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Biosynthesis and function of rhizobacterial secondary metabolites in plant abiotic stress tolerance

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KEYWORDS

Abiotic stress, metabolic pathways, osmoprotectants, plant growth-promoting rhizobacteria, stress tolerance

HIGHLIGHTS

- Rhizobacterial strains (RK1, RT2, RT3) produced diverse bioactive secondary metabolites detected by GC–MS.
- Proline was the most abundant metabolite, acting as a key osmoprotectant under drought stress.
- RT3 strain significantly enhanced lettuce drought tolerance compared to other treatments.
- Inoculated plants showed higher survival rates and fresh biomass after rewatering.
- Specific metabolites such as proline, glycine, and vitamins contributed to improved plant stress resilience.

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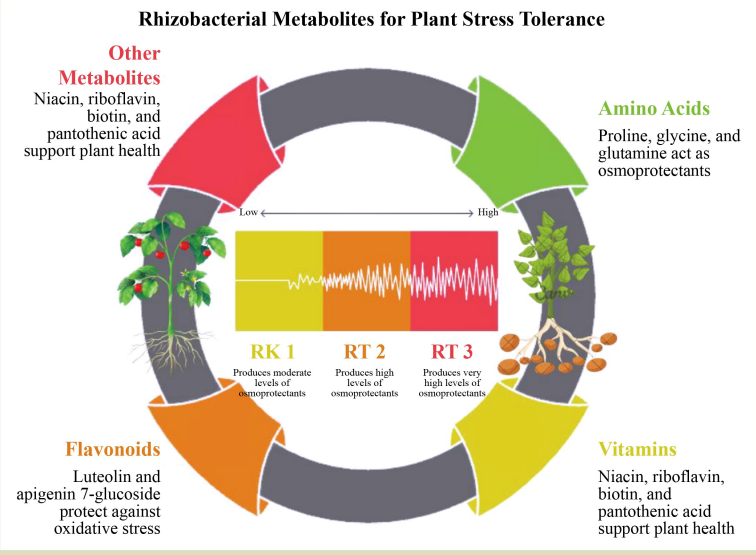
GRAPHICAL ABSTRACT



ABSTRACT

Plant growth-promoting rhizobacteria enhance plant growth and stress resilience, but the metabolite-based mechanisms behind these effects remain insufficiently characterized. This study aimed to assess the metabolite profiles of three rhizobacterial treatments (RK1, RT2 and RT3) and evaluate their effects on drought tolerance in lettuce (*Lactuca sativa*). The strains were cultured under standard laboratory conditions, and their intracellular metabolites were analyzed using gas chromatography-mass spectrometry. Results showed production of key compounds such as proline, glycine,

glutamine, niacin, riboflavin, biotin, pantothenic acid, luteolin and apigenin 7-glucoside, with proline being the most abundant across strains. Lettuce plants were grown under controlled conditions and inoculated by soil drenching at transplantation. Drought stress was imposed 5 days after inoculation by withholding water for 7 days. Survival rate and fresh weight were measured after rewatering. Plants treated with rhizobacterial strains, particularly RT3, had significantly higher survival rates and fresh weight compared to the uninoculated control. These findings highlight the distinct contribution of specific rhizobacterial metabolites to drought tolerance and demonstrate their potential as microbial bioinoculants for improving plant performance under water-limited conditions.

1 Introduction

The plant growth-promoting rhizobacteria (PGPR) are key for in boosting plant growth and yield, unique among all the beneficial plant microorganisms, because they improve nutrient uptake, which in turn triggers plant defense and response to environmental stress. PGPR can help to achieve sustainable agriculture; they can increase production and strengthen plant systems against biotic and abiotic stresses by collaborating with ecologically friendly farming practices. Both abiotic and biotic factors reduce plant growth and production[1,2]. The reduction in agricultural production can lead to changes in global commodity prices and is a major threat to food security, particularly in areas where farming is a key industry[3]. Currently, crops are susceptible to abiotic stress on about 20% of arable land[4], and on about 45% of arable and irrigated land by 2050[5]. When environmental problems affect land, it is advisable to combat land degradation economically and sustainably[6]. PGPR have been found to be able improve plant tolerance to various stresses, such as drought, salinity, high temperature, cold and waterlogging stress[7]. This is because PGPR mediate plant growth by producing hormones, siderophores and exopolysaccharides, and solubilizing nutrients in the rhizosphere.

Chang et al.[7] reported that volatile organic compounds, phytohormones and lipopolysaccharides produced by PGPR protect plants against abiotic stress. According to Choudhar et al.[8], such bacterial metabolites are known to trigger some plant responses against biotic and abiotic stress agents. According to Zarei[9], PGPR, apart from proline, produce other osmolytes, such as amino acids and soluble sugars, in response to plant stress under drought conditions. Plants may invoke osmotic protection pathways as drought is generally a harsh environmental condition. PGPR may stimulate production in the internal plant cells and exudation of osmoprotection in the soil[10]. These bioactive microorganisms can produce osmoprotectants, including amino acids, sugars, vitamins, phenolic compounds and flavonoids, which they can also exude[11]. These classes of osmoprotectants are toggled to bring about recovery in plant health from damage inflicted by environmental stressors[12]. For example, in stress conditions, proline and glycine betaine accumulate in the plant cells to participate in osmotic adjustment, protection against oxidative stress and counteracting reactive oxygen species (ROS) under stress conditions[13]. PGPR have also been found to increase the accumulation of sugars in the leaves of plants under drought stress, acting as osmoprotectants[14]. Also, the accumulated soluble sugars constitute another form of drought adaptation with an osmoprotective role in reestablishing osmotic pressure within plants[15].

