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Harnessing methyl jasmonate signalling to counteract salt stress in papaya (*Carica papaya* L.) – A physiological and biochemical perspective

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Abstract

Salinity is a critical abiotic constraint limiting papaya cultivation in salt-prone regions due to its high sensitivity to ionic and osmotic stress. This study investigated the role of exogenous methyl jasmonate (MeJA) in mitigating salt-induced physiological and biochemical impairments in papaya seedlings. Uniform seedlings of cv. Red Lady were exposed to 100 mM NaCl to simulate moderate salinity (7.0 dS m^{-1}) and subsequently treated with foliar MeJA @ 0, 25, 50, 75, and 100 µM under controlled greenhouse conditions. Salinity significantly reduced chlorophyll content, relative leaf water content (RLWC), and antioxidant enzyme activities, accompanied by elevated proline and malondialdehyde (MDA) accumulation. MeJA application markedly reversed these effects, with 75 µM proving most effective. This concentration enhanced chlorophyll stability (increased 11.4% total chlorophyll), RLWC (83.1 %), soluble sugars, phenolic content, elevated superoxide dismutase (74.4%) activity, while reduced activity of catalase, and ascorbate peroxidase. Simultaneously, MDA levels declined (28.0%) with MeJA application, indicating reduced lipid peroxidation and improved membrane integrity. However, higher MeJA concentration (100 µM) induced slight inhibition of some stress management parameters, revealing a biphasic response typical of jasmonate signalling. 75 µM MeJA gave best balanced physiological response, while some biochemical parameters peaked at 100 µM. Overall, MeJA at moderate dose (75 µM) effectively primed defense pathways, stabilized cellular redox homeostasis, and enhanced salinity tolerance in papaya seedlings.

Key words: Methyl jasmonate, salt stress, antioxidant enzymes, membrane stability, papaya

Introduction

Papaya (*Carica papaya* L.) is a fast-growing tropical and subtropical fruit crop valued for its economic, nutritional, and industrial significance. Native to Central America but now widely cultivated across Asia, Africa, and tropical America, papaya is consumed both as a fresh fruit and as a raw material for juices, jams, and health products. The crop is rich in sugars, vitamins A and C, minerals, dietary fibre, and bioactive compounds, making it an important contributor to nutritional security (Pares and Basso, 2013; Ahmed *et al*., 2024). Beyond its dietary role, papaya latex provides papain, an industrially important proteolytic enzyme used in pharmaceuticals, food processing, and leather industries. Globally, India, Indonesia, Nigeria, Brazil, and the Philippines are among the leading producers. Despite its potential, papaya remains vulnerable to a wide array of abiotic stresses, with soil salinity emerging as a major constraint in many production zones. Because papaya seedlings have shallow roots, high transpiration demand, and limited ion exclusion mechanisms, they are particularly susceptible to salt-induced growth inhibition and physiological damage, which restricts expansion into marginal lands increasingly affected by salinization.

Soil salinity poses a formidable challenge to modern agriculture, with estimates suggesting that more than 20% of irrigated farmland is already salt-affected, and the affected area is predicted to expand further due to intensive irrigation, seawater intrusion, and climate change. Excess salts impair plant performance through two interlinked mechanisms: osmotic stress, which restricts water uptake and induces leaf wilting, and ionic toxicity, caused mainly by sodium and chloride accumulation in tissues (Lu and Fricke, 2023). These effects destabilize photosynthetic pigments, disrupt nutrient balance, and trigger oxidative damage through uncontrolled generation of reactive oxygen species (ROS). Papaya seedlings under salt stress typically exhibit chlorosis, reduced relative water content, lowered chlorophyll and carotenoid pools, and accumulation of malondialdehyde (MDA), reflecting lipid peroxidation and membrane injury as similarly reported Wang *et al*. (2022) in case of *Malus* species. Plants naturally activate enzymatic defenses such as superoxide dismutase (SOD), catalase (CAT), and peroxidases (POD, APX, PPO), along with osmolyte accumulation like proline, to scavenge ROS and maintain cellular homeostasis. However, in salt-sensitive species like papaya, these defenses are often insufficient, and external interventions are required to strengthen tolerance. In this context, plant hormones and signaling molecules capable of priming stress defense pathways are gaining attention as low-cost, environmentally compatible strategies to enhance resilience.

