



Exploring the role of bacterial endophytes in mitigating salinity stress in tomato (*Solanum lycopersicum*)

S LAKSHMI¹, G R PARINITH¹, S NAKKEERAN¹, P R RENGANAYAKI¹, S AMBIKA^{2*}
and D THIRUSENDURA SELVI¹

Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu 641 003, India

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ABSTRACT

One of the most significant factors influencing global crop production is salt stress. Plants adapt to salinity stress using a variety of physiological, morphological and molecular mechanisms. Microbial agents, particularly bacterial endophytes, have shown to enhance salinity tolerance, thereby improving plant growth, survival and physiological performance under saline stress. The present study was carried out during 2023–25 at Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu to evaluate the efficacy of bacterial endophyte seed biopriming for enhancing tomato (*Solanum lycopersicum* L.) growth, physiological performance and salinity tolerance under saline conditions to find the most efficient endophyte and to elucidate the biochemical mechanism by profiling the root exudate metabolites using Gas Chromatography-Mass Spectrometry (GC-MS). Tomato cv. PKM 1 seed were bioprimed with *Bacillus firmis* (1:1), *Bacillus paralicheniformis* (undiluted broth), *Bacillus amyloliquefaciens* (undiluted broth) and *Bacillus velezensis* (1:1) along with water (hydropriming) for 12 h. Non-primed seeds were used as control. The primed and control seeds were sown in pots with different levels of salinity (0 mM, 25 mM, 50 mM and 75 mM NaCl). Among the tested isolates, *B. paralicheniformis* performed the best followed by *B. firmis* under different salinity levels at different durations such as 30, 45 and 60 days. *B. paralicheniformis* recorded highest leaf area (85.7 cm), chlorophyll content (2.0 mg/g) and relative water content (77.5%) at 60 days. The best-performed isolates (*B. paralicheniformis* suspension, *B. firmis* suspension) along with the control under pot culture were selected and raised for 15 days using hydroponic method. The root exudates were collected and analysed through GC-MS. The seeds primed with *B. paralicheniformis* recorded more biomolecules such as niacinamide, 2,4-di-tert-butylphenol, α -terpinyl acetate and fatty acid derivatives such as methyl cis-13,16-docosadienoate and hexadecanoic acid butyl ester which possess stress-protective and antioxidant properties that may be responsible for phytohormone production, stimulation of antioxidant activity and resulted in improved physiological performance of tomato seedlings under salinity.

Keywords: Biopriming, Germination, Salt tolerance, Seed treatment, Tomato

India's food grain demand is projected to reach 350 metric tonnes by 2050 for a population of 1.8 billion (Kumar and Sharma 2020). Achieving food security requires higher crop productivity but soil salinity remains a major barrier causing yield loss of 20–50% (Eswar *et al.* 2021). Globally, salinity impacts 33% of irrigated land and 20% of all cultivated land, with projected loss exceeding US \$12 billion annually by 2050 (Jägermeyr and Frieler 2018).

Salinity stress results from excessive salt accumulation, disrupting plant physiology by reducing photosynthesis, transpiration, seedling growth, protein synthesis and nutrient uptake (Ali *et al.* 2022b). It increases reactive oxygen species (ROS), leading to oxidative stress and osmotic imbalance

(Atta *et al.* 2023). Tomato (*Solanum lycopersicum* L.), a key vegetable crop, is mildly sensitive to salinity and particularly vulnerable in semi-arid regions with saline irrigation water and fertiliser use (Al Busaidi *et al.* 2010).

In sustainable agriculture, microbial-based solutions, especially endophytic bacteria, offer eco-friendly ways to improve plant growth under salt stress. These microbes reduce ROS levels, regulate antioxidant enzymes, produce growth hormones and release beneficial metabolites (Sahu *et al.* 2021). Root exudates, which can account for up to 20% of plant dry weight, provide essential nutrients for rhizosphere microbes, aiding colonisation (Hawes and Pueppke 1986). Although bacterial endophytes have been reported to improve salinity tolerance in plants, their relative efficiency as seed biopriming agents in tomato and the effect of biopriming on root exudate metabolites are poorly understood. Hence, the present study was carried out to evaluate the efficacy of bacterial endophyte seed biopriming

¹Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu; ²SRM College of Agricultural Sciences, Baburayanpettai, Chengalpattu, Tamil Nadu. *Corresponding author email: ambikasingaram@gmail.com

for enhancing tomato growth, physiological performance and salinity tolerance under saline conditions to find the most efficient endophyte and to elucidate the biochemical mechanism by profiling the root exudate metabolites using Gas Chromatography-Mass Spectrometry (GC-MS).

