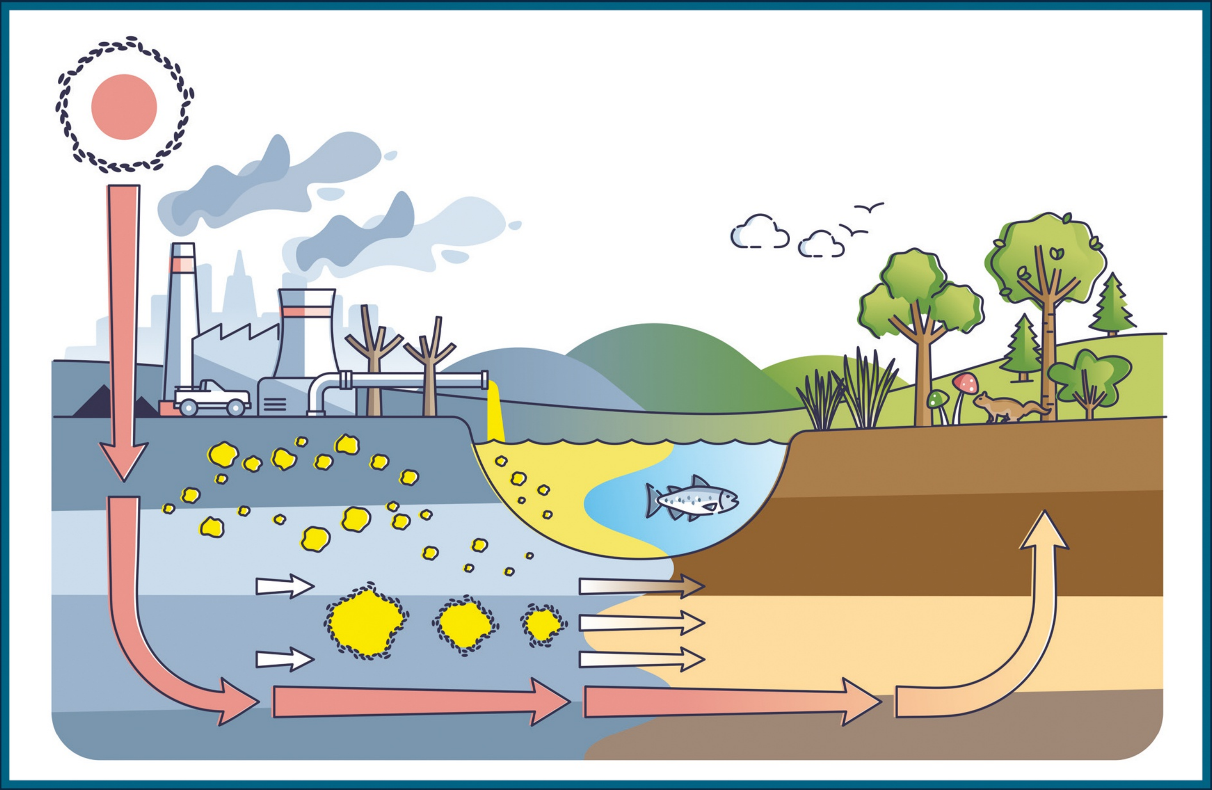
Progress in Biochemistry and Biotechnology

BIOTECHNOLOGY OF EMERGING MICROBES

Prospects for Agriculture and Environment



Edited by

Hemen Sarma and Sanket J. Joshi

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Prospects for Agriculture and Environment

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Preface

Over the course of the last three to four decades, our planet has seen unprecedented challenges related to a wide range of anthropogenic occurrences. Although the future direction of these shifts is uncertain, there is unilateral agreement that such negative developments might be unfavorable for the survival of the human race. In addition, the rate of expected change is likely to be abrupt, and the most likely outcome of this ongoing process could lead to catastrophic consequences, especially for agriculture and the environment. Although different environmental engineering strategies have been developed, none of them seem to address carbon dioxide accumulation, the biosphere, and ecosystem safety. The rapidly increasing potential for the development of living systems is an alternative possibility under consideration in this regard. It may require novel biotechnological approaches such as the design of synthetic microbes that reproduce and expand to large geographic areas in order to achieve long-term restoration of the biosphere and the ecosystem. This will take into account not only the proper design of organisms but also the understanding of their location and adaptability within ecological networks. This is a future scenario likely to involve ideas from current rhizosphere engineering, biosphere engineering, and ecosystem engineering.

This book highlights these ideas and the latest developments contributed by leading biotechnologists and bioengineers. The chapters cover various aspects of microbe-mediated agriculture and environmental engineering, with a focus on the restoration and management of the rhizosphere, the biosphere, and the ecosystem through the use of microbes for a sustainable future. Recycling, regenerating, and rejuvenating resources are challenges for a sustainable future. In addition to that, toxic contaminants remain a major concern. The population is rapidly affected by this catastrophic situation, industrialization, and the overuse of chemical compounds. A number of bioengineering strategies have recently been developed to address these challenges. With the stated objective, this book was designed to address various technical and application details of microorganisms and their products in the light of bioengineering approaches, and to provide up-to-date knowledge to researchers, bioengineers, and those who can support the sustainable management of our ecosystems. Experts from different parts of the world contributed to this book, covering different microbial aspects and applications.

We would like to emphasize that utmost care was taken during reviewing and all stages from copyediting to production; therefore, any mistakes that remain are purely unintentional, kindly excuse them. We would like to take the opportunity to acknowledge the extensive support provided by the Elsevier Inc. team, from book proposal to publication: Linda Versteeg-Buschman, Timothy Bennett, and the copyediting team. We would also like to sincerely acknowledge our universities for supporting and encouraging these scholarly activities.

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CHAPTER 1

Potential microbes for environment and agriculture: Bioengineering strategies for a sustainable future

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1 Introduction

Microbes are considered to be essential to our ecosystem, without which it would be impossible for any living organism to survive. The study of microorganisms on every level is considered a necessity. Various microbes from different niches constitute their unique role in the bioengineering of the environment. One of those niches is the rhizosphere, where microbes increase soil fertility and plant health (Dutta and Bora, 2019). The rhizosphere is a chemically complex environment composed of the association between soil and the plant roots, which helps in the growth and development of the plant and many microbial communities dwelling within the root area of the plant. Studies have proved that rhizosphere science enables the development of biotechnological applications in several sectors such as agriculture, ecological engineering, and habitat restoration (Haldar and Sengupta, 2017). Some of the features of the rhizosphere include plant growth-promoting rhizobacteria which provide nutrition for plants. This includes various other activities like abiotic stress suppression and protection from harmful phytopathogenic infections (Haldar et al., 2022).

Factors such as climate fluctuations, growth of human population, and limited resources make it a priority to enhance agricultural production. The rhizospheric microbial community assembly (MCA) fails to hold the framework of a consistent ecological system, which is the main component of the dynamic interactions between the plant and bacteria (Munoz-Ucros et al., 2021).

Rhizospheric microbe engineering is acquiring more attention in advanced agricultural research due to its importance to plants and agriculture. This not only allows for plant health maintenance and fitness but also improves plant yield on a very large scale as compared to normal conditions. Nevertheless, the success of engineered microbes may be hampered by soil factors along with the combined effects of uneven morphological and functional networks dictated by soil conditions (Bano et al., 2021). The

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understanding of improvement of functions that are driven by certain precursors strengthens the desired results even in a very complex environment. In addition to this, a particular microbe can be subjected to various culturing conditions tailored to a specific purpose (Sivasubramaniam and Franks, 2016).

The exploitation of the biofilm formation process in industries has also gained much attention due to bacterial cells being immobilized and highly resistant to environmental insult and has a potential for long-term stability that allows for the performance of constant bioprocessing activities (Li et al., 2006). Applications include the removal of wastes from the environment, referred to as bioremediation (Singh et al., 2006). This application is good for the biosynthesis of chemical production (Zhang et al., 2004), biotransformation, and fermentation processes (Li et al., 2007), as well as wastewater treatment (Nicolella et al., 2000).

A significant obstacle in saline aquatic environments is acclimation of the microorganisms to salinity and high osmotic stress in water. This hampers the diversity of the microbe composition on a very large scale worldwide (Auguet et al., 2010; Lozupone and Knight, 2007). In short, increasing salinity decreases biodiversity, followed by considerable loss in metabolic functions (Oren, 1999). This serves as a good standard for configuring the essential ecological changes that take place along the salt gradient (Gasol et al., 2004).

For halophiles and halotolerant microorganisms, an osmotic regulation strategy avoids water deficits and plasmolysis. Hence, it is considered crucial for its adaptability and survivability in changing salt concentrations (Booth and Louis, 1999; Wood, 2011). It is estimated that bioremediation of contaminated saline soil is possible if the salinity concentration is less than 15%. Reduction of saline concentration can also be done by adding fresh water (Riis et al., 2003). In a competitive environment, maximum benefit is achieved by quorum sensing (QS). QS is a regulatory mechanism adopted by planktonic bacteria to integrate gene expression and systematize physiological processes in a local population (Dong, 2005). Many applications of QS have recently emerged that facilitates the identification of pathogenic microbes associated with a host through engineering of whole-cell microbial biosensors. Promising applications include creating selectable engineered microbes that successfully penetrates and invades cancerous cells and thereby a novel anticancer medicine. Also, transgenic plants that are resistant to common microbial pathogens can be achieved through QS (Choudhary and Schmidt-Dannert, 2010).

Microorganisms are ubiquitous, and because of their significance to food, beverage, pharmaceutical, and enzyme industries, they are a major topic of study. Industries use several different microorganisms, such as yeast, bacteria, and fungus. To thrive, they need specialized media that is high in carbon, nitrogen, phosphate, vitamins, and other nutrients. In addition to these, other elements are utilized to prepare media for optimal growth (Arora and Bose, 2022).

Overuse of dangerous pesticides and mineral fertilizers has resulted in pollution and major health problems. One solution is nanoparticles which are objects between 1 and 100 nm in size, and because of their small size, they differ from bulk material. By developing higher performing nanomaterials, these issues may be solved through nanoscience. N, P, K, Fe, Mn, Zn, Cu, Mo, and carbon nanotubes are examples of nanofertilizers that exhibit improved targeted delivery efficiency. Ag, Cu, SiO_2, ZnO, and other nanoformulations are examples of nanopesticides that outperform traditional pesticides in terms of broad-spectrum insect protection (Chhipa, 2016).

Microorganisms may biosynthesize nanoparticles, which are a green alternative and a more environmentally friendly technology. Metallic nanoparticles are produced by prokaryotes and eukaryotes. These microorganisms include bacteria, fungus, algae, and actinomycetes (Hasan, 2015). Silica, selenium, gold, silver, copper, copper oxide, Pd, Mn, ZnO, Fe_2O_3, TiO_2, and $Ca_5(PO_4)_3OH$ are all examples of nanofertilizers for plant growth stimulation.

Silica, sulfur, gold, silver, Ag_2O/Ag, Ag_3O_4, nickel, platinum, copper, copper oxide, zinc oxide, chitosan, titanium dioxide nanoparticles, $Fe_3O_4/ZnO/AgBr$ nanocomposite, and reduced graphene oxide nanosheets are used as nanobiopesticides through nanobioformulations (Pestovsky and Antonio, 2017). Numerous studies have examined the makeup and alterations of the microbiota and raised novel questions and theories about their role in health and disease. Bacteria are now recognized as a significant cause of noninfectious chronic diseases such as allergies, chronic inflammatory bowel disorders, colon cancer, diabetes, and neurodegenerative diseases (Autenrieth, 2017).

2 Rhizosphere microbes in bioengineering

A small ecological region called the "rhizosphere" around the plant roots which serves as a home for beneficial microorganisms in which a plant depends on. fungi, bacteria, and different kinds of microbial consortia act as important plant growth regulators, disease suppressors, and promote various other fundamental processes for a plant to thrive. The interactions of plant and microbes can be seen in this zone. Rhizosphere microbiome is defined as the total set of microbial communities residing in a particular locality of a root zone (Ali et al., 2017). The composition of these microbes generally includes fungi, bacteria, and archaea among which bacteria are considered to be the most effective tool in promoting plant growth.

Bacteria can be used in agriculture as microbial agents that enhance various essential procedures in plants (Zhang et al., 2021b). The uptake of phosphorous and nitrogen is done by mycorrhiza and rhizobia, respectively. Likewise, the microbes are capable of biodegradation of persistent inorganic pollutants and the weathering of minerals in nature. In return, the microbes can use the root exudates as a carbon source for nutrition (Bais et al., 2006; van der Heijden et al., 2008).

2.1 Rhizosphere microbes for crop improvement

2.1.1 The plant-microbe interaction and its significance in crop improvement

The interaction that takes place in the rhizosphere may be direct or indirect which includes plant-plant, microbe-microbe, and plant-microbe interactions. The interaction with several other soil inhabitants can also be seen within the rizosphere (Bais et al., 2006; Quiza et al., 2015).

It is a difficult process to examine how plants and microbes interact, which often relies on various factors such as the type of soil, plant species, environment, climate, and anthropogenic effects. These factors and conditions determine plant species-dependent physiological interactions as well as exudation patterns (Quiza et al., 2015). Rhizodeposits, root exudates, and root border cells are considered the most essential components for the enhancement of root colonization capacity, the growth rate of rhizo-microbes, and organic bioactive compound secretions (Hassan et al., 2019).

A study revealed that the microbial biomass was almost doubled in the rhizosphere contrasted with that of nonrhizospheric soil due to the excess supply of carbon from plants in the rhizospheric zone (Bonkowski et al., 2000). It has been found that about 5%–20% of net photosynthetically fixed carbon is released by plants into the rhizosphere. This released carbon is also referred to as rhizodeposits (Marschner, 2011). Rhizodeposits consist of 27%–50% of carbon in the roots and are subsequently deposited into the soil. Rhizodeposits contribute approximately 11% of the net fixed carbon.

There are different types of rhizodeposits that can consist of mono or polysaccharides, phenolic compounds, proteins, and plant cells (Tian et al., 2020). The rhizodeposit composition is dynamic in nature. In specific root tissues, different types of rhizodeposits and as well as distribution can be determined. Hence, contributing to a diversity of rhizodeposits in the rhizosphere, leading to the significantly strong influence on the microbes in the rizosphere (Hirsch et al., 2013). A wide variety of rhizodeposits originates as a result of unloading root tissues and lysates from root cells (Dennis et al., 2010). The saying *the hidden half of the hidden half* refers to the high dynamic nature between microorganisms and soil organic matter. Other possibilities include converting it to CO_2, regardless of its essential role in carbon and nutrient cycling. For this reason, rhizodeposition remains an undetermined part of the carbon cycle in terrestrial ecosystems (Pausch and Kuzyakov, 2018).

The root exudates are yet another crucial element of the rhizosphere. Exudates are helpful in maintaining and shaping a particular type of rhizosphere's microbial population. It functions as a signal that successfully begins a symbiotic relationship with mycorrhizal fungi and rhizobia present in a given plant species (Badri and Vivanco, 2009). Root exudation includes ions, water, free oxygen, enzymes, mucilage secretion, and metabolites. In two active processes, root exudation can be comprehensively examined. First, removal of unknown substances takes place through a gradient-dependent process. This is followed by secretion of known compounds such as defense and lubrication (Bais et al., 2006).

Each pattern of root exudation is unique as well as specific to different plant species. This influences specific rhizosphere microflora. This may be due to a composition of beneficial microbes along with unwanted pathogenic bacteria as well (Neumann et al., 2014). The ability of root tips to detect and migrate toward nutrients and water in the soil aids in a plant's survival (Hawes et al., 2000). It is well known that root tips create lots of cells daily in many species that are metabolically active, which enables the study of gene expression from the specialized patterns (Hawes et al., 2016).

Root tips release border cells and border-like cells in the nature of solitary cells or in a group of cells. These are considered a functioning biological component in the root system which helps in managing the root interactions with rhizospheric microflora. After separation, the root border cells synthesize and secrete mucilaginous compounds rich in secondary metabolites, polysaccharides, antimicrobial proteins, and extracellular DNA (Driouich et al., 2013). Border cells are beneficial as they control and inhibit microbes and pathogenic invasions, respectively. This is due to its rapid attraction, stimulation, repelling, and inhibition of microbial growth (Hawes et al., 1998).

2.1.2 Recent advances in crop improvement

Interactions between microbes and plants are important for a plant's growth and development. Based on studies of these interactions, current agricultural challenges can be solved by bacteria belonging to the genera, viz. *Rhizobium, Achromobacter, Paenibacillus, Azospirillum, Streptomyces Aspergillus, Gluconoacetobacter, Azotobacter, Methylobacterium, Arthrobacter, Pantoea, Penicillium, Piriformospora, Planomonospora, Bacillus, Pseudomonas, Serratia,* and *Burkholderia*. The bacteria are considered to be useful in sustainable agriculture as biofertilizers, instead of synthetic agrochemicals (Yadav, 2020). Among them, *Methylobacterium* is a good potential inoculum due to its substantial part in improving plant health, nutrition, balanced phytohormone levels, and most importantly protection against pathogens (Zhang et al., 2021a).

In biotic remediation, recombinant protein production through bioengineering of nonmammalian expression systems is considered a novel approach. In contrast, fungi, microalgae, and protozoa are associated with large quantities of antibiotic production (Matthews et al., 2017). A soil borne root-colonizing bacteria *Pseudomonasaureofuciens*, specifically from strains 30–84 and strain PGS 12, produce phenazine antibiotics (Pierson and Pierson, 1996) that functions to prevent approximately 90% of *G. graminis* var. *tritici*. Moreover, other antibiotics are also known to suppress disease in plants (Pierson, 1992).

Biocontrol is another application where rhizospheric bacteria are largely involved in killing and suppressing pathogens. One example is the fluorescent bacteria, *Pseudomonas* which can be used as a biocontrol agent due to its root colonizing, organic substrate utilization, ease of culture in vitro, secondary metabolite production, and compatibility with other chemically used pesticide properties (Sindhu et al., 2016). *P. fluorescens* strains act as antagonists in browning roots disease in *M. truncatula* plants caused by the phytopathogen *Botrytiscinerea* (Hernández-León et al., 2015). This is due to producing antibiotics, bacteriocins, siderophores, volatile organic compounds, phytoalexins, hydrolytic enzymes such as chitinases along with other metabolites (Sindhu et al., 2009).

2.2 Rhizosphere microbes for bioremediation of emerging pollutants

The main cause of metals in water and soil is mainly industrial effluents which serves as a source for diverse pollutants to be dispersed in nature. Here, selected microorganisms can be utilized for clean-up and recovery of the contaminated water and soil in order to facilitate bioremediation (Bajpai et al., 2022). Both physical and chemical treatments can be applied in small areas of remediation, however, it may not be cost effective. An environmentally healthy and carbon-neutral strategy for the eradication of harmful and enduring contaminants is phytoremediation. In this strategy, the plants are associated with heavy metals remediation by hyperaccumulating and sequestering them in situ (Yan et al., 2020). The processes of phytodegradation, phytovolatilization, phytoaccumulation, and phytoextraction are the foundation of phytoremediation. These techniques are effective, sustainable, and affordable (Muthusaravanan et al., 2018).

