# Plant-Microbial Interactions for Sustainable Agriculture

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Edited by

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# CHAPTER ONE

# PLANT–MICROBE INTERACTIONS IN EXTREME ENVIRONMENT – INSIGHT AND PROSPECTS IN SUSTAINABLE AGRICULTURE

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## Abstract

The plant–microbe associations in extreme ecological niches are intriguingly complex and dynamic because of abiotic stresses imparted by the surrounding environment. This chapter emphasises on plant–microbe association in extreme terrestrial and aquatic environments around the globe, describes the manipulation of the mechanism of such unique interactions towards agriculture sustainability. The specific adaptation strategies and evolutionary processes for both the host plant and the associated microorganisms in an unfavorable environment are highlighted in this chapter to develop successful methods of bioformulation to be applied in agriculture.

**Keywords:** Extreme environment, Stresses, Plant–microbe interactions, Adaptation strategies, Evolutionary processes, Bioformulation, Sustainable agriculture.

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# Introduction

Theoretically, it is difficult to describe an extreme environment for a plant as harsh micro–environments can exist in the so–called ideal environment of a plant (e.g. rocky outcrop in a rainforest). Alternatively, the plants can find the surroundings optimum for growth and development even in hostile environments (e.g. the growth of short–lived plants after sporadic rainfall in arid regions). Plants require a range of optimal conditions for proper growth and existence, and if they are devoid of these factors for a substantial time phase, it results in an overall reduction in plant growth and fitness. Therefore, extreme environments refer to conditions challenging for plants to thrive in as they limit their normal physiological processes. The abiotic factors in extreme environments are very close to the upper or lower limits for most growing crop varieties (Fernández-Marín et al 2020). These factors include extremities and fluctuations in temperature intensity, availability of nutrients and water, concentrations of gases ($O_2$ and $CO_2$), UV radiation, and salinity (Xu et al 2020).

The physiology of plants is highly altered due to these abiotic stresses, and the negative impact of these environmental stressors results in reduced crop yield, leading to global food insecurity (Egamberdieva et al 2017). Recent reports have shown the loss of 2000 million hectares of land throughout the world due to global warming, resulting in scarcity of food, water and a rise of salinity in soil (Duchenne-Moutien et al 2021; Mukhopadhyay et al 2021). Therefore, sustenance in hostile environmental scenarios is an excellent challenge for plant species. This challenge of mitigation of abiotic stressors for survival and reproduction in extreme environments is met through various mechanisms adapted by the plants that include both physical (size, posture, structural adaptations) and chemical responses (volatile organic compounds [VOCs], secondary metabolites, secondary messengers like $Ca^{2+}$, phytohormones, defence molecules). Due to high selective pressures in extreme environments, the phylogenetically distinct plant species have undergone convergent evolution and have developed similar survival strategies, adapting features, and acclimatizing behaviours (Xu et al 2020).

In this regard, the microbiome associated with plants also plays a vital role, as they can produce various phytohormones or their analogs, secondary metabolites, and VOCs (Zhao et al 2022). The establishment of a stable phytomicrobiome is an essential component during plant adaptation in any environment. With the evolution, the plants develop associations with microbial organisms to promote adaptation to the growing environments (Lyu et al 2021). This indicates that the coevolution of plants and microbes underpins sustainable agriculture, and hence, gaining deep perspectives on the manipulative and tolerance strategies of the plants and their associated microflora is essential for better crop management in extreme environmental situations. The plant growth–promoting bacteria (PGPB) associated with plant species in extreme environments are evolutionary well–adapted, can increase soil fertility, and efficiently regulate stress response genes to enhance better plant development (Alsharif et al 2020). Therefore, exploitation of the potential of phyto–microbiome from extreme environmental conditions will add to agricultural sustainability in otherwise non–agricultural lands of extreme terrains of the world. The microbial technology and genetic engineering of microbes and plants are at the forefront of research applied for the betterment of agriculture (Thakur et al 2023). In this respect, low–input biotechnology is one of the strategies suggested by agriculturists and environmentalists to enhance plant stress tolerance through microbial species (Gupta et al 2022). The greatest challenge to be considered during sustainable agriculture development is optimizing the levels of biochemical produced by the plant–associated microorganisms under abiotic stressors of extreme environments. For this, a better understanding of plant–specific traits, genetic mechanisms, receptor functions, and plant–microbe interactions in extreme environments is of the utmost importance.

Therefore, the following chapter encompasses the adaptive mechanisms of plants from extreme terrestrial and aquatic environments around the world, the plant–microbe and microbe–microbe crosstalk in these environmental scenarios, and the strategies of manipulation of these associations toward the development of eco–friendly and economically feasible sustainable agriculture.

## Extreme Environments

Due to small–scale deviations and gradual changeover of the physical environment along the earth's surface, dividing the world into a few ecological zones is challenging. However, through arbitrary boundaries based on average predominating environmental features, the world’s ecological zone has been divided into five major biomes *viz.* aquatic (freshwater and marine), grassland (tropical and temperate), forest (tropical, temperate and boreal), desert and tundra (arctic and alpine).

However, forests covering one–third of the world bear the highest terrestrial biodiversity among these biomes. The others, including boreal, desert, and tundra, have limited and specific vegetation and microbiome distribution due to the extreme temperatures and low precipitation amounts. The living species from these latter biomes require special adaptations for survival.