According to Kurniawan and Chuang[16], PGPR that produce phytohormones stimulate one of the plant defense mechanisms that enhances several plant phytohormone signaling pathways associated with abiotic stress tolerance. The monoterpene content in plants increased significantly after treatment with osmoprotectant-producing PGPR[17]. PGPR produce organic acids and other secondary metabolites, which increase the solubility of macro and micronutrients as well as improve plant performance under stressed conditions[18]. According to Mohanan et al.[19] plants treated with PGPR that produce 1-aminocyclopropane-1-carboxylate deaminase and trehalose grow better under salt stress conditions due to enhanced

pigment photosynthesis[20]. Tissue under stress conditions maintains turgor and water balance within the plant with several secondary metabolites such as proline, betaine, glycine and polyols (including malate and mannitol)[21]. Also, PGPR-treated chickpea plants had increased phenolic and flavonoids concentrations[22]. The antioxidant group includes phenolic acids and flavonoids, which can protect plants against drought stress[23]. The limited water availability in the soil will stimulate the same accumulation process of both compounds, directly contributing to increasing plant growth and production[24]. This study aimed to evaluate metabolite compounds secreted by PGPR that potentially act as osmoprotectants.

2 Materials and methods

2.1 Bacterial isolation

Three rhizobacterial strains were isolated from the roots of tomato (*Solanum lycopersicum*) and potato (*Solanum tuberosum*) plants from an experimental field of University of Muhammadiyah Malang and from farmer fields at Sumber Brantas, East Java, Indonesia. Soil samples, consisting of plant roots and root zone, were collected from five locations with heavy densities of plant roots up to 8 plants m^{-2}. A sample (~5 g) of the root zone was added to 30 mL of sterile distilled water and vortexed for 5 min to give an homogeneous suspension. This was then serially diluted from 10^{-1} to 10^{-5} to enable dilution of the bacterial population to a number isolatable on an agar plate. This suspension was for plated on a nutrient agar (NA) medium for initial isolation and purification of bacteria.

2.2 Bacterial culture

An aliquot (100 μL) of each dilution (10^{-1} to 10^{-5}) of rhizobacterial suspension was plated to NA medium. The plates were then inverted and incubated at 28 °C for 24 h to facilitate the growth. Following the incubation, individual colonies were picked from the plate for streaking at least twice on fresh plates to allow for pure cultures. This ensured that a single, isolated colony was picked for streaking. This was repeated at least three times to ensure that the isolated cultures were pure. Then, purified strains were inoculated onto NA media containing cyclohexylamine at 100 $mg{\cdot}L^{-1}$, which induces osmotic stress conditions. The growth under such conditions was used to select a strain with high osmotic stress tolerance. The selected bacterial strains were characterized for growth kinetics in nutrient broth (liquid medium) supplemented with 0.1% glucose as the carbon source and ammonium chloride as the sole nitrogen source. These cultures grown at 28 °C with constant shaking. Optical density at 600 nm was measured at 0, 12, 24, 48 and 72 h to determine the growth rate and behavior of the strains under minimal nutrient conditions, to provide information on their metabolic activity and growth.

2.3 Plant experimental design

Lettuce (*Lactuca sativa*) plants were used as a model to evaluate the effect of rhizobacterial strains on drought tolerance. Seeds were germinated in a growth chamber under controlled conditions (25 ± 2 °C, 60%–70% RH, 16/8 h light/dark photoperiod) in a sterile growth medium. After germination, uniform plants were transplanted into seed tray (3.5 cm diameter) containing autoclaved soil and allowed to acclimate for 3 days. The experiment had four treatments: an uninoculated control, and three inoculated treatments, RK1, RT2 and RT3 (the latter being the strain designation and applied dilution). Each treatment had three biological replicates each consisting of a single plant. Bacterial suspensions were applied by drenching 20 mL of inoculum into the around the seedling following transplantation. Drought stress was imposed 5 days post-inoculation by withholding water for 7 days. During this period, survival was recorded. Water was then applied to assess recovery by measuring fresh weight (g per plant) after 3 days.

2.4 Detection of osmoprotectants

Culturing was done on nutrient broth (liquid medium) minimal media containing 0.2% glucose as a carbon source to study some selected rhizobacterial strains for osmoprotectants produced. The culture was incubated at 150 $r{\cdot}min^{-1}$ at 28 °C for 48 h to keep the cells in good growth along with production of metabolites. Following incubation, the culture was centrifuged for 10 min at 10,000 $r{\cdot}min^{-1}$ to remove the bulk of the bacterial cells. The bacterial osmoprotectant-producing supernatants were pipetted carefully into sterile clean tubes. The supernatant was further passed through a 0.22 $\mu mol{\cdot}L^{-1}$ membrane filter to remove any residual bacterial cells or particulate matter. The filtered supernatant was subjected to chemical analysis to detect major osmoprotectants, namely proline, glycine betaine, trehalose, mannitol and glutathione

analyzed by GC-MS, following the method reported by Agami et al.[25]. All the supernatants were derivatized with BSTFA prior to analysis in GC-MS to enhance the volatility of the osmoprotectants to improve detection and quantification during analysis by GC-MS.

2.5 Data analysis

Quantitative production levels of these osmoprotectants determined by GC-MS were compared and visualized using Python (version 3.11) such as package *matplotlib*, *seaborn*, and *pandas* to generate bar charts and diagrams that illustrate differential production patterns between strains. Data obtained from drought stress experiments were analyzed using one-way ANOVA followed by Tukey's HSD test at a 5% significance level ($p < 0.05$) using with SAS software (version 9.3.1.).

