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RESEARCH ARTICLE

Evaluation of thermotolerant bacteria from a heat tolerant tomato genotype (IIHR-2202) for plant growth-promoting traits under *in vitro* conditions

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Abstract

Heat stress is a major abiotic constraint that reduces tomato productivity by disrupting plant physiological processes. It is hypothesised that thermotolerant bacteria within the plant microbiome can help sustain plant growth and physiological performance under high temperatures, thereby offering a novel strategy for plant growth promotion and heat stress alleviation. In the present study, 22 thermotolerant bacterial isolates associated with the heat-tolerant tomato genotype IIHR-2202 were isolated and evaluated for their plant growth-promoting traits at 30 °C and 42 °C under *in vitro* conditions. Ammonia production ranged from 12.86 to 34.10 µg mL^{-1} at 30 °C, while it ranged from 7.01 to 24.47 µg mL^{-1} at 42 °C. Phosphate solubilisation ranged from 41.86 to 88.83 µg mL^{-1} at 30 °C and from 13.40 to 61.95 µg mL^{-1} at 42 °C. Potassium solubilisation ranged from 31.45 to 63.92 µg mL^{-1} at 30 °C, whereas at 42 °C it ranged from 48.39 to 66.49 µg mL^{-1}. Zinc solubilisation ranged from 32.70 to 48.95 µg mL^{-1} at 30 °C and 28.45 to 40.95 µg mL^{-1} at 42 °C. Siderophore production ranged from 32.11 to 47.36 PSU at 30 °C and 22.75 to 40.21 PSU at 42 °C. The isolates also retained significant indole-3-acetic acid (IAA) and gibberellic acid (GA_3) production under heat stress conditions. Based on their overall plant growth promotion traits six superior thermotolerant isolates were further identified by 16S rRNA gene sequencing as *Fictibacillus phosphorivorans* strain S3, *Stenotrophomonas maltophilia* strain S9, *Glutamicibacter mishrai* strain R6, *Exiguobacterium indicum* strain R7, *Enterobacter soli* strain R21 and *Enterobacter hormaechei* subsp. *xiangfangensis* strain S7. This is the first study evaluating multifunctional thermotolerant plant growth-promoting bacteria (PGPB) associated with the heat tolerant tomato genotype IIHR-2202 under *in vitro* elevated temperature. These thermotolerant PGPB are promising candidates for the development of microbial inoculants to improve tomato productivity under elevated temperature scenarios.

Keywords: bioinoculants; heat stress; multifunctional; plant growth-promoting bacteria; thermotolerant; tomato

Introduction

Global warming and the resulting increase in ambient temperatures have emerged as a major constraint to agricultural sustainability. Rising temperatures intensify abiotic stresses such as heat, drought and salinity, which collectively pose serious threats to crop productivity. Heat stress is particularly detrimental because it disrupts physiological and metabolic processes, impairs membrane stability and reduces nutrient uptake, ultimately leading to yield losses (1). The adverse effects of heat stress are more pronounced during critical growth stages, as it hampers root development, alters plant metabolism and compromises overall plant performance.

Beyond its direct impact on plant physiology, elevated temperatures also influence the rhizosphere environment by altering microbial community structure and dynamics, thereby affecting plant-microbe interactions (2). In this context, plant growth-promoting bacteria (PGPB) have gained considerable attention as sustainable and eco-friendly tools for enhancing plant resilience under abiotic stress conditions. These beneficial microbes are known to promote plant growth through diverse direct and indirect mechanisms. The GPB facilitate plant growth by mechanisms such as biological nitrogen fixation, solubilisation of essential nutrients including phosphorus, zinc and potassium, production of siderophores for improved iron acquisition and synthesis of phytohormones (3, 4). Through these multifaceted actions, PGPB can enhance nutrient acquisition, improve root architecture and regulate plant metabolism under stress conditions.

Research has underscored the importance of thermotolerant bacteria in mitigating the adverse effects of elevated temperatures. These specialised bacterial strains can survive and maintain their functional traits under high-temperature conditions, thereby supporting plant growth even in adverse environments (5). Recent evidence suggests that thermotolerant bacteria with plant growth promoting traits contribute to plant stress tolerance by

regulating antioxidant defence systems, improving photosynthetic efficiency and maintaining hormonal homeostasis (6, 7). Auxin-producing isolates have been shown to stimulate root growth and enhance stress tolerance by activating gene expression pathways associated with heat stress adaptation (8).

Studies indicates that plant growth-promoting bacteria mediated stress alleviation involves complex physiological and molecular mechanisms, including enhanced nutrient uptake, osmotic adjustment and induction of stress-responsive genes (9, 10). Despite these advancements, there is a limited understanding of the functional diversity and heat tolerance mechanisms of thermotolerant bacterial strains, particularly regarding their capacity for nutrient mobilisation, siderophore production and phytohormone synthesis under heat stress conditions.

Tomato is highly sensitive to elevated temperatures, especially during reproductive and fruit-setting stages, resulting in severe reduction in growth and yield. Despite increasing interest in stress-resilient plant growth promoting strains, limited information is available on thermotolerant bacterial communities associated with heat-tolerant tomato genotypes and their ability to retain multifunctional plant growth-promoting traits under *in vitro* conditions. In particular, the functional characterisation of thermotolerant bacteria capable of nutrient solubilisation, siderophore production and phytohormone synthesis under heat stress remains insufficiently explored. Identification of such microbial resources is essential for developing sustainable bioinoculants suitable for climate-resilient agriculture.

Although several thermotolerant PGPB have been reported, comparative information regarding their ability to retain multiple plant growth-promoting traits under elevated temperature conditions remains limited, particularly in those associated with heat -tolerant tomato genotypes. Therefore, the present investigation was undertaken to characterise thermotolerant bacterial isolates associated with a heat-tolerant tomato genotype and to evaluate their plant growth-promoting traits under *in vitro* normal and elevated temperature conditions. The temperature of 42 °C was selected to represent severe heat stress frequently encountered during summer conditions in tropical tomato-growing conditions. Efficient isolates exhibiting stable multifunctional traits under heat stress were further subjected to morphological and molecular characterisation to identify potential candidates to support the development of climate-resilient microbial inoculants for sustainable tomato production.

