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Research Article

Plant Growth-Promoting Rhizobacteria (PGPR) Reduce Adverse Effects of Salinity and Drought Stresses by Regulating Nutritional Profile of Barley

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With the growing emphasis on sustainable agriculture, food security, and environmental protection, the use of beneficial soil microbes is imperative, as the use of chemicals such as fertilizers, pesticides, and herbicides has resulted in food contamination, disease, weed resistance, and negative environmental consequences, which ultimately impacted human health. Climate change is a major factor and is of great concern for crop production. Abiotic stresses, including salt and drought stress, restrain the crop yield. The aim of this particular study is to understand what role do plant growth-promoting rhizobacteria (PGPR) play in combating the salinity and drought stresses through modification of nutritional profile. In the current study, inoculated barley (*Hordeum vulgare* L.) plants were subjected to various stresses such as 200 mM and 1000 mM salinity stress as well as drought stress, and then their various parameters such as seed germination as well as shoot and root biomasses and photosynthetic activity were compared with non-treated stressed barley plants. Our data depicted an improvement or significant enhancement of these parameters in PGPR (*Pseudomonas fluorescens* SBW25 and *Pseudomonas putida* KT2440) applied barley plants. Furthermore, the particle-induced X-ray emission (PIXE) technique was used for the elemental analysis of PGPR-inoculated and non-inoculated plants under stress vs. no stress conditions. Our PIXE analysis of various macro- and micronutrients revealed an enhancement of Ca, Mg, K, P, S, Al, and Si uptake in PGPR-treated plants. PGPR applications depicted reduced Cl^- contents in 200 mM salt-stressed barley roots (KT2440 = 7.7 mg/kg and SBW25 = 6.3 mg/kg) and stems (KT2440 = 406.4 mg/kg and SBW25 = 365.5 mg/kg) as compared to controls (roots = 8.9 and stems = 469.5), while they displayed a significant increase in the barley leaves (KT2440 = 405 mg/kg and SBW25 = 416.4 mg/kg) when compared to control (110.6 mg/kg) under the same stress condition. In 1000 mM salt stress, a significant reduction in the Cl^- content was observed in PGPR-applied barley roots (KT2440 = 7.6 mg/kg), stems (KT2440 = 1205.8 mg/kg and SBW25 = 1008.3 mg/kg), and leaves (KT2440 = 967.8 mg/kg and SBW25 = 530.8 mg/kg) when compared to controls (roots = 15.2 mg/kg, stems = 1605.2 mg/kg, and leaves = 1165.2 mg/kg). On the other hand, a significant increase in the Cl^- content was noticed in PGPR-applied barley roots (KT2440 = 29.5 mg/kg and SBW25 = 25.8 mg/kg), stems (KT2440 = 1023.8 mg/kg and SBW25 = 894.9 mg/kg), and leaves (KT2440 = 369.2 mg/kg and SBW25 = 409.8 mg/kg) when compared to controls (roots = 13.5 mg/kg, stems = 505.3 mg/kg, and leaves = 219.9 mg/kg) under drought stress condition. PGPR application was also found to be effective for enhancing the uptake of micronutrients (Mn, Fe, Co, Ni, Cu, and Zn) in barley plant parts under control and also under stressed conditions. Overall, our findings revealed an improvement in the uptake of macro- and micronutrients for the enhancement of salinity and drought stress tolerance. Conclusively, these PGPR species are an effective source of plant stress tolerance and elevated growth of barley and related plants under stress conditions.

1. Introduction

According to the United Nations' World Population Prospects, the world population is continuously rising at an alarming rate of 74 million people/year and is thought to reach around 9.7 billion in 2050 and more than 65% of people would solely rely on agriculture, so to ensure their survival, food security would be a big challenge (https://www.un.org/esa/population/unpop.htm). Almost all of this growth increase is expected to occur in developing countries [1]. Similarly, urbanization is also expected to continue at an accelerating pace, and in 2050, it would account for 70% of the world population, while on the other hand, rural population would decline at the same pace. This would be a major concern for developing countries where food insecurity is a major issue due to population increase, poverty, rapid industrialization, debt burden, and political instability. In addition to these, many other factors decrease crop productivity further. The most important of these factors are the ever-escalating negative effects of various environmental stress factors [2]. Plant stresses are usually divided into biotic and abiotic stresses. Abiotic stresses such as salinity, drought, water logging, mineral toxicity, and extreme temperatures severely affect seed quality, growth, development, and yield of crop and other plants [3]. There is quite similarity in the genetic, molecular, biochemical, and physiological effects of both salinity and drought stresses [4]. Both of these affect the nutrient uptake in plants through impacting their availability, assimilation, and transport in the plants [5]. Proper nutrition is the basic need of life. The nutrients required in large amounts by plants are known as major or macronutrients and these are C, H, O, N, P, S, Ca, Mg, and K. Micronutrients are required in small amount and these are Cu, Zn, Mn, Fe, Cl, Ni, B, and Mo [6]. Deficiency of essential nutrients is one of the major causes reducing plant growth and productivity [7, 8]. Nutrients of plants not only play a role in the growth and development of plants but also assist in coping with various abiotic and biotic stresses. Provision of mineral nutrients to plants plays an essential role in improving their tolerance potential against various environmental stresses, i.e., drought, salinity, temperature, and disease. Therefore, it is necessary to find a strategy for improving crop tolerance against salinity and drought stresses through enhancement of nutrient uptake.

One of the strategies adopted for enhancing the mineral nutrients in plants under stress includes the use of various chemical fertilizers which play an important role in enhancing the global agricultural production. Excessive and indiscriminate use of these chemicals such as fertilizers, pesticides, and herbicides enhances the accumulation of toxic compounds in soil that are absorbed by several crops. Various acid radicals, such as H_2SO_4 and HCl, are found in most of the synthetic fertilizers that increase the soil acidity and adversely affect plant health. In addition, some plants also absorb recalcitrant compounds and the continuous consumption of such crops can cause systemic disorders in human beings. A large number of herbicides and pesticides have carcinogenicity potential [9]. Hence, for sustainable agriculture, there is a need of some alternative technologies for improving both the quality and quantity of crops without jeopardizing human health. One of the effective, safe, and reliable alternate strategies is the use of environmentally friendly microbial inoculants. They contribute in enhancing agronomic efficiency by reducing production costs and environmental pollution. Plant growth-promoting rhizobacteria (PGPR) are naturally occurring soil bacteria inhabiting the rhizosphere [10]. They act as biofertilizers, biocontrol, biopesticides, and bioherbicide agents. *Bacillus, Pseudomonas*, *Rhizobium*, *Bradyrhizobium*, and *Azospirillum* are some of the examples of PGPR [11, 12]. Rhizobacteria are beneficial and important for having plant growth-promoting ability, and this growth improvement is because of certain traits of the PGPR. PGPR make use of various mechanisms under various conditions for plant growth improvement. They usually promote plant growth and alleviate salinity and drought stress damage through absorbing nutrients either by fixing atmospheric nitrogen or by direct uptake of various macro- and micronutrients such a phosphorus, potassium, zinc, and iron [13, 14]. They also produce various phytohormones such as indole acetic acid, gibberellins, and cytokines which play a role in signal transduction and modification of immune responses for optimal growth [15]. Yield gap is the major issue of developing countries due to inadequacy of soil nutrition. So, the utilization of environmentally friendly PGPR may facilitate farmers in obtaining potential yield on hostile soils by coping with such stress challenges.

Barley (*Hordeum vulgare* L.), grown in the world today, is the most ancient cereal crop. Globally, it is one of the top most cultivated crops. In terms of production, it ranks fourth after wheat, rice, and maize among the cereal grains and is being used both as human food as well as animal feed [16]. It is mostly grown in the arid and semiarid regions. In 2021/2022, the production of barley grains was estimated to be about 147.05 million tons [17]. Barley is a good source of protein, starch, vitamins, minerals, and dietary fibers particularly β-glucan. These attributes of barley play a role in combating various degenerative diseases such as colon inflammation, obesity, diabetes, and hypertension [18]. Barley is more economical to cultivate because of its outperformance under various environmental stress conditions [19]. Despite its high tolerance to various environmental stresses, the growth and development of barley are significantly affected both by salinity and drought stresses [20, 21].

Although several studies have been reported regarding the impact of PGPR on nutrition profile in various plants, little attention has been paid on the comprehensive study of various mineral (macro and micro) nutrients in different parts (leaves, stems, and roots) of barley plants under abiotic stress conditions. Therefore, the present study hypothesized that PGPR inoculation would help in stimulating the various organs, i.e., stems, roots, and leaves, to enhance mineral nutrients' uptake and will help in ameliorating salinity and drought stress of a high value vegetable crop such as barley. For this purpose, a pot experiment was conducted, physiological parameters were measured, and the particle-induced X-ray emission (PIXE) technique was performed for evaluating the efficacy of PGPR for enhancing the

growth, photosynthesis, and chlorophyll fluorescence parameters as well as the nutritional profile in various parts of barley plant under salinity and drought stress conditions.

2. Materials and Methods

2.1. PGPR Inoculation, Plant Growth, and Stress Treatments. *P. fluorescens* SBW25 and *P. putida* KT2440 strains were assessed for their potential ameliorating role for drought and salt stresses. The strains used for this study were kindly provided by Dr. George O'Toole (Department of Microbiology and Immunology, Geisel School of Medicine, Dartmouth College, Hanover, NH, USA), and their selection for current research was based on their growth-promoting abilities as reported in previous studies [22, 23]. PGPR were grown in Luria broth (LB) medium for 24 h on continuous shaking in an incubator (200 rpm) at $28 \pm 2^{\circ}$C followed by centrifugation to collect pellets which were washed thrice and re-suspended in sterile distilled water to set an OD (optical density) of 1 at 600 nm (to obtain final concentration of 8×10^8 CFU/mL). Seeds (var. Snober-96) of barley obtained from National Agricultural Research Centre (NARC), Islamabad, Pakistan, were surface sterilized using Clorox 10% solution (3 min) and subsequently washed with 95% ethanol and water. Surface sterilized seeds were used for the inoculation of PGPR in the form of suspensions and distilled water (control) for 3 h and were grown in Petri plates with moistened cotton in the dark. After three to five days, the emergence of the radicals from the seeds was taken as a germinated seed. The following formula was used for the calculation of germination percentage:

$$\text{Germination percentage} = \left(\frac{\text{number of seeds germinated}}{\text{number of seeds sown}}\right) \times 100. \quad (1)$$

After three to five days of the emergence of the radical and plumule, seedlings were placed in plastic pots of sterilized soil and sand (3 : 1) for growth under controlled environmental conditions [24]. The experiment was set up according to Kang et al. [25] with some modifications. There were eight sets of plants: control barley plants with PGPR and without PGPR application, 200 mM salinity-stressed plants with PGPR and without PGPR application, 1000 mM salinity-stressed plants with PGPR and without PGPR application, and drought-stressed plants with PGPR and without PGPR application. Stress treatments (30 plants per treatment) were applied on 30-day-old mature plants. Salt stress was given following the pattern of Habib et al. [26], gradually starting irrigation with 50 mM NaCl with an increment of 50 mM per day until the 200 mM final NaCl concentration was attained in four days for one set of plants. 200 mM salt stress is the usual salt stress applied on various plants including barley. As barley is a salt-tolerant plant, we also tested it with high salt stress (1000 mM) treatment. High salt stress was given to another set of plants gradually starting from 250 mM with an increment of 250 mM per day until the 1000 mM final concentration was attained. We used a water withholding strategy of one week for drought stress.

