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Biodiversity, mechanisms, and potential biotechnological applications of minerals solubilizing extremophilic microbes: A review

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ABSTRACT

The earth's surface consists of arid, semi-arid, and hyper-arid lands, where life is profoundly challenged by harsh conditions such as temperature fluctuations, water scarcity, high levels of solar radiations, and soil salinity. The harsh environmental conditions pose serious consequences on plant survival, growth, and productivity accessibility of nutrients reduces. To cope with the harsh environments and increase plant productivity, an extremophilic microbe has attracted agriculturists and environmentalists. The extremophilic microbes, adapted to extreme environmental conditions, offer an unexploited reservoir for biofertilizers, which could provide various forms of nutrients and alleviate the stress caused by the abiotic factors in an environment friendly manner. Worldwide, minerals solubilizing extremophilic microbes are distributed in various hotspots and belong to three domains of life including, archaea, bacteria, and eukarya. The minerals solubilizing extremophilic microbes belongs to diverse phyla, namely, Ascomycota, Actinobacteria, Basidiomycota, Bacteroidetes, Crenarchaeota, Deinococcus-Thermus, Euryarchaeota, Firmicutes, and Proteobacteria. Mineral solubilizing extremophilic microbes achieve the mineral solubilization of phosphorus, potassium, zinc, and selenium by secreting special compounds such as organic acid, exopolysaccharides, and different enzymes. Consequently, extremophilic microbes are becoming increasingly important in agriculture, industries and environmental biotechnology as well, paving the way for novel sequencing technologies and "metaomics" methods, including metagenomics, metatranscriptomics, and metaproteomics. The extremophilic microbial diversity and their biotechnological application in agriculture and industrial applications will be a milestone for future needs. The present review deals with biodiversity, mechanisms and potential biotechnological applications of minerals solubilizing extremophilic microbes.

1. INTRODUCTION

Food production per unit surface area must be considerably expanded to fulfill the rising population's demand as is expected, by 2050, the food demand is expected to grow up to 70%. Agricultural food production is largely affected by various abiotic stresses which lower the nutrients accessibility rate of the plants. Various abiotic factors of the environment such as acidity, alkalinity, drought, salinity, and low/high temperature are known to affect the production of crops. It has been estimated that the world's maximum land is facing harsh environmental conditions [1]. Globally, 15% of the soil is acidic, 6% has high salt concentration, approximately 57% of the soil is under cold stress, and more than 60% of the land is affected by drought [2,3]. Under such harsh environmental conditions the production of

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food is not be possible without additional inputs. Modern agriculture has largely expanded agricultural productivity and contributed significantly to the objective of food access and poverty alleviation through utilization of agrochemicals. The widespread and unrestricted use of agrochemicals has resulted in the contamination of food, surface, groundwater, soil salinization, and pathogen resistance to many chemical agents cause serious effects on health of humans and food safety. Moreover, the physical, chemical, and biological health of cultivable soils has also declined due to overexploitation of chemicals. The food demand fulfillment of ever-growing population needs more excellence for enhancement of crop productivity in the 21st century.

The extremophilic microbes thriving in harsh environmental conditions could serve as bioinoculants having plant growth-promoting ability which enhance the growth and yield of crops grown under abiotic stress conditions [4]. Extremophilic microbes have been known to thrive in environments having high concentrations of heavy metals, salt, organic solvents, radiation exposure, toxic waste; low and high temperature, pH, and pressure [5]. The microbiota surviving in such harsh conditions belongs to all three domains of life including bacteria, archaea, and eukarya. The extremophilic microbiomes belong to various phyla such as Ascomycota, Actinobacteria, Basidiomycota, Bacteroidetes, Crenarchaeota, Euryarcheota, Firmicutes, Deinococcus-Thermus, and Proteobacteria. The discovered extremophile PGP (plant growth promoting) bacteria included *Arthrobacter, Bacillus, Burkholderia, Brevundimonas, Citricoccus, Cocuria, Exigobacterium, Flavobacterium, Lycinibacillus, Methylobacterium, Mycobacterium, Paenibacillus, Pseudomonas, Providencia, Serratia,* and *Xanthinobacterium* [6-8]. Among all archaebacteria are known to have high flexibility and ability to survive in harsh environmental conditions. The extremophilic microbes promote plant through various mechanisms including the production of hydrolytic enzymes, hormones (cytokinin and gibberellic acids), solubilization and chelation of nutrients (phosphorus, potassium, zinc, iron, and selenium) which helps them to survive in such conditions. The microbial survival mechanism could help in the production of the plants.

The extremophilic microbiome plays a substantial role in plant growth, nutrient uptake as well as stress alleviation. The stress-adaptive microbes has the ability to produce extracellular hydrolytic enzymes (amylase, β-glucosidase, β-galactosidase, chitinase, cellulase, laccase, lipase, pectinase, protease, and xylanase), anti-freezing compounds could alleviate the abiotic stress through 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity. The mineral solubilizing extremophilic microbiomes also have a wide range of applications in various fields such as biodegradation, chemical processing, bioconversion of hemicellulose, dairy industry, composting, detergent industry, food industry, leather industry, feed industry, molecular biology, cellulose, and paper industry. The present review focus on the biodiversity, mechanism of plant growth promotion under abiotic stress and "omics" approaches along with their biotechnological application of mineral solubilizing extremophilic microbiomes.

2. MINERAL SOLUBILIZING EXTREMOPHILIC MICROBES

2.1. Archaea

Archaea are single-celled prokaryotic microbes with unique phenotypic and molecular characteristics, differentiating them from other domains of life, bacteria, and eukaryotes [4]. They are the most common microbes found in harsh conditions such as ocean floor, hot water, seawater, low temperature, dry soil environments, alkaline and acidic conditions, acute anoxia, arid, and semi-arid soils [9,10]. They are also known to survive in high-salinity concentrations by maintaining the intracellular osmotic pressure equal to or greater than that extracellular environment [11]. Different mineral solubilizing archaea species belonging to phylum Euryarchaeota and Crenarchaeota have been reported from different extreme environments. Some species of archaea, including *Halolamina, Halosarcina, Halostagnicola, Halobacterium, Haloarcula, Halococcus, Haloterrigena, Haloferax, Natrialba, Natrinema*, and *Natronoarchaeum* have been sorted out from halophilic plants (*Abutilon, Cenchrus, Dicanthium, Suaeda nudiflora,* and *Sporobolous*) from hypersaline regions and exhibit phosphorus solubilization activity [12]. In a similar report, P-solubilizing archaea *Haloferax* sp. was reported from sediment and brine from a solar saltern [13].

2.2. Bacteria

Bacteria make up a large domain of prokaryotic microbes and diverse species have been found in various extreme habitats including glacial, lakes, ocean, hot water, cold water, periglacial, dry soil, and acidic and alkaline soil [14]. Diverse species of bacteria belonging to phylum Actinobacteria, Bacteroidetes, Cyanobacteria, Chlamydiae, Chloroflexi, Firmicutes, Gemmatimonadetes, Nitrospirae, α/β/γ/δ-Proteobacteria, Planctomycetes, Spirochaetes, and Verrucomicrobia have been known to inhabit extreme environmental conditions [15]. These bacteria undergo exclusive biological and genetic changes to survive in such hostile conditions [16]. In a report, bacterial species, namely, *Aurantimonas, Alishewanella, Arthrobacter, Brachybacterium, Brevundimonas, Bacillus, Citricoccus, Cellulosimicrobium, Desemzia, Exiguobacterium, Flavobacterium, Janthinobacterium, Kocuria, Klebsiella, Lysinibacillus, Paenibacillus, Planococcus, Paracoccus, Providencia, Pseudomonas, Pontibacillus, Psychrobacter Sanguibacter, Sphingobacterium, Sinobaca, Staphylococcus, Sporosarcina, Stenotrophomonas,* and *Vibrio* were isolated from Leh Ladakh (India), cold desert [17].

The plant growth-promoting bacteria including *Acinetobacter, Bacillus, Enterobacter, Marinobacterium, Pseudomonas, Pantoea, Rhizobium,* and *Sinorhizobium* were isolated from salt-affected barren soils of weed (*P. corylifolia*) [18]. In a report, Patel *et al*. [19] isolated bacterial species *Aneurinibacillus aneurinilyticus* and *Bacillus* spp. from hot springs showed phosphorus solubilization activity. The drought tolerant and P-solubilizing bacterial species, *Pseudomonas fluorescens*, *Enterobacter hormaechei*, *Pantoea ananatis*, *Pantoea agglomerans*, *Klebsiella oxytoca*, *Arthrobacter pascens,* and *Ochrobactrum intermedium,* were reported from foxtail millet (*Setaria italica* L.) growing in semi-arid conditions [20]. The three strains of halotolerant and P-solubilizers bacteria strains *Halomonas* sp., *Micrococcus luteus*, and *Bacillus* sp. were reported from salt pan [21].