3 Results

3.1 Variability of osmoprotectants produced by the tested rhizobacteria strains

The variability of compounds produced by rhizobacteria strains RK1, RT2 and RT3 was examined in relation to their potential in mitigating abiotic stress in plants. These compounds contributed to cellular stabilization, reduction of oxidative stress and enhancement of metabolic function. Notable compounds produced by the bacterial strains included amino acids (glutamine, glycine and proline), vitamins (biotin, pantothenic acid and riboflavin), and other secondary metabolites such as flavonoids (kaempferol and luteolin), phenolic compounds (luteolin 7-glucoside) and sugars (arabinose, rhamnose and xylose). High concentrations of proline were particularly important, as it is known to contribute to osmotic adjustment under drought and salinity stress. The analysis also showed that other non-osmoprotectant compounds, such as luteolin, pantothenic acid and phenylalanine, have the potential to contribute to oxidative stress mitigation. Additionally, lactic acid and various amino acids supported plant growth and vigor, further enhancing plant resilience under environmental stress (Fig. 1).

3.2 Metabolic pathways of the tested rhizobacteria strains

Metabolic pathway analysis revealed that several amino acids, including glycine, serine and threonine, were involved in critical cellular functions, particularly under stress conditions. These amino acids had a significant impact score and were linked to nitrogen metabolism, protein synthesis and cellular energy production. Other pathways involved the biosynthesis of isoleucine, leucine and valine, as well as sulfur metabolism and CoA biosynthesis (Table 1).

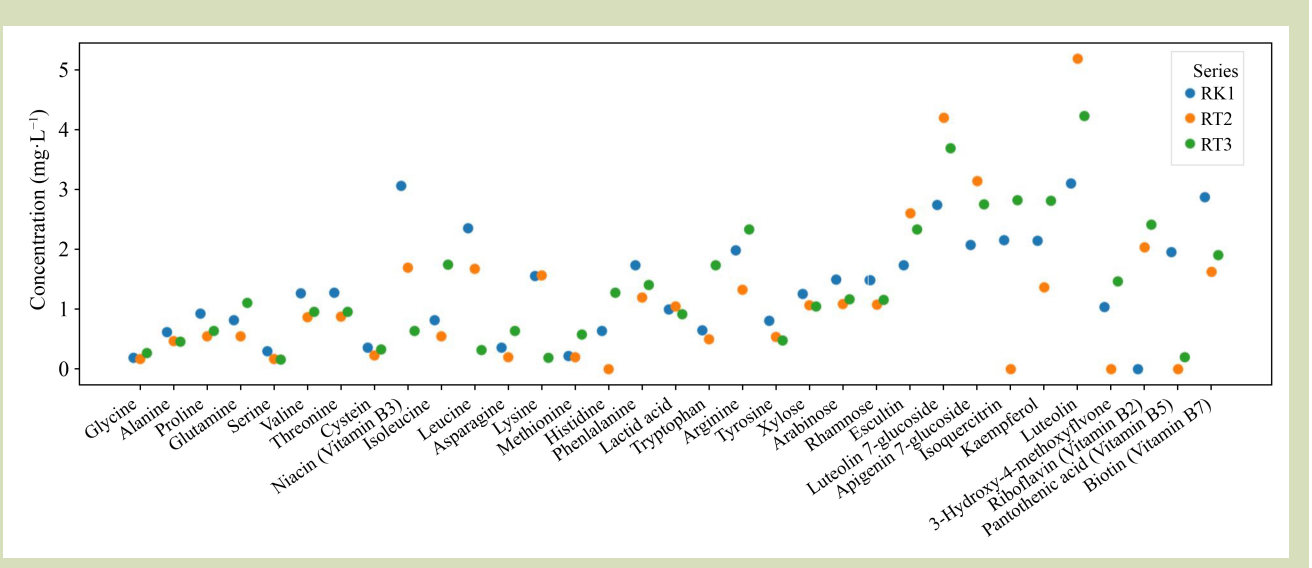


Fig. 1 Metabolite concentration distribution from three tested rhizobacterial strains.

Table 1 Summary of significant metabolic pathways from three PGPR strains

Metabolic pathway	Total compound	Expected hits	Observed hits	Raw *p*-value	Significance score (–lg *p*)	Holm-corrected *p*-value	FDR-adjusted *p*-value	Impact
Glycine, serine and threonine metabolism	37	0.563	7	0.004	63.909	3.74	0.37	0.511
Valine, leucine and isoleucine biosynthesis	22	0.335	4	0.0002	3.633	0.021	0.008	0.107
One carbon pool by folate	23	0.350	4	0.0003	35.542	0.025	0.008	0.216
Pantothenate and CoA biosynthesis	24	0.365	4	0.0003	34.792	0.029	0.008	0.090
Tyrosine metabolism	35	0.532	4	0.001	28.325	0.129	0.027	0.206
Phenylalanine metabolism	17	0.258	3	0.002	27.527	0.154	0.027	0.05
Thiamine metabolism	21	2.221	3	0.003	2.478	0.286	0.044	0
Cysteine and methionine metabolism	45	0.685	4	0.004	24.202	0.323	0.044	0.278
Sulfur metabolism	23	0.350	3	0.004	2.362	0.253	0.044	0.075
Phenylalanine, tyrosine and tryptophan	24	0.365	3	0.005	23.082	0.408	0.045	0.139

In addition, important metabolites produced by the three strains are the constellation of the glycine, serine and threonine pathways. These three amino acids are essential for plant cell metabolism (Fig. 2). Glycine (C00037) converted from serine (C00065) via serine hydroxy methyltransferase serves as a one-carbon source in the purine and nucleic acid synthesis pathways. Glyoxylate is produced as a product with C00188, among others, as with serine participating in the energy metabolism of C00213. The amino acid serine (C00065) is involved in the synthesis of phosphatidylserine (C02737) in membranes. Threonine (C00022) is a precursor of serine that produces succinyl-CoA (C00740), which plays a role in the citric acid cycle. All these amino acids are involved in protein synthesis, energy production and resistance to oxidative stress, thereby stimulating the metabolism of rhizobacteria to enhance plant growth under stressful environmental conditions (Fig. 2).