2.2. Measurement of Plant Growth Parameters and Photosynthetic Activity. Root and shoot fresh and dry weights of control and stress-treated plants were measured for harvested barley plants with and without PGPR inoculations. For the measurement of dry weights, plants were kept in an oven for 72 h at 70°C. For the measurement of root length of soil plants, their roots were first dug out and washed carefully and then their lengths were measured from the start to the tip of primary roots. For the measurement of photosynthetic activity of control and stress-treated plants, chlorophyll fluorescence parameters, i.e., Fv/Fm ratio and performance index (PI), were measured using Pocket PEA chlorophyll fluorimeter (Hansatech). Prior to measurement, leaves were dark-adapted for 15 minutes using leaf clips. The chlorophyll fluorescence signal received during recording is digitized in the control unit which is recorded. For many plant species, an Fv/Fm value in the range of 0.79 to 0.84 is considered optimal value, while the lower values indicate plant stress [27].

2.3. PIXE (Particle-InducedX-Ray Emission) Analysis. PIXE is a powerful elemental analysis technique which is non-destructive in nature. It is the measurement of X-rays emitted from a sample bombarded with high energy ion beam. In PIXE, the samples are bombarded with particles (generally 1–4 MeV protons) accelerated in an accelerator and the characteristic X-rays produced by the de-excitation of the atoms in the sample are measured using semiconductor detector. Interaction of protons with matter generates the X-ray spectrum; from these spectra, elements as well as their concentrations can be determined in the sample [28].

2.3.1. Sample Preparation. Leaves, stems, and roots were collected from non-treated and PGPR-treated barley plants under control and stressed conditions and kept in an oven at 80°C until dried properly. The dried samples were ground manually using pestle and mortar in order to form a very fine homogenous powder. The ground samples were pelletized using a manual pellet press machine (Carver, USA, Model: 4350L: Serial No. 4160505). 24,000 pounds pressure was used to make a pellet of 13 mm diameter. 2-3 pellets were formed for each sample. For the avoidance of moisture and environmental contamination, pellets were placed in a desiccator.

2.3.2. Experimental Setup. Pellets were used as a target in PIXE setup and mounted on sample holder, which can easily be rotated forward, backward, horizontally, and vertically in the scattering chamber. The target was irradiated with a 3 MeV proton beam from 5 MV Pelletron Tandem Accelerator at Experimental Physics Laboratory (EPL), National Centre for Physics (NCP), Islamabad. The proton beam was collimated to 2 mm diameter. During irradiation, the beam current was in the range of 10 nA–20 nA and 2 μC total charge was collected. The emitted X-rays in this process were measured using silicon drift detector (SDD) with high resolution, which was placed at an angle of 45° to the incident beam, in order to collect maximum characteristic X-rays and minimum background radiations. For the reduction of low-energy background, Mylar absorber sheet of 100 μm thickness with no hole was used between target and detector. The distance between the target and the detector was 6 cm. The vacuum inside the scattering chamber was 10–60 torr. NIST apple leaf (SRM1515) was used as standard reference material.

2.4. PIXE Data Analysis. The X-ray spectrum was analyzed using GUPIXWIN software, which automatically fits the spectrum to obtain elemental concentrations [29]. Its calibration was done using Copper. GUPIXWIN converts spectral data into elemental concentrations which are finally transformed into Microsoft Excel format.

2.5. Statistical Analysis. For statistical analysis, statistical program SPSS version 20.0 was used. Means of three or five replicates of non-treated and PGPR-treated barley plants were determined for control and stress-treated groups. Data were analyzed using two-way analysis of variance (ANOVA) followed by Tukey's HSD post hoc test for multiple comparisons at $p \leq 0.05$ significance level. PCA (principal component analysis) was performed to compare the means of macro- and micronutrient uptake with treatments under control and stressed conditions.

3. Results

3.1. Effect of PGPR on Barley Seed Germination. Initially, we inoculated barley seeds with *P. putida* KT2440 and *P. fluorescens* SBW25 strains of PGPR to check their effects on seed germination. Application of both PGPR significantly increased the germination percentage with the more significant effect observed for *P. fluorescens* SBW25 (94%) with respect to non-inoculated (control) seeds as shown in Figure 1.

3.2. Effect of PGPR on Biomass and Photosynthetic Activity of Barley Plants under Salinity and Drought Stress Conditions. 200 mM and 1000 mM salt stress as well as drought stress treatments significantly decreased the shoot fresh weights in non-inoculated plants with more significant reduction observed under drought stress (0.36 g/plant). Under drought stress, *P. fluorescens* SBW25 application showed a more

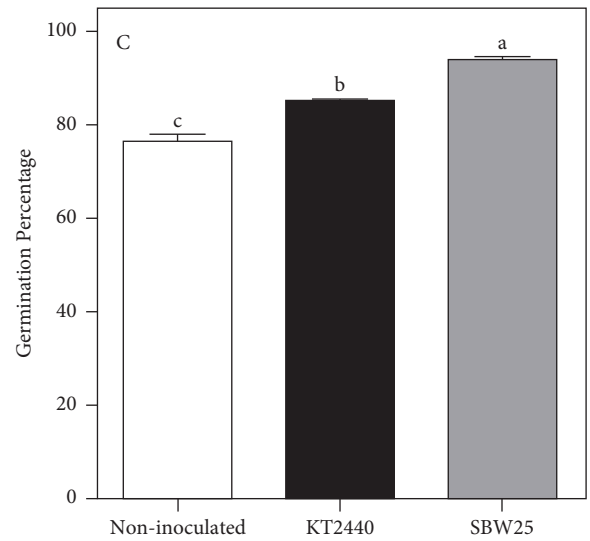

Figure 1: Effect of PGPR inoculation on barley seed germination. Bars are means ± SE, while $n = 3$. Bars represented by different letters are significantly different at $p \leq 0.05$.

pronounced effect by significantly (3.18 g/plant) increasing the shoot fresh weight. Under 200 mM salt stress, *P. putida* KT2440 application was found to be effective for significant (1.98 g/plant) enhancement of shoot fresh weight with respect to non-inoculated salt-stressed barley plant. Although an improvement was observed, however, statistically no significant difference was observed between treated and non-treated plants under 1000 mM salt stress treatment. Similarly, PGPR applications improved shoot dry weights of barley plants; however, statistically no significant difference was observed between non-inoculated and inoculated barley plants under no stress control condition and under 200 mM and 1000 mM salt-stressed conditions. However, under drought stress, PGPR application helped in ameliorating the stress by significantly increasing dry weights. The effect of *P. fluorescens* SBW25 (0.93 g/plant) was more pronounced than *P. putida* KT2440 (0.67 g/plant) for enhancing the dry weights. Drought stress more adversely affected the root fresh weight in non-inoculated plants. PGPR-inoculated drought-stressed plants exhibited significantly higher fresh weights of roots with the statistically more significant effect observed for *P. fluorescens* SBW25 (1.24 g/plant) inoculated drought-stressed plants. Similarly, under control (no stress) condition and 200 mM and 1000 mM salt stress conditions, PGPR-inoculated plants showed significantly higher root fresh weights with more pronounced effects observed for *P. fluorescens*SBW25-treated plants (1.21, 1.62, and 0.72 g/plant). We obtained almost similar results for root dry weights as for the root fresh weights except that statistically no significant difference was observed between PGPR-inoculated and non-inoculated plants under 1000 mM salt stress treatment (Table 1).

The Fv/Fm ratio characterizes the maximum quantum yield of photochemical reactions in dark-adapted leaves. In our study, Fv/Fm was affected by the application of stress treatments. Fv/Fm values decreased both in non-inoculated

Table 1: Effect of PGPR on the shoot and root biomasses and photosynthetic activity of barley plants under salinity and drought stress conditions.

Treatments	Shoot FW (g plant^{-1})	Shoot DW (g plant^{-1})	Root FW (g plant^{-1})	Root DW (g plant^{-1})	Root length (cm)	Fv/Fm ratio	PI values
Control							
Non-inoculated	1.66 ± 0.47^{ab}	0.17 ± 0.004^{cd}	0.6 ± 0.08^{def}	0.06 ± 0.004^{ef}	11.83 ± 1.63^{bc}	0.82 ± 0.01^{a}	3.64 ± 0.13^{bcd}
P. putida KT2440	1.52 ± 0.40^{ab}	0.26 ± 0.05^{cd}	0.64 ± 0.05^{bcdef}	0.17 ± 0.01^{bc}	17.1 ± 0.68^{ab}	0.82 ± 0.003^{a}	3.05 ± 0.35^{d}
P. fluorescens SBW25	1.65 ± 0.12^{ab}	0.21 ± 0.03^{cd}	1.21 ± 0.09^{abc}	0.20 ± 0.01^{ab}	12 ± 0.92^{bc}	0.81 ± 0.003^{a}	3.99 ± 0.12^{abcd}
NaCl 200 mM							
Non-inoculated	1.46 ± 0.54^{b}	0.11 ± 0.01^{cd}	0.56 ± 0.09^{def}	0.12 ± 0.008^{cde}	15.83 ± 0.83^{bc}	0.807 ± 0.003^{a}	4.01 ± 0.13^{abcd}
P. putida KT2440	1.98 ± 0.50^{ab}	0.21 ± 0.08^{cd}	1.09 ± 0.08^{abcd}	0.17 ± 0.02^{bc}	17 ± 3.06^{ab}	0.79 ± 0.01^{a}	4.53 ± 0.08^{abcd}
P. fluorescens SBW25	1.43 ± 0.43^{b}	0.19 ± 0.03^{cd}	1.62 ± 0.23^{a}	0.25 ± 0.02^{a}	23.5 ± 1.25^{a}	0.81 ± 0.0^{a}	5.33 ± 0.51^{a}
NaCl 1000 mM							
Non-inoculated	0.84 ± 0.14^{b}	0.09 ± 0.005^{cd}	0.61 ± 0.02^{cdef}	0.08 ± 0.01^{ef}	14.1 ± 1.42^{bc}	0.807 ± 0.009^{a}	4.48 ± 0.49^{abcd}
P. putida KT2440	1.07 ± 0.11^{b}	0.14 ± 0.008^{cd}	0.89 ± 0.19^{bcde}	0.10 ± 0.005^{ef}	18.6 ± 2.02^{ab}	0.81 ± 0.006^{a}	4.92 ± 0.45^{abc}
P. fluorescens SBW25	1.13 ± 0.21^{b}	0.17 ± 0.006^{cd}	0.72 ± 0.17^{bcdef}	0.07 ± 0.01^{ef}	16.6 ± 1.66^{ab}	0.807 ± 0.003^{a}	4.63 ± 0.10^{abcd}
Drought							
Non-inoculated	0.36 ± 0.09^{b}	0.18 ± 0.02^{cd}	0.19 ± 0.09^{f}	0.04 ± 0.004^{f}	8.73 ± 1.17^{c}	0.81 ± 0.006^{a}	4.23 ± 0.34^{abcd}
P. putida KT2440	1.42 ± 0.08^{b}	0.67 ± 0.03^{b}	0.44 ± 0.02^{ef}	0.07 ± 0.01^{ef}	13.7 ± 0.79^{bc}	0.82 ± 0.006^{a}	5.18 ± 0.38^{ab}
P. fluorescens SBW25	3.18 ± 0.29^{a}	0.93 ± 0.04^{a}	1.24 ± 0.09^{ab}	0.16 ± 0.01^{bcd}	15.6 ± 1.47^{bc}	0.81 ± 0.003^{a}	3.56 ± 0.19^{cd}

Data are expressed as means ± SE, while n = 5. Different letters show a significant difference at $p \leq 0.05$.

and PGPR-applied stressed barley plants with respect to control plants; however, overall, for Fv/Fm ratio, statistically no significant difference was observed between PGPR-inoculated and non-inoculated plants under control, 200 mM and 1000 mM salt stress, and drought stress conditions. PI (performance index) value increased significantly both in non-inoculated and PGPR-inoculated barley plants under 200 mM and 1000 mM salt stress and drought stress conditions, except *P. fluorescens*SBW25-inoculated drought-stressed plants which showed a significant decrease (3.56 ± 0.19) with respect to non-inoculated drought-stressed plants. However, an increase in PI values in *P. fluorescens* SBW25 (5.33 ± 0.51) inoculated plants under 200 mM salt stress and in *P. putida*KT2440-inoculated plants under 1000 mM salt stress (4.92 ± 0.45) and drought stress (5.18 ± 0.38) conditions were found to be statistically significant with respect to non-inoculated stressed counterparts (Table 1).