The extreme ecosystems discussed in the following chapter include desert, cold, marine, wetland, and flooded ecosystems. The desert biome covers one–third (33%) of the earth's land area but is home to one–sixth of the earth's total population and is one of the indispensable reserves for minerals. The diversities of micro– and macro–organisms from deserts are significantly less studied, possibly due to the extremities of temperature and uncertenities in precipitation. But this is to be borne in mind that the desert harbours a rich niche of diverse life forms and provides benefits of water, food supply, medicines, and raw materials to the local inhabitants and neighbouring areas. Deserts also act as carbon sinks that store $CO_2$ and prevent its entry into the atmosphere (Flanagan and Flanagan 2018). However, global warming threatens this ecosystem by increasing the risk of wildfires and destroying slow–growing trees and shrubs. Therefore, the restoration of the desert ecosystem is highly important. On the other hand, the knowledge of adaptive features of dry desert species is vital to manipulate agriculture worldwide under increasing global warming (Flanagan and Flanagan 2018).

The biodiversity in the cold ecosystem is low due to very little precipitation and permanent layers of ice. However, in the recent on–going climate change scenario, the cold regions' biome is mostly affected (Cordes et al 2023). The mortality of species markedly increases with the changes in climatic conditions of cold regions. However, unlike the other biomes, the cold ecosystem has a unique adaptive micro–and macro population. These are also important for agricultural and industrial purposes like pigment production (Sajjad et al 2020). Though some studies have been done on mesophilic microorganisms for bioformulations, these species have failed to protect plants from pathogens under low temperatures. However, the biocontrol agents (BCA) derived from cold regions are effective at low temperatures (Torracchi et al 2020). Still, studies on isolating and identifying such BCA from cold regions are limited. Therefore, accounting for microbial species diversity and abundance and highlighting their importance in sustainable agriculture is needed.

The marine ecosystem includes salt marshes, estuaries, mangrove forests, coral reefs, open oceans, and the deep–sea oceans cover 70% of the Earth's surface area and supports a wide range of plant and animal population. It adds to 50% of the total world's oxygen, 97% of the water resources and provides essential ecosystem services for the normal functioning of the living world. Additionally, it provides food security, raw materials for animal fodders, pharmaceuticals and buildings, and protection against erosion and floods. But climate change and anthropometric activities like overfishing, agricultural and industrial wastes, plastic pollutants, medicinal remnants, and cosmetic chemicals threaten this vast ecosystem. Considering all these, protecting the marine ecosystem and knowing the biodiversity of this largest ecosystem is essential (Lotze 2021).

Wetlands and flooded ecosystems, covering 40% of the world's biome, are natural reservoirs for flood storage and reduce the severity of downstream erosion during heavy rainfalls. These lands offer protection against storm surges and wind waves. It also protects surface waters from overloading of nutrients by the removal of excess nutrients. Also, the wetland is the abode of various flora and fauna that provide essential living for a large population worldwide. Therefore, the preservation of the flora in the wetlands and the reconstruction of coastal marshes are necessary worldwide. The adaptation of the wetlands plants (hydrophytes) makes it the most unique in the world. However, anthropometric activities, natural calamities, and ever–increasing pollution are the leading causes of the destruction of wetlands worldwide. Therefore, the study on the biodiversity of wetland and flood storage areas to restore and protect the same is an essential note of discussion for ecologists (Wang et al 2021; Pétillon et al 2023; Jones et al 2020; Palit et al 2022; Xu et al 2019).

## Terrestrial Extreme Environments

### Desert Ecosystems

The high temperatures, solar radiation, and water scarcity due to annual precipitation below 250–300 mm and higher evapotranspiration than precipitation result in drought stress in arid and semi–arid desert regions. These environmental conditions result in the generation of oxidative stress among the desert plants. Hence, to cope with the developing oxidative stress, innumerable secondary metabolites, like alkaloids and isoprenoids (monoterpenes and sesquiterpenes), oxygenated compounds like acetaldehyde, acetic acid, ethanol and other volatile compounds like green leaf volatiles (GLV) and phenols are being synthesized by the plants as an early line of defence (Rinnan et al 2014). The high emission of VOCs results in the development of strong aroma which is responsible for attracting pollinators like bats and moths. They take part in the ecological cycle of deserts. Later, these are replaced by more effective and protective non–volatile antioxidants like xanthophylls. Dehydrogeosmin (DHG) is another VOC released in diurnal rhythms by the flowers from diverse cactus plants in deserts that attract pollinators (Rinnan et al 2014). Another process implemented by the poikilochlorophyllous species is to lose the chlorophyll and thylakoids under arid conditions and re–synthesize them with increased hydration (Beckett et al 2012). On the other hand, at high UV–radiation, the emission of salicylic esters like 2–ethylhexenyl salicylate and 3,3,5–trimethylcyclohexenyl salicylate protect the plants in desert (Matsunaga et al 2008). Additionally, diverse oxygenated VOCs, aromatics (acetophenone, benzene, benzaldehyde, phenol, xylene, and 1–chloro–2–methoxybenzene) and oxidized fatty acid products were found to be emitted among dessert plants from North and South America (Jardine et al 2010). The distribution and competition of the desert shrubs are regulated through root–root communication by releasing VOCs in *Ambrosia* sp. and *Larrea* sp. (Rinnan et al 2014). Additionally, Crassulacean acid metabolism (CAM), photorespiration, and expression of heat–shock proteins (HSPs) are other ways of adaptation in desert plants by which they can reduce the absorption of excessive heat and energy and also can maintain the proper protein folding under extremely high temperatures (Alsharif et al 2020)