3.3 Distribution of compounds in biological pathways

This study investigated the distribution of compounds in the biological pathway produced by the three rhizobacterial strains. The highest compound values were found in high antioxidant and energy metabolism pathways, particularly osmoprotectants, protein biosynthesis, nitrogen assimilation, metabolic regulation and ROS scavenging. The highest compound values were for as osmoprotectants and ROS reduction, energy regulation, ion homeostasis, lignin biosynthesis, auxin synthesis, polyamine synthesis, and secondary metabolism (Fig. 3).

3.4 Adaptive responses of lettuce plants under drought stress

The application of rhizobacterial strains significantly influenced the survival and post-drought recovery of lettuce under water stress conditions (Fig. 4). Plants treated with RT3 gave the highest survival rate, followed by RT2, RK1 and the control (Fig. 4(c)). A similar trend was observed in fresh weight after rewatering, where RT2 gave the highest biomass, significantly greater than RT3, RK1 and the control (Fig. 4(d)). Overall, these synergistic effects explain the improved survival and fresh weight in drought-stressed lettuce, especially under RT2 treatment, and highlight the promising role of microbial inoculants in sustainable agriculture under changing climate conditions.

3.5 Potential role of bioactive compounds in enhancing plant defense mechanisms against stress

The data obtained from this study indicated that the compounds produced by strains RK1 and RT2 evaluated could affect various environmental stresses (Fig. 5). Proline and valine, in particular, were among the most effective, enhancing stress recovery, protein synthesis and energy production under abiotic stress conditions, such as drought and heat. Luteolin was an important contributor to antioxidant activity and

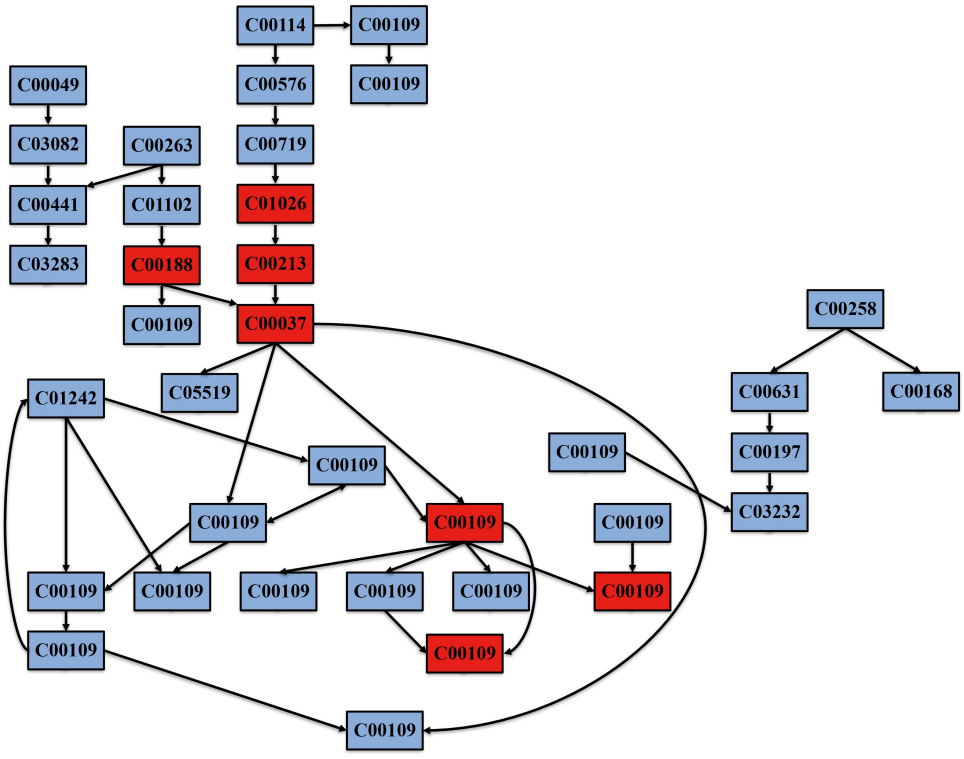


Fig. 2 Putative glycine, serine and threonine metabolic pathways based on compounds identified in bacterial isolates.