Phytodegradation of organic materials can occur inside of the plant or in the rhizosphere. Numerous chemicals and types of molecules, including as solvents in groundwater, petroleum, aromatic compounds in soils, and volatile compounds in the air, can be eliminated from the environment using this technology. (Newman and Reynolds, 2004). Volatile organic chemicals may be released into the air or soil by plant root activities (indirect phytovolatilization) or directly from stems or leaves. Across scales, from local chemical spills to global changes of methane coming from ecosystems biochemically degrading carbon, pollutants volatilizing from plants play a significant role (Limmer and Burken, 2016). The roots of plants absorb pollutants then transported to and deposited in the plant's upper leaf areas by phytoabsorption, phytosequestration, or phytoaccumulation. This mostly happens during intake of organic chemicals and heavy metals (Abdel-Shafy and Mansour, 2018). In oil contaminated soils, aliphatic, polyaromatic hydrocarbons (PAHs), and asphaltenes are bioremediated by various bacteria that are a member of the phyla *Proteobacteria*, *Bacteroidetes*, *Actinobacteria*, *Nocardioides*, or *Firmicutes* (Table 1) (Singha and Pandey, 2021).

3 Saline microbes in bioengineering

3.1 Bioengineering of saline sodic soils

A saline environment is mainly described as a condition of extreme soil salinity where plant development and yield are limited. In dry and semidry environments, sodicity-induced soil deterioration has a significant detrimental influence on agricultural output

Table 1 Isolation and characterization of some potential microbes with significant applications.

Sl. no.	Microbes	Secreted compounds	Detection methods	Applications	References
1.	*Pseudomonas aeruginosa*-Strain FP10	2,4-Diacetylphloroglucinol (DAPG)	Traits and sequence similarity of partial 622-bp fragment of 16S ribosomal DNA	*Fusarium oxysporum* f. sp. *cubense* FOC caused the vascular discoloration that was decreased by FP10 and increased plant height in the banana plant	Ayyadurai et al. (2006)
2.	*Stenotrophomonas maltophilia* (PM-1, PM-26), *Bacillus fusiformis* (PM-5, PM-24), and *Pseudomonas fluorescens* (PM-13)	Indole-3-acetic acid (IAA)	Phenotypic and 16S rDNA sequences analysis	Nitrogenase activity above 150 nmol h^{-1} mg^{-1} protein	Park et al. (2005)
3.	*Stenotrophomonas* spp. (AJK-3 and AJK-9 strain)	Indole-3-acetic acid	16S rRNA gene sequence analysis	Promotes nitrogenase activity and solubilization of insoluble phosphate and zinc	Majeed et al. (2015)
4.	*Pseudomonas putida* NCIB 98164, *Comamonastestosteroni* GZ42, *Sphingomonasyanoikuyae* B1, and *Mycobacterium* sp. strain PY01	–	Southern hybridization	Polyaromatic hydrocarbon (PAH) degradation	Daane et al. (2001)
5.	Halophilic and halotolerant *Bacilli* (AT2RP4, HL1RS13, NRS4HaP9, and LK3HaP7)	Lipase, protease, cellulase, amylase, gelatinase, and catalase enzymes at 1.0–1.5 M NaCl concentration	16S rRNA gene analysis	Employed under harsh environments to bioconvert organic compounds to valuable products	Mukhtar et al. (2019)
6.	*Pseudomonas stutzeri*, *Bacillus subtilis*, *Stenotrophomonas maltophilia*, and *Bacillus amyloliquefaciens*	Indole-3-acetic acid (26.78–51.28 μg mL^{-1})	Phylogenetic analysis of 16S rRNA sequences	Suppressed *Phytophthora* crown rot caused by *Phytophthora capsici*	Islam et al. (2016)

Continued

Table 1 Isolation and characterization of some potential microbes with significant applications—cont'd

Sl. no.	Microbes	Secreted compounds	Detection methods	Applications	References
7.	*Bacillus* species	Siderophore, solubilized phosphate, and indole-3-acetic acid	Microbial identification system (BIOLOG) and 16S rDNA sequencing	Antagonistic activity against *Sclerotium rolfsii* and *Colletotrichum capsici* and plant growth-promoting traits	Kumar et al. (2010)
8.	*Azotobacter paspali* and *Azotobacter vinelandii*	–	Morphological and biochemical methods	Fixes nitrogen in the soil	Hala and Ali (2019)
9.	*Pseudomonas aeruginosa*-strain DSM 50071 and strain NBRC 12689 (AK20 and AK31), *P. fluorescens* strain ATCC 13525, strain IAM 12022 (AK18 and AK45), *B. subtilis* strain NCDO 1769 (AK38)	Indoleacetic acid (IAA), hydrogen cyanide, phosphate solubilization, and siderophore	RNA analysis	Plant growth-promoting effects on rice	Karnwal (2017)
10.	*Pseudomonas* spp., *Bacillus* sp., *Acinetobacter* sp.	IAA production, phosphate solubilization, ammonia production, catalase production, siderophore production	Biochemical and16 S rDNA gene sequencing analysis	Antagonistic activity against phytopathogenic *Rhizoctonia solani*	Kumari et al. (2018)

and sustainability. A substantial class of salt-affected soils known as sodic soils is distinguished by an excess of sodium ions (Na^+) on the cation exchange complex as well as in the soil solution phase. Due to specific physical processes (clay slaking, swelling, and dispersion) and environmental factors (surface crusting and hard setting), these soils have specific structural problems (Qadir et al., 2007). The degradation and decomposition of soil organic matter and the stability of soil aggregates are all processes that are heavily reliant on microbial activity (Singh, 2016).

The microbial diversity, however, is of great value in the exploration of crop improvement applications due to its high tolerance of salinity (Yadav et al., 2020). The coastal areas and landscapes affect plants through aerosols that originate from the ocean and in snowy areas where salts are mostly used to clear pathways and adversely damage the surrounding plants (Hingole and Pathak, 2016). As a consequence, water translocation becomes difficult for plants leading to the increase in toxicity levels which lowers the transpiration rate, leaf expansion, senescence of older leaves increases, and ultimately, the closure of stomata as well. Leaf burn, defoliation, and foliar symptoms like leaf bronzing and necrotic spots are some common symptoms that occur from excess accumulation of sodium and chloride ions in the leaves (Munns and Tester, 2008; Podmore, 2009; Rahnama et al., 2010).

Halophiles survive and thrive in saline environments. These microorganisms are very diverse and include bacteria that oxidize sulfur, cyanobacteria, heterotrophic bacteria, archaea, algae, protozoa, moderately aerobic and anaerobic bacteria, and many multicellular eukaryotic organisms. Halophiles are known as halotolerant due their ability to grow in the presence of salt. Some halophiles are able to tolerate high concentrations of NaCl which are considered to be extremely halotolerant (Das Sarma and Arora, 2001).

Halophiles need to keep the cytoplasm's osmotic pressure in balance with the surrounding environment in order to survive. Intracellular accumulation of KCl in the cell in exchange for Na^+ ions from the cytoplasm is one of the main mechanisms featured in most halotolerant bacteria and archaea (Galinski, 1995; Grant et al., 2004; Oren, 1999; Ventosa et al., 1998). Osmoadaptation, accumulation of some adaptive solutes like amino acids, glutamate and proline, derivatives of amino acids, and the sugar trehalose are some of the most commonly performed mechanisms that microorganisms utilize for tolerating salinity (Tsuzuki et al., 2011).

Exposure of high metal salt concentration leads to the interaction and reduction of metal ions to smaller particles of desired shapes and structures in the marine ecosystem (Baker et al., 2013). The genera *Haloarcula*, *Haloferax*, *Halorubrum*, *Halobacterium*, and *Halomonas* belonging to the order Actinomycetales (*Rhodococcus ovatensis*), and some *Bacillus* species are commonly isolated microorganisms from Romanian salt lakes. These species are able to synthesize enzymes such as lipase, inulinase, caseinase, and gelatinase. These enzymes also known as extremozymes are synthesized in saline environments.

Some produced as bioproducts (polyhydroxybutyrate (PHB), carotenoid pigments, melanin) are useful in plant growth, development or can be used for various bioremediation techniques.

Stimulation of phytohormones is associated with different physiological functions of plants such as utilization of nutrients (Enache et al., 2013; Nagaraju and Nagaraju, 2018; Ruginescu et al., 2020; Yadav and Saxena, 2018). Through bioengineering analysis, it has been shown that enzymes of halophilic archaea and bacteria can function in arid conditions due to exposure to acidic conditions causing the organism to adapt to negatively charged and hydrophobic conditions. Advances in bioengineering have allowed for substitution of fuel for biofuels generated from halophilic microorganisms (DasSarma et al., 2010). Moreover, halophiles are associated with the production of biosurfactants, oil recovery with biopolymers, enzymes (amylase and protease) in the detergent industry as well as exopolysaccharide production (Kanekar et al., 2012).

Another example is bacteriorhodopsin, ahaloarchaeal retinal protein. Bacteriorhodopsin is a sensory rhodopsin that enables the organism to sense light and grow phototrophically. Through the aid of this retinal protein, a huge range of optical devices such as photosensors have been developed in optical industries (DasSarma and DasSarma, 2015). Bacteriorhodopsin also has the capacity to transform light energy into chemical energy and electricity. These extremozymes are useful attributing to their unique ability to perform under harsh conditions of high ionic concentrations (Kanekar et al., 2012).

3.2 Applications of saline microbes

Various hypersaline environments serve as a hotspot of halophilic microorganism biodiversity which are primarily archaeal, bacterial, and fungal species with novel and halotolerant functions (Yadav and Saxena, 2018). Halophiles have the capability to grow and adapt in high salt environments which are the sources of 5% of the world's effluents. This demonstrates their potential for bioremediation (Sivaprakasam et al., 2008). Different genera such as *Streptomyces, Tenuibacillus, Thalassobacillus,* and *Virgibacills* are some of the common Eubacteria known to thrive in saline environments.

The halophilic fungal isolates such as *Alternaria, Aspergillus, Cladosporium, Debaryomyces, Hortaea, Myrothecium,* and *Wallemia* have also been identified along with bacterial isolates from saline environments from many global regions (Saxena et al., 2016; Yadav et al., 2015, 2017). These organisms have the potential to bioremediate wastewater that contains high concentrations of salt where other bioremediating bacteria cannot perform these functions due to their low survivability in saline water. Such high concentrations of saline would normally cause destruction of the cell plasma membrane, osmotic stress, and enzyme denaturation. Therefore, efforts have been made to use halophilic microorganisms as a suitable alternative in bioremediation processes mainly due to its ability to grow under salt stress conditions (Peyton et al., 2004).

Loss of activity of bacteria in conventional activated sludge units is common due to high salt concentrations (>1%). High salt concentration leads to cell desiccation by osmotic fluctuations across cell membranes. This is an effect of salinity in the biodegradation process which results in the chemical and biological oxygen removal resulting in low degradation performance (>2%) (Dinçer and Kargi, 2000).

Biodegradation of both hydrocarbons has been reported in extreme halophilic bacteria, for e.g., some species of *Halobacterium* genus are able to degrade *n*-alkanes and polynuclear aromatic hydrocarbons in the presence of 30% salt concentration (Al-Mailem et al., 2010; Kulichevskaya et al., 1992). The archaea, *Haloferax denitrificans*, removes nitrate from brines through a membrane bioreactor which follows the denitrification process (Cyplik et al., 2007). Denitrification of saline groundwater in coastal areas can also be done with the help of *Haloferax mediterranei* (Martínez-Espinosa et al., 2007).

The isolation of halophilic enzymes and osmotic solutes demonstrated stabile adaptation in saline conditions. These enzymes can be used for improving nutrient supplements, immune boosters, antioxidants, cosmetics, and coloring agents (Oren, 2010). Ectoine is an osmotic solute first discovered in *E. halochloris* (a haloalkaliphilic photosynthetic sulfur bacterium). Later, studies (Buommino et al., 2005; Zhang et al., 2009) could isolate this compound along with a 5-hydroxy derivative from various halophilic and halotolerant bacteria. Ectoine is useful for its ability to increase shelf life and enzyme activity by serving as a protectant of biomolecules (unstable enzymes and nucleic acids) against salt stress, thermal denaturation, dehydration, and freezing conditions (Kolp et al., 2006; Lippert and Galinski, 1992). Inhibition of trypsinogen to trypsin (spontaneous conversion), chymotrypsinogen to chymotrypsin (trypsin-catalyzed conversion), and stabilization of trypsin and chymotrypsin activity are some of the examples of other uses for ectoine (Kolp et al., 2006). Moreover, biopolymer-degrading enzymes are now used in the efficient treatment of waste in oilfields where high temperature and salinity usually fluctuate (de Lourdes Moreno et al., 2013).

In dermatological cosmetic industries, ectoine is utilized to protect the skin from UV-A rays, resolve skin aging problems, and moisturize dry or irritated skin conditions (Oren, 2010). This compound also reduces "sunburn cell" formation in UV exposed cells through heat shock proteins and stimulation of Langerhan's cell immunity (Buenger and Driller, 2004). Ectoine can also be used to inhibit or suppress aggregation and toxicity in neurons caused by the Alzheimer's disease (Kanapathipillai et al., 2005).

The presence of high concentration of sodium salt in soil retards the natural growth of plants and crops (Yadav and Saxena, 2018). In this regard, halophilic bacteria are useful in developing a sustainable agricultural approach by promoting the growth of plants in high salt environments (Sharma et al., 2016). Agricultural productions are reduced due to the serious effect and stress caused by salinity. Various physiological processes like phytohormone regulation, development of roots or shoots, and uptake of nutrients and photosynthesis are greatly affected in this regard (Sharma et al., 2016).

Halophiles fix nitrogen in the soil, solubilize nutrients, and promote phytohormone secretion, thereby acting as a possible tool to recover degraded lands by eliminating salt from soils (Arora, 2020). Significant increase of total fresh weight of plants along with the increase in root and shoot length (62.2%–78.1%) was visualized in experimentation with halophilic bacterial strains under salt stress of 200 mM of NaCl. Salt sensitive plants are now able to flourish and survive through bioengineered applications of halophilic and halotolerant bacteria (Orhan, 2016). Moreover, microbes enable further study of agricultural crops that go through pressure (adaptation, stress resistance, and response processes) that occur as a result of climate modifications (Grover et al., 2011).

Pigments can also be isolated from halophiles. Salinixanthin, a novel carotenoid pigment, is a pigment that provides protection from photodegradation in organisms, controls the stability in cell membranes, and promotes light harvesting (Lutnaes et al., 2002). Xanthorhodopsin also promotes harvesting light energy by acting as a transmembrane proton transporter (Balashov et al., 2005).

4 Microbial biofilms in bioengineering

Microenvironments provide a platform to perform and adapt many processes which are regulated by localized cells within a matrix of extracellular polysaccharide secretions (EPS) measured in micrometer spatial scales of microorganisms also known as "microbial biofilms" (Decho, 2000). Exopolysaccharides, proteins, organic matter, lipids, enzymes, nucleic acid, bacterial refractory compounds, and membrane vesicles are some common components of EPS (Jamal et al., 2018). These compounds are believed to be involved in biofilm matrix formation which promotes crucial functions in biofilm formation and maintaining stability (Fong and Yildiz, 2015). Biofilms are made of polysaccharides, detritus, and exudates by the critical community of diverse microorganisms (fungi, bacteria, algae, and protozoa) or also by a single bacterial species (Costerton et al., 1978; Teschler et al., 2015; Wimpenny et al., 2000).

Various mechanisms and strategies are adapted in the growth and attachment of the biofilm formation process. Here, EPS carries out the fundamental mechanism for microorganisms to attach and colonize to food surfaces (Kumar and Anand, 1998). The medical and industrial industries have primarily been taken into account for research studies on microbial biofilms. However, the agricultural sector is also able to utilize biofilms to increase crop-yields and provide protection from phytopathogenic diseases. Moreover, surface colonization of plants and soil colloids by biofilms helps to enhance a particular role or function of an organism as well as boosting the fertility of the soil (Ansari et al., 2021).

Our understanding of this branch of microbial biology has been expanded by the use of modern technologies in biofilm investigations. Using these technologies, researchers have demonstrated that biofilms are highly organized biological systems where microbes are organized, coordinated, and functioning communities (O'Toole et al., 2003). Biofilm structure can be influenced by a different factors, including surface and interface qualities, nutrient availability, the population of the microbial community (Stoodley et al., 1997). For instance, a dental plaque biofilm is often stratified and compact when subjected to significant shear pressures, as those experienced on the surface of teeth when chewing (Bowden and Li, 1997; Wimpenny and Colasanti, 2006).

When biofilms were discovered to be connected to plants, it was recognized that some bacteria cannot only boost plant growth but also participate in biocontrol of plants to defend against infections. Additionally, when used at high cell densities, biofilms can be used for biofertilizers (biofilmed biofertilizers), bioremediation, and nutrient mobilization (Ghiasian, 2020).

4.1 Microbial biofilm in bioremediation of pollutants

Biotechnological methods can also be used to create biofilms that are better able to break down harmful contaminants and thereby prevent their release into the environment through altering regulatory networks and controlling gene expression. The capacity to modify biofilms to enhance their ability to biodegrade has been made possible by advances in synthetic biology (Mishra et al., 2022). The potential for bioremediation of contaminants using immobilized microbial cells has been demonstrated in various publications. Studies of bacterial biofilms show that these structures have certain properties that are good for use in a variety of processes, such as the degradation of industrial and agricultural wastes and water filtration (Bhattacharjee et al., 2022). Additionally, biofilms can develop in a variety of harsh conditions, where they utilize the sulfur cycle (Edwards et al., 2000).

Cyanobacterial mat biofilms have been thoroughly investigated for potential benefits (Ramsing et al., 2000; Ward et al., 1998). More recently, scientists have begun to look into biofilms that cover in Antarctica (Paerl and Priscu, 1998). In these harsh settings, complex organized communities have been shown to carry out a variety of biological processes, including N_2 fixation and fermentation (Davey and O'toole, 2000).

"Anaerobic granules" are multitrophic bio-aggregates made up of methanogenic isolates that can convert organic waste into a methane-rich biogas that can be used as a renewable energy. The development of the anaerobic ammonium oxidizing (anammox), aerobic, hydrogenic, oxygenic photo, and numerous other granules in the previous years has created new prospects in wastewater treatment (Trego et al., 2021).

4.2 Microbial biofilm in bioreactor and its application

In the last 20 years, there has been a higher amount of utilization of membrane bioreactors (MBR), a relatively new technology based on the activated sludge process. Much focus has been done in the development and optimization of this technology concurrently with its commercial development (Ivanovic and Leiknes, 2012). Even with low hydraulic influent loading, biofilm reactors can house biomass for long durations. Since the wastewater concentrations are too low to sustain the formation of activated sludge flocs, MBRs are especially well suited when the treatment calls for slow-growing organisms with low biomass yield. The metabolic activity can be kept high regardless of the biological aggregates settling characteristics or the hydraulic influent loading (Wilderer and McSwain, 2004).

The identification and characterization of microbes from the phylum *Chloroflexi* are capable of biodegrading organohalides and have provided information on the potential application of the microbial mechanism for the breakdown of halogenated hydrocarbons (Löffler et al., 2013). The *Dehalococcoides* species is acknowledged as beneficial inhabitants of a biofilm community for reductive dechlorination (Chung et al., 2008). In one study, the treatment of wastewater in a submerged biofilm membrane bioreactor allowed for nitrification and denitrification. The dominating genera, Simplicispira, and Acinetobacter showed that nitrifying bacteria, heterotrophic denitrifiers, and aerobic denitrifiers are able to co-exist in the same submerged biofilm membrane bioreactor (SBF-MBR) (Han et al., 2018).