Materials and Methods

Screening the isolates for their plant growth promoting traits

Twenty-two thermotolerant bacterial isolates previously isolated from leaf (I2L1, I2L2, I2L9, I2L10, I2L15), stem (I2S3, I2S4, I2S6, I2S7, I2S9, I2S10, I2S11) root (I2R5, I2R6, I2R7, I2R8, I2R12, I2R13, I2R17, I2R20, I2R21) and rhizoplane (I2RH3) of heat tolerant tomato genotype IIHR-2202 were screened for ammonia production, potassium solubilisation, zinc solubilisation, phosphate solubilisation, siderophore production and phytohormone production at 30 and 42 °C. A reference strain *Bacillus amyloliquefaciens* P-72 (MTCC 12351) was used for comparison purposes.

Ammonia production

Individual thermotolerant bacterial isolates were grown in nutrient broth (pH 7.2) for 24 hr for inoculum standardisation and the cell density was adjusted to OD_{600} = 0.5 (10^8 cells mL^{-1}). Subsequently, 1 mL of the standardised inoculum was grown in 10 mL of nutrient broth of pH 7.2 at 30 and 42 °C on a rotary shaker at 120 rpm for 48 hr. The samples were centrifuged at 8000 rpm for 10 min to eliminate suspended cells and particulate debris. A 1 mL of culture supernatant was mixed with 0.5 mL Nessler's reagent, incubated for 10 min and the final volume adjusted to 9 mL and absorbance was recorded at 450 nm (11, 12). The NH_3 concentration was determined from a standard curve prepared using ammonium sulphate concentrations ranging from 500 to 4000 µM.

Phosphate solubilisation

Phosphate solubilisation was determined using the National Botanical Research Institute's phosphate (NBRIP) growth medium containing tri-calcium phosphate (0.5 %) as an insoluble phosphate source. About 50 mL of NBRIP medium (pH 7), prepared in 100 mL Erlenmeyer flasks were inoculated with 1 mL of the standardised inoculum (10^8 cells mL^{-1}) of each thermotolerant culture and incubated at 30 and 42 °C in an orbital shaker at 120 rpm for 10 days. Following incubation, the cultures were centrifuged at 8000 rpm for 10 min to obtain a cell-free supernatant and the soluble phosphorus content in the supernatant was quantified by the colorimetric method (13).

Potassium solubilisation

Thermotolerant bacterial isolates were cultured in 25 mL of Alexandrov broth (pH 7.2) supplemented with 0.2 % potassium aluminium silicate. The flasks were then inoculated with 1 mL of standardised inoculum (10^8 cells mL^{-1}) of individual actively growing bacterial cultures and incubated at 30 °C and 42 °C under shaking conditions at 120 rpm for 10 days. The cultures were centrifuged at 8000 rpm for 10 min to separate the cells and debris. Subsequently, 1mL of the cell-free supernatant was added into a 50 mL volumetric flask, diluted to 50 mL with distilled water and mixed thoroughly. A 1 mL of this supernatant was fed to a flame photometer (ELICO CL 378, ELICO Ltd., Hyderabad, India) to determine K content. Potassium solubilisation by the bacterial isolates was quantified using a standard curve generated with various concentrations of KCl (14).

Zinc solubilisation

The thermotolerant bacterial isolates were inoculated in mineral salt broth of pH 7.2 supplemented with 0.1 % insoluble zinc phosphate. Fifty mL of the medium prepared in 100 mL Erlenmeyer flasks were inoculated with an 1 mL of standardised inoculum (10^8 cells mL^{-1}) suspension of the individual isolates and incubated at 30 and 42 °C at 120 rpm for 10 days. The cultures were then centrifuged at 8000 rpm for 10 min to remove the debris and cells. An aliquot of 1 mL was transferred in a 50 mL volumetric flask and the volume made up to 50 mL using sterile distilled water and fed to an Atomic Absorption Spectrophotometer (AAS) (Agilent Technologies, Santa Clara, CA, USA) to determine the available zinc content (15).

Siderophore production

The thermotolerant bacterial isolates were grown in 10 mL nutrient broth (pH 7.2) and inoculated with 1 mL of the standardised inoculum (10^8 cells mL^{-1}) of the individual cultures and incubated at 30 and 42 °C at 120 rpm for 48 hr. After incubation, they were centrifuged at 8000 rpm for ten min to separate the debris and cells

and 100 µL of the supernatant was transferred to microplates, followed by the addition of 100 µL of Chrome Azurol S (CAS) reagent and incubated for 20 min. The absorbance was recorded at 600 nm (16). The percent siderophore units (PSU) were calculated using the following formula:

$$\text{Siderophore production (psu)} = \frac{Ar - As}{Ar} \times 100$$

Where, Ar is the absorbance of reference and As is the absorbance of the sample.

Phytohormone production

All the thermotolerant bacterial isolates were initially screened for IAA and GA_3 production by spectrophotometric method at 30 °C and 42 °C.

Indole-3-acetic acid production

A 1 mL standardised inoculum (10^8 cells mL^{-1}) of the individual thermotolerant bacterial isolates were inoculated in 10 mL of nutrient broth (pH 7.2). While one set was supplemented with 0.5 % tryptophan and the other was without tryptophan. The cultures were incubated at 30 and 42 °C at 120 rpm for 5 days in dark conditions. After incubation the IAA concentration was determined by the colorimetric procedure method using Salkowski reagent the absorbance was measured at 530 nm (17). The IAA concentration of the sample was determined using a standard curve (10–100 µg mL^{-1}) prepared using IAA, using the regression equation, $y = 0.0017x + 0.0138$.

Gibberellic acid production

One mL standardised inoculum (10^8 cells mL^{-1}) of the individual thermotolerant bacterial isolates was inoculated into 25 mL nutrient broth (pH 7.2) and incubated at 30 and 42 °C at 120 rpm for 7 days. After 7 days of incubation, the concentration of gibberellic acid was determined by the colorimetric method and the absorbance was measured at 254 nm (18), using a standard curve prepared with GA_3 (15 and 20 µg mL^{-1}) using the regression equation, $y = 0.0128x + 0.0007$.