Among such regulators, jasmonic acid (JA) and its volatile derivative methyl jasmonate (MeJA) have emerged as versatile modulators of plant defense and adaptation. Derived from fatty acid metabolism, jasmonates orchestrate a wide spectrum of processes, from growth and development to responses against biotic and abiotic stresses (Rehman *et al*., 2023). Exogenous application of MeJA has been reported in several crops to improve tolerance to salinity, drought, temperature extremes, and heavy metals by activating antioxidative enzymes, stabilizing chlorophyll, modulating stomatal conductance, and enhancing osmolyte accumulation (Gul *et al*., 2023). However, the action of MeJA is strongly dose-dependent: low concentrations often prime protective responses, whereas higher doses may trigger senescence or inhibit growth (Jiang *et al*., 2021). While beneficial roles of MeJA have been demonstrated in cereals, legumes, and vegetables, very limited evidence exists for papaya, despite its economic importance and pronounced salt sensitivity (Rehman *et al*., 2023). The lack of systematic studies exploring dose–response relationships of MeJA in papaya seedlings under saline environments constitutes a significant research gap. This experiment was therefore designed to evaluate the efficacy of different MeJA doses in mitigating salt-induced physiological and biochemical perturbations in papaya seedlings. Specifically, the study examined pigment dynamics, chlorosis index, antioxidative enzymes, osmolyte accumulation, relative water content, and lipid peroxidation to determine whether exogenous MeJA can alleviate salt stress and to identify the concentration that provides the most effective protection. It was hypothesized that MeJA application at moderate concentrations would mitigate salt-induced oxidative stress and improve physiological performance in papaya seedlings.

Materials and methods

Experimental site and plant material: The present investigation was executed under strictly regulated greenhouse conditions in the Department of Horticulture and Postharvest Technology, Institute of Agriculture, Visva-Bharati, Sriniketan, West Bengal during the cropping years 2023–24 and 2024–25. Vigorous and uniform seedlings of papaya (cv. Red Lady) were raised from surface-sterilized seeds in a sterilized mixture of sand, soil, and compost blended in equal proportions (1:1:1, v/v/v). The seedlings were maintained at 28 ± 2 °C temperature, 65 ± 5 % relative humidity, and a photoperiod of 14 h per day with daily light integral (DLI) of 16 mol m^{-1} d^{-1}. After completing four weeks of growth, morphologically similar and healthy plants were selected for further treatment application.

Induction of salt stress: Artificial salinity stress was generated by introducing analytical-grade sodium chloride (NaCl) into the potting medium. Preliminary standardization trials confirmed that 100 mM NaCl consistently produced visible symptoms of growth inhibition without inflicting permanent damage. The saline solution was administered to the pots (plugged holes to prevent the leaching) periodically until the substrate's electrical conductivity (EC) stabilized around 7.0 dS m^{-1} (measured at an interval of 3 days), representing a moderate salinity level (Huang *et al*., 2022). The Control plants were also grown under identical conditions. The salinity induction continued for seven consecutive days and stopped before methyl jasmonate (MeJA) application to ensure physiological acclimatization of seedlings to saline stress.

Preparation and application of methyl jasmonate: Methyl jasmonate (procured from Sigma–Aldrich, 98.5 % purity) was initially dissolved in a minimal volume of ethanol and subsequently diluted using double-distilled water containing 0.05 % (v/v) Tween-20 as a wetting agent. The resulting solutions contained final MeJA concentrations of 0 (only solvent), 25, 50, 75, and 100 µM. These were designated as treatment combinations T_1 (control, only solvent), T_2 (25 µM), T_3 (50 µM), T_4 (75 µM), and T_5 (100 µM). Foliar sprays were administered as a fine mist using a hand atomizer until uniform runoff was achieved on both sides of the leaf surface, at 30 days after germination. To minimize volatilization losses, spraying was done during early morning hours. Two subsequent sprays were provided at 15-day intervals to maintain a consistent hormonal effect throughout the experiment.

Experimental design and treatment layout: The study followed a completely randomized design (CRD) comprising five treatment levels with four replications, each replication including ten seedlings. To counter positional effects, pots were periodically rearranged within the greenhouse. All plants received identical management practices, such as regular irrigation with Hoagland's nutrient solution and manual weeding. Observations were recorded 60 days after the initial MeJA application, the stage when treatment-induced variations became most distinct.

