Journal of Tropical Crop Science Vol. 13 No. 2, June 2026
www.j-tropical-crops.com

Received 6/18/2025; Revised 4/25/2026; Accepted 6/22/2026
https://doi.org/10.29244/jtcs.13.02.529-543

Study of Salinity Tolerance in Several Mutant Rice Lines Using Morphophysiological and Biochemical Approaches

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Abstract

Salinity is a major limitation to rice production. ‘Atomita 2’, a mutation-derived rice variety released in 1983, was originally reported to be salinity-tolerant, but detailed evidence of its tolerance remains limited. This study aimed to identify salinity-tolerant mutant lines of ‘Atomita 2’ and to characterize their morphological, physiological, and biochemical responses in the M4 generation under salt stress. The experiment was conducted in a greenhouse through two stages: initial screening of mutant lines under 60 mM NaCl and subsequent evaluation of selected genotypes for morphophysiological and biochemical traits. Screening identified 38 surviving genotypes. Salinity stress reduced plant height, tiller number, 100-grain weight, and grain yield, and decreased photosynthetic rate, stomatal conductance, transpiration rate, and SPAD value. In contrast, APX and CAT activities, proline, and MDA increased with NaCl concentration, indicating stress adaptation. ‘Atomita 90’ and ‘Atomita 146’ showed greater tolerance than ‘Atomita 2’ and ‘Pokkali’, as indicated by stress tolerance index values and their physiological and biochemical responses.

Keywords: antioxidant enzyme, mutant strains, reactive oxygen species

Introduction

Salinity is one of the major challenges currently affecting agricultural land. Saline soil is defined as soil containing sodium (Na) levels that exceed the tolerance threshold of crops (Rachman et al., 2018). In Indonesia, land is classified as saline when the sodium content in the soil solution ranges from 8% to 15%, and seawater intrusion occurs for more than four months per year (Sopandie, 2013). Saline soils exhibit an electrical conductivity (EC) value greater than 4 dS/m, equivalent to 40 mM NaCl (Rachman et al., 2018). These soils are commonly found in coastal areas, irrigated lands, over-fertilized fields, and naturally saline regions. Rice (*Oryza sativa* L.) is a staple food crop for over half of the global population, particularly in Indonesia. By 2050, the global population will reach 9.6 billion people (Leridon, 2020). This population growth will drive a continuous increase in rice demand. However, crop production in many areas is currently facing serious challenges due to climate change, which contributes to various abiotic stresses, including salinity (Munn, 2002). At present, 4.03 billion people live in 13 countries severely affected by soil salinity, and this number is expected to rise to 5.02 billion by 2050 (Liu et al., 2020). According to Zhu (2016), nearly 50% of all cultivated land worldwide is expected to be affected by salinization by 2050, posing a major obstacle to sustainable agricultural development and food security.

Numerous studies have reported salinity stress as one of the most prevalent abiotic stresses affecting rice (Shahid et al., 2018). Rachman et al. (2018) noted that salinity stress poses a significant barrier to rice growth and development. Salinity stress inhibits growth and

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photosynthesis, reduces biomass, and leads to partial grain sterility, ultimately decreasing rice yields (Tsai et al., 2019). Salinity imposes two types of stress on rice plants: osmotic stress and ion toxicity (Karolinoerita & Yusuf, 2020). Elevated levels of sodium (Na^+) and chloride (Cl^-) ions in the soil solution interfere with plant-water relations by reducing soil water availability, thereby lowering osmotic potential (Grewal, 2010). High Na^+ concentrations also limit potassium (K^+) uptake by plant roots, thereby reducing the K^+/Na^+ ratio (Ueda et al., 2013). The expansion of saline land in Indonesia is likely to continue, necessitating the development of appropriate rice varieties and cultivation methods for saline conditions. This would enable the effective use of marginal lands, including those affected by salinity. Rice is particularly sensitive to salinity during critical stages such as germination, seedling development, and flowering. Screening during the early growth stages (2–4 weeks) is more practical than during flowering, as it allows for faster selection, requires less space, and is more efficient in terms of time and cost (Bado et al., 2016).

‘Atomita 2’ is a rice variety developed through breeding and officially released in 1983. It has demonstrated initial tolerance to salinity at concentrations of 4–6 mm HOS/cm (Balai Pengkajian Teknologi Pertanian, 2014). To improve its agronomic performance and salinity tolerance, further radiation-induced mutation breeding is necessary. However, the morpho-physiological and biochemical characteristics of the ‘Atomita 2’ variety and its mutants under salinity stress have not yet been thoroughly investigated. Therefore, this study is essential and is expected to serve as a theoretical foundation for the development of salinity-tolerant rice varieties.