MATERIALS AND METHODS

The present study was carried out during 2023–24 and 2024–25 at Tamil Nadu Agricultural University, Coimbatore (11°0'44.5"N and 76°56'08.1"E; 426 m AMSL), Tamil Nadu. Tomato cv. PKM 1 seeds (85% germination) were obtained from the Department of Vegetable Sciences, Horticultural College and Research Institute, Periyakulam, Tamil Nadu. Salinity tolerant bacterial endophyte cultures *Bacillus paralicheniformis* strain NB 11, *Bacillus firmus* (reference strain), *Bacillus amyloliquefaciens* isolate Pokkali Leaf 08 and *Bacillus velezensis* isolate Pokkali Leaf 10 were obtained from the Department of Plant Pathology, Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu and were used for this study.

Preparation of bacterial suspension for biopriming and its dilution: Lysogeny broth (LB) (tryptone 10 g, yeast extract 5 g, NaCl 5 g and Agar 25 g) was prepared in conical flasks, autoclaved for 20 min and was cooled. Using inoculation loop, bacterial cultures were inoculated and kept in a mechanical shaker at 150 rpm at 30°C for 48 h. The 10⁹ CFU/mL bacterial cultures were used for biopriming of tomato seeds throughout the experiment.

Treatment details: Tomato cv. PKM 1 seed were primed with water (T₁), *B. firmus* (1 part broth:1 part distilled water) (T₂), *B. paralicheniformis* (undiluted broth) (T₃), *B. amyloliquefaciens* (undiluted broth) (T₄) and *B. velezensis* (1 part broth:2 parts distilled water) (T₅) for 12 h with the volume of 1:2 (seed: solution) ratio (Selvarani *et al.* 2021). The seeds were dried back to their original seed moisture content. The seeds without any treatment were used as control (T₀).

Raising pro tray nursery: Primed seeds along with hydroprimed and control seeds were raised in pro trays. Cocopeat, neem cake, *Azospirillum* spp. and *Phosphobacteria* spp. (240:5:1:1, respectively) were used as nursery media.

Preparation for pot culture experiment: The soil collected from Department of Seed Science and Technology, Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu had red sandy loam texture having pH of 7.81 and EC of 0.35 dS/m. Each pot (14 inches × 14 inches) was filled with 10 kg of soil adjusted at various salinity levels i.e., 0 mM (0 g NaCl/L) (S₀), 25 mM (1.461 g NaCl/L) (S₁), 50 mM (2.922 g NaCl/L) (S₂) and 75 mM NaCl (4.207 g NaCl/L) (S₃). Seedlings (25 days old) of bioprimed, hydro-primed and control seeds were transplanted @8 seedlings/pot. The study was laid out using factorial completely randomised block design (F-CRBD) with three replications.

Leaf area: Leaf area was determined by measuring the length and breadth of the third leaf from the top of the plant at 30, 45 and 60 days after transplanting (DAT) by using the formula given by Montgomery (1911):

$$\text{Leaf area (cm}^2\text{)} = L \times W \times K$$

Where L, Maximum length of the third leaf (cm); W, Maximum width of the third leaf (cm); K, Constant factor (0.5) (Montgomery parameter).

Chlorophyll content: Total chlorophyll/g of fresh leaf was determined using the given formula (Arnon 1949):

$$\text{Total chlorophyll} = \frac{(8.02 \times \text{OD @663}) + (20.02 \times \text{OD @645}) \times V}{100 \times W}$$

Where OD, Optical density; V, Final volume of supernatant (25 mL); W, Weight of leaf sample (0.25 g).

Relative water content: The leaf was cut into small discs and fresh weight of discs was taken. These leaf discs were allowed to float in water for 4 h to attain full turgidity. The water droplets stuck to the leaf surface were removed with filter paper and the turgid weight was recorded. The leaf discs were then placed on a butter paper cover and heated to 80°C for 48 h in a hot air oven. The dry weight was then recorded and reported as percentage (Barrs and Weatherly 1962).