Besides morphological and genetic adaptations, desert plants recruit specific microorganisms on the phyllosphere, endosphere, rhizosphere, rhizosheath, and rhizoplane and develop successful communication with the microbiome (Alsharif et al 2020). Though the association of endophytic microorganisms with the enhancemnet of growth in plants and maintenance of fitness has been widely accepted, identification of endophytes from arid regions is rarely performed. The high–throughput 16S–rRNA sequencing studies of extreme arid regions of the Atacama and Patagonia deserts of Noth and South Chili have demonstrated differences in distribution, richness, and variety of endophytic bacterial species in these two regions. The identified species belonged to the genera of Proteobacteria, Firmicutes, Actinobacteria, and Bacteroidetes (Maza et al 2019; Gaete et al 2020). Bacillaceae and Enterobacteriaceae are the keystone species. Therefore, this study on plant–microbe holobiont might be an important base for developing proficient methods for conserving native plants and using the knowledge of sustainable agriculture during extreme climate changes (Zhang et al 2019). Similar bacterial phyla were observed from the pioneer native desert plants of Saudi Arabia, Cacti from Mexico, and Caragana, a perennial shrub of arid regions of North China

(Osman et al 2016; Na et al 2018). This latter study identified Gemmatimonadetes, Acidobacteria, and Cyanobacteria as well. The most dominant genera identified belonged to *Acinetobacter*, *Arthrobacter*, *Bacillus*, *Burkholderia*, *Chitinophaga*, *Chryseobacterium*, *Flavobacterium*, *Kocuria*, *Microbacterium*, *Paenibacillus*, *Pseudomonas*, *Rhizobium*, *Sphingobacterium*, and *Stenotrophomonas* (Na et al 2018). It is widely known that plant genotype affects the composition of associated microbes. However, studies with desert plants showed that the soil has a more significant impact on microbiota composition than the host type (Marasco et al 2018; Osman et al 2016). The abundance of Proteobacteria and Actinobacteria demonstrates their wide–range adaptability and versatility under high selective pressures in arid soils (Pini et al 2011; Mohammadipanah and Wink 2016). These characteristics and their plant growth–promoting activities have made them excellent candidates for bioinoculants.

The halotolerant *Klebsiella* strains from the genera Enterobacteriaceae with aminocyclopropane–1–carboxylic acid (ACC) deaminase activities, siderophore–producing abilities, auxin synthesis capabilities identified as rhizobacteria from the native shrub, *Parastrephia quadrangularis* of Atacama Desert were found to increase biomass and superoxide dismutase activities in the roots of wheat crop (Acuña et al 2019). The positive effects on biomass of root and shoots of cucumber were observed after inoculation with rhizobacterial strains having high phytase activities and isolated from *Larrea tridentata* of the Mojave Desert of North America (Jorquera et al 2012).

Similar studies were performed with *Bacillus* and *Serratia* sp. isolated from the rhizosphere of *Atriplex* sp. of arid soil and with *Enterobacter* and *Bacillus* sp. from agroecosystems of Atacama and Aconcagua Valley (Inostroza et al 2017). This experiment showed that the agro–ecosystem–derived species could improve plant growth under natural conditions, while the species from arid deserts functioned well under water–stressed conditions. Therefore, this knowledge can be harnessed to isolate PGPR from arid and semi–arid regions to promote agriculture in the upcoming global warming scenarios. The degraded soil restoration and revegetation was successfully performed by the use of *Azospirillum brasilense* and *Bacillus pumilus* bioinoculants in the Sonoran Desert of North America (Bashan et al 2012; Galaviz Bustamante et al 2018). This bioinoculation increased the activity of other PGPR in the soil, like *Rhizobia*, through augmentation of soil fertility and soil organic carbon content.

*Bacillus* sp. and *Pseudomonas lini* with halophilic properties combined with ACC–deaminase activity, siderophore synthesis, phosphate–solubilization, and indole–acetic–acid (IAA) production abilities were isolated from the roots of the perennial grass *Distichlis spicata* of Chihuahuan Desert. These isolates enhanced the growth of cucumber, *Arabidopsis* sp. and watermelon under normal and salt–stressed conditions (Palacio–Rodríguez et al 2017). *Pseudomonas* sp. M30–35 isolated from the rhizosphere of succulent xerophytic shrub *Haloxylon ammodendron* from the Northwestern Chinese desert could also improve salt–tolerance, catalase activity, and total biomass of ryegrass plants, and genome sequencing identified 34 genes from these species involved in PGP traits (He et al 2018).

Visible increases in the growth of plants, germination of seeds, ammonia and nitrogen fixation, and altered activities of antioxidant enzymes were observed in pomegranates with co–inoculation of *Azotobacter chroococcum*, and AM fungi (*Glomus mosseae*), cowpea plants with *Bacillus* sp. and wheat plants with *Serratia marcescens* from the great Indian Thar Desert revealing biofertilizer potential of these isolates under salt–stressed conditions (Alsharif et al 2020). AM fungi in association with PGPR (*Pseudomonas fluorescens* and *Pseudomonas putida*) could also stimulate efficiently the increase in biomass and alleviate the negative effects of severe droughts by increasing retention of water in Common myrtle of semi-arid regions of Iran (Azizi et al 2022). *Bacillus cereus, Bacillus subtilis,* and *Bacillus circulans* identified from the Thar Desert of Pakistan enhanced the growth of *Arabidopsis thaliana* under salt stress (Bokhari et al 2019).

