



Exploring the Role of Microorganisms in Enhancing Pearl millet Growth and Productivity

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Abstract: Arid and semi-arid regions are vast reservoirs of hardy organisms, including plant species and the associated microorganisms. An important crop of these regions is the pearl millet which serves as a source of food and feed, especially in the rainfed tracts. The inherent hardiness of the crop has attracted researchers from all over the world to unveil its underlying biology as well as to assess the role of associated microflora in imparting the hardiness that allow pearl millet to survive under very harsh climatic conditions. The pearl millet-associated microbiome consists of the rhizospheric (within the rhizosphere), phyllospheric (on the leaf surfaces) and endophytic (within the internal tissues) microbial communities. These microorganisms play a critical role in plant health and growth by improving the uptake of essential nutrients, protecting plants from pathogens, and enhancing drought and disease tolerance. This has been demonstrated in several studies wherein microbial inoculation of pearl millet resulted in increased protection from diseases like downy mildew, enhanced drought and high temperature tolerance and improved plant characteristics including yield. Exploring native stress tolerant and plant growth promoting microorganisms and unraveling their effect on molecular biology and biochemistry of pearl millet plants holds huge potential for their utilization in sustainable arid and semi-arid agriculture systems.

Key words: Downy mildew, drought stress, microbiome, mycorrhiza, pearl millet, PGPR.

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] contributes nearly half of the global millet production, and is grown on 30 mha area of the arid and semi-arid tropical regions of Asia and Africa (Satyavathi *et al.*, 2021). In India, pearl millet is the fourth most widely cultivated food crop after rice, wheat, and maize, with an area of 6.93 mha, production of 8.61 mt and average productivity of 1,243 kg ha⁻¹ (Anonymous, 2020; Reddy *et al.*, 2021). Western Rajasthan has the largest area under pearl millet (4.6 mha) and the highest production (2.8 mt) in the country with a productivity of 400 kg ha⁻¹ (APEDA, 2023). Western Rajasthan encompasses 62% of the total arid area of India, characterized by high solar incidence, coupled with relatively high wind velocities, sandy soils with low fertility, poor microbial activity and low organic matter content

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(Singh and Joshi, 1988). The inherent climate resilience of pearl millet plant, attributed by the C4 photosynthetic machinery, enables it to survive under these harsh conditions and to be the dominant cereal crop of these regions by providing food and dry fodder in livestock-based farming systems.

Like climate-hardy crops, arid regions are also a vast reservoir of stress tolerant microorganisms, including bacteria, archaea, fungi, protozoa, and nematodes, which are known to play an important role in maintaining the health of arid soils. They are responsible for operating diverse processes, such as decomposition of organic matter, cycling of nutrients, and maintenance of soil fertility. Besides, they provide a variety of benefits to plants, including improved root growth, increased nutrient uptake, enhanced tolerance to multiple abiotic stresses, bio-control of plant pathogens, improved plant growth and enhanced crop yield (Mohanram and Kumar, 2019). Bioprospecting activities to tap native microbial resources associated with extreme habitats would unveil novel, underutilized microbes and their derived bio-molecules with immense potential in sustainable agriculture systems (Saritha *et al.*, 2015).

The beneficial association of plants and soil microbes is an important aspect in sustainable agriculture. Plant rhizosphere is considered as hotspot of microbial activity wherein diverse soil microorganisms interact not only with each other, but also with the host plants. The association of these rhizospheric soil microorganisms with plants confers protection from several biotic and abiotic stressors, thereby enhancing their adaptability to hostile environments, besides promoting crop productivity through various mechanisms. Hence, combining the climate-hardiness of pearl millet and the benefits of the associated soil microflora has enormous potential in sustainable arid agriculture. This review aims to collate information on microbial community associated with rhizosphere, phyllosphere and endosphere of pearl millet and the possibility of exploiting their potential to sustainably enhance pearl millet production, besides improving soil fertility.

Methodology

The study is based on literature review and is designed to cover the beneficial aspects and

scope of plant-microorganism interactions in facilitating growth and productivity of pearl millet. The discussion is mainly focused on the plant-associated microbiome of millets, in general, and pearl millet, in particular.