3.3. Effect of PGPR on Macronutrients of Barley Leaves under Salinity and Drought Stress Conditions. Applications of *P. fluorescens* SBW25 and *P. putida* KT2440 strains improved nutrient acquisition in treated barley leaves under control (no stress) and under stressed (salt + drought) conditions. Under the control condition in comparison to non-inoculated plants, PGPR-treated plants were found to have significantly higher Mg content of leaves with a more pronounced effect observed for *P. fluorescens* SBW25 (871069.1 mg/kg) inoculated barley plants. Exposure of 200 mM salt stress significantly decreased Mg content in non-treated and PGPR-treated plants; however, PGPR-inoculated salt-stressed plants still maintained significantly higher Mg level when compared to non-inoculated salt-stressed plants and the effect of *P. fluorescens* SBW25 (400573.9 mg/kg) was statistically more significant for this enhancement. In 1000 mM salt stress treatment, PGPR application improved uptake of Mg content in comparison to non-inoculated salt-stressed barley leaves. In drought stress, *P. putida* KT2440 (32507.9 mg/kg) inoculated plants showed significantly higher Mg contents in comparison to non-inoculated drought-stressed plants. For Ca content, *P. fluorescens* SBW25 depicted enhanced uptake in control-condition. Similarly, the PGPR application also helped in enhancing the Ca content in 200 mM salt stress and drought stress conditions. However, in 1000 mM salt stress, applications of PGPR were found to be effective for enhancing Ca uptake significantly, and among the two strains tested, the effect of *P. putida* KT2440 (1314.1 mg/kg) was more pronounced than that of *P. fluorescens* SBW25 (846.5 mg/kg). Similarly, the application of *P. fluorescens* SBW25 was also found to be effective for enhancing K content in control condition. Likewise, an enhanced uptake was also observed in PGPR-applied barley leaves as compared to non-treated leaves under 200 mM salt stress condition. Under 1000 mM salt stress, when compared to non-PGPR-appliedsalt-stressed leaves, PGPR application displayed significant enhancement of K with statistically more pronounced significant effects observed for *P. putida* KT2440 (8565.3 mg/kg). Drought stress significantly decreased K content in non-inoculated plants; however, PGPR applications helped in significant enhancement of K under the same stressed condition. Both PGPR-treated plants displayed significantly higher sulfur uptake in comparison to non-inoculated plants under control conditions. The application of 200 mM salt stress showed a significant decrease in S content, while it was not detected under 1000 mM salt stress in non-treated plants. PGPR applications were found to be effective for enhancing S uptake under saline conditions with more pronounced significant effects observed for *P. fluorescens* SBW25 (1718 mg/kg) inoculated barley leaves in 200 mM stress condition. Drought stress also reduced S content significantly in non-treated plants, while the inoculations of PGPR improved S uptake; however, statistically no significant difference was observed among treated and non-treated drought-stressed barley leaves. Like Mg, PGPR applications also increased phosphorus (P) content significantly in comparison to non-inoculated plants with more prominent significant effects observed for *P. fluorescens*SBW25-inoculated leaves under control (2662.6 mg/kg) and 200 mM salt stress (1308.5 mg/kg) conditions. In 1000 mM salt stress, PGPR applications also enhanced P uptake, while in drought stress, P content increased significantly in both non-inoculated and PGPR-inoculated barley leaves with respect to control condition. However, this increase was statistically more significant in PGPR (*P. putida* KT2440 and *P. fluorescens* SBW25) treated plants, and among the two strains tested, the effect of *P. fluorescens* SBW25 (2608.9 mg/kg) was more pronounced for enhancing P uptake than that of *P. putida* KT2440. Applications of PGPR significantly enhanced Al uptake under 200 mM salt stress condition with a statistically more significant effect observed with *P. fluorescens* SBW25 (23069.4 mg/kg) application. Similarly, they also improved Al uptake in 1000 mM salt stress and drought stress conditions. Si contents were found to be significantly higher in PGPR-treated barley leaves with a more statistically significant effect observed for *P. fluorescens* SBW25 (3921.5 mg/kg) inoculated plants under control and 200 mM salt stress conditions. Si was not detected in non-treated plants in 200 mM salt stress. In 1000 mM salt stress, Si uptake increased in non-treated plants in comparison to control plants. As barley is a salt-tolerant plant and Si plays a beneficial role in stress tolerance, it might be due to the plant's innate ability to cope with the stress situations. However, inoculations of PGPR under the same stress condition showed relatively higher uptake of Si when compared to non-treated counterparts. Similarly, PGPR-treated plants depicted statistically more significant uptake of Si content in comparison to non-inoculated drought-stressed plants (Table 2).

3.4. Effect of PGPR on Micronutrients of Barley Leaves under Salinity and Drought Stress Conditions. Application of PGPR also improved the acquisition of micronutrients in comparison to non-inoculated barley leaves under our experimental conditions. Cl^- contents were found to be significantly higher in PGPR-treated plants with statistically

Table 2: Effect of PGPR on macronutrients of barley leaves under salinity and drought stress conditions.

	Mg	Ca	K	S	P	Al	Si
Control							
Non-inoculated	24051^{e}	221.2^{c}	1165.2^{cd}	15.4^{e}	8^{d}	1494.3^{d}	19.4^{d}
P. putida KT2440	244911.7^{c}	206.6^{c}	1090.6^{cd}	2206.4^{a}	1074.2^{cd}	15609.8^{bc}	2784.3^{bc}
P. fluorescens SBW25	871069.1^{a}	296.6^{c}	1384^{cd}	2333.2^{a}	2662.6^{a}	46556.5^{a}	7804^{a}
NaCl 200 mM							
Non-inoculated	6906^{e}	120.6^{c}	427.5^{d}	7.6^{e}	3.8^{d}	371.2^{d}	ND
P. putida KT2440	135238.7^{d}	176.1^{c}	580.8^{d}	1255.5^{c}	535.9^{cd}	8763.1^{cd}	1500.1^{c}
P. fluorescens SBW25	400573.9^{b}	187.4^{c}	670.1^{d}	1718^{b}	1308.5^{bc}	23069.4^{b}	3921.5^{b}
NaCl 1000 mM							
Non-inoculated	33732.2^{de}	349.3^{c}	2127^{c}	ND	19.5^{d}	904.3^{d}	27.9^{d}
P. putida KT2440	50977.8^{de}	1314.1^{a}	8565.3^{a}	586^{d}	51.4^{d}	2669.7^{d}	53.4^{d}
P. fluorescens SBW25	38127.5^{de}	846.5^{b}	3431.3^{b}	487.6^{d}	21^{d}	1420.6^{d}	47.4^{d}
Drought							
Non-inoculated	16112.3^{e}	44^{c}	360.2^{d}	5.4^{e}	851.6^{cd}	751.1^{d}	2597.5^{bc}
P. putida KT2440	32507.9^{de}	157.2^{c}	1340.8^{cd}	17.7^{e}	2367.9^{ab}	1426.1^{d}	6960.5^{a}
P. fluorescens SBW25	25779.9^{e}	144.6^{c}	1343.8^{cd}	14.7^{e}	2608.9^{a}	1563.8^{d}	7657.4^{a}

ND: not detected. Means ($n = 3$). Different letters show a significant difference at $p \leq 0.05$. Unit: mg/kg.

more significant uptake observed with *P. putida* KT2440 (745.4 mg/kg) application in control condition. When compared to non-treated control plants, Cl^- contents reduced in non-inoculated 200 mM salt-stressed plants; however, under the same stressed conditions, PGPR treatments significantly improved Cl^- uptake. In comparison to control condition, exposure of 1000 mM salt stress showed a significant increase of Cl^- content in non-treated barley leaves. However, inoculations of PGPR significantly reduced Cl^- content, and among the tested PGPR strains, *P. fluorescens* SBW25 (530.8 mg/kg) showed a more significant reduction in Cl^- contents with respect to non-inoculated stressed leaves. Drought stress significantly decreased Cl^- content in non-inoculated plants; however, PGPR applications helped in significant enhancement of Cl^- content with statistically more significant effects observed with *P. fluorescens* SBW25 strain (409.8 mg/kg). Mn contents were found to be significantly higher in PGPR-treated plants in comparison to non-treated plants under control condition. In 200 mM salt stress, *P. fluorescens* SBW25 (9.6 mg/kg) inoculation depicted significantly higher Mn uptake as compared to non-inoculated stressed leaves. Under 1000 mM salt stress, treatments of both PGPR significantly enhanced Mn uptake with more statistically significant effects observed for *P. putida* KT2440 (100.4 mg/kg) inoculation when compared to non-treated counterparts. In the same way, in drought stress, Mn reduced significantly in non-inoculated leaves and PGPR treatments were found to be effective in ameliorating this stress through significant enhancement of Mn content, and more significant effects were observed with *P. putida* KT2440 strain (17.5 mg/kg). Similar results were obtained for iron (Fe), except that *P. putida* KT2440 (15.3 mg/kg) displayed more significant uptake of Fe under drought stress condition. Co was not detected in non-inoculated barley leaves under control condition and was also not detected in *P. putida* KT2440- and *P. fluorescens*SBW25-inoculated leaves under 200 mM salt stress condition. Co was found to be significantly higher in PGPR-inoculated leaves with the more significant effect observed for *P. fluorescens* SBW25 (11.3 mg/kg) strain as compared to non-inoculated barley leaves in 1000 mM salt stress. In drought stress, PGPR applications also improved Co uptake, but that was not statistically significant in comparison to non-treated leaves. Ni was not detected in non-inoculated leaves under control, 200 mM, and 1000 mM salt stress conditions. Both PGPR treatments displayed significantly higher Ni content under control conditions. The effect of *P. fluorescens* SBW25 was (0.016 mg/kg) more pronounced than that of *P. putida* KT2440 (0.009 mg/kg) in 200 mM salt stress, while in 1000 mM salt stress, *P. putida* KT2440 (0.032 mg/kg) was found to be more effective for significant enhancement of Ni content with respect to the other strain. Under drought stress, in comparison to non-inoculated plants, the application of both PGPR significantly improved Ni uptake with a statistically more significant effect observed for *P. fluorescens* SBW25 (0.13 mg/kg) inoculation. For Cu, *P. fluorescens* SBW25 treatment depicted significant enhancement under control condition. In 200 mM salt stress, non-inoculated barley leaves showed a statistically significant increase in Cu content when compared to PGPR (*P. putida* KT2440 and *P. fluorescens* SBW25) inoculated leaves, while the increase in Cu uptake with PGPR applications was not statistically significant with respect to non-treated plants under 1000 mM salt stress conditions. However, in drought stress, PGPR applications showed increased uptake of Cu, and significant uptake was observed with *P. fluorescens* SBW25 (0.59 mg/kg) treatment. For Zn, statistically no significant difference was observed among treated and non-treated barley leaves under control condition. Applications of 200 mM and 1000 mM salt stress, as well as drought stress, significantly reduced Zn content in non-treated barley leaves, while the applications of PGPR increased its uptake which in 200 mM salt stress and drought stress conditions was found to be statistically non-significant when compared to untreated plants. However, in 1000 mM salt stress, application of *P. putida* KT2440 (83.1 mg/kg)

significantly improved Zn content as compared to non-treated stressed leaves (Table 3).