5 Microbes for biofuel and bioelectricity

Gasoline and aviation fuel are now being replaced by biologically derived alternatives through microorganisms. About 10% of the world's energy demand is met by biomass. Biofuels such as ethanol are a good alternative because of its high energy and low freezing point (Dunlop, 2011). There are various reasons for crude oil price increase in many countries worldwide. These include resource depletion, insecurity of politics in production, and environmental problems. Beyond major risks and challenges, biomass has the potential to relieve struggling civilizations (Antoni et al., 2007). Ethanol is a widely used fuel in the transportation sector. Ethanol can now be easily produced by microorganisms. Ethanol biofuel may be beneficial and cost effective due to its low energy content, limitation of storage infrastructure, and existing fuel distribution compatibility (Peralta-Yahya and Keasling, 2010).

5.1 Algal biofuel

Algal biofuel production is a promising sustainable source of bioenergy due to the fact that it doesn't compete with food crops for arable land (Kazamia et al., 2012). Algae, especially green unicellular microalgae, have long been suggested as potential renewable fuel sources. Significant amounts of biomass and oil that can be used to make biodiesel can also be produced by microalgae (Pittman et al., 2011). The production of algal biomasses is now one of the most economically viable system designs for producing large quantities of biofuels (Smith and Mcbride, 2015).

The halophilic alga *Dunaliella* is used in the manufacturing of glycerol and is a potential source of carotene, making it a viable raw material for biofuels. *Dunaliella* cellular material is catalytically pyrolyzed at 200–240°C to provide an oil-like product that is soluble in benzene. The entire process is exothermic, allowing for the recovery of most of the heat energy required to start the reaction. In an algae-seawater slurry, up to 75% of the cell material may be transformed into oil that can be extracted (Oren, 2010).

5.2 Microbial fuel cell

Through the action of microorganisms, microbial fuel cells (MFCs) can be used as a power source to transform chemical energy into electrical energy. (Hoang et al., 2022). The MFC consists of two compartments separated by a proton exchange membrane (PEM), which allows only protons to pass through. One compartment contains the anode, where bacteria oxidize organic matter and release electrons, while the other compartment contains the cathode, where oxygen or other oxidants accept the electrons and produce water or other reduced products (Fig. 1). The flow of electrons from the anode to the cathode generates a current that can be used to power electronic devices

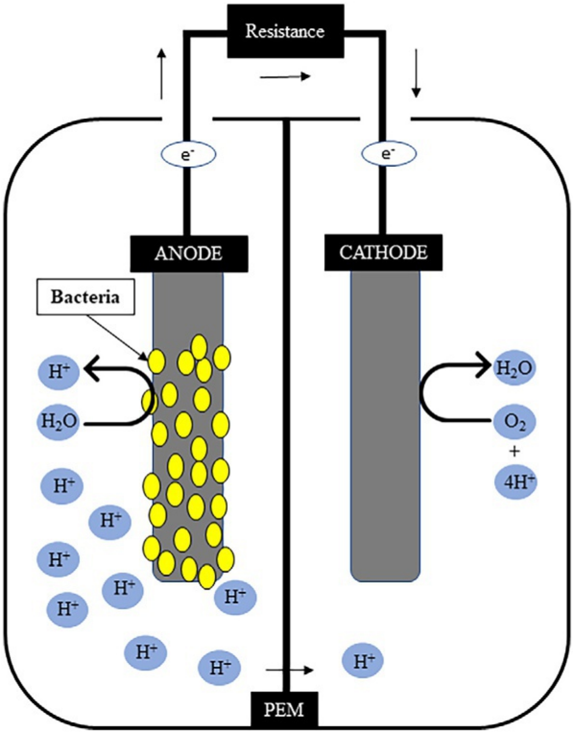

Fig. 1 Generaion of current in a microbial fuel cell.

(Chen et al., 2023; Ida and Mandal, 2023). The MFC is potentially able to address both the energy crises and environmental pollutants. In addition, the artificial mediator that facilitates electron transfer (by collecting electrons from the microorganisms and transferring them to the anode), can also serve as the electron donor. Alternatively, it can be a reduced by-product of microbial metabolism (Lovley, 2006). MFCs have a lot of potential as a new type of energy source, a method of treating wastewater, and a biosensor for contaminants and oxygen. However, further study is needed to fully utilize the microbial potential (Kim et al., 2007). Scanning electron microscopy (Fig. 1) was used to study the biofilm that had developed on the anodic electrode and found that it grew larger the more MFC cycles were performed. From the first cycle (1,310.0 ± 22.3 mA/m^2) to the last cycle (1,539.4 ± 25.8 mA/m^2) of the MFC experiment, the maximum current output increased significantly. Furthermore, Coulombic efficiency was raised from 89.4% ± 0.2% to 98.9% ± 0.5% (Eaktasang et al., 2013). The development of electroactive biofilms (EABs) in a constrained organic environment increased their phenol removal activity, which was crucial for determining how to apply a microbial electrochemical system (MES) in order to treat industrial wastewater (Li et al., 2023). Improvements in the way MFCs are used to extract resources from valuable waste such as "human urine" and generate electricity from it (Sharma et al., 2022). Some of the general issues with commercializing MFC technology include concerns about how well the proton exchange membrane or cation exchange membrane will hold up over time as well as concerns about power output (Table 2) (Prathiba et al., 2022).

6 Role of quorum sensing in bioengineering

In cell population density, regulating gene expression occurring as a response to environmental fluctuations is quorum sensing (QS). Autoinducers are a type of chemical signaling molecules produced and released by quorum sensing bacteria as a result of increasing cell population (Miller and Bassler, 2001).

The *Photobacterium fischeri* (*Vibrio fischeri*) is a luminous marine bacterium where QS was first described in 1970 by Kenneth H. Nealson and John W. Hastings of Harvard University. In their experiment, the luminescing character was only functionable if the cell population reached a high-density level. The regulation of molecular messengers (autoinducers) then travels between cells of microorganisms causing bioluminescence. The term "autoinducers" are used in the sense that it has the potential to activate gene expression of target cells which resulted in bioluminescence (Fuqua et al., 2001; Losick and Kaiser, 1997; Nealson et al., 1970; Nealson and Hastings, 1979).

6.1 Quorum sensing in biochemical production

Quorum sensing is a crucial component of pathogenesis since it is the biochemical communication system that bacteria use to spread virulence factors. This strategy maximizes

Table 2 Sources, microbes, and mechanism involved in biofuel production.

Biofuels	Extracted from the sources	Microbes included	Mechanism/strategy involved	Product yield	References
Biohydrogen	*Chlamydomonas* sp. MACC-549 and *Chlamydomonas reinhardtii* cc124	*Brevundimonas* sp., *Rhodococcus* sp., and *Leifsonia* sp.	Effective bacterial respiration eliminates oxygen, which is necessary for *Chlamydomonas* to activate a Fe-dependent hydrogenase	1196.06 ± 4.42 μL H_2 L^{-1} and 5800.54 ± 65.73 μL H_2 L^{-1}	Lakatos et al. (2014)
Hydrogen and methane	*Chlorella vulgaris*	*Clostridium thermocellum*	*C. thermocellum* bioaugmentation enhanced the degradation of *C. vulgaris* biomass, increasing the levels of methane and hydrogen produced	9.4% increase in bioenergy yield	Lü et al. (2013)
Formate	Eukaryotic cells	*Saccharomyces cerevisiae*	Electrochemical reduction of CO_2	–	Wegat et al. (2022)
Bioethanol	*Gracilaria verrucosa*	*Saccharomyces cerevisiae*	The enzymatic hydrolysate on fermentation with *S. cerevisiae*	0.43 g/g	Kumar et al. (2013)
	Corn stover	*Geobacillus thermoglucosidasius*	Fermentation and consolidated bioprocessing	0.45 g/g	Madhuvanthi et al. (2022)
	Cellulose, oat-spelt xylan, and plant fiber	*Rhizopus* strains	Anaerobic stress	31 g/L	Skory et al. (1997)

the roles that the highly populated bacterial population plays in terms of metabolism and behavior as well as the creation of the accompanying response to diffuse or secrete signaling molecules. As a result, quorum sensing's multilayered signal transduction networks aid in the creation of biofilms while also enhancing bacteria's ability to combat the disadvantages (Tabassum et al., 2021). Gram-positive and gram-negative bacteria both show crucial phenotypes through quorum sensing regulation. These include production of antibiotics, development of fruiting bodies, and sporulation. Moreover, it is helpful in demonstrating the virulence of a number of pathogenic microorganisms such as *Pseudomonas aeruginosa* and *Vibrio cholerae* (Diggle et al., 2007).

Some bacterial phenotypes are also responsible for promoting symbiotic pathogenic initiation with eukaryotic hosts through quorum sensing which regulates motility, production of exopolysaccharide, biofilms, and toxins. Eukaryote hosts can respond to the bacterial signaling network by producing quorum-sensing-interfering (QSI) compounds which might inhibit quorum sensing and hence, biofilm colonization (González and Keshavan, 2006).

The synthesis of the biosurfactant and rhamnolipid is one such process controlled by quorum sensing molecules. *Pseudomonas* spp. produces rhamnolipids, which are surface-active compounds generated from microbes (Dusane et al., 2010). *Ruegeria pomeroyi* DSS-3, a heterotrophic marine bacterium, was able to grow on dimethylsulfoniopropionate (DMSP), and *N*-(3-oxotetradecanoyl)-L-homoserine lactone was produced by *R. pomeroyi* on DMSP at levels that were substantially greater than those observed during growth on propionate. Observation of the varied production of metabolites, such as glutamine, vitamin B2, and cyclic amino acid biosynthetic intermediates, was coincident with the formation of QS molecules (Johnson et al., 2016).

6.2 Quorum sensing in designing microbial biosensors

Quorum quenching (QQ) is another strategy that interferes the QS system of microbes. QQ has been widely used for its potential to control diseases by suppressing the expression of virulent genes which seems to be a better strategy than cell growth restriction only. Drug toxicities, complex infections, and resistance to antibiotics are also some challenges that QQ can overcome (Chen et al., 2013). Signaling molecules act as precursors for the QS process. Inactivation by enzymatic degradation causes reduction in the effect of processes controlled by QS. Two classes of *N*-acyl homoserine lactone (AHL) inactivating enzymes were found to control this effect, via AHL lactonases, which are known to engage in hydrolyzing AHL acylases releasing fatty acids as well as free homoserine lactone (Czajkowski and Jafra, 2009). Reduction in signal concentrations in the bacterial environment diminishes virulence level and formation of biofilm. Hence, applications have been developed accordingly which includes biocontrol agents where signal degrading bacteria suppresses soft rot disease and protects crop plants (Yebra et al., 2004).

Furthermore, gram-negative AHLs are recognized by whole-cell QS biosensors. There are generally two components in a typical AHL biosensor: a transcriptional regulator and promoter. Both pathogenic (*Agrobacterium*, *Erwinia*, *Pantoea*, and *Xanthomonas*) and beneficial bacterial isolates (*Rhizobium*, *Sinorhizobium*, and *Pseudomonas*) especially from plant associated genera produce AHL (Choudhary and Schmidt-Dannert, 2010).

Bacteria, cyanobacteria, algae, fungi, sponges, and tunicates are the main organisms in a marine ecosystem with the ability to control microbial colonization by successful disruption of bacterial biofilms. QS thus can disrupt biofilms through inhibitor compound production (Dobretsov et al., 2011; Hentzer et al., 2002; Ng et al., 2012; Ni et al., 2009). The red macro-alga, *Delisea pulchra,* is responsible for the first isolated QS inhibitor (Givskov et al., 1996).

Biofouling is a major problem caused by macro as well as microorganisms forming on surfaces in the marine environment. This creates various challenges in developing aquaculture and for industries associated with the marine environment. Persistent biofouling elimination through quorum quenching enzymes in membrane bioreactors with probiotics in aquaculture is a sustainable method (Fetzner, 2015; Yebra et al., 2004).

Development of a synthetic biological system should contain a strong programmable QS system with a potential to recognize cell regulation of target genes when there is a high cell density. Recent advances in bioengineering of QS-based genetic devices are solving a major problem by controlling gene expression, cancer cell invasion, limiting the size of population, and artificial ecosystem management (Choudhary and Schmidt-Dannert, 2010).

In clinical and environmental samples, QS signals are utilized as indicators to detect harmful microorganisms. However, its efficacy is eventually lost due to QS-deficient mutations occurring after complete colonization of the host (Choudhary and Schmidt-Dannert, 2010; Köhler et al., 2009). On some occasions, human commensal microbes are responsible for developing cancer metastasis. QS peptides such as EDF-derived (*Escherichia coli*) peptides initiate the invasion of the HCT-8/E11 colon cancer cells (Wynendaele et al., 2015).

7 Conclusion and future perspectives

Implementation of microbes for various applications has met with success depending on the substrates used. Microbes will respond differently under varying conditions in order to survive. New techniques can be developed for a wide variety of applications including bioremediation. Taking sustainable measures would ensure a cleaner environment. Conducting sustainable experiments would help to remove toxic and harmful contaminants.

The fate of these contaminants may arise particularly from toxic chemicals that were used during culturing of the plants. Replacing these chemicals with compounds that are more sustainable and better for the environment would be more ideal. The introduction of new technologies, resource inputs, and financial incentives will also increase agricultural output. Future technological advancements in food production and handling systems should be nonpolluting to the environment and human health as well as discourage the creation of additional toxic chemicals (Wittwer, 1979). It is crucial to recognize that compelling market variables will continue to have a significant impact on the price of energy when considering future patterns of energy supply and demand. Future prices of fossil fuels are expected to rise as they are at the root of historical and ongoing conflicts in addition to environmental damage and climate change (Wegat et al., 2022).

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CHAPTER 2

Endophytic bacteria-mediated resistance to plant diseases: Bioengineering approaches

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Abbreviations

ACC-1	aminocyclopropane-1-carboxylic acid.
BCA	biological control agent
Bt	*Bacillus thuringiensis*
CMC	carboxymethyl cellulose
DNA	deoxyribonucleic acid
EPS	exopolysaccharides
GA	gibberellin
HCN	hydrogen cyanide
ISR	induced systemic resistance
JA	jasmonic acid
mRNA	messenger RNA
N2	nitrogen gas
PAL	phenyl ammonia lyase
PGPB	plant growth promoting rhizobacteria
PO	peroxidase
PPO	polyphenol oxidase
PR	pathogen resistance
RNA	ribonucleic acid
ROS	reactive oxygen species
SA	salicylic acid
SDS-PAGE	sodium dodecyl-sulfate polyacrylamide gel electrophoresis
SOD	superoxide dismutase
VOC	volatile organic compounds

1 Introduction

Endophytic bacteria can colonize and progress their growth within plant tissues without making any harmful impact on plants. They are subclass of rhizospheric bacteria and termed as plant growth-promoting rhizobacteria. They share all the important characteristics found in rhizobacteria that are required for beneficial aspects in host plants (Beneduzi et al., 2012).

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Endophytic bacteria mostly enter host tissues through natural openings or actively penetrate plant cells and can colonize the inner tissues, intercellular gaps, or vascular system of the plant (Gai et al., 2009). The mutualistic connection causes significant physiological variations in the host plant. Endophytes take advantage of the nutrients provided by plants in exchange for the ability to control plant infections, stop the spread of disease, and aid the plant in tolerating stressful situations (Xavier et al., 2021). Endophytes use a variety of direct or indirect plant growth-supporting events, such as solubilization of inorganic phosphates, N2 fixation, siderophore biosynthesis, and plant hormone synthesis (Hayat et al., 2010). The common approaches for the biocontrol of phytopathogens include the production of novel antibiotics, food restriction, the synthesis of fungal cell wall-loosening enzymes, and plant defense priming. Some endophytes have the ability to degrade xenobiotics, and some may serve as carriers of genes that can introduce degradative traits (Ryan et al., 2008). Endophytes, therefore, provide considerable promise for the creation of a secure, productive, and sustainable agricultural system.

2 Types of endophytic bacteria

Endophytic bacteria are grouped into obligate endophytes and facultative endophytes depending on the necessity of the host plant for their life cycle (Egamberdieva et al., 2017). The obligate endophytes are completely dependent on the host plant for all of their needs. They require plant metabolites for their existence and to achieve their life cycle within the plant tissue (Frank et al., 2017). They are incapable of surviving in soil. Obligate endophytes are either not culturable or require complex culture conditions to grow in the laboratory (Xavier et al., 2021). They are protected from severe temperatures, UV rays, water shortages, and competition with faster-growing antagonistic microorganisms for their needs.

In comparison, facultative endophytes usually entered to host plants from a nearby environment and can reside outside the plant tissue at some period of their growth (Abreu-Tarazi et al., 2010). When conditions are favorable, they carry out colonization and infection, which promotes their growth and development. They can enter plant endophytic niches through fractures in the secondary roots, injuries, and cracks on the plant produced by phytopathogens or nematodes, or natural openings in flowers, stems, and cotyledons (Fadiji and Babalola, 2020). They can also enter the host by active migration through the xylem and phloem (Mengistu, 2020) or by the action of enzymes that loosen and breakdown cellulose fiber (Verma et al., 2021).

3 Plant colonization with endophytic bacteria

Endophytic bacteria primarily adhere to the surface of roots by recognizing some root exudates and exploring the possible entry positions to contact the internal plant tissues.

Organic acids, amino acids, and cell wall polymers such as arabinogalactan, flavonoids, and other biomolecules present in root exudates can communicate with endophytes (Kumar et al., 2020). Natural openings like stomata, lateral roots, wounds, natural fissures at the lateral root, and leaf tip pores are the major access points of the endophytes (Hardoim et al., 2015). Additionally, some bacterial endophytes enter easily and distribute within the plant tissues by secreting enzymes that breakdown the plant cell wall (Compant et al., 2005).

After biofilm formation, endophytic bacteria begin to enter the interior of the root passively or actively. Passive entry of bacteria occurs through the fissure at root development areas and root tips (Hardoim, 2011), while active penetration can be accomplished by attachment ofbacteria to host plant cells using their flagella or by compounds that aid in the penetration process. Exopolysaccharides (EPS), cellulase and pectinase enzymes, and numerous quorum-sensing molecules are the majority of these metabolites (Hardoim et al., 2015). The interaction and colonization of endophytes in the host plant is shown in Fig. 1.

The initial contact between *Burkholderia phytofirmans* PsJN and host plant for endophytism is facilitated by oxyalates produced by plant roots. The colonization of the wheat and rice roots by *Azorhizobium caulinodans* and *Serratia* sp. is facilitated by some flavonoids (Dudeja et al., 2021). The endophyte *Bacillus subtilis* BSn5 synthesizes subtilomycin in *Arabidopsis thaliana*, which limits flagellin peptide-mediated plant defense and improves the colonization process (Deng et al., 2019).