Material and Methods

Study Area

This Study consisted of two experiments: (1) Initial screening to determine potential mutant lines of rice variety ‘Atomita 2’ tolerant to salinity stress, (2) Identification of morphophysiological and biochemical characteristics of mutant lines of rice variety ‘Atomita 2’ against salinity stress. The first experiment was conducted in the greenhouse of Cikabayan Bawah experimental garden, Department of Agronomy and Horticulture IPB, from March 2023 to June 2024. The genetic materials used in the first experiment were 100 3rd generation (M3) mutant lines of ‘Atomita 2’, and national varieties namely ‘Atomita 2’, ‘Pokkali’, ‘IR64’, ‘Biosalin 1’, and ‘Biosalin 2’. The second experiment was conducted in the greenhouse of the Radiation Process Technology Research Center - Nuclear Energy Research Organization - BRIN Jakarta, from July 2024 to January 2025. The genetic materials used in the second experiment were 10 rice genotypes, including: 3 genotypes selected at 120 mM NaCl, namely ‘Atomita 77’, ‘Atomita 90’, and ‘Atomita 69’ (from other previous experiments); 4 genotypes selected at 60 mM NaCl, namely ‘Atomita 29’, ‘Atomita 146’, ‘Atomita 325’, and ‘Atomita 81’ (experiment 1); and 3 genotypes from comparison varieties (‘Atomita 2’, ‘Pokkali’, ‘IR64’).

Procedures

Salinity Tolerance Scoring at Two Weeks After Treatment

Salinity Tolerance Scoring at Two Weeks After Treatment experiment used an augmented randomized complete block design with a single NaCl concentration (60 mM) for selection. A total of 100 rice genotypes were selected, along with 5 check varieties, ‘Atomita 2’, ‘Pokkali’, ‘IR64’, ‘Biosalin 1’, and ‘Biosalin 2’, which were replicated four times. The experiment was conducted using Yoshida solution and soil as media. The seeds were sown hydroponically in seedling trays containing Yoshida solution. After 1–2 weeks of growth in the Yoshida solution (when seedlings had developed 2–3 leaves), salinity stress was imposed by adding NaCl to the solution to reach a final concentration of 60 mM. NaCl was fully dissolved in the Yoshida

Received 6/18/2025; Revised 4/25/2026; Accepted 6/22/2026
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solution, and the solution's electrical conductivity (EC) was measured with a conductivity meter to confirm the target salinity level. The solution was monitored every 2-3 days and adjusted as needed to maintain a stable salinity concentration throughout the treatment period.

The salinity treatment was maintained for two weeks. Selected seedlings were then transplanted into plastic buckets containing soil media. No additional NaCl was applied after transplanting into soil. Therefore, salinity exposure in this experiment was limited to the seedling stage under hydroponic conditions. Measurements included salinity tolerance scoring based on the International Rice Research Institute (2013) Standard Evaluation Score (SES), plant height, and root length at 2 weeks after treatment.

The Effect of NaCl Concentration and Genotype on Morphological Characteristics of Rice Plants

This experiment used a split-plot design within a completely randomized block design. The main plot consisted of salinity stress treatments at three levels: 0, 60, and 120 mM NaCl. The subplot factor was rice genotype, consisting of 10 genotypes: 'Atomita 77', 'Atomita 90', 'Atomita 69', 'Atomita 29', 'Atomita 146', 'Atomita 325', 'Atomita 81', 'Atomita 2', 'Pokkali', and 'IR64'. 'Atomita 2' was used as the parent, 'IR64' as the sensitive check, and 'Pokkali' as the tolerant check. Each treatment was replicated four times, resulting in 120 experimental units. Seedlings were sown and transplanted at 22 days after sowing into plastic buckets filled with planting media. Each bucket (capacity ±10-15 L) was filled with approximately 8-10 kg of soil and maintained under flooded conditions, with a water layer of approximately 2-3 cm above the soil surface to simulate lowland rice cultivation. Salinity stress was initiated at the panicle initiation stage.

Salinity was initially imposed at the start of the treatment period by applying NaCl solutions at designated concentrations (0, 60, and 120 mM). The NaCl was dissolved in water and applied uniformly to each bucket at approximately 1.5–2.0 L per bucket to achieve near-field-capacity conditions and ensure uniform distribution of salt within the root zone. To account for potential changes in soil salinity due to leaching, evaporation, and plant uptake, soil salinity was monitored periodically. Soil electrical conductivity (EC) was measured every 5–7 days. Soil moisture was maintained by adding distilled water to sustain a flooded layer (2–3 cm), while drainage was minimized to reduce salt loss. When EC values fell below an acceptable threshold (±15% of the target level), a small volume of NaCl solution at the corresponding treatment concentration (approximately 200–300 ml per bucket) was gradually added to restore the intended salinity level. These additions were made to maintain salinity conditions rather than as repeated treatment applications.

Measurements in the second experiment included morphological, physiological, and biochemical variables. Morphological variables included plant height, number of tillers, and yield components included number of panicles per clump, number of grains per panicle per clump, number of filled grains per panicle per clump, 100-grain weight, and grain weight per clump. Physiological variables observed included photosynthetic rate, stomatal conductance, transpiration rate, leaf water content, SPAD, and stomatal density. Biochemical variables observed included APX enzyme activity, measured using the method of Asada and Nakano modified by Kumar (2022), and CAT enzyme activity, proline content, and MDA levels, measured using the method of Chen and Zhang (2016) as modified by Chen and Zhang (2023).

Data Analysis

The first experiment was analyzed using the *F* test and the LSD (least significant difference) test at a 5% significance level. The second experiment was analyzed using the *F* test and the HSD (honestly significant difference) test at a 5% significance level. All analyses were performed using the RStudio software.