3.5. Effect of PGPR on Macronutrients of Barley Stems under Salinity and Drought Stress Conditions. PGPR treatments also improved macronutrient acquisition in treated barley stems under control and also in stressed conditions. Exposure of 200 mM salt stress drastically reduced Mg contents in non-inoculated barley stem, while PGPR applications helped for statistically more significant enhancement of Mg content. In 1000 mM salt stress, PGPR inoculations were found to be effective for significant improvement of Mg uptake. *P. putida* KT2440 (280623.7 mg/kg) showed statistically more significant uptake of Mg than *P. fluorescens* SBW25 strain when compared to non-inoculated stressed plants. In drought stress, only *P. fluorescens* SBW25 (226255.3 mg/kg) inoculation displayed significant uptake of Mg content with respect to non-treated plants. Similarly, Ca uptake was found to be significantly higher in PGPR-inoculated barley stems. In 200 mM salt stress, *P. fluorescens* SBW25 (145.7 mg/kg) inoculation helped in increasing the Ca uptake, while in 1000 mM salt stress, *P. putida* KT2440 (1352.8 mg/kg) inoculated barley stems showed significantly higher Ca content as compared to non-inoculated barley stems. Drought stress significantly decreased Ca content in non-inoculated stems, while inoculation with PGPR helped in significant improvement of Ca uptake with the statistically more significant effect observed for *P. putida* KT2440 (1385 mg/kg) inoculation. 200 mM salt stress significantly lowered K content in non-treated barley stems. However, increased K contents in PGPR-inoculated stems were not found to be statistically different from the non-inoculated stems. K contents also reduced significantly in 1000 mM salt stress and drought stress conditions in non-inoculated stems, while PGPR applications significantly enhanced K uptake. *P. putida* KT2440 (7611.3 mg/kg) in 1000 mM salt stress and *P. fluorescens* SBW25 (7824.5 mg/kg) strain in drought stress showed statistically more significant uptake of K content. Under control condition, PGPR-inoculated stems (with a more pronounced significant effect of *P. fluorescens* SBW25 (2464.4 mg/kg)) showed significantly higher S uptake than non-inoculated barley stems. In 200 mM salt stress, treatments of both PGPR enhanced the S content significantly in comparison to non-treated stems. *P. fluorescens* SBW25 (810.3 mg/kg) inoculated stems also depicted significantly higher S content in comparison to non-inoculated stems in 1000 mM salt stress. S was not detected in non-inoculated and *P. putida*KT2440-inoculated stems in drought stress, while under the same condition, *P. fluorescens*SBW25-inoculated stems displayed S uptake. P was not detected in non-inoculated and *P. fluorescens*SBW25-inoculated barley stems, while it was detected in *P. putida*KT2440-inoculated stems in control condition. In 200 mM salt stress, inoculations of both *P. putida* KT2440 (2353.7 mg/kg) and *P. fluorescens* SBW25 (2430.8 mg/kg) more significantly increased P contents in comparison to the non-inoculated salt-stressed stem, while in 1000 mM salt stress, an increase in P content in PGPR-inoculated stems was not found to be significantly different from non-inoculated stressed stems. P was also not detected in non-inoculated drought-stressed barley stems, while PGPR-inoculated drought-stressed barley stems showed uptake of P element. Al was not detected in *P. putida*KT2440-inoculated barley stems, while *P. fluorescens* SBW25 (666.9 mg/kg) inoculated stem displayed significantly higher Al content in comparison to non-inoculated stems in control condition. Applications of 200 mM and 1000 mM salt stresses showed a gradual significant increase in Al content in non-inoculated barley stems, while the application of PGPR boosted this effect by significantly increasing Al uptake with respect to non-inoculated salt-stressed plants. The effect of *P. putida* KT2440 (2426 mg/kg and 2085.2 mg/kg) was more pronounced than that of *P. fluorescens* SBW25 strain. Al was not detected in *P. fluorescens*SBW25-inoculated stems in 1000 mM salt stress condition. Drought stress also increased Al content significantly in non-inoculated barley stems in comparison to control condition; however, Al was not detected in both *P. fluorescens* SBW25- and *P. putida*KT2440-inoculated stems under the same stress condition. 200 mM salt stress application depicted a more significant reduction of Si content in non-inoculated barley stems, while PGPR (7004.7 mg/kg and 7176.5 mg/kg) applications helped in more significant uptake of Si under the same condition. Both 1000 mM salt stress and drought stress also decreased Si contents in non-inoculated stems, while enhancement with PGPR application was not found to be statistically significant when compared to non-treated plants under the same stressed conditions (Table 4).

3.6. Effect of PGPR on Micronutrients of Barley Stems under Salinity and Drought Stress Conditions. Applications of PGPR also improved the acquisition of micronutrients in barley stems. Under control condition, non-inoculated stems showed significantly higher (2367.1 mg/kg) Cl^- contents in comparison to PGPR-applied stems, and among the two strains, *P. putida* KT2440 (756.8 mg/kg) displayed significantly lower Cl^- contents when compared to non-treated barley stems. A significant decrease in Cl^- contents was also observed under 200 mM and 1000 mM salt stress conditions in non-treated barley stems with more significant reduction observed under 200 mM salt stress condition. PGPR-applied stems showed significantly lower Cl^- content with respect to non-treated stems under the same stress conditions. The effect of *P. fluorescens* SBW25 (365.5 mg/kg) was significantly more pronounced for lowering Cl^- content under 1000 mM salt stress condition. Cl^- contents also reduced significantly in non-inoculated barley stems under drought condition when compared to the control condition. However, PGPR treatments showed relatively higher Cl^- contents as compared to non-treated drought-stressed stems. 200 mM and 1000 mM salt stress, as well as drought stress, significantly lowered the Mn contents in non-inoculated stems; however, PGPR applications significantly improved Mn uptake under the same stressed

Table 3: Effect of PGPR on micronutrients of barley leaves under salinity and drought stress conditions.

	Cl	Mn	Fe	Co	Ni	Cu	Zn
Control							
Non-inoculated	307.8^{de}	6.2^{de}	17.9^{bcd}	ND	ND	0.095^{c}	157.4^{a}
P. putida KT2440	745.4^{bc}	9^{cde}	18.1^{bc}	0.046^{c}	0.13^{a}	0.078^{c}	145.1^{a}
P. fluorescens SBW25	418.1^{cde}	7.1^{cde}	18.6^{bc}	0.82^{c}	0.14^{a}	0.32^{b}	157.4^{a}
NaCl 200 mM							
Non-inoculated	110.6^{e}	3.9^{de}	3.8^{e}	0.016^{c}	ND	0.52^{a}	13.1^{c}
P. putida KT2440	405^{cde}	6.8^{de}	4.9^{e}	ND	0.009^{d}	0.11^{c}	21.6^{c}
P. fluorescens SBW25	416.4^{cde}	9.6^{cde}	5.6^{de}	ND	0.016^{cd}	0.092^{c}	19.8^{c}
NaCl 1000 mM							
Non-inoculated	1165.2^{a}	14^{bcd}	22.3^{bc}	1.6^{c}	ND	0.026^{c}	18.6^{c}
P. putida KT2440	967.8^{ab}	100.4^{a}	73^{a}	4.8^{b}	0.032^{bcd}	0.071^{c}	83.1^{b}
P. fluorescens SBW25	530.8^{cd}	20.3^{b}	26.7^{b}	11.3^{a}	0.015^{d}	0.087^{c}	8.5^{c}
Drought							
Non-inoculated	219.9^{de}	3^{e}	3.9^{e}	0.034^{c}	0.049^{bc}	0.022^{c}	3.5^{c}
P. putida KT2440	369.2^{de}	17.5^{bc}	15.3^{bcde}	0.14^{c}	0.062^{b}	0.084^{c}	8.4^{c}
P. fluorescens SBW25	409.8^{cde}	13^{bcde}	12.7^{cde}	0.25^{c}	0.13^{a}	0.59^{a}	3.9^{c}

ND: not detected. Means ($n = 3$). Different letters show a significant difference at $p \leq 0.05$. Unit: mg/kg.

Table 4: Effect of PGPR on macronutrients of barley stems under salinity and drought stress conditions.

	Mg	Ca	K	S	P	Al	Si
Control							
Non-inoculated	336442^{cd}	828.6^{de}	12157.6^{c}	934.2^{de}	ND	3.3^{f}	866.1^{bc}
P. putida KT2440	581454.4^{b}	2546.7^{b}	14420.6^{b}	1653.7^{c}	522.2^{b}	ND	1644.1^{b}
P. fluorescens SBW25	454693^{bc}	3870.5^{a}	23182.1^{a}	2464.4^{a}	ND	666.9^{e}	1664.5^{b}
NaCl 200 mM							
Non-inoculated	21087.6^{f}	139^{f}	476^{g}	1110.5^{d}	27.9^{b}	1106.5^{d}	24.8^{c}
P. putida KT2440	785929.1^{a}	133.4^{f}	1085.4^{g}	2187.7^{b}	2353.7^{a}	2426^{a}	7004.7^{a}
P. fluorescens SBW25	811969.9^{a}	145.7^{f}	1201.8^{g}	2115.3^{b}	2430.8^{a}	2199.7^{ab}	7176.5^{a}
NaCl 1000 mM							
Non-inoculated	177074.6^{def}	972.9^{cde}	6173^{ef}	316.1^{g}	73.7^{b}	1576.7^{c}	390.7^{bc}
P. putida KT2440	280623.7^{cde}	1352.8^{cd}	7611.3^{de}	457.5^{g}	175^{b}	2085.2^{b}	1151.5^{bc}
P. fluorescens SBW25	210646.4^{de}	1011^{cde}	6793.2^{def}	810.3^{ef}	359.3^{b}	ND	1099.1^{bc}
Drought							
Non-inoculated	126820.1^{ef}	569^{ef}	5857.3^{f}	ND	ND	1669.9^{c}	552.8^{bc}
P. putida KT2440	122124.5^{ef}	1385^{c}	7668.8^{de}	ND	25.3^{b}	ND	934^{bc}
P. fluorescens SBW25	226255.3^{de}	881.1^{cde}	7824.5^{d}	700.7^{f}	133.4^{b}	ND	1037.4^{bc}