Recording of observations: Relative leaf water content (RLWC) was quantified following the method described by Barrs and Weatherley (1962). Stomatal density was evaluated using nail-polish imprints taken from the abaxial leaf surface considering five leaves per replication and observed under a compound microscope at 40× magnification. Leaf chlorophyll a, chlorophyll b, and total chlorophyll were estimated following the standard protocol. Leaf tissue was cut into pieces and samples were cooled to room temperature for 30 minutes, filtered and absorption measured at 665 nm and 648 nm being the final stages using DMSO as standard with LABMAN double beam UV-Visible spectrophotometer (LMSPUV 1200) (Sadasivam and Manickam, 1992). Chlorophyll concentration (a, b and total) was expressed as mg/g fresh weight and determined by the following formula (Barnes *et al*., 1992):

Chlorophyll a (mg/g F.W) = (14.85 A_{665} -5.14 A_{648});

Chlorophyll b (mg/g F.W) = (25.48 A_{665} – 7.36 A_{648});

Total chlorophyll (mg/g F.W) = (7.49 A_{665} + 20.34 A_{648});

where: A_{665} = absorption value at 665 nm, A_{648}= absorption value at 648 nm.

Soluble sugar content was determined by the anthrone method, employing glucose as a calibration standard (Lane and Eynon, 1923).

Biochemical and antioxidative enzyme assays: Freshly sampled leaf tissues were frozen immediately in liquid nitrogen and preserved at −80 °C for biochemical analyses. Proline content was estimated according to Bates *et al*. (1973) using 3 % sulfosalicylic acid extraction and reaction with acid-ninhydrin reagent; absorbance was measured at 520 nm. Lipid peroxidation, expressed as malondialdehyde (MDA) concentration, was quantified following Heath and Packer (1968) and represented as µmol g^{-1} fresh weight. Total phenolic content was determined by the Folin–Ciocalteu method (Singleton and Rossi, 1965) and expressed as mg gallic acid equivalents (GAE) per 100 g FW, while antioxidant capacity was evaluated through the DPPH radical-scavenging assay (Prieto *et al*., 1999).

Enzymatic assays: For enzymatic assays, crude enzyme extracts were prepared by homogenizing 0.5 g of fresh leaf tissue in 5 ml of ice-cold 50 mM phosphate buffer (pH 7.0) containing 1 mM EDTA and 1 % polyvinyl pyrrolidone (PVP). The homogenate was centrifuged at 12,000 × g for 15 min at 4 °C, and the resulting supernatant was immediately used for analysis. Superoxide dismutase (SOD) activity was determined based on the inhibition of photochemical reduction of nitro blue tetrazolium (Sigma Aldrich, 98.0%) (Beauchamp and Fridovich, 1971). Catalase (CAT) activity was estimated by measuring the decomposition rate of hydrogen peroxide (Sigma Aldrich, 85%) at 240 nm (Aebi, 1984). Ascorbate peroxidase (APX) was assayed by monitoring the decline in ascorbate absorbance at 290 nm (Nakano and Asada, 1981). Peroxidase (POD) activity was estimated using guaiacol (97.5) and catechol (98.5%) as substrates, recording the rise in absorbance at 470 nm and 420 nm, respectively (Shevyakova *et al*., 2002). Before all the above enzymatic assays protein estimation was done by colorimetric method based on the Biuret reaction and the reduction of the Folin-Ciocalteu reagent by tyrosine and tryptophan (Lowry *et al*., 1951) and the enzyme activity normalization done by specific enzyme activity calculation taking the ratio of total enzyme activity and protein concentration (Jesani *et al*., 2002).

Statistical analysis: All obtained data were expressed as mean ± standard error (SE) from four replications of five treatments (19 degrees of freedom) along with the treatment difference in superscripts. One-way analysis of variance (ANOVA) was performed for both the years (2023-24 and 2024-25) using SPSS v.26 (IBM Corp., USA), and the treatment means were compared employing the least significant difference (LSD) test at a significance level of $P \leq 0.05$. Data recorded in both the years were pooled, and year × treatment interaction was tested and found non-significant, thus the only pooled data have been considered for presentation of results.

