Nutritional content analysis of plant growth-promoting rhizobacteria species

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ABSTRACT

Agricultural production requires the continuous application of mineral fertilizers, which not only disrupt the natural balance but also reduce economic efficiency. The objective of this study was to understand the effects of plant growth-promoting rhizobacteria (PGPR) species (Bacillus megaterium M3, Bacillus subtilis OSU142, Bacillus pumilus C26, Paenibacillus polymyxa RC05, Azospirillum brasilense sp245, Burkholderia cepacia OSU7, B. cepacia OSU7 AMP Res and Raoultella terrigena TFI08) on their host plants. The maximum levels of arginine, histidine, tartaric acid, citric acid, and gibberellic acid were observed in B. megaterium M3 with maximum levels of glycine and threonine in B. subtilis OSU142, maximum lysine and lactic acid levels in R. terrigena TFI08 and maximum asparagine, serine, and asbiscic acid levels in A. brasilense sp245. The highest Ca and P concentrations were observed in B. megaterium M3, while high concentrations of K, S, Na, Mn, Cd, and Ni were obtained from A. brasilense sp245. These data suggest that the B. megaterium M3, A. brasilense sp245, and R. terrigena TFI08 strains have the potential to be used as organic fertilizers to facilitate plant growth in sustainable and organic farming.

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1. Introduction

Plant Growth-Promoting Rhizobacteria (PGPR) is free-living microorganisms that exert beneficial effects on plants by colonizing their rhizospheres or phyllospheres [1]. PGPRs can improve plant growth and yield directly and indirectly. Direct mechanisms include the following: 1) releasing plant growth regulators such as auxins, cytokinins, and gibberellins, 2) lowering ethylene in plants, 3) solubilizing inorganic phosphate, 4) mineralizing organic phosphate, 5) Asymbiotic fixation of atmospheric nitrogen, 6) producing organic matter, including amino acids, 7) releasing enzymes and 8) stimulating disease-resistance mechanisms (systemic acquired or induced resistance) [1,2]. As an indirect mechanism, PGPR may have an antagonistic effect against phytopathogenic microorganisms and act as biocontrol agents, controlling plant disease-causing organisms, stimulating beneficial symbioses, and/or protecting the plant by degrading xenobiotics in contaminated soils [3]. Additionally, PGPR alleviate drought, cold, high salinity, and metal toxicity stresses [1–5].

Many PGPR produce phytohormones that enhance root growth and surface area. Phytohormones consist of auxins (IAA), cytokinins and gibberellins produced by natural soil microbial communities [6]. However, hormone and organic acid contributions from PGPR have not been determined, and their involvement in promoting plant growth is speculative. Therefore, PGPR have been formulated for use in agriculture, on the scale of fermentation microorganisms, with management of the quality and effectiveness of the product [7]. To ensure survival and activity of PGPR in the field, seeds have been inoculated with PGPR, or PGPR have been applied as a powder or liquid.

Intensive farming practices, which warrant high yield and quality, require the extensive use of chemical fertilizers, which are costly and create environmental problems. Therefore, there has been a recent resurgence of interest in environmentally friendly, sustainable and organic agricultural practices. This system avoids or largely excludes the use of synthetic fertilizers, pesticides, growth regulators and livestock feed additives. Environmentally friendly organic agricultural systems depend heavily on bio-fertilization, green manure, farm manure, crop rotation, legumes, mineral-bearing rocks, and aspects of biological pest control to sustain soil productivity. However, yield reduction is a serious problem in the organic production system [8]. The use of organic fertilizers containing sewage sludge, seaweed, and lichen is known...
to improve plant growth and help sustain environmental health and soil productivity [9,10]. Crops, vegetables and fruits are reliably produced using organic fertilizer sources if enough nutrients are available. To our knowledge, no study has previously investigated the chemical composition of PGPR exudates. Therefore, in the present study, our objectives were to understand how PGPR act on their host plant and to evaluate various chemical properties of PGPR strains as a nutrient source for sustainable and organic agriculture.