ND: not detected. Means ($n = 3$). Different letters show a significant difference at $p \leq 0.05$. Unit: mg/kg.

conditions. *P. putida* KT2440 (52.2 mg/kg) in 1000 mM salt stress and *P. fluorescens* SBW25 (32 mg/kg) in drought stress displayed statistically more significant enhancement of Mn content. Mn was not detected in *P. putida*KT2440-inoculated stems under drought stress condition. Almost similar results were obtained for Fe, except that increase in Fe uptake in PGPR-inoculated stems was not found to be statistically different from non-inoculated stems in 200 mM salt stress condition, and the applications of both PGPR significantly increased Fe uptake in comparison to non-inoculated stems in 1000 mM salt stress condition. Co was not detected in non-inoculated stems under 200 mM salt stress, while *P. fluorescens* SBW25 (55.5 mg/kg) inoculated stems displayed significantly higher Co content as compared to *P. putida*KT2440-inoculated stems under the same stress condition. Co was not detected in *P. putida*KT2440-inoculated stems in 1000 mM salt as well as drought stress conditions. Co uptake reduced significantly in non-inoculated stems in 1000 mM salt and drought stress conditions, while the increased uptake of Co in *P. fluorescens*SBW25-inoculated stems was not found to be statistically significant when compared to non-inoculated stems under the same stressed conditions. For Ni, inoculations of both PGPR found to be effective for its significant enhancement in the control condition, while statistically non-significant enhancement of Ni was observed with PGPR application in 200 mM salt stress and drought stress conditions. In 1000 mM salt stress, PGPR-treated stems displayed non-significant decrease with respect to stressed counterparts. Both PGPR showed significantly higher Cu contents under control condition. Cu was not detected in non-inoculated stems, and statistically no significant difference was found among the two strains for Cu uptake under 200 mM salt stress condition. In 1000 mM salt stress, increased uptake of Cu in PGPR-inoculated barley stems was not statistically significant as compared to non-

inoculated stems, while in drought stress, *P. putida* KT2440 (1.7 mg/kg) inoculation showed significantly higher Cu content as compared to non-inoculated stems. For Zn, PGPR inoculations displayed significantly higher uptake under control condition. In 200 mM salt stress, *P. putida* KT2440 (22.4 mg/kg) inoculated stems showed a significant decrease in Zn content, while *P. fluorescens*SBW25-inoculated stems displayed a non-significant increase in comparison to non-inoculated stems. On the other hand, under 1000 mM salt stress, PGPR inoculations showed significantly higher Zn uptake. Among the two strains, the effect of *P. fluorescens* SBW25 (222.63 mg/kg) was more pronounced for enhancing the Zn content. Similarly, *P. fluorescens* SBW25 strain (231.3 mg/kg) was also found to be effective for more significant enhancement of Zn uptake, while *P. putida* KT2440 (5.03 mg/kg) inoculated stems displayed a significant decrease of Zn content in comparison to non-inoculated drought-stressed stems (Table 5).

3.7. Effect of PGPR on Macronutrients of Barley Roots under Salinity and Drought Stress Conditions. PGPR were also found to be useful for enhancing macronutrient uptake in treated barley roots under our experimental conditions. 200 mM and 1000 mM salt stress as well as drought stress conditions lowered the Mg uptake significantly in non-inoculated barley roots. *P. fluorescens* SBW25 (3411.6 mg/kg) in 200 mM salt stress and *P. putida* KT2440 (11107.9 mg/kg) in 1000 mM salt stress conditions enhanced the Mg uptake significantly as compared to non-inoculated roots. In drought stress, both PGPR significantly improved Mg uptake with respect to non-inoculated roots. However, the effect of *P. putida* KT2440 (5789.9 mg/kg) was more pronounced than that of *P. fluorescens* SBW25 strain. Stress conditions significantly lowered the Ca content in non-inoculated stressed barley roots. Inoculation of *P. fluorescens* SBW25 was found to be useful for significant enhancement of Ca content under 200 mM salt stress (257.5 mg/kg), while under 1000 mM salt stress (1586.8 mg/kg) and drought stress (1709.5 mg/kg) conditions, enhancement of Ca in PGPR-treated barley roots was not found to be statistically significant in comparison to non-inoculated counterparts. Stress applications significantly reduced K uptake in non-inoculated roots. Although an enhancement was observed, statistically no significant difference was observed among treated and non-treated roots in 200 mM salt stress condition. In 1000 mM salt stress, only *P. putida* KT2440 strain more significantly (401.6 mg/kg) raised K contents in comparison to non-inoculated roots. In drought stress, both PGPR treatments significantly improved K uptake. The effect of *P. putida* KT2440 (191 mg/kg) was more pronounced than that of the other strain when compared to non-inoculated stressed roots. Exposure of 200 mM and 1000 mM salt stress, as well as drought stress, significantly lowered S content in non-inoculated roots. In 200 mM salt stress, an increase in S content due to PGPR inoculation was not found to be statistically different from non-treated roots. Under 1000 mM salt stress, *P. putida* KT2440 inoculation helped in significant (64.6 mg/kg) enhancement of S uptake, while under drought stress, although both *P. putida* KT2440 and *P. fluorescens* SBW25 strains helped for significant improvement of S uptake, more pronounced significant effects were observed with *P. putida* KT2440 (44.6 mg/kg) inoculated barley roots when compared to non-inoculated stressed roots. P was not detected in non-inoculated and *P. fluorescens*SBW25-inoculated barley roots, while *P. putida*KT2440-inoculated roots showed significantly higher (29.3 mg/kg) P uptake in control condition as compared to stressed conditions. Similarly, P was also not detected in non-inoculated and *P. fluorescens*SBW25-inoculated roots in 200 mM salt stress. Under 1000 mM salt stress, P was not detected in *P. putida*KT2440-inoculated roots, while the increase in P uptake owing to *P. fluorescens* SBW25 inoculation was not found to be statistically significant when compared to non-inoculated roots. P was also not detected in non-inoculated drought-stressed roots, while both *P. putida* KT2440- and *P. fluorescens*SBW25-inoculated drought-stressed roots displayed higher P contents which were not statistically different from each other. Exposure of the stresses significantly reduced Al content with a more significant reduction observed in 1000 mM salt stress condition. Treatments of both PGPR significantly enhanced Al uptake under 200 mM and 1000 mM salt stress conditions. *P. fluorescens* SBW25 in 200 mM salt stress (926.7 mg/kg) and *P. putida* KT2440 in 1000 mM salt stress (798.4 mg/kg) displayed a more significant uptake of Al. In drought stress, only *P. putida*KT2440-inoculated roots showed a statistically significant (892.9 mg/kg) increase of Al with respect to non-inoculated roots. Applications of the stresses significantly lowered Si contents in non-inoculated roots. Increase in Si contents due to PGPR inoculations under 200 mM salt stress was not found to be statistically different from non-inoculated roots. In 1000 mM salt stress, only *P. putida*KT2440-inoculated roots displayed a significant (367.8 mg/kg) increase, and in drought stress, both PGPR strains significantly increased Si uptake as compared to non-inoculated roots (Table 6).

3.8. Effect of PGPR on Micronutrients of Barley Roots under Salinity and Drought Stress Conditions. PGPR inoculations also improved the acquisition of micronutrients in comparison to non-inoculated barley roots under our experimental conditions. For Cl^- content, both PGPR inoculations showed a significant decrease with respect to non-treated roots under control condition. Exposure of 200 mM also showed a significant decrease of Cl^- contents in both non-treated as well as PGPR-treated barley roots in comparison to control condition. The decrease in Cl^- uptake was more significant in PGPR-treated barley roots when compared to non-treated roots under the same stress condition. 1000 mM salt-stressed non-treated barley roots showed increased uptake of Cl^- in comparison to control plants. *P. putida* KT2440 application significantly (7.6 mg/kg) reduced Cl^- uptake, whereas *P. fluorescens*SBW25-treated roots showed significantly (26.7 mg/kg) raised Cl^- contents when compared to non-treated roots. Both PGPR treatments under

Table 5: Effect of PGPR on micronutrients of barley stems under salinity and drought stress conditions.

	Cl	Mn	Fe	Co	Ni	Cu	Zn
Control							
Non-inoculated	2367.1^{a}	76.7^{c}	65.1^{c}	12.2^{c}	0.4^{b}	1.8^{b}	212.2^{ab}
P. putida KT2440	756.8^{bc}	138.8^{b}	90.4^{b}	32.3^{b}	5.1^{a}	3.3^{a}	260.4^{a}
P. fluorescens SBW25	1299.3^{abc}	232.9^{a}	112.4^{a}	55.5^{a}	4.3^{a}	3.5^{a}	267.7^{a}
NaCl 200 mM							
Non-inoculated	469.5^{bc}	6.6^{gh}	6.9^{fg}	ND	0.012^{b}	ND	25.9^{cd}
P. putida KT2440	406.4^{c}	10.4^{fgh}	9.8^{fg}	0.019^{d}	0.032^{b}	0.069^{c}	22.4^{d}
P. fluorescens SBW25	365.5^{c}	10.5^{fgh}	10.8^{fg}	0.26^{cd}	0.087^{b}	0.11^{c}	28^{cd}
NaCl 1000 mM							
Non-inoculated	1605.2^{ab}	18.3^{efgh}	17.5^{ef}	4.7^{cd}	0.183^{b}	0.11^{c}	51.8^{cd}
P. putida KT2440	1205.8^{abc}	52.2^{d}	40.3^{d}	ND	0.099^{b}	0.16^{c}	118.7^{bc}
P. fluorescens SBW25	1008.3^{bc}	26.5^{ef}	40.7^{d}	11.7^{cd}	0.09^{b}	0.23^{c}	222.63^{a}
Drought							
Non-inoculated	505.3^{bc}	19.1^{efg}	30.6^{de}	4.3^{cd}	0.33^{b}	0.064^{c}	51.3^{cd}
P. putida KT2440	1023.8^{bc}	ND	ND	ND	0.36^{b}	1.7^{b}	5.03^{d}
P. fluorescens SBW25	894.9^{bc}	32^{e}	35.7^{d}	8.4^{cd}	0.607^{b}	0.151^{c}	231.3^{a}

ND: not detected. Means ($n = 3$). Different letters show a significant difference at $p \leq 0.05$. Unit: mg/kg.

Table 6: Effect of PGPR on macronutrients of barley roots under salinity and drought stress conditions.