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Results

Salinity Tolerance Scoring at Two Weeks After Treatment

The salinity tolerance scores for 105 rice genotypes (100 test genotypes and 5 check genotypes) under 60 mM NaCl selection are shown in Table 1. A total of 20 genotypes scored 1 (highly tolerant), including: ‘Atomita 2’, ‘Pokkali’, A9, A51, A52, A64, A65, A66, A83, A100, A137, A146, A210, A237, A251, A281, A303, A325, A367, and A389. Eight genotypes scored 3 (tolerant): A57, A85, A155, A208, A224, A255, A285, and A296. Meanwhile, 10 genotypes scored 5 (moderately tolerant), including: ‘Biosalin 1’, A29, A81, A87, A129, A149, A249, A304, A313, and A317. Three genotypes scored 7 (sensitive), and the remaining 64 genotypes scored 9 (highly sensitive). Among the five check genotypes used in this study, only ‘Atomita 2’, ‘Pokkali’, and ‘Biosalin 1’ showed tolerance to 60 mM NaCl stress. The application of 60 mM NaCl successfully selected 38 genotypes ranging from moderately tolerant to highly tolerant.

Effect of Salinity Stress on Plant Height

Changes in plant height after 60 mM NaCl salinity treatment for two weeks are presented in Table 2. Based on the selection results, some rice genotypes showed significantly taller plant height than the check parent and the tolerant checks. Genotype A137 was the best based on plant height after treatment, having a taller stature than the parent genotype ‘Atomita 2’, and the tolerant checks ‘Pokkali’, ‘Biosalin 1’, and ‘Biosalin 2’. Among all the observed genotypes, the shortest plant height was found in genotype A295 (8.5 cm). A decrease in plant height is one of the morphological responses of plants to salinity stress (Sopandie, 2013).

Effect of Salinity Stress on Root Length

The performance of root length after a 60 mM NaCl salinity treatment for 2 weeks is shown in Table 3. Rice root length changed significantly after the treatment. Genotype A65 had the longest root length after salinity stress, measuring 30.5 cm, which was significantly longer than those of all the check genotypes. The shortest root among all observed plants was in genotype A182 (3.8 cm), significantly shorter than that of the check genotype ‘Pokkali’; however, this plant died after two weeks of salinity stress. Among the plants that survived the treatment, the genotype with the shortest root length was the check genotype ‘Biosalin 1’, with a root length of 8 cm.

Table 1

Salinity Tolerance Scores under 60 Mm Nacl Salinity at the Seedling Stage

Score	Tolerance	Observation	Number of selected genotypes
1	Highly tolerant	Normal growth, leaves are asymptomatic	20
3	Tolerant	Growth is almost normal, but leaf tips are slightly whitish and curled	8
5	Moderately tolerant	Growth is severely stunted, most leaves curl, and only a few elongate	10
7	Sensitive	Total growth cessation, most leaves dry up, and some plants died	3
9	Highly Sensitive	The majority of the plants died	64

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www.j-tropical-crops.com

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Table 2

Rice Plant Height Two Weeks After 60 mM NaCl Salinity Treatment

Genotypes	Plant height (cm)	Genotypes	Plant height (cm)	Genotypes	Plant height (cm)
A5	19.9 b	A139	15.2 b	A267	11.8 bde
A7	17.2 b	A140	21 ac	A268	20.5 ac
A8	21.2 ac	A146^h	27.8 abcde	A269	22 ace
A9^h	27 acde	A149^h	21.5 ac	A270	18.1 b
A17	13.1 bde	A153	12.4 bde	A271	21.9 ace
A29^h	25.1 acde	A155^h	26 acde	A281^h	11.8 bde
A30	15.6 bd	A160	19 b	A284	16.5 b
A36	22 ac	A165	16.7 b	A285^h	22.3 ace
A51^h	26.3 acde	A182	12 bde	A295	8.5 abcde
A52^h	26.3 acde	A187	22.2 ace	A296^h	19.7 ac
A53	14.5 bde	A207	19.5 a	A302	17.4 b
A57^h	27.5 acde	A208^h	23.2 acde	A303^h	24.6 acde
A58	12 abcde	A209	14.3 bd	A304^h	22.3 ace
A59	19.7 b	A210^h	25.3 acde	A313^h	15.6 b
A64^h	25.2 acde	A215	16 b	A317^h	19 a
A65^h	28.5 acde	A216	11 bde	A325^h	23.6 acde
A66^h	28.8 acde	A221	16.1 b	A326	16.8 b
A76	16.8 b	A222	15 b	A343	12.1 bde
A79	19 b	A223	16 b	A347	18 b
A81^h	21.1 ac	A224^h	22 ace	A359	21.5 ac
A82	22.8 ac	A229	16.5 b	A367^h	24 acde
A83^h	24.4 acde	A233	15.3 b	A368^h	21.2 ac
A85^h	27.5 acde	A237^h	28.2 abcde	A369	16 b
A86	13.2 bde	A239	20.2 ac	A375	17.3 b
A87^h	21.5 ac	A240	24.2 acde	A376	13.5 bd
A99	18.9 b	A241	20.2 ac	A379	14.2 bd
A100^h	29.6 abcde	A249^h	25.1 acde	A380	13.1 bde
A106	19.2	A250	16.8 b	A385	14.2 bd
A113	14.2 bd	A251^h	26.4 acde	A386	17.7 b
A121	15.5 b	A255^h	24 acde	A389^h	23.7 acde
A123	15.9 b	A256	22.4 ace	‘Atomita 2’^{h}	15.25
A129^h	24.2 acde	A259	15.8 b	‘Pokkali’^{h}	23.52
A131	14.5 bd	A263	17.6 b	‘IR64’	15.60
A137^h	30.2 abcde	A265	18.5 b	‘Biosalin 1’^{h}	19
A138	17.8 b	A266	23.6 acde	‘Biosalin 2’	18.18

Notes. The letter index in the same column is the result of the least significant difference (LSD) test, a= significantly different from ‘Atomita 2’, b= significantly different from ‘Pokkali’, c= significantly different from ‘IR64’, d= significantly different from ‘Bosalin 1’, e= significantly different from ‘Biosalin 2’. ^{h} plants survived after being treated with NaCl stress for 2 weeks.