2.3. Fungi

Fungi are one of the most essential taxonomic groups of microbes which belong to the eukarya domain and it includes yeast, molds, mushrooms, and also puffballs [22]. They are found in different habitats such as soil, animals, dead matter, deserts, and some species are found in extreme environmental conditions, including deep oceans, seas, and coral reefs, glaciers, hot springs, acidic, alkaline, drought, pressure, salinity, and temperatures and associated with plants [23]. In another investigation, Ali *et al*. [24] illustrate the significant roles of PGP fungi *Trichoderma longibrachiatum* isolated from hot desert plant which showed heat stress tolerance in cucumber plants. The psychrotolerant fungi *Auxarthron alboluteum*, *Alternaria tenuissima*, *Ascomycota* sp., *Arthrinium gitiae*, *Aureobasidium* sp., *Curvularia* sp., *Dothideomycetes* sp., *Mucor hiemalis*, *Penicillium chrysogenum*, and *Sordariomycetes* sp. were isolated from different region of Mexican glaciers [25]. Salt-tolerant endophytic fungi, namely, *Alternaria tenuissima, Aspergillus ochraceus, A. hiratsukae, Chaetomium* sp., *C. globosum,* and *Curvularia lunata* were sorted out from seawater [26].

3. DIVERSITY AND DISTRIBUTION OF EXTREMOPHILIC MINERAL SOLUBILIZING MICROBES

The diversity of microbes is distributed in extreme environments such as oceans, deserts, deep glaciers, hot springs, mine, and coastal region (saline areas) [Table 1]. Several researchers have been investigated, characterized mineral solubilizing microbes and can be used as microbial consortium and bioinoculants for reducing abiotic stress for crop production [27].

3.1. Psychrophiles

Psychrophilic microbiomes are able to grow at a temperature close to the freezing point of water and have been found in low-temperature environments such as cold and polar regions, glaciers, deep sea depths, shallow landmasses, refrigerated equipment, temperate regions, and upper atmospheres [28]. Cold stress triggers a major physiological reaction in plants, shorting their growing periods and lowering agricultural crop output. Consequently, bacteria has an essential role in the growth promotion of plants in the short-term as part of a comprehensive cold stress management strategy. Active phosphorylation and dephosphorylation pathways are used by bacteria to detect a decrease in ambient temperature across cellular membranes. Here, some of the ways in which microorganisms adapt to cold temperatures are explored such as changes associated with the cell membrane, cryoprotectants, cold shock proteins, antifreeze proteins, RNA degradosome, and ice nucleator proteins. Other mechanisms of adaptations to cold temperatures include proliferation in the rate of translation and transcription of various metabolically essential molecules and acceleration of metabolic pathways, that is, entering the pathway of pentose phosphate and viable but non-culturable states [29]. Many psychrophilic mineral solubilizing microbes have been reported to be used as bio-inoculants to enhance plant growth and produce of agricultural yield including *Arthrobacter*, *Bacillus*, *Pseudomonas*, *Pseudoalteromonas*, and *Vibrio* [30,31].

In a report, psychrophilic bacteria, namely, *Sphingomonas glacialis* was isolated from alpine glacier cryoconite region [32]. In an another report, *Pedobacter daechungensis, P. heparinus, P. terricola, P. glucosidilyticus,* and *P. lentus* were isolated from Arctic soil [33]. Albert *et al*. [34] reported psychrophilic bacterium *Sphingobacterium psychroaquaticum* from Lake Michigan water. Lee *et al*. [35] reported *Lacinutrix jangbogonensis* from Antarctic marine. A study concluded that, psychrophilic bacteria *Massilia eurypsychrophila* was sorted out from the ice core [36], and *Psychrobacter pocilloporae* from coral *Pocillopora eydouxi* [37]. Another finding reported that, bacterial species including *Aurantimonas altamirensis, Alishewanella* sp., *Bacillus marisflavi*, *B. baekryungensis*, *Desemzia incerta*, *Pseudomonas frederiksbergensis*, *Providencia* sp., *Pontibacillus* sp., *P. xylanexedens*, *Sinobaca beijingensis,* and *Vibrio metschnikovii*, were isolated from low temperature and high altitude environments of Indian Himalayas [17]. Other cold stress adapted bacteria such as *Pseudomonas rhodesiae,* and *Arthrobacter methylotrophus* were sorted out from rhizospheric region of wheat of North zone of India [38].

In another report, P-solubilizing microbes, namely, *Pseudomonas*, *Bacillus*, *Enterobacter,* and *Rhizobium* have been reported from

Table 1: Distribution of mineral solubilizing microbes.

Microbes	Habitat	References
Pseudomonas libanensis EU-LWNA-33	Drought	Kour *et al*. [200]
Bacillus subtilis GB03	Saline	Zhang *et al*. [201]
Paenibacillus brassicacearum E85	Drought	Aarab *et al*. [202]
Pseudomonas fluorescens 153	Saline	Abbaspoor *et al*. [203]
Paenibacillus fluorescens SorgP4	Drought	Ali *et al*. [204]
Glomus intraradices BEG 123	Salt	Aroca *et al*. [205]
Azospirillum lipoferum B3	Drought	Arzanesh *et al*. [206]
Aeromonas hydrophila MAS-765	Saline	Ashraf *et al*. [207]
Bacillus aquimaris SU8	Salt	Bal *et al*. [208]
Dietzia natronolimnaea STR1	Drought	Barnawal *et al*. [209]
Achromobacter xylosoxidans 249	Saline	Barra *et al*. [210]
Pseudomonas syringae DC3000	Saline	Barriuso *et al*. [211]
Bacillus safensis W10	Drought and heat stress	Chakraborty *et al*. [212]
Pantoea intestinalis DSM 28113T	Drought and heat stress	Chen *et al*. [213]
Arthrobacter arilaitensis R15	Drought	Chukwuneme *et al*. [214]
Streptomyces werraensis S4	Drought	Chukwuneme *et al*. [214]
Micrococcus roseus SW1	Acidic	El-Azeem *et al*. [215]
Pantoea agglomerans R-42	Saline	Farhat *et al*. [216]
Helmithosporium velutinum 41-1	High tempreture	Hidayat [217]
Veronaeopsis simplex Y34	High tempreture	Hidayat [217]
Aeromonas vaga BAM-77	Alkalinity	Jha *et al*. [218]
Azospirillum brasilense NO40	Drought and heat stress	Kasim *et al*. [219]
Pseudomonas koreensis strain AK-1	Saline	Kasotia *et al*. [220]
Streptomyces laurentii EU-LWT3-69	Drought	Kour *et al*. [93]
Burkholderia phytofirmans PsJN	Drought and heat stress	Naveed *et al*. [221]
Trichoderma asperellum Q1	Saline	Qi, Zhao [222]
Fusarium verticillioides RK01	Saline	Radhakrishnan *et al*. [223]
Bacillus halodenitrificans PU62	Saline	Ramadoss *et al*. [224]
Brevundimonas diminuta AW7	Drought	Rana *et al*. [225]

(*Contd...*)

Table 1: (*Continued*).

Microbes	Habitat	References
Paenibacillus plecoglossicida S1	Drought stress	Rolli *et al*. [226]
Pseudomonas aeruginosa GGRJ21	Drought	Sarma, Saikia [227]
Pseudomonas lurida M2 RH3	Cold stress	Selvakumar *et al*.[228]
Xanthomonas campestris RMLU-26	Saline	Sharan *et al*. [229]
Bacillus licheniformis HSW-16	Salinity stress	Singh, Jha [230]
Pseudomonas putida AK MP7	High temperature	Singh *et al*. [231]
Streptococcus thoraltensis 5CR-F	Drought	Toribio-Jiménez *et al*. [232]
Lysinibacillus fusiformis IARI-THD-4	Acidic stress	Verma *et al*. [60]
Bacillus nanhaiensis IARI-THD-20	Alkalinity stress	Verma *et al*. [60]
Bacillus altitudinis IARI-HHS2-2	Cold stress	Verma *et al*. [138]
Flavobacterium psychrophilum HHS2-37	Cold stress	Verma *et al*. [6]
Bacillus aerophilus BSH15	Acidic stress	Verma *et al*. [7]
Planococcus salinarum BSH13	Acidic stress	Verma *et al*. [7]
Bacillus endophyticus BNW9	Alkalinity stress	Verma *et al*. [7]
Paenibacillus xylanexedens BNW24	Alkalinity stress	Verma *et al*. [7]
Pseudomonas rhizosphaerae IARI-DV-26	Alkalinity stress	Verma *et al*. [7]
Paenibacillus polymyxa BNH18	Cold stress	Verma *et al*. [7]
Bacillus alcalophilus BCZ14	Drought and heat stress	Verma *et al*. [7]
Arthrobacter sulfonivorans IARI-L-16	Cold stress	Yadav *et al*. [17]
Cellulomonas turbata AS1	Cold stress	Yadav *et al*. [23]
Piriformospora indica (Pi)	Drought and heat stress	Yaghoubian *et al*. [233]
Paenibacillus fluorescens 153	Drought	Zabihi *et al*. [234]
Pseudomonas lini DT6	Drought	Zhang *et al*. [235]
Serratia plymuthica DT8	Drought	Zhang *et al*. [235]