Results and discussion

Influence of methyl jasmonate on leaf pigment composition: Exposure of papaya seedlings to salt stress substantially reduced the chlorophyll content compared with non-salinized controls, reflecting a decline in photosynthetic competence under ionic and osmotic stress. However, foliar supplementation of methyl jasmonate (MeJA) significantly modulated pigment dynamics (Table 1). Chlorophyll a and total chlorophyll contents increased progressively with MeJA concentration up to 75 µM (T_4), reaching 169.2, and 217.9 mg 100 g^{-1} FW, respectively - values about 30–35 % higher than the untreated control (T_1), while chlorophyll b content decreased with increase in concentration of MeJA. A marginal decline was observed at 100 µM (T_5), indicating a threshold beyond which excessive jasmonate may impair chloroplast function.

The restoration of chlorophyll under MeJA treatment suggests that exogenous jasmonate alleviated salt-induced degradation of photosynthetic pigments, possibly by suppressing chlorophyllase activity and enhancing the stability of pigment-protein complexes within thylakoid membranes. Similar chlorophyll retention effects of MeJA were observed in pearl millet (Ndiaye *et al*., 2022) and tomato (Gul *et al*., 2023) under NaCl stress. Jasmonates are known to upregulate genes associated with chlorophyll biosynthesis (e.g., *CHLH*, *PORB*) while down regulating chlorophyll degradation pathways, thereby sustaining light-harvesting efficiency. The slight reduction at 100 µM supports the view that supraoptimal MeJA levels may trigger senescence-like responses mediated by reactive oxygen species (ROS) and lipid signaling intermediates.

Stomatal density and water relations: Salt stress typically limits gas exchange by causing stomatal closure, thereby restricting CO_2 assimilation. In this study, MeJA application substantially altered stomatal density (Table 1). The control (T_1) exhibited 455 mm^{-2} stomata, whereas densities increased progressively to 588 mm^{-2} under 75 µM MeJA (T_4). A slight reduction at 100 µM indicated stomatal over compaction or partial inhibition of epidermal differentiation at higher jasmonate levels. Enhanced stomatal density under moderate MeJA supply may reflect improved leaf expansion and epidermal cell differentiation due to optimized hormonal crosstalk between jasmonates, abscisic acid (ABA), and auxins. This adjustment allows plants to maintain photosynthetic activity while preserving water economy. Previous research reported similar improvements in many crop plants (Li *et al*., 2018) treated with MeJA, suggesting that jasmonate-mediated signaling can fine-tune stomatal development to counter salinity-induced physiological drought.

Relative leaf water content (RLWC) exhibited a parallel trend, rising from 66.0 % in the control to a maximum of 83.1 % at 75 µM MeJA (Table 1). This considerable enhancement demonstrates the ability of MeJA to sustain cellular hydration under saline conditions. The increased RLWC may be attributed to MeJA-induced accumulation of compatible solutes such as proline and sugars, which enhance osmotic adjustment and maintain turgor. Moreover, MeJA may stabilize aquaporin expression, improving water transport across membranes. These findings are consistent with MeJA-induced increases in leaf relative water content in *Anchusa italica* under salinity stress, confirming the universal role of jasmonates in enhancing water-use efficiency (Taheri *et al*., 2020).

Soluble sugar accumulation: Soluble sugars act as osmoprotectants and energy reservoirs under abiotic stress. In the present investigation, the soluble sugar concentration in papaya leaves increased from 43.4 mg g^{-1} FW in control seedlings to 61.7 mg g^{-1} FW in 75 µM MeJA-treated plants, and slightly to 62.3 mg g^{-1} FW at 100 µM (Table 1).

Table 1. Leaf chlorophyll content, stomatal density, relative leaf water content and soluble sugar content of papaya seedlings as influenced by foliar application of methyl jasmonate at 60th day after germination