Some genes required for the colonization process are expressed under the influence of many plant exudates. The plant extract induces the rice endophyte *Burkholderia kururiensis* M130 to trigger the genes responsible for adhesion and motility (Coutinho et al., 2015). A gene that encodes tyrosinase enzyme is found in the *Streptomyces* strains 303 and 209

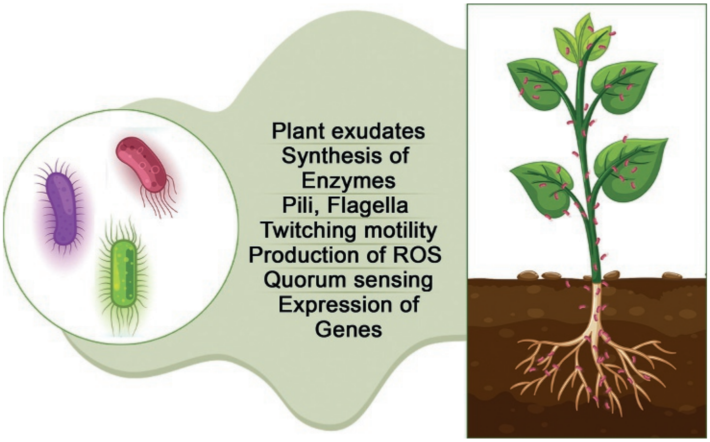

Fig. 1 Plant–microbe interaction and colonization.

responsible for the oxidation of a phenolic molecule, salicylic acid (SA), which facilitates the colonization of them in *A. thaliana*. Again, the tyrosinase activity relatively shields the *Streptomyces* from toxic phenolic chemicals produced by plants during their transition into endophytism. Genes involved in chemotaxis, sporulation, teichuronic acid production, and motility are shown downregulated, but genes associated with stress responses, metabolism, and nutrition transport are shown upregulated in *B. subtilis* when it is primed with rice seeds during their germination (Xie et al., 2015). Several mutation studies reported that pilin Pil X, pilA, and serine–threonine kinase are involved in the endophytism and establishment of *Azoarcus* sp. BH72 inside the plant tissues. *Gluconacetobacter diazotrophicus* expresses ROS-detoxifying genes (glutathione reductase and superoxide dismutase) in larger quantities during the initial stage of rice root colonization (Bhattacharjee et al., 2008).

4 Interactions of plants with endophytic bacteria

4.1 Production of metabolites and antioxidants

Secondary metabolites produced by bacteria, fungi, plants, and other species influence their interaction with the environment. Antibiosis is the activity of inhibiting the growth of phytopathogens by novel metabolites secreted by antagonists. These chemicals include poisonous substances, antibiotics, and volatile chemicals. These chemicals inhibit the growth of pathogens at low concentrations. For example, after settling into root systems, Pseudomonas produces antibiotics that prevent the growth of harmful bacteria.

4.1.1 Siderophores

Siderophores belongs to iron-chelating substances that attach with ferric ions and make them available to the host plants. Siderophores accelerates the growth of the host plants by giving iron nutrients and rendering them inaccessible to phytopathogens (Aftab Uddin et al., 2021). Siderophore synthesis makes microbes an efficient competitor along with promoting plant-microbe relationships and colonization. By the synthesis of siderophore, endophytic bacteria colonized within potato plants are able to prevent the growth of *Xanthomonas campestris* and *Streptomyces scabies* (Castillo et al., 2006). The occurrence of bacterial wilt diseases in banana is highly reduced by bacilibactin type of siderophore synthesized by endophytic Bacillus sp. (Kumari et al., 2022).

4.1.2 Hydrogen cyanide (HCN)

Numerous bacterial genera can make HCN, which appears to inhibit the growth of phytopathogens by biogenic cyanogenesis. Cyanide is able to inhibit number of metalloenzymes and cytochrome C oxidase produced by plant pathogens and defend against various plant diseases (Rani et al., 2022). For example, HCN has been credited with suppressing tomato root-knot disease, and controlling *Odontotermes obesusin* (termites).

Enterobacter cloacae and *Pantoea ananatis* produce HCN as a result of their antagonistic action against Ralstonia sp. (Jisha et al., 2013).

4.1.3 Antibiotics

Some bacteria can kill other microorganisms by the synthesis of antibiotics. Bacterial endophytes are the finest source for such potential antibiotics. The main antibiotics that are crucial in the control of plant infections are mostly categorized as nonvolatile antibiotic compounds. They are lantibiotics produced by *Enterococcus, Bacillus, Streptococcus, Micrococcus, and Staphylococcus*. For example, homicorcin, a lantibiotic synthesized by *Staphylococcus hominis* MBL AB63, makes strong action against *Staphylococci* sp. (Aftab Uddin et al., 2021). Munumbicins are antibiotics generated by endophyte *Streptomyces* sp. strain NRRL 30562 which show activity against *Bacillus anthracis* and *Mycobacterium tuberculosis* (Castillo et al., 2006). Phloroglucinols are broad-spectrum antibiotics that bring systemic resistance in plant hosts (Dwivedi and Johri, 2003). Phenazines synthesized by some *Archaea*and *Eubacteria* prevent fungal diseases in plants (Anjaiah et al., 1998).

4.1.4 Lipopeptides

Lipopeptides are secondary metabolites which contain a combination of short peptides and lipophilic molecules. Endophytes produce lipopeptide isoforms fengycin, iturin, and surfactin to protect the plant from pathogens. Bacillomycin, an iturin produced by the rhizobacterium *B. amyloliquefacines* FZB42, protects the host from harmful actions of *Fusarium oxysporum* (Koumoutsi et al., 2007). Fengycin inhibits the growth of filamentous fungi by creating pores that drastically affect the cell membrane permeability. Surfactins produced by endophytes in Arabidopsis plants are able to inhibit the growth of *P. syringae* (Bais et al., 2004).

4.1.5 Volatile organic compounds (VOCs)

Volatile organic compounds are active in plant defense to protect them from diseases. For example, in wheat plants, the antagonist *P. fluorescens* prevents the take-all disease by the synthesis of 2-acetamidophenol. Salicylic acid, a phenyl propanoid, and jasmonic acid, a product of the lipoxygenase pathway, are powerful inducers that bring plant responses against pathogenesis (Díaz et al., 2003). 2,3-Butanediolgenerated by strain GB03 induces induced systemic resistance and prevent the growth of *Erwinia carotovora* subsp. (Ryu et al., 2003).

4.2 Promote plant growth

Endophytic bacteria support the plants directly in nutrient uptake from the environment or by controlling the synthesis of growth-related hormones, which can advance plant growth under normal and stressful conditions. An important characteristic of endophytic bacteria that helps plant growth is biological N_2 fixation, which is the process by which

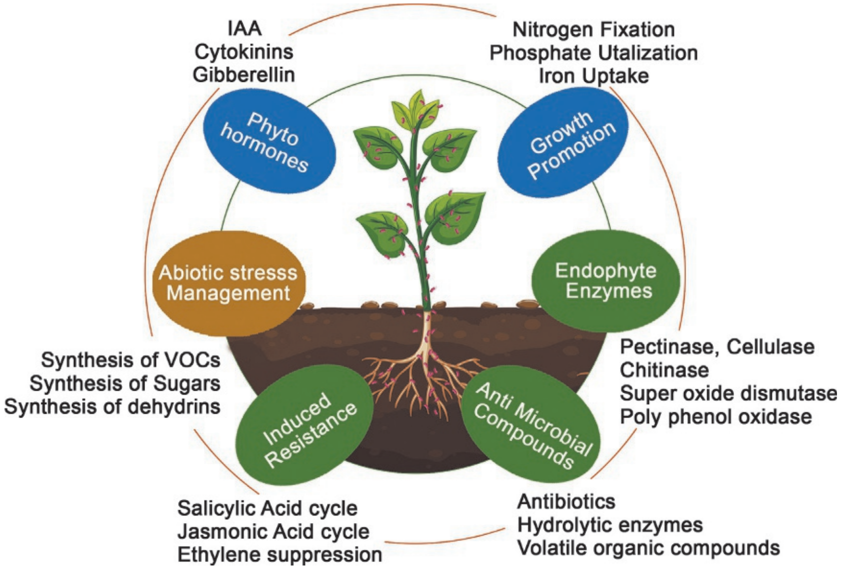

Fig. 2 Mechanisms of plant growth promotion by endophytic bacteria.

microbes convert atmospheric N_2 into ammonia (Zhang et al., 2020). Nitrogenase-producing bacteria can provide their host plants with fixed atmospheric nitrogen. Certain endophytic bacteria express nitrogen-fixing genes that allow bacteria to make nitrate and ammonium from atmospheric nitrogen gas (Santi et al., 2013). Fig. 2 cites various molecular mechanisms of plant growth promotion by endophytic bacteria.

Phosphorous, a micronutrient essential for enzymatic processes, exists in the soil in precipitated, immobilized, and insoluble forms. However, their insoluble nature prevents plants from using them (Mahanty et al., 2017). Endophytic bacteria can solubilize organic phosphorus by either secreting phosphatase enzyme or by using processes including acidification, ion exchange, chelation, and organic acid generation (Singh et al., 2020). By releasing growth-regulating plant hormones such as IAA, cytokinins, ethylene, and gibberellins, endophytic colonization increases nutrient absorption in plants and promote their growth under various stresses (Trivedi et al., 2020). Besides cell elongation and proliferation, IAA secreted by endophytes is responsible for the growth improvement by increasing the number of roots, height, and biomass (Kandel et al., 2017). The production of transgenic plants by expressing ACC deaminase genes of PGP rhizobacteria making them better growth under abiotic stress situations (Rani et al., 2022).

4.3 Control of plant diseases

Plant pathogens are the main threat to the sustainability of agriculture and the ecosystem. Fungal pathogens can be difficult to manage because of their varied host ranges, as well as their soilborne nature. To control phytopathogens, chemical fungicides are frequently utilized at larger dosages. However, the increased use of fungicides has led to some unfavorable outcomes such as disease resistance development and unintended ecological effects. The practice of endophytes as a biological control strategy for plant diseases has several advantages over chemical control, eco-friendliness, high effectiveness, durability, and strong specificity. In general, PGPB inhibits the progression of the disease by either damaging the plant pathogen, slowing its growth inside the host, or indirectly boosting the plant cell's immunity through an ISR mechanism, thereby reducing pathogen growth (Tariq et al., 2020).

Endophytes can attack plant infections through a process known as antibiosis, which depends on the synthesis of enzymes, volatile organic compounds, and other antimicrobial chemicals. Some bacteria produce enzymes can kill the oospores of plant disease causing fungi (Frankowski et al., 2001). Some extracellular enzymes secreted by endophytes make damage in pathogen morphology and retard pathogen growth. By secreting protease, amylase, and chitinase, *Klebsiella pneumoniae* HR1 prevented *Modiolula phaseolina* from causing the deadly root rot disease (Dey et al., 2019).

Bacterial chitinase enzymes have been widely shown to limit fungal growth, making them useful for managing plant-pathogenic fungal infections (Cavlae et al., 1991). The fungus's chitin cell wall is broken down by the chitinase enzyme, allowing DNA or RNA, or proteins to be released from the cell. Four family chitinase genes (chiA-chiD) can be found in the genome of *Serratia proteamaculans* 568, as well as two thermostable chitinases produced by the novel strain *Brevibacillus laterosporus,* which exhibits antifungal and pesticidal properties ((Prasanna et al., 2013; Purushotham et al., 2012). By generating extracellular chitinase enzyme, *Bacillus licheniformis* prevents the growth of *Aspergillus niger, and Gibberella saubinetii*. *B. pumilus* SG2 shows antifungal action against *B. sorokiniana*and *F. graminearum* by secreting two chitinases, ChiL, and ChiS. The PR-4 gene encodes the endochitinase enzyme which promotes plant defenses by loosening fungal cell wall and inhibits hyphal growth and spore germination (Shali et al., 2010).

Esterases are involved in the degradation and detoxification of various virulence factors and quorum-sensing signal molecules produced by plant pathogens (Mavrodi et al., 2010). For example, brefeldin A secreted by *Alternaria carthami* (the fungus that causes safflower blight) and albicidin synthesized by *Xanthomonas albilineans* (causative agent of leaf scald disease in sugar cane) are degraded by esterase. Gelatinases are protease enzymes which able to degrade the gelatin in fungal pathogens such as *Colletotrichum coccodes, Fusarium solani, Alternaria* sp., *F. udum,* and *Rhizoctonia* sp. (Bawa et al., 2019). The expression of PR-2 gene leads to the synthesis glucanase enzyme which destroys fungal cell wall by hydrolyzing glucans in the cell wall (Balasubramanian et al., 2012).

Some endophytic bacteria trigger a defense system known as induced systemic resistance (ISR) in order to defend the host plant against various phytopathogens (Alvin et al., 2014). Jasmonic acid, salicylic acid, and orethylene induced pathways are used by endophytic bacteria to start ISR in host plants (Pieterse et al., 2012). ISR is again brought by high-level expression of pathogen resistance genes (PR2, PR3, PR4, and PR5), as well as genes involved in various plant defense pathways (Ali et al., 2018). .The upregulation of PR-1 and PR-4 for inducing systematic acquired resistance has been reported in endophytic actinobacteria separated from wheat tissues (Doornbos et al., 2011). .Therefore, by boosting the plant immune system, BCAs can prevent pests and diseases from spreading. BCAs such as *Pseudomonas fluorescens*, *Bacillus amyloliquefaciens, Bacillus cereus, and Bacillus atrophaeus* can generate ISR against various phytopathogens (Lahlali et al., 2022). *B. phytofirmans* PsJN produces ISR in grapevines to act against *Botrytis cinerea* (Frank et al., 2017). Several endophytes expressing ROS scavenging enzymes like SOD, PAL, PO, and PPO are connected with ISR in plants (Alquéres et al., 2013).

5 Applications

5.1 Resistance against cotton bollworm

The "white gold," cotton (Gossypium sp.), is the major raw material for the cloth industry and is involved in the economic and social concerns of over 60 million people worldwide through its production (Rajendran et al., 2007). The most harmful insect pest of cotton is the cotton bollworm *(Helicoverpa armigera)* (Cunningham et al., 1999). An effective method of managing cotton bollworm causing pests is a biological control using endophytic bacteria. The making and application of talc-based bioformulations would facilitate the control of major pests of cotton plant (Rajendran et al., 2007).

Rajendran et al. identified *Pseudomonas fluorescens* strain Pf1 and *Bacillus* strains from the cotton plant's stem, root, leaves, and seeds and recognized their effectiveness in protecting cotton against American bollworm infestation. The application of talc-based bioformulations of the above strains with and without chitin dramatically decreased the prevalence of bollworm (Rajendran et al., 2007). The bacterial suspension is first mixed with purified talc powder and carboxymethyl cellulose (CMC) under hygienic conditions. The pH is adjusted to neutral with calcium carbonate. After sterilization, the cotton seeds are soaked in endophytic bacterial suspension for 24 h. After planting the treated cotton seeds in a pot, a talc-based formulation is applied to the plant either by soil application or by foliar application. When larvae feed on the cotton plant, the bacterial species can inhibit American bollworm through ISR by synthesizing defense enzymes (Rajendran et al., 2007). .To increase the influence of induced systemic resistance, chitin can be added to talc-based formulations (Delvasto et al., 2008). In a normal plant, peroxidases are only active during the early stages of a bollworm infestation; however, in plants treated with endophytic bacteria, the peroxidase activity will be continued even after a week of infestation.

5.2 Plant–microbe interaction studies using multiomics data analysis

Next-generation sequencing (NGS) and multiomics data provide the gene expression level of plant–microbe interaction which improves the research in this field (Sharma et al., 2020). Genomics works with complete genome sequences, and transcriptomics observes mRNA levels to provide expression patterns of genes (Mahanty et al., 2017). Proteomics studies can understand the native conformations, functions, and communications of proteins in different types of cells, and metabolomics seeks to grasp the activities of various metabolites in a specific organism (Hall, 2011). Thus, a combination of omics techniques can link every facet of cellular level variation and give a comprehensive understanding about the complicated dynamics of cellular processes of plant-microbe endophytism is summarized in Fig. 3.

Genes expressed for the colonization and the synthesis of bioactive compounds, such as hormones and antibiotics, have been characterized by genome analysis (Firrincieli et al., 2015). A comparison between whole proteins of endophyte-colonized and endophyte-free plants provides the list of specific proteins involved in the plant-microbe interactions. During the colonization between *G. diazotrophicus* and sugarcane roots, 30 different bacterial proteins are expressed. Among these, nine genes mainly involved in oxidative and osmotic stress regulation as well as chemotaxis are controlled by host

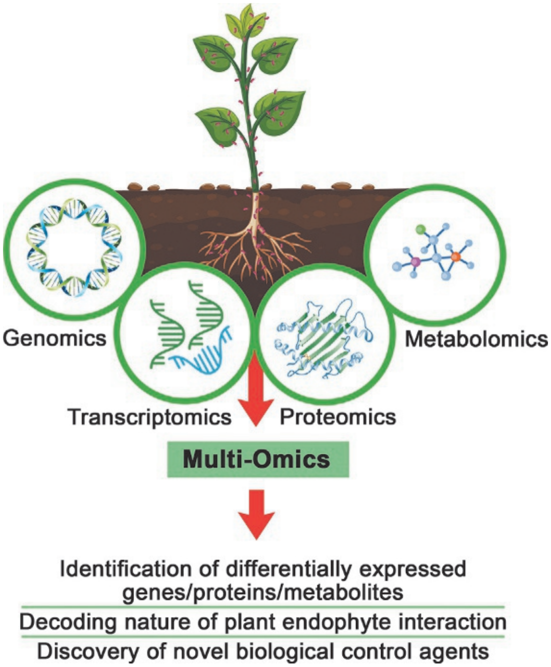

Fig. 3 Plant–microbe interaction studies using multiomics data analysis.

signals (Lery et al., 2011). The differential gene expression analysis identified the role of flavonoid synthesis to prevent anthracnose in *Camellia oleifera* (Yang et al., 2022). In the study of endophyte colonization, stress tolerance, and the identification of bioactive metabolites, multiomics analysis unquestionably continues to perform vital functions. However, there are still several difficulties in analyzing multiomics data. One of the key issues that requires ongoing research is how to effectively link different omics data and reveal more meaningful information (Huang et al., 2017).

5.3 Production of microbial pesticides

Biopesticides are microorganisms or products of living organisms for controlling plant-affected pests. The biopesticide *Bacillus thuringiensis* (Bt) had the greatest degree of commercial success. Bt generates endotoxins, which can be used as biopesticides, and can be used to produce insect-resistant transgenic plants, particularly against lepidopteran insects (Schünemann et al., 2014). Genetically modified strains of endophytic bacteria facilitated improved pest control in plants. The endophytes have some necessary traits to construct genetically engineered organisms. First, the pest-controlling component must be delivered to easily accessible points to the pathogen. Second, endophyte should lack the major disease-posing potential for crops. Third, genetic modification of the endophyte must be simple. The capacity for ready expression and long-term stability of the foreign gene(s) in endophytes are other criteria that must be taken into account while creating recombinant microorganisms (Dwivedi and Johri, 2003).

Yang Lia demonstrated the cloning of the Cry218 gene into bacterial endophyte *Burkholderia pyrrocinia* JK-SH007 using pHKT2 expression vector to create insecticidal activity against lepidoptera larvae. This is achieved by cloning 3.5 kb of Cry218 gene into 5.3 kb of pHKT2 expression vector in which the insecticidal crystal protein expression is regulated by the PrPl promoter of lambda phage as shown in Fig. 4. The vector system

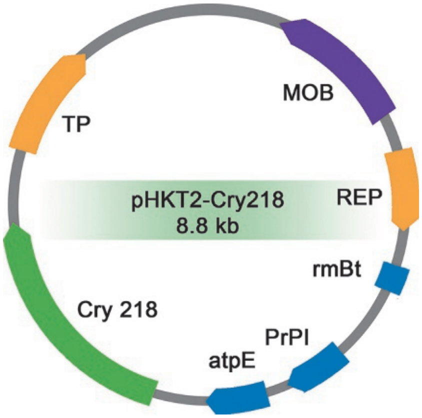

Fig. 4 pHKT2-Cry218 vector.

is transformed to *B. pyrrocinia* strain JK-SH007 by electroporation method. Expression of Cry218 protein is confirmed by SDS-PAGE and western blotting techniques (Barazani et al., 2001).

