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Methyl Jasmonate Alleviates the Deleterious Effects of Salinity Stress by Augmenting Antioxidant Enzyme Activity and Ion Homeostasis in Rice (*Oryza sativa* L.)

Shahid Hussain [1], Rui Zhang [1], Shuli Liu [1], Rongkai Li [1], Yang Wang [1], Yinglong Chen [1], Hongyan Hou [2] and Qigen Dai [1,*]

[1] Jiangsu Key Laboratory of Crop Genetics and Physiology, Jiangsu Key Laboratory of Crop Cultivation and Physiology, Jiangsu Co-innovation Center for Modern Production Technology of Grain Crops, Research Institute of Rice Industrial Engineering Technology, Key Laboratory of Saline-alkali Soil Improvement and Utilization (Coastal Saline-alkali Lands), Ministry of Agriculture and Rural Affairs, Yangzhou University, Yangzhou 225009, China

[2] Yibang Agriculture Technology Development Co., Ltd., Dongying 257000, China

* Correspondence: qgdai@yzu.edu.cn

Abstract: Methyl jasmonate (MeJA) is a potent player that fine-tunes growth and developmental activities under salinity stress. In this study, we investigated the influence of MeJA on two rice cultivars (NJ9108 and XD22) subjected to different salinity stresses. Following stress treatment, reduction in the water use efficiency, relative water contents, and membrane stability index in both cultivars were observed, whereas MeJA treatment partially alleviated the negative effects. MeJA treatment significantly increased the maximum photochemical efficiency (Fv/Fm) and electron transfer to photosystem II (Fv/Fo). Under salinity stress, MeJA treatment significantly triggered the H_2O_2 and APX accumulation, while POD and SOD remained unchanged in both cultivars. Salt stress increased Na^+ concentration in the roots and leaves but decreased K^+ concentration and the K^+/Na^+ ratio in both cultivars. However, MeJA-treated plants had the maximum K^+ accumulation in both leaves and roots under saline conditions. The differential expression pattern of *OsHKT* and *OsHAK* genes implied that ion homeostasis is crucial to growth under salt stress. These findings suggest that the application of MeJA can be an alternative source of reducing salinity without compromising growth and yield.

Keywords: rice (*Oryza sativa* L.); salinity stress; fluorescence; rice growth; gas exchange attributes; methyl jasmonate; yield components

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1. Introduction

Due to global industrialization, urbanization, and salinization, especially in developing countries such as China, land suitable for crop productivity is rapidly declining [1]. Irrigated lands may experience salinization issues, and a portion of these areas are lost each year [2]. Over 6% of land worldwide, which means more than 800 million hectares, suffers either salinity or alkalinity [3,4]. About 99.13 million hectares of saline land in China is located in the northern regions [5]. Saline soils are divided into coastal saline mudflats, inland saline lands, and heavily irrigated soil [6]. Tidal intrusion causes coastal salinity, when very saline seawater mixes with fresh water, rendering its saline at dangerous levels [7–9]. The deposition of oceanic salts delivered via wind and rain is another source of salt accumulation in irrigated soils, particularly sodium chloride [10]. China's coastal mudflats reserves in the future will be the main resources for crop cultivation, while the salinity in these regions is the major obstacle to the soil [11,12]. Therefore, multiple strategies were used to improve and utilize the saline-alkali regions [13,14], such as cultivated cereal crops and halophytes for food and grazing and to ensure food security.

The rice plant is susceptible to salt stress, particularly during the seedling and early vegetative stages [15,16], decreasing seed germination, deformed leaves, reduced dry mass, increased infertility, and reduced crop productivity [17]. High rhizosphere salinity negatively influences the physiological characteristics of plants [17], seed germination, plant life and crop productivity [18]. Salt stress inhibits rice development by inducing metabolic changes and reducing the plant's ability to absorb water and nutrients [14]. Furthermore, salt stress weakened the growth of rice spikelets, particularly inferior spikelets, which considerably reduced rice grain production [17,19].

Salt stress is one of the most significant abiotic stresses and an unavoidable constraint that negatively impacts plant growth and productivity [20–23]. The root is the plant's first organ to be affected by salt stress, which disrupts the ionic balance of cells, resulting in an overproduction of Reactive Oxygen Species (ROS) [24]. Thus, excessive ROS is triggered, which destroys genetic material and causes significant oxidation of crucial biomolecules such as membrane lipids, proteins, and carbohydrates, altering the redox homeostasis in plant tissues, hindering plant growth and is effective at varying levels of stress-induced deterioration [25–28].

Hormones, such as methyl jasmonate (MeJA) and jasmonic acid (JA), can help plants cope with salt stress [29,30]. Jasmonate is a vital cell regulator that responds to different environmental stresses, such as salt, drought, and heavy metals [31–33]. MeJA diminishes the inhibitory effect of NaCl on photosynthesis rate and enhances plant growth and development [34–36]. Plant growth regulators (i.e., abscisic acid, salicylic acid, brassinosteroids and methyl jasmonate) cope with stress in plant-produced proteins and cause potential osmotic resistance to various stresses [29,37–39]. MeJA specifically mitigates the severe effects of the salinity and drought stress of multiple crops, such as soybean [31,39], barley [34], strawberry [40], pea [41], and broccoli [39]. Furthermore, MeJA causes cellular signaling and regulatory phenomena that influence seed germination, tuberculosis, aging, root and reproductive growth, and fruit maturation [42,43]. It also seems that the MeJA treatments minimized the unfavorable effects of salinity through chlorophyll content, photosynthetic rate (P*n*), leaves transpiration rate (T*r*), and proline content [29]. The hormone also increases photosynthetic rate, relative water, and soluble sugar contents [44]. MeJA enhances the recovery of salinity-stressed rice plants by changing abscisic acid balance and diminishing salt stress's inhibitory effect on the rate of photosynthesis [45,46].

Ion homeostasis plays a crucial role in mitigating salt stress. Several ion transporter genes, such as the high-affinity potassium transporter (*HKT*) and the high-affinity K^+ transporter (*HAK*), are crucial for balancing ion accumulation in plant cells under salinity stress [47–49]. For instance, [50] used exogenous chemicals on rice plants subjected to salinity stress and observed a better tolerance with augmented Na^+/K^+ homeostasis. In this study, we suggest that MeJA can regulate ion homeostasis in rice plants exposed to salt stress. MeJA also mitigates the negative influence of osmotic stress by regulating the penetration of inorganic and organic ions to suppress the absorption of toxic ions. It was hypothesized that MeJA facilitates plant growth and development in stressful environments and could enable plants to cope with salinity-induced stress by reducing oxidative stress. Thus, this research aimed to investigate the impact of MeJA on rice agronomical, physiological, and antioxidants under salinity stress conditions.

2. Materials and Methods

2.1. Plant Materials, Design, and Experiment

We examined two rice cultivars (XD22 and NJ9108) in this pot experiment. The seed cultivars were obtained from the College of Agriculture, Yangzhou University, Jiangsu, China (33°57′ N, 120°240′ E) in 2019–2020 during the growth season. The soil in the experimental field has a sandy loam texture with 0.43–0.44.8 g/kg total nitrogen, 72–80.5 mg kg^{-1} potassium, 18–20 mg kg^{-1} phosphorus, and 3–3.8 g kg^{-1} organic carbon in the 0–20 cm soil layer and the soil conductivity was 5.5–6.5 µS/cm. The pots were arranged in a randomized complete block design in three-factor factorial, two cultivars, salt stress, and MeJA,

containing eight replicates. Three NaCl concentrations were considered for each treatment, i.e., CK = 0, S1 = 30, S2 = 60, and S3 = 90 millimole/liter (mM), and both cultivars were placed in two groups.

The experimental pots were placed in a transparent polyethylene shelter to shield them from rainwater. The soil collected from the farmland was mixed carefully. The dried soil sample was passed through a 10 mm mesh and the tagged pots were filled with 10 kg of the soil sample from the mixed soil (placed in six rows and separated 1.5 m apart). Urea, superphosphate, and potassium chloride were the sources of nitrogen, phosphorus, and potassium. Urea was added at a rate of 1.305 g pot^{-1} in the pre-transplanting stage, tillering stage, panicle initiation stage and booting stage. Superphosphate was added as the basic fertilizer, about 8.3 g pot^{-1}, and potassium chloride was added as the basic fertilizer and panicle fertilizer at a rate of 1.665 g pot^{-1}. All pots were well flooded a day before transplanting. On the second day, at 7:00 a.m., four plants were transplanted from the rice nursery onto four hills in each pot. During the growth period, the rice plant was regularly irrigated as required.