Novel *Pantoea* sp. isolated from different parts of *Alhagi sparsifolia* in the Taklamakan and Gobi Desert of North China revealed *in vitro* characteristics of PGPT (plant growth promoting traits) of exopolysaccharide (EPS) and protease production. Additionally, these bacterial species demonstrated tolerance towards water stress, extreme heat, salt and enhanced the growth of wheat when inoculated. They increased sugar and chlorophyll and decreased the inoculated plants' proline contents (Chen et al 2017). The EPS and lipopolysaccharides (LPS) secretion is recognized as a mechanism for *Shinorizobium meliloti*, *Bradyrhizobium diazoefficiens*, *Bacillus cereus*, and *Rhizobium* sp. in tomato, forming a protective layer on plant surfaces and helping in water retention and accumulation of HSPs (Khan et al 2023).

The bacterial isolates *Arthrobacter agilis*, *Bacillus endophyticus*, *Bacillus tequilensis*, *Planococcus rifietoensis*, and *Variovorax paradoxus* isolated from different parts of *Salicornia europaea* from Gurbantunggut Desert of China also displayed strong salt and drought tolerance activities (Zhao et al 2016). *Bacillus amyloliquefaciens* FZB42 from dry Gansu Province, China, induced tolerance to drought conditions in *Glycyrrhiza* *uralensis* Fisch. by inducing root–elongation and IAA production (Yue et al 2022). High thriving capabilities in nitrogen–deficient soils and protein contents in seeds in non–nodulating legume *Tylosema esculentum* of South African deserts could be attributed to the presence of inter–transmissible endophytic bacterial strains of *Rhizobium*, *Bacillus*, *Burkholderia*, *Microbacteria*, *Chitinophaga and Stenotrophomonas* sp., indicating these species to be important as biofertilizers (Chimwamurombe et al 2016). The date–palm trees from the Tunisian Sahara Desert in North Africa harboured similar bacterial phyla with an abundance of *Pseudomonas* sp., and all of them showed high PGPT that helped the plants to thrive under drought stress (Cherif et al 2015). *Streptomyces* sp. strain PT2 and *Streptomyces rochei* strain PTL2 showed potential biocontrol activities and could protect plants from fungal threats like soil–borne pathogenic fungus *Rhizoctonia solani*. *Nocardiopsis dassonvillei* MB22 proved to be an efficient biofertilizer and biocontrol agent among all the isolates from native plants of the Sahara deserts (Zamoum et al 2017; Allali et al 2019). Comparative genomics studies have identified potential genes responsible for developing stress tolerance among 2500 microbial strains with biofertilizer and antimicrobial potential including *Bacillus sp.*, *B. megaterium*, *B. pumilus*, *B. licheniformis*, *Micrococcus luteus, Paenibacillus sp.*, *Pseudomonas sp., and Acinetobacter calcoaceticus* from various native plant species of South Arabian Peninsular Deserts and the cultured–isolates showed positive plant growth promoting traits when tested on cucumber, cabbage, tomato, alfalfa, maize, Arabidopsis and wheat plants (Alsharif et al 2020).

## Cold Ecosystems

The vegetation in cold ecosystems is dwarf and consists of bryophytes, shrubs, and sedges due to the limited nutrients and harsh environmental conditions. The vegetation in these ecosystems suffers from cold stress and freeze–thaw events, particularly during autumn, winter, and spring. The most common technique the plants use to combat the cold stress is higher emission of VOCs (Rinnan et al 2014). A higher emission of isoprenoids, including monoterpenes and sesquiterpenes, have been observed from plants like willows and mosses from arctic tundra regions than temperate species, indicating the adaptive mechanisms for these plants in extremely cold environments. Similarly, a high emission peak of monoterpenes was observed from boreal forests at temperatures below 10°C

Conversely, microorganisms have developed intricate adaptive features in their cellular compositions, including membranes, energy–synthesizing compartments, nutrient utilization capabilities, and cryotolerance. Reports have shown that the microorganisms isolated from extreme low–temperature regions could serve as efficient PGPR under cold stress such as psychrotrophic strain of *Acinetobacter oleivorans* IRS14 was found to enhance biomass, antioxidant and chlorophyll contents, pigments (carotenoid), proline, and endogenous phytohormones in wheat and helped them to combat cold stress (Ali et al 2023). PGPR isolated from the rhizosphere of mustard and apple plants of Uttarakhand regions of India, when co–cultured in pea, showed promising and stable plant growth, antifungal activities, various PGPT and cold tolerance (Anwar et al 2019). Though, field–or pot–based studies were not performed, genetic analyses revealed the presence of genes associated with the synthesis of plant growth hormones like auxin, abscisic acid, cytokinin, ethylene, and salicylic acid in *Cryobacterium* sp. from Arctic glaciers. This indicates the high potency of this isolate to perform as PGPR under cold stress (Singh et al 2015). *Pseudomonas protegens* isolated from the anthropogenic soil of Russia stimulated the growth of bread wheat under cold and drought stress by stimulating water reabsorption by the plants (Bakaeva et al 2022).