Treatments	Chlorophyll a content (mg100g^{-1} FW)	Chlorophyll b content (mg/ 100g^{-1} FW)	Total chlorophyll content (mg100g^{-1} FW)	Stomatal density (per mm^2)	Relative leaf water content (%)	Soluble sugar content (mg g^{-1})
T_1	130.2 ± 7.8^{e}	62.1 ± 3.5^{a}	193.2 ± 7.9^{de}	455.2 ± 16.3^{e}	66.0 ± 3.8^{e}	43.4 ± 3.1^{de}
T_2	147.3 ± 6.4^{d}	58.7 ± 2.9^{b}	206.5 ± 8.3^{cd}	502.4 ± 14.2^{d}	74.5 ± 4.7^{bcd}	47.9 ± 3.7^{d}
T_3	156.7 ± 6.8^{c}	51.9 ± 3.7^{c}	207.3 ± 9.3^{bc}	556.2 ± 20.7^{abc}	79.3 ± 4.9^{bc}	55.2 ± 4.2^{c}
T_4	169.2 ± 7.5^{ab}	47.3 ± 4.1^{cd}	217.9 ± 7.6^{ab}	588.5 ± 19.3^{a}	83.1 ± 5.4^{a}	61.7 ± 4.9^{ab}
T_5	171.4 ± 8.2^{a}	45.8 ± 2.8^{de}	218.2 ± 8.9^{a}	572.7 ± 18.8^{ab}	79.4 ± 5.1^{ab}	62.3 ± 4.7^{a}
SE(m)	2.7	1.8	5.1	7.8	1.8	1.8
CD(0.05)	8.2	5.4	15.7	23.5	5.4	5.3

This significant elevation indicates that MeJA enhanced carbon partitioning toward soluble carbohydrate synthesis, which contributes to osmotic balance and ROS scavenging (Taheri *et al*., 2020). The mechanism may involve MeJA-mediated activation of sucrose phosphate synthase and invertase enzymes, facilitating sugar accumulation as a stress-responsive adaptation (Miron and Schaffer, 1991). Comparable responses were reported in sorghum

(Mulaudzi *et al*., 2023) where MeJA pretreatment enhanced soluble sugar levels under salinity, supporting improved osmotic regulation and membrane integrity.

Leaf proline dynamics: Proline serves as a key osmolyte and ROS quencher in salt-stressed plants. In this experiment, proline content declined progressively with increasing MeJA concentrations, from 45.2 µmol g^{-1} FW in the control to 31.0 µmol g^{-1} FW at 75 µM and further to 26.5 µmol g^{-1} FW at 100 µM (Table 2).

Although proline accumulation is a common stress marker, its reduction here indicates that MeJA effectively mitigated cellular stress, thereby reducing the requirement for osmolyte accumulation (Liang *et al*., 2013). Similar changes in proline following MeJA supplementation has been documented in sugar beet (Finger *et al*., 2021) subjected to postharvest storage, where the hormone improved antioxidant protection and maintained ionic balance.

Activation of antioxidant enzymes: A major physiological consequence of salt stress is overproduction of reactive oxygen species (ROS), leading to oxidative damage of membranes, proteins, and nucleic acids. In this study, foliar-applied MeJA substantially reduced the requirement of antioxidant enzymes like superoxide dismutase (SOD), ascorbate peroxidase (APX), and catalase (CAT) in a concentration-dependent manner due to reduced production of ROS (Table 2).

SOD activity increased from 22.3 U mg^{-1} protein in the control to 38.9 U mg^{-1} protein at 100 µM MeJA, representing a considerable enhancement (Table 2). This enzyme is the first line of defense against superoxide radicals, catalyzing their conversion into hydrogen peroxide (Jomova *et al*., 2024). The concurrent rise in CAT and APX activities peaking at 12.1, 5.2, and 5.8 µmol H_2O_2 min^{-1} mg^{-1} protein, respectively suggests that MeJA treatment efficiently detoxified hydrogen peroxide, thereby maintaining redox equilibrium (Dai *et al*., 2023). The decline in APX and CAT activity at 100 µM may result from excessive ROS or feedback inhibition due to over-activation of JA signaling, consistent with the biphasic nature of jasmonate action.

Lipid peroxidation and membrane integrity: Lipid peroxidation, expressed as malondialdehyde (MDA) content, serves as a biochemical marker of oxidative membrane damage. MDA levels in untreated control plants were high (49.6 µmol g^{-1} FW), reflecting severe oxidative stress under salinity. Application of MeJA significantly reduced MDA concentration, reaching a minimum of 35.7 µmol g^{-1} FW at 75 µM (T_4), corresponding to a 28 % decrease relative to control (Table 2). The suppression of lipid peroxidation demonstrates that MeJA effectively curtailed ROS-induced membrane damage by enhancing the antioxidant enzyme system and stabilizing membrane lipids.