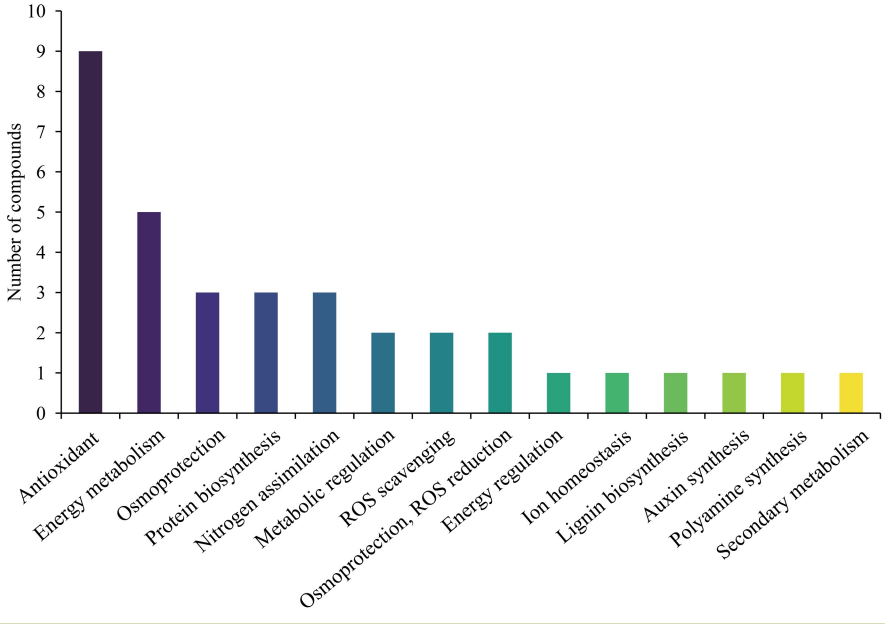


Fig. 3 Categorization of identified compounds from bacterial isolates based on their biological pathway associations.

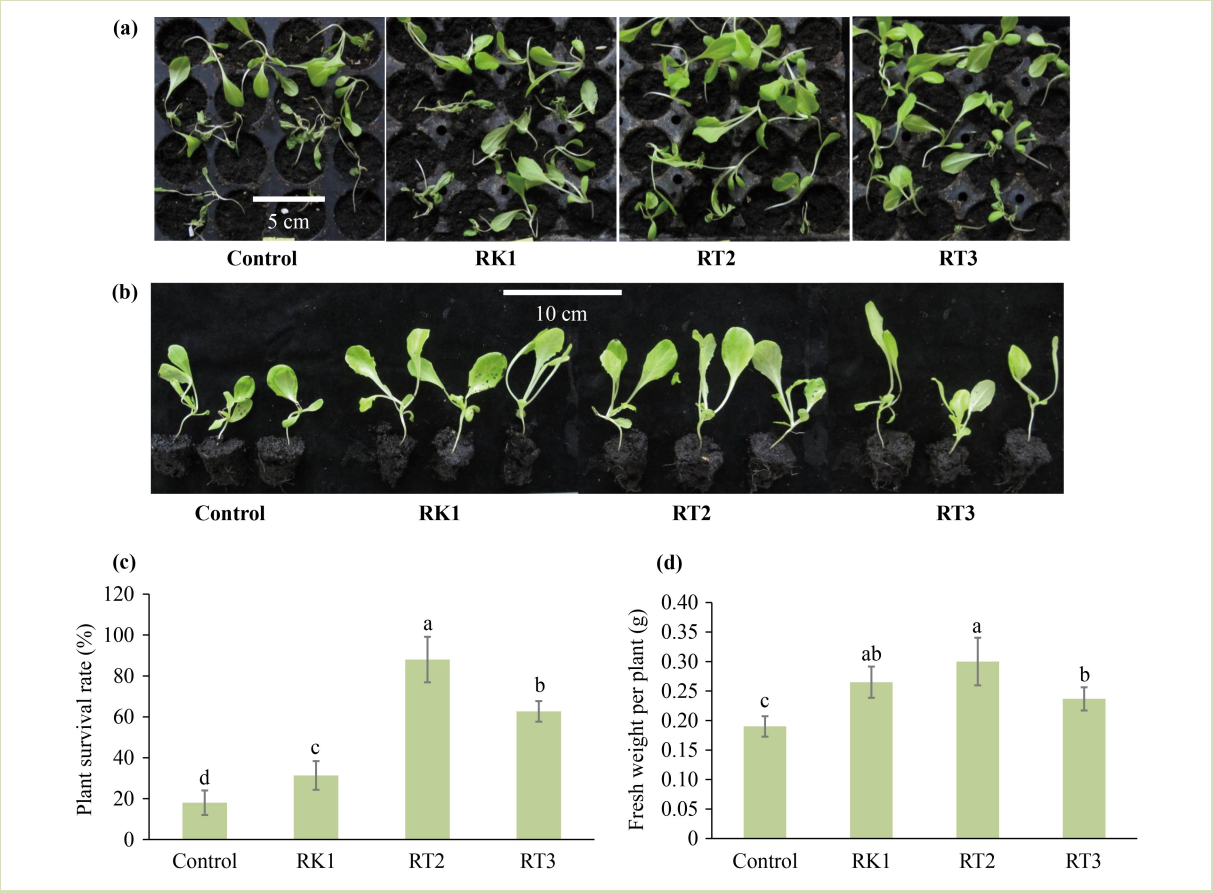


Fig. 4 Plant condition and biomass recovery of lettuce under drought stress. (a) Lettuce plants after 7 days of drought stress. (b) Lettuce plants after rewatering. (c) Survival rate following the drought period. (d) Fresh weight of plants measured after rewatering. Ten-day-old seedlings were treated with three bacterial strains, while control plants received an equal volume of water. One day after treatment, all plants were transferred to a 23 °C growth chamber. Different letters above the bars in (c) and (d) indicate statistically significant differences ($p < 0.05$).

reduction of oxidative damage. Pantothenic acid (vitamin B5) and riboflavin (vitamin B2) enhanced energy metabolism and antioxidant activity, further supporting stress tolerance. Biotin (vitamin B7) enhanced antioxidant responses and reduced ROS scavenging, which is essential for cellular integrity under oxidative stress. Compounds such as tryptophan, isoleucine and tyrosine enhanced nitrogen storage and stress recovery, thus aiding plant growth under nutrient-limited conditions (Fig. 5). Overall, compounds such as proline, valine, luteolin, and pantothenic acid were valuable in enhancing plant resistance, highlighting the potential of compounds derived from rhizobacteria in enhancing plant growth and survival under environmental stress.