2.2. Preparation of MeJA Foliar Spray

MeJA ($C_{13}H_{20}O_9$) used in this experiment was purchased from Sigma-Aldrich Sigma Aldrich, Shanghai, China. We prepared two solutions of MeJA, i.e., C1 = 0, C2 = 125 and C3 = 250 micromoles/liter (μM). The desired amount of concentration was dissolved in ethanol (0.1%) and then added to an appropriate volume with double-distilled water. Furthermore, the MeJA were sprayed at tillering initiation, jointing, and spiking stages and the control plants were sprayed with the same ethanol, and double distilled water used for the MeJA solution.

2.3. Measurements of Plant Growth and Yield Parameters

2.3.1. Plant Growth Parameters

We randomly collected four plants from each treatment to determine growth parameters, such as plant length (PH), flag leaf area (FLA), root length (RL), fresh root weight (FRW), fresh leaf weight (FLW), stem thickness (StTh), fresh stem weight (StFW) green yellow leaf numbers (GLN/hill) and yellow leaf numbers (YLN/hill). Plant height was measured from the soil surface to the last leaf tip by using a meter ruler. Four plants were randomly selected to determine the flag leaf area using the formula:

$$\text{FLA} = \text{leaf width (cm)} \times \text{leaf length (cm)} \times 0.75$$

We randomly selected three pots for root length, and the plant was carefully taken out and washed clearly; finally, the root length was measured using a meter ruler graded in cm. The plant's fresh root, stem, and root weight were measured using an electronic scale (extra moist removal using tissue paper). Stem thickness was measured using an electrical vernier caliper. The green and yellow leaves were first separated and then the green and yellow leaves per hill tillers were considered per replicate in each treatment.

2.3.2. Yield Components

For the yield components, we selected three plants at maturity stage (at full dryness stage) from three pots of each treatment and measured the infertile spikelet sets per panicle (IFSpl/pan), filled seed sets $panicle^{-1}$ (FSS/pan), and the total number of spikelets per panicle (TSpl/pan), the total seed sets $panicle^{-1}$ (TSdS/pan), grain weight pot^{-1} (GW/pot), and 1000 grain weight (ThGW) (g). Three panicles were selected from each treatment; the fertile and infertile spikelets were first counted and then averaged. The average of fertile and infertile seed sets was considered total seed sets per panicle. The rice plant's roots, leaves, and stems were separated and dried in an oven at 80 °C for 24 h. The oven-dried samples were stored in paper envelopes for chemical analysis.

2.4. Physiological Parameters

2.4.1. Chlorophyll Determination

We used the tip, middle, and base of the flag leaves during the anthesis stage, of three plants in each pot for the soil plant analysis development (SPAD) using a chlorophyll meter (chlorophyll meter SPAD-502 plus, Konica Minolta, Osaka, Japan).

2.4.2. Leaf Relative Water Contents (RWC)

Four plants were taken from each treatment and put directly in a water pot to maintain water flow and control water loss in the plant. From each plant, flag leaves were selected from all treatments to determine the RWC. The leaves were cut into small equal sizes from the flat green parts and one-third of each leaf was left uncut from the tip of the leaf [51]. The cut samples were weighed to determine the fresh weight (FW), soaked in 10 mL distilled water at 4 °C in dark cooling storage for 24 h, and weighed again to record the turgid weight. Subsequently, the samples were dried in an oven at 85 °C for 24 h to determine the dry weight (DW). The RWC of the leaves was calculated according to the following formula [52]:

$$\text{RWC} = (\text{FW} - \text{DW})/(\text{TW} - \text{DW}) \times 100$$

2.4.3. Membrane Stability Index (MSI)

To determine the membrane stability index (MSI), 0.2 g of flag leaves were cut into small uniform-sized discs (6 cm) and placed into two sets of test tubes containing 10 mL of double-distilled water. One set was heated in a water bath at 40 °C for 30 min. The other was boiled in a boiling water bath for 15 min. According to [53,54], the samples were cooled to 25 °C and the electric conductivities (EC1 and EC2) of the first and second groups were measured, respectively, using a conductivity meter (CM-115, Kyoto Electronics, Kyoto, Japan). The following formula was used to calculate the MSI:

$$\text{MSI} = 1 - \text{EC1}/\text{EC2} \times 100$$

2.4.4. Leaf Chlorophyll Fluorescence (LCf)

The LCf was measured using a pulse amplitude modulation chlorophyll fluorometer (MINI-PAM Walz, Effeltrich, Germany). The minimum fluorescence F_0 was measured after 30 min. Dark-adapted leaf and maximum fluorescence Fm were determined after a 30 s saturation of the light pulse of the extant leaf. We determined the fluorescence using the fluorescence variable (Fv), maximum photochemical efficiency of PSII (Fv/Fm), and efficiency of electron transfer to photosystem II (PSII) (Fv/Fo) active reaction center of the photosynthetic apparatus. According to the calculation methods of [55], the maximum photochemical efficiency of PSII is $\text{Fv}/\text{Fm} = (\text{Fm} - F_0)/\text{Fm}$.

2.4.5. Gas Exchange Attributes

The gas exchange parameters were determined at the anthesis stage using a portable gas exchange system (Li-6400XT, USA) from 9 a.m. to 11:30 a.m. on sunny days. The first fully developed healthy flag leaf of rice plants with the same vigor was selected to measure the leaf gas exchange parameters in each treatment along with replicates. The measurement was taken in the middle of the upper part of the leaf, carefully avoiding the central leaf vein. Two replicates were considered for each treatment in the anthesis stage. Additionally, the leaf photosynthetic rate (P*n*, $\mu\text{molm}^{-2}\ \text{s}^{-1}$), conductance to H_2O (Cond), transpiration ratio (T*r*, mmol), intercellular CO_2 concentration (C*i*), water use efficiency (WUE), and stomatal conductance (G*s*) were measured. Finally, the PAR in the leaf chamber was fixed to 1000 $\mu\text{mol m}^{-2}\ \text{s}^{-1}$ and the rice saturated light intensity.

2.5. Measurements of MDA, H_2O_2, APX, POD, and SOD Activities

Fresh leaf samples were stored in a −80 °C refrigerator to analyze different biochemical properties. For lipid peroxidation (MDA) determination, about 0.5 g of fresh leaf tissue

was ground using liquid nitrogen. An amount of 5.0 mL of 0.05 M precooled phosphate buffer (pH 7.8) was mixed and homogenate then centrifuged at 15,000 rpm for 20 min at 4 °C and the supernatant was used to determine antioxidant activities [56], with minor changes. The absorbance of archived supernatant was analyzed at 440, 532 and 600 nm. For hydrogen peroxide (H_2O_2), the mixture containing 200 µL leaves supernatant and 2 mL 20% H_2SO_4 with 0.1% $TiCl_4$ was centrifuged and the absorbance of obtained supernatants was measured at 410 nm [57].

To measure ascorbate peroxidase (APX) activity, frozen leaves were crushed in 5.0 mL of 50 mM Tris-HCl buffer (pH 7.0) with 1.0 mM sodium ascorbate, 1 mM DTT, 1.0 mM EDTA, 1 mM reduced glutathione, 5.0 mM $MgCl_2$, and 1% PVPP (w/v), while homogenate was centrifuged at 20,000 rpm for 20 min at 4 °C [58]. Peroxidase (POD) activity was measured by the determination of guaiacol oxidation by H_2O_2 at 470 nm absorbance [57]. Superoxide dismutase (SOD) activity was determined spectrophotometrically from the inhibition of the photochemical reduction of nitro blue tetrazolium at 560 nm [59]. All kits used in this study were purchased from Suzhou Keming Biotechnology Co., Ltd., Suzhou, China, (www.cominbio.com) (accessed on 30 March 2022); the kits were operated strictly as directed by the manufacturer.