A slight increase in MDA at 100 µM may indicate that higher jasmonate levels disrupt membrane integrity through excess signaling intermediates such as oxylipins (Dave and Graham, 2012). Similar biphasic trends were reported in tomato (Gul *et al*., 2023), where moderate MeJA concentrations alleviated oxidative injury, whereas higher doses induced mild stress. These findings reinforce the concept that MeJA operates as a stress modulator, balancing defense activation and growth regulation depending on concentration (Yu *et al*., 2024).

Total phenolic content and antioxidant capacity: Phenolic compounds function as non-enzymatic antioxidants, directly scavenging free radicals and chelating metal ions. In the present study, total phenolic content increased steadily with MeJA concentration, peaking at 42.8 mg GAE 100 g^{-1} FW under 100 µM treatment (Table 2). Likewise, antioxidant capacity, measured via DPPH radical scavenging, improved from 52.7 % in the control to 71.3 % at 75 µM before slightly declining to 68.4 % at 100 µM.

The positive association between phenolic accumulation and DPPH activity suggests that MeJA stimulated the phenyl propanoid pathway, increasing the synthesis of phenolics such as flavonoids and lignin precursors that contribute to ROS detoxification (Ninkuu *et al*., 2025). Jasmonates are known to enhanced antioxidant potential observed. Similar observations in *Capsicum annuum* under salinity and MeJA treatment confirm that jasmonates act as potent elicitors of secondary metabolites linked to oxidative protection (Sohn *et al*., 2022).

Integration of biochemical and physiological responses: The integrated analysis of physiological and biochemical traits reveals a coherent picture of MeJA-induced salt stress mitigation in papaya seedlings. At moderate concentrations (50–75 µM), MeJA improved chlorophyll retention, stomatal behaviour, water status, and sugar accumulation, while concurrently activating antioxidant enzymes and phenolic metabolism.

These coordinated effects culminated in reduced lipid peroxidation and improved redox stability, thereby sustaining photosynthetic efficiency and cellular homeostasis (Guan *et al*., 2019). The observed decline in some parameters at the highest MeJA dose (100 µM) underscores the dual role of jasmonates: beneficial at low to moderate levels but potentially inhibitory when overapplied (Bao *et al*., 2024). This biphasic response aligns

Table 2. Physio-metabolic expression of papaya seedlings as influenced by foliar application of methyl jasmonate at 60th day after germination

Treatments	Leaf proline content (µ mole g^{-1} FW)	Superoxide dismutase (SOD) unit mg^{-1}	Phenol ($mgGAE100g^{-1}$)	Antioxidation capacity (DPPH radical scavenging %)	Lipid peroxidation (MDA)(µ mole g^{-1} FW)	Ascorbate peroxidase (µmole min^{-1} mg^{-1} protein)	Catalase (µmole H_2O_2 min^{-1} mg^{-1} protein)
T_1	45.2 ± 3.1^{a}	22.3 ± 1.8^{e}	27.8 ± 2.9^{de}	52.7 ± 4.6^{e}	49.6 ± 3.2^{a}	11.7 ± 1.3^{a}	12.1 ± 1.0^{a}
T_2	37.8 ± 2.9^{b}	25.5 ± 1.7^{d}	30.0 ± 2.5^{cd}	61.2 ± 5.4^{cd}	45.3 ± 3.1^{b}	9.1 ± 0.9^{b}	9.4 ± 1.2^{b}
T_3	35.6 ± 3.3^{bc}	29.6 ± 2.6^{bc}	35.2 ± 2.8^{bc}	65.8 ± 5.1^{bc}	42.5 ± 2.9^{bc}	8.4 ± 1.0^{bc}	7.7 ± 0.9^{c}
T_4	31.0 ± 3.7^{d}	32.3 ± 2.5^{b}	37.5 ± 3.1^{b}	71.3 ± 5.3^{a}	35.7 ± 3.2^{de}	6.8 ± 0.7^{d}	5.2 ± 0.7^{e}
T_5	26.5 ± 2.2^{e}	38.9 ± 2.8^{a}	42.8 ± 3.4^{a}	68.4 ± 4.9^{ab}	36.4 ± 2.7^{d}	5.6 ± 0.8^{de}	5.8 ± 0.8^{d}
SE(m)	0.9	1.0	1.6	1.6	1.1	0.5	0.3
CD(0.05)	2.6	3.1	4.7	4.9	3.2	1.5	0.9

T_1: Control (water), T_2 : Methyl jasmonate (MeJA) @ 25 µM, T_3 : MeJA@ 50 µM, T_4 : MeJA@ 75 µM, T_5: MeJA@ 100 µM. (values are means ± SE, n = 4, superscripted letters are statistically different) with the hormetic model of plant hormone action, wherein mild stress signaling enhances tolerance, whereas excessive activation triggers growth inhibition or senescence.