Millet-associated soil microbial community

Roots and soils are considered key components for adaptation of crops since they impact the availability of water and minerals. The properties of structural units of soil determine overall soil physical and mechanical properties such as retention and movement of water, aeration, and temperature that have direct impacts on plant growth, and this in turn is strongly influenced by carbon content of soil (Haynes and Swift, 1990). Plants are known to exude ~11% of net photosynthetically fixed carbon and 10–16% of total plant nitrogen as rhizodeposits via roots into the rhizospheric region (Jones *et al.*, 2009). The localized availability of this labile carbon and other readily utilizable nutrients provide inputs for bioprocesses (Kuzyakov and Blagodatskaya, 2015). Components of plant root exudates get varied, both qualitatively and quantitatively, depending on the nutritional status of the plant and the plant growth stage, leading to a plant-driven selection of specific rhizosphere microbial communities (Mohanram and Kumar, 2019). This natural selection of associated soil microflora by millets has been proved by several researchers (Table 1) and this phenomenon contributes to the adaptation mechanisms of the plants for their growth and survival in harsh environments.

Comparison of the bacterial microbiota composition in the root-adhering soil fraction of nine pearl millet lines revealed a dominance of the phyla *Proteobacteria*, *Firmicutes*, and *Actinobacteria* (Ndour *et al.*, 2017). These phyla contain agriculturally important bacterial genera predominantly belonging to *Pseudomonas*, *Bacillus*, and actinomycetes, respectively. Also, 184 strains of culturable exo-polysaccharides-producing bacteria have been obtained from the rhizosphere of some pearl millet lines, representing members from *Rhizobiales* and *Bacillales* (Ndour *et al.*, 2017). Recent research has shown that domesticated and wild species of pearl millet display contrasting patterns of abundance and co-occurrence in their root mycobiome (Mofini *et al.*, 2022).

Table 1. Microbial diversity associated with the rhizosphere of millets

Host plant	Dominant members of the rhizosphere microbiome	Role of rhizosphere microbiome	Reference
Pearl millet (<i>Pennisetum glaucum</i>)	Dominant phyla (abundance > 20%) belonged to the <i>Proteobacteria</i> , <i>Firmicutes</i> , and <i>Actinobacteria</i> , and to a lesser extent to <i>Bacteroidetes</i> , <i>Acidobacteria</i> , <i>Chloroflexi</i> , <i>Planctomycetes</i> and <i>Gemmatimonadetes</i> (abundance < 20%)	Carbon, nitrogen, and sulphur cycling, suppression of plant-pathogens	Ndour <i>et al.</i> (2017)
Pearl millet (<i>Pennisetum glaucum</i>)	Core fungal taxa belonged to four fungal phyla: Ascomycota, Basidiomycota, Chytridiomycota and Glomeromycota. Ascomycota, the most dominant, represented from 63.8 to 97% of the core OTUs with 22 families, with <i>Pleosporaceae</i> (31 OTUs) and <i>Nectriaceae</i> (31 OTUs) with relative abundance of 4.9% and 4.46%, respectively, being the dominant families	Decomposers and nutrient recyclers	Mofini <i>et al.</i> (2022)
Finger millet (<i>Eleusine coracana</i>)	Abundance of culturable <i>Bacillus cereus</i> and <i>Paenibacillus</i> spp., <i>Pseudomonas</i> , <i>Serratia</i> , <i>Stenotrophomonas</i> , and <i>Streptomyces</i> , and fungal genera <i>Ampelomyces</i> , <i>Coniothyrium</i> , and <i>Trichoderma</i>	Plant growth promotion, nutrient uptake, and hormonestimulation	Dheeman <i>et al.</i> (2017), Choudhary <i>et al.</i> (2020)
Foxtail millet (<i>Setaria italica</i>), Pearl millet (<i>Pennisetum glaucum</i>), Prosomillet (<i>Panicum miliaceum</i>), Japanese millet (<i>Echinochloa esculenta</i>)	The predominant indicator taxa under drought belonged to <i>Actinobacteria</i> , while indicator taxa of watered condition belonged to <i>Firmicutes</i> and <i>Chloroflexi</i>	Decomposition, carbon and nutrient cycling	Simmons <i>et al.</i> (2020)