Morphological and molecular characterisation of selected efficient isolates

Based on their overall superiority in terms of plant growth promoting traits under *in vitro* elevated temperature conditions, six efficient thermotolerant isolates were further selected for characterisation. Morphological characteristics including colony colour, texture, margin and shape were recorded following growth on nutrient agar medium. Characterisation included Gram staining and endospore staining.

The selected efficient isolates were identified at the National Centre for Microbial Resource (NCMR), National Centre for Cell Science, Pune. The 16S rRNA was amplified using consensus primers 16F 27(5'-CCA GAG TTT GAT CMT GGC TCA G-3') and 16R 1492 (5'-TAC GGY TAC CTT GTT ACG ACT T-3'). The amplified polymerase chain reaction (PCR) product was purified by PEG-NaCl precipitation prior to direct sequencing using an ABI® 3730XL automated DNA sequencer (Applied Biosystems, Inc., Foster City, CA) according to manufacturer's instructions. The PCR conditions were as follows: 95 °C for 10 min; 35 cycles of 94 °C for 1 min; 55 °C for 1 min; 72 °C for 1 min followed by 72 °C for 10 min. Sequencing was performed from both terminals with additional internal primers to confirm that each nucleotide position was sequenced at least twice to get full length 16S rRNA (≈1500 bp). The resulting sequences were assembled using the Lasergene package and identified with the sequences available in the EzBioCloud database (19).

Statistical analysis

The experiment was conducted using a factorial completely randomised design (FCRD) with two temperature conditions (30 and 42 °C) and three replications for each isolate × temperature combination. The 3 replications represent independent biological replicates and no technical replicates were included. The data were subjected to two-way analysis of variance (ANOVA) to determine the effects of temperature, bacterial isolate and their interaction (temperature × isolate). Statistical analyses were performed using R software version 4.5.1. Differences among treatment means were compared using Duncan's multiple range test (DMRT) at a significance level of $p \leq 0.05$. The results are presented as mean ± standard error (SE).

Results

Ammonia production

All thermotolerant isolates produced ammonia at both temperature conditions; however, ammonia production was reduced under elevated temperature conditions (42 °C). At 30 °C, ammonia production ranged from 12.86 to 34.10 µg mL^{-1}, whereas at 42 °C it ranged from 7.01 to 24.47 µg mL^{-1} (Table 1). The highest ammonia production at 30 °C was recorded in isolate P-72 (34.10 µg mL^{-1}), followed by isolates I2S7 and I2R6 (31.94 µg mL^{-1}). Under elevated temperature conditions, isolate I2R6 exhibited the maximum ammonia production (24.47 µg mL^{-1}), followed by I2R21 (22.76 µg mL^{-1}) and I2S3 (22.02 µg mL^{-1}).

Phosphate solubilisation

Phosphate solubilisation by thermotolerant isolates varied significantly with isolate and temperature (Table 1). At 30 °C, phosphate solubilisation ranged from 41.86 to 88.83 µg mL^{-1}, while at 42 °C it ranged from 13.40 to 61.95 µg mL^{-1}. Overall, phosphate solubilisation showed reduction at 42 °C compared with 30 °C, indicating that elevated temperature negatively affected phosphate solubilisation across the isolates. The highest phosphate solubilisation at 30 °C was recorded by I2R6 (88.83 µg mL^{-1}), followed by I2R21 (88.68 µg mL^{-1}), I2S7 (88.54 µg mL^{-1}) and I2R7 (87.77 µg mL^{-1}). At 42 °C, I2S9 and I2R21 recorded the highest phosphate solubilisation (61.95 µg mL^{-1}), followed by I2R7 (61.50 µg mL^{-1}).

Potassium solubilisation

Potassium solubilisation differed significantly among the isolates under both temperature conditions (Table 1). At 30 °C, potassium solubilisation ranged from 31.45 to 63.92 µg mL^{-1}, whereas under elevated temperature it ranged from 48.39 to 66.49 µg mL^{-1}. Isolate I2S3 exhibited the highest potassium solubilisation at 30 °C (63.92 µg mL^{-1}). Under heat stress conditions, isolate I2R7 recorded the maximum potassium solubilisation (66.49 µg mL^{-1}), followed by I2R21 (62.27 µg mL^{-1}) and I2S7 (61.96 µg mL^{-1}). In contrast to ammonia and phosphate solubilisation, potassium solubilisation increased in several isolates under elevated temperature, suggesting enhanced mineral-solubilising activity under heat stress.

Zinc solubilisation

All thermotolerant bacterial isolates exhibited zinc solubilisation ability under both normal and elevated temperature conditions (Table 1). Zinc solubilisation at 30 °C ranged from 32.70 to 48.95 µg

Table 1. Plant growth promotional activities of thermotolerant bacterial isolates