2.6. Analysis of Different Genes

To examine the temporal expression patterns of selected genes, we performed qRT-PCR for four genes in the rice plants subjected to four NaCl treatments, i.e., 0, 30, 60, and 90 mM. The qRT-PCR was performed in a CFX-96 Real-time PCR Detection System (Bio-Rad, Hercules, CA, USA). Reactions were conducted in a total volume of 20 µL containing 50 ng of cDNA, 10 pmol of forward and reverse primers, and 10 µL of 2x SsoFast EvaGreen qPCR Supermix (Bio-Rad, State College, PA, USA). The cycling conditions followed the manufacturer's protocol at a primer-specific annealing temperature. The threshold cycle (Ct) was automatically determined for each reaction using the system with default parameters. We normalized the transcript levels to actin transcript and calculated the fold differences of each amplified product in the samples using the $2^{-\Delta\Delta Ct}$ method. All the primer sequences were designed using the NCBI-Primer blast online tool (https://www.ncbi.nlm.nih.gov/tools/primer-blast/) (accessed on 10 February 2022). The sequences are listed in Table S1.

2.7. Measurements of Na^+, K^+, and Na^+/K^+ Ratio

After harvesting, the plant's roots, leaves, stems, and seeds from each experimental unit were sampled. Dried samples were ground into a fine powder, and two replicates of 0.445 to 0.460 g from each sample were weighed. The weighed dry powder (containing 5 mL HNO_3, 3 mL double-distilled water, and two drops of H_2O_2) was digested using the MARS-6 microwave digestion system and prepared for the micro–macro nutrient analysis. Each sample was filtered using the Whatman filter paper (0.45 µm) and stored in 10 mL plastic tubes before analysis. According to [60,61], the total Na^+, K^+, and Na^+/K^+ ratio of the digested filtrate was measured using an inductively coupled plasma atomic emission spectrometry (Model iCAP 6300, Thermo fisher scientific, ICP Spectrometer, MA, USA).

$$\text{Macro content concentrations} = \frac{\text{Tested value} \times 10 \times 50}{\text{Sample weight}} \ (\text{mg/g})$$

2.8. Statistical Analysis

All the experiments were conducted with a minimum of three replicates and the results were expressed as mean ± standard deviation (SD). We used Microsoft Excel for data entry, statistical analysis, and SD calculation. For the interaction of MeJA and salinity stresses, the data were analyzed by factorial two-way ANOVA and the least significant difference (LSD) test ($p \leq 0.05$) was performed using Statistic 9. However, the figures were generated by GraphPad Prism 7.0.

3. Results

3.1. Influence of Salinity and MeJA Foliar Applications on Agronomical Attributes

Under high salinity stress, the plant height (PH) was reduced ($p \leq 0.05$) in both rice cultivars NJ9108 (30.66 cm) and XD22 (36.63 cm). However, the MeJA (125 µM) application resulted in an increase in PH of XD22 compared to the NJ9108 cultivar under salinity stress conditions. In NJ9108, the sole application of MeJA reduced the fresh leaf weight (FLW) in S3C2 (15.27) and S3C3 (20.26) compared with that of the control plants.

The salinity stress also reduced the RFW, RDW, FLW, StTh, StFW (g), and GLN/hill in both cultivars (NJ9108 and XD22). However, the application of MeJA enhanced the RL (38.53 and 46), FRW (26.25 and 31.74), FLW (18.78 and 20.37), StTh (54.83 and 65.84), and GLN/hill (37.66 and 53) in the NJ9108 and XD22 cultivar, respectively, as shown in (Tables 1 and 2).

Table 1. Effects of different levels of MeJA and salinity stress on plant height (PH), flag leaf area (FLA), root length (RL), fresh root weight (FRW), fresh leaf weight (FLW), stem thickness (mm), and stem fresh weight (SFW) of two rice cultivars during anthesis stage.

	Salinity	MeJA	PH (cm)	FLA	RL (cm)	FRW (g)	FLW (g)	StFW (g)	StTh (mm)
NJ9108	0	0	85.01 a	52.40 a	35.2 a	15.6 bc	13.34 b	37.96 b	9.07 a
		125	74.01 bc	52.94 a	38.53 a	26.25 a	18.76 a	54.83 a	8.53 ab
		250	68.79 cd	40.78 b	37.53 a	13.02 cd	12.23 bc	30.57 bcd	8.03 abc
	30	0	77.78 b	36.62 bc	23.5 bc	14.23 bc	7.98 de	21.66 efg	7.95 a–d
		125	72.24 c	38.59 b	23.53 bc	17.7 b	9.67 d	36.53 bc	7.58 b–e
		250	64.52 d	27.81 d	23.2 bc	7.93 ef	9.55 d	16.72 ghi	6.64 de
	60	0	72.35 c	39.92 b	31.00 ab	12.11 cde	9.99 d	29.46 cde	7.27 b–e
		125	66.81d	30.84 cd	23.20 bc	14.83 bc	7.88 de	25.70 def	7.06 cde
		250	65.32 d	24.40 de	24.00 bc	7.93 ef	5.04 fg	12.99 hi	6.29 e
	90	0	37.89 e	38.47 b	21.83 c	8.93 def	6.71 ef	17.80 fgh	7.63 b–e
		125	30.66 e	15.27 f	13.53 d	2.07 g	1.52 h	11.86 hi	8.53 ab
		250	38.63 f	20.26 ef	23.50 bc	5.07 fg	3.96 g	9.04 i	6.56 e
CV			4.24	12.7	17.73	21.73	15.40	18.57	10.70
XD22	0	0	82.02 a	41.77 c	35.10 bc	28.04 a	16.23 c	53.74 ab	8.73 ab
		125	79.73 a	48.00 b	46.00 a	31.74 a	20.37 a	65.84 a	8.99 a
		250	79.48 a	52.86 a	35.17 b	17.35 b	19.65 abc	55.823 ab	8.79 a
	30	0	71.94 b	36.51 d	31.57 bcd	29.10 a	9.66 d	35.14 cd	7.68 abc
		125	72.27 b	38.94 cd	26.97 def	18.73 b	19.75 ab	47.23 bc	8.90 a
		250	68.56 b	34.96 de	27.70 cde	17.94 b	16.17 c	45.23 bc	7.85 abc
	60	0	60.52 cd	30.49 fg	19.17 gh	6.16 cd	5.06 e	21.55 ef	6.67 cd
		125	63.22 c	31.65 ef	21.63 efg	7.64 cd	9.36 d	33.22 de	7.38 bc
		250	57.13 d	27.13 gh	19.67 fgh	6.46 cd	6.83 de	24.81 def	5.97 d
	90	0	38.17 e	21.71 i	25.60 d-g	13.49 bc	4.02 e	23.09 def	7.26 cd
		125	36.89 e	23.78 hi	13.87 h	5.58 d	10.39 d	21.99 ef	7.06 cd
		250	36.63 e	20.59 i	22.20 efg	4.64 d	3.54 e	14.85 f	6.67 cd
CV			4.86	7.67	16.18	28.75	17.93	17.78	10.41

Values are the average of three replications of each treatment of 2 hills pot^{-1}. In the both cultivars, column with different letters (a–i) denoted significant difference among salinity and MeJA applications interaction at $p \leq 0.05$, according to the LSD test.

Table 2. Effects of different levels of MeJA and salinity stress on green leaf number hill^{-1} (GLN/hill), yellow leaf number hill^{-1} (YLN/hill) (at anthesis stage), whereas infertile spikelets panicle^{-1} (IFSpl/pan), filled seed sets panicle^{-1} (FSS/pan) total spikelets panicle^{-1} (TSpl/pan), total seed sets panicle^{-1} (TSdS/pan), grain weight pot^{-1} (GW/pot), and 1000 grain weight (ThGW) of two rice cultivars during maturity stage.