They reported that the fungal communities associated with pearl millet were significantly structured according to sites and the plant type, with a higher fungal diversity in cultivated compared to wild pearl millet (Mofini *et al.*, 2022). Moreover, shift in microbial community in pearl millet root zone soils have been demonstrated with intercropping. For instance, intercropping of pearl millet with the shrub, *Guiera senegalensis* in Senegal, Africa, shifted certain predicted bacterial metabolic pathways and enriched some bacterial and fungal genera, leading to an abundance of genera having plant growth promoting properties like *Enterobacter* and *Paraburkholderia* (Mason *et al.*, 2022).

These studies illustrate the vastness in millet-associated soil microbiome and the influence of millets on rhizospheric soil microbial diversity. Pearl millet acts as a potential reservoir of these soil microorganisms which play crucial roles for agricultural benefits such as improved plant health and increased soil fertility.

Millet-associated phyllospheric and endophytic microbiome

In an ecological perspective, plants are more than individual entities as they co-habit with the plant core-microbiota that impact plant

growth, yield and productivity. These include the phyllospheric microorganisms that survive on plant's leaf surfaces and the endophytic microorganisms that survive within the internal plant tissues (Mohanram and Kumar, 2019). This microbiome plays vital roles in the host plant's nutrient uptake, metabolic capabilities and tolerance to biotic and abiotic stresses (Bulgarelli *et al.*, 2013).

An earlier study by Kumar and Balasubramanian (1981) reported the analysis of phyllosphere microflora in pearl millet and reported that the resistant pearl millet cultivar (PHB-14) had a significantly higher population of fungi, gram-positive and gram-negative bacteria, as compared to susceptible cultivar (NHB-3) under healthy and diseased situations. Among the fungi isolated, *Cladosporium* dominated the phyllosphere of resistant cultivar under the influence of downy mildew, indicating the role of phyllosphere microflora in biotic stress tolerance (Kumar and Balasubramanian, 1981). The presence of C1-compound utilizing *Methylobacterium*, a ubiquitous symbiont in the phylloplane, has been found to enhance barnyard millet growth and yield (Poorniammal *et al.*, 2020). Several diazotrophic bacteria (fix gaseous nitrogen) has

been reported in the phyllosphere of foxtail millet (*Setaria italica* L. Beauv) (Mohammed, 2000).

Apart from the phyllospheric microorganisms, endophytes also play a role in maintaining plant health. Endophytes, mostly represented by bacteria and fungi, are frequently reported from all parts of the plant including root, stem, leaves, fruits, and seeds. In a recent study, seed endophytic bacteria, *Kosakonia cowanii*, *Bacillus subtilis*, *Bacillus tequilensis*, *Pantoea stewartii*, *Paenibacillus dendritiformis*, *Pseudomonas aeruginosa* and *Bacillus velezensis* were obtained from pearl millet seeds (Kumar *et al.*, 2021). These isolates were found to be plant growth promoting and inhibited the growth of fungal phytopathogens, mainly *Fusarium* sp. In another study, 102 endophytic *Bacillus* strains from root, leaf and stem of pearl millet plants were isolated and were found to belong to the species, *Bacillus albus*, *B. amyloliquefaciens*, *B. aryabhatai*, *B. halotolerans*, *B. haynesii*, *B. pacific*, *B. paramycoides*, *B. proteolyticus*, *B. pumilus*, *B. subtilis*, *B. siamensis*, *B. tequilensis*, *B. wiedmannii* and *B. zhangzhouensis* (Kushwaha *et al.*, 2020). Endophytic *Bacillus* strains have been reported to enhance pearl millet growth and nutrient uptake, especially under conditions of low soil phosphorus, because of their ability to solubilize phosphates, produce siderophores and indole-acetic acid (IAA) (Ribeiro *et al.*, 2018). Even diazotrophic endophytic bacteria such as *Pseudomonas aeruginosa* have been found to be associated with pearl millet (Gupta *et al.*, 2022). Similarly, the natural resistance of finger millet to various fungal pathogens including *Fusarium* sp. has been attributed to the endophytic microbes which produce antifungal compounds *viz.* viridicatol, tenuazonic acid, alternariol, and alternariol monomethyl ether (Mousa *et al.*, 2015). Antagonistic activities of bacterial endophytes obtained from millets against *Rhizoctonia solani* in foxtail millet has also been reported (Reddy and Shivaprakash, 2018). In another study isolated bacterial species belonging to the genera *Pantoea*, *Pseudomonas*, *Enterobacter*, *Sphingobacterium*, *Microbacterium* and *Curtobacterium* from finger millet seeds and were found to produce IAA, were able to grow on nitrogen free medium and solubilized phosphate (Misganaw *et al.*, 2019). More interestingly, Misganaw *et al.* (2019) also reported geo-specific variations in