Isolates	Ammonia production (µg mL^{-1})		Phosphate solubilisation (µg mL^{-1})		Potassium solubilisation (µg mL^{-1})		Zinc solubilisation (µg mL^{-1})		Siderophore production (PSU)	
	30 °C	42 °C	30 °C	42 °C	30 °C	42 °C	30 °C	42 °C	30 °C	42 °C
I2L1	25.59 ± 1.48 ^{bc}	17.22 ± 0.99 ^{cde}	76.40 ± 4.41 ^{cd}	55.59 ± 3.21 ^{ab}	41.03 ± 2.37 ^{fgh}	54.95 ± 3.17 ^{bc}	45.90 ± 2.65 ^{ab}	38.85 ± 2.24 ^{a}	39.27 ± 2.27 ^{bcdef}	34.56 ± 2.00 ^{abcd}
I2L2	24.92 ± 1.44 ^{bc}	17.13 ± 0.99 ^{cde}	73.72 ± 4.26 ^{cd}	46.45 ± 2.68 ^{bc}	45.23 ± 2.61 ^{defgh}	53.45 ± 3.09 ^{bc}	37.58 ± 3.18 ^{bcde}	37.50 ± 2.17 ^{a}	38.90 ± 2.25 ^{bcdefg}	34.23 ± 1.98 ^{abcd}
I2L9	24.38 ± 1.41 ^{bc}	15.87 ± 0.92 ^{def}	71.90 ± 4.15 ^{cd}	44.68 ± 2.58 ^{cd}	51.03 ± 2.95 ^{bcdef}	56.19 ± 3.24 ^{bc}	45.65 ± 2.64 ^{ab}	32.90 ± 1.90 ^{ab}	38.78 ± 2.24 ^{bcdefg}	33.16 ± 1.91 ^{bcde}
I2L10	24.24 ± 1.40 ^{bc}	15.74 ± 0.91 ^{defg}	71.22 ± 4.11 ^{cd}	44.27 ± 2.56 ^{cd}	47.31 ± 2.73 ^{bcdefg}	52.86 ± 3.05 ^{bc}	45.55 ± 2.63 ^{ab}	37.20 ± 2.15 ^{a}	38.26 ± 2.21 ^{bcdefg}	31.29 ± 1.81 ^{cdef}
I2L15	22.08 ± 1.27 ^{cd}	15.42 ± 0.89 ^{efg}	69.00 ± 3.98 ^{cd}	43.13 ± 2.49 ^{cd}	52.93 ± 3.06 ^{bcd}	56.19 ± 3.24 ^{bc}	45.45 ± 2.62 ^{ab}	39.05 ± 2.25 ^{a}	38.20 ± 2.21 ^{bcdefg}	30.21 ± 1.74 ^{cdef}
I2S3	31.89 ± 1.84 ^{a}	22.02 ± 1.27 ^{ab}	78.68 ± 4.54 ^{abc}	58.09 ± 3.35 ^{a}	63.92 ± 3.69 ^{a}	58.76 ± 3.39 ^{abc}	42.75 ± 2.95 ^{abcd}	40.50 ± 2.34 ^{a}	39.73 ± 2.29 ^{bcd}	36.04 ± 2.08 ^{abc}
I2S4	20.37 ± 1.18 ^{de}	14.25 ± 0.82 ^{efgh}	68.54 ± 3.96 ^{cd}	42.72 ± 2.47 ^{cd}	51.28 ± 2.96 ^{bcde}	53.61 ± 3.10 ^{bc}	43.58 ± 3.10 ^{abc}	37.10 ± 2.14 ^{a}	37.04 ± 2.14 ^{bcdefg}	30.19 ± 1.74 ^{cdef}
I2S6	19.97 ± 1.15 ^{de}	14.07 ± 0.81 ^{efgh}	68.22 ± 3.94 ^{cd}	41.27 ± 2.38 ^{cd}	48.45 ± 2.80 ^{bcdefg}	53.82 ± 3.11 ^{bc}	43.13 ± 3.08 ^{abcd}	36.60 ± 2.11 ^{ab}	35.31 ± 2.04 ^{cdefg}	29.46 ± 1.70 ^{cdefg}
I2S7	31.94 ± 1.84 ^{a}	19.43 ± 1.12 ^{bcd}	88.54 ± 5.11 ^{a}	58.09 ± 3.35 ^{a}	56.86 ± 3.28 ^{ab}	61.96 ± 3.58 ^{ab}	47.50 ± 2.74 ^{a}	40.95 ± 2.36 ^{a}	39.58 ± 2.29 ^{bcde}	39.02 ± 2.25 ^{ab}
I2S9	26.72 ± 1.54 ^{b}	17.27 ± 1.00 ^{cde}	77.59 ± 4.48 ^{bc}	61.95 ± 3.58 ^{a}	56.18 ± 3.24 ^{abc}	58.76 ± 3.39 ^{abc}	48.95 ± 2.83 ^{a}	40.00 ± 2.31 ^{a}	39.89 ± 2.30 ^{bcd}	36.14 ± 2.09 ^{abc}
I2S10	18.98 ± 1.10 ^{def}	13.04 ± 0.75 ^{fgh}	65.89 ± 3.80 ^{de}	40.50 ± 2.34 ^{cd}	48.45 ± 2.80 ^{bcdefg}	53.61 ± 3.10 ^{bc}	42.83 ± 3.06 ^{abcd}	36.50 ± 2.11 ^{ab}	34.82 ± 2.01 ^{defg}	29.28 ± 1.69 ^{defgh}
I2R5	18.57 ± 1.07 ^{def}	12.41 ± 0.72 ^{fghi}	65.81 ± 3.80 ^{de}	37.36 ± 2.16 ^{cd}	47.45 ± 2.74 ^{bcdefg}	53.74 ± 3.10 ^{bc}	44.50 ± 2.57 ^{abc}	34.80 ± 2.01 ^{ab}	33.86 ± 1.95 ^{defg}	28.56 ± 1.65 ^{defgh}
I2R6	31.94 ± 1.84 ^{a}	24.47 ± 1.41 ^{a}	88.83 ± 5.13 ^{a}	55.59 ± 3.21 ^{ab}	56.19 ± 3.24 ^{abc}	58.76 ± 3.39 ^{abc}	40.83 ± 1.67 ^{abcd}	40.45 ± 2.34 ^{a}	47.36 ± 2.73 ^{a}	38.22 ± 2.21 ^{ab}
I2R7	30.59 ± 1.77 ^{a}	19.88 ± 1.15 ^{bc}	87.77 ± 5.07 ^{ab}	61.50 ± 3.55 ^{a}	53.61 ± 3.10 ^{bcd}	66.49 ± 3.84 ^{a}	41.05 ± 4.80 ^{abcd}	40.10 ± 2.32 ^{a}	43.24 ± 2.50 ^{ab}	36.16 ± 2.09 ^{abc}
I2R8	17.18 ± 0.99 ^{efg}	12.23 ± 0.71 ^{fghi}	57.77 ± 3.34 ^{ef}	35.00 ± 2.02 ^{d}	42.45 ± 2.45 ^{efgh}	53.61 ± 3.10 ^{bc}	43.70 ± 2.52 ^{abc}	34.75 ± 2.01 ^{ab}	33.64 ± 1.94 ^{defg}	28.08 ± 1.62 ^{defgh}
I2R12	16.86 ± 0.97 ^{efg}	12.09 ± 0.70 ^{fghi}	57.68 ± 3.33 ^{ef}	25.27 ± 1.46 ^{e}	48.45 ± 2.80 ^{bcdefg}	51.08 ± 2.95 ^{c}	43.45 ± 2.51 ^{abc}	34.55 ± 1.99 ^{ab}	33.59 ± 1.94 ^{defg}	27.98 ± 1.62 ^{defgh}
I2R13	15.83 ± 0.91 ^{fgh}	11.91 ± 0.69 ^{ghi}	53.31 ± 3.08 ^{fg}	22.45 ± 1.30 ^{ef}	38.45 ± 2.22 ^{ghi}	56.25 ± 3.25 ^{bc}	36.33 ± 2.03 ^{cde}	34.50 ± 1.99 ^{ab}	33.37 ± 1.93 ^{defg}	26.68 ± 1.54 ^{efgh}
I2R17	15.60 ± 0.90 ^{fgh}	10.83 ± 0.63 ^{hi}	51.31 ± 2.96 ^{fgh}	20.36 ± 1.18 ^{ef}	37.45 ± 2.16 ^{hi}	51.03 ± 2.95 ^{c}	41.85 ± 2.42 ^{abcd}	34.30 ± 1.98 ^{ab}	32.80 ± 1.89 ^{efg}	26.30 ± 1.52 ^{fgh}
I2RH3	15.29 ± 0.88 ^{fgh}	10.52 ± 0.61 ^{hi}	45.95 ± 2.65 ^{gh}	19.50 ± 1.13 ^{ef}	31.45 ± 1.82 ^{i}	48.39 ± 2.79 ^{c}	41.25 ± 2.38 ^{abcd}	33.75 ± 1.95 ^{ab}	32.78 ± 1.89 ^{efg}	26.01 ± 1.50 ^{fgh}
I2S11	14.30 ± 0.83 ^{gh}	9.03 ± 0.52 ^{ij}	44.68 ± 2.58 ^{gh}	17.22 ± 0.99 ^{ef}	49.45 ± 2.86 ^{bcdef}	54.01 ± 3.12 ^{bc}	34.92 ± 4.00 ^{de}	33.50 ± 1.93 ^{ab}	32.44 ± 1.87 ^{fg}	23.24 ± 1.34 ^{gh}
I2R20	12.86 ± 0.74 ^{h}	7.01 ± 0.40 ^{j}	41.86 ± 2.42 ^{h}	13.40 ± 0.77 ^{f}	45.88 ± 2.65 ^{cdefgh}	48.45 ± 2.80 ^{c}	32.70 ± 3.30 ^{e}	28.45 ± 1.64 ^{b}	32.11 ± 1.85 ^{g}	22.75 ± 1.31 ^{h}
I2R21	27.08 ± 1.56 ^{b}	22.76 ± 1.31 ^{ab}	88.68 ± 5.12 ^{a}	61.95 ± 3.58 ^{a}	53.61 ± 3.10 ^{bcd}	62.27 ± 3.60 ^{ab}	46.05 ± 2.66 ^{ab}	39.90 ± 2.30 ^{a}	39.89 ± 2.30 ^{bcd}	40.21 ± 2.32 ^{a}
P72	34.10 ± 1.97 ^{a}	19.88 ± 1.15 ^{bc}	77.77 ± 4.49 ^{bc}	61.50 ± 3.55 ^{a}	53.61 ± 3.10 ^{bcd}	58.76 ± 3.39 ^{abc}	48.90 ± 2.82 ^{a}	39.50 ± 2.28 ^{a}	41.92 ± 2.42 ^{abc}	36.16 ± 2.09 ^{abc}
	I	T	I × T	I	T	I × T	I	T	I × T	I	T	I × T	I	T	I × T
CD at 5 %	2.309	0.681	3.265	6.724	1.982	9.509	6.027	1.777	8.524	5.051	1.489	7.144	3.986	1.175	5.638