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CHAPTER 3

Rhizobacteria that boost plant growth while lowering abiotic stress—A profitable solution

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1 Introduction

Plants experience a variety of abiotic and biotic stresses. Abiotic (50%) and biotic (30%) stressors have been shown in several studies as potential threats to future food security because they reduce agricultural productivity globally (Sharma et al., 2021). The extent and intensity of abiotic stress have increased in an unprecedented manner during the present regime of global warming and climate change accompanied by high temperatures, droughts, floods, and increased contamination, which has implications for soil health, microbial diversity, and crop production. Many agricultural sites have suffered from the effects of abiotic stress factors. Soil contamination is a ubiquitous environmental problem of global concern. Over the past few decades, pollutant concentrations have been rising in different environmental domains. They are produced by a variety of human activities, most notably fast industrialization, inappropriate waste management, extensive use of pesticides and chemical fertilizers, and mining, and they accumulate in the environment (Mondal et al., 2019; Briffa et al., 2020). The majority of pollutants have a persistent character; some have the ability to traverse trophic boundaries. They have a negative impact on crop production, quality of soil and water, the health of the biota, including humans, and the entire ecosystem services (Gavrilescus, 2021).

A strong management strategy for agricultural soils is necessary to maintain output, achieve economic growth, safeguard biodiversity, and satisfy rising food demand due to the shrinkage of arable agricultural lands. In this regard, good agricultural practices and organic farming techniques have been prescribed over the years to safeguard and maintain sustainable agricultural land in this environment. These sustainable agricultural approaches include the use of beneficial microbes including bacteria, mycorrhizae, and insects. Plants and microorganisms have close evolutionary interactions between them (Chagas et al., 2018). Positively interacting microorganisms including rhizobia, mycorrhiza, endophytes (plant growth promoting), and epiphytes provide benefits to the

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associated plants, such as protection against stresses, promotion of growth, and increased availability of nutrients. The plants also provide protection and nutrients to the associated microbes (Chagas et al., 2018) whereas, the negatively interacting microbes cause disease and damage to their host plants (Venturi and Fuqua, 2013). Root colonization is the first step of plant-microbe interactions. The relationship between microorganisms and plants is initiated by the production of signals from both the host and colonizer (Chaparro et al., 2014; Yu et al., 2022). The rhizosphere is the source of the majority of microorganisms that colonize to plants (Yu et al., 2022). The rhizosphere is a zone in the soil next to roots, while the rhizoplane is the entire surface area of roots (Coats and Rumpho, 2014).

The interactions between plants and microbes are crucial to both partners' ability to survive and adapt to their surroundings, even in contaminated soil (Rajkumar et al., 2012). Environmental stress can be alleviated in plants by their associated microbes (Ali et al., 2022). The contaminants resistant plant growth promoting bacteria (PGPB) belonging to the genera of *Pseudomonas*, *Azotobacter*, *Achromobacter*, *Azospirillum*, *Bacillus*, *Variovorax, Enterobacter*, *Aeromonas*, *Klebsiella*, etc., are capable of inducing plant development under environmental stress conditions mediated by synthesis of IAA, gibberellic acid (GA), 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, phosphate solubilization, siderophores, organic acids, biosurfactants, exopolymers, etc. (Glick, 2010; Rajkumar et al., 2012; Sandilya et al., 2022).

2 Abiotic stresses

2.1 Drought

The term "drought" takes into consideration a number of important variables including the hydrometeorological state, socioeconomic circumstances, and stochastic tendency of water (American Meteorological Society Council, 2004). In the last 40 years, more people have been impacted by drought stress than by any other natural hazard because of its nearly universal occurrence (Montwé et al., 2016). Drought is a complex natural occurrence with a range of severity levels, occurrence times, geographic coverage, and impacts, and it is getting worse, lasting longer, and being more severe as a result of global climate change (Basak et al., 2022; Vicente-Serrano et al., 2020; Biswas et al., 2018a, b). Most prevalent important factors influencing crop development is drought stress. Researchers have been interested in this issue since drought has such catastrophic effects on crop plants (Barooah et al., 2021). Significantly lower biomass, poor vegetative and reproductive growth are the results of drought stress, which also negatively affects seed germination rates, seedling growth, photosynthesis, stomatal conductance, and other biological processes (Seleiman et al., 2021). In general, there are four different types of droughts: meteorological, hydrological, socioeconomic, and agricultural (Zeng et al., 2022). Whereas meteorological drought is caused by a protracted delay in precipitation, hydrological drought is caused by inadequate water resources including surface and underground water; socioeconomic drought is caused by inadequate water management systems to fulfil the water requirement of household and community; and agricultural drought is designated as reduction of soil moisture due to inadequate water supply that affects crop development and crop produce (Barooah et al., 2021; Zeng et al., 2022). Interacting metabolic processes are triggered by drought stress, including the inhibition of antioxidant enzyme activity and the production of reactive oxygen species (ROS) in metabolic pathways (Laxa et al., 2019). The life cycle of plants is significantly influenced by the ROS species.

2.2 Temperature

The term "suboptimal temperature stress" refers to conditions above or below the thermal thresholds, which is characterized by a decline in plant growth, a decrease in metabolic activity, and damage at cellular or tissue level (Greaves, 1996). Both exposures to extremely high temperatures for a brief period of time and moderately high temperatures for an extended period of time are harmful to plant growth and development. High temperature has an adverse impact on the biochemical processes, physiological traits, and morphological development of various plant species (Aslam et al., 2022). The effects of high temperatures include leaf senescence and abscission, burnt branches, leaves, stems, and also the growth of root (Nievola et al., 2017). Plants produce more metabolites under high temperatures, including heat-shock proteins, antioxidants, and osmoprotectants (Bokszczanin et al., 2013). Antioxidant enzymes are synthesized at varying levels to combat the ROS generated due to stress of different degrees, serving as signaling molecules (Laxa et al., 2019).

Plants are affected by low temperatures in two different ways, including chilling injury and freezing injury. Plants grown in tropical and subtropical regions typically suffer from chilling injury. When exposed to low temperatures below 12°C, these plants exhibit conspicuous physiological malfunctions (Lyons, 1973; McWilliam, 2019) whereas freezing damage occurs at temperatures below 0°C due to intracellular and extracellular freezing (Román-Figueroa et al., 2021). Solid ice forms when extracellular water freezes and causes mechanical damage to plant cell membranes (Steponkus et al., 1993; Román-Figueroa et al., 2021). Plants enhance membrane cryo-stability to prevent freezing damage, which may be related to changes in the plasma membrane's constitution (Miki et al., 2019). In general, the hydrophilic substances including sugar, enzymes, and dehydrins promote alteration in proteins and lipids associated with plasma membrane to improve the membrane cryo-stability (Pirzadah et al., 2014).

2.3 Salinity

Soil salinity, a global problem affecting both developed and developing countries has an adverse impact on agricultural production (Shokat and Großkinsky, 2019). The salinity of the soil has increased worldwide as a result of intensive agriculture and unfavorable environmental regimes. The term "salt impacted" describes soil that is saline (salt build-up) or sodic (excess sodium in combination with negatively charged clay particles) (Litalien and Zeeb, 2020). Saline soils are those which have an electrical conductivity of the saturation soil extract of more than 4 dSm^{-1}, ESP $<15\%$ and pH below 8.5 (Szabolcs, 1994; Shahid et al., 2018). There are two categories of salinity: primary and secondary. Primary salinity refers to naturally existing saline in soil and water, whereas secondary salinity refers to salinity brought on by human activities such as agriculture and land development (Srivastava et al., 2019). A cocktail of ions including sodium, calcium, magnesium, sulfate, and chloride make up saline soils, with sodium chloride frequently predominant (Zaman et al., 2018). The normal processes of plant development are hampered or impacted by the high concentration of soluble salts present. In plants, the osmotic or water-deficit are imposed due to salt stress, which reduced the water uptake capacity of the plants, resulting slower growth (Gupta et al., 2021). In addition to water and other solutes, the roots excessively absorb salt from the soil, and these materials enter the plants' transpiration stream, damaging the cells involved in the transpiration process, thereby reducing plant development (Gavrilescu, 2021). The excess accumulation of Na^+ and Cl^- in plant cells have an adverse effect because these ions impact the activity of enzymes (Shrivastava and Kumar, 2015).

2.4 Flood

Every year, sporadic, unforeseen flash floods overwhelm one-fourth of the world's rice crops that occur less frequently now than in the past. Flood stress generally occurs in rice growing areas (Bin Rahman and Zhang, 2022). The plants require oxygen to survive, but heavy flooding lowers the amount of oxygen in the soil, thereby aerobic respiration can be reduced (Zhou et al., 2020). Depending on the condition of the submerged plant components, flooding also leads to ethylene accumulation and raises the CO_2 level (De Pedro et al., 2020). Light intensity can also be a problem in flood-affected agricultural areas, which will reduce photosynthetic activity (Bui et al., 2019). The ability of some plant species to adapt to low oxygen levels may be shown in their production of lateral and adventitious roots, cellular changes, and the creation of aerenchyma tissue (Pedersen et al., 2021).

2.5 Toxic metal(loid)s

Environmental contamination arises when an extraneous substance (element, compound, or ion) enters into the environment and causes some adverse impacts on its physicochemical and biological attributes. Contamination by toxic metal(loid)s (TMs) is a ubiquitous environmental problem of global concern. The TM contamination of water and soil can cause toxicity in living organisms of an ecosystem, and degrade the water/soil quality and adversely affect ecosystem health and services, which have significant negative connotation for soil fertility, agricultural productivity, and human health. As, Pb, Hg, Cd, Cr(VI), Ni, and Cu are ranked first, second, third, seventh, seventeenth, 57th, and 118th on the list of 275 chemicals classified as "priority substances" by the Agency for Toxic Substance and Disease Registry (ATSDR, 2019). Widespread TM contamination is a result of growing urbanization, industrialization, intense agriculture, mining, industrial output, sewage discharge from populated areas, irrigation, and overuse of fungicides and herbicides. The majority of these TMs have a persistent character, and some of them may even cross trophic boundaries. They have a negative impact on ecosystem services and overall ecosystem health, including the soil and water quality, crop produce, and health of the biota including humans (Gavrilescu, 2021). For instance, many metals (Cu, Ni, and Zn) that are contemplated as micronutrients for plants can be hazardous when present in excessive amounts (Khandelwal et al., 2022; Mondal et al., 2022). Non-essential TMs that plants encounter, such as Cd, Pb, Hg, and As, have a negative impact on enzyme activity, mitosis, photosynthesis, plant development, respiration, germination, and production (Khandelwal et al., 2022; Mondal et al., 2022).

3 Rhizobacteria

The term "rhizosphere" refers to the region around a root of plant where there are intricate interactions between the soil, plant, and the microbes, which is a dynamic micro-environment of the soil ecosystem. It has the power to influence the development of roots, uptake of nutrients, exudation from root, and rhizodeposition (Schnepf et al., 2022). Rhizodeposits comprise dead and lysed root cells, exudates, lost root cap and border cells, mucigel, and lost gases (Schnepf et al., 2022). It is known that rhizodeposits increase microbial activity and production of enzymes, which in turn impacts on nutrient availability and organic matter degradation in the soil (Hinsinger et al., 2009). Due to the distinctive physicochemical and biological soil properties associated with roots, the rhizosphere milieu has a greater quantity, diversity, and activity of microorganisms than bulk soil (de la Porte et al., 2020). Microorganisms in the rhizosphere have a great potential to affect plant development and agricultural productivity (Nosheen et al., 2021). The bacteria that colonize in the rhizosphere have an advantageous impact on the development and growth of plants, designated as "plant growth promoting rhizobacteria" (PGPR) (Oleńska et al., 2020). The PGPR can promote plant growth both directly and indirectly through combating plant infections (bioprotectants), improving uptake and availability of nutrients (biofertilizers), and producing phytohormone (biostimulants). Numerous rhizobacteria from the genera of *Rhizobium*, *Bradyrhizobium*, *Azotobacter*, *Bacillus*, *Azospirillum*, *Burkholderia*, *Aeromonas*, *Pantoea*, *Methylobacterium*, *Pseudomonas*, etc. have been shown plant growth promotion under a variety of abiotic stresses (Miransari, 2014; Barooah et al., 2021; Mondal et al., 2019, 2022). A special plant-soil-microbe interaction happens in the rhizosphere zone, which is facilitated by the chemical constituents extricated by microorganisms and plants (Das et al., 2022). In agricultural plants, PGPRs enhance germination of seed, development of root, ripening of fruit, fluorescence, branching and tillering (Mondal et al., 2022). Furthermore, PGPRs provide resistance to both biotic and abiotic stressors (Shameer and Prasad, 2018).

4 Plant growth promotion by PGPR under abiotic stress

Plant-microbe interactions play a crucial role in the endurance and adaptation of both the associates in the environment, even under abiotic stresses (Rajkumar et al., 2012; Shameer and Prasad, 2018). Environmental stress can be alleviated in plants by its associated microbes (Ali et al., 2022). The genera of PGPB including *Pseudomonas*, *Azotobacter*, *Azospirillum*, *Achromobacter*, *Bacillus*, *Enterobacter*, *Klebsiella*, *Aeromonas*, *Variovorax*, etc., are capable of inducing plant development under environmental stress mediated by synthesis of IAA, ACC deaminase, organic acids, siderophores, biosurfactants, exopolymers, biogenic compounds, and phosphate solubilization (Fig. 1) (Glick, 2010; Rajkumar et al., 2012; Sandilya et al., 2022).

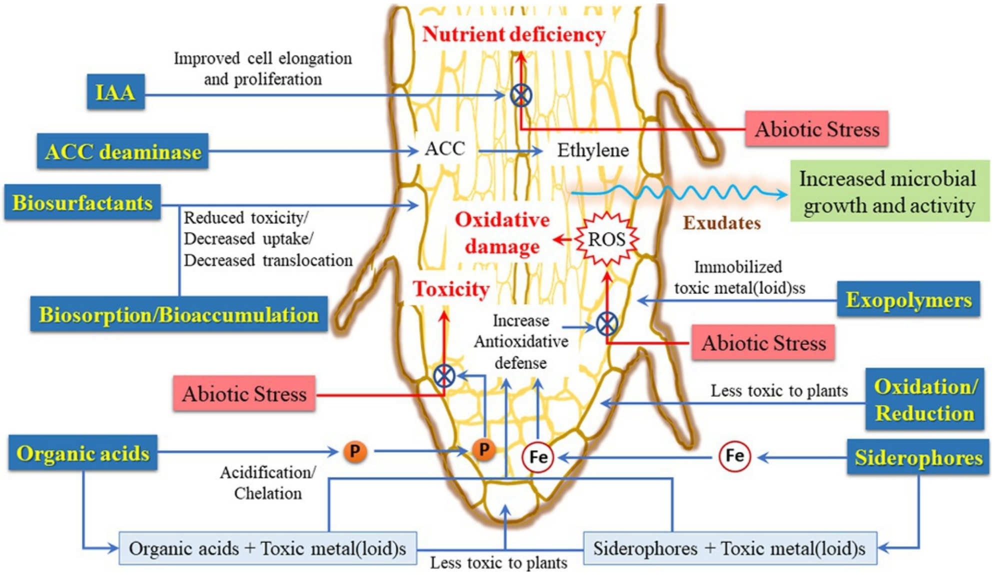

Fig. 1 Promotion of plant growth and alleviation of abiotic stress in plant by rhizobacteria. *(Modified after Rajkumar, M., Sandhya, S., Prasad, M.N.V., Freitas, H., 2012. Perspectives of plant-associated microbes in heavy metal phytoremediation. Biotechnol. Adv., 30(6), 1562–1574.)*

4.1 Production of phytohormones

Abiotic stress induces hormonal imbalance in plants (Khanna et al., 2020). Plant hormones including auxins, GA, abscisic acid (ABA), salicylic acid (SA), cytokinins (CKs), and brassinosteroids (BRs) have a considerable impact on how plants respond adaptively to abiotic stress (Waadt et al., 2022). Many bacteria have the potential to produce these phytohormones, which stimulate plant development under both normal and stressful conditions (Babalola, 2010; Biswas et al., 2017; Biswas et al., 2018a,b; Banerjee et al., 2019; Mondal et al., 2019, 2022). These bacterial phytohormones also modulate hormonal imbalance in plant and their stress-resilient response (Etesami et al., 2015).

IAA is the most significant and prevalent auxin in plants, and is produced by about 80% of the rhizospheric bacteria (Patten and Glick 1996). Plant's abiotic stress can be reduced by the bacterial IAA through the increase in nutrient absorption by proliferating plant roots and promotion of adaptative capacity and resistance to stress (Mondal et al., 2019, 2022; Munir et al., 2022) (Fig. 1). Many studies show that the bacterial IAA reinforces numerous cellular defence mechanisms to withstand stresses (Etesami, 2018). Most often opted plant's strategy is the secretion of root exudates to prevent the entrance of stress via chelation in the apoplast or rhizosphere (Magdziak et al., 2011). The IAA synthesized from bacteria can loosen the cell walls of plant root followed by the increasing root exudation, which also facilitates microbial colonization in rhizosphere (Etesami et al., 2015).

Many bacterial species also synthesize other phytohormones such as GA and SA through induction of antioxidant system, and controlling the activity of the enzymes peroxidase, catalase, and proteases, which can alleviate abiotic stress including TMs toxicity in plants inflicted by oxidative stress, lipid peroxidation, and hormonal imbalance (Zhu et al., 2012; Egamberdieva et al., 2017).

4.2 Synthesis of ACC deaminase

In many plants, abiotic stress can cause an increase in ethylene biosynthesis, which reduces root elongation, hydrogen peroxide accumulation, and induction of apoptosis (Sun and Guo, 2013; Chmielowska-Bąk et al., 2014). Under abiotic stress, bacterial ACC deaminase can alleviate the toxicity caused by the stressor and enhance tolerance in plants, followed by the promotion of root growth through reducing plant ethylene levels by hydrolysing ACC to NH_3 and α-ketobutyrate (Glick, 2005, 2010). Introduction of exogenous ACC deaminase-producing bacteria have been shown to enhance plants' ability to grow under abiotic stress conditions (Glick, 2014; Zhang et al., 2011; Rajkumar et al., 2012) (Fig. 1). The bacterial species including *Bacillus* spp., *Pseudomonas* spp., *Enterobacter* spp., *Proteobacteria* sp., *Arthrobacter* sp., *Firmicutes* sp. and *Actinobacteria* sp. are able to synthesize ACC deaminase which could reduce the abiotic stresses in plants (Rajkumar et al., 2012; Mondal et al., 2019, 2022).

4.3 Production of siderophores

Iron is considered as one of the necessary elements for plants to grow and develop, but under abiotic stress, its uptake is hampered resulting in inhibition in chlorophyll biosynthesis (Kumar et al., 2022). A few plants can overcome this Fe deficiency either by making phytosiderophores and/or rhizosphere acidification (Etesami, 2018). Bacteria can also help plants under such condition in acquiring Fe through siderophores production (Glick, 2010). The bacterial siderophore enhances the quantity of chlorophyll and promotes plant development under stressful conditions by selectively absorbing Fe from a complex of metal(loid)s cations (Dimkpa et al., 2009) (Fig. 1). Many studies reported that the siderophores produced by bacteria have greater affinity to Fe than phytosiderophores, thereby promoting higher chlorophyll synthesis in plants by PGPR (Rasouli-Sadaghianiet al., 2010).