	Mg	Ca	K	S	P	Al	Si
Control							
Non-inoculated	9210.8^{bc}	13098.3^{b}	295.3^{bc}	44.4^{b}	ND	1204.2^{ab}	661^{ab}
P. putida KT2440	11285.8^{ab}	5385.6^{c}	402.4^{ab}	74.4^{a}	29.3^{a}	1633.2^{a}	431.3^{bc}
P. fluorescens SBW25	14039.6^{a}	18557.7^{a}	501.5^{a}	76.9^{a}	ND	$927.9b^{c}$	932.5^{a}
NaCl 200 mM							
Non-inoculated	1056.7^{e}	184.3^{d}	36.4^{f}	6.3^{e}	ND	435.1^{cd}	5^{e}
P. putida KT2440	1771.7^{e}	213.6^{d}	44.2^{f}	8.3^{e}	0.12^{c}	682.3^{bcd}	26^{e}
P. fluorescens SBW25	3411.6^{de}	257.5^{cd}	45.1^{f}	7.3^{e}	ND	926.7^{bc}	18.8^{e}
NaCl 1000 mM							
Non-inoculated	2946.8^{de}	725.8^{cd}	84.4^{def}	24.5^{cd}	9.4^{b}	307.9^{d}	80.8^{de}
P. putida KT2440	11107.9^{ab}	2947.6^{cd}	401.6^{ab}	64.6^{a}	ND	798.4^{bcd}	367.8^{bcd}
P. fluorescens SBW25	3742.3^{de}	1586.8^{cd}	121.1^{def}	26.3^{cd}	15.3^{b}	490.4^{cd}	120.8^{de}
Drought							
Non-inoculated	4233.5^{de}	1286.8^{cd}	78^{ef}	13.9^{de}	ND	413.3^{cd}	90.6^{de}
P. putida KT2440	5789.9^{d}	2502.9^{cd}	191^{cd}	44.6^{b}	17.5^{b}	892.9^{bc}	164.8^{cde}
P. fluorescens SBW25	5973.9^{c}	1709.5^{cd}	181.8^{de}	30.7^{bc}	17.4^{b}	570^{cd}	148.7^{cde}

ND: not detected. Means ($n = 3$). Different letters show a significant difference at $p \leq 0.05$. Unit: mg/kg.

drought stress displayed significantly higher Cl^- uptake in comparison to non-treated drought-stressed roots. The effect of *P. putida* KT2440 for increasing the Cl^- uptake was statistically more significant (29.5 mg/kg) than that of *P. fluorescens* SBW25 strain (25.8 mg/kg). In the case of Mn, PGPR applications depicted significantly enhanced uptake with statistically more significant uptake observed with *P. fluorescens* SBW25 application (121.2 mg/kg). Stress treatments significantly reduced Mn contents in non-treated barley roots. The enhancement in Mn uptake with PGPR application was not statistically significant when compared to non-PGPR-applied barley roots under 200 mM salt stress condition. In 1000 mM salt stress and also in drought stress conditions, PGPR applications significantly raised Mn level with respect to non-treated roots. *P. putida* KT2440 in 1000 mM salt stress (74.4 mg/kg) and *P. fluorescens* SBW25 in drought stress (50.4 mg/kg) showed a more significant improvement of Mn uptake. Similar to Mn, Fe contents were also increased significantly in PGPR-treated roots with the more significant effect observed for *P. fluorescens* SBW25 (457.1 mg/kg) inoculation under control condition. Stress applications showed a significant reduction of Fe contents in non-inoculated plants. Applications of both PGPR strains significantly increased Fe contents under 200 mM salt stress and drought stress conditions. In 1000 mM salt stress, *P. putida*KT2440-inoculated roots displayed significant (410.1 mg/kg) enhancement of Fe uptake. Co contents were found to be significantly higher in PGPR-treated barley roots with more significant effects observed for *P. putida* KT2440 (1.2 mg/kg) strain under control condition. Exposure of the stress conditions significantly reduced Co contents in non-inoculated roots. The increase of Co uptake with PGPR application in 200 mM salt stress was not statistically significant as compared to non-inoculated roots. However, in 1000 mM salt stress and also under drought stress, enhancement in Co in PGPR-treated roots was statistically

significant in comparison to non-treated roots. The effect of *P. putida* KT2440 was more pronounced than that of *P. fluorescens* SBW25 strain. Ni element showed a significant reduction in PGPR-treated roots with more significant reduction observed for *P. putida* KT2440 (0.0681 mg/kg) inoculation when compared to non-inoculated roots under control condition. Stress applications significantly reduced Ni uptake in non-inoculated roots. Increased uptake of Ni with PGPR applications was not statistically significant when compared to non-treated roots in 200 mM salt stress. In 1000 mM salt stress and drought stress, *P. putida* KT2440 (0.35 mg/kg and 0.32 mg/kg) inoculation depicted a significant increase in Ni uptake with respect to non-inoculated roots. Ni was not detected in *P. fluorescens*SBW25-inoculated drought-stressed roots. Cu reduced significantly in the non-inoculated root on the exposure of 200 mM and 1000 mM salt stress as well as drought stress. Applications of both PGPR strains significantly increased Cu uptake in 200 mM salt stress. Similarly, PGPR application also enhanced Cu uptake under 1000 mM salt stress and drought stress conditions. The effect of *P. putida* KT2440 was more pronounced than that of *P. fluorescens* SBW25 strain when compared to non-inoculated roots. *P. fluorescens* SBW25 (494.2 mg/kg) inoculated roots showed significantly higher Zn uptake under control condition. Exposure of the 200 mM and 1000 mM salt stress, as well as drought stress conditions, significantly decreased Zn contents in non-inoculated roots. The increased Zn contents due to PGPR applications were not found to be statistically significant in comparison to non-treated roots under 200 mM salt stress conditions. Applications of both PGPR strains significantly improved Zn uptake under 1000 mM salt stress and drought stress conditions. The effect of *P. putida* KT2440 was more pronounced than that of *P. fluorescens* SBW25 strain for enhancing the Zn uptake (Table 7).

3.9. Result Evaluation through PCA. PCA was used to investigate the relationship between the applied treatments with macro- and micronutrient uptake in leaves, stems, and roots of barley plants under control and stressed conditions. PCA1 of macronutrient uptake in leaves revealed that PC1, PC2, and PC3 accounted for 54.06%, 28.27%, and 14.88% of the data variation, respectively (Figure 2). PC1 was found to be associated with Mg, S, P, Al, and Si, and it showed strong correlation with KT2440 (Control), SBW25 (200 mM NaCl), and KT2440 (200 mM NaCl). PC2 was found to be associated with Ca and K, and it showed strong correlation with SBW25 (1000 mM NaCl) and KT2440 (1000 mM NaCl).

PCA2 of micronutrient uptake in leaves revealed that PC1, PC2, and PC3 accounted for 42.04%, 22.01%, and 14.75% of the data variation, respectively (Figure 3). PC1 was found to be associated with Cl, Mn, Fe, and Co, and it displayed strong correlation with non-inoculated (Control) and KT2440 (Drought). PC2 was found to be associated with Ni, Zn, and Cu, and it showed strong correlation with SBW25 (Drought and Control) and KT2440 (Control).

PCA3 of macronutrient uptake in stems revealed that PC1 alone explained 55.61% of the total variance and PC2 explained 32.62% of the total variance (Figure 4). PC1 was found to be associated with Mg, P, Al, and Si, and it showed strong relation with SBW25 (Drought, 200 mM NaCl, and 1000 mM NaCl), non-inoculated (Control), and SBW25 (200 mM NaCl). PC2 was found to be associated with Ca, K, and S, and it showed strong relation with SBW25 (Control) and KT2440 (Control).

PCA4 of micronutrient uptake in stems revealed that PC1 and PC2 accounted for 75.53% and 14.64% of the data variation, respectively (Figure 5). PC1 was comprised of Mn, Fe, Co, Ni, Cu, and Zn, and it showed strong correlation with KT2440 (Drought) and SBW25 (Drought). PC2 was comprised of Cl, and it showed strong correlation with SBW25 (1000 mM NaCl), KT2440 (1000 mM NaCl), and non-inoculated (1000 mM NaCl).

PCA5 of macronutrient uptake in roots revealed that PC1 accounted 71.48% and PC2 18.35% of total variance (Figure 6). PC1 was found to be associated with Mg, Ca, K, S, Al, and Si, and it showed strong relation with *P. putida* KT2440 (1000 mM NaCl). PC2 was found to be associated with P and showed strong relation with KT2440 (Drought), SBW25 (Drought), and SBW25 (1000 mM NaCl).

PCA6 of micronutrient uptake in roots revealed that PC1 and PC2 accounted for 76.02% and 14.25% of the data variation (Figure 7). PC1 was found to be associated with Mn, Fe, Co, Ni, Cu, and Zn, and it showed strong relation with SBW25 (Control) and non-inoculated (Control). PC2 was found to be associated with Cl, and it showed strong relation with SBW25 (Drought and 1000 mM NaCl).

4. Discussion

There is need to enhance the food production in order the meet the feeding challenge of the world in 2050. This could be possible through enhancing the production of food in limited available arable land that must be done in an environmentally safe manner. Unremitting use of chemical fertilizers reduces essential natural nutrients of fertile soil [30]. Imbalance of nutrients and low fertility of soil are the major challenges faced by the farmers, as the nutrient deficiencies are highly correlated with low productivity of crops as well as low nutrition value of food [31]. Therefore, there is a need to utilize alternate environmentally safe approaches. PGPR are beneficial microbes. PGPR increase the availability of nutrients in the rhizosphere region and hence stimulate the growth of their host plants by increasing the mobility, uptake, and enrichment of plant nutrients. They produce plant growth-promoting compounds and also play an important role in the rotation of macro- and micronutrients by altering the root morphology and consequently enhancing the root surface area for the enhanced uptake of these nutrients. Hence, they play an important role in the circulation of plant nutrients and reduce the need for chemical fertilizers [12, 32].

According to recent studies, microbes can help plants for coping with salinity and drought stresses. Although various mechanisms for PGPR-conferred stress tolerance in plants

Table 7: Effect of PGPR on micronutrients of barley roots under salinity and drought stress conditions.

	Cl	Mn	Fe	Co	Ni	Cu	Zn
Control							
Non-inoculated	12.1^{abc}	72.3^{c}	278.2^{c}	0.8^{bcd}	0.679^{a}	0.95^{bc}	355.8^{b}
P. putida KT2440	7.4^{c}	94.2^{b}	325.3^{bc}	1.2^{a}	0.0681^{de}	1.3^{ab}	357^{b}
P. fluorescens SBW25	9.8^{bc}	121.2^{a}	457.1^{a}	0.96^{abc}	0.516^{b}	1.5^{a}	494.2^{a}
NaCl 200 mM							
Non-inoculated	8.9^{bc}	5.9^{f}	34^{e}	0.14^{f}	0.039^{de}	0.06^{f}	27.5^{d}
P. putida KT2440	7.7^{c}	6.3^{f}	57.7^{de}	0.18^{f}	0.042^{de}	0.08^{ef}	28^{d}
P. fluorescens SBW25	6.3^{c}	6.6^{f}	54.5^{de}	0.16^{f}	0.041^{de}	0.1^{ef}	35.1^{d}
NaCl 1000 mM							
Non-inoculated	15.2^{abc}	22.6^{f}	60.5^{de}	0.141^{f}	0.058^{de}	0.21^{def}	52.2^{d}
P. putida KT2440	7.6^{c}	74.4^{c}	410.1^{ab}	1.1^{ab}	0.35^{c}	1.1^{ab}	504.3^{a}
P. fluorescens SBW25	26.7^{ab}	45^{d}	89.2^{de}	0.26^{ef}	0.084^{de}	0.43^{def}	64.1^{cd}
Drought							
Non-inoculated	13.5^{abc}	22.8^{ef}	41.8^{de}	0.125^{f}	0.12^{d}	0.3^{def}	48.9^{d}
P. putida KT2440	29.5^{a}	40.2^{de}	154.9^{d}	0.618^{cde}	0.32^{c}	0.59^{cd}	179.3^{c}
P. fluorescens SBW25	25.8^{ab}	50.4^{d}	158.4^{d}	0.499^{def}	ND	0.47^{de}	129^{cd}

ND: not detected. Means ($n = 3$). Different letters show a significant difference at $p \leq 0.05$. Unit: mg/kg.