I2- IIHR 2202, L: leaf, S:- stem, R: root, RH: rhizoplane, I: isolate, T: temperature. Values are mean ± SE(m) of three replications. Means followed by different superscript letters differ significantly according to Duncan's multiple range test (DMRT) at $p \leq 0.05$.

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mL^{-1}, while at 42 °C it ranged from 28.45 to 40.95 µg mL^{-1}. The highest zinc solubilisation at normal temperature was recoded in isolate I2S9 (48.95 µg mL^{-1}), followed by P-72 (48.90 µg mL^{-1}) and I2S7 (47.50 µg mL^{-1}). Under elevated temperature conditions, isolate I2S7 showed the maximum zinc solubilisation (40.95 µg mL^{-1}), followed by I2S3 (40.50 µg mL^{-1}) and I2R6 (40.45 µg mL^{-1}).

Siderophore production

Siderophore production by thermotolerant bacterial isolates was significantly influenced by temperature (Table 1). At 30 °C, siderophore production ranged from 32.11 to 47.36 PSU, while at 42 °C it ranged from 22.75 to 40.21 PSU. The highest siderophore production at normal temperature was observed in isolate I2R6 (47.36 PSU), followed by I2R7 (43.24 PSU) and P-72 (41.92 PSU). Under elevated temperature conditions, isolate I2R21 recorded the highest siderophore production (40.21 PSU), followed by I2S7 (39.02 PSU) and I2R6 (38.22 PSU).

Phytohormone production

The thermotolerant bacterial isolates exhibited varying levels of IAA and GA_3 production under both normal and elevated temperature conditions (Fig. 1 and 2). Several isolates maintained relatively high phytohormone production even under heat stress conditions, indicating their potential role in regulating plant growth and stress adaptation. Significant variation in phytohormone production was observed among the isolates, at 30 °C, IAA production ranged from 40.63 to 87.69 µg mL^{-1}, while at 42 °C it ranged from 36.47 to 50.43 µg mL^{-1}. The highest IAA production at normal temperature was observed in isolate I2R21 (87.69 µg mL^{-1}), followed by I2S7 (82.59 µg mL^{-1}). Under elevated temperature conditions, isolate I2S3 recorded the highest IAA production (50.43 µg mL^{-1}), followed by I2S7 (49.45 µg mL^{-1}). Similarly at 30 °C, GA_3 production ranged from 41.52 to 99.96 µg mL^{-1}, while at 42 °C it ranged from 28.63 to 88.01 µg mL^{-1}. The highest GA_3 production at normal temperature was observed in isolate I2S7 (99.96 µg mL^{-1}), followed by I2S9 (97.80 µg mL^{-1}). Under elevated temperature conditions, isolate I2R6 recorded the highest GA_3 production (88.01 µg mL^{-1}), followed by P-72 (80.11 µg mL^{-1}). Although IAA production declined under elevated temperature, several isolates maintained relatively high production, indicating good thermotolerance.