4.4 Phosphate solubilization

Many rhizospheric bacteria can convert insoluble phosphate compounds to plant accessible soluble form through the synthesis of organic acids and resulting in the decrease of pH (Gyaneshwar et al., 2002). Additionally, the phosphate-solubilizing bacteria have been isolated from a variety of environments, including stressed soils, rhizospheres, phyllospheres, and rock phosphate deposits (Zaidi et al., 2009). The phosphate solubilizing bacteria can play significant roles in decreasing uptake of toxic metal by the plants and their translocation to aerial parts as a result of their binding to the bacterial cell wall and immobilization as metal-phosphate complexes (Rajkumar et al., 2012; Etesami, 2018; Khanna et al., 2022) (Fig. 1). The soluble phosphate also immobilizes TMs in contaminated soil and increases TMs resistance of plants via insoluble TMs-phosphate complex formation, as observed in the immobilization of Pb by the production of pyromorphite $[Pb_5(PO_4)_3]$ and Cd^{2+} through Cd-phosphate precipitation (Zheng et al., 2021; Li et al., 2022).

4.5 Production of organic acids

Many bacteria that boost plant growth and development are capable of synthesizing low-molecular-weight organic acids including citric acid, oxalic acid, succinic acid, gluconic acid, etc. (Archana et al., 2012). The bacterial organic acids show greater affinity for chelation to TMs compared to the essential nutrients (Najeeb et al., 2009). These organic acid-producing bacteria can alleviate abiotic stress in plants through (i) complex formation with TMs having less phytotoxicity than the free form (Gao et al., 2010; Nabi et al., 2021); (ii) induction of organic compounds secretion by plants to form complexes with TMs (Matusik et al., 2008); (iii) beneficial contribution in essential nutrient acquisition (Gadd, 2004); (iv) modulation of antioxidant enzyme responses (Kavita et al., 2008); (v) solubilization of rock phosphate, and subsequently precipitation of insoluble metal(loid)-phosphate complexes (Cao et al., 2008; Sharma and Archana, 2016) (Fig. 1).

4.6 Production of biosurfactants

Biosurfactants or surface-active agents are amphiphilic, surface tension reducing compounds, which decrease surface and interfacial tensions and are either generated on the cell surfaces of microbes or expelled extracellularly (Etesami, 2018). The primary components of the biosurfactants are fatty acids, mycolic acid, glycolipids, phospholipids, and lipoproteins (Kashif et al., 2022). The amphiphilic biosurfactants produced by bacteria have higher and stronger affinity to toxic metal(loid)s than the typical soil metal cations, followed by the increment in TMs tolerance and removal (Pacwa-Płociniczak et al., 2011) (Fig. 1).

4.7 Production of extracellular polymeric substances

Extracellular polymeric substances, also known as exopolymers, are natural polymers of homo- or hetero-polysaccharides, that are either released into the environment by bacteria or adhered to the exterior of their cells as a slime or capsule (Staudt et al., 2004; Rajkumar et al., 2012). Bacterial exopolymers have a considerable indirect impact on plant growth under abiotic stress by complexing with toxic metal(loid)s, capturing the precipitated metal sulfides and oxides, and decreasing their mobility as well as bioavailability to plants (Banerjee et al., 2019; Morcillo and Manzanera, 2021) (Fig. 1). The acyl group of exopolymers provides its anionic property, which also enhances its lipophilicity and interaction with other polysaccharides and cations (Kaushal and Wani, 2016).

5 Future prospects and concluding comments

The researchers are compelled to develop a variety of solutions that can aid in developing a sustainable agricultural ecosystem that can prevent and anticipate the issues brought on by the changing climate by the compelling daily increase in information concerning agricultural productivity losses. PGPR can increase the host plant's tolerance to both biotic and abiotic stresses and be used to alleviate their adverse effects (Tabassum et al., 2017). As a result, it will be crucial to identify and thoroughly analyze rhizobacterial strains with the ability to provide cross-protection against a variety of stressors (Dimkpa et al., 2009a, b). The capacity of rhizobacteria to counteract the impacts of environmental stress may be significantly impacted by the induced systemic response (ISR) of crop plants. In order to understand the signaling cascades caused by PGPR, which lead to increased tolerance to abiotic stressors, it will be useful to conduct a thorough investigation of ISR against plant pathogens. Creating microbiological tools and methods of plant-microbe-soil interaction is the most promising way to deal with various abiotic stressors. It is now necessary and also demanded by the commercial sector to construct a beneficial soil microbial consortia with a long shelf life.

However, the degree of efficacy in accomplishing the advantages of PGPR tends to decrease as it moves from laboratory studies to greenhouses, and then to fields, which suggests that there is a need for study on the multiple facets of PGPR under real life settings and field environments. Thus, in order to increase field level accomplishments, research is now needed on screening procedures, strain enhancement, and the development of optimum rhizobacterial strains for rhizosphere competence and sustainability. Although using PGPR to assist plants in the agricultural field with stress management appears challenging, there is still much untapped potential (Ilangumaran and Smith, 2017). Researchers are attempting to create speedier and more reliable remedies as many forms of abiotic stressors are severe risks to the global crop output. Annual crop production is seriously impacted to a greater extent by abiotic stresses. Therefore, it is crucial to concentrate on expanding the geographic region, developing novel techniques of breeding for abiotic stress tolerance, and conducting a thorough investigation of rhizobacteria-mediated abiotic stress relief. Since it can effectively accomplish the goal in question, PGPR-assisted abiotic stress management has grown immensely popular and received a great deal of attention. Native microorganisms should be given top priority for the effective completion of the assignment since they have superior adaptation capacity to an imported strain (Sarma et al., 2012). However, to unveil the actual mechanisms involved in the process, thorough experimental investigation must be conducted. Utilization of PGPR to enhance plant growth and disease management under abiotic stress appears promising. It must be used to sustainably increase plant growth and productivity.

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CHAPTER 4

Rhizoremediation as a green technology for heavy metal remediation: Prospects and challenges

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1 Introduction

Although heavy metal is immobile in nature but interacts with many biotic components and gets transported to different parts of the plants like leaves, vegetables, fruits, roots, and seeds (Ganesan, 2014). Upon consequence, it can enter human and animal bodies through the food chain, which is ingested about 98% heavy metals and the remaining 1% each drinking water and aquatic foods (Clijsters and Van Assche, 1985). Removing heavy metals from medium to low levels of contamination using physical and chemical treatments like landfilling, incineration, leaching, and chemical methods is usually expensive, inefficient, unsafe, laborious, and environmentally invasive (Segura et al., 2009; Ganesan, 2014). These treatments are based on transporting and recycling contaminants from soils to material forms. Furthermore, it is responsible for disrupting soil characteristics and thereby ecology by rendering the land unsuitable for usage in agriculture and various purposes. In this context, rhizoremediation can be considered a suitable option for remediation of the heavy metal contaminated site. The degradation of pollutants by rhizoremediation is higher than that of phytoremediation in plants and microbes alone.

2 Heavy metal

Over the years, heavy metals became synonymous with the most deleterious pollutants because of their persistence, nondegradable feature, toxicity, biomagnification, and bioaccumulation nature (Alfaifi et al., 2021; Zhao et al., 2021). Heavy metals are defined as a subset of 40 elements with a specific density of more than 5 g/cm^3 according to their chemical properties and environmental behavior, which includes transition metals, metalloids, lanthanides, and actinides, for example, mercury (Hg), silver (Ag), nickel (Ni), cobalt (Co), zinc (Zn), copper (Cu), selenium (Se), cadmium (Cd), lead (Pb), molybdenum (Mo), uranium (U), and arsenic (As) (Ganesan, 2014; Yang et al., 2018). It is also

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known to possess characteristics of metallic properties such as ductility, ligand specificity, and conductivity. Among them, heavy metals can be classified biologically into two classes based on their role in the metabolism and nutrition function of both prokaryotes and eukaryotes: essential elements (micronutrients: Mo, Ni, Cu, Zn, Co, and Se) that are crucial for the growth and development of plants and animals up to certain levels and nonessential elements (As, Ag, U, Cd, Hg, and Pb) that are often considered to be toxic contaminants due to potential biomagnification and bioaccumulation risk on exposure through the food chain (Appenroth, 2010; Gadd, 2010; Zhao et al., 2021).

3 Heavy metal pollution

Pollution caused by heavy metals is generally regarded as a persistent threat to public health, crop production, ecology, and environment (Chun et al., 2021). Approximately, 0.8 million tons of lead (Pd) and 0.03 million tons of chromium (Cr) have accumulated in soils in Chinese industrial and agricultural regions (Yang et al., 2018). Moreover, abandoned mine areas and tailing regions typically exhibit a high amount of heavy metal concentrations. From soil and water, heavy metal gets adsorbed and accumulated in the plant and then enters the animal kingdom causing health risk (Ganesan, 2014). It is responsible for water pollution, ecological imbalance, and various environmental issues. Investigating the pollution of heavy metal in the surface sediments of Haizhou Bay, China with characteristics and spatial distribution found that the highest potential ecological risk coefficient of heavy metals in Hg, followed by Cd, As, Pb, Cu, Cr, and Zn (Liu et al., 2021). High ecological risk of Hg pollution in soil and high health risk of As pollution in crops is recorded in Jiangbei, China (Xiang et al., 2021). Another study showed above permissible limits of heavy metal concentration, namely Mn, As, Cr, Ni, Zn, and Se, in the drinking water of southern Saudi Arabia (Alfaifi et al., 2021). The author added that only 20%–52% of the groundwater samples may be suitable for agricultural and domestic purposes based on calculated pollution indices. The plant may be adversely affected by heavy metals that lead to changes in the photosynthesis metabolic pathways, uptake of nutrients, ethylene synthesis, protein metabolism, nitrogen metabolism, decreased cytokinin level, and sugar and water metabolism (Ganesan, 2014). Indeed, exposure to heavy metals to human beings could result in many health-related problems, for example, as exposure induces cardiovascular disorders and cancer disease (Yang et al., 2018). High metal indexes (MI) of synergistic contamination of heavy metals (Cu, Pb, and Ni) in the surface water are reported to be 12.4, indicative of the severity case (Hoang et al., 2021). The author stated that the level of Cu concentration is recorded as the highest noncarcinogenic risk at the "adverse effect" level, whereas the level of Ni and Cr is found as the highest carcinogenic risk at an "unacceptable" level. The teratogenic effects of heavy metals such as U, Pb, Cd, and Hg may alter the expression of gene and proliferation of cell, thus leading to cancerous diseases (Table 1) (Ganesan, 2014).

Table 1 Rhizoremediation of heavy metals.

Sl. no.	Heavy metal	Rhizo-microbes	Plant	References
1.	Cd^{2+}	*Pseudomonas aeruginosa* MKRh3	*Vigna mungo*	Ganesan (2008)
2.	Cd	*Pseudomonad* strain MKRh3	Black gram	Ganesan (2008)
3.	Cu and Cd	*Serratia* sp. SY5	*Echinochloa crus-galli*	Koo and Cho (2009)
4.	Cr	*Mesorhizobium* strains RC1 and RC4	*Cicer arietinum*	Wani et al. (2009)
5.	Cr	*Bacillus* sp. PSB10	*Cicer arietinum*	Wani and Khan (2010)
6.	Zn, Cu, As, and Pd	*B. aryabhattai SMT50*, *Bacillus methylotrophicus SMT38*, *Bacillus licheniformis SMT51*, and *Bacillus aryabhattai SMT48*	*Spartina maritima*	Mesa et al. (2015)
7.	Cu	*Enterobacter* spp. and *Pseudomonas* spp.	Mung bean	Sharaff et al. (2017)
8.	Cr (VI) and Cd (II)	*Azotobacter* sp.	*Lepidium sativum*	Sobariu et al. (2017)
9.	Cu, Zn, Pd, and As	*Microbacterium* sp. CE3R2, *Microbacterium* sp. NM3E9, *Curtobacterium* sp. NM1R1, and *Microbacterium* sp. NE1R5	*Brassica nigra*	Roman-ponce et al. (2017)
10.	As	*Kocuria flava* and *Bacillus vietnamensis*	Rice	Mallick et al. (2018)
11.	Zn, Cu, Pb, and Cd	*Glomus macrocarpum*, *Paraglomus occultum*, and *Glomus* sp.	*Urochloa brizantha*, *Sorghum bicolor*, and *Acacia mangium*	de Fátima Pedroso et al. (2018)
12.	Cd	*Claroideoglomus etunicatum*	Sorghum	Babadi et al. (2019)
13.	Pb and Zn	Rhizobiales	*Miscanthus sinensis*	Sun et al. (2021)
14.	Cu (II) ions	*Pantoeadispersa*	*Sphaeranthus indicus*	Yaashikaa et al. (2020)
15.	Cd	*Bacillus paramycoides* and *Bacillus subtilis*	*Pennisetum purpureum*	Viji et al. (2022)
16.	Cd	*Bacillus wudalianchiensis*, *Bacillus drentensis*, *Bacillus amyloliquefaciens*, *Alcaligenes* sp., *Bacillus subtilis*, *Planococcus ruber*, and *Bacillus foraminis*	*Pennisetum pedicellatum*	Kumar and Fulekar (2022)
17.	Cd^{2+}, Pb^{2+} and Zn^{2+}	*Trichoderma harzianum* and *Bacillus subtilis biofilm*	Potato	Henagamage et al. (2022)
18.	Cu and Pb	*Novosphingobium* sp. CuT1	*Festucaarundinacea* L.	Lee and Lee (2022)

4 Source of heavy metal pollution

Major sources of heavy metal contamination in the environment are natural activities and anthropogenic activities. This natural activity includes volcanic eruptions, forest fires, leaching, withering, and erosion of parent rocks, whereby transferring large quantities of heavy metals to water bodies and land (Gadd, 2010). Examination of heavy metals in freshwater wetlands, brackish wetlands, and salt marshes observed that the highest mean values of heavy metals concentration in salt marsh with 11.03 mg/kg of As, 0.28 mg/kg of Cd, 43.68 mg/kg of Cr, 23.48 mg/kg of Cu, 538.15 mg/kg of Mn, 14.41 mg/kg of Pb, 58.5 mg/kg of Zn, and 2.67% of Fe in the top 50 cm soils (Zhao et al., 2021). Usman et al. (2020) reported that the highest concentration of Fe with 36,300 mg/kg in the Jijal complex and the lowest concentration of Cd with 1.07 mg/kg in the Kohistan batholith. Ecological risk index (ERI) values indicate a low risk (ERI <150).

While possible anthropogenic activities that contribute to heavy metal are mining, solid waste disposal, metal processing, smelting, fuel combustion, chemical production, solar cells, metal alloys, electroplating, electronic goods, factory emissions, domestic effluents, industrial effluents, Ni-Cd batteries, stabilizer in PVC, pigment in plastics, sewage irrigation, and synthetic fertilizers (Gadd, 2010; Yang et al., 2018; Alfaifi et al., 2021). For example, 40%–70% of heavy metal discharged into the environment is largely contributed by industrial activities like smelters in the Daye site and Zhuzhou site (Xu et al., 2021). Additionally, the Pb and As contents at the Daye site are higher than that of the Zhuzhou site, but Cu, Ni, and Cd contents are lower than at the Zhuzhou site. This has led to the accelerated discharge of heavy metal in the soil.

Assessing eight different roadside sites nearby Buddha Nullahin Ludhiana, India found that the maximum contents of heavy metals like Co, Cd, Cu, Zn, and Pb, which is above the permissible limit (Kaur et al., 2022). Across the five continents, the dominant factors for discharging heavy metals into river and lake water bodies from 1972 to 2017 differ variably rock weathering, fertilizer, and pesticide use in Africa; rock weathering, manufacturing, and mining in Europe and Asia; manufacturing, fertilizer, pesticide use, and mining in North America; and mining, waste discharge, fertilizer, rock weathering, pesticide use, and manufacturing in South America (Zhou et al., 2020). The average abundance of metal contamination in sediment heavy metals of the Netravati River basin is in the order of $Pb > Mn > Ni > Zn > Cr > Cu > Co$, whereby it could pose a great risk to aquatic biota (Gayathri et al., 2021).

5 Rhizoremediation

Rhizoremediation is a remediation technique that combined both rhizospheres of plants and their associated rhizosphere microbes by forming a mutual relationship to degrade pollutants in the environment (Saravanan et al., 2019). This technique is typically considered eco-friendly and cost-effective. While the microbes inhabiting this area provide the plant with protection, N_2 fixation, preserve the soil chemistry, regulate the biogeochemical cycles, and degrade organic materials (Ganesan, 2014). Here, in this process, the exudates secreted from the plant roots in the form of organic acids certain monosaccharides, sterols, and ions as necessary food stimulate the growth and activity of the microbial community in the rhizosphere; thereby leading to the effective degradation of pollutants. Kuiper et al. (2004) stated that bacterial or fungal activity in the rhizosphere degrades the organic or inorganic contaminants in soils. It also helps spread and permeate the rhizome microbes through the impermeable soil layers soil (Saravanan et al., 2019).

Some of the techniques that enhance remediation efficiency are bio-stimulation, bioaugmentation, and rhizoengineering (Shah, 2020). The bio-stimulation process is done by inducing the activity of the microorganisms with added fertilizer, minerals, and bio-surfactants in the rhizosphere. While bioaugmentation process of microorganisms' catabolic ability is carried out through the introduction of soil drenching, root dipping, and seed coating to increase the contaminants degradation in rhizosphere (Ganesan, 2014). The rhizoengineering process is the augmenting of transgenic plants to produce more root exudates and enhance the plant-microbial interaction, thereby resulting in effective contaminants removal from the soil (Arabi et al., 2021).

Rhizoremediation secretes root exudates such as phenolics, organic acid, and proteins that stimulate the functionality and viability of the plant growth-promoting rhizobacteria (PGPR) and led to more efficient degradation of environmental pollutants (Saravanan et al., 2019). Moreover, the biomass of microbes acting as a sink could prevent toxic heavy metals from uptake and accumulating in different parts of plants (Gadd, 2010). Whereas soil organic matter could influence the sorption processes of contaminants in the rhizosphere; thus controlling its movements in the soil profile (Saravanan et al., 2019). Other soil properties soil texture, pH, humidity, and soil temperature decide the way of interaction between the plant and microbes. Increase in soil temperature tends to reduce oxygen solubility and bioavailability, resulting in a slow and ineffective remediation process (Shah, 2020). Furthermore, the optimum soil pH is essential for the activity and growth of the microbes that stimulate the contaminant's biodegradation. High microbial population in the rhizosphere plays a major role effective degradation of contaminants than of a single strain alone (Fig. 1).