pea plants (*Pisum sativum* L.) growing under low temperature condition [39]. Yarzábal *et al*. [40] reported various P-solubilizing bacterial species *Pseudomonas brenneri, P. antarctica*, *P. fluorescens*, *P. fredericksbergensis*, *P. psychrophila*, *P. poae,* and *P. orientalis* from Antarctic soils, Greenwich Island. Phosphate solubilizing bacteria *Pseudomonas orientalis*, *P. brenneri*, and *P. antarctica* were isolated from Venezuelan tropical glaciers [41]. Psychrophilic and psychrotolerant plant growth promoting microbes *Mrakia*, *Pseudomonas,* and *Rhodotorula* were sorted out from high-altitude volcano crater in Mexico [42]. Four phosphorus solubilizing microbes, namely, *Pseudomonas* sp., *P. palleroniana*, *P. proteolytica*, and *P. azotoformans* were isolated from high-altitude Himalayan soil under a low temperature [43].

3.2. Thermophile

It is interesting to think that life can be present in extreme temperature. Only microbes have the ability to grow and survive in such extreme temperatures which are known as thermophiles. Over the last few years, a large number of thermophilic microbial taxa were sorted out from both man-made (acid mine effluents, biological waste and waste treatment plants, and self-heated compost piles) and natural (deep-sea, geothermal fields, volcanic fields, terrestrial fumaroles, and terrestrial hot springs) sources. A large number of metagenomic studies are being conducted in these situations to explore the complete microbial and viral ecosystem. The microbes that grow at high temperatures (103–110°C) belongs to genera of archaea such as *Pyrococcus, Melanopyrus, Pyrodictium,* and fungi including *Aspergillus, Candida, Myceliophthora, Thermomucor,* and *Thermomyces* [44], whereas bacteria belongs to the *Thermotoga maritime* and *Aquifex pyrophilus* [45,46]. Thermo-tolerant microbiomes play a great role in solubilizing minerals. In a study, *Bacillus borstelensis, B. coagulans, B. licheniformis, B. smithii, Streptococcus thermophilus,* and *S. thermonitrificans* were thermo-tolerant microbes and grew more rapidly at 50°C than at 25°C. All the strains examined were able to solubilize phosphate at high temperatures during composting [47].

Another study reported mineral solubilizing thermotolerant bacterium *Bacillus altitudinis* from hot springs [6]. Microbes including *Thermotoga elfii* [48], *Thermotoga hypogeal* [49], *Thermoanaerobacter uzonensis* [50], *Bacillus thermophilus* [51], and *Herbinix luporum* [52] were isolated from hot springs areas. Mineral solubilizing thermotolerant microbes including *Arthrobacter* sp., *Alcaligenes faecalis*, *Bacillus siamensis*, *B. subtilis*, *Delftia acidovorans*, *Methylobacterium* sp., *M. mesophilicum*, *Pseudomonas* poae, *P. putida,* and *P. stutzeri* exhibited more than six diverse plant growth promoting activities at high temperature [53]. The thermotolerant microbes *Rhodothermus marinus* and *B. methanolicus* were extracted from hot water pre-treatment [54]. Phosphorus solubilizing thermo-tolerant microbes *Streptomyces californicus, S. chromogenus, S. exfoliates, S. fulvissimus, S. lydicus, S. rimosus, S. violaceus, S. xanthochromogenes,* and *S. olivoverticillatum,* were sorted out from villages around Barshi Dist-Solapur, MS, India [54]. The thermophilic bacteria *Klebsiella* sp. was isolated from Paniphala hot spring [55]. Thermotolerant bacterium *Pseudomonas putida* isolated from rhizospheric soil solubilized phosphorus, and produced siderophores [56].

3.3. Acidophiles

Acidophiles are a group of microbes that survive in both acidic natural (solfataric fields and sulfuric pools), and artificial (areas connected with human activities, i.e., coal and metal ore mining) environments. Acidophiles survive in acidic atmospheres with a pH level of <3.0 [57]. Several acid-tolerant microbes belonging to the genera *Acidithiobacillus, Flavobacterium, Lysinibacillus, Methylobacterium,* and *Pseudomonas* have been reported from acidic environments [58]. An acidophilic microbe has been reported from diverse acidophilic conditions including *Bacillus aerophilus, B. amyloliquefaciens, B. circulans*, *B. cereus*, *B. licheniformis, B. pumilus*, *Lysinibacillus fusiformis*, *Planomicrobium* sp., and *Paenibacillus polymyxa* [59].

Verma *et al*. [60] reported mineral-solubilizing acidophilic microbes *Bacillus cereus*, *B. pumilus*, *B. thuringiensis*, *Lysinibacillus fusiformis, Pseudomonas rhodesiae, Planococcus salinarum,* and *Variovorax soli*. In a different study Chen *et al*. [61] reported mineral solubilizing microbes from acidic soil such as *B. megaterium, P. xylanilyticus*, *Pantoea dispersa*, and *P.cypripedii*. Phosphorous solubilizing bacteria *B. thuringiensis* was isolated from the cassava roots. This bacterial strain *B. thuringiensis* was inoculated to an acidic soil to study its effect on phosphate solubilization and the growth of peanuts (*Arachis hypogeae*). The study concluded that bacterial strains have the ability to enhance plant height. Number of branches, crude protein contents and showed potential as a biological phosphorus fertilizer [62].

Twenty phosphorus solubilizing bacteria (PSB) were sorted out from calcareous rhizosphere soils, namely, *Acinetobacter* sp., *B. megaterium*, *B. subtilis*, *P. aeruginosa*, *P. oryzihabitans,* and *Rhizobium* sp. [63]. Similarly, four strains of acidophilic manganese (Mn) solubilizing bacteria *B. cereus*, *B. nealsonii*, *Enterobacter* sp., and *Staphylococcus hominis* were isolated from mining effluents [64]. Another study was conducted, in which potassium solubilizing microbes like *P. orientalis, P. agglomerans*, and *Rahnella aquatilis* were isolated from the rhizospheric soil of paddy. They have ability to solubilize potassium under acidic conditions [65]. Similarly, Lee *et al*. [66] reported the high silicate and phosphorus solubilizing bacteria *Enterobacter ludwigii* from paddy soil having low pH condition. *B. subtilis, B. cereus, B. amyloliquefaciens, B. thuringiensis, B. wiedmanni, B. siamensis, B. subtilis, Burkholderia paludis, B. cenocepacia, B. contaminans, B. cepacia,* and *Paenibacillus sp*., were isolated from wet land paddy field of Mizoram, and have capability to solubilize phosphate in acidic conditions [67].

3.4. Alkaliphiles

Alkaliphilic species require an alkaline field (pH of 9.0 or greater) to grow, with a pH of 10.0 being optimum. Based on pH preference, such alkaliphiles are divided into two groups: alkali-tolerant organisms that grow best in the pH range of 7.0–9.0 but cannot thrive above pH 9.5, and alkaliphilic organisms that grow best between pH 10.0 and 12.0. Alkaline habitats, which include naturally occurring, alkaline springs, desert soils and soils and also artificially generated industrial-derived waters, are typical severe environments and various mineral solubilizing microbes have been known to survive in such conditions. In neutral soil, alkaliphilic gram positive and endospore forming *Bacillus* sp., and non-sporing species of *Actinopolyspora, Aeromonas*, *Corynebacterium*, *Micrococcus*, *Pseudomonas,* and *Paracoccus* fungi have been isolated [68]. Numerous alkaliphilic microbes reported as mineral solubilizing including *Burkholderia*, *Bacillus*, *Klebsiella*, *Lysinibacillus*, *Variovorax*, *Psychrobacter*, *Planococcus*, *Paenibacillus*, *Pseudomonas*, *Micrococcus*, *Rhizobium*, and *Stenotrophomonas* [69]. These alkaliphilic bacteria were isolated from different rhizospheric and non-rhizospheric soil such as wheat [60] tobacco [70] tea [71] and sugarcane [72].