Heatmap analysis of plant growth-promoting traits

Hierarchical clustering heatmap analysis indicated considerable variation in the quantitative expression of plant growth-promoting traits among the thermotolerant isolates under normal and elevated temperature conditions (Fig. 3). The heatmap clearly distinguished efficient multifunctional isolates from comparatively less active isolates based on nutrient solubilisation, siderophore production and ammonia production profiles. Isolates I2S7, I2R6, I2R7, I2R21, I2S3, I2S9 and P-72 clustered together due to their consistently superior performance under elevated temperature conditions, indicating strong thermotolerance and multifunctional plant growth -promoting potential.

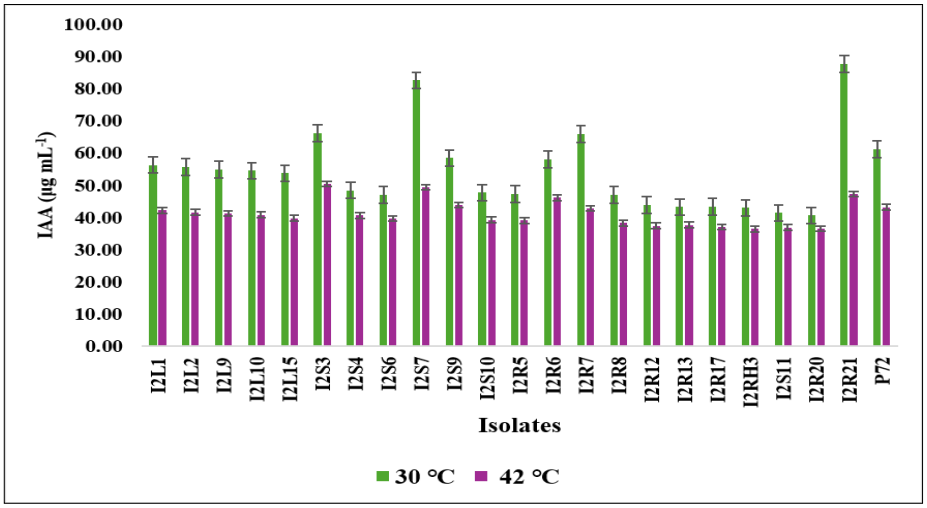


Fig. 1. Indole-3-acetic acid production by thermotolerant bacterial isolates.

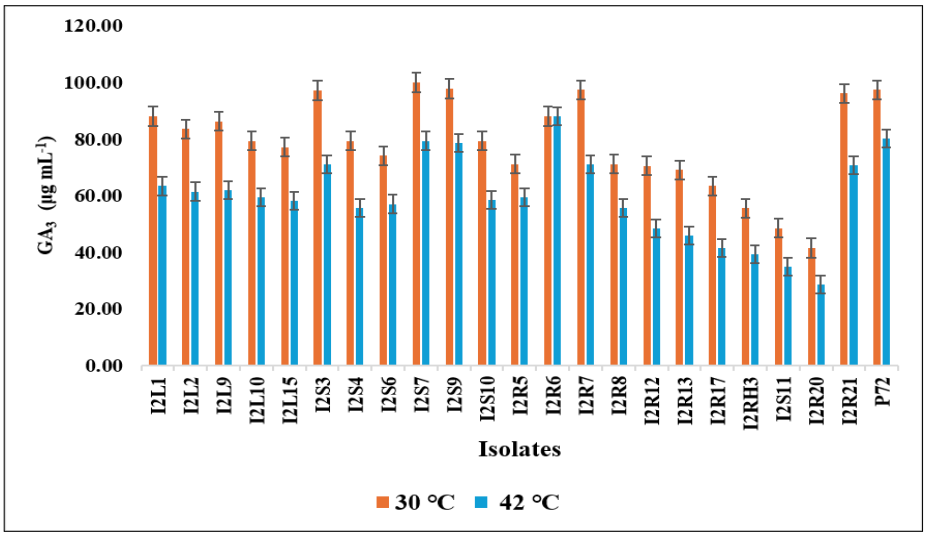


Fig. 2. Gibberellic acid (GA_3) production by thermotolerant bacterial isolates.