	Salinity	MeJA	GLN/hill	YLN/hill	IFSpl/pan	FSS/pan	TSpl/pan	TSdS/pan	GW/pot (g)	ThGW (g)
NJ9108	0	0	29.66 b	6 bc	0.00 e	119.00 a	13.67 ab	150.67 ab	93.997 a	25.35 ab
		125	37.66 a	3 de	0.00 e	97.00 b	14.00 a	158.67 a	63.397 b	26.1 ab
		250	27.66 bcd	3 de	0.33 de	107.67 ab	13.67 ab	165.33 a	60.407 bc	28.1 a
	30	0	27.33 bcd	2.67 de	0.00 e	104.67 b	11.33 abc	130.67 b	49.86 cd	24.2 ab
		125	29.00 bc	2.33 de	2.33 cd	20.33 de	9.33 cde	101.00 c	32.01 e	23.6 ab
		250	21.00 d	4.67 cd	0.00 e	64.33 c	11.00 bcd	96.00 cd	38.43 de	24.47 ab
	60	0	31.33 ab	4.33 cd	0.00 e	31..33 d	8.33 de	82.00 cde	16.58 f	22.58 ab
		125	21.33 d	7.00 bc	8.00 a	1.67 f	9.33 cde	77.00 def	3.13 g	20.35 b
		250	21.00 d	8.33 b	6.00 ab	7.33 ef	9.00 cde	65.67 efg	9.82 fg	13.38 c
	90	0	22.00 cd	8.33 b	3.33 c	8.33 ef	8.33 de	52.67 gh	6.29 fg	0 d
		125	03.00 f	1.66 e	6.67 ab	0.00 f	6.67 e	33.00 h	0.00 g	0 d
		250	11.00 e	13.00 a	5.67 b	3.33 f	8.33 de	61.00 fg	2.11 g	0 d
CV			19.03	31.09	47.66	18.08	15.54	12.58	21.79	20.8
XD22	0	0	43.00 bc	3.67 cde	0.00 d	118.67 a	13.00 a	141.00 a	92.21 a	29.17 a
		125	47.67 ab	7.00 bcd	0.00 d	70.67 bc	11.33 ab	95.33 bc	80.13 b	29.43 a
		250	53.00 a	6.67 cde	0.00 d	80.67 b	10.67 ab	110.67 b	88.55 ab	28.67 ab
	30	0	32.33 de	3.00 de	0.00 d	58.33 cd	9.33 bcd	75.67 cde	45.82 c	26.75 bc
		125	36.67 cd	2.33 e	0.00 d	39.00 e	10.33 bc	89.67 bcd	39.89 c	25.68 c
		250	52.00 ab	8.00 bc	1.00 cd	44.33 de	10.00 bc	76.33 cde	43.11 c	25.88 c
	60	0	14.33 gh	11.33 ab	1.33 cd	19.67 f	8.00 cde	59.33 ef	4.68 d	22.47 d
		125	25.00 ef	13.67 a	5.67 b	12.00 fg	9.67 bcd	66.33 def	7.57 d	12.9 e
		250	22.33 fg	15.67 a	4.00 bc	9.67 fg	7.33 de	68.00 c–f	3.07 d	21.25 d
	90	0	15.67 gh	5.67 cde	5.67 b	3.00 g	7.33 de	66.33 def	0.73 d	0 f
		125	7.67 h	7.67 bc	11.67 a	3.67 g	6.00 e	47.33 f	1.49 d	0 f
		250	9.67 h	15.00 a	6.00 b	0.00 g	11.67 ab	51.67 ef	0.00 d	0 f
CV			17.96	32.04	72.36	23.01	12.32	20.96	18.77	6.64

Values are the average of 4 replicates of each treatment of 2 hills pot^{-1}. In the both cultivars, column with different letters (a–h) denoted the significant difference among salinity and MeJA applications interaction at $p \leq 0.05$, according to the LSD test.

3.2. Influence of Salinity and MeJA Foliar Applications on Rice Yield Components

Salinity stress significantly reduced ($p \leq 0.05$) the TSpl/pan by 52.4% and 53.8% in NJ9108 and XD22, respectively, as compared to the control plants (Table 2). The application of the MeJA treatment with salinity stress slightly increased the number of TSpl/pan compared with the untreated plants (see Table 2). In both cultivars, salinity stress increased the number of YLN/hill and IFSpl/pan. However, MeJA treatment (125 µM) alleviated the effect of salt-induced stresses by decreasing the YLN/hill. Conversely, the IFSpl/pan in both cultivars was not increased by MeJA applications under salinity stress. The interaction of high salinity (90 mM) and the MeJA (250 µM) application increased the ratio of green and yellow leaf numbers per hill and similarly decreased the numbers of IFSpl/pan by 93.3% and 80.5% in the NJ9108 and XD22 cultivars, respectively, compared to control plants (see Table 2).

In both cultivars, salinity stress reduced the FSS/pan by 93% and 97.5% in the NJ9108 and XD22, respectively. However, the MeJA application increased the FSS/pan from low to high salt concentrations. Under salinity stress, TSdS/pan was significantly ($p \leq 0.05$) reduced by 80% and 66.4%, in the NJ9108 and XD22 cultivars, respectively, compared to

the control. On the other hand, TSdS/pan indicated a non-significant (p = 0.05) increase when sprayed with MeJA under salinity stress (see Table 2). Under salinity stress, both cultivars NJ9108 and XD22 reduced the GW/pot by 93.3 and 99.2%, while ThGW by 52.4 and 56.2%. The maximum GW/pot was recorded in the untreated salinity stress plants treated with MeJA (125 and 250 µM) applications.

3.3. Influence of Salinity and MeJA on Rice Chlorophyll Content, RWC, and MSI

Under salinity stress, leaf chlorophyll content and MSI were negatively influenced, whereas RWC increased with increasing NaCl concentration. However, at higher concentrations of salinity stress (>90 mM), MeJA (250 µM) treatments reduced the RWC in XD22 when compared to the same group of salinity stress alone (see Table 3). The chlorophyll content decreased as salinity concentration increased while the MeJA (250 µM) treatment increased the chlorophyll content in NJ9108 (43.94) and XD22 (44.39) under the saline condition. Compared with the control treatment, the high salinity stress treatment reduced the MSI value, which was higher at 30 mM and 60 mM of NaCl when treated with 250 µM of the MeJA application. Moreover, MSI value increased particularly with the application of 125 µM of MeJA under high salinity stress (90 mM) (see Table 3).

Table 3. Influences of different levels of MeJA and salinity stress on Chlorophyll contents, relative water contents, and membrane stability index of two rice cultivars during anthesis stage. Treatments S0 = 0, S2 = 30 and S2 = 60, S3 = 90 mM (NaCl) and C1 = 0, C2 = 125, C3 = 250 µM (MeJA).

Cultivars		NJ9108			XD22		
NaCl	**MeJA(µM)**	**Chl.C**	**RWC**	**MSI**	**Chl.C**	**RWC**	**MSI**
S0	0	42.59 a	81.08 d	83.76 a	40.91 bc	88.44 bc	81.58 abc
	125	41.68 ab	92.60 a	87.68 a	39.61 c	94.54 a	80.95 abc
	250	41.97 ab	83.65 cd	85.89 a	39.53 c	92.99 ab	83.96 ab
S1	0	42.12 ab	90.47 ab	76.48 bc	44.39 a	92.62 ab	87.62 a
	125	40.96 ab	85.07 bcd	81.85 ab	41.94 abc	69.25 e	78.21 abc
	250	43.94 a	85.25 bcd	87.45 a	41.56 abc	91.11 ab	84.71 ab
S2	0	38.03 b	84.47 cd	80.92 ab	41.50 abc	87.94 bc	82.47 abc
	125	40.97 ab	94.43 a	73.06 c	43.36 ab	83.72 cd	87.07 ab
	250	43.13 a	89.14 abc	81.44 ab	43.50 ab	91.31 ab	77.22 bc
S3	0	41.18 ab	92.09 a	80.85 ab	39.60 c	93.79 a	79.31 abc
	125	42.46 a	92.97 a	83.35 ab	41.52 abc	95.51 a	80.36 abc
	250	44.39 a	82.16 d	73.17 c	36.02 d	82.17 d	73.17 c
Salinity		**	**	***	**	*	ns
MeJA		**	ns	ns	ns	*	ns
Salinity * MeJA		**	ns	*	ns	*	ns
CV		3.4	4.58	5.37	4.76	3.38	7.27

In the both cultivars, column with different letters (a–e) denoted the significant difference among salinity and MeJA applications interaction. Here, ns, not significant; *, $p \leq 0.05$; **, $p \leq 0.01$; and ***, $p \leq 0.001$; respectively.