the distribution of various taxonomic groups of endophytes along with differences in their plant growth promotion potential.

The phyllospheric and endophytic components of the millet-associated microbiome along with the soil microbiome are often involved in nutrient cycling, nutrient uptake, plant protection from pathogens and plant growth promotion and hence, have immense potential to be utilized in developing microbial formulations for boosting crop growth, yield and productivity. However, the composition of these microbiomes is highly dependent on the plant species, environment, and the season. To better understand the impact of these plant-associated microbiomes, unraveling the mechanisms involved in the plant-microorganism inter-relations is warranted.

Biochemical and molecular mechanisms underlying the pearl millet-microorganism interaction

Microorganisms find a range of uses in improving pearl millet growth, ranging from their direct effects in enhancing nutrient mobilization and plant nutrient uptake to indirect effects by enhancing tolerance to biotic and abiotic stresses (Fig. 1). Plant growth promoting bacteria are known to enhance plant growth directly by producing phytohormones like IAA (indole-3-acetic acid), IBA (indole butyric acid), GA (gibberellic acid), by producing siderophores, known as Fe-chelating compounds that supply Fe to plants and minimize competition from pathogens, by producing HCN (hydrogen cyanide) which is deleterious to harmful microorganisms, by fixing nitrogen in soil, by solubilizing and mobilizing nutrients like phosphorus (Ahmad and Kibret, 2014). PGPR are also known to produce ACC deaminase enzyme, which is responsible for dissociation of stress induced ACC (1-aminocyclopropane-1-carboxylate), secreted as root exudates, which otherwise gets forwarded to produce ethylene that has a drastic impact on physiology, growth and development of plants (Gupta and Pandey, 2019).

Plant growth promoting *Pseudomonas* sp. was found to improve pearl millet plant height, fresh weight, dry weight and leaf area over the control, simultaneously offering 59.7-73.3% protection against downy mildew, caused by