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Table 3

Rice Root Length Two Weeks After 60 mM NaCl Salinity Treatment

Genotypes	Root length (cm)	Genotypes	Root length (cm)	Genotypes	Root length (cm)
A5	7 b	A139	16.8 acde	A267	5.5 bd
A7	7 b	A140	12.3 c	A268	7.5 b
A8	7.1 b	A146[h]	29.5 abcde	A269	8.4 b
A9[h]	21.7 acde	A149[h]	24 abcde	A270	5.5 bd
A17	4.1 abde	A153	4 b	A271	13.8 acde
A29[h]	19.6 acde	A155[h]	27.4 abcde	A281[h]	13 c
A30	5.9 b	A160	10.7	A284	6.1 b
A36	17 acd	A165	8.7 b	A285[h]	18.5 acde
A51[h]	23.1 acde	A182	3.8 b	A295	4.7 b
A52[h]	24 acde	A187	20.2 acde	A296[h]	16.5 acde
A53	4.9 abde	A207	14.8 acde	A302	7.6 b
A57[h]	25.5 abcde	A208[h]	22.7 abcde	A303[h]	18.1 acde
A58	5.5 bd	A209	5.4 b	A304[h]	21 acde
A59	13.7 b	A210[h]	25.7 abcde	A313[h]	19.1 acde
A64[h]	27.5 abcde	A215	10.5 c	A317[h]	16.7 acde
A65[h]	30.5 abcde	A216	4.1 b	A325[h]	13.4 cde
A66[h]	30.1 abcde	A221	15.2 acde	A326	12.3 c
A76	5.5 abd	A222	4.1 b	A343	4.9 b
A79	17.8 acde	A223	8.2 b	A347	6.8 b
A81[h]	18 acde	A224[h]	28.1 abcde	A359	16.1 acde
A82	8.8 b	A229	5.2 b	A367[h]	13.5 acde
A83[h]	24 acde	A233	6.5 b	A368[h]	13.6 acde
A85[h]	24.3 acde	A237[h]	30.3 abcde	A369	7.2 b
A86	4.7 abde	A239	15.5 acde	A375	13 ce
A87[h]	19.9 acde	A240	16.5 acde	A376	7.2 b
A99	6.8 b	A241	21.7 abcde	A379	13.2 ce
A100[h]	23.5 abcde	A249[h]	21.7 abcde	A380	5.5 b
A106	13.2 acde	A250	7.2 b	A385	7.8 b
A113	5.2 b	A251[h]	25.1 abcde	A386	8.3 b
A121	5.9 b	A255[h]	21.5 abcde	A389[h]	19.8 acde
A123	8.9 b	A256	7.2 b	'Atomita 2'[h]	8.12
A129[h]	19.9 acde	A259	4.7 b	'Pokkali'[h]	16.63
A131	5.5 bd	A263	9.7 c	'IR64'	5.60
A137[h]	22.2 abde	A265	18.4 acde	'Biosalin 1'[h]	8.00
A138	7.6 b	A266	13.4 acde	'Biosalin 2'	7.42

Notes. The letter index in the same column is the result of the Least Significant Difference (LSD) test, a= significantly different from 'Atomita 2', b= significantly different from 'Pokkali', c= significantly different from 'IR64', d= significantly different from 'Bosalin 1', e= significantly different from 'Biosalin 2'. [h] plants survived after being treated with NaCl stress for 2 weeks.

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The Effect of NaCl Concentration and Genotype on Morphological Characteristics of Rice Plants

Changes in plant height and number of tillers were measured two weeks after the application of salinity treatment, whereas yield components, including number of panicles, number of grains, number of filled grains, 100-grain weight, and weight of grains, were recorded at the end of the experiment.

Salinity treatment significantly reduced plant height, as shown in Table 4. The average plant height under control conditions (0 mM NaCl) was 108.11 cm and decreased significantly under salinity stress, with further reductions at higher NaCl concentrations. The average number of tillers under 120 mM NaCl was the lowest at 16 tillers. Rice genotypes significantly influenced plant height and tiller number after salinity treatment. The 'Pokkali' genotype had the highest plant height and the lowest number of tillers after salinity treatment. Salinity-tolerant rice plants exhibited higher values of morphological traits, including plant height, biomass, root and shoot lengths, and root fresh weight (Alkahtani & Dwiningsih, 2023).