Alkaliphilic zinc solubilizing microbes *Agromyces aurantiacus*, *Alkalibacterium* sp., *A. pelagium*, and *B. foraminis* were isolated from fly ash landfill site [73]. Alkaliphiles *B. marisflavi,* and haloalkaliphile *Chromohalobacter israelensis* were isolated from the Batim salt pan, were able to solubilize phosphate at high salt concentrations and pH [74]. Seker *et al*. [75] reported, Pseudorhodoplanes from Photinia fraseri and able to solubilize phosphorus nitrogen fixation and IAA production under alkaline condition. Alkaliphilic bacteria *B. marisflavi* was isolated from sediment samples of mangrove ecosystem located in Quellossim, Goa, India, and this strain was able to solubilize phosphorus under alkaline conditions [76]. Samreen *et al*. [77] observed *Bacillus* sp. sorted out from soil with ability to solubilize phosphorus under alkaline conditions. In a similar finding, *E. aerogenes*, *Enteriobacter* sp., and *Pantoea* sp. were isolated from the root zone of wheat plants and these strains were capable of solubilizing phosphorus under alkaline conditions [78]. The alkaliphilic phosphorus solubilizing bacteria *E. ludwigii, P. agglomerans, P. vagans, P. azotoformans,* and *S. quinivorans* these microbes were sorted out from wheat rhizosphere under alkaline conditions. *E. ludwigii*, *Hafnia alvei*, *P. eucalypti*, *P. chlororaphis,* and *Yokenella regensburgei* were isolated from *Lotus tenuis* plants of rhizospheric soil and capable of solubilizing phosphate under a broad range of alkaline-sodic conditions [79].

3.5. Halophiles

Halophiles are types of microbes that thrive in atmospheres with extremely high salt concentrations for agriculture crop production, particularly in arid/semiarid regions in the world. Halophiles include microbes that can grow at concentrations of 0.2–0.85 M NaCl (1–5%), moderate halophiles grown at concentrations of 0.85–3.4 M NaCl (5–20%), and halophilic microbes that can grow at concentrations of 3.4–5.2 M NaCl (21–31%). [80,5]. They belong to phyla Proteobacteria α, β, and δ, Bacteroidetes and Verrucomicrobia are convoluted in relieving the salt stress. Many halophilic and halotolerant bacterial genera such as *P. Planococcus, Halobacillus, Halomonas, Micrococcus, Marinococcus,* and *Virgibacillus* from the different halophytes have been reported [81,82]. In a study Yang *et al*. [83] reported the bacterium *Achromobacter piechaudii* from tomato seedlings growing under high salinity stress conditions. Some halophilic microbiome such as *B. aquimaris*, *B.s siamensis, B. alcalophilus, Halobacillus, L. xylanilyticus*, and *P. dendritiformis* has reported [84]. In the study, Yadav *et al*. [17] reported, various halophilic and halotolerant species such as *Ammoniphilus* sp., *B. halodurans, B. methanolicus*, *B. vallismortis*, *Halobacillus dabanensis*, and *H. trueperi* isolated from Sambhar lake, these were reported and described for diverse possible PGP traits for agriculture.

Phosphorus solubilizing bacteria *Alcaligenes faecalis, B. subtilis*, and *P. geniculate* were sorted out from saline soils [85]. In a study, *B. megaterium*, *B. velezensis*, *B. methylotrophicus*, *B. atrophaeus*, *B. aryabhattai*, *B. amyloliquefaciens,* and *B. subtilis* were isolated from rhizosphere of healthy pepper growing in salinized soil of Shihezi, Xinjiang, China. These bacterial strains have the ability to solubilize phosphorus, fixation of N and production of IAA [86]. *Paenibacillus* sp., and *Aneurinibacillus aneurinilyticus* were isolated from garlic (*Allium sativum*) and showed activity of ACC deaminase, and solubilization of phosphorus under saline conditions [87]. Salt-tolerant phosphate solubilizing bacteria (PSB) *Acinetobacter pittii, Brevibacillus schisleri, Ensifer sesbaniae, Gordonia terrace, Pseudomonas hunanensis,* and *Paenibacillus illinoisensis* were isolated from peanut rhizosphere [88]. *Bacillus subtilis*, *B. megaterium*, *Kocuria kristinae,* and *Sphingomonas paucimobilis* were isolated from rhizospheric saline soils of coastal Odisha, India and estimated their phosphate solubilizing ability [89].

3.6. Xerophiles

Xerophiles are microorganisms that have the capability to grow in arid environmental conditions or the existence of very little water movement. Some potassium solubilizing microbes *Acidithiobacillus ferrooxidans*, *Bacillus pumilus*, *B. mucilaginosus*, *B. edaphicus, B. megaterium, Paenibacillus polymyxa*, *Planococcus salinarum*, and *Sporosarcina* sp. were reported from water stressed condition [90]. Another study Verma *et al*. [91] reported, drought-tolerant PSM *B. megaterium*, *Duganella violaceusniger*, *P. amylolyticus*, *P. dendritiformis*, *P. monteilii*, *P. thivervalensis*, *P. lini*, *Psychrobacter fozii*, *Stenotrophomonas* sp., and *S. maltophilia*, from wheat crops growing in water lacking conditions. In an investigation, *Azotobacter* sp. was isolated from rhizospheric region of soil and crops grown in semi-arid regions across Tehran, Alborz, Qazvin and Qom Provinces of Iran. The strain was reported for solubilizing of phosphate and potassium, producing of siderophores and IAA [92]. In a report, *Penicillium* sp., and *Streptomyces laurentii* were isolated from rhizospheric soil of different cereal crops. These strains have been showing P, and K solubilization, and siderophores, HCN, NH_3, ACC and IAA production under the condition of drought stress [93]. Drought tolerating rhizobacteria *E. ludwigii* and *B. megaterium* were isolated from Seosan, Chungcheongnam-do Province, and having ability to solubilization of phosphorus, potassium, calcium, and magnesium [94].

4. MECHANISMS OF MINERALS SOLUBILIZATIONS UNDER ABIOTIC STRESS CONDITIONS

The mineral solubilizing microbiome acts as direct mechanism for the development of plant growth, and improving soil health. These mechanisms may be activated simultaneously at various stages of plant development. In general, the PGP microbiomes promotes plant growth directly by either nutrient acquisition (P, K, Zn, and Se) or modulating plant hormone levels or indirectly by reducing the inhibitory effects of numerous pathogens on plant growth and developing the plant in the forms of biocontrol agents [Figure 1; Table 2] [95].

4.1. Solubilization of Phosphorus

Phosphorus is the second most important macronutrient needed for the overall growth of plants and developments [96,97]. It influences various vital metabolic processes such as development, cell division, signal transduction, macromolecular biosynthesis, energy transport, respiration, and photosynthesis of plants. Phosphorus helps in the proliferation and elongation of root to obtain additional nutrients and water from the soil. Compared to other crucial macronutrients phosphorus is one of the least plentiful elements in the lithosphere (0.1%). It is present at 400–1200 mg/kg in soil. In the soil, P is available in two forms such as organic P (Po) and inorganic P (Pi) that fluctuate in soil pH, vegetation cover, parent material, time, and pedogenesis extent [98]. Both types of phosphorus occur in mineral complexes that contain alkaline earth metal and non-metal such as calcium and transition metals such as aluminum, iron, and manganese, Al, Fe, and Mn. These component can fluctuate depending on soil pH and mineral conditions; for example, P forms complexes with almunum, iron, and manganese in acidic soil, but Ca reacts strongly in alkaline soil [99]. Inorganic forms of phosphorus make up approximately 35–75% of the total P in the soil, and it can be classified to exist in three diverse collections such as primary minerals (i.e., apatite), secondary minerals (i.e., CaP, FeP, AlP, and MnP) and sorbed minerals (i.e., clay minerals, Al, Fe and Ca). Calcium-phosphate primarily source of apatite and present in the form of hydroxyapatite ($Ca_5\ (PO_4)_3OH$), fluorapatite ($Ca_5\ (PO_4)_3\ F$), and francolites ($Ca_5\ (PO_4,\ CO_3)_3F$) in natural alkaline soils, this is a primary source of Pi, whereas Fe and Al are present as oxy(hydr)oxides, that is, variscite ($AlPO_4.2H_2O$) strengite ($FePO_4.2H_2O$), and wavellite ($Al_3(OH)_3(PO_4)_2 \cdot 5H_2O$), in acidic soil [100]. Another type of phosphorus, known as (Po), is found in the soil in about 30–65%. The main notorious forms of Po such as inositol, phospholipids, phosphates, and nucleic acids are most prevalent in soil, where inositol being the greatest abundant and dominant form. Inositol is more adjustable and comprises phosphate monoesters (hexakisphosphate and inositol monophosphate), however phospholipids are composed phosphoglycerides. Carboxylic acid, organophosphorus (phytin), monophosphoryted, sugar phosphate, and teichoic acid are additional Po forms in soil [101].