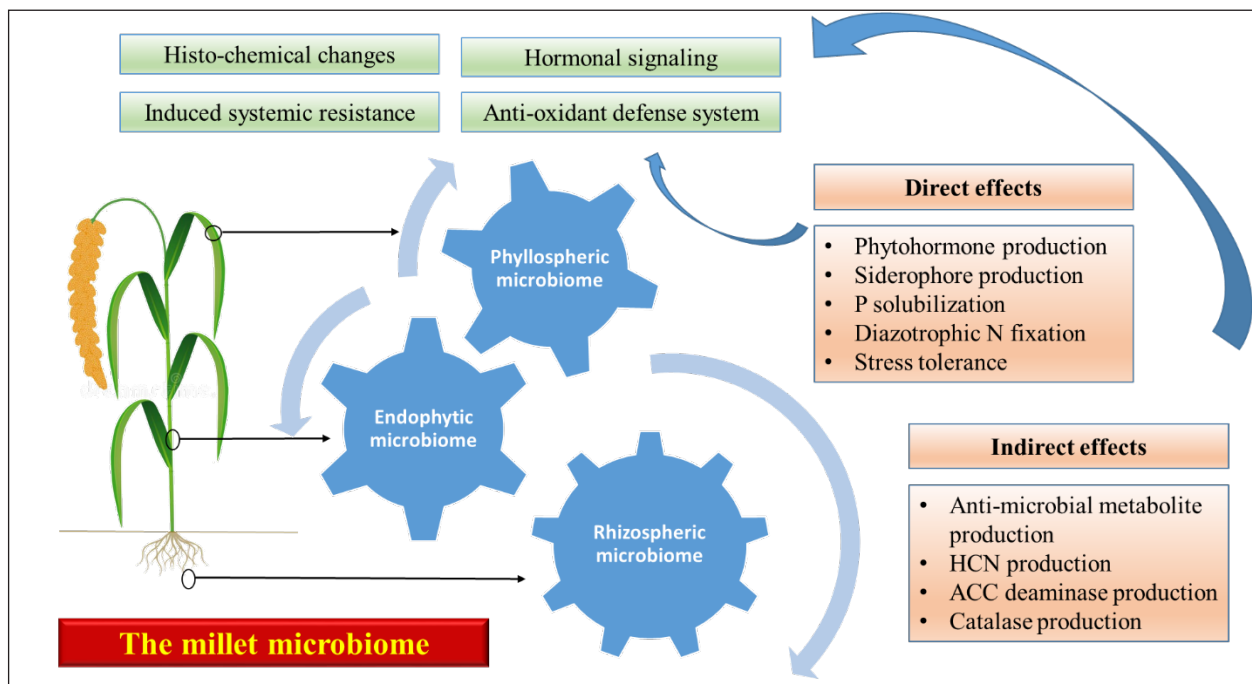


Fig. 1. The role of millet-associated microbes in enhancing plant growth, yield and productivity

Sclerospora graminicola (Jogaiah *et al.*, 2010). The plant growth promoting rhizobacteria belonging to the genus *Bacillus* - *B. pumilus* and *B. subtilis* - were reported to offer 40-50% protection, compared with the untreated control (Raj *et al.*, 2003). *B. pumilus* mediated induced systemic resistance (ISR) was found to be associated with the expression of hypersensitive response (HR) and enhanced lignification, in addition to the increased expression of the defense enzymes β -1,3-glucanase, chitinase, phenylalanine ammonia lyase (PAL), peroxidase (POX), and polyphenol oxidase (PPO) (Raj *et al.*, 2012). Similarly, inoculation of pearl millet with *Trichoderma hamatum* was reported to significantly enhance the activities of defense enzymes such as glucanase, peroxidase, phenylalanine ammonia-lyase, and polyphenol oxidase along with over-expression of pathogenesis-related (PR) proteins PR-1, PR-5, cell wall defense HRGPs (Hydroxyproline-rich glycoproteins) and upregulation of salicylic acid biosynthesis gene, isochorismate synthase (Siddaiah *et al.*, 2017). These cellular mechanisms are pivotal for the mounting systemic immunity in pearl millet against downy mildew pathogen upon microbial inoculation.

Bacillus sp. have also been utilized for induction of drought tolerance in pearl millet.

Inoculation of pearl millet with ACC deaminase producing PGPR (Plant Growth Promoting Rhizobacteria)- *Bacillus amyloliquefaciens* showed a 3.3 and 1.8 fold decrease in the relative expression of drought-responsive factor (DREB-1E) and ethylene-responsive factor (ERF-1B), respectively and an increase of 2.2 and 2.9 fold in the relative expression of APX1 (ascorbate peroxidase) and SOD1 (superoxide dismutase), respectively over control, indicating the activation of an enzymatic anti-oxidant defense system in pearl millet upon simulated drought stress condition (Murali *et al.*, 2021). Recently, the PGPR *Shewanella putrefaciens* and *Cronobacter dublinensis* were also found to enhance drought tolerance in pearl millet by modulating hormones and stress-responsive genes. The expression level of genes involved in phytohormone biosynthesis (SbNCED, SbGA20oX, SbYUC) and coding drought-responsive transcription factors (SbAP2, SbSNAC1 PgDREB2A) was significantly higher in inoculated plants as compared to uninoculated plants (Manjunatha *et al.*, 2022). The Arbuscular Mycorrhizal Fungi (AMF), *Rhizophagus aggregatus* and *Funneliformis mosseae* were found to ameliorate the negative effects of temperature stress in millet lines by increasing the chlorophyll concentration, root dry weight and shoot dry weight as compared to non-inoculated plants (Ndeko *et al.*, 2022).