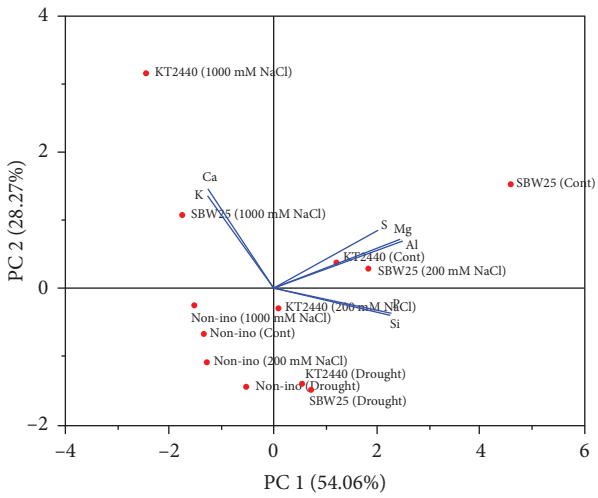

Figure 2: PCA of macronutrient uptake by PGPR in leaves of barley plants under control and stressed conditions. Ca: calcium, K: potassium, Mg: magnesium, Al: aluminium, S: sulfur, P: phosphorus, and Si: silicon.

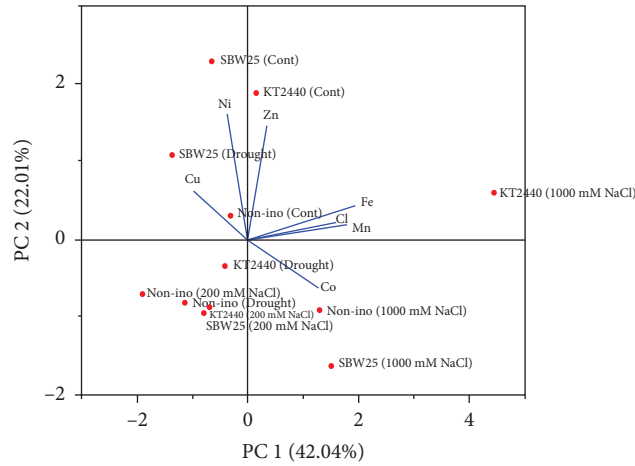

Figure 3: PCA of micronutrient uptake by PGPR in leaves of barley plants under control and stressed conditions. Cu: copper, Ni: nickel, Zn: zinc, Fe: iron, Cl: chlorine, Mn: manganese, and Co: cobalt.

have been proposed, the exact mechanism is still speculative. The stress ameliorating mechanisms followed by the PGPR application are complex and are not well understood. A complex network of signaling events that occur during the plant-microbe interaction regulates these mechanisms and subsequently ensure stress mitigation [33]. Salt stress causes the precipitation and depletion of available P, and phosphate solubilizing bacteria (PSB) can solubilize precipitated form of P and make them available to plants under salt stress [12, 34, 35]. PGPR do this by stimulating the ion transport systems in the root. Besides, H^+ ion production in the rhizosphere changes the pH sufficiently that helps in the mineralization of soil elements [36]. Rhizobacterial strains also assist in the provision of micronutrient like iron by producing low molecular weight and high affinity iron chelating siderophore agents [37]. Potassium solubilizing bacteria (KSB) such as *Pseudomonas* and *Bacillus* species are reported to enhance the K availability in soil for plant uptake through certain biological processes [38, 39]. Moreover, PGPR assist in the scavenging of free radicals by producing antioxidant enzymes. Besides, increased root surface area triggered by the beneficial soil bacteria helps in increasing the nutrient uptake [12, 40].

The most basic criterion for crop growth and yield is the efficient germination of seeds. In our study, inoculation of barley seeds with *P. putida* KT2440 and *P. fluorescens* SBW25 strains enhanced germination of barley seeds. Although germination percentage varied among the two species, both the inoculated treatments showed a significantly higher germination rate than the non-inoculated control (Figure 1). Our experimental results are in agreement with one of the previous studies where PGPR inoculation improved seed germination percentage in maize

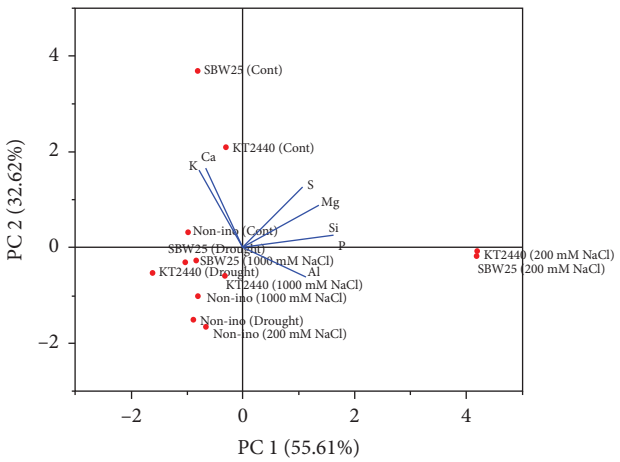

Figure 4: PCA of macronutrient uptake by PGPR in stems of barley plants under control and stressed conditions. Ca: calcium, K: potassium, Mg: magnesium, Al: aluminium, S: sulfur, P: phosphorus, and Si: silicon.

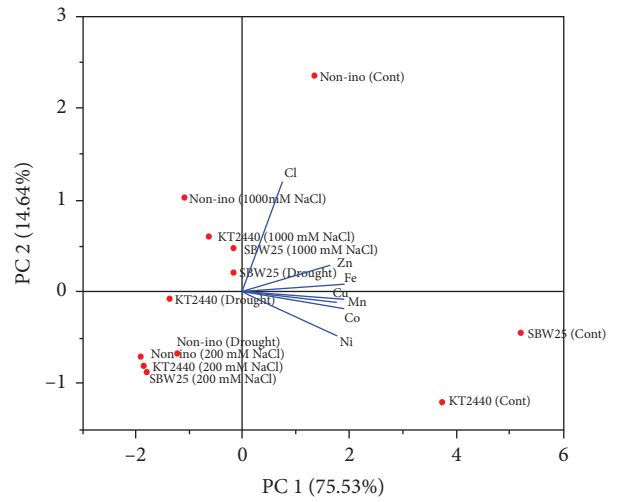

Figure 5: PCA of micronutrient uptake by PGPR in stems of barley plants under control and stressed conditions. Cu: copper, Ni: nickel, Zn: zinc, Fe: iron, Cl: chlorine, Mn: manganese, and Co: cobalt.

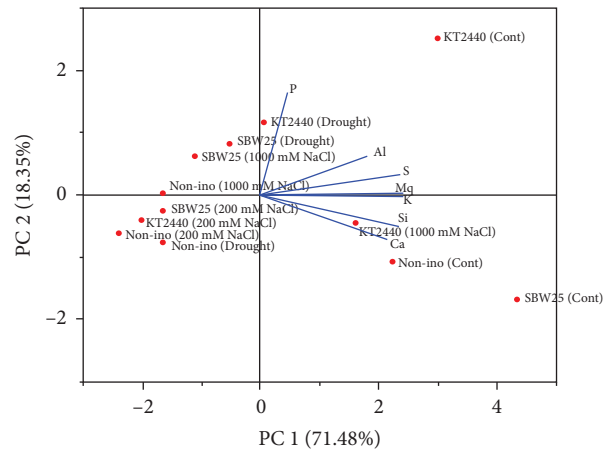

Figure 6: PCA of macronutrient uptake by PGPR in roots of barley plants under control and stressed conditions. Ca: calcium, K: potassium, Mg: magnesium, Al: aluminium, S: sulfur, P: phosphorus, and Si: silicon.

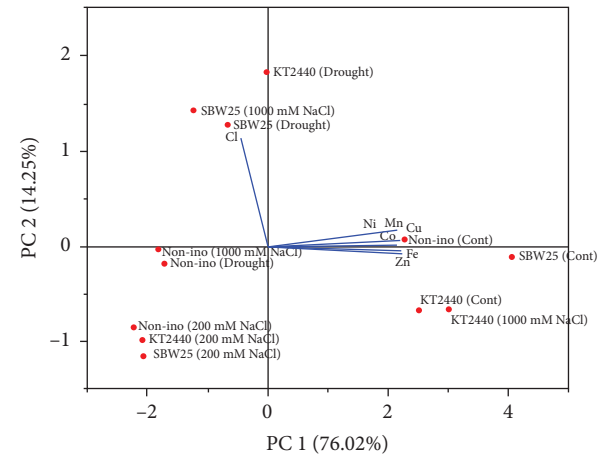

Figure 7: PCA of micronutrient uptake by PGPR in roots of barley plants under control and stressed conditions. Cu: copper, Ni: nickel, Zn: zinc, Fe: iron, Cl: chlorine, Mn: manganese, and Co: cobalt.

[41]. Enhanced seed germination might be due to attachment of PGPR to the seed surface and synthesis of growth phytohormones, which perhaps activate specific enzymes involved in starch assimilation and promote seed germination [41].

Salinity and drought are the major environmental stresses reducing the growth and development of plants. These stresses significantly reduce the growth traits such as plant height, fresh and dry biomasses, photosynthetic activity, and nutrient availability of barley plants [15, 42]. Moreover, they also induce overproduction of reactive oxygen species (ROS), causing lipid peroxidation and protein injury leading to programmed cell death [43]. For the determination of stress tolerance ability of plant, growth is an important attribute. Stress usually influences the growth and development of plants by affecting their root and shoot biomasses. The reduced growth rate is usually the initial response of any plant to salt or drought stress [44]. Basically, barley is considered as salt as well as drought-tolerant plant, but our results depicted a significant decrease in barley growth once exposed to 200 mM and 1000 mM NaCl stress treatment and also under the drought stress condition (Table 1). In one of the previously reported studies, it was shown that drought stress imposed at the vegetative stage significantly decreased growth of two selected genotypes of barley plants [45]. However, application of PGPR can significantly enhance growth by reducing the deleterious effects of salt or drought stresses as evident by the significant improvement of fresh and dry weights of shoots and roots of barley plants under our experimental conditions (Table 1). Similar findings of plant growth promotion and stress tolerance were also reported previously [25, 26, 46, 47].

Roots are also important plant organs playing an essential role in plant growth and development by controlling

the uptake of water and mineral nutrients. Environmental conditions are rarely optimum for the extensive and effective growth of plant roots [48]. Under stress, assimilation of CO_2 decreases, which is the major source of energy for plant growth and development, so eventually it reduces the root growth [49]. Under stress, a reduction in root length causes a decrease in plant biomass [50]. Our current assessment also showed a significant reduction of root length in non-inoculated stressed plants (Table 1). PGPR are well known for inducing longer roots [51]. Our study also proved the enhancement of root lengths with PGPR treatment in the stressed plants when compared to non-inoculated plants (Table 1). Indole-3-acetic acid (IAA) produced by the PGPR have ability to increase root length, size, and the number of root tip cells enabling plants to access nutrients more efficiently from the soil and ultimately improving plant under stressed conditions [52].