Plants absorb P from the soil through their roots as anion charged primary and secondary ions of orthophosphate such as $H_2PO_4^-$ and HPO_4^{2-}; however, phosphorus is mostly found in the complex mineral source in the soil, and accessible form is virtually low. Therefore,

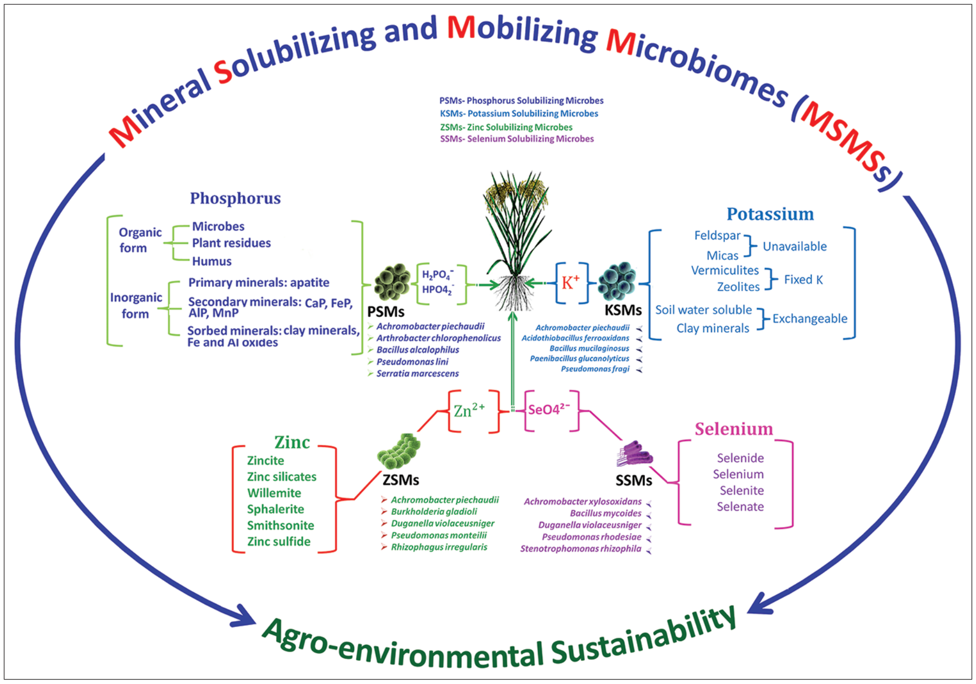

Figure 1: Role of mineral solubilizing and mobilizing microbiomes. Adapted with permission from Devi *et al*. [240].

Table 2: Role of mineral solubilizing microbes under extremophilic conditions.

Microbes	Condition	Sources	Role	References
Azospirillum lipoferum B3	Drought	Wheat	P-solubilization	Arzanesh *et al*. [206]
Providencia rettgeri sp. TPM23	Saline	Saline soils	P-solubilization	Jiang *et al*. [236]
Bacillus licheniformis BGBA 1	Drought	Rice	P-solubilization and siderophores production	Pahari, Mishra [237]
Trichoderma asperellum Q1	Saline	Cucumber	Siderophores producing	Qi, Zhao [222]
Fusarium verticillioides RK01	Saline	Soybean	P-solubilization	Radhakrishnan *et al*. [223]
Humicola sp. KNU01	Saline	Soybean	P-solubilization	Radhakrishnan *et al*. [223]
Bacillus halodenitrificans PU62	Saline	Wheat	P-solubilization and siderophores production	Ramadoss *et al*. [224]
Brevundimonas diminuta AW7	Drought	Wheat	P-solubilization and siderophores production	Rana *et al*. [225]
Pseudomonas aeruginosa GGRJ21	Drought	Mung bean	Siderophores production	Sarma, Saikia [227]
Bacillus megaterium IARI-IIWP-9	Drought	Wheat	P-solubilization and siderophores production	Verma *et al*. [91]
Bacillus aquimaris IARI-IHD-17	Drought	Wheat	P-solubilization	Verma *et al*. [91]
Paenibacillus durus IARI-IIWP-40	Drought	Wheat	P-solubilization	Verma *et al*. [91]
Acinetobacter sp. M05	Drought	Mushroom	P-solubilization and siderophores production	Zhang *et al*. [238]
Kushneria sp. YCWA18	Halophilic	Yellow Sea	P-solubilization	Zhu *et al*. [239]

solubilization is more essential as P scarcity can stifle plant growth by reducing root development and blooming. Soil microbes are capable of solubilizing phosphorus, which are known as phosphate solubilizers. Several mechanisms have been involved in the solubilization of phosphorus in soil through release of complex or mineral liquefying compounds such as production of organic acid (acetate, lactate, malate, oxalate, succinate, gluconate, citrate, and also ketogluconate), lowering the pH in soil, siderophores, protons, hydroxyl ions and also CO_2, release extracellular enzymes such as biochemical phosphorus mineralization and also release phosphorus during degradation of substrate such as biological phosphorus mineralization [102]. Exopolysaccharides (EPS) released by microbes, also discharge P from the complex metals including Al, Cu, Fe, Mg, K, and Zn. Extracellular phosphatases, a microbial enzyme that acts as a catalyst for the hydrolysis reaction of anhydride and esters of H_3PO_4 and boosts the concentration of orthophosphate and is employed through plants, can also increase P solubility [103].

Phosphorus solubilizing microbiome has been used as bioinoculants/microbial consortium to improve phosphate assimilation and provides a number of benefits for growth of plant [104]. Numerous studies has been found in which rhizospheric soil bacteria convert insoluble to the soluble P and boost for plant development. In a study, phosphorus solubilizing bacteria belonging to genera *Burkholderia*, *Pseudomonas,* and *Pantoea* were sorted out from acidic soil of northeast of Argentina. Gulati *et al.* [105] reported phosphate solubilizing plant growth promoting bacteria *Acinetobacter rhizosphaerae* BIHB from the cold deserts of trans-Himalayas. *Acinetobacter rhizosphaerae* BIHB bacterial strain was able to produce organic acid gluconic, 2-keto gluconic, lactic, malic, oxalic, and formic acids during the solubilization of numerous inorganic phosphates. In another study, twelve psychrotolerant phosphate solubilizing microbes *P. lurida*, *P. jessani*, *P. fluorescens*, and *P. koreensis* were isolated from high-altitude of the Uttarakhand state NW Indian Himalayan region (IHR) [106].

Taurian *et al*. [107] reported PSB *Pantoea* sp. and *P. fluorescens* from peanut tissues. They were inoculated on the crop of peanut (*Arachis hypogaea* L.) and showed the highest shoot and root weight in both reproductive growth stages. In an investigation pH and salt tolerant PSB namely, *Klebsiella oxytoca* was isolated from metal contaminated soil. This microbial strain was inoculated into the mung bean crop and showed higher plant height and root length over the untreated control [108]. The PSB *P. cedrina*, *Rhizobium nepotum*, *R. tibeticum*, and *R. aquatilis*, were isolated from faba bean rhizosphere growing in Meknes region [109]. In another report, *B. subtilis*, *P. putida*, and *P. fluorescens* were having ability to solubilize TCP under salinity stress. These isolates dramatically increased the number of leaves, stem height, and plant biomass when inoculated into the plant of *Curcuma longa* [110]. Shahid, Khan [111], reported PSB *Burkholderia cepacia* was isolated from *Vicia faba* rhizosphere and have ability to solubilized of P (50.8 $\mu g\ ml^{-1}$). This single strain was inoculated on the chickpea plants and showed enhancement in chickpea production. In addition, PGP bacteria *Pseudomonas libanensis* was able to solubilize phosphorus under drought stress conditions [112].

4.2. Solubilization of Potassium

Potassium is the third vital macronutrient solubilized by soil microbes for plant growth promotion. K is the 7th most copious element on earth that is involved in several physiological and biological functions of plants such as osmotic cell regulation, and enzyme activation [113]. It exists from three different forms such as readily available or exchangeable potassium, unavailable K, and slowly available or fixed potassium. Almost 90–98% of the K is in unavailable form i.e. feldspars ($KAlSi_3O_8$), muscovite ($KAl_3Si_3O_{10}(OH)_2$), orthoclase, biotite ($K_2Fe_6Si_6Al_2O_{20}(OH)_4$), illite, vermiculite, micas and smectite [39]. In the soil, another type of K found is fixed potassium (slowly accessible), which accounts for 1-10% of total soil K. In soil, this form serves as potassium storage and is found among a layer of clay minerals. Soluble potassium (K^+) is the 3rd form of exchangeable K (K^+). This type of K is formed when soil and water mix and can be found in the range of 1–2% on the surface.