2. Materials and methods

2.1. Bacterial strains

PGPR strains (Bacillus megaterium M3, Bacillus subtilis OSU142, Bacillus pumilus C26, Paenibacillus polymyxa RC05, Azospirillum brasilense sp245, Burkholderia cepacia OSU7, B. cepacia OSU7 AMP Res., and Raoultella terrigena TFi08) were obtained from the culture collection in the Department of Genetics and Bioengineering, Faculty of Engineering and Architecture at Yeditepe University, Istanbul, Turkey. These bacteria were previously reported to have plant growth-promoting characteristics and to be potential biocontrol agents against a wide range of bacterial and fungal pathogens that cause economically important crop losses in agriculture [11–15]. The bacterial strains used in this study were identified using the Sherlock Microbial Identification System version 6.0 (MIDI, Newark, DE).

2.2. Bacterial growth and laboratory experiment

Pure bacterial cultures were grown on National Botanical Research Institute Phosphate (NBRIP) growth medium [16]. The bacterial culture suspensions were kept in a nutrient broth with 15% glycerol at –80 °C for long-term storage. For these experiments, a single colony was transferred to a 500 mL flask containing NBRIP and grown aerobically on a rotating shaker (Merck KGaA, Darmstadt, Germany) for 48 h at 27 °C and 150 rpm. The culture was diluted to a final concentration of 108 colony forming units (CFU) mL⁻¹ using sterile distilled water containing 0.025% Tween 20. Twenty-five samples of PGPR bacterial suspensions in replicate were used to determine the organic acid, amino acid, hormone, and nutrient contents, along with enzyme activity.

2.3. Amino acids analysis

For the amino acid analysis, 5 mL of 0.1 N HCl was added to 5 mL bacterial culture suspensions. The cultures were homogenized and dispersed using an IKA Ultra Turrax D125 Basic homogenizer and incubated at 40 °C for 12 h. Then, the homogenized bacterial culture suspensions were vortexed. After these bacterial suspensions were centrifuged at 1200 rpm for 50 min, the supernatants were filtered through a 0.22 μm pore Millex Millipore filter. The supernatants were subjected to HPLC analysis using a Zorbax Eclipse-AAA 4.6 × 250 mm, 5 μm column (Agilent 1200 HPLC), and the absorbance at 220 nm was read using a UV detector. The flow speed was 1 mL min⁻¹, and the column temperature was 250 °C. The organic acid contents of the bacterial suspensions, including oxalic and propionic acids, were determined using 25 mM potassium phosphate pH 2.5 as the mobile phase.

2.4. Organic acid analysis

For the analysis of organic acids, 10 mL of deionized water was added to 5 mL bacterial culture suspensions, which were homogenized using an IKA Ultra Turrax D125 Basic homogenizer. After centrifugation at 1200 rpm for 50 min, the supernatants were filtered through a 0.22 μm pore Millex Millipore filter and collected in vials. The supernatants were subjected to HPLC analysis using a Zorbax Eclipse-AAA 4.6 × 250 mm, 5 μm column (Agilent 1200 HPLC), and the absorbance at 220 nm was read using a UV detector. The flow speed was 1 mL min⁻¹, and the column temperature was 250 °C. The organic acid contents of the bacterial suspensions, including oxalic and propionic acids, were determined using 25 mM potassium phosphate pH 2.5 as the mobile phase.

2.5. Hormone analysis

The extraction and purification processes were executed as described [18]. For hormone analysis, 5 mL of cold (–400 °C) 80% methanol was added to 5 mL bacterial culture suspensions. The bacterial suspensions were homogenized for 10 min using an IKA Ultra Turrax D125 Basic homogenizer, and then the bacterial suspensions were incubated for 24 h in the dark. The bacterial suspensions were filtered using a Whatman No: 1 filter, and the supernatants were filtered again using a 0.45 μm pore filter. The hormones were analyzed by HPLC using a Zorbax Eclipse-AAA C-18 column (Agilent 1200 HPLC), and the absorbance was read at 265 nm using a UV detector. Gibberellic acid, salicylic acid, indole acetic acid (IAA), and abscisic acid (ABA) were determined using 13% acetonitrile (pH 4.98) as the mobile phase.