3.6 Impact of stress conditions on metabolite concentrations

This study also showed its involvement in mitigating various abiotic stresses. It revealed that the compounds produced by the three strains were responsive to abiotic stress conditions, including drought, salinity, heat stress and oxidative stress (Figs. 6 and 7). Proline and glutamine showed high concentration levels under drought and salinity stress conditions, indicating their participation in osmotic regulation and nitrogen metabolism under water and salt stress conditions. In addition, under various abiotic stress conditions, three strains gave different responses. Figure 6 illustrated that strain RT2 had higher variability in compound concentrations

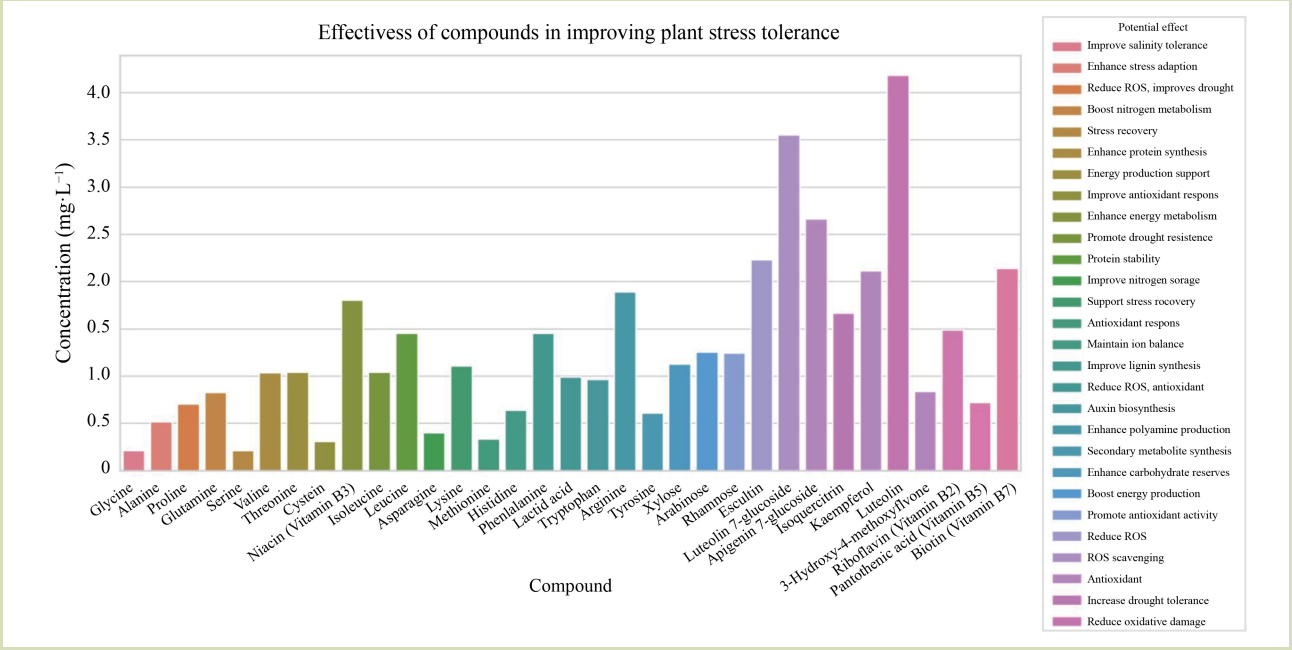


Fig. 5 Exploring the potential of bacterial strain-derived compounds to enhance plant tolerance to abiotic stress.

under oxidative stress conditions compared to strains RK1 and RT2. However, under general stress conditions including salinity and drought conditions, strain RT3 had a greater response than the other two strains. Under heat stress and nitrogen deficiency, data demonstrated that three strains had the same response to stress due to unfavorable conditions. These indicated that three rhizobacteria strains have different abilities in mitigating plant stress conditions. These findings agreed with previous work which showed that bacterial strains have different abilities in producing metabolite compounds involved in mitigating abiotic stress. This ability can affect its efficiency in increasing plant growth and plant resistance under unfavorable conditions.

4 Discussion

This study provides valuable insights into the role of rhizobacterial metabolites in mitigating abiotic stress in plants, with particular emphasis on their osmoprotective effects and contributions to cellular stability under adverse conditions. The diversity of metabolites produced by the rhizobacterial strains RK1, RT2, and RT3 underscores the potential for using these microorganisms to enhance plant resilience. Proline, glycine and glutamine were the main compounds produced by these rhizobacterial strains contributing to overcoming oxidative stress. Proline, a well-known osmoprotectant, was synthesized in large quantities by all strains. This compound has been shown to help plants manage osmotic stress by stabilizing proteins and cellular structures during periods of water deficit or salinity[19,26]. The accumulation of proline under drought and salinity stress in this study supports its role in osmotic adjustment, turgor recovery and protection against oxidative damage[27]. Glycine, another important amino acid, acts as a precursor for various metabolic processes, including protein synthesis, and also contributes to maintaining cellular osmotic balance under stress conditions[28]. In the context of saline environments, glycine has been shown to enhance stress tolerance by aiding in osmotic regulation and stabilizing cellular integrity[29].