Characterising the profile of biomolecules produced under salinity

Preparation of root exudates: Tomato seeds were surface sterilised with 80% ethanol for 5 min and were rinsed thoroughly with distilled water. Seeds primed with *B. paralicheniformis* and *B. firmus* and control seeds were germinated using the roll towel method. Uniformly sized seedlings were transplanted into glass test tubes in 50 mL Hoaglands nutrient solution prepared with deionised water. On 14th day, root exudates were collected. The collected liquid was filtered via a column (20 mm in diameter) containing 100 mL of XAD-4 resin, then washed with 50 mL of methanol before being condensed on a rotary evaporator at 40°C. The solution (25 mL) was then placed in a -20°C freezer until usage. Root exudates were analysed using GC-MS as per Bacilio-Jiménez *et al.* (2003) with slight modifications at the Department of Plant Molecular Biology and Biotechnology, Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu.

Identification of root metabolites: A concentrated solution of methanol (5 mL) was transferred to a column packed with XAD-4 resin. To allow the methanol to naturally evaporate, the column was eluted with 200 mL solution containing 80% ether and 20% acetate. The eluted substance was then concentrated under vacuum until it dried out completely (Zhong Qun *et al.* 2012). The dried material was subsequently dissolved in 1 mL of HPLC grade methanol. The primary component obtained from this process was used for identifying the root exudates through GC-MS analysis. For analysis, 1 µL of the reaction mixture was directly injected into the gas chromatograph. Total GC run time was 30 min with initial temperature of 80°C kept for 1 min, then raised to 250°C at a rate of 8°C/min, then raised to 300°C at a rate of 12°C/min and held for 5 min. The injector temperature was 240°C.

Statistical analysis: The F test was used to assess the significance of data from different experiments, as explained

by Panse and Sukhatme (1985). For comparison among treatments, differences at ($p \leq 0.05$), standard error deviation (SEd) and critical difference (CD) were calculated.

RESULTS AND DISCUSSION

The bioprimered seeds recorded 35%, 41% and 27% increase in leaf area at 25 mM (S_1), 50 mM (S_2) and 75 mM (S_3) salinity levels, respectively, compared to control seeds (Table 1). The improvement may be due to increased osmotic adjustment, maintenance of ionic homeostasis by improving K^+ uptake and reducing Na^+ and better nutrient uptake. Additionally, enhanced antioxidant (Catalase, Peroxidase, Glutathione reductase and Superoxide dismutase) and non-enzymatic antioxidant activities may reduce oxidative damage and maintain photosynthetic activity in plants thereby increasing leaf area under saline conditions. Similar results have been reported by Kumar *et al.* (2020).

Salinity stress was counteracted by seeds bioprimering with *B. parlicheniformis*. Results revealed that the seeds primed with *B. parlicheniformis* (T_3) recorded 32%, 19% and 42% increase of chlorophyll content over control at S_1 , S_2 and S_3 , respectively at 45 DAT. Similar results were observed under 30 and 60 DAT growth periods (Table 2). This can be due to the low photosynthetic activity caused by salinity stress by decreasing leaf water potential and increasing stomatal and mesophyll resistance to gas fluxes (Dadkhah and Rassam 2017). The major component of the chlorophyll molecule, Mg^{2+} may be inhibited from being absorbed by sodium ions. This lowered the chlorophyll concentration and impeded tomato seedling growth as well as the formation of biomass in their roots and leaves. Ion toxicity also interferes with photosynthesis in plants by disrupting the oxygen-evolving complex, electron transport chain and photosystem II reaction centres (Lanquar *et al.* 2005). Furthermore, stomatal closure can increase CO_2 deficit in plants, resulting in decreased activity of Calvin cycle enzymes. Salinity has a negative impact on delaying flowering, reduced fertility and lowering yield (Egamberdieva *et al.* 2019). Enhancement of salinity tolerance by maintaining better ionic balance, chlorophyll content and reducing oxidative damage under saline conditions was also reported by Gul *et al.* (2025) in rice. Endophytic bacteria may regulate the expression of genes responsible for producing various ROS-scavenging enzymes, siderophores, antioxidant enzymes, volatile organic compounds and phytohormones (Ali *et al.* 2022, Shahid *et al.* 2022). Endophytic bacteria (isolated from *Fagonia indica* and *Ajuga bracteosa*) enhanced the performance of tomato plants under salinity. The endophytic bacteria enhanced IAA, ammonia, phosphate solubilisation, siderophore production, proline accumulation and antioxidant activity (Younis *et al.* 2024).