PGPR strains not only enhanced the growth of plants but also modulated the rhizosphere bacterial composition eg. *Sinorhizobium* sp. A15, *Bacillus* sp. A28, *Sphingomonas* sp. A55 and *Enterobacter* sp. P24 significantly increased the yield of grains and also stimulated the abundance of Acidobacteria, Chloroflexi, and Verrucomicrobia in maize plants in the extremely cold climate of Northeast China (Chen et al 2020). Similar observations were noticed for the same maize plants under chilling conditions where the abundance of Cellvibrionaceae, Comamonadaceae, Caulobacteraceae, Enterobacteriaceae, Flavobacteriaceae, Methylophilaceae, Opitutaceae, Phyllobacteriaceae, Pseudomonadaceae, Sphingobacteriaceae, Sphingomonadaceae, and Xanthomonadaceae increased and Burkholderiaceae, Chitinophagaceae, and Streptomycetaceae significantly got depleted. Moraxellaceae and Flavobacteriacae showed potential PGPT under chilling conditions (Beirinckx et al 2020).

Recent studies showed that the cold-adaptive PGPR *Pseudomonas jesenii* MP1 and *Pseudomonas palleroniana* N26 enhanced the nutritional status of the soil and yields of kidney beans in field conditions of Harsil and Chakrata locations of Indian Central Himalayas and could serve as potent bioinoculants for biofortification of crops (Khan et al 2023). *Bacillus* sp. IHBT-705 from the rhizosphere of saffron plants from Himachal Pradesh of North India displayed tolerance over a wide range of temperatures from 4°C-50°C along with other stress adaptabilities like tolerance to high salinity, pH and osmotic changes along with other PGPT like siderophore synthesis, phosphate and potassium solubilization. Genetic analyses identified versatile clusters of genes that could survive at both high and low temperatures (Ali et al 2023)

PGPR *Burkholderia phytofirmans* PsJN reversed the cold–induced changes in grapevines and *Arabidopsis thaliana* by modifying the rate of photosynthesis and carbohydrate metabolism and thus revealing their potential to be used as biofertilizers under extreme chilling conditions (Fernandez et al 2012; Theocharis et al 2012; Su et al 2015).

The genetic studies revealed the cold stress response abilities of psychrophilic *Bacillus* sp. CJCL2, RJGP41, and temperate *Bacillus velezensis* FZB42 and wheat inoculated with these strains showed higher phytohormone, abscisic acid, and proline accumulation and a decrease in lipid peroxidation, resulting in higher growth and development under extreme environments of Qinghai–Tibetan plateau (Zubair et al 2019). The mechanisms involved in cold–adaptation in *Pseudomonads*, *Bacillus* sp. while developing interactions with wheat, CJCL2, and RJGP41 from the Northern Himalayas showed the secretion of EPS, secondary metabolites, and formation of biofilms on the root surfaces. These mechanisms inhibited plants' sodium uptake and cold dehydration in the Himalayan regions (Khan et al 2023). *Pseudomonas koreensis* P2 isolated from Sela Lake, India, also showed similar PGPT and genetic screening identified genes involved in siderophore production, phosphate solubilization, temperature tolerance, multidrug resistance, and glycine–betaine production (Srivastava et al 2019).

Micropropagation is an alternative solution for the conservation of endangered plant species. However, the survival of such species in greenhouses or fields is a challenge. To overcome this, PGPR–priming is a method used, and it has been used in various cold–climate regions to save the natural vegetation. For example, bio inoculation with *Serratia quinivorans* PKL:12 isolated from the rhizosphere of medicinal herb, *Picrorhiza kurroa* of Himachal Pradesh increased the growth of this herb in cold regions of Himachal Pradesh. Genetic screening of this bacterial strain revealed biocontrol, plant–growth–promoting, and cold–adapting potential (Kumar et al 2021). Bio–priming is an emerging method of treating seeds with bioinoculants before applying them to field trials. At low–root temperatures, *Bacillus megaterium* and *Bradyrhizobium japonicum* strains isolated from rhizosphere and bulk soil as well as non–agricultural lands of different locations in Siberia increased germination rates and initial growth of seedlings in different soybean cultivars when used for seed bio–priming (Miljaković et al 2022).

## Aquatic Ecosystems

### Marine Ecosystems

The saline water is most dominantly widespread globally, while the arid/semiarid regions suffer from scarcity of fresh water. Therefore, establishing agriculture with saline water is an alternative solution for the growth of crops in those areas. Additionally, soil salinity is one of the pioneer causes of the decline in cultivable lands and plant productivity globally.

Therefore, to cope with this problem, an increase in the growth of halotolerant plants as well as saline tolerance in non–halophytes, is essential (Wang et al 2022). Bioformulations synthesized from plant growth–promoting microorganisms isolated from halotolerant varieties of saline soil might be a helpful avenue for agricultural practice in saline environments. Extensive research is being conducted worldwide to identify PGPR with salt–tolerance capabilities along marine ecosystems. The mainly distributed microbial taxa that form biofilms on aquatic plants and participate in nutrient assimilation include Actinobacteria, Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria, Firmicutes and Bacteroidetes (Srivastava et al 2017). The plant–microbial symbioses in coastal systems include mycorrhizal association, nitrogen fixation symbioses, endophyte colonization, rhizosphere association, and pathogenic interactions. These interactions facilitate the coastal plants' growth and build resilience against biotic and abiotic stresses. Additionally, these also dictate soil aggregate formation, nitrification and denitrification, soil organic matter accumulation, decomposition, and formation of recalcitrant organic matter with the aid of extracellular enzymes (Farrer et al 2022).