Glutamine was also present in high concentrations and contributed significantly to plant stress adaptation, as it supports nitrogen metabolism and protein synthesis, both of which are critical during stress conditions. Its role in regulating cellular functions and aiding in the synthesis of essential molecules under stress conditions is consistent with findings of other studies[30,31]. The ability of these compounds to protect cellular structures from oxidative stress is further emphasized

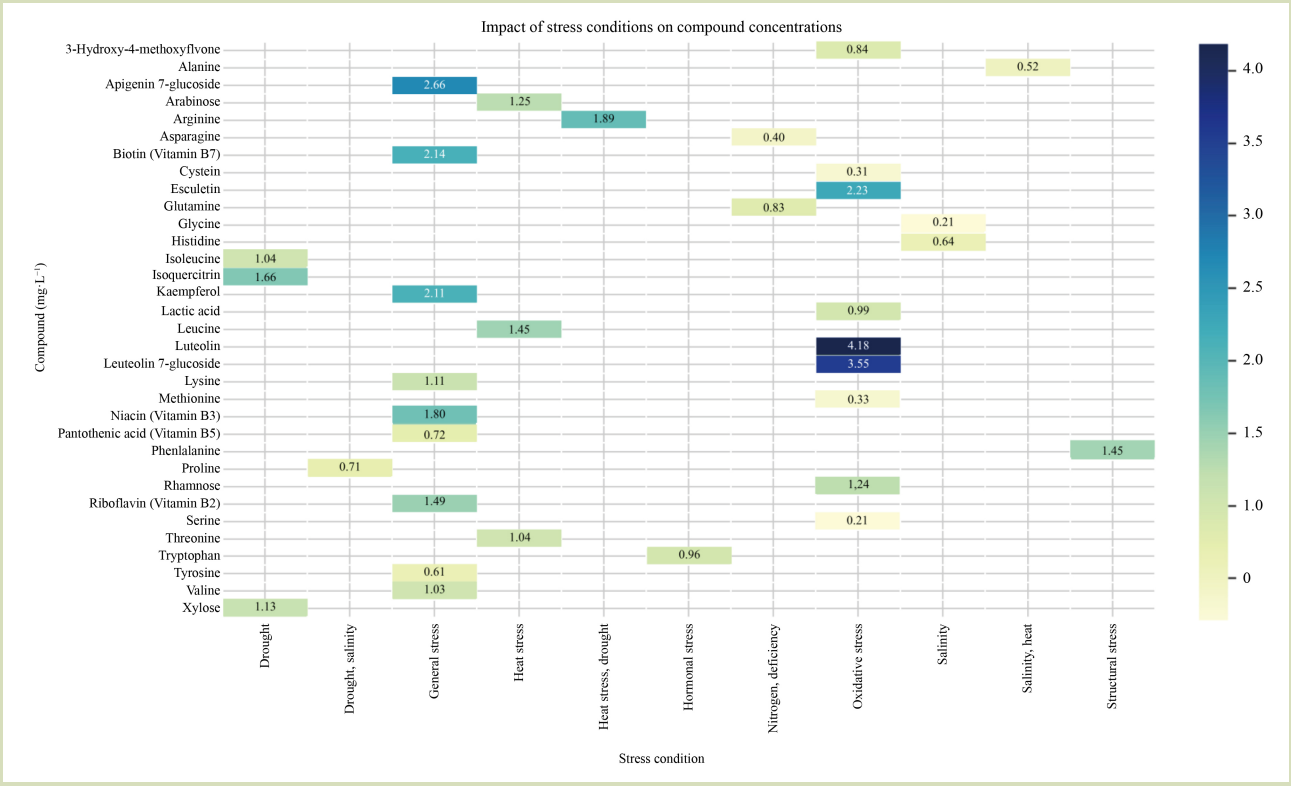


Fig. 6 Potential alterations in compound levels synthesized by bacterial strains under stress conditions.

by the high concentration of phenylalanine, an amino acid precursor involved in the production of phenolic compounds, which are important in oxidative stress responses[32]. Luteolin, a flavonoid compound, had protective activity under heat stress, consistent with other research showing its role in defending plants against UV radiation and extreme temperatures[33].

The study also identified the role of vitamins, such as pantothenic acid (vitamin B5) and riboflavin (vitamin B2), in supporting energy metabolism and antioxidant defenses in plants under stress conditions.

Notably, the study also highlighted the role of vitamins, such as pantothenic acid (vitamin B5) and riboflavin (vitamin B2), which support energy metabolism and antioxidant defenses in plants under stress conditions. Pantothenic acid, in particular, is involved in metabolic processes and stress responses, helping plants adapt to unfavorable conditions[34]. Riboflavin, also essential for coenzyme synthesis, enhances the overall metabolic efficiency of plants, especially during stress[35]. Biotin (vitamin B7), another essential vitamin, is critical for enzyme activation that is necessary for cellular function and stress resilience[36]. These findings further corroborate the idea that rhizobacterial metabolites can support plant stress tolerance by enhancing metabolic activity and reducing oxidative damage. Additionally, the accumulation of amino acids, such as alanine, isoleucine and tyrosine, under various abiotic stresses indicates that these compounds are essential for stress adaptation through protein synthesis and metabolic adjustments. Isoleucine and leucine, for example, contribute to the production of amino acids that help stabilize cell membranes and maintain protein function under water scarcity[37]. These amino acids also play a role in signaling pathways that regulate stress responses, highlighting their importance in plant survival during adverse environmental conditions[38].