An increase in relative water content (RWC) of 5%, 5% and 10% was observed in primed seeds over nonprimed seeds at 25 mM (S_1), 50 mM (S_2) and 75 mM (S_3) salinity levels, respectively at 45 DAT (Table 3). The osmotic potential is raised by the presence of water-soluble salts

Table 3 Effect of different bacterial endophytes on relative water content in bioprimered tomato cv. PKM 1 seedling against salinity stress at different concentrations in pot culture.

Treatments	Relative water content (%)														
	30 DAT					45 DAT					60 DAT				
	S ₀	S ₁	S ₂	S ₃	Mean	S ₀	S ₁	S ₂	S ₃	Mean	S ₀	S ₁	S ₂	S ₃	Mean
T ₀	73.1	69.6	65.9	60.4	67.2	77.6	71.2	67.9	62.4	69.8	78.6	76.3	72.9	67.4	73.8
T ₁	72.8	71.3	66.5	61.9	68.1	74.8	72.8	68.8	63.7	70.0	79.5	77.3	73.0	67.7	74.4
T ₂	76.3	73.8	70.4	70.5	72.7	77.5	74.8	72.4	69.5	73.6	81.5	79.6	76.4	72.6	77.5
T ₃	74.1	72.7	69.1	67.0	70.7	75.7	74.4	70.7	68.2	72.3	80.5	78.8	75.6	72.2	76.8
T ₄	73.6	71.8	69.0	66.9	70.3	74.8	72.9	70.0	67.1	71.2	79.6	77.9	74.9	71.6	76.0
T ₅	73.1	70.9	68.0	65.1	69.3	75.0	73.5	70.6	68.5	71.9	79.5	77.5	74.6	73.1	76.2
Mean	73.8	71.7	68.1	65.3	69.7	75.9	73.3	70.1	66.6	71.5	79.9	77.9	74.6	70.8	75.8
	T	S	T × S			T	S	T × S			T	S	T × S		
SEd	0.93	0.76	1.86			1.08	0.88	2.17			0.98	0.80	1.97		
CD (<i>p</i> = 0.05)	1.92**	1.57**	3.84**			2.24**	1.83**	4.49**			2.04**	1.66**	4.08**		

**, Significant at 0.01 level of significance; DAT, Days after transplanting. Treatment details are given under Materials and Methods.

Table 4 Root metabolites produced by tomato cv. PKM 1 seed without biopriming treatment on 15 Days after sowing under hydroponics condition.

S. no.	RT (min)	Peak area (%)	Compound's name	Molecular formula	Function
1.	13.417	1.84	Alpha-terpinyl acetate	C ₁₂ H ₂₀ O ₂	Antimicrobial and antioxidant
2.	15.469	0.63	Phenol, 3,5-bis (1,1-dimethylethyl)-	C ₁₄ H ₂₂ O	Antioxidant
3.	18.750	0.34	n-Pentadecanol	C ₁₅ H ₃₂ O	Antifungal
4.	19.455	1.10	1,2-Benzenedicarboxylic acid, bis (2-methylpro)	C ₁₆ H ₂₂ O ₄	Antifungal, antibacterial and antioxidant
5.	20.408	18.54	1,4-Dibutyl benzene-1,4-dicarboxylate	C ₁₆ H ₂₂ O ₄	-
6.	20.460	3.50	Phthalic acid, butyl neopentyl ester	C ₁₇ H ₂₄ O ₄	Antifungal, antibacterial and antioxidant
7.	20.650	0.63	Methyl cis-11,14-Icosadienoate	C ₂₂ H ₄₀ O ₂	-
8.	21.238	0.40	Hexadecanoic acid, butyl ester	C ₂₀ H ₄₀ O ₂	Antimicrobial
9.	24.344	0.41	1-Nonadecene	C ₁₉ H ₃₈	Antioxidant
10.	31.300	0.41	Linoleic acid	C ₁₈ H ₃₂ O ₂	Antioxidant
11.	27.705	0.17	Urocanic acid-TMS	C ₆ H ₆ N ₂ O ₂	Algicidal
12.	30.235	0.66	3-Hydroxyanthranilic acid	C ₇ H ₇ NO ₃	Antioxidant and antimicrobial
13.	32.205	0.18	Juniperic acid	C ₁₆ H ₃₂ O ₃	Antioxidant

RT (min), Retention time in minutes.