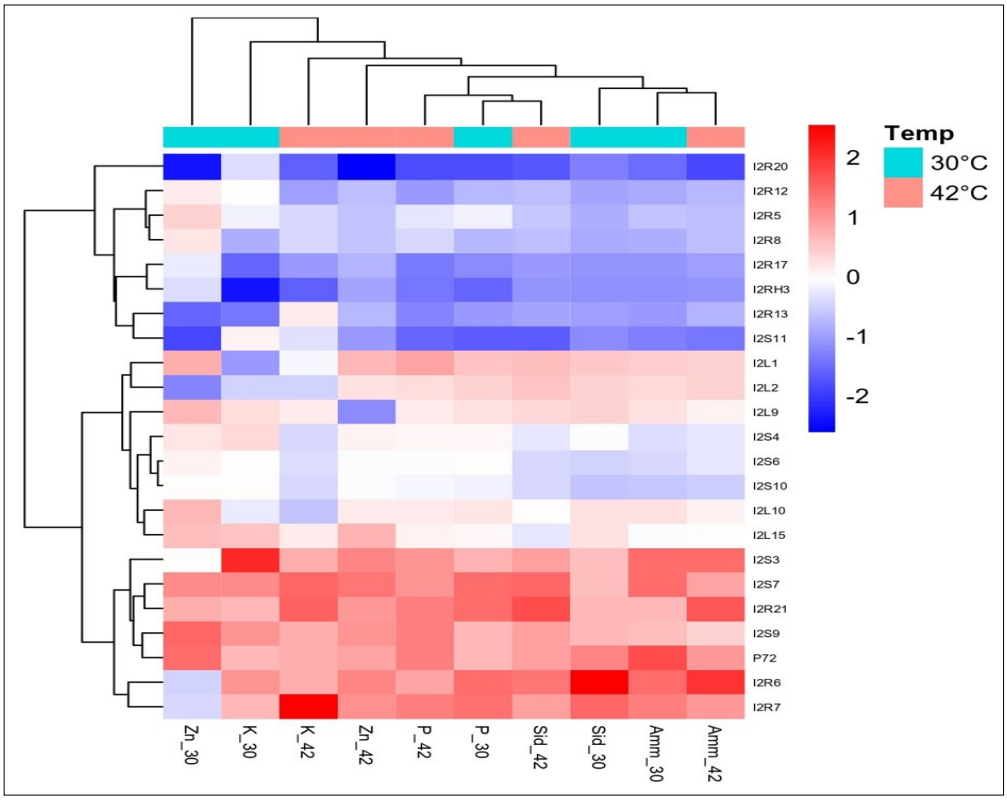


Fig. 3. Hierarchical clustering heatmap illustrating the quantitative variation in plant growth-promoting traits of the thermotolerant bacterial isolates under normal (30 °C) and elevated temperature (42 °C) conditions. The heatmap represents the relative performance of individual bacterial isolates for key plant growth-promoting parameters, including ammonia production, phosphate solubilisation, potassium solubilisation, zinc solubilisation and siderophore production, evaluated quantitatively at two temperature regimes. The colour intensity reflects normalised trait values, where warmer colours indicate higher activity and cooler colours indicate lower activity.

Morphological and molecular characterisation of efficient isolates

Based on overall plant growth-promoting efficiency under elevated temperature conditions, six superior thermotolerant bacterial isolates (I2S7, I2R6, I2R7, I2R21, I2S3 and I2S9) were selected for detailed characterisation (Table 2). Morphological characterisation revealed variations in colony colour, texture and margin among the isolates. Gram staining showed both Gram-positive and Gram-negative bacterial groups among the selected isolates. Molecular characterisation based on 16S rRNA identified the efficient isolates as *Fictibacillus phosphorivorans* strain S3, *Stenotrophomonas maltophilia* strain S9, *Glutamicibacter mishrai* strain R6, *Exiguobacterium indicum* strain R7, *Enterobacter soli* strain R21 and *Enterobacter hormaechei* subsp. *xiangfangensis* strain S7. The nucleotide sequences were accessioned in the National Center for Biotechnology Information (NCBI) database (Table 2).

Discussion

The ability of selected thermotolerant bacterial isolates to retain multiple plant growth-promoting traits at 42 °C demonstrates their physiological adaptation to elevated temperature and highlights their potential for developing climate-resilient microbial inoculants. The variation observed among leaf, stem and root derived isolates may related to differences in their respective plant habitats. Root-associated bacteria interact with root exudates and rhizospheric microorganisms, while leaf-associated bacteria experience a more exposed and nutrient-limited environment with fluctuations in temperature, moisture and radiation (20, 21) Bacteria obtained from stem tissues are subject to a different type of ecological niches closely related to the plant's physiology. The differences in bacterial community composition and diversity among the rhizosphere, phyllosphere and endosphere of tomato, including differences between roots, rhizoplane, stems and leaves has been previously reported (22). In addition, stress conditions can alter the tomato root microbiome and favour bacterial groups (23).

Ammonia production is an important trait contributing to nitrogen availability and plant growth stimulation in the rhizosphere. In the present study, ammonia production declined under elevated temperature conditions compared to normal temperature conditions among the isolates, indicating the sensitivity of nitrogen metabolism to heat stress. Although the reference strain *B. amyloliquefaciens* P-72 recorded the highest ammonia production at 30 °C, isolates I2R6, I2R21 and I2S3 maintained comparatively higher ammonia production under heat-stress conditions (42 °C). suggesting enhanced metabolic stability under stress conditions. Elevated temperature is known to influence microbial enzymatic activity and nitrogen transformation processes, thereby affecting ammonia synthesis (12). The sustained ammonia production observed in efficient isolates may therefore contribute to maintaining nitrogen availability in the rhizosphere under heat stress conditions.

Phosphate solubilisation remained comparatively stable in several thermotolerant isolates despite elevated temperature stress. Isolates I2R21, I2S9 and I2R7 exhibited high phosphate solubilization efficiency at 42 °C, on par with the reference strain *B. amyloliquefaciens* P-72, indicating the persistence of phosphate-mobilising mechanisms under thermal stress. Phosphate-solubilising bacteria enhance phosphorus availability primarily through secretion of organic acids and phosphatases that convert insoluble phosphates into plant-accessible forms (24).

Table 2 Morphological and molecular characterization of thermotolerant bacterial isolates

Isolate name	Identification	Closest type strain	Percent similarity	NCBI accession number	Morphological characteristics					
					Colony colour	Colony texture	Colony margin	Colony shape	Gram staining	Endospore staining
I2S3	*Fictibacillus phosphorivorans* strain S3	*Fictibacillus phosphorivorans* strain Ca7 (JX258924)	100	PZ251385	Creamish yellow	Smooth	Undulated	Circular	+	+
I2R6	*Glutamicibacter mishrai* strain R6	*Glutamicibacter mishrai* strain S5-52 (KT444697)	99.77	PZ251387	Light Yellow	Mucoid	Entire	Circular	+	-
I2R7	*Exiguobacterium indicum* strain R7	*Exiguobacterium indicum* strain HHS 31T (AJ846291)	99.85	PZ251388	Light orange	Smooth	Entire	Circular	+	-
I2S9	*Stenotrophomonas maltophilia* strain S9	*Stenotrophomonas maltophilia* strain MTCC 434 (JALV01000036.1)	97.36	PZ251386	Light Yellow	Smooth	Undulated	Circular	-	-
I2R21	*Enterobacter soli* strain R21	*Enterobacter soli* strain ATCC BAA-2102 (LXES01000062)	99.66	PZ251389	Cream	Mucoid	Entire	Circular	-	-
I2S7	*Enterobacter hormaechei* subsp. *xiangfangensis* strain S7	*Enterobacter xiangfangensis* LMG 27915T (FYB01000083)	99.63	PZ251390	Creamish white	Butyrous	Entire	Circular	-	-

Thermotolerant plant growth-promoting bacteria capable of maintaining phosphorus mobilisation under high temperature conditions may therefore support plant nutrient acquisition and root growth under stress environments. Similar observations have demonstrated that stress-adapted PGPB sustain nutrient cycling processes through temperature-resilient metabolic pathways and stress-responsive gene regulation (2, 10).