Mechanistic interpretation: The amelioration of salt stress by MeJA can be mechanistically attributed to several interconnected physiological processes: MeJA functions as a signal transducer that activates defense gene expression, leading to elevated antioxidant enzyme synthesis and reduced ROS accumulation. The increase in soluble sugars and stabilization of RLWC indicate improved osmotic balance, enabling cells to maintain turgor and metabolic activity under high external Na^+ concentrations.

Photosynthetic protection: Retention of chlorophyll and higher stomatal density suggest improved gas exchange and light-harvesting capacity, preventing photo-inhibition. Elevated phenolic and flavonoid levels imply an enhanced non-enzymatic antioxidant pool that complements enzymatic defenses. Reduced MDA content reflects preserved membrane fluidity and reduced ion leakage, indicative of overall physiological recovery. Together, these mechanisms illustrate the multifaceted role of MeJA in reprogramming papaya metabolism toward resilience under saline conditions.

Comparative performance and optimal dosage: Among the treatments, 75 µM MeJA (T_4) consistently provided the most favourable balance between growth maintenance and stress protection. This concentration achieved the highest chlorophyll and water content, maximum enzymatic antioxidant activity, and the lowest lipid peroxidation. The marginal decline at 100 µM L^{-1} reinforces the necessity of dosage optimization for exogenous hormone application. The dose-dependent pattern also reflects the delicate equilibrium between MeJA-induced ROS signaling and ROS detoxification. At optimal levels, MeJA induces a controlled oxidative burst that triggers defense gene expression, while at excessive levels, ROS accumulation surpasses detoxification capacity, leading to oxidative injury. Hence, the 75 µM concentration may represent the physiological “sweet spot” for balancing signaling and protection in papaya seedlings.

Implications for salinity management in papaya: The capacity of MeJA to enhance salinity tolerance in papaya has substantial agronomic implications. Papaya is highly sensitive to soil EC above 4 dS m^{-1}, which restricts its cultivation in saline-prone regions. The present findings demonstrate that exogenous MeJA can fortify the antioxidant machinery and osmotic regulation systems, enabling seedlings to withstand EC levels of approximately 7 dS m^{-1} without irreversible damage. Application of MeJA could thus serve as a cost-effective, eco-friendly strategy for improving papaya establishment in marginal soils, complementing conventional soil reclamation and irrigation management practices.Beyond papaya, these findings contribute to the broader understanding of jasmonate-mediated stress mitigation in perennial fruit crops, where hormonal interventions remain underexplored compared with cereals and vegetables. The consistency of MeJA responses across diverse physiological indices highlights its potential as a universal resilience enhancer in fruit crop physiology.

Although the current findings clearly demonstrate the efficacy of MeJA in mitigating salt stress in papaya seedlings, further studies involving molecular and transcriptomic analyses are warranted to identify key genes and signaling networks involved in jasmonate-mediated tolerance. Evaluating MeJA effects on ion homeostasis (Na^+/K^+ ratio), chlorophyll fluorescence parameters, and growth recovery after stress release would provide deeper mechanistic insights. Field-level validation under naturally saline conditions is also essential to assess the practical applicability of MeJA in commercial papaya cultivation.

Exogenous application of methyl jasmonate effectively alleviated the adverse effects of salinity in papaya seedlings by improving photosynthetic pigment stability, water retention, osmotic regulation, and antioxidant defense. Although several biochemical traits continued to increase at 100 µM MeJA, 75 µM appeared to provide the most balanced physiological response, combining high RLWC and antioxidant capacity with the lowest lipid peroxidation enabling seedlings to withstand EC 7.0dS m^{-1} without irreversible damage. The study underscores methyl jasmonate as a potent eco-compatible elicitor for enhancing salt tolerance in papaya and potentially other tropical fruit crops, although greenhouse-level observations require further field validation.

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