Salinity significantly affected the number of panicles, grains, and filled grains (Table 4). The highest number of panicles was recorded at 60 mM NaCl, although it was not significantly different from the control. Control treatment (0 mM NaCl) produced the highest number of grains and filled grains (171 and 122 grains), while 120 mM NaCl resulted in the lowest values (141 and 84 grains). Salinity significantly affected grain number and grain filling. This result aligns with Subekti et al. (2020), who reported that high soil salinity reduced panicle number, grains per panicle, and 1000-grain weight, while increasing the number of empty grains. The increase in panicle number under 60 mM NaCl suggests that mild salinity stress may stimulate tiller-to-panicle differentiation in certain genotypes, likely through

Table 4

Effects of NaCl Concentrations on Morphological Traits and Yield Components of Ten Rice Genotypes

Treatments	Plant height (cm)	Number of tillers	Number of panicles	Number of grains	Number of filled grains	Weight of 100 grains (g)	Grain weight (g)
NaCl concentrations (mM)							
0	108.11 a	19 a	18 ab	171 a	122 a	2.23 a	33.66 a
60	101.10 b	21 a	20 a	163 a	113 a	2.05 b	28.33 b
120	93.54 c	16 b	16 b	141 b	84 b	1.81 c	14.54 c
Genotypes							
'Atomita 77'	94.79 cd	19 a	19 a	172 ab	114 ab	2.00 ab	27.11 a
'Atomita 90'	93.83 d	19 a	18 a	164 ab	117 ab	2.05 ab	27.00 a
'Atomita 69'	94.45 cd	22 a	16 a	156 ab	119 ab	2.00 ab	29.66 a
'Atomita 29'	95.29 cd	20 a	19 a	155 ab	102 abc	2.05 ab	25.27 ab
'Atomita 146'	97.79 cd	18 ab	18 a	166 ab	120 ab	2.04 ab	25.55 ab
'Atomita 325'	94.17 cd	18 ab	18 a	146 ab	97 bc	2.02 ab	25.17 ab
'Atomita 81'	98.37 c	20 a	17 a	167 ab	107 abc	2.03 ab	26.19 ab
'Atomita 2'	95.08 cd	22 a	19 a	181 a	125 a	2.05 ab	30.94 a
'Pokkali'	137.58a	13 c	17 a	143 ab	80 c	2.18 a	21.66 ab
'IR 64'	107.79b	15 bc	19 a	131 b	80 c	1.87 b	16.43 b

Note. Values followed by the same letter in the same column are not significantly different in each character based on the 5% HSD test.

Received 6/18/2025; Revised 4/25/2026; Accepted 6/22/2026
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stress-induced hormonal regulation and altered assimilate partitioning. However, this response does not enhance final grain production, indicating that reproductive processes such as grain filling are more sensitive to sustained salinity stress than early panicle initiation. The 'IR64' genotype, which serves as the sensitive check, exhibited the fewest panicles and filled grains (131 and 80, respectively) among the genotypes. The 'Pokkali' genotype, used as the tolerant check, showed relatively high panicle number but low filled grain number, similar to 'IR64'. This indicates that 'Pokkali' maintains vegetative growth and panicle development under salinity stress but exhibits limited grain-filling efficiency, suggesting a stress-avoidance strategy rather than full reproductive tolerance. Meanwhile, the mutant genotype did not differ significantly from the parental genotype in most yield components.

The 100-grain weight and the grain weight per clump decreased significantly as NaCl concentration increased (Table 4). Under control conditions, rice plants exhibited the highest 100-grain weight (2.23 g) and grain weight per clump (33.66 g). The 'Pokkali' genotype had the highest 100-grain weight (2.18 g), while the 'IR64' genotype showed the lowest (1.87 g). The 'Atomita 2' genotype produced the highest grain yield per clump, although it was not significantly different from 'Atomita 77', 'Atomita 90', and 'Atomita 69'.

The interaction between NaCl concentration and genotype significantly affected grain weight per clump (Table 5). The highest grain weight (81.25 g) was recorded in the 'Atomita 2' genotype at 0 mM NaCl, whereas the lowest was observed in the 'IR64' genotype at 120 mM NaCl. The salinity tolerance index (STI) was calculated based on grain weight per clump using the formula: STI (%) = (grain weight under salinity stress/grain weight under control) × 100. This index was used to evaluate the ability of genotypes to maintain yield under salinity stress relative to non-stress conditions, with values >100% indicating stable or improved performance and values <100% indicating yield reduction. STI is considered a reliable indicator for comparing genotypic tolerance because it integrates yield potential under both stress and non-stress conditions. Low salinity levels (50 mM) did not significantly alter the salinity tolerance index, whereas significant differences were observed at higher concentrations (200 mM) (Arajmand et al., 2020).

Table 5

Effect of Interactions Between NaCl Concentration and Genotypes on Grain Weight per Clump and Salinity Tolerance Index (STI)

Genotypes	Grain weight per clump (g)			STI (%)	
	0 mM	60 mM	120 mM	60 mM	120 mM
'Atomita 77'	73.47 ab	58.61 abcd	30.56 cdef	79.8	41.6
'Atomita 90'	69.87 abcd	62.87 abcd	29.28 def	90.0	41.9
'Atomita 69'	70.49 abcd	74.32 ab	33.16 bcdef	105.4	47.0
'Atomita 29'	64.37 abcd	55.11 abcd	32.13 bcdef	85.6	49.9
'Atomita 146'	70.87 abcd	44.27 abcd	38.19 bcdef	62.5	53.9
'Atomita 325'	72.41 abc	52.68 abcd	25.95 ef	72.8	35.8
'Atomita 81'	70.89 abcd	57.13 abcd	29.73 def	80.6	41.9
'Atomita 2'	81.25 a	70.71 abcd	33.67 bcdef	87.0	41.4
'Pokkali'	57.76 abcd	47.49 abcd	24.73 ef	82.2	42.8
'IR64'	41.85 abcd	43.43 abcd	13.33 f	103.8	31.9

Note. Values followed by the same letter in the same line and column are not significantly different in each character based on the 5% HSD test.