The salinity is a determining factor for establishing the rhizosphere bacterial population and modulates the rhizosphere microbiome and metabolite composition, allowing specific keystone species to be established. These bacterial species become the signature of the halotolerant plant’s holobiome, which interacts with the plants to help them combat salt–stress. Such keystone species with PGPT were isolated from sea–rice cultivars of China and were found to promote salt–tolerance in those plants (Wang et al 2022). On the Yellow River delta of China, *Sinorhizobium/Ensifer* sp. isolated from the nodules of soybean proved to be a potent candidate for increasing nitrogen fixation in soybean plants by improving salt resistance (Yang et al 2020). Heavy–metal degrading capabilities were identified among the rhizo–isolates (*Pantoea agglomerans* and *Bacillus aryabhattai*) from the halophyte *Spartina* *densiflora* along highly metal–polluted estuarine regions of Tinto and Odiel rivers, Spain (Paredes–Páliz et al 2018). The plants inoculated with these strains showed better management of metal stress with decreased antioxidant activities and increased lignin synthesis. PGPR *Bacillus aryabhattai*, *Stenotrophomonas rhizophila*, *Pseudomonas oryzihabitans*, and *Salinicola endophyticus* isolated from coastal salt–marshes of Portugal increased photoprotection ability and reduced antioxidant activities in *Halimione portulacoides* thereby augmented the overall plant fitness under high salt–stress (Carreiras et al 2022).

Halotolerant *Streptomyces* sp. isolated from the rhizosphere of *Salicornia bigelovii* on the westnorth coast of the UAE produced IAA, ACC–deaminase, and polyamines and stimulated the growth and seed yield of this halophytic crop (Mathew et al 2020). High ACC–deaminase activity was also identified among the rhizobacterial strains of the Oceanospirillales family isolated from the rice cultivars grown along saline coastal agricultural fields of Kerala, India. These isolates also showed other PGPT, including phosphate solubilization, siderophore, and biofilm production (Krishnan et al 2018). *Brachybacterium saurashtrense* JG06, characterized as halotolerant diazotrophic bacteria, was found to develop changes in *Arachis hypogaea* and tobacco plants during nitrogen starvation and salt–stress and positively modulated the photosynthesis in these plants (Alexander et al 2022). *Pseudomonas putida*, *Pseudomonas mendocina*, and *Stenotrophomonas maltophilia* were isolated from sea–water of Eastern Harbour of Alexandria, Egypt, and were shown to possess PGPT of IAA and HCN (hydrogen cyanide) production, phosphate solubilization and various enzyme activities. The halotolerance, thermostability, and capacity to boost hyperaccumulation of heavy metals in treated plants (sunflower) proved their potential for biofertilization and bioremediation (Sorour et al 2022). In addition to *Pseudomonas and Stenotrophomonas sp., Aeromonas, Bacillus, Vibrio, Pseudoalteromonas, Staphylococcus, and Marinobacter* sp. have been tested as biofertilizers in edible halophyte *Salicornia ramosissima* and have been shown to modulate the metabolism of fatty acids, oxalates and phenols in response to salt and drought stress (Mesa–Marín et al 2023). *Bacillus amyloliquefaciens* isolated from *Sasamorpha borealis*, a temperate plant in Japan that can grow at –20$^0$C, displayed several PGPT, including nitrogen fixation and production of IAA, siderophore, ACC–deaminase activities. The growth of pepper plants was enhanced even under high saline, drought, and heavy–metal–contaminated conditions when inoculated with *Bacillus amyloliquefaciens* (Kazerooni et al 2021). This *Bacillus* sp., isolated from the same plants along Korean coastal lands, showed antifungal activity against *Botrytis* and *Alternaria* sp., the two pathogenic fungi causing *Botrytis* gray mold and *Alternaria* leaf spot diseases. These bacterial strains improved the health of the plants by alleviating the biotic stress through increased production of salicylic acid and sugar and mitigated the fungal growth through enzyme hydrolysis (Kazerooni et al 2021). Rhizobia consortia, composed of bacterial isolates *Pseudomonas*, *Pseudarthrobacter*, *Bacillus*, and *Aeromonas* species obtained from different halophytes of coastal lands of southwest Spain significantly improved the heat–tolerance of grapevines by enhancing photosynthetic capabilities, osmoprotectant abilities, antioxidant mechanisms, and membrane stability (Carreiras et al 2023). *Pantoea*, *Bacillus*, *Azotobacter*, and *Pseudomonas* from Poland coasts in greenhouse experiments could enhance the contents of chlorophyll in strawberry plants under water–deficit conditions, indicating that these marine microbial isolates could be used as potent biofertilizers during droughts (Paliwoda et al 2022). Halotolerant PGPR strains of *Bacillus*, *Oceanobacillus* and *Halomonas* sp. isolated from the rhizosphere and endorhizosphere of durum wheat of Ghar regions of the Dead Sea boosted the growth of wheat plants under salt and water stress and showed antagonistic actions against *Fusarium culmorum* (Albdaiwi et al 2019). *Isoptericola* sp. AK164 isolated from the rhizosphere of *Avicennia marina* of Red Sea Coast elevated stress responses in *Arabidopsis thaliana* under salt stress by synthesizing ACC–deaminase and various enzymes (Alghamdi et al 2023). Tomato plants treated with halotolerant *Enterobacter hormaechei* (MF957335) isolated from the Arabian Sea's saline water showed better growth and biomass improvement. These strains could also solubilize potassium and calcium (Ranawat et al 2021).