Table 5 Root metabolites produced by bioprimed tomato cv. PKM 1 seed with undiluted *Bacillus paralicheniformis* on 15 days after sowing under hydroponics condition

S. no.	RT (min)	Peak area (%)	Compound's name	Molecular formula	Function
1.	13.417	0.50	Alpha-terpinyl acetate	C ₁₂ H ₂₀ O ₂	Antimicrobial and antioxidant
2.	15.465	0.41	2, 4-di-tert-butylphenol	C ₁₄ H ₂₂ O	Antioxidant
3.	19.455	1.08	1,2-Benzenedicarboxylic acid, bis (2-methylpro)	C ₁₆ H ₂₂ O ₄	Antifungal, antibacterial and antioxidant
4.	19.807	6.48	Dibutyl phthalate	C ₁₆ H ₂₂ O ₄	Phytotoxicity
5.	19.983	0.85	Phthalic acid, di(2-methylbutyl) ester	C ₂₅ H ₄₀ O ₄	Antibacterial and antioxidant
6.	20.408	18.54	1,4-Dibutyl benzene-1,4-dicarboxylate	C ₁₆ H ₂₂ O ₄	-
7.	20.460	3.50	Phthalic acid, butyl neopentyl ester	C ₁₇ H ₂₄ O ₄	Antibacterial and antifungal
8.	21.238	0.40	Hexadecanoic acid, butyl ester	C ₂₀ H ₄₀ O ₂	Antimicrobial
9.	24.344	0.41	1-Nonadecene	C ₁₉ H ₃₈	Antioxidant
10.	20.650	0.63	Methyl cis-13,16-docosadienoic	C ₂₂ H ₄₀ O ₂	Antioxidant
11.	21.385	0.38	Phenol-TMS	C ₆ H ₅ OH	Antioxidant
12.	22.690	0.23	Methyl butanoate	C ₅ H ₁₀ O ₂	Antioxidant
13.	22.035	0.75	Niacinamide	C ₉ H ₁₄ N ₂ OSi	Antioxidant
14.	24.345	0.62	1-Hexacosanol	C ₂₆ H ₅₄ O	Antioxidant
15.	25.920	0.98	Nonadecyl pentafluoropropionate	C ₂₂ H ₃₉ F ₅ O ₂	Antioxidant and antifungal
16.	27.375	0.24	Fendiline	C ₂₃ H ₂₅ N	Anticancer
17.	29.590	0.36	4-Aminobenzoic acid-2TMS	C ₇ H ₇ NO ₂	Antifungal

RT (min), Retention time in minutes.

in the soil. As a result, the roots ability to absorb water decreases, placing the plant under drought stress. Plant roots can actively pump water from the soil and move it further upwards to a certain extent (Stavi *et al.* 2021). RWC is known to decrease as salinity increases while the tolerant cultivars exhibit less decrease in RWC (Hussain *et al.* 2022). Endophytic bacteria may increase the production of some plant hormones in seeds, including cytokinins, indole acetic acid, 1-aminocyclopropane-1-carboxylate (ACC)-deaminase enzyme and the production of gibberellic acid which reduces ethylene levels in roots and increases root vigour (Penrose and Glick 2001). Some PGPR can alleviate salinity stress by generating chemical and physical changes in plants through a process known as induced systemic tolerance (IST) (Yang *et al.* 2009). Similar results have been reported by Chakraborty *et al.* (2011) in mung bean, chickpea and rice, by Ali *et al.* (2017) in wheat and Kanti *et al.* (2013) in soyabean.