Journal of Tropical Crop Science Vol. 13 No. 2, June 2026
www.j-tropical-crops.com

Received 6/18/2025; Revised 4/25/2026; Accepted 6/22/2026
https://doi.org/10.29244/jtcs.13.02.529-543

Under 60 mM NaCl, ‘Atomita 69’ and ‘Atomita 90’ showed higher STI values than their parent and ‘Pokkali’, with ‘Atomita 69’ exceeding 100% (105.4%), indicating stable performance under moderate salinity. At 120 mM NaCl, STI decreased across all genotypes; however, ‘Atomita 146’, ‘Atomita 29’, and ‘Atomita 69’ maintained relatively higher STI values, indicating better tolerance under severe stress. Physiological response supported these results, where ‘Atomita 90’ showed a high photosynthetic rate and stomatal density, accompanied by the highest proline accumulation. Meanwhile, ‘Atomita 146’ exhibited the highest photosynthetic rate, stomatal conductance, and transpiration rate, along with low MDA accumulation and the highest APX activity. The elevated APX activity reflects this genotype’s ability to scavenge ROS, thereby enhancing its tolerance to salinity stress. Conversely, the ‘IR64’ genotype exhibited the highest sensitivity to salinity, as evidenced by the lowest grain yield per clump and STI values at 120 mM NaCl, while remaining relatively tolerant at 60 mM NaCl. This result is supported by the high MDA content in ‘IR64’, indicating greater membrane damage due to ROS accumulation.

The Effect of NaCl Concentration and Genotype on Physiological Characteristics of Rice Plants

The application of 120 mM NaCl significantly reduced photosynthetic rate, stomatal conductance, transpiration rate, and SPAD value, but increased stomatal density and leaf water content in rice plants (Table 6).

Under 120 mM NaCl, the lowest values were observed for photosynthetic rate (9.23 $\mu mol \cdot m^{-2} \cdot s^{-1}$), stomatal conductance (0.15 $mol \cdot m^{-2} \cdot s^{-1}$), transpiration rate (3.69 $mmol \cdot m^{-2} \cdot s^{-1}$), and SPAD value (39.09). The ‘Atomita 146’ genotype exhibited the highest photosynthetic rate, stomatal conductance, transpiration rate, and stomatal density,

Table 6

Effects of NaCl Concentrations on Physiological Traits of Ten Rice Genotypes

Treatments	Photosynthesis rates ($\mu mol.m^{-2}.s^{-1}$)	Stomatal conductance ($mol.m^{-2}.s^{-1}$)	Transpiration rates ($mmol.m^{-2}.s^{-1}$)	SPAD values	Stomatal density ($stomata/mm^2$)	Leaf water content (%)
NaCl concentrations (mM)						
0	10.54 ab	0.23 a	4.92 a	42.43 a	439.87 b	35.70 b
60	12.00 a	0.22 a	5.03 a	39.49 b	476.69 ab	37.29 b
120	9.23 b	0.15 b	3.69 b	39.09 b	482.55 a	40.72 a
Genotypes						
‘Atomita 77’	9.54 ab	0.16 ab	3.87 ab	40.36 a	485.77 a	39.09 a
‘Atomita 90’	11.28 ab	0.19 ab	4.52 ab	41.24 a	524.84 a	38.86 a
‘Atomita 69’	8.38 b	0.14 b	3.22 b	40.31 a	457.32 a	37.66 a
‘Atomita 29’	10.42 ab	0.18 ab	4.22 ab	40.99 a	517.19 a	38.60 a
‘Atomita 146’	13.79 a	0.29 a	5.98 a	40.10 a	488.32 a	39.06 a
‘Atomita 325’	11.03 ab	0.23 ab	4.93 ab	39.56 a	472.61 a	39.34 a
‘Atomita 81’	11.74 ab	0.23 ab	5.11 ab	39.25 a	466.67 a	37.38 a
‘Atomita 2’	9.25 ab	0.19 ab	4.49 ab	39.07 a	466.24 a	36.94 a
‘Pokkali’	8.53 b	0.16 ab	3.77 ab	42.33 a	439.07 ab	38.00 a
‘IR 64’	11.95 ab	0.26 ab	5.36 ab	40.17 a	345.65 b	34.12 a

Note. Values followed by the same letter in the same column are not significantly different in each character based on the 5% HSD test.

Journal of Tropical Crop Science Vol. 13 No. 2, June 2026
www.j-tropical-crops.com
Received 6/18/2025; Revised 4/25/2026; Accepted 6/22/2026
https://doi.org/10.29244/jtcs.13.02.529-543

indicating superior salinity tolerance compared to the other genotypes. In contrast, the 'Atomita 69' genotype recorded the lowest photosynthetic rate, stomatal conductance, and transpiration rate.