The other saline–stress adaptations in extreme hypersaline marine environments include algae adaptations that have contributed to the maximum global atmospheric dimethyl sulfide (DMS) where the micro– and macro–algae release DMS in addition to little amounts of isoprene as stress–adaptor molecules (Rinnan et al 2014). DMS production has been reported from the brine channels of Arctic and Antarctic Seasonal Ice zones by the ice algae in addition to the accretion of DMSP (dimethylsulphoniopropionate) and other osmoprotectants to counteract the external high salts (NaCl). High DMS observations have also been found at hypersaline inland Salton Sea, soda–lake microbial mats, and Antarctic lakes (Rinnan et al 2014).

Another significant symbiotic association is the holobiont of corals that includes endosymbiotic dinoflagellate partner *Symbiodinium*, bacteria (Endozoicomonas), viruses, archaea, fungi, endolithic algae and protists.

These coral–associated microbes participate in nutrient cycling, synthesis of antibiotics and quorum sensing molecules, and offer bio–controlling of pathogenic microorganisms. Therefore, manipulation of the coral microbiome can be a solution to enhance coral health under stressful environments (Peixoto et al 2017).

## Wetland Ecosystems and Flooded Environments

The wetlands are the areas that are overflown with water from the nearby sea, river, lake, spring, and groundwater. The wetlands and flood storage ecosystem form the areas covered with salt and fresh water that provide habitats for various life forms, storing flood waters and maintaining surface water flow during dry periods. The water saturation determines the wetland vegetation. Except for Antarctica, all continents contain wetlands classified as bogs, fens, marshes, muskegs, potholes, peatlands, swamps, sloughs, and mires. However, the anoxic niche created around the flooded water–logged systems with fluctuating water table, the intertidal zones of mangrove vegetation, and salt–marshes form an extreme environment for vegetation as these regions develop stress and the plants show stress–adaptive responses like production of VOCs. Due to the lack of oxygen, fermentation produces ethanol, acetaldehyde, and acetic acid. The abundance of aerenchyma in the roots and rhizosphere of plants growing in wetlands is another mechanism for the fast transport of air and gases. The wetland plants of colder arctic and boreal regions also produce isoprenoids with the aid of the microorganisms associated with the rhizosphere. The emission of isoprenoids has also been observed from the mangrove flowers and leaves in response to the hypersaline environment of marshy wetlands. The VOCs released by the mangrove species inhibit the growth of other species and are directly proportional to the concentration of salts in the wetlands (Basyuni et al 2009).

The microorganisms inhabiting wetland systems associated with plants offer an excellent solution for the plants to thrive under environmental stresses. Besides, the contaminations from domestic, industrial, and agricultural wastes form a massive deposit in the wetlands at the river–sea estuaries, and wetlands become the sink for pollutants such as heavy metals. The pollutant, heavy metal, and pesticide accumulation result in abundant bacterial and fungal isolates with bioremediation capabilities in wetland areas (Chen et al 2020). *Achromobacter mucicolens*, *Diaphorobacter nitroreducens*, *Rhizobium daejeonense*, *Pseudomonas veronii*, *Pseudomonas lini* isolated from *Phragmites australis* of wetlands of tropical and temperate regions showed high production of IAA, siderophore and phosphate solubilization. In addition, they could degrade

90% of the carbamazepine, a hazardous pharmaceutical found in wastewater (Sauvêtre and Schröder 2015). Extremely halophilic archaeon (WN019T) was isolated from the wetland soil of Tianjin, China, and these isolates were found to grow in 15.0–20.0% (w/v) NaCl and pH 7.5–8.0. However, PGPT has not been studied in this isolate but can be tested for the growth of plants in hypersaline environments (Gong et al 2021). Studies in constructed wetlands revealed that the *Typha latifolia* and *Cyperus laevigatus* plants that showed better biomass and growth harbored hydrocarbon–degrading bacterial strains belonging to *Pseudomonas*, *Acinetobacter*, and *Bacillus*. These isolates displayed various PGPT and could degrade hydrocarbon. This indicates that the isolates can be potent candidates for bioremediation in constructed wetlands to alleviate hydrocarbon contamination and improve wetland vegetation (Hashmat et al 2019). *Bacillus*, *Nesterenkonia*and *Halomonas*, having abilities to solubilize phosphorus and potassium, fix nitrogen and utilize iron–ammonia–salt, were isolated from the rhizosphere of *Populus euphratica* Olivier of wetland reserves of Mulei, China. These isolates also promoted plant height, dry mass, and germination rate of maize plants in pot experiments (Anwar et al 2022). PGPRs like *Stenotrophomonas* sp., *Pseudomonas* sp. and *Sphingobium* sp., *Streptomyces* sp. and *Micromonospora* sp. colonizing as endophytes in the roots of wetland plant *Tamarix chinensis* in China with IAA and siderophore production and phosphate solubilization abilities. In addition, these isolates accumulate and transform nickel and promote the growth of wheat seedlings under pot trials, indicating that these potentials can be harnessed for both biofertilization and bioremediation of heavy–metal polluted wetland plants (Chen et al 2020; Gong et al 2018). Similarly, *Klebsiella*, *Pseudomonas*, *Agrobacterium*, and *Ochrobactrum* sp. isolated from *Arthrocnemum indicum* of salt–marshes in Gujarat coastlines promoted growth, augmented salt-tolerance balanced the ion homeostasis and decreased oxidative stress in peanut plants under salt–stress (Sharma et al 2016). The rhizosphere of *Cyperus laevigatus*, sedge along the coastline of Gujarat, India, harbours PGPR like *Delftia tsuruhatensis* and *Exiguobacterium indicum*. *Stenotrophomonas maltophilia* isolated from the rhizosphere of *Cyperus laevigatus* enhanced the development of peanut plants under $N_2$ deficit conditions (Alexandar et al 2019). Bacterial isolates from aerial parts, rhizosphere, and roots of *Arthrocnemum macrostachyum* from the western wetlands of Spain also showed multiple PGPT and resistance to heavy metals and increased efficiency of germination of seeds of these plants in the presence of heavy metal contamination (Navarro–Torre et al 2016).