2.6. Enzyme activities of PGPR

Phosphatase activity was determined using para-nitrophenyl phosphate (pNPP) as an ortho-phosphate monoester analog substrate [19]. We calculated the p-nitrophenol content using a calibration curve obtained with standards containing 0, 10, 20, 30, 40 and 50 ppm of p-nitrophenol.

2.7. Antioxidant enzymes analysis of PGPR

For antioxidant enzyme assays, frozen cell samples were ground to a fine powder with liquid nitrogen and extracted with ice-cold 0.1 mM phosphate buffer, pH 7.8, containing 1 mM ethylenediaminetetraacetic acid (EDTA), 1 mM phenylmethanesulfonylfluoride (PMSF) and 0.5% polyvinylpyrrolidone (PVP). The superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT) enzyme activities in the apoplastic fractions were measured using a spectrophotometer [20].

2.8. Element analysis

The Kjeldahl method and a Vapodest 10 Rapid Kjeldahl Distillation Unit (Gerhardt, Königswinter, Germany) were used to determine the total N content [21] of PGPR strains. The Ca, Mg, Na, K, P, S, Fe, Cu, Mn, Zn, Pb, Ni and Cd contents were determined using an Inductively Coupled Plasma spectrometer (Perkin–Elmer, Optima 2100 DV, ICP/OES, Shelton, CT 06484-4794, USA) [22].

2.9. Statistical analysis

Data were sorted by PGPR species, and differences among species were identified using the Duncan test option in the analysis of variance [23]. Differences were considered significant at P < 0.05.

3. Results

3.1. Amino acids and organic acids produced from PGPR

B. megaterium M3 had the highest glutamate (26,814 pmol μl⁻¹), isoleucine (25,562 pmol μl⁻¹), arginine (35,727 pmol μl⁻¹),
Fig. 1. Amino acid content of some studied PGPR species (mean ± standard deviation). Different letters within a PGPR species indicate that they are significantly different at $P \leq 0.05$. 
histidine (25,172 pmol μl⁻¹), tryptophan (14,871 pmol μl⁻¹),
cysteine (12,290 pmol μl⁻¹), proline (8604 pmol μl⁻¹), alanine
(7416 pmol μl⁻¹), methionine (4337 pmol μl⁻¹), and glutamine
(1723 pmol μl⁻¹) levels, whereas B. cepacia OSU7 had the lowest
levels of these amino acids. Conversely, the lysine
(36,996 pmol μl⁻¹), valine (6323 pmol μl⁻¹), and leucine
(2124 pmol μl⁻¹) levels were the highest in R. terrigena TFi08. The
sarcosine (20,058 pmol μl⁻¹), asparagine (3345 pmol μl⁻¹), tyrosine
(4432 pmol μl⁻¹), serine (1971 pmol μl⁻¹), and aspartate
(2155 pmol μl⁻¹) levels were the highest in A. brasilense sp245,
while the glycine (5025 pmol μl⁻¹), threonine (5737 pmol μl⁻¹),
phenylalanine (13,331 pmol μl⁻¹), and hydroxyproline
(1243 pmol μl⁻¹) levels were the highest in B. subtilis OSU142
(Fig. 1).

The maximum oxalic (1313 ng μl⁻¹), propionic (2284 ng μl⁻¹),
and succinic (85,878 ng μl⁻¹) acid levels were observed in
P. polymyxa RC05. The maximum tartaric (2996 ng μl⁻¹), citric
(12,776 ng μl⁻¹), and maleic (6715 ng μl⁻¹) acid levels were observed
in B. megaterium M3. The maximum fumaric acid
(1247 ng μl⁻¹) levels were identified in A. brasilense sp245, while
the maximum malic (4526 ng μl⁻¹), malonic (29,547 ng μl⁻¹), and
lactic (125,788 ng μl⁻¹) acid levels were identified in R. terrigena
TFi08. B. cepacia OSU7 AMP Res. displayed the maximum levels of
butyric acid (20,293 ng μl⁻¹) (Fig. 2).
3.2. Hormone and nutrient content of PGPR

In this study, the hormone contents of different PGPR species were examined. The highest gibberellic acid (6388 ng μl⁻¹), salicylic acid (4548 ng μl⁻¹), and IAA (1116 ng μl⁻¹) levels were obtained from B. megaterium M3, while the highest levels of ABA (1220 ng μl⁻¹) were detected in A. brasilense sp245. The lowest gibberellic acid (1056 ng μl⁻¹) and salicylic acid (905 ng μl⁻¹) levels were observed in B. pumilus C26, and the lowest IAA (105.8 ng μl⁻¹) and ABA (8.50 ng μl⁻¹) levels were detected in B. subtilis OSU142 (Fig. 3).