Interestingly, Zn tolerance rhizobacteria bacterial strains isolated from a Zn-polluted soil enhance the mycorrhizal and nodulation efficiency in plants, which relates to the stimulation of symbiotic structures (Vivas et al., 2006). Bio-inoculant like *Bacillus* species PSB10 not only reduces chromium toxicity but also promotes leghemoglobin, nodulation, growth, grain protein, chlorophyll, and seed yield of chickpea crop grown in chromium-contaminated sites (Wani and Khan, 2010). An increase in remediation efficiency is reported in heavy-metal-contaminated soil (Cu and Cd) using *Serratia* sp. SY5, isolated from the rhizoplane of barnyard grass (*Echinochloa crus-galli*) (Koo and Cho,

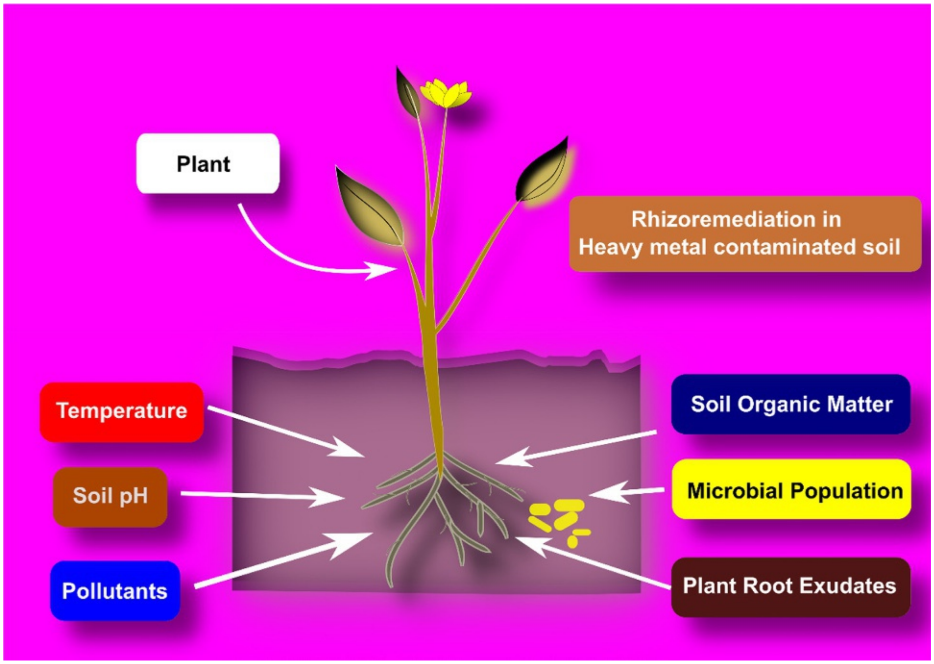

Fig. 1 Factor affecting rhizoremediation of heavy metal in soil involving plant-microbes relationship.

2009). Wani et al. (2009) demonstrated that *Mesorhizobium* strains RC1 and RC4 isolated from chickpea nodules are capable of reducing chromium by 84% and 83%, respectively, within 120 h of incubation at pH 7.

Due to the seed coating of *Pseudomonad aeruginosa* MKRh3, plants can be grown without cadmium toxicity and cadmium accumulation (Ganesan, 2008). Under in situ conditions, the biofilm of *Trichoderma harzianum* and *Bacillus subtilis* with 50% of recommended chemical fertilizers reduces the soil availability of Pb^{2+} by 77%, Cd^{2+} by 78%, and Zn^{2+} by 62% than that of 100% recommended chemical fertilizers (Henagamage et al., 2022). Lee and Lee (2022) underlined that the ability of *Ovosphingobium* sp. CuT1 to grow on 1/10 LB-agar plates containing 5 mM of Cu or 5 mM of Pb for rhizoremediation in heavy metal-contaminated soils. Another study reported the isolation of two As-resistant halophilic bacterial strains (*Kocuriaflava* AB402 and *Bacillus vietnamensis* AB403) from the mangrove rhizosphere of Sundarban that could easily tolerate 35 and 20 mM of arsenite, respectively, due to As adsorption on the cell surfaces and intracellular accumulation under hypersaline condition (Mallick et al., 2018). The author also stated the strains promoted both the growth of rice seedlings and decreased As uptake and accumulation in the plant because of the formation of static biofilm and production of extracellular polymeric compounds to colonizein rice roots.

The use of *P. aeruginosa* MKRh3 seed coating in protecting plants from growth inhibition owing to cadmium toxicity is documented in black gram, where the microbes prevent Cd uptake by immobilization and detoxification (Ganesan, 2008). It was observed that the sorghum inoculation of *Claroideoglomus etunicatum* induces plant tolerance to Cd contamination due to solubilize and transfer of it from the soil to rhizosphere (Babadi et al., 2019). Moreover, the amount of carbohydrates and glomalin in the soil rhizosphere is higher than that of bulk soils using rhizoboxes. Sun et al. (2021) found that the root-associated microbiome not only provides essential ecological services but also nutrient acquisition and pathogen resistance during plant growth. Inoculating *Brassica nigra* seeds with *Microbacterium* sp. NM3E9, *Microbacterium* sp. NE1R5, *Microbacterium* sp. CE3R2, and *Curtobacterium* sp. NM1R1 could facilitate root development and seed germination in the presence of 2.2 mmol/L of Zn (II) (Roman-ponce et al., 2017). Kumar and Fulekar (2022) found that *P. pedicellatum* could restore cadmium-contaminated effectively soil by 83% from the 100 ppm spiked soil after 60 days. Mesa et al. (2015) also suggested that the inoculation of *S. maritima* coupled with metal-resistant PGP rhizobacteria might increase the adaptation and growth of the plant in contaminated estuaries through the restoration program.

Study on Cu tolerant rhizobacterium *Enterobacter* sp. P36 from rhizosphere soil samples in mung bean plants found that Cu toxicity is reduced and promotes plant growth in $CuSO_4$-amended soils. This improves in the revegetation of agricultural soils polluted by Cu and restores the agroecosystem in the industrial zone of the Amlakhadi region, Gujarat, India (Sharaff et al., 2017). Although the growth of *Lepidium sativum* is affected by Cd (II) solutions compared to that of Cr (VI) due to its higher toxicity, the symbiosis relationship of *L. sativum* and *Azotobacter* sp. tends to provide a beneficial synergistic system by increased tolerance even at high heavy metal ions concentrations for bioremediation purpose (Sobariu et al., 2017). When *Pennisetum purpureum* plants are bioaugmented with the bacterial co-culture of *Bacillus paramycoides* and *Bacillus subtilis*, they can tolerate higher cadmium concentrations and bioaccumulation without hindering plant growth and effectively remediate the soil polluted with cadmium (Viji et al., 2022). AMF inoculation of plants contributes revegetation of heavy metal-contaminated soil due to litter formation and rhizospheric activity (de Fátima Pedroso et al., 2018). Investigation of copper-resistant bacteria found that *Sphaeranthus indicus* could result from the expansion of Cu (II) ion translocation factor acquired at the centralization of Cu (II) ion in the soil at 150 mg/L Cu (II) (Yaashikaa et al., 2020).

6 Removal mechanism

The three major mechanisms in rhizoremediation are the production of bio-surfactant, formation of biofilm, and production of organic acid for removing heavy metals from the environment (Saravanan et al., 2019). Apart from these mechanisms, other processes involved are respiration, redox reaction, exudation, chelation, precipitation, adsorption, complexation, transportation, acidification, and desorption. Bio-surfactants secreted by the microbes as extracellular compounds are amphiphilic in nature that degrade contaminants with the formation of micelle inside the rhizosphere (Kuiper et al., 2004). Secreting organic acids in the rhizosphere such as oxalic acid, gluconic acid, malic acid, citric acid, succinic acid, malonic acid, and lactic acid act as chelating agents and degrade the contaminants (Saravanan et al., 2019). The formation of biofilms by a community or aggregate of microorganisms at a specific area immobilizes and degrades contaminants in the rhizosphere (Segura et al., 2009). Lugtenberg and Kamilova (2009) also reported the formation of micro-colonies around the roots covered by a mucoid layer called biofilm that involves the use of mycorrhizae and rhizobacteria. It was also shown that the use of engineered rhizobacterium such as EC20-expressing *P. putida* 06909 inoculums to sunflower roots decreases cadmium phytotoxicity as well as increases 40% in cadmium accumulation (Wu et al., 2006).

7 Factors affecting

There are several factors affecting the rhizoremediation of heavy metals as follows:

1. Microbial population
2. Plant root exudates
3. Contaminants nature
4. Contaminant concentration
4. Soil organic matter
6. Energy sources
7. Soil properties and
8. Nutrient availability

Generally, plant root exudates consist of complex mixtures of soluble organic compounds such as enzymes, amino acids, sugars, and organic acids that possess the ability to attract microbial community; in turn, enhance plant growth and protect from contaminants (Saravanan et al., 2019). These organic acids in root exudates include malonic acid, malic acid, acetic acid, fumaric acid, oxalic acid, lactic acid, citric acid, and tartaric acid that could solubilize minerals present inside the rhizosphere (Kuiper et al., 2004). However, the developmental stage and species age of plants could affect the secretion rate, composition, and quality of the root exudates (Segura et al., 2009). The rhizoremediation process is dependent on the type, concentration, and solubility of pollutants in a rhizosphere (Saravanan et al., 2019). For microbial growth and development in the rhizosphere, root exudates, organic matter contents, and contaminants act as the source of energy and nutrient (Shah, 2020).

8 Conclusion

Rapid industrialization has led to increasing heavy metal contamination such as Zn, Ni, Cr, Pb, Cd, and Cu in soil and water environment. It is extremely toxic, nonbiodegradable, and accumulating nature properties. Many factors play an important role in the rhizoremediation process that includes concentration, types of heavy metals, availability of nutrients for rhizosphere microorganisms, soil properties, and types of plants and microorganisms, which affect the degradation and removal of heavy metals from the rhizosphere. However, this rhizoremediation approach offers cost-effective and eco-friendly options, where the microbes and plant rhizosphere interaction involve reducing the toxicity of heavy metals worldwide.

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CHAPTER 5

Maximizing soil carbon storage: Leveraging microbial factors and limitations for carbon remediation

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1 Soil-based carbon sequestration

Carbon sequestration and storage (CSS) refers to the "catching" of carbon from the atmosphere and safe, stable storage in other sink (Kowalska et al., 2020). It is considered that soil is a promising sink for C storage; however, many studies consider involving building industry for C storage (Arehart et al., 2021). Nevertheless, soil carbon sequestration is considered an easy and low-cost practice helping in the mitigation of climate change (Dynarski et al., 2020). It has been noticed that C is sequestered in the soil mainly as a soil organic carbon (SOC), and what else, it has been estimated that soil is able to sequester over 5% of total carbon (Zhang et al., 2018). Moreover, the SOC pool is crucial for climate since even the smallest changes in SOC may highly affect the climate changes at a global scale (Lan et al., 2021). The soil-based carbon sequestration allows for the lowering of the CO_2 concentration in the atmosphere and storage underground. This process is closely correlated with the photosynthetic activity of plants. At present, we are observing a huge interest in carbon sequestration worldwide, which is a response to the need of humanity to stabilize the greenhouse gases (GHGs) concentration in the atmosphere and further limit climate change (Sanaullah et al., 2019). Moreover, the capacity of the soil to capture and store carbon from the atmosphere not only plays a key role for climatic issue but also influences and determines soil functions (Wiesmeier et al., 2019). However, the capacity of soil to capture CO_2 and store it in deeper soil layers differs in the climatic zones and soil physical parameters.

There are many factors that drive soil-based carbon sequestration. Among climatic conditions, temperature and precipitation are considered the main drivers for carbon sequestration. Temperature highly affects the microbial activity in the soil and consequently determines SOC decomposition by microbes. It has been noticed that the SOC content in the soil falls down with an increase in temperature (Black et al., 2016). Moreover, Black et al. (2016) suggested that combined higher CO_2 and increased temperature elevate the losses in soil carbon in agricultural lands. On the other hand,

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Köhler et al. (2018) suggested that increased temperature may play an important role in safeguarding the nutritive features of crops in elevated CO_2 concentrations. In turn, precipitation determines the net primary production (NPP) and thus influences soil productivity. The amount of precipitation is essentially important for water-limited areas. Depending on the physical soil features, the lack of precipitation may limit soil carbon sequestration by reducing photosynthesis, but the excess precipitation may negatively affect the soil's capacity to store carbon by causing floods. However, the humid conditions in the soil are considered to be favorable for formation of SOC stabilizing mineralization. Therefore, humidity in the soil also affects the soil pH and, in most cases, influences on soil acidification that positively limits SOC decomposition. Therefore, the studies indicate that moist and cool areas are richer in SOC, while dry and warm areas are poorer in SOC. In this aspect, also topography plays an important role in SOC sequestration. It is so since topography regulates precipitation and water accumulation in the soil and thus indirectly may drive or limit soil-based carbon sequestration at local scale. Therefore, it has been noticed that the vegetation type and land use may highly contribute to the changes which are SOC stock. The different climatic zones and connected with it various flora control the input of SOC pool and its decomposition in the soil. However, the influence of vegetation on the distribution of SOC seems to be vertical. Therefore, this impact has been noticed mainly in a topsoil, while in the deeper soil layers, it is lesser noticeable (Hou et al., 2019). At a spatial scale, it has been observed that SOC pool is positively correlated with a plant diversity. Therefore, it is considered that in coniferous forests, SOC stock is much higher in comparison with other forest types which are correlated with high content of acidic litter in the ground. Beside vegetation, microbial community highly influences the soil C sequestration capacity. It is connected with decomposition processes in the soil and possible aspect of reduction of sequestered SOC. However, the microbial population and diversity are closely related with soil quality and climatic conditions including soil moisture, soil fertility, temperature, nutritional aspect as well (Frindte et al., 2019). The SOC stock in the soil may be boosted by microbial application, and this issue will be more describe along this chapter.

Soil-based carbon sequestration has a positively role in the ecosystem as besides lowering the CO_2 concentration in the atmosphere mitigating climate change, it contributes the soil protection against soil degradation. Therefore, an increase release of CO_2 from the soil has been noticed at the degraded areas. Thus, also in this aspect of lowering soil degradation, the soil-based carbon sequestration has an important role for public health and climatic policy. What else, soil-based carbon sequestration may help in the efforts of food production for increasing population in the world by enriching soil in organic carbon and thus improving its quality and productivity (Xu et al., 2021).

Storage of sequestered C in the soil strictly depends on the transformation of C compounds. Only formation of stable C forms may stabilize SOC sequestration. Aromatic compounds and alkyl-C fraction show a high half-life time and thus indicate a long persistence in the soil being nonsusceptible for microbial decomposition. These two C fractions are favorable for SOC sequestration purposes and mitigation of climate change. Aromatic compounds as well as alkyl-C fraction are considered to be stable in the soil even for centuries, while O-alkyl C and carbonyl C fractions show a high liability and resistance for the decomposition (Kowalska, 2021).

1.1 Climate changes affect carbon storage

Since soil-based carbon sequestration and its storage underground depend on the climatic conditions, the observing climate change highly influences on its efficiency. The main boosters of climate change and global warming are GHGs, while we are observing a still increasing their concentration in the atmosphere. The NOAA's Global Monitoring Lab estimated that the global concentration of only CO_2 in atmosphere is above 418.43 ppm in May 2022 (Fig. 1) reaching a record value (Global Monitoring Laboratory; Lindsey, 2022). Even the observed economic stagnation did not inhibit the growth of GHGs emission (Lindsey, 2022). The long-term modulations in temperature and weather pattern cause a huge concern worldwide in many ecological and society aspects.

The consequences of climate changes are still studied; however, we already know that increase in temperature (which is observed year by year) may seriously altereach ecosystems. As mentioned before, the soil-based C sequestration is less efficient along the temperature increase; thus, we can suggest that the SOC sequestration may be limited by a still growing tendency of temperature. It is predicted that the surface temperature my increase by up to 4.8°C up to 21 century. The rise of soil temperature under deeping

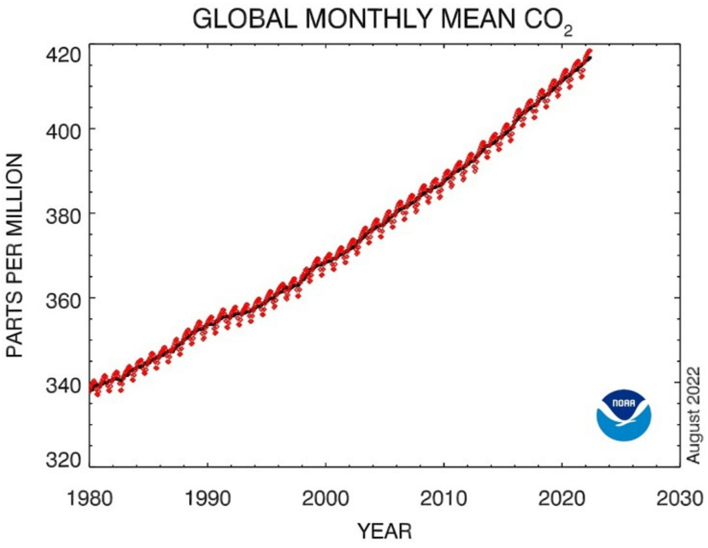

Fig. 1 Global monthly mean CO_2 in atmosphere since 1980 (NOAA, 2022).

climate change causes difficulties in controlling of soil quality, e.g., pH value. All alternations in soil characteristic even in a low scale may have a number of environmental consequences, including difficulties in monitoring and controlling plant, soil productivity, and consequently reduction of soil sequestration. The increasing soil temperature may accelerate microbial activity and thus force the decomposition processes. Therefore, Raza et al. (2021) suggested that soil inorganic carbon (SIC) depletion caused by increased soil acidification may jeopardize soil potential to mitigate climate change. It would be originated from the offset from the benefits of carbon sequestration and CO_2 emission caused by the processes of neutralization of soil acidity. Therefore, the increased periods of droughts often followed by more and more frequent floods do not stabilize SOC sequestration. The often changing soil properties and high alternations in soil moisture under a deeping climate change may seriously disturb the processes of stable carbon binding in the soil. Therefore, frequently altering weathers do not promote the stability of ecosystems, including plant developments. The disturbed ecosystem balance does not allow for a efficient productivity and consequently may limit soil-based carbon sequestration but also may promote a decomposition processes, or, in the worst perspective, lead to the soil erosion, and degradation deeping further climate change.

1.2 Reduction of CO_2 emissions through sustainable remediation

Soil degradation beside climate change causes more and more fears worldwide of mankind. Worldwide degraded areas take even 40% of lands what exacerbates the climate problem even more but also deeps the problem of hunger and poverty in the world (Kacprzak et al., 2022). It has been noticed that the effects of degraded soil are fall in fertility, yield reduction, deterioration of the crops quality, loss in biodiversity, and loss of agricultural land. Since each changes in natures forces appearing the next changes, the disturbances of the ecological balance lead to a catastrophe on many levels. Among various effects of soil degradation, the losses in biodiversity seem to have an serious impact. Why? Biodiversity is so important for the proper functioning of the whole ecosystem since greater diverse influence in the higher stability and resistance to changes. Each species have a specific function in nature, and its disappearance affects the loss of the balance of the ecosystem.

Remediation of degraded soils contributes to the enriching in the plant production which is promising for the removing of CO_2 from the atmosphere. It allows for the entering of atmosphericCO_2 into carbon flow in the ecosystem (Kadulin and Koptsik, 2019). Absorption of CO_2 by plants and its incorporation into plant biomass cause that concentration of CO_2 in atmosphere falls down. Thus, degradation of soil plays a crucial role in regulation of CO_2 uptake and release by vegetation but also in controlling of decomposition processes (Ma et al., 2018). It indicates that the restoration of natural ecosystems and soil repair is essentially important for climatic issues. Moreover, in a still increasing trends of CO_2 concentration of the soil, the soil remediation would be helpful due to the increased plant production. It has been observed that under higher CO_2 levels in the atmosphere that surround plants, they are able to "catch" more of CO_2 than in the lower CO_2 concentrations increasing a net gain of C in the soil (Cassia et al., 2018). Such phenomenon in itself demonstrates the necessity to use remediation techniques in the face of deteriorating climatic conditions. What else, global warming effects on the elongation of vegetation seasons what additionally would contribute to the increased CO_2 sequestration through the year (Kirschbaum and McMillan, 2018).