3.4. Influence of Salinity and MeJA Foliar Application on Rice Leaf Chlorophyll Fluorescence (LCf)

The salinity stresses and MeJA applications significantly ($p \leq 0.05$) induced the chlorophyll fluorescence, particularly in Fv/Fo values. Moreover, the results showed that PSII Fv/Fm and Fv/Fo were increased at 125 µM of MeJA ($\leq$30 mM NaCl) in both cultivars, such as NJ108 (0.86, 6.39) and XD22 (0.84, 5.29) at the control concentration. In NJ9108, the MeJA treatments decreased the Fv/Fm (0.83, 0.83) and Fv/Fo (4.89, 5.01) ($\geq$60 mM). In NJ9108 cultivar, a non-significant decrease were found at higher salinity stresses (60–90 mM), while significant at XD22 cultivar compared to the control treatment (see Figure 1).

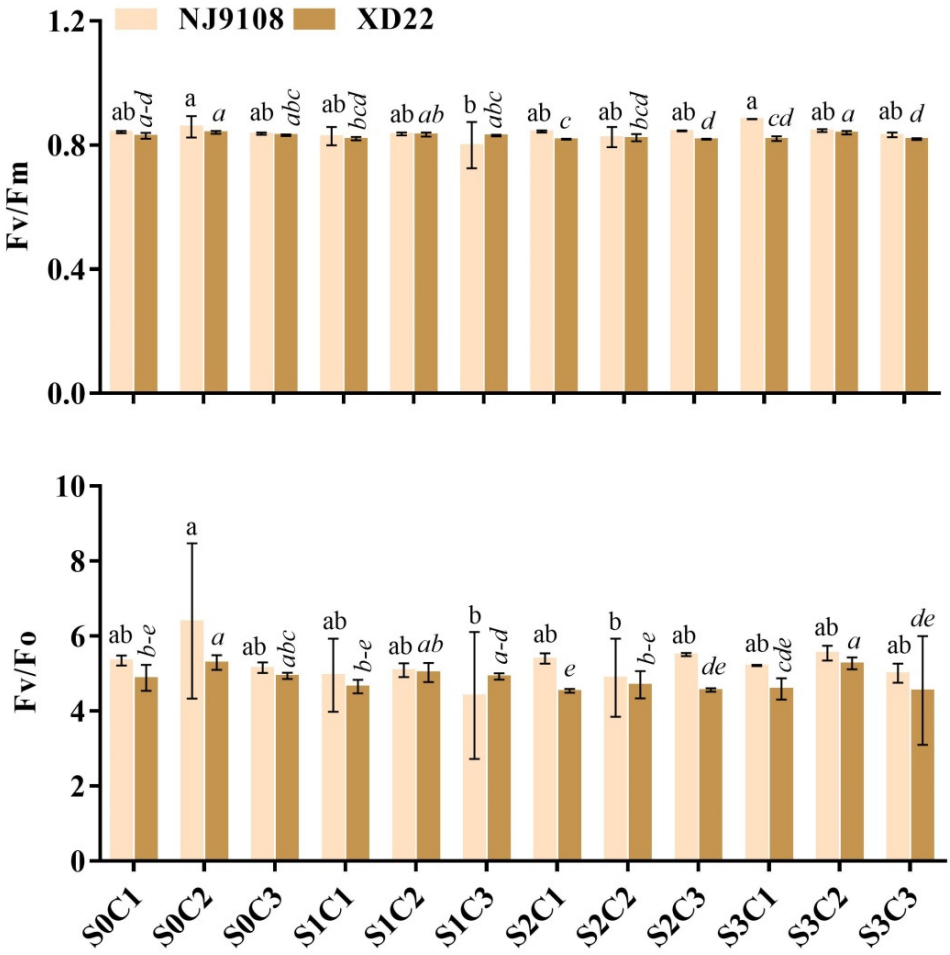

Figure 1. Influence of MeJA and salinity stress on leaf fluorescence maximum photochemical efficiency of PSII (Fv/Fo) and the efficiency of electron transfer to the PSII (Fv/Fm) activities. Salinity and MeJA foliar spray treatments S0 = 0, S1 = 30 and S2 = 60, S3 = 90 mM and MeJA applications, i.e., C1 = 0, C2 = 125, C3 = 250 µM. Bars represent the means of three replications. Bars represent the means ± SD of three replications. The letters a–e showed the significant difference between salinity and MeJA applications interaction, whereas NJ9108 represented by uniform and XD22 cultivar by italic letters.

3.5. Influence of Salinity and MeJA Foliar Application on Rice Gas Exchange Attributes

The salinity stress significantly ($p \leq 0.05$) declined the P*n* and H_2O (Cond) in both cultivars. Under high-saline conditions (90 mM), plant death occurred before panicle initiation in the NJ9108 cultivar, while the XD22 cultivar showed resistance. The value of intercellular CO_2 concentration (C*i*) significantly increased ($p \leq 0.05$) as the salinity levels increased in both cultivars. A decreasing trend in T*r* was observed at low and high salinity stresses, whereas WUE significantly ($p \leq 0.05$) increased with an increase in salinity stress in both cultivars. The sole application of NaCl stress (>60 mM) increased the WUE by 46.3% and 26.3% in NJ9108 and XD22, respectively (see Figure 2). In contrast, the plant's stomatal conductance (G*s*) decreased with increasing salinity stress in both cultivars.

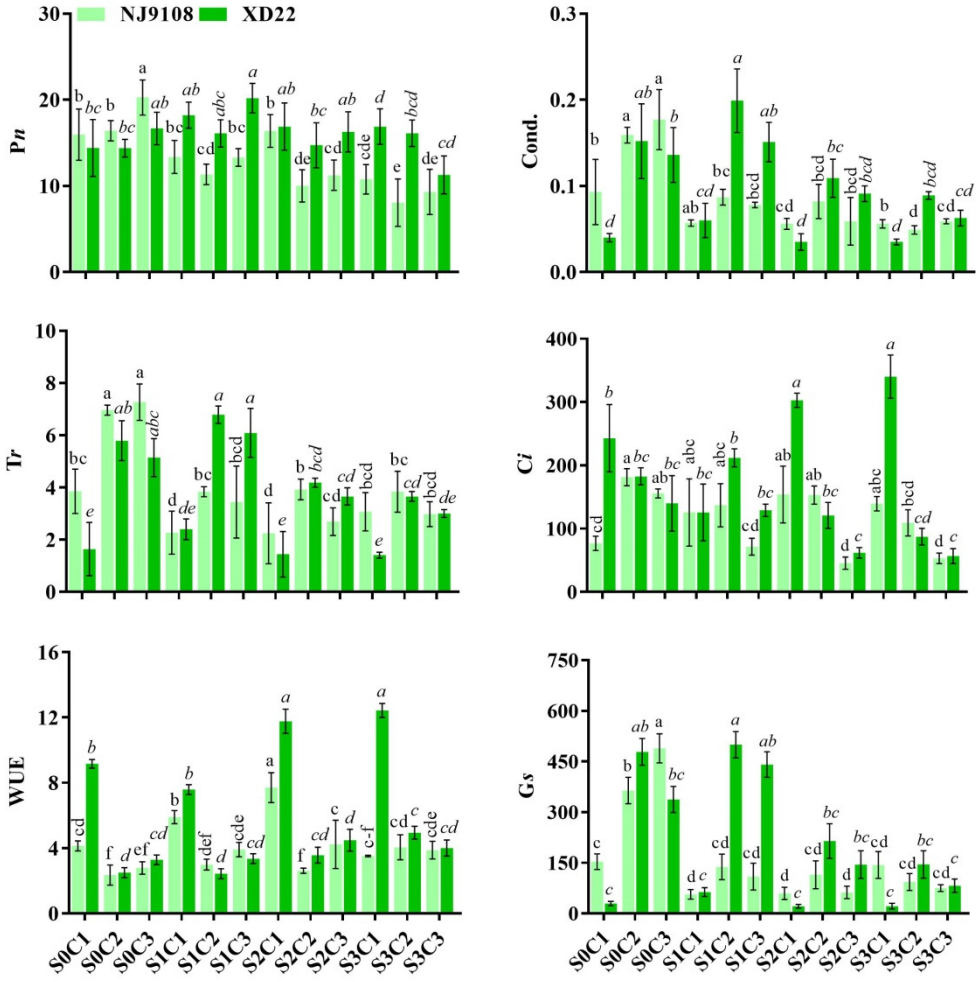

Figure 2. Influence of MeJA and salinity stress on photosynthetic parameters, i.e., Photosynthetic rate (P*n*), Conductance to H_2O (Cond), transpiration rate (Trmmol), intercellular CO_2 concentration (C*i*), Water use efficiency (WUE), and stomatal conductance (G*s*) on rice two cultivars (NJ9108 and XD22). Salinity treatments, i.e., S0 = 0, S1 = 30 and S2 = 60, S3 = 90 mM and MeJA applications, i.e., C1 = 0, C2 = 125, C3 = 250 µM. The letters a–f showed the significant difference between salinity and MeJA applications interaction, whereas NJ9108 represented by uniform and XD22 cultivar by italic letters.