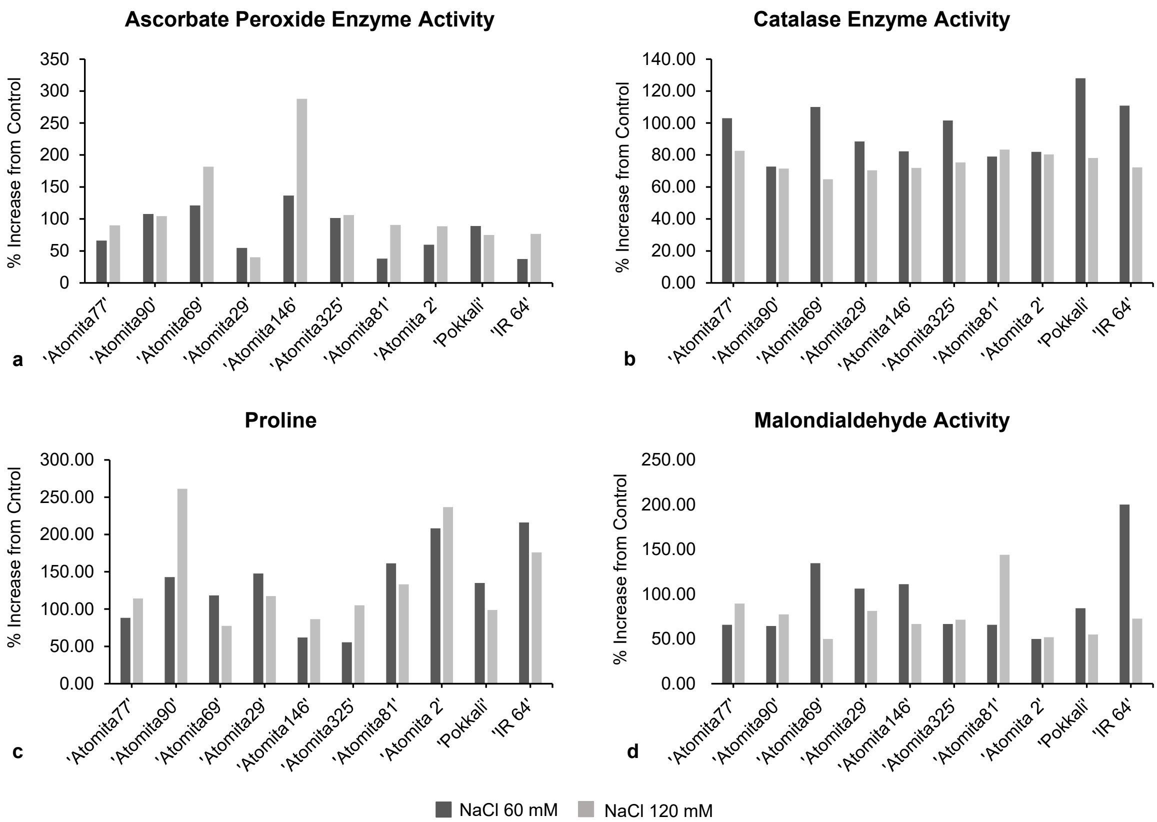
The Effect of NaCl Concentrations and Genotypes on Biochemical Characteristics of Rice Plants

The accumulation of reactive oxygen species (ROS) under salinity stress leads to oxidative damage to membrane lipids, proteins, and nucleic acids. However, plants can mitigate these effects through enzymatic and non-enzymatic antioxidant systems, with catalase (CAT) and ascorbate peroxidase (APX) serving as key antioxidant enzymes involved in ROS scavenging (Sopandie, 2024). In the research, increasing NaCl concentrations triggered the accumulation of biochemical compounds, including antioxidant enzyme activities (APX and CAT), proline, and malondialdehyde (MDA), indicating the plant's adaptive response to salinity stress. The percentage increases in ascorbate peroxidase (APX) and catalase (CAT) activities, as well as proline and malondialdehyde (MDA) contents, are presented in Figure 1.

The 'Atomita 90' genotype exhibited the highest proline accumulation among all genotypes. Proline accumulation can serve as an indicator of plant tolerance to salinity stress. The IR64 genotype showed the greatest increase in MDA content among the genotypes. Higher MDA accumulation was predominantly observed in salinity-sensitive genotypes, such as 'IR64', reflecting greater membrane damage from oxidative stress. The 'Pokkali' and 'Atomita 146' genotypes exhibited the most significant increases in antioxidant enzyme activities (APX and CAT) among the genotypes.

Figure 1

Percentage of Increase in the Activities of Ascorbate Peroxidase (a), Catalase (b), Proline (c), and Malondialdehyde (d) Enzymes in Ten Rice Genotypes at Two NaCl Concentrations



Journal of Tropical Crop Science Vol. 13 No. 2, June 2026
www.j-tropical-crops.com
Received 6/18/2025; Revised 4/25/2026; Accepted 6/22/2026
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Discussion

The salinity tolerance scores recorded after two weeks of treatment showed a significant effect of salinity on the early growth of rice plants. A consistent decrease in tolerance scores as salinity concentrations increase indicates a progressive decline in plant tolerance (Samidanane et al., 2024). Salinity tolerance scores are closely related to plant survival (Kanawapee et al., 2011). High salinity negatively affects the survival of each genotype used in this study, according to Hariadi et al. (2015). Increased salinity inhibits plant growth, including plant height. Higher salinity levels adversely impact rice plant growth (Hariadi et al., 2015). This is consistent with Singh et al. (2022), who reported a significant decrease in plant height under salinity stress. In this study, rice plant height and survival significantly decreased under 60 mM NaCl treatment. A decrease in root length is also a growth barrier caused by salinity stress. High salinity concentrations inhibit seed germination, root elongation, shoot length, and fresh weight of rice plants (Zhang et al., 2021).