Plants absorb K from the soil through the root system and the high-affinity transport system (HATS) or by a low-affinity transport system (LATS) and carry it to each cell of the plant tissues *via* xylem and phloem for many plant functions [114]. Although this mineral is not found in chemical structure as nitrogen and phosphorus in the plant, it is still an essential macronutrient. It aids in activating plant enzymes, preserving osmotic rigidity and turgor, protein synthesis, transport of water, and the absorption of essential minerals and biological compounds. In addition, K assists in the regulation of stomatal cell function to reduce water loss through transpiration, photosynthesis and confers resistance to plants such as bacteria and fungi. The lack of potassium in plant can cause many problems like lowering in crop yield and growth inhibition, internodes shortening, blackening of scorching of some tubers such as potatoes, all small grains, and photosynthesis reduction [115,116]. The level of its soluble form of K in soil has fallen worldwide, resulting in reduced availability of K to plants. To fulfill the K necessity for plants, farmers utilize ago-chemical fertilizers known as potash. The efficacy and cost of potash have skyrocketed, resulting in a number of environmental consequences. The KSM predominantly consists of fungus and bacteria, although bacteria perform a crucial function in the K solubilization minerals that are commonly known as potassium solubilizing bacteria (KSB). The potassium solubilization by microbes was considered via different research all over the biosphere to expose the various mechanism used by the microbes such as solubilization in direct way, solubilization in indirect way, polysaccharides exudation and biofilm formation on the surface of minerals. In the process of direct solubilization through bacteria help in solubilization of K through the organic acid production, acidolysis, carbonic acid based chemical [114,117]. These bacteria produce organic acid, citric acids, oxalic acid, and tartaric acid and H^+ ions which help in lowering the pH around the soil [118,119]. Organic acid exudation is an important process of K solubilizing minerals (biotite, illite, feldspar, mica, muscovite, and orthoclase) [120,121].

Microbes also release low molecular weight of organic molecules through chelation, metabolic activities, extracellular enzymes, and organic ligands that help in solubilization of K mineral via pH regulation of the microenvironment [122]. Another mechanism of K solubilization is the secretion of polysaccharides; although; the process of K is difficult to understand, microbes accept variety of methods to mobilize K in soil. Capsular exopolysaccharides are additional possible method for the solubilization of K minerals. In this process, microbes secrete acidic or slime polysaccharides externally, which interact with surface on minerals to form bacterial- minimal complexes and release K minerals from silicates. In addition, EPS binds with K^+ and SiO_2, maintaining the balance between soil and minerals, and as a result, eventually increasing K^+ bioavailability [123]. When bacteria secrete exopolysaccharides, the excreted molecular compound absorbs SiO_2, after that the stability among the mineral and liquid phase gets overstated, and leads to response around K^+ and SiO_2 solubilization. Biofilm formation is the last mechanism of solubilization. Biofilm is a type of early stage of plant–microbiome interaction in which germ cells become trapped on biotic and abiotic surfaces [114]. Several reports have been showed to investigate potassium solubilizing microbes in normal conditions, but extreme conditions have few studies. In an investigation Selvakumar *et al*. [124] reported *Bacillus, Staphylococcus,* and *Kocuria* from the plants rhizosphere, grown high salty soils in Uttarakhand Himalayas, which have ability to solubilize potassium, and this strain was applied in the strawberry under saline conditions, increasing plant growth, fruit yield, and nutrition. Potassium solubilizing microbes *B. megaterium*, *Duganella violaceusniger*, *P. thivervalensis*, *P. dendritiformis, Psychrobacter fozii*, *Stenotrophomonas* sp., and *S. maltophilia,* were isolated from plant of wheat and under the acidity conditions [91]. Ahmad, Zargar [125] reported, 27 K solubilizing bacteria in which *Bacillus* and *Pseudomonas* were isolated from rhizospheric region of soil of apple var. delicious collected from sixty different orchards of Kashmir valley. Similarly, three potassium solubilizing bacteria *P. agglomerans*, *P. orientalis* and *R. aquatilis* were sorted out from paddy rhizospheric soil under saline condition and these bio-inoculants increased the grain yield [65].

In a study, potassium solubilizing fungi *Penicillium pinophilum* was sorted out from the rhizosphere of pomegranate in semi-arid regions. The effect of bioinoculants on the plants of pomegranate (*Punica granatum* L.), increasing fruit yield and quality was much higher [126]. Kushwaha *et al*. [127] reported salt tolerating endophytic microbes *Bacillus amyloliquefaciens, B. albus*, *B. aryabhattai*, *B. halotolerans*, *B. haynesii*, *B. pacific*, *B. paramycoides*, *B. proteolyticus*, *B. siamensis*, *B. tequilensis*, *B. wiedmannii,* and *B. zhangzhouensis* isolated from pearl millet (*Pennisetum glaucum*). They were able to solubilize K, P, and Zn, production of IAA and siderophores. In another report, potassium solubilizing microbes *Acinetobacter pittii*, *A. pittii*, *Cupriavidus oxalaticus*, *Ochrobactrum ciceri*, and *Rhizobium pusense* were inoculated on paddy plants, and resulted in increased height of plant, fresh, and dry weight of the root/shoot, and chlorophyll content under saline conditions [128]. Additional investigation Muthuraja, Muthukumar [129] reported potassium solubilizing fungi *Aspergillus terreus*, *A. niger*, and *A. violaceofuscus* from Maruthamalai Hills and Kolli Hills in Tamil Nadu, Southern India. These fungi have ability to produce diverse organic acids such as acetic, ascorbic, benzoic, citric, malic, and oxalic acid and also IAA (0.678–46.326 μg L^{-1}), under *in vitro* conditions. Four potassium solubilizing microbes (KSM) *Bacillus subtilis*, *B. licheniformis*, and *Burkholderia cenocepacia* were isolated from saxicolous habitat (rockdwelling) Maruthamalai Hills. These microbes has been inoculated on the tomato plant for, results showed growth parameters such as plant height, total root length, leaf area, root/shoot ratio, and tissue K content in sterilized and unsterilized soils under greenhouse conditions and also have the ability to producing organic acids [130].

4.3. Solubilizing of Zinc

Zinc (Zn) is necessary micronutrient that function as a metal activator and cofactor of various plant enzymes including synthesis of tryptophan and plays an important role in their plant life cycle [131]. Tryptophan is liable for the tryptophan synthesis, biosynthesis of IAA, isomerase, hydrolysis, lysis, ligase, transferases, and oxidoreductases. It aids plant growth, root development, crop output, and water intake both directly and indirectly. To maintain proper physiological function zinc is needed in a small quantity in human beings and other living organisms. A substantial amount of inorganic zinc present in soil is converted into unavailable form. In soil, Zn exists in the fixed form such as franklinite ($ZnFe_2O_4$), hopeite ($Zn_3(PO_4)_2\cdot 4H_2O$), smithsonite ($ZnCO_3$), sphalerite (ZnS), wellemite (Zn_2SiO_4), and zincite (ZnO) ultimately created the hampers on Zn availability [132]. Plant absorb zinc from soil in the form of (Zn^{2+}), which are present in low amount in the soil as same way while other plant nutrients absorb. Mostly zinc is found in the soil in insoluble form that cannot absorb or utilize by plants. As a result, solubilization and mineralization are crucial, as a lack of zinc causes growth abnormalities in plants, lowering yield.

Furthermore, the low concentration of Zn in the soil hinders crop production and substantially reduces zinc accretion in the production of crop. Zinc deficiency in plants causes stunted growth due to changes in auxin metabolism, destruction of chloroplast, chlorosis, and photosystems (PS-I and II), pollen sterility, decline in rubisco activity, water absorption, heat stress vulnerability, and poor root development. Microbes can assist the solubilization of zinc in two ways: Through single or multiple mechanisms. Lowering pH, which improves zinc availability, is one of the several processes of solubilization used by microbes [133]. Mineral chelation is another method of solubilization of Zn. Chelation may be achieved through the excretion of Zn chelating substances [134]. Bioactive mixture secreted through soil inhibits the interaction of zinc with clay and chelates, forming a complex ion with the metal cation Zn^{2+} [135]. Chelation also enhances the amount of zinc ions in the soil which can be uptakes by the roots of plant. This process is the most prevailing way for solubilization of Zn through microbes [133]. Microorganism solubilize Zn through numerous organic acids production, that is, gluconate or derivatives of gluconic acid, including 2-ketogluconic and 5-ketogluconic acid, which contain low pH and zinc accessible in plants [136]. Organic acid synthesis is essential for dissolving mixture Zn into a soluble form by lowering the pH of microbial habitats, resulting in increased Zn availability and decreased Zn consumption in plants, a process known as assimilation [137].

A few studies have been reported zinc solubilizing microbes under extreme conditions such as psychrotolerant bacteria *Arthrobacter nicotinovorans*, *A. methylotrophus*, *Achromobacter piechaudii*, *Bacillus horikoshii*, *B. amyloliquefaciens*, *B. megaterium*, *B. thuringiensis*, *B. muralis*, *Bordetella bronchiseptica*, *Exiguobacterium* sp., *E. antarcticum*, *Flavobacterium psychrophilum*, *Kocuria kristinae*, *Providencia* sp., *Pseudomonas peli*, *P. extremorientalis*, *P. aeruginosa*, *P. rhodesiae*, *Pantoea dispersa*, and *Staphylococcus arlettae* from wheat (*Triticum aestivum*) growing in the northern hills zone of India [138]. In additional, Othman *et al*. [139] reported *Acinetobacter* sp. and *Serratia* sp., from rice fields which were having ability to solubilize zinc sources, that is, $ZnSO_4$ and ZnO through the production of oxalic acid. These zinc-solubilizing bacteria inoculated on rice plants (*Oryza sativa*) showed the greater enhancement in plant growth parameters and root development. Two salt tolerance bacteria *B. pumilus* and *P. pseudoalcaligenes* were reported for the solubilization of zinc under salt stress conditions.