The diversity of metabolic pathways observed in this study further underscores the complexity of the rhizobacterial role in plant stress mitigation. The pathways involved in amino acid synthesis, coenzyme production and antioxidant activity were

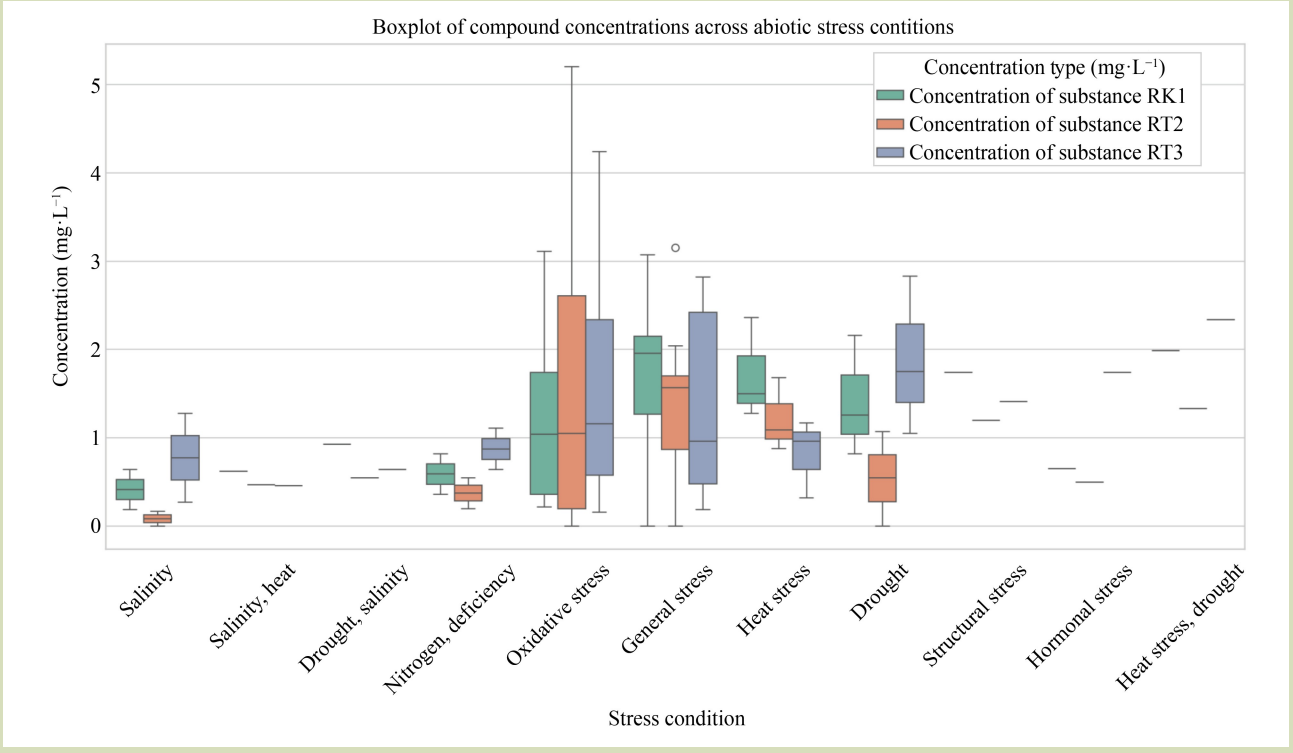


Fig. 7 Comparative boxplots of bioactive compound concentrations from bacterial strains under abiotic stress.

prominently represented, indicating their crucial roles in supporting plant cellular function and stability under stress. The high impact of compounds such as glycine, serine and threonine, which are involved in nucleic acid and protein synthesis, demonstrates the importance of nitrogen metabolism and protein stabilization in stress adaptation[39]. The involvement of tyrosine and phenylalanine metabolism in synthesizing phenolic compounds that provide antioxidant protection aligns with findings from other studies on the role of phenolics in plant stress tolerance[40]. The study also revealed how different rhizobacterial strains exhibited variable responses to stress conditions, reflecting the diverse capabilities of rhizobacteria in mitigating abiotic stress. For example, strain RT2 showed higher variability of compound concentrations under oxidative stress compared to RK1 and RT3. This finding highlights the potential for selecting specific bacterial strains based on the type of stress encountered by plants, thereby optimizing the use of rhizobacterial inoculants for improving plant resilience. Similarly, strain RT3 exhibited a stronger response to drought and salinity stress, suggesting that specific strains may be more effective under different environmental conditions. These findings are consistent with previous research showing that bacterial strains vary in their capacity to produce metabolites that alleviate stress[40].

Overall, the compounds produced by these rhizobacterial strains demonstrate their potential for enhancing plant growth and stress tolerance in agricultural systems. Their ability to mitigate oxidative stress, stabilize cellular structures and improve metabolic efficiency makes them valuable tools for promoting plant health, particularly in environments characterized by abiotic stresses such as drought, salinity, heat and oxidative damage. By exploiting the metabolic potential of these rhizobacteria, it may be possible to develop more sustainable agricultural practices that can improve crop productivity and resilience in the face of changing environmental conditions.

5 Conclusions

The outcome of the investigation provides evidence that PGPRs produced a number of metabolites acting as osmoprotectants that may ameliorate plant resilience under

abiotic stresses. These compounds from the isolated bacteria are recognized as having important osmoprotective activity to mitigate abiotic stresses. Proline, glutamine, phenylalanine, luteolin and pantothenic acid, identified as inducing resistance to drought, salinity and heat stresses, are particularly notable as they enhance plant resilience under stress conditions. These compounds contribute to stabilizing cellular structures, minimize oxidative damage and assist in maintaining metabolic functionality to increase stress tolerance. The metabolic pathways associated with the biosynthesis of amino acid, energy metabolism and antioxidant defense, help in plant growth and survival during stress conditions. Such findings show that compounds from rhizobacteria could contribute to improving stress tolerance, which is important for future prospects in sustainable agriculture and crop protection against abiotic stress conditions.

Compliance with ethics guidelines

Erfan Dani Septia, Nur Izzatul Maulidah, and Andi Kurniawan declare that they have no conflicts of interest or financial conflicts to disclose. This article does not contain any studies with human or animal subjects performed by any of the authors.

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