Under the low saline stress (<30 mM), the MeJA foliar application (250 µM) significantly enhanced P*n*, while at high salinity stress (60–90 mM), the MeJA foliar treatment (250 µM) reduced P*n* followed by MeJA foliar application (250 µM), compared with that of the control treatment (see Figure 2). Comparatively, the MeJA application increased the T*r* in the NJ9108 as compared to the XD22 cultivarwhen subjected to higher salinity (90 mM) compared to lower salinity stress (30 mM). Meanwhile, both MeJA treatments (125 and 250 µM) reduced the value of C*i* under salt stress treatments (see Figure 2). MeJA treatment (125 µM) enhanced the value of C*i* in control of NJ9108 and XD22. We also observed that, among both cultivars, XD22 showed lower C*i* in all sole salinity treatments than where MeJA applications were applied. Under saline conditions, both the cultivars' transpiration rates (T*r*) positively responded to MeJA applications. The MeJA foliar (125 µM) spray enhanced the value of T*r* in both cultivars in the applied salinity treatments, except in the non-saline stressed treatment.

3.6. Influence of Salinity and MeJA Foliar Applications on MDA, H_2O_2, APX, POD, and SOD

A higher level of salinity (90 mM) significantly ($p \leq 0.05$) increased the level of MDA and H_2O_2 in the rice leaves (Figure 3). In comparison, the applications of MeJA declined the MDA and H_2O_2 contents in the rice leaves at higher NaCl concentrations. Overall, in

NJ1908, MeJA (125 µM) treatment significantly reduced the MDA and H_2O_2 contents by 27.8% and 38.8% at low NaCl levels (0–30 mM), and at high NaCl (90 mM), 13.12%, and 6.9%, respectively. In the XD22 cultivar, MDA and H_2O_2 contents were decreased in the leaves of plants treated with MeJA (125 and 250 µM) by 46.9% and 60.2% at low (30 mM NaCl) and high (90 mM NaCl) salinity stress and high salinity stress by 14.1% and 30.7%, respectively (see Figure 3).

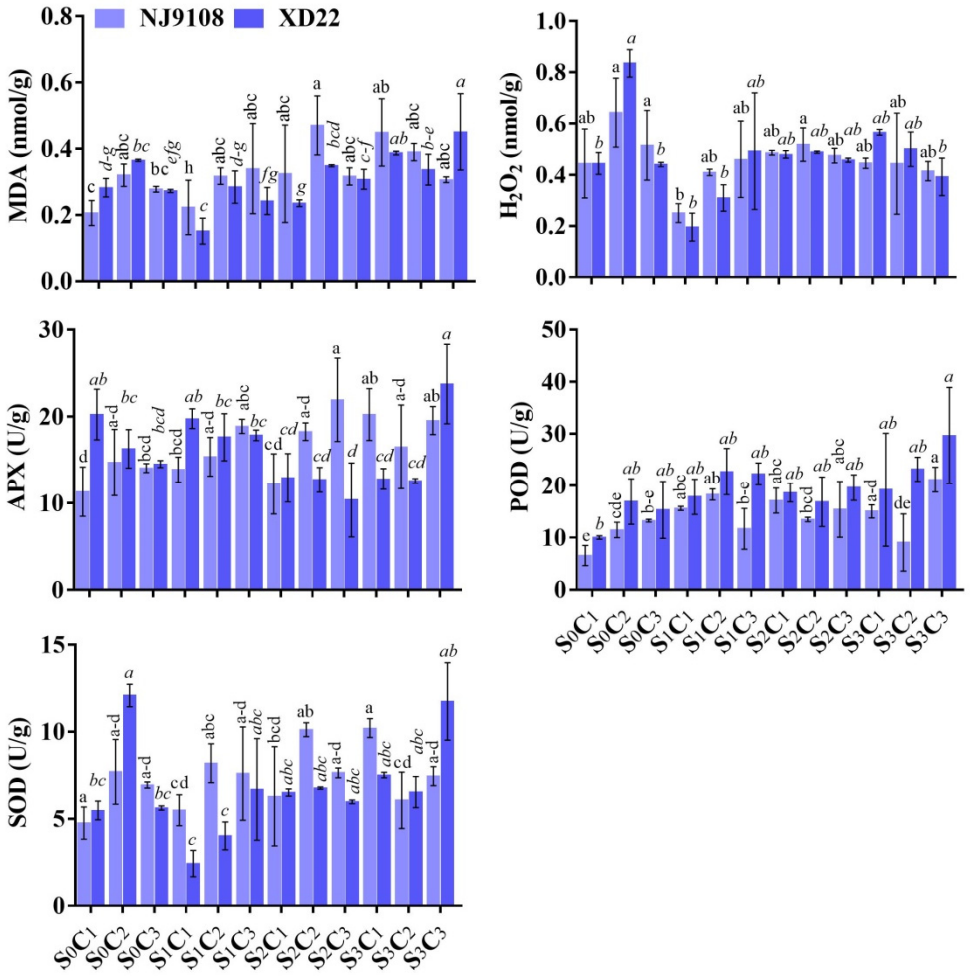

Figure 3. Influence of MeJA and salinity stress on activities of Malondialdehyde (MDA), hydrogen peroxide (H_2O_2), ascorbate peroxidase (APX), peroxidase (POD), and superoxide dismutase (SOD), in the leaves of rice plants. Salinity stresses, i.e., S0 = 0, S1 = 30, S2 = 60, and S3 = 90 mM and MeJA applications, i.e., C1 = 0, C2 = 125, and C3 = 250 µM. Bars represent the means ± SD of three replications. The letters a–h showed the significant difference between salinity and MeJA applications interaction, whereas NJ9108 represented by uniform and XD22 cultivar by italic letters.

Figure 3 showed that the APX and SOD activities in plant leaves increased significantly under salt stresses with 125 µM of MeJA compared with the control but POD activity increased significantly ($p \leq 0.05$). However, under salt stress, when treated with 250 µM of MeJA, SOD activities in leaves increased significantly, and the SOD activity initially decreased in XD22 and then increased with higher salinity and MeJA treatments (90 mM and 250 µM).

However, MeJA treatment (125 µM) at a low NaCl concentration (30 mM) significantly increased APX, POD, and SOD activities by 7.9%, 14.6%, and 32.9% in NJ9108, respectively; the same results were observed with MeJA treatment (125 µM) at high salinity stress (90 mM NaCl). In XD22, the MeJA reduces the salinity effect by increasing the APX by 46.1%, 10.4%, POD by 36.1% and 6.1%, and SOD activities by 10.4%, and 36.1% under low

and high salinity stresses (see Figure 3). Moreover, MeJA (125 and 250 µM) treatments improved the activity of the antioxidant enzymes in stressed plants differently under saline conditions (see Figure 3).

3.7. Influence of Salinity and MeJA Foliar Applications on Expression Analysis of Stress Genes

In NJ9108, *OsHKT1* was induced significantly under all the NaCl treatments (0, 30, 60, and 90 mM). A higher expression was recorded in XD22 than in NJ9108. Conversely, an opposite expression trend was observed in *OsHKT7* for the NJ9108 and XD22 cultivars under the NaCl (30–90 mM) treatments. Compared with the gene of the control, the *OsHAK1* gene was triggered strongly in NJ9108 under 30 and 90 mM of NaCl treatments (Figure 4). However, *OsHAK1* was not prominently expressed in XD22 compared with its expression in NJ9108. The *OsHAK5* gene exhibited an increased expression pattern in NJ9108 and XD22 under all the NaCl treatments. The highest expression was recorded in XD22 under the 90 mM of NaCl treatment, where it reached a maximum of 18 fold (Figure 4).