According to GC-MS analysis, the exudates of roots taken from seeds primed with *B. paralicheniformis* (17 biomolecules) and *B. firmis* (15 biomolecules) had maximum number of chemical compounds compared to control (13 biomolecules) (Table 4, 5, 6 and Fig. 1). Major biomolecules, with highest peaks for 1,4-dibutyl benzene-1,4-dicarboxylate (19.57%), phthalic acid, butyl neopentyl ester (3.28%), alpha-terpinyl acetate

(1.34%) and diamyl phthalate (0.96%), along with minor compounds such as hypoxanthine, 1-nonadecene, methyl butanoate and tetracosanol, possessed antioxidant and antibacterial properties that promote germination whereas 1,2-benzenedicarboxylic acid had antifungal, antibacterial and antioxidant functions (Deepak *et al.* 2017). The antimicrobial and antioxidant property were also reported by Bhat *et al.* (2022) in alpha-terpinyl acetate, Elmaa *et al.* (2018) in nonadecyl pentafluoropropionate, Sathishkumar *et al.* (2015) in phthalic acid and Yang *et al.* (2018) in palmitic acid. Similarly, the antibacterial, antifungal and antioxidant activities of phthalic acid was reported in tomato under water stress condition by Pagadala Damodaram *et al.* (2021). Hexadecanoic acid has antioxidant properties which help in combating abiotic stress conditions. Similarly, niacinamide has been identified to possess antioxidant property in the salinity stress condition, through which it alleviates salinity stress. Antifungal activity against *Pseudomonas syringae* in tomato has been reported in 4-aminobenzoic acid-2 TMS by Goodwin *et al.* (2018). Role of catalase in promoting seed germination due to antioxidant activity has also been reported by Eshghi *et al.* (2014) with Methyl butanoate and Makhafole *et al.* (2017) with tetracosanol.

Thus, it can be concluded that biopriming of tomato seeds with *B. paralicheniformis*, a bacterial endophyte, efficiently alleviated salinity stress by improving