Unraveling different mechanisms of microorganism-mediated plant growth promotion in pearl millet have gained enormous interest with recent research and development. The involvement of numerous biomolecules and signaling pathways has been implicated in the plant-microorganism crosstalk by several researchers. Hence, plants and microorganisms interact in complex ways, providing mutual benefits and further research to unlock these aspects could lead to advancements in agriculture, food security, and biotechnology.

Current status and future prospects

Literature review suggests that research has primarily focused on exploring the role of microorganisms in enhancing biotic stress tolerance in pearl millet. Several researches have evaluated plant-growth promoting bacteria and fungi for their ability to impart host tolerance to downy mildew. This is due to the innate climate-hardiness of the crop attributed to various biochemical and physiological mechanisms that render the crop's adaptation to arid and semi-arid conditions. Transcriptomic studies have revealed the role of differentially expressed genes that participate in plant hormone-related signaling pathways and oxidoreductase pathways in pearl millet that contribute to the crop's drought stress tolerance (Ji *et al.*, 2021). Imparting abiotic stress resilience has been another area of research which has garnered lots of interest lately, especially under the changing climate scenario. Rhizobacteria, endophytes and mycorrhizal fungi are the prime candidates for such studies. Recent developments in "omics-based" research have even tried to understand the molecular biology behind these plant-microorganism interactions, a few of which have been detailed out in an earlier section.

There are a few studies showing the direct impact of beneficial microorganisms in improving pearl millet plant characteristics. Joshi and Rao (1989) reported that *Azospirillum brasiliense* inoculation on pearl millet increased tillers by 37.9%, heads by 44.3% and test weight by 32.1%. Positive effects of phosphate solubilizing bacteria in utilizing native P in arid soils in pearl millet has also been recorded (Tarafdar *et al.*, 1991). The application of *Serratia marcescens*, *Pseudomonas* sp. and *Bacillus circulans* along with composts

was found to significantly increase the growth of pearl millet in terms of shoot length, leaf area, root length density, and plant weight, by 80% in glass house conditions (Hameeda *et al.*, 2006). Similarly, field application of *Azospirillum* along with recommended dose of FYM and 75% recommended dose of chemical fertilizers was found to enhance pearl millet plant height, number of leaves per plant, shoot and root dry biomass and nutrient (N, P, K) uptake (Rekha *et al.*, 2018). In another study, combined application of *Pseudomonas fluorescens*, *Azotobacter chroococcum*, *Azospirillum lipoferum*, and *Acetobacter diazotrophicus* with the fungus *Trichoderma viride* in pearl millet crop improved the plant height, dry weight, ear length, grain and stover yield, grain quality (58.9% protein and 17% carbohydrate), nitrogen uptake (grain 59.03 and stover 79.76 kg ha⁻¹) and phosphorus uptake (grain 9.21 and stover 8.73 kg ha⁻¹) (Singh *et al.*, 2017).

However, further research is needed in assessing the performance of beneficial microorganisms in realizing enhanced yield and yield attributes of pearl millet, under actual field conditions. This would require rigorous bioprospecting of beneficial microorganisms associated with pearl millet followed by their screening based on multiple plant growth promoting parameters so as to select for the better performing ones. The utilization of microorganisms native to arid and semi-arid regions also have an added advantage of the cultures being adapted to the harsh environmental conditions, thereby having greater chances of survival. Utilizing these organisms, either alone or in combination, holds great potential in sustainable management options. Renewed interest in research on millets and deep insights into the mechanisms of microorganism mediated phytostimulation would pave the way to obtain more competent and smart microbial strains which may work to enhance pearl millet growth and productivity under diverse agro-ecological conditions.

Conclusion

In conclusion, the role of microorganisms in pearl millet growth is highly significant and should not be overlooked. The presence of beneficial microorganisms can help improve soil fertility, nutrient availability and crop yield. Furthermore, microorganisms can also help

protect pearl millet against certain diseases and also enhance their abiotic stress resilience. Therefore, it is essential to understand and utilize the beneficial roles of microorganisms in pearl millet production systems.

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