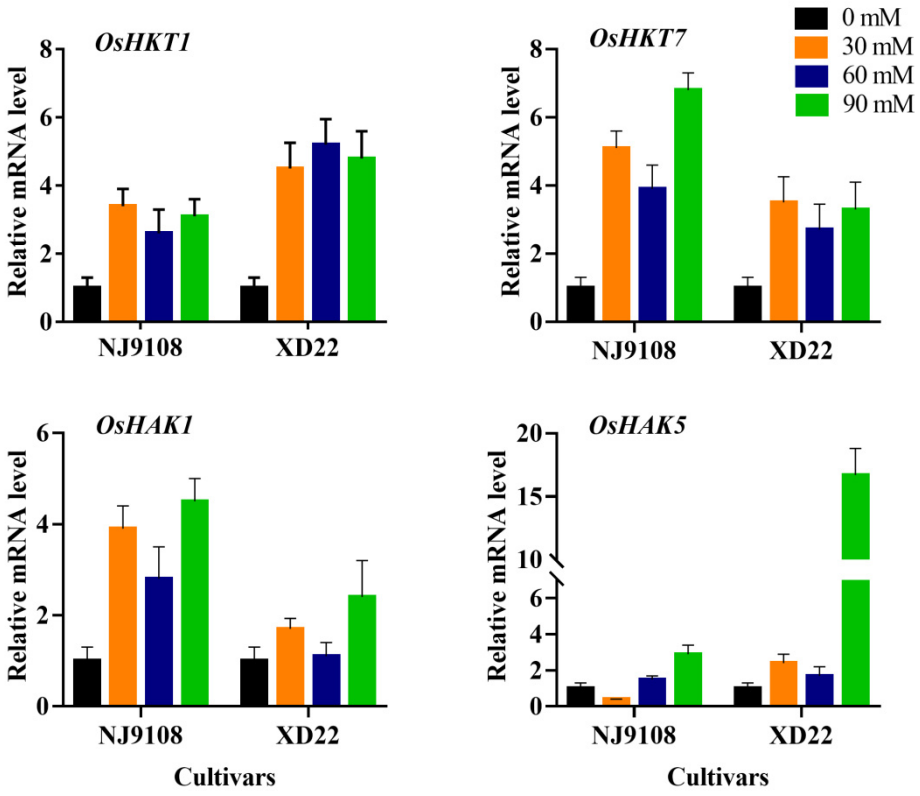

Figure 4. Influence of salinity and MeJA on the relative expression patterns of *OsHKT1*, *OsHKT7*, *OsHAK1* and *OSHAK5* genes in the leaf of both rice cultivars. Salinity stresses, i.e., S0 = 0, S1 = 30, S2 = 60, and S3 = 90 mM and MeJA applications, i.e., C1 = 0, C2 = 125, and C3 = 250 µM, respectively. Error bars represent the means ± SD of three replications.

3.8. Na^+, K^+, and Na^+/K^+ Homeostasis

Figure 5 illustrates the root and leaf ion contents (i.e., Na^+, K^+, and Na^+/K^+ ratio) of the rice plants. Salinity and MeJA treatments, as well as their interaction, significantly ($p \leq 0.05$) influenced the accumulation of Na^+, K^+, and Na^+/K^+ ratios in both cultivars. At high salinity, the maximum accumulation of Na^+ was found in the root of XD22 (95.2%) and the leaf of NJ9108 (95.7%) compared with that of the non-stressed plants (see Figure 5). However, both cultivars significantly ($p \leq 0.05$) reduced the Na^+ content at the highest salinity. In higher salinity stresses, a considerable decrease in K^+ content was observed in the roots of the NJ9108 and XD22 cultivars. In both parts (root and leaf) of the plants in both cultivars, the highest accumulation of K^+ was estimated when 250 µM of MeJA treatment

was applied at all salinity levels, including non-stress treatments. Figure 5 shows that the ratio of Na^+/K^+ increased in the roots and shoots of the highest salt-stressed plant, while a substantial decrease was observed when MeJA foliar spray was applied. Additionally, the exogenous treatment of MeJA diminished the ratio of Na^+/K^+ in the root of NJ9108 and leaf of XD22 compared with that of the cultivars under sole high-salinity conditions (Figure 5).

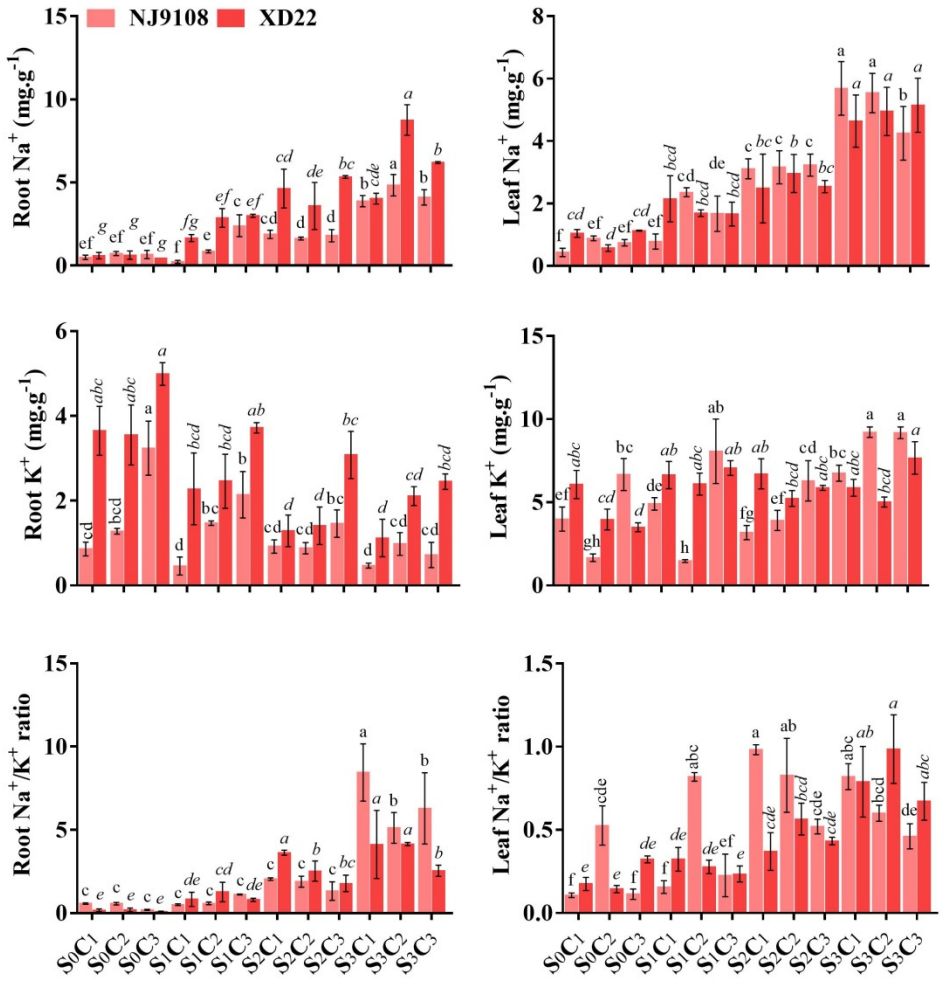

Figure 5. Influence of MeJA and salinity stress on sodium (Na^+), potassium (K^+) and K^+/Na^+ ratios in root and leaves of two wheat cultivars, NJ9108 and XD22. Salinity stresses, i.e., 0, 30, 60 and 90 mM and MeJA applications, i.e., C1 = 0, C2 = 125, and C3 = 250 µM, respectively. Bars represent the means ± SD of three replications. The letters a–h showed the significant difference between salinity and MeJA applications interaction, whereas NJ9108 represented by uniform and XD22 cultivar by italic letters.