Another study, Galeano *et al*. [140] have been reported *Bacillus cereus* isolated from Ironstone outcrops under drought conditions. This microbe has ability to solubilize zinc and phosphorus and the production of ammonia, catalase, hydrolytic enzyme activity (cellulase, protease, and amylase) and exopolysaccharides (EPS). Patel *et al*. [141] reported Zn solubilizer *Acinetobacter* sp. from sugarcane rhizospheric soil of Madhi village. These bacterial species exhibited plant growth promoting attributes including fixation of nitrogen, phosphorus, potassium solubilization and production of IAA under salinity stress condition. This strain was inoculated in sugarcane under greenhouse and resulted in increased plant growth parameters such as fresh and dry weight of root and shoot fresh/dry weight, plant height, and number of leaves were significantly improved as compared to positive control. Initially, six potential zinc solubilizing bacteria including *A. globiformi, B. cereus*, *P. polymyxa*, *Streptomyces*, *Stenotrophomonas maltophilia*, and *Ochrobactrum intermedium* were sorted out from rhizosphere of chickpea (*Cicer arietinum* L.). These strains were able to enhance shoot and root length as compared to untreated control [142].

4.4. Solubilization of Selenium

Selenium (Se) is a trace element that is needed by plants, human and animals. This mineral plays pivotal role in cell metabolism by acting as a protector against oxidative stress and as supervisors of cell redox status [143]. Selenium is present all over the biosphere including hydrosphere, lithosphere, and atmosphere. Globally, Se content is approximately 0.05–1.5 mg kg^{-1}, and the average is calculated to be 0.44 mg kg^{-1}. Selenium occurs in two different chemical forms, namely organic and inorganic, and present in less amounts in soil, plant, atmosphere, aquatic, and freshwater systems. The organic forms of selenium includes methylselenol, selenomethionine (SeMet), and Se-methylselenocysteine (MetSeCys) [144], and inorganic form exist in the two forms, that is, selenite (SeO_3^{2-}), selenate (SeO_4^{2-}), and selenide (Se^{2-}) in soil. Selenate is the most soluble form of Se in the soil. These forms are present in diverse oxidation reaction in the environments, that is, selenate [SeO_4^{2-}, Se (VI)], selenite [SeO_3^{2-}, Se (IV)], selenide (Se^{2-}), and elemental (Se0).

However, Se (VI) and Se (IV) are commonly present in an aquatic system, and they are readily assimilated and absorbed by plants. In addition, Se (IV) is more harmful than Se (VI). In acidic soil, Se is mostly found as selenite, whereas in alkaline soil, it is mostly found as selenate. Both of the forms are metabolized to seleno-compound, although their uptake and mobility within the plant. Se absorb through plant cells through plasma membrane sulfate transporter, and converted into Se amino acid through the sulfur (S) absorption pathway [145]. Selenium found in low quantity has been revealed to protect the plants from abiotic stimuli, that is, cold, drought, heat, salt, and UV-B radiation, all of which cause oxidative damage [146]. Mainly, three mechanisms involve the soil's controlled Se speciation, oxidation versus reduction mineralization, immobilization, and volatilization. The amount of Se fluctuates mostly varies mostly the microbial actions of Se species depending on the base of redox condition, pH, and other soil factors [147].

In general, abnormal skin color, dysfunction of the heart muscle, weakness of the heart muscle, swelling, fragile red blood cells, Keshan and Kashin–Beck diseases, including cancer susceptibility, are caused by Se deficiency in humans. In contrast, Se toxicity causes blood clotting, necrosis of the heart, nausea, liver, hair; nail loss and kidney damage and vomiting, whereas Se toxicity caused blood clotting, liver and kidney destruction, necrosis of heart, nausea, liver, vomiting hair, and nail loss [148]. Despite the fact that plants do not require selenium, it has showed potential for growth of plant and stress tolerance. Although several reports have shown, low concentrations of selenium are enough to improve the plant growth [149,150]. Plants with high Se levels have a variety of detrimental effects, including reduced efficiency of photosynthetic and growth of plant, chlorosis, and eventual death [151]. On the other hand, plant species vary greatly in their vulnerability to high doses of Se, with some even showing encouragement of growth in high Se soils and the ability to absorb Se to astoundingly highest concentration [152]. Se insufficiency issues are becoming more prevalent in human health around the world. The solution to this problem can be accomplished through selenium biofortification of diverse crops like rice [153], wheat [154], and cruciferous vegetables [155]. Se is mostly utilized in agriculture, as a source ingredient in a variety of fertilizers, like foliar sprays, and insecticidal, mostly as sodium selenite (Na_2-SeO_3). A modest amount of Se is expanded used for fortified compound in vitamins, other nutritional supplements, and cattle feedstuffs. Various studies have been reported for plant growth using biofortification techniques, but no investigation of the solubility of Se from extreme environments is available.

In a study, the inoculation of Se solubilizing bacteria *Bacillus* sp. in wheat plant significantly increased acid phosphatase activity, and plant growth [156]. Some bacterial species are associated with Se biofortification in different crops and its effects on Se uptake in plants. *Paenibacillus* sp. and *Bacillus* sp. bacteria is used mineral for biofortification in wheat [157]. In a report *Acinetobacter* sp., *Bacillus* sp., *Klebsiella* sp., and *Paenibacillus* sp., are found as efficient solubilizer of selenium phosphorus [158]. Other Se solubilizing microbes *Bacillus* sp., *Glomus claroideum, Enterobacter* sp., *Pseudomonas* sp., and *Stenotrophomonas* sp., rise the selenium content of wheat grains [159]. *Caulobacter vibrioides* is a Gram-negative bacteria, isolated from a selenium mining area in Enshi, southwest China found to solubilize Se mineral into Se (IV) [160]. Some Arbuscular mycorrhizal fungi (AMFs) and root endophytic fungi (REFs) frequently used for Se biofortification such as *Glomus versiform* [161], *Glomus fasciculatum* [162], *Glomus mosseae* [163], *Glomus claroideum* [159], *Funneliformis mosseae* [164,165], and *Glomus irtraradices* [164,166].

5. BIOTECHNOLOGICAL APPLICATIONS

Biotechnology has opened up new opportunities to apply beneficial extremophilic microbiome in the soil to promote plant growth, biological control against plant pathogens and soil-borne pathogens. Microbial inoculants have a better stimulatory effect on plant growth promotion in nutrient deficient soil than nutrient-rich soil.

5.1. Plant Growth Promotion

Biofertilizers consisting of living organisms such as bacteria, algae, and fungi isolated from water, air, rhizospheric soil and plants, use in the agriculture could improve the health of soil and plant [167]. The production of sufficient food to satisfy the requirements of the world's extended population, has largely depend upon the chemical fertilizers for providing nutrients to the plants, but chemical fertilizers are more reliable in terms of harming the environment and affecting human beings. Therefore, microbe's uses as bioinoculants/biofertilizers are being viewed as viable alternative to chemical fertilizers to enhance crop productivity and soil fertility. Biofertilizers have been used for the higher production of crops which significantly increases crop productivity by various mechanisms including solubilization and mobilization of potassium, phosphorus, zinc, and selenium; fixation of nitrogen, and production of growth hormone [168]. Numerous biofertilizers are available, which could be used to enhance the crop productivity such as *Funneliformis mosseae,* and *Rhizophagus irregularis* having capability of fixing nitrogen and solubilizing phosphorus. There inoculation of higher biomass accumulation on the crop of two *cajanus cajan* (pigeon pea) [169]. Similarly, Zhao *et al*. [82] isolated 105 bacterial species of *Arthrobacter*, *Bacillus*, *Brevibacterium*, *Brachybacterium*, *Glycomyces*, *Isoptericola*, *Kocuria*, *Planococcus*, *Phyllobacterium*, *Streptomyces*, and *Variovorax* genera from the *Salicornia europea* L., a plant considered one of the best salt-accumulating bacteria. According to Abdelaziz *et al*. [170], the PGPMs belongs to *Pseudomonas* and *Bacillus* genera and the well-known N-fixing bacteria *Azotobacter*, *Azospirillum*, *Frankia*, *Halobacillus, Klebsiella*, *Serratia*, *Pseudomonas*, *Paenibacillus*, *Pantoea*, *Rhizobium,* and *Salinibacter*. Extremophilic microbiomes could be applied as microbial inoculants for PGP and as biocontrol agents for crop growing under extreme eco-friendly conditions [171].