The levels of minerals important for plant nutrition are presented in Table 1. B. megaterium M3 had the highest concentration of Ca (119.4 mg kg⁻¹) and P (814 mg kg⁻¹), followed by B. cepacia OSU7 (73.22 mg kg⁻¹) and B. pumilus C26 (35.37 mg kg⁻¹). B. subtilis OSU142 had the highest N content (15,870 mg kg⁻¹). The richest sources of K, S, and Na were found in A. brasilense sp245 (664 mg kg⁻¹, 754 mg kg⁻¹, and 8755 mg kg⁻¹, respectively), followed by B. cepacia OSU7 (635 mg kg⁻¹, 698 mg kg⁻¹, and 8248 mg kg⁻¹, respectively). B. cepacia OSU7 had the highest concentration of Mg (24.48 mg kg⁻¹), followed by A. brasilense sp245 (21.66 mg kg⁻¹). The lowest Ca, P, K, S, Mg and Na levels were observed in B. subtilis OSU142 (4.55 mg kg⁻¹, 48 mg kg⁻¹, 87 mg kg⁻¹, 158 mg kg⁻¹, 3.08 mg kg⁻¹, and 1251 mg kg⁻¹, respectively).

There were statistically significant differences in the total microelement concentration between PGPR species (Table 2). B. cepacia OSU7 had the highest total Fe content (10.91 mg kg⁻¹). The Cu levels were highest in R. terrigena TFi08 (5.38 mg kg⁻¹), while B. cepacia OSU7 AMP Res showed the highest levels of Zn (30.14 mg kg⁻¹). P. polymyxa RC05 had the highest levels of B (167 mg kg⁻¹), Cr (0.083 mg kg⁻¹), Pb (0.13 mg kg⁻¹) and Al (5.79 mg kg⁻¹), while A. brasilense sp245 displayed the highest levels of Mn (0.53 mg kg⁻¹), Cd (0.032 mg kg⁻¹), and Ni (0.042 mg kg⁻¹) (Table 2).

3.3. Enzyme activity of PGPR

The highest SOD (250 EU g⁻¹), POD (27,890 EU g⁻¹), and CAT (45 EU g⁻¹) activities were observed in R. terrigena TFi08 (Fig. 4), while B. pumilus C26 displayed the lowest activities.

B. subtilis OSU142 displayed the highest alkaline phosphatase (ALPE; 1589 μg TPF g⁻¹) and acid phosphatase (APE; 774 μg TPF g⁻¹) activities (Fig. 5).

4. Discussion

4.1. Amino acids and organic acids produced from PGPR on plant growth

In this study, the B. megaterium M3, A. brasilense sp245, and R. terrigena TFi08 strains showed high levels of amino and organic acid content. A considerable number of fertilizer sources, mostly those associated with hormonal, organic or amino acid contents, promote plant growth. These ingredients render insoluble forms of plant nutrients into soluble forms through acidification, chelation and exchange reactions. These processes compensate for the higher cost of manufacturing fertilizers in industry and mobilize the fertilizers added to soil. Organic fertilizer, especially low grade, has received great attention as a source of PGPR and for use in...
Natural organic foliar fertilizer is an effective method for feeding plants in soil that is deficient or contains unavailable forms of nutrients because plants absorb nutrients through their roots and foliage. Because macronutrients are required in very high amounts, their supply through foliage is impractical. However, when soil conditions are unfavorable, such as when macronutrient and micronutrients are fixated and/or leaching, it may be desirable to utilize foliar applications of plant nutrients. These results are in accordance with the results obtained by Deelip et al. [24], who found that alanine, tyrosine, arginine, lysine, and succinic acid were produced by PGPR play a vital role in plant growth and nutrition, leading to healthy plants, an important aspect in increasing crop yields and nutrient uptake [26] (Bloemberg et al., 2001). Sayyed et al. [27] found that methionine, isoleucine, tyrosine and proline produced by A. faecalis enhanced plant sidereophore production, while Deelip and Deelipkumar [24] found that alanine, tyrosine, arginine, lysine and succinic acid produced by P. fluorescens NCIM 5096 and P. putida NCIM 2847, and A. faecalis [25]. These products produced by PGPR play a vital role in plant growth and nutrition, leading to healthy plants, an important aspect in increasing crop yield, and to efficient nutrient uptake [26] (Bloemberg et al., 2001).}