4. Discussion

Jasmonates and MeJA play a dynamic role in reducing the negative impacts of environmental constraints, especially salinity stress on crops. Aside from their role in stress, MeJA participates in a diversity of growth, physiological, and developmental processes, including root elongation, fertility, reproductive phases, senescence, ripening, oxidants, and interactions with other plant hormones. Salt stress causes a cessation in plant height, grain yield, and relative water content [62]. In our results, both cultivars of MeJA treatments increased stem thickness and fresh weight, green leaf number, fresh leaf weight, root length, and fresh root weight under saline conditions. Similarly, JAs effectively protected wheat from high-salinity stress (150 mM NaCl) and increased the plant height, root length, branch weight, and dry root weight compared with untreated plants [33]. Our findings are also

consistent with previous results, where the high concentrations of JAs inhibited growth as well as fresh and dry weights in rice and legume crops [63,64]. Exposing plants to different MeJA treatments can reduce plant growth due to JAs metabolic activity, which delays the production and bio-activities of endogenous gibberellins [65,66]. Plant gibberellin hormones can interact with MeJA synergistically or antigenically, inhibiting growth [67].

Leaf gas exchange and chlorophyll fluorescence are essential attributes that mitigate different biotic stresses, especially under salinity stress. In a saline environment, decreases in the Fv/Fm ratio might be due to damage to the thylakoid membrane and chloroplast [64]. Similar to our result, it was found that the salinity influenced the Fv/Fm in rice, sugar beet, and cabbage; it also seems that the observed stress considerably inhibited the Fv/Fo and Fv/Fm in plant leaf tissues (*C. tinctoria*) under salt-treated conditions [68–70]. However, our experimental analysis showed that the lower concentration of MeJA could strengthen the Fv/Fm and Fv/Fo of leaves during the anthesis stage under salinity stress. Similarly, according to [71,72], specific concentrations and durations of MeJA treatments are critical for enhancing Fv/Fm in an expanded leaf. MeJA treatments strengthened the Fv/Fm and Fm/Fo ratios in rice plants while the maximum Fv/Fm ratio was found in MeJA-treated plants [70]. The Fv/Fo changes showed that the light vitality absorbed through PSII and used to decrease the efficacy of QA and the potential of the PSII system [73]. Regulation of photosynthetic properties could increase the plant's tolerance to many biotic and abiotic stresses, as previously investigated when the MeJA pre-treatment reduced the NaCl inhibition of the CO_2 fixed rate and increased the value of Fv/Fm by increasing chlorophyll content and transpiration rate [17,74], resulting in an increase in photosynthetic efficiencies. Salt stress influences the photosynthetic efficiencies in rice plants by disrupting the stomatal performance [75]. The reduction in photosynthetic efficiencies may be due to the decrease in the leaf area and chlorophyll contents (i.e., P*n*, G*s*, T*r*, and chlorophyll synthesis), which lowers the intercellular CO_2 stomatal conductance and other fluorescence activities [47,76]. The water potential, enzyme activities, and chlorophyll content were also affected while damaging chloroplast ROS production [77,78]. However, the application of MeJA may also promote the quantities of total soluble proteins, sugars, proline, RWC, chlorophyll contents, as well as the transpiration ratio [45,66], which could mediate the photosynthetic efficiencies.

Salinity stress causes osmotic pressure in plants that affects RWC directly, due to a decrease in RWC by osmotic stress closing the stomata, limiting the metabolic efficiency, which indirectly decreases the plant growth and yield of crops [79,80]. However, the application of MeJA (125 µM) increased the RWC in both cultivars under stressed and unstressed saline conditions, which is due to the retention of water in plant tissues. Salinity stress considerably increases oxidative stresses because of a disturbance in the production of H_2O_2 and MDA levels, which are injurious to cells. On the other hand, MeJA considerably lowers the toxicity of Na^+ and molecular oxygen ions, as well as H_2O_2, and boosts the activities of SOD and APX; these effects were found when the leaves of diploid and tetraploid *Robinia pseudoacacia* were treated with MeJA [81]. The findings are similar to those obtained by [82], that MeJA enhances antioxidant activities (APX, POD, and SOD) and reduces the ratio of Na^+/K^+ to alleviate the detrimental effects of salinity stress in strawberry leaves sprayed with MeJA. Our results showed that MeJA decreased the oxidant (MDA and H_2O_2) levels while unregulated the antioxidant defense system of leaves such as APX, CAT, and POD activities under salinity stress. This finding is consistent with the results of [33,83], where exogenous JA treatment significantly increased SOD and CAT activities. Similarly, the exogenous application of JAs significantly increases SOD and APX activities, which was reported as an essential antioxidative defense required for salt tolerance in plants [31,84]. Thus, our results revealed that the coordination of APX, POD, and CAT activities with SOD activity plays a central protective role in MDA, H_2O_2, and the O_2 scavenging process [83,85,86].

HKT channels are expressed in all plant parts, from roots to shoot and leaves to flowers [48]. *HKT* gene expression is often affected by stress conditions, such as high

sodium or low potassium concentrations. A decreased expression of *AtHKT1* in NJ9108 roots enhanced tolerance to salinity stress [48,87,88]. Similarly, from our findings, we observed a reduced expression of *OsHKT1* in NJ9108 than in XD22, and this expression explains the high tolerance of NJ9108 to salinity stress. In contrast, *OsHKT7* exhibited a lower expression in XD22 than in NJ9108. We assume that *OsHKT1* and *OsHKT7* work simultaneously to regulate plant response to salinity stress. Previous studies have shown that cluster I *HAKs* confer the activity of high-affinity K^+ uptake. In contrast, the cluster transcript levels increase under K^+ starvation or saline conditions, thereby reinforcing potassium supply and adaptation [48,89–91]. Existing studies have addressed the roles of K^+ selective *HAK* transporters under low K^+ and salt-stress conditions [88]. In this study, we observed a higher expression of *OsHAK1* in NJ9108 than in XD22. This higher expression of *OsHAK1* might contribute to regulating shoot Na^+ exclusion while enhancing salt tolerance, possibly by recovering Na^+ from the xylem sap; this phenomenon provides a novel mechanistic understanding of the salt-tolerant role of *HAK* family transporters.

Ionic toxicity depends on the main component of salinity stress that commences with the accumulation of damaging concentrations of ions (Na^+ and Cl^-) in plant cells [92,93]. Both Na^+ and K^+ ions compete to enter plant root cells and the replacement of K^+ with Na^+ often causes nutritional imbalances [94]. In this study, the accumulation of Na^+ in the leaves and roots induced nutrient imbalance in both parts, as indicated by a decrease in the K^+/Na^+ ratio. Maintaining a low Na^+ concentration and lower Na^+/K^+ ratio in the leaf is vital for stress tolerance [95]. High Na^+ concentration reduces the amounts of available K^+, Mg, and Ca for plants [95,96]. However, pre-treatment with JA prior to salt stress reduced Na^+ deposition, thereby linking JA to Na^+ homeostasis [97]. The mitigation of growth inhibition under NaCl-salt stress can be attributed to enhanced ion homeostasis with MeJA, especially at 125 µM. Hence, the applied concentrations of the MeJA, salinity stress varying sensitivity and exogenous MeJA applications could avert the plants' diverse growth, and physiological and developmental responses.

5. Conclusions

We found that increasing salinity stress inhibited the agronomical parameters, fluorescence, and leaf gas exchange attributes. Meanwhile, MeJA foliar treatment on rice plants under salt stress substantially changed fluorescence and gas exchange activities. The most significant enhancements were observed in the gas exchange activities when MeJA was applied at a concentration of 125 µM. MeJA also played a role in mediating the oxidant level (MDA and H_2O_2) and protecting the antioxidants from deleterious conditions caused by salinity stress. Additionally, the NJ9018 cultivar performed better than the XD22 cultivar, as shown by the differential expression of *OsHKT* and *OsHAK* genes. Statistically, our results show that a MeJA treatment (125 µM) can alleviate the negative effects of salinity stress and improve rice plant agronomical parameters, fluorescence, and gas exchange traits.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy12102343/s1, Table S1: Primers Sequences for qRT PCR.

Author Contributions: Conceptualization, S.H.; methodology, S.H. and Y.C.; software, S.H.; formal analysis, S.H. and S.L.; investigation, S.H.; resources, R.L. and Y.W.; data curation, S.H.; writing—original draft preparation, S.H.; writing—review and editing, S.H., H.H. and R.Z.; supervision, Q.D.; project administration, Q.D.; funding acquisition, Q.D. and Y.C. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

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