5.2. Plant Protection

Biopesticides are environmentally acceptable substitute to chemical pesticides for killing pest such as weeds, insects, and fungi that diminish crop output. In the literature, there are many studies available of PGPM which can also be used bio based pesticides and promotes plant growth of plant. They have a variety of pest-control techniques, including as the production of auxin, vitamins, siderophores, antibiotics against pathogens, and stimulating the plant defense by inducing flavonoids and phytoalexin [172]. Various PGPMs have been reported for the plant protection as biopesticides *Alcaligenes*, *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Glomus mossae, G. fasciculatum*, *Gigaspora margarita*, *Serratia*, *Enterobacter*, *Klebsiella*, *Pseudomonas*, *Paenibacillus,* and *Streptomyces* [173,174].

6. METAOMICS APPROACHES

Recent advances in omics approches have produced huge information that has been used to stimulate research activities in all possible areas. Meta-omics techniques are used to help the study of microbes living under the extreme condition from different environments [175]. Well-established omics technologies, microbes could be studied at the genomic, transcriptomic, proteomic, and metabolomics, as well as modern approaches such as RNA omics and multi-omics perform a crucial role in interpreting responses of plant stresses, and crop improvements. This technique is used to study plants associated microbes for better understanding for their further applications in a variety of harsh situations [176]. Using this technique plant microbiome has been used in efficient way for improvement of production under extreme environmental conditions. Metagenomics, metatranscriptomics, and metaproteomics studies on the interactions between plants and microorganisms have the potential to reveal a wealth of information on plants' stress responses that are mediated by microbes [177].

6.1. Metagenomics

Metagenomics is a promising approach for leading about microbe-microbes and plant-microbe interaction, and it has a lot of potential for increasing long-term plant productivity [178]. It is estimated that about <1% of microbes has been cultured using metagenomics approaches. Only culture-independent technologies or metagenomics approaches have been used to access the enormous majority of the bacteriological world [179]. Analysis of 16S rRNA sequence and molecular phylogeny, they can only evaluate the microbial diversity of various settings without cultivating [180]. Sanger sequencing, Roche 454 pyrosequencing, and Illumina (sequencing by synthesis) have been employed to investigate bacterial populations with PGP from the rhizospheric plant from various harsh conditions. The Sanger sequencing approches was first metagenomics sequencing phases [181]. Although next-generation sequencing (NGS) systems allow for improved sequencing efficiency at a lower cost over time [182]. Furthermore, modern NGS platforms can generate 5000Mb of DNA sequences per day, which is more than twice as much as the 6Mb of the data generated by Sanger sequencing [183]. Shotgun metagenomics studies allow classification of PGP microbe at the gene level and the direct inference of molecular function. In this study, the microbial community will allow underlying surveying associates of various microbiomes in a specific ecosystem concerning diverse biotic and abiotic stresses. The functional metagenomics method emphasizes identifying genes related to a particular function. The development of next-generation sequencing technologies has boosted interest in uncultureable microorganisms found in the rhizosphere of plants that grow in harsh settings. Metagenomics and metaproteomic investigations have been used to functionally characterize the rhizosphere microbial communities in a range of severe settings [184,185]. Metagenomics analysis has been used to characterize genes involved in the survival of microbes in harsh environments, including suitable solutes, heat shock proteins, and pH homeostasis [186,187]. Numerous researches on the impact of PGP bacteria on potato, wheat, maize, and rice plants have revealed ACC deaminase genes for reducing salt stress [188,189]. In a study concluded that first metagenomic research of the Red Sea mangroves' microbiome and the first use of unbiased 454-pyrosequencing to examine the microbiome of *Avicennia* marina rhizosphere.

6.2. Metatranscriptomics

Metatranscriptomics is the study of gene expression of microbes found in a natural environment at a time. Metatranscriptomics studies can be performed by high throughput sequencing techniques, including microarray techniques, third Generation Single-Molecule Long Read Sequencing, and Next Generation Sequencing (NGS). Microarray technology was one of the essential techniques for quantifying the impression of transcript (mRNA) from known organisms or entire microbial communities [190]. Many PGP features, like as ACC deaminase production in rhizobacteria and phytohormones production were subsequently triggered by these proteins to boost growth under abiotic stressors [191]. A few stress induced bacterial genes activated miRNA, which increased the expression of genes implicated in abiotic stress mitigation in plants such as *Arabidopsis*, rice, *Medicago,* and wheat [192]. MiRNA169 was utilized to minimize drought and salinity stress in rice crops, and miRNA169c was utilize to alleviate stress of drought in tomato plants [193,194]. Using the RT-PCR method, researchers compared different miRNAs to investigate microbe-mediated aluminum stress in two rice varieties [195]. In a study, concluded that, analysis of various environmental stresses and compared with public transcriptomics data to identify overlapping stress controlled gene in induced response to *Botrytis cinerea* and other biotic (*Pseudomonas syringae* PV. tomato DC3000 *virulent* and *avirulent Rpm1* strains, *Arabidopsis brassicicola* and *Pseudomonas rapae*), abiotic (oxidative stress and wounding), and hormonal (SA, ET, JA, and ABA) stresses [196].

6.3. Metaproteomics

The term "metaproteomics" refers to the analysis of an environmental sample's whole microbial protein complement at a certain time [197]. Metaproteomics analysis recently has been widely employed to detect the functioning of microbial communities from various critical habitats around the world. Plant-microbe and microbe-microbe interaction have been studied using metaproteomics analyses [198]. Many studies have been conducted on the importance of metaproteomics in various environments. Metaproteomics research on plant microbes aids in the understanding of complex metabolic pathways as well as the various discoveries available in the many microbial gene and protein activities. The reports on plant microbes help to understand complex metabolic pathways, and discover many functions of genes and proteins microbes. The particular identification of protein is supported by a comparison of the plant microbe's interactions under the condition of stressed and non-stressed. Other proteins and enzymes involved in abiotic stress mitigation can be identified by comparing the protein profiles of various plant-associated microorganisms with and without stress. Metaproteomics techniques were used to study bacterial groups associated with various crops such as *Arabidopsis*, barley, maize, oilseed rape, rice, soybean, and wheat developing under abiotic stresses [199]. Metaproteomics techniques could be utilized to classify protein–protein interactions, a diverse protein involved in metabolic pathways, synthesis of enzymes and protein, which are used as osmolytes to respond to stress of abiotic conditions and proteins associated with the cell wall and cytoskeleton maintain intracellular osmotic balance.

7. CONCLUSIONS

Extremophilic microbiomes that survive in unique and extreme conditions have very diverse possible biotechnological applications in the environment and agriculture. Mineral solubilizing extremophilic microbial strains could be useful as bioinoculants and biocontrol agents in agriculture to encourage plant growth under various abiotic stress conditions. Many arable lands urgently need a natural and environmental friendly alternative to synthetic fertilizers for crop production and also help in the alleviation abiotic stresses on crops cultivated in harsh environments. Bioinoculants/biofertilizer has been developed, and some developed countries are already taking advantage of green technology. The capability of the mineral solubilizing extremophilic microorganisms to promote the growth of plant and biomolecule production has raised the interest of scientific groups. Mineral solubilizing extremophilic microbes can improve crop output under abiotic challenges by applying meta-omics methods, including metagenomics, metatranscriptomics, and metaproteomics; it could provide several evidences on the microbes mediated stress response of plants. In conclusion, mineral solubilizing extremophilic microbes are sustainable resources that can be utilize in various biotechnological sectors to develop the economy. In future, the genotype-specific microbiome will eventually be available and used as a diagnostic for creating climate resistant cultivars. Consortia of advantageous microbes will also play a role in assisting plants in withstanding stressful conditions, or they will be employed to encourage plants to expel a particular set of root exudates that will provide them a survival advantage in extreme environmental conditions.

8. AUTHOR CONTRIBUTIONS

All authors made substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data; took part in drafting the article or revising it critically for important intellectual content; agreed to submit to the current journal; gave final approval of the version to be published; and agree to be accountable for all aspects of the work. All the authors are eligible to be an author as per the international committee of medical journal editors (ICMJE) requirements/guidelines.

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10. CONFLICTS OF INTEREST

The authors report no financial or any other conflicts of interest in this work.

11. ETHICAL APPROVALS

This study does not involve experiments on animals or human subjects.

12. DATA AVAILABILITY

All the data is available with the authors and shall be provided upon request.

13. PUBLISHER'S NOTE

14. USE OF ARTIFICIAL INTELLIGENCE (AI)-ASSISTED TECHNOLOGY

The authors declares that they have not used artificial intelligence (AI)-tools for writing and editing of the manuscript, and no images were manipulated using AI.

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