### 4.2. Hormone and nutrient content of PGPR on plant nutrition

Our results showed that the highest gibberellic acid, salicylic acid and IAA levels were obtained from B. megaterium M3, but ABA was highest in A. brasilense sp245 (Fig. 3). The direct mechanisms by which PGPR facilitate plant growth include the production of plant growth regulators or phytohormones [27]. The production of phytohormones such as auxins (IAA), cytokinins and gibberellins by natural soil microbial communities has been reported by various sources over the past 20 years [31,32].

Recent investigations revealed that PGPR can promote plant growth by producing ACC deaminase, which reduces ethylene levels in the roots of developing plants [33], and by producing plant growth regulators such as indole acetic acid (IAA) [34], gibberellic acid [35], and cytokinins [36]. Several studies have shown that many soil bacteria in general, and PGPR in particular, can produce cytokinins, gibberellins or both [37]. For example, cytokinins have been detected in the cell-free medium of some strains of Azotobacter spp., Rhizobium spp., Pantoea agglomerans, Rhodospirillum rubrum, P. fluorescens, B. subtilis and P. polymyxa. However, plant growth promotion by some cytokinin- or gibberellin-producing PGPR has been reported [38]. Similarly, Swain et al. [39] reported that IAA producing strains of B. subtilis a positive effect on Dioscorea rotundata. A suspension of B. subtilis was applied on the surface of the plant, which resulted in an increase in the root: stem ratio and the number of sprouts compared with the non-inoculated plants. The potential for Azotobacter spp., to produce a high amount of IAA in agriculture was reported by Ahmad et al. [40].
Indole-3-acetic acid, a main auxin in plants, is known to control many important physiological processes, such as cell enlargement, cell division, root initiation, the growth rate, phototropism, geotropisms, and apical dominance [41]. In plant cells, IAA is largely formed by de-novo synthesis from tryptophan that undergoes either oxidative deamination or decarboxylation with indole-3-acetic aldehyde as an intermediate. Indole-3-acetic acid (IAA) controls a wide variety of processes in plant development, including many of the important physiological processes of plants, such as cell enlargement, cell division, root initiation, growth rate, phototropism, geotropisms, and apical dominance. IAA also plays a key role in shaping plant root architecture through the regulation of lateral root initiation, root vascular tissue differentiation, polar root hair positioning, root meristem maintenance and root gravitropism [29]. The production of IAA is widespread among rhizobacteria, with increasing numbers of endophytic IAA-producing PGPR being reported [42].

Environmental stresses such as salinity, alkalinity, acidity, osmotic and matrix stress, and carbon starvation affect auxin biosynthesis in bacteria. Bacterial IAA causes increased lateral and adventitious rooting, leading to improved mineral and nutrient uptake and root exudation [43–45].

Cytokinins stimulate plant cell division, control root meristem differentiation, and inhibit primary root elongation and lateral root formation but can also promote root hair development [46]. Cytokinin production has been reported in various PGPRs, including Arthrobacter spp., Azospirillum spp., P. fluorescens, and P. polymyxa [47,48]. The cytokinin receptors play a complimentary role in plant growth promotion due to B. megaterium [36]. Gibberellins enhance

Fig. 4. Antioxidant enzyme activity of some studied PGPR species (mean ± standard deviation). Different letters within a PGPR species indicate that they are significantly different at $P \leq 0.05$. 