Salinity tolerance is best measured by the ability to maintain yield under saline conditions (Negrao et al., 2017). A reduction in grain yield under saline conditions reflects salinity's adverse effects on rice (Samidanane et al., 2024). Non-tolerant rice varieties are significantly affected by high soil salinity, resulting in plant desiccation and crop failure (Subekti et al., 2020). The salinity tolerance index can be used to identify sensitive or tolerant rice varieties and is positively correlated with yield under pot salinity conditions (Anshori et al., 2018). Arajmand et al. (2020) explained that the tolerance index, expressed as a percentage, reflects the cultivar's ability to tolerate salinity. Lower values indicate lower genotypic tolerance to salinity stress.

Salinity stress induces physiological and biochemical responses that inhibit growth, and these responses vary by plant genotype (Pamuta et al., 2022). The present findings are consistent with previous studies (Babar et al., 2022; Behera et al., 2023; Hariadi et al., 2015), which reported that increasing salinity significantly reduces photosynthetic rate, transpiration rate, stomatal conductance, and SPAD value, thereby negatively affecting rice growth. Salinity disrupts the activity of enzymes involved in chlorophyll biosynthesis and damages chloroplast structures, resulting in a decline in the photosynthetic rate (Zahra et al., 2022). Short-term exposure to high salinity concentrations induces ultrastructural changes in chloroplasts, including thylakoid swelling and starch accumulation (Sopandie, 2024). Salinity stress also triggers stomatal closure, leading to decreased stomatal conductance and transpiration rate (Zuo et al., 2024). The impairment of chlorophyll synthesis and chloroplast damage under salinity stress reduces chlorophyll content, as reflected in lower SPAD values.

Under salinity stress, plants produce large amounts of ROS (Hartatik et al., 2024; Pamuta et al., 2022). High salinity levels elevate Reactive Oxygen Species (ROS) production, resulting in oxidative damage to rice plants through increased lipid peroxidation and membrane injury (Parinaz et al., 2019). Malondialdehyde (MDA) content is widely recognized as a marker of lipid peroxidation and an indicator of oxidative damage under stress conditions (Simon & Akkara, 2020; Simon & Yusuf, 2020). High NaCl concentrations promote MDA accumulation via lipid peroxidation, thereby compromising cell membrane integrity (Hnilickova et al., 2021). Furthermore, Wang et al. (2022) reported that salinity-sensitive rice varieties exhibited greater increases in MDA levels, indicating more severe lipid peroxidation and membrane damage than salinity-tolerant varieties. CAT and APX enzymes play essential roles in reducing ROS and H_2O_2 accumulation generated under stress conditions (Simon & Yusuf, 2020). Plants regulate ROS production and scavenging through enzymatic mechanisms by enhancing the activity of various antioxidant enzymes (Kumar et al., 2021). Proline is a compatible osmolyte that plays an important role in plant tolerance mechanisms against abiotic stress (Guo et al., 2022). As an osmoprotectant, proline contributes to cellular osmotic balance, thereby facilitating plant adaptation to salinity-induced osmotic stress,

Received 6/18/2025; Revised 4/25/2026; Accepted 6/22/2026
https://doi.org/10.29244/jtcs.13.02.529-543

and its accumulation is positively correlated with salinity tolerance (Spormann et al., 2023). The present results demonstrate a stronger adaptive capacity to salinity stress, which is consistent with previous studies (Alkahtani & Dwiningsih, 2023; Pamuta et al., 2022). Salinity treatment significantly increased proline and MDA contents, as well as antioxidant enzyme (APX and CAT) activities, as part of the plant's response to salinity stress.

Conclusions

Application of 60 mM NaCl successfully selected 38 genotypes from a total of 100 surviving genotypes after two weeks of treatment. Differences in genotype responses to salinity stress reflect tolerance levels. Based on morphological responses (STI values) and physiological and biochemical parameters, the 'Atomita 90' and 'Atomita 146' genotypes exhibited greater salinity tolerance than their parent genotype ('Atomita 2') and 'Pokkali'. 'Atomita 90' showed higher STI values than its parent and 'Pokkali' under 60 mM NaCl treatment and, physiologically, exhibited the highest photosynthetic rate, stomatal density, and proline accumulation. Meanwhile, 'Atomita 146' exhibited the highest STI under 120 mM NaCl, supported by the highest transpiration rate, stomatal conductance, and stomatal density, and the lowest MDA accumulation, along with the highest APX enzyme activity.

Acknowledgement

The author gratefully acknowledges the Ministry of Finance of the Republic of Indonesia, through the Education Fund Management Institute (LPDP), for providing scholarship support and research funding.

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Received 6/18/2025; Revised 4/25/2026; Accepted 6/22/2026
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