Maintenance of photosynthetic activity is necessary for alleviating the stress effect on plant growth [53]. Chlorophyll fluorescence reveals the integrity of the thylakoid membrane and the relative efficiency of electron transport from photosystem II (PS II) to photosystem I (PS I) [54]. Fv/Fm ratio is the most commonly used measuring parameter of chlorophyll fluorescence, which indicates the quantum efficiency of PS II [55]. We measured the Fv/Fm ratios of non-inoculated and PGPR-primed barley leaves; however, our study revealed statistically no significant enhancement of Fv/Fm ratio in PGPR-treated plants under control and stressed conditions (Table 1). A similar finding was also reported previously where the PGPR application was found to have no significant effects on the photochemical efficiency of PS II under stress conditions [56].

Performance index (PI) is another indicator of photosystem II functioning. PI is one of the most convenient parameters used for comparative studies of plant stresses [57]. It allows to assess the efficiency of photosystem II and to identify the eventual changes in the activity of photosynthetic apparatus caused by salt stress [58], drought stress [59], and other stresses. By analogy, water stress decreases PI, whereas high PI value implies favorable soil moisture conditions. Our study also showed significantly higher PI values in PGPR-treated plants under different stress treatments (Table 1).

Furthermore, this study identified the changes in nutrition profile contributing to salinity and drought tolerance in PGPR-inoculated barley plants under control and stressed conditions. For this purpose, the PIXE technique was used for the analysis of various macro- and micronutrients in various parts (leaves, roots, and stems) of barley plants.

Foods derived from the plants are an important source of minerals and proteins for the bulging population particularly in developing countries. Biofortification or increasing the bioavailable nutrients in staple crops is thought to be a feasible option. Among the various strategies used for the biofortification of micronutrients, PGPR play a role in the enhanced uptake of minerals from the rhizosphere. *P. fluorescens* has the ability to enhance N, P, K, Mg, Mn, Fe, and Zn nutrient availability as well as organic matter in the soil, which lessens the need of use of chemical fertilizers and thus facilitates in maintaining the ecological balance of soil [60, 61]. Our study also revealed statistically significant effects of PGPR application on the macronutrient uptake, e.g., Ca, Mg, K, P, S, Al, and Si (Tables 2, 4, and 6), and also on micronutrient uptake, e.g., Mn, Fe, Co, Ni, Cu, and Zn (Tables 3, 5, and 7), in barley plants under control conditions, but these mineral uptake responses were strain-specific (either *P. putida* KT2440 or *P. fluorescens* SBW25 or both strain applications). These findings show the potential role of these PGPR strains in the biofortification of food.

Besides, PGPR application was also found to be effective under stressed conditions. In our current investigation, drought and salt (200 mM and 1000 mM) stress applications significantly decreased macronutrients in non-inoculated barley plants. However, inoculation with PGPR helped in ameliorating these stress conditions by enhancing macronutrient uptake (Tables 2, 4, and 6 and Figures 2, 4, and 6). Similar findings were also reported by Numan et al. [62], where the enhanced absorption of Mg^{2+} and Ca^{2+} and reduced absorption of Na^{+} were observed in PGPR-treated cotton plants.

It has been demonstrated that PGPR inoculations increase the K^{+} concentration, which in turn leads to a high K^{+}/Na^{+} ratio in plants and thus plays an effective role in salinity tolerance [63]. Our current findings of K^{+} enhancement with PGPR application under salt stress conditions are in accordance with a previous study, where the application of *Azospirillum* increased the K^{+}/Na^{+} ratios in salt-stressed maize plants [38, 64, 65]. Similarly, a significant increase of K level was also observed in PGPR-inoculated drought-stressed barley roots, stems, and leaves (Tables 2, 4, and 6 and Figures 2, 4, and 6). According to one study, enhanced K uptake in plants was observed by the application of three PGPR strains *Azotobacter chroococcum*, *Rhizobium* sp., and *B. mucilaginosus* [46].

Various studies depicted the salinity-induced reduction in P concentrations in plants which might be because of ionic strength effects and also because of the poor solubility of Ca-P minerals. P improves drought tolerance by increasing stomatal conductance, photosynthesis, and cell membrane stability [66]. According to our present investigation, PGPR applications were found to be effective for significant enhancement of P in barley leaves and stems and roots under 200 mM, 1000 mM salt-stressed and drought-stressed conditions (Tables 2, 4, and 6 and Figures 2, 4, and 6). Our findings are in agreement with the previous study of Castillo-Aguilar et al. [67], where the PGPR-treated capsicum plants showed 40 and 50% increase uptake of P and K in comparison to non-treated plants.

According to our data, the application of PGPR also showed a significant increase of Al in treated barley plants under stressed conditions (Tables 2, 4, and 6 and Figures 2, 4, and 6). In a previous study, highest Mg, K, Al, and Zn values were observed with *P. fluorescens* rhizobacteria applications compared to control application, which could be linked to PGPR potential of enhancing Ca, N, P, K, Mn, Fe, and Zn nutrient elements [68]. Si not only improves plant growth but is also found to be valuable for the amelioration of

various plant stresses including nutrient imbalances [69]. It has been demonstrated that Si generates salt tolerance in various crops like rice, wheat, barley, maize, and tomato [70]. During salt stress, Si helps in preventing plant desiccation by lowering the transpiration rate. Our data showed significant improvements of Si uptake with PGPR applications in barley plants (Tables 2, 4, and 6 and Figures 2, 4, and 6).

Thus, inoculation of barley plants with PGPR strains helped in relieving the abiotic stresses. The higher nutrient accumulation in PGPR-treated leaves might be attributed to their proficiency in improving nutrient absorption and translocation [71]. Microbial-induced changes like change of rhizosphere pH through organic acid excretion and chelation with siderophores make the nutrients more accessible to plants. Most importantly they play an important role in enhancing the K^+/Na^+ ratio. In summary, PGPR can (1) enhance the nutrient availability by the acceleration of nutrient cycling [72]; (2) promote the absorption of nutrients through alteration in the root physiology; and (3) reinforce the Na^+ detoxification potential of the plant [73] and thus help in the enhancement of plant biomass.

Barley is well known for its ability to tolerate high Na^+ and Cl^- concentrations in leaf tissues [74]. Excessive concentrations of Na^+ and more importantly Cl^- affect various enzymes in plants and cause cell swelling, which lessens energy production. The high concentrations of Na^+ and Cl^- in the rhizosphere competitively interact with other nutrient ions for the binding site and transport protein in root cells [75]. Although Na^+ and Cl^- toxic ions can benefit plant adaptation to salt stress by the compartmentalization at the cellular and intracellular level, with time, toxicity builds due to high Na^+ concentration in the older leaves [76]. After the exhaustion of salt storage capacity in cells, salts accumulate in the intracellular spaces, which leads to dehydration and ultimate death of plant cells [77]. Microbes can modify the uptake of toxic ions and nutrients in roots by altering the host physiology, i.e., by regulating the expression or activity of ion transporter or through the modification of physical barriers around the roots, i.e., formation of the more extensive rhizosheath by bacterial exopolysaccharides or by directly reducing the foliar accumulation of toxic ions (Na^+, Cl^-), hence improving the overall nutritional status of both macro- and micronutrients. In our study, applications of PGPR showed a significant decrease of Cl^- contents in 200 mM salt-stressed barley roots and stems and a significant increase in stressed leaves. Similarly, in 1000 mM salt stress, Cl^- contents decreased significantly in PGPR-inoculated barley leaves, stems, and also in *P. putida*KT2440-inoculated barley roots (Tables 3, 5, and 7 and Figures 3, 5, and 7). Hence, suppression of toxic ion uptake with PGPR application can resume the growth of plants by protecting them from the toxic effects of salt ions and keeping the homeostasis of ions in the barley.

Cl^- is also well known for its role in cell hydric, osmotic, and turgor regulation [78]. The stomatal opening and closing are mediated by the fluxes of K^+ and associated anions, i.e., chloride and malate. A balance is probably needed between the use of Na^+ and Cl^- by the plant for the maintenance of turgor and to avoid chemical toxicity, which depends on the species and conditions. Impairment of stomatal regulation in Cl^--deficient palm trees was thought to be a major reason for wilting symptoms and plant growth depression [79]. The effects of water stress on Cl^- content are not well studied. In papaya, an increase in Cl^- as well as Na^+ concentrations in both leaves and roots was observed under water stress conditions [80]. Likewise, according to our present investigation, PGPR-inoculated drought-stressed barley leaves, stems, and roots depicted significant enhanced Cl^- content and hence helped the plant in coping with the drought stress condition (Tables 3, 5, and 7 and Figures 3, 5, and 7).

In addition to macronutrients, micronutrients also play an essential role in plant growth and development. Before the translocation of micronutrients to seeds, their uptake from the rhizosphere is the initial step in the process of nutrient accumulation in the plant, and PGPR are well known for the solubilization and supply of nutrients to plants [12, 32]. In our experimental conditions, PGPR inoculation led to an enhancement in the Mn, Fe, Co, Ni, Cu, and Zn contents in barley plants (Tables 3, 5, and 7 and Figures 3, 5, and 7), which indicate the possible role of PGPR in improving the translocation and mobilization of micronutrients under control and stressed conditions.

The results of the present investigation are consistent with those reported in the literature. Rana et al. [81] investigated PGPR capability for increasing the micronutrients in wheat plants and found a significant enhancement in relation to control. According to one study, salinity reduced Fe content in barley and corn [82], while another study depicted improved Zn and Fe uptake in PGPR-inoculated tomato plants. Similarly, Sharma et al. [83] found that applications of *P. putida*, *P. fluorescence*, and *A. lipoferum* in rice significantly increased micronutrients. Other researchers also reported similar results in different crops like increased micronutrients (Mn, Fe, Cu, and Zn) in the wheat [84] and barley plants [85]. Likewise, the findings of various other studies are also in accordance with our current findings [86–88].

5. Conclusions

More food production through meeting the environmental stress challenges is the need of time for satisfying the food demand of ever-growing world population. Moreover, for sustainable agriculture, there is a need to replace synthetic chemical fertilizers (costly and harmful for human health) with environmentally safe biological agents. This comprehensive study was designed to know the effects of beneficial PGPR on nutritional profile of various parts (leaf, stem, and root) of barley plants under abiotic stress conditions. The findings of this study demonstrated that the inoculation of barley plants with the *Pseudomonas* species strains, i.e., *P. putida* KT2440 and *P. fluorescens* SBW25, proved to be very helpful in conferring tolerance against salinity and drought stresses possibly through improving the physiological parameters (seed germination, shoot and root biomasses, and photosynthetic activity) as well as through the

improvement of elemental profile. Our PIXE analysis (except for 200 mM salt-stressed leaves) confirmed the lower uptake of Cl^- under salt stress conditions and higher uptake under drought stress conditions along with the enhancement of macronutrients, i.e., Mg, Ca, K, P, S Al, and Si, and micronutrients, i.e., Mn, Fe, Co, Ni, Cu, and Zn, in PGPR-inoculated barley plants under salinity and drought stress conditions, supporting the mechanism that PGPR could decrease the acquisition of toxic ions, maintain the intracellular ion homeostasis, and increase the availability of nutrients in plants. The results of this study suggest that these bacterial strains have the ability to improve the productivity of barley plants by reducing the adverse effects of salinity and drought stresses, and hence these *Pseudomonas* species can be used to benefit barley plants or related crops under stressed conditions.

Data Availability

The data used to support the findings of this study are available from the corresponding author upon reasonable request.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

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