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the development of plant tissues, particularly stem tissue, and promote root elongation and lateral root extension [49]. The production of gibberellins has been documented in several PGPR, including Azospirillum spp., Azotobacter spp., \textit{B. pumilus}, \textit{Bacillus licheniformis}, \textit{Herbaspirillum seropedicae}, \textit{Glucanobacter diazotrophicus} and rhizobia [50].

Sweet potato cultivars inoculated with PGPR strains that are capable of IAA production exhibited significantly increased plant growth as the result of enhanced N, P, K, Ca and Mg uptake [51]. Most of the PGPR strains analyzed in the present study were found to contain significant quantities of a variety of essential nutrients. The highest P, K, S, and Na contents were present in \textit{A. brasilense} sp245, but Ca was highest in \textit{B. pumilus} C26. These data suggest that some of the PGPR strains tested have a high nutritional potential, and their mineral content is higher than some organic fertilizer sources.
Acetic, glycolic, malonic, oxalic, and formic acids play a crucial role in the acquisition of P, Fe and Mn by plants growing in low-nutrient soils. The release of these acids in response to nutrient starvation differs between plant species [52,53]. The concentrations of fumaric, malic and citric acids can also chelate Fe and Mn in iron and manganese oxides (i.e., Fe$_2$O$_3$ and MnO$_2$), thus making them available for uptake by the plant [54]. Similarly, these acid anions form complexes with Ca, Al and Fe present in the soil as insoluble phosphates of calcium, iron and aluminium and liberate P for uptake by the roots [55]. Additionally, these acids can desorb P from sesquioxide surfaces by anion exchange [56,57] and maintain sulfate mobility in rhizosphere soil through competitive displacement from adsorption sites [58].

4.3. The enzyme activity of PGPR on plant growth under stress conditions

Our data showed that the SOD, POD and CAT contents of R. terrigena TF108 were higher than the other PGPR species tested in this study. Antioxidant enzyme activities have been reported to increase under cold, saline, high light and soil pollution conditions in the case of cucumber seedlings [59]. PGPR application may also assist growth by alleviating the negative effects of cold stress by promoting the accumulation of antioxidant enzyme activities and decreasing reactive oxidative oxygen species (ROS) such as H$_2$O$_2$, O$_2$ and OH in response to cold stress [60].

P-Solubilizing PGPR strain applications also altered the ALPE and APE concentrations of soil. The highest ALPE and APE activities were obtained from soil with B. megaterium M3 (Fig. 5). ALPE and APE are involved in the transformation of organic and inorganic compounds in soil. An increase of phosphatase activity can improve the P nutrient status of the soil. Mineralization of soil organic P (Po) plays an important role in the phosphorus cycling of a farming system. Alkaline and APE use organic phosphate as a substrate and convert it into an inorganic form. The principal mechanism for the mineralization of soil organic P is the production of acid phosphatases [61]. The release of organic anions and the production of siderophores and acid phosphatase by plant roots/microbes or alkaline phosphatase [62] enzymes hydrolizes the soil organic P or splits P from organic residues.

5. Conclusions

The present study reveals that the tested PGPR species were rich in organic acids, amino acids, hormones and nutrients. In agreement with other reports, the data suggest that the bio-inoculation of PGPR strains can improve growth, nutrient uptake, and the nutritional quality, as shown for barley [63], pearl millet and black gram [64]. The potential to improve plant yields by combining PGPR by co-inoculation has been the subject of several studies for more than a decade [65,66]. Seed inoculation with A. brasilense, B. subtilis OSU142 and B. megaterium M3 strains alone or under dual inoculation increased plant growth as determined by shoot or root length and increased the nutrient uptake in plants. In general, the microbial inoculation of seeds with B. subtilis OSU142 and A. brasilense sp245 alone or in mixed inoculation with B. megaterium M3 may be used in organic and sustainable agriculture crop production as a substitute for costly mineral fertilizers. Seed inoculation with Azospirillium and Bacillus species is widely used in organic production systems because they are important N$_2$-fixing, P-solubilizing, and phytohormone-producing microorganisms, resulting in improved crop growth and yield [67]. In Turkey, the most commonly reported PGPR are B. subtilis OSU142 and B. megaterium M3, which have a range of reported properties including N$_2$-fixation, P-solubilization, IAA and cytokinin production, and increased root and shoot growth and crop yield [63].

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