Potassium solubilisation was notably enhanced in several isolates under elevated temperature conditions, particularly in isolate I2R7, which recorded the highest potassium solubilisation at 42 °C which is significantly higher than the reference strain *B. amyloliquefaciens* P-72. Unlike ammonia and phosphate solubilisation, potassium solubilisation increased in several isolates under elevated temperature, suggesting that potassium-mobilising pathways remain active or are enhanced under thermal stress. Thermotolerant potassium-solubilising bacteria are capable of maintaining the production of organic acids, including gluconic, citric, oxalic and malic acids, under elevated temperature conditions. These organic acids lower the pH of the surrounding medium and facilitate the dissolution of potassium-bearing minerals, thereby increasing the availability of soluble potassium (25, 26). Efficient potassium-solubilising bacteria may therefore contribute to improved plant water relations and thermotolerance. The enhanced potassium mobilisation observed in the present *in vitro* study suggests that thermotolerant isolates possess adaptive physiological mechanisms that remain functional even under elevated temperature conditions. Similar findings have indicated that thermotolerant PGPB improves nutrient uptake efficiency and regulates physiological responses associated with stress adaptation (6).

Zinc solubilisation also remained relatively stable among the isolates under heat stress conditions. Zinc is an essential micronutrient involved in several enzymatic and antioxidant processes in plants. The ability of isolates I2S7, I2S3 and I2R6 to sustain zinc solubilisation under elevated temperature conditions highlights their potential to enhance micronutrient availability under *in vitro* heat stress, comparable to the reference strain *B. amyloliquefaciens* P-72. Maintenance of micronutrient balance is particularly important under heat stress, as elevated temperature often disrupts nutrient uptake and assimilation in plants (10). Thermotolerant zinc-solubilising bacteria may therefore contribute to enhanced metabolic stability and stress tolerance in plants cultivated under high-temperature environments.

Siderophore production was another important trait that was retained by efficient isolates under elevated temperature conditions. Isolates I2R21, I2S7 and I2R6 exhibited comparatively higher siderophore production than the reference strain *B. amyloliquefaciens* P-72 at 42 °C, indicating efficient iron-chelating ability under *in vitro* stress conditions. Iron availability in soil is often reduced under elevated temperatures due to altered oxidation states and reduced solubility, which can limit plant growth and microbial activity. Siderophore-producing bacteria improve iron acquisition by chelating ferric ions and making them available to plants and microorganisms (27). In addition to iron mobilisation, siderophore-producing PGPB are also associated with enhanced antioxidant activity and reduction of oxidative stress in plants subjected to abiotic stress conditions (4). The retention of siderophore production under elevated temperature conditions therefore reflects the ecological adaptability and functional significance of the thermotolerant isolates.

Phytohormone production, particularly IAA and GA_3, were consistently observed among efficient isolates under both normal and elevated temperature conditions *in vitro*. Phytohormone-producing PGPB influences root development, nutrient uptake and stress-responsive signalling pathways in plants. Isolates I2S7, I2R6, I2R7 and I2R21 maintained higher IAA and GA_3 production under *in vitro* heat-stress conditions than the reference strain *B. amyloliquefaciens* P-72, demonstrating superior phytohormone-producing potential. This *in vitro* performance suggests their potential as candidates for further evaluation of plant growth promotion under heat-stress conditions auxin-producing bacteria stimulate root elongation and lateral root formation, thereby improving nutrient and water uptake under stress conditions (28). In addition, bacterial phytohormones regulate stress-responsive genes and contribute to maintenance of hormonal balance during abiotic stress (7, 8). Sustained phytohormone production under elevated temperature conditions therefore represents an important adaptive feature of thermotolerant PGPB.

Hierarchical clustering heatmap analysis further revealed distinct variation in the expression of plant growth-promoting traits among the thermotolerant isolates. Efficient isolates viz., I2S7, I2R6, I2R7, I2R21, I2S3, I2S9 and the reference strain *B. amyloliquefaciens* P-72 clustered together due to their superior multifunctional performance under elevated temperature conditions. The clustering pattern clearly demonstrated that only a few isolates retained stable expression of multiple plant growth-promoting traits under stress conditions, emphasising the importance of screening for multifunctional thermotolerant bacteria for agricultural applications. An earlier report suggested that endophytes from tomato roots exposed to temperatures of 45–47 °C, reported several plant growth-promoting traits, including phosphate solubilisation, IAA, siderophore and ammonia production. This suggests that heat-exposed tomato tissues can serve as a source of bacteria with useful thermotolerance and plant growth-promoting traits (29).

Molecular characterisation identified the efficient isolates, I2S3 as *F. phosphorivorans* strain S3, I2S9 as *S. maltophilia* strain S9, I2R6 as *G. mishrai* strain R6, I2R7 as *E. indicum* strain R7, I2R21 as *E. soli* strain R21 and I2S7 as *E. hormaechei* subsp. *xiangfangensis* strain S7. Members of these genera have been widely associated with nutrient mobilisation, phytohormone production and multi stress tolerance in different crop systems (30–34). The identification of these isolates further supports their potential use as microbial inoculants for enhancing crop productivity under high-temperature conditions. Future studies should investigate additional stress-related traits, such as 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity, exopolysaccharide production, biofilm formation and antioxidant responses and further evaluate these isolates under greenhouse and field conditions to validate their potential for agricultural application.

Conclusion

The present study demonstrated that thermotolerant bacterial isolates obtained from the heat tolerant tomato genotype IIHR-2202 retained multifunctional growth-promoting attributes under elevated temperature conditions *in vitro*. The combined ability to solubilise nutrients, produce siderophores and synthesise phytohormones under heat stress highlights their potential as promising candidates for further validation in plants under heat-stress conditions. Six thermotolerant bacterial isolates belonging to the genera *Fictibacillus*, *Glutamicibacter*, *Exiguobacterium*, *Stenotrophomonas* and *Enterobacter* were identified as the most promising candidates. These isolates hold promise for enhancing plant growth and resilience under heat stress in the changing climatic scenario, subject to further evaluation.

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Authors' contributions

SS conducted the experiments, analysed the data and prepared the manuscript. GS formulated and supervised the experiments and edited the manuscript. UN, RTK and RHL advised and critically reviewed the manuscript. All authors have read and approved the manuscript.

Compliance with ethical standards

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Ethical issues: None

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT to improve language and clarity. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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