*Kocuria flava* AB402 and *Bacillus vietnamensis* AB403 from the rhizosphere of Sundarban mangrove plants have been found to promote the growth of rice plants and enhance the uptake of arsenic from the soil (Mallick et al 2018). *Arthrobacter* sp., *Bacillus* sp., *Kocuria rosea*, *Pseudomonas plecoglossicida* from the rhizosphere of Sundarbans displayed PGPT–like IAA production, siderophore synthesis, phosphate, and zinc solubilization. These isolates improved the growth of pea plants upon inoculation and inhibited the growth of the pathogenic fungus *Macrophomina phaseolina* (Pallavi et al 2023). *Halomonas* sp. from the rhizosphere of *Avicennia marina* of Sundarbans has been found to promote the growth of rice in hypersaline and heavy metal–exposed soil through the secretion of EPS (Mukherjee et al 2019).

Screening for PGPT among the bacterial isolates from propagules of the mangrove species *Avicennia marina* and using bacterial isolates as inoculants to enhance barley and rice production under salt–stress showed positive results. The isolate that performed the best was *Gordonia terrae* (Soldan et al 2019). *Staphylococcus*, *Bacillus*, *Pantoea* and *Salmonella* species isolated from the rhizosphere of *Spartina maritima*, grown in metal–polluted wetlands of Tinto and Odiel estuary, Spain, displayed resistance to salt and heavy metals as well as plant growth promoting potential. Of these, *Pantoea agglomerans*, *Bacillus methylotrophicus*, *Bacillus licheniformis and Bacillus aryabhattai* enhanced the growth of *Spartina maritima* in metal–polluted fields. These observations indicate that these PGPR can be efficient candidates for wetland restoration (Mesa et al 2015; Paredes–Páliz et al 2016). *Pseudomonas stutzeri* identified as endophyte from the bulk soil associated with *Typha angustifolia* growing in the borderline wetlands promoted nitrogen metabolism and growth of these plants and rice cultivars (Saha et al 2016).

The flooded fields are one of the stressful environments that inhibit the proper cultivation of crops. The isolation of methane–utilizing bacteria from five rice–growing regions of India at different stages of cultivation led to the identification of species from *Burkholderia*, *Hyphomicrobium*, *Methylobacterium*, *Meyerozyma*, *Paenibacillus*, *Pseudomonas*, *Pantoea*, *Enterobacter*, *Paenibacillus* and *Rahnella* with PGPT and promoted the growth of rice cultivars upon inoculation (Rani et al 2021; Vishwakarma et al 2020; Rani et al 2022). Therefore, these studies conclude that the flooded fields might also be a potent reservoir of PGPR, and isolation of these species is needed to formulate bioinoculants for crops to mitigate abiotic stresses.

### Conclusion and Future Prospects

Agriculture is an assorted interface between plants and soil microorganisms. In modern agriculture, weightage is given to economically sustainable and environment–friendly tactics to promote agroecosystems' sustainability without compromising product quality and quantity. However, to balance the sustainability of agriculture and feeding the ever–growing population worldwide, the agriculturists and the food industries face real challenges due to various biotic and abiotic stresses, particularly the changes in the climatic scenarios. Here, microorganisms offer an alternative solution by participating in agricultural management and promoting healthy crop growth, disease suppression, and protection against abiotic and biotic stresses. The factors determining these activities are the long–term coevolution and stable association of microorganisms with the plants and the microbes' adaptability in extreme environments. However, due to limited knowledge about this diverse plant–microbe association in extreme environments, harnessing the activities toward the benefits of agriculture is challenging. The recent understanding of plants as part of holobionts in extreme environments is giving rise to complex yet pertinent arguments, the answer to which would need holistic approaches to develop well–versed hypotheses. The ecological and molecular biological investigations will be combined with progressive genetic technologies of metagenomics and metatranscriptomics, addressing the crosstalk between the plant and the colonizing microbes in extreme environments.

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## Conflict of Interest

The authors declare that there is no conflict of interest.

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