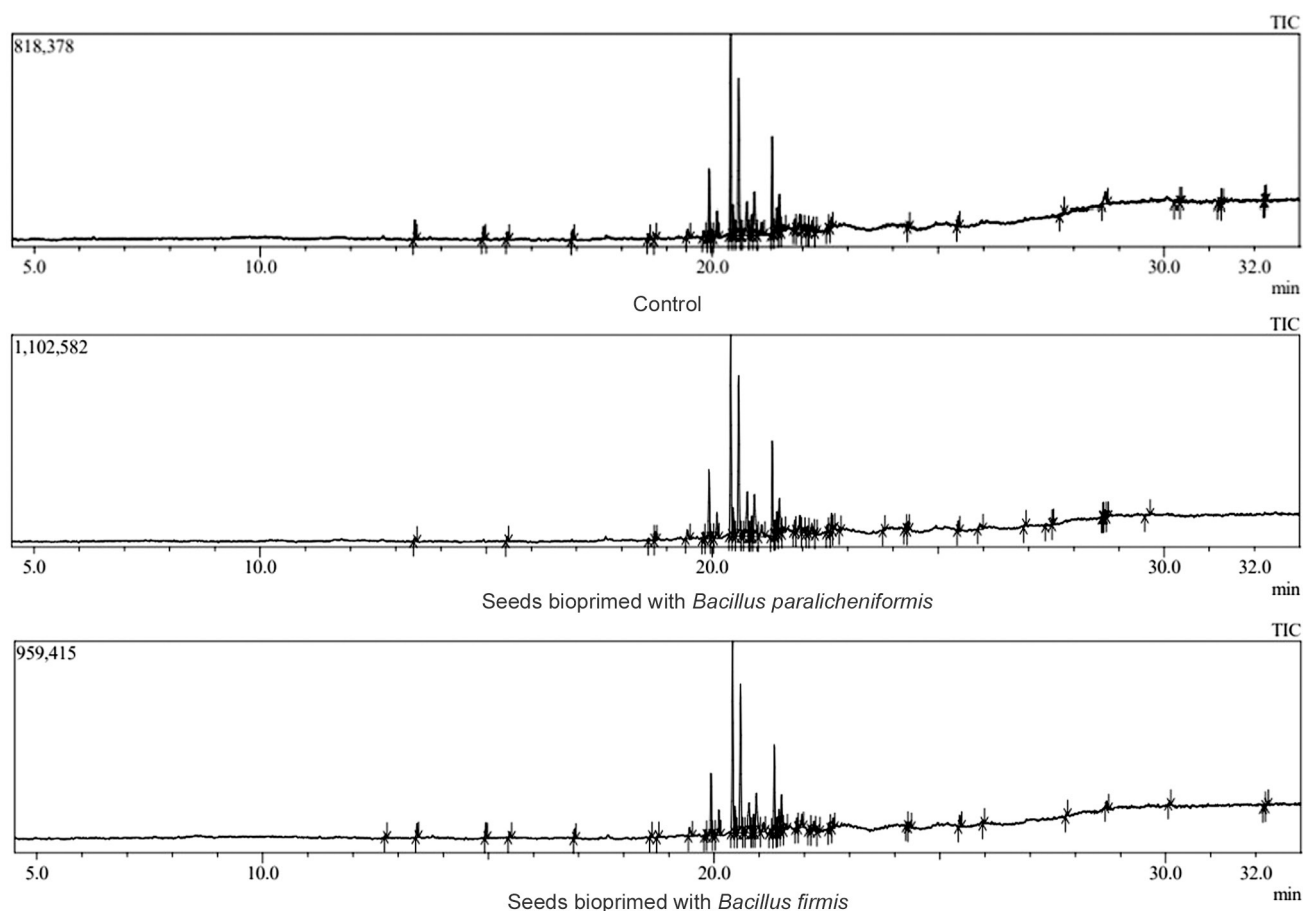


Fig. 1 GC-MS Chromatogram of control, *Bacillus paralicheniformis* and *Bacillus firmis* bioprimed tomato PKM 1 seedlings root exudates.

Table 6 Root metabolites produced by bioprimered tomato cv. PKM 1 seed with *Bacillus firmis* at 1:1 dilution suspension on 15 days after sowing under hydroponics condition

S. no.	RT (min.)	Peak area (%)	Compound's name	Molecular formula	Function
1.	13.418	1.34	Alpha-Terpinyl acetate	C ₁₂ H ₂₀ O ₂	Antimicrobial and antioxidant
2.	19.454	1.28	1,2-Benzenedicarboxylic acid, bis (2-methyl pro)	C ₁₆ H ₂₂ O ₄	Antifungal, antibacterial and antioxidant
3.	20.106	2.81	Phthalic acid, di(2-methylbutyl) ester	C ₂₅ H ₄₀ O ₄	Antibacterial and antifungal
4.	20.409	19.57	1,4-Dibutyl benzene-1,4-dicarboxylate	C ₁₆ H ₂₂ O ₄	-
5.	20.462	3.28	Phthalic acid, butyl neopentyl ester	C ₁₇ H ₂₄ O ₄	Antibacterial and antifungal
6.	22.549	0.66	Hexadecanoic acid, butyl ester	C ₂₀ H ₄₀ O ₂	Antimicrobial
7.	18.747	0.24	1-Nonadecene	C ₁₉ H ₃₈	Antioxidant
8.	15.468	0.70	2, 4-di-tert-butylphenol	C ₁₄ H ₂₂ O	Antioxidant
9.	20.655	0.62	Methyl butanoate	C ₅ H ₁₀ O ₂	Antioxidant
10.	21.238	0.40	Palmitic acid	C ₁₆ H ₃₂ O ₂	Antioxidant
11.	22.207	0.96	Diamyl phthalate	C ₁₈ H ₂₆ O ₄	Antioxidant
12.	24.343	0.55	Tetracosanol	C ₂₄ H ₅₀ O	Antioxidant
13.	30.085	0.24	Hypoxanthine	C ₅ H ₄ N ₄ O	Antioxidant
14.	32.265	0.32	Batyl alcohol	C ₂₁ H ₄₄ O ₃	-
15.	19.995	0.84	P-Cresol	CH ₃ C ₆ H ₄ OH	Antioxidant

RT (min), Retention time in minutes.

physiological performance and inducing stress-protective bioactive compounds. The GC-MS analysis indicated that unique bioactive compounds related to stress existed in the bioprimered seeds. These findings demonstrated that bacterial endophytes are cost-effective, sustainable and eco-friendly bioinoculants for enhancing salinity tolerance in tomato.

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