Impoverishment of soil functionality at degraded areas contributes to the higher soil respiration rates and increased emissions of CO_2 from the soil. It has been noticed that exacerbated degradation of grassland areas leads to the increased emissions of CO_2 in nongrowing seasons (Ma et al., 2018). Others showed in in vitro study that production of CO_2 at intact soil was consistently lower in comparison with its much higher production at heavily degraded areas along the forest in the tropical peatlands (van Lent et al., 2019).

Anthropogenic activity continuously changes the surrounding environment. The deforestation and forest degradation which is widely known especially in Amazon forests achieve a historical levels. It has been estimated that over 165 Gt of CO_2 emission comes from the deforestation in the time period of 2001–2020 (FAO, 2020). Therefore, the CO_2 emission at those are as highly contributes to the climatic problems. The soil restoration techniques, especially afforestation and reforestation, are considered as an effective remediation techniques that contribute to the mitigation of climate change (Zhang et al., 2019). However, it has been noticed that in the case of degraded tropical lands, the afforestation may recover soil C stock over few decades; however, it also may decrease soil carbon stability (Zhang et al., 2019). In turn, the case of restoration of productive wetlands in a quick perspective may become a net CO_2 sink supporting the fight against climate change (Valach et al., 2021). The soil degradation may come also from the industry. The open-cast mining is one of the most degrading branches of the industry. Therefore, the remediation of postmining areas generates a huge costs due to the large surface at open-cast mining. The implementation of thoughtful, prudent, and balanced remediation technology into the soil would repair to generate a multiple props (increased plant biomass, improved biodiversity, etc.), but also it can generate a good climatic feedback. For example, the remediation of postmining soil with compost from plant residues resulted, beside improved soil quality, in a lowest CO_2 emissions in contrast to unamended and natural sites (Soria et al., 2021). Moreover, Kadulin and Koptsik (2019) proposed that intensity of CO_2 emission by soils and the structure of its production could be implemented in monitoring the efficiency of remediation of barren lands.

2 Microbial contributions to carbon storage

Microbial community plays an important role in atmospheric-terrestrial carbon exchange. Thus, processes of SOC decomposition, transformation, and stabilization are of a high value in changing climate. Soil carbon is constantly changing in the soil, and properly functioning soil contributes to its higher stabilization which effects in lower CO_2 emissions to the air. A majority of carbon transformations are conducted with microorganisms living in the soil. It has been noticed that their absence negatively affect carbon sequestration. The importance of microbial organisms results from their activity which allows for the achieving of a sustainability via assuring soil health and proper carbon and nutrition exchange (Singh and Gupta, 2018). The soil with a higher microbial diversity shows a better self-regulation properties and thus a better capability to sustain the ecological processes which is resulted by a microbial buffering (Singh and Gupta, 2018).

The microbial role in soil carbon sequestration depends strongly on soil quality, quantity, and quality of soil microorganisms. The set of enzymes produced by the microbial biomass determines the directions of changes in carbon compounds in the soil (Ren et al., 2017). The microbial decomposition of SOC contributes to the soil respiration catalyzed by a C-degrading extracellular enzymes (EEs) (Qadeer et al., 2022). Moreover, it is suggested that microbial activity would be the most limiting agent in the soil for carbon sequestration purposes. Nevertheless, the processes of SOC decomposition resulted from microbial activity are strictly limited by a weather condition, soil aeration, and moisture (Zhang et al., 2022). It causes that the microbial activity will be constantly changing in response to changing climatic conditions. Especially, problematic may be an extended dry periods connected with a high soil salinity in irrigated areas. Such connection may result in the successive occurrence of the drought and high salinity leading to soil degradation (D'Odorico et al., 2019). It has been noticed that increased salinity results in the lower microbial activity and biomass; however, it influenced on the increased metabolic quotient (qCO_2). The reduction of salinity effect and improvement in plantation can lower a negative impact of CO_2 release into the atmosphere (Boyrahmadi and Raiesi, 2018).

The real projections of microbial contribution to the carbon storage in the soil have a dual structure (Fig. 2). The growing CO_2 concentration in the atmosphere may influence on the microorganisms in the soil which will more quickly decompose the organic matter driving release even more amounts of CO_2. It is not clear what will be the overall effect of climate change since different regions vary in a amounts of emitted and absorbed GHGs (Liu et al., 2022). Nevertheless, it generate a serious fear on the issue on stimulation of enzymatic activity of microorganisms in warming temperatures which would warm the climate even more in a self-winding spiral. The second projection assumes that in some European parts, the warming climate may accelerate the vegetation and microbial proliferation what will result in higher soil-based carbon sequestration and thus higher SOC stock in the soil (Yang et al., 2019). Thus, the scenarios in future perspective would be various, and it is considered that each changes will be site-specific for SOC sequestration (Fig. 3).

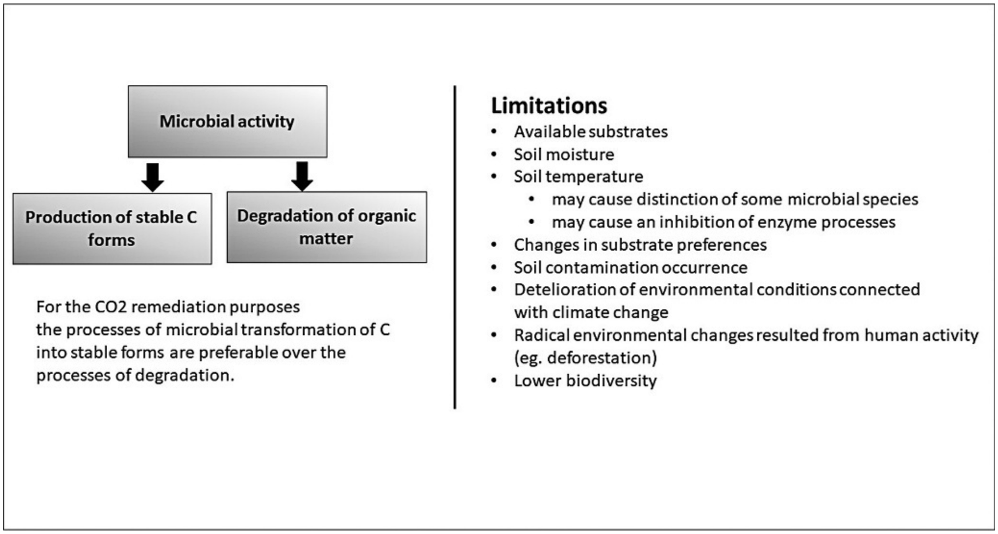

Fig. 2 Possible directions of microbial activity in the soil.

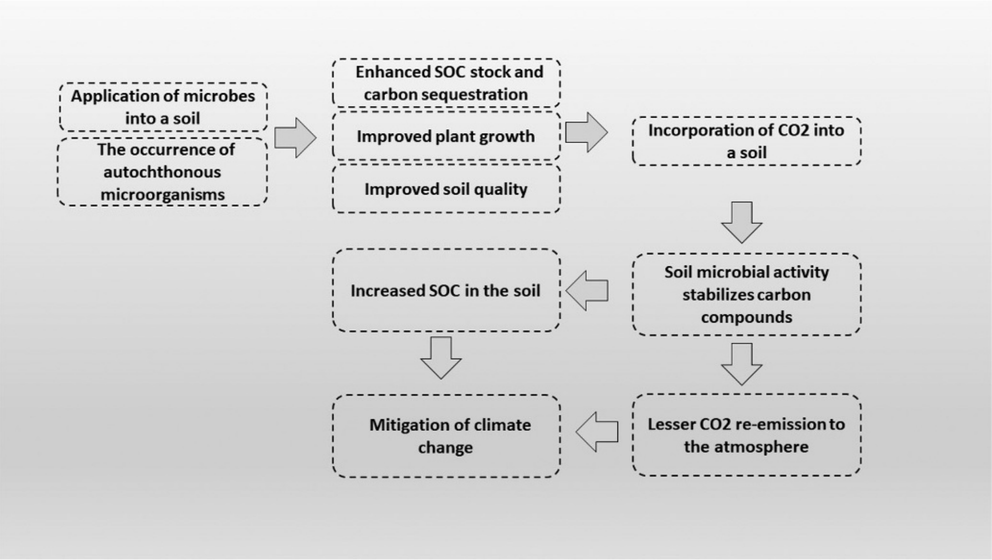

Fig. 3 Potential direction of microbial activity in CO_2 remediation.

2.1 Soil microbial diversity and carbon sequestration

Climate changes are supposed to influence on the lowering in biodiversity. Changing environmental condition may led to the distinction of many species which are more susceptible for temperature increases, etc. (Sintayehu, 2018). The limitation of microbial diversity in the soil may disturb a number of soil processes and thus reduce the stability of sequestered carbon. Yang et al. (2018) studied the possible association between the composition of soil bacterial community and soil carbon storage on the Loess Plateau. In turn, Prommer et al. (2020) indicated that increased microbial growth connected with it higher and richer microbial community positively influences on the stabilization of organic carbon and increases its accumulation in the soil.

Following the idea of improving the carbon sequestration capability in soil as a result of increasing microbial activity, a soil bioaugmentation would to be a successive technique in assisting mitigation climate changes (Fig. 4). The soil bioaugmentation refers to the introduction of living microorganisms (both, or separately bacteria and fungi) into the soil which may improve or even, in some cases, may initiate the soil microbial activity. Such modification is supposed to lower soil CO_2 release into the atmosphere by improved soil properties and higher soil production followed by acceleration of the formulation of stable C compounds in the soil. The bioaugmentation can be essentially necessary at the areas with a high soil depletion characterized with high CO_2 emissions. The application of living organisms, their proliferation, and development in the soil may highly contribute to the growing capability of the soil to carbon sequestration. What else,

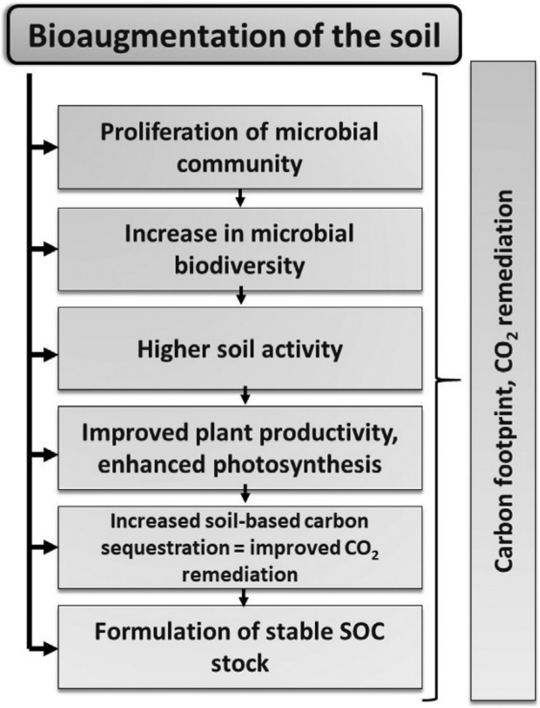

Fig. 4 Soil microbial input in SOC stabilization.

bioaugmentation with living microorganisms with specific functions may contribute to cleaning-up the soil as microorganisms have the ability to immobilize heavy metals (Zeng et al., 2020), degrade polycyclic aromatic hydrocarbons (PAHs) (Lu et al., 2019), remediate petroleum-contaminated soil (Yuniati, 2018), etc. For instance, actinobacteria have a potential to degrade pesticides and are nonsusceptible for negative influence of heavy metals which may be present in the soil (Mawang et al., 2021).

The bioaugmentation and its method depend on the initial soil quality but also on the type of soil contamination to be remediated (Fig. 5). Allochthonous bioaugmentation refers to the usage of a microbes from the another site. The selection of microorganisms to be introduced to a new environment is a bottleneck of each remediation technique. Such approach refers in majority of bioaugmentation applied to soil remediation at totally depleted areas. In turn, re-injection of microorganisms back to the soil which were initially isolated from this soil and multiplied in laboratory is called autochthonous bioaugmentation. This approach will enhance the rate of soil remediation and highly contribute to the improvement of soil quality and soil carbon sequestration. The example of this approach is bioaugmentation with autochthonous fungi in remediation of mining soil contaminated with total petroleum hydrocarbons (Hernández-Adame et al., 2021). It has been noticed that allochthonous bioaugmentation is more often used in comparison with autochthonous bioaugmentation (Nwankwegu et al., 2022). Therefore, the present advances molecular techniques allow for genetic modification of microbes what let to achieve high efficiency of soil remediation. Bioaugmentation with genetically engineered microorganisms (GEMs) is called gene bioaugmentation (Mawang et al., 2021). A genome of GEMs contains a desirable genes which allows to play a specific function in the soil. Such genetic inoculum has a mobile genes which after application into a soil are horizontally transferred and involved into the genome of autochthonic microorganisms enriching them in a new functions.

2.2 Formulation of microaggregates in the soil by microorganisms

It has been noticed that formulation of microaggregates in the soil essentially limits the decomposition losses. The formulation of microaggregates is limited by a numerous factors such as organic matter load, mechanical disturbances, soil moisture, and soil temperature. Nevertheless, some bacteria and arbuscular mycorrhizal fungi (AMF) considerably contribute to their formulation. Otherwise, the respiration with organic matter by microorganisms connected with the participation in carbon cycling and positive activity in formulation of aggregates would offset those CO_2 losses. Such phenomenon seems to preferably influence on the CO_2 remediation emphasizing an important role of microorganisms. Therefore, it has been noticed that glomalin-related soil proteins (GRSP) produced by AMF and some bacteria are essential for C fixation in the soil and consist the most essential source of SOC (Kumar et al., 2020). Therefore, it has been noted that

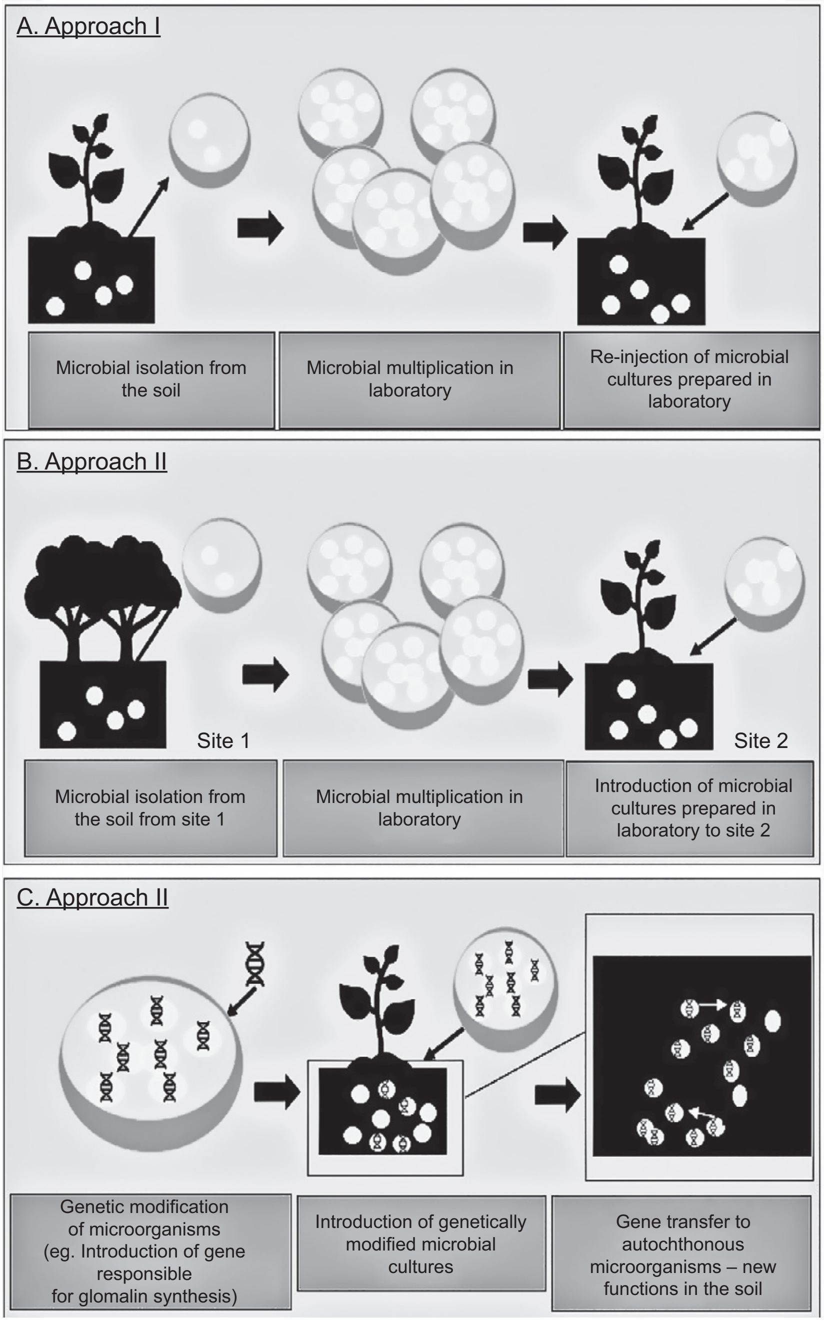

Fig. 5 Bioaugmentation methods: (A) autochthonous bioaugmentation; (B) allochthonous bioaugmentation; (C) gene bioaugmentation.

higher CO_2 concentration stimulates AMF proliferation with a positive influence on GRSP (Agnihotri et al., 2022).

The myccorhizal fungi's contribution to the formulation of microaggregates flows probably from the synthesis of specific proteins such as glomalin. Among fungi that synthesis of glomalin is *Acaulosporamorroaiae, Acaulosporalaevis, Glomus versiforme, Glomus verruculosum, Glomus luteum, Glomus mossae, Glomus intraradices*, and many others (Wang et al., 2020; He et al., 2020; Gao et al., 2019). This glycoprotein is a homolog of heat shock protein which influences on hydration and in the effect affects the accessibility of hydrolytic enzymes to bulk organic matter. Since a term "glomalin" refers only to the clear gene product; in the soil matter, it is defined as glomalin-related soil protein (GRSP). It has been proposed that GRSP positively affects the aggregates hydrophobicity and stability by their improvement (Mothay and Ramesh, 2021). The GRSP released into the soil is incorporated to the soil organic matter. The specific characteristic of GRSP enhances soil physical stability (Staunton et al., 2020). Moreover, GSPR has been proposed to be applicated as an indicator for soil physical stability, fungal activity, and turnover (Emran et al., 2020) but also for a good agricultural practice (Agnihotri et al., 2022). GRSP improves water retention, nutrient cycling, and enzyme activity and limits the soil erosion. It has been noticed that GRSP may also stimulate microorganisms to extracellular production of polysaccharides, which may positively increase and stabilize SOC (Agnihotri et al., 2022). GRSP, therefore, enhances soil porosity and contributes to the higher roots system productivity (Zbíral et al., 2017). Therefore, GRSP is consider that behind influence on soil organic matter, it may also be involved in sediment-associated heavy metal accumulation as GRSP has the ability to chelate heavy metal ions (Wang et al., 2019). It has been noticed that GRSP may sequestrate $0.24\,\mathrm{Mg\,Cha}^{-1}$ in soil, while its concentration in the soil is around $1.1 \pm 0.04\,\mathrm{mg\,g}^{-1}$ (Wang et al., 2018). Therefore, Wang et al. noticed that in this concentration of glomalin, AMF contributes $0.24\,\mathrm{Mg\,C\,ha}^{-1}$. By disregarding the role of GRSP in carbon sequestration and CO_2 remediation, the source of the appearance of these proteins in the soil has been questioned. At present, it is controversial to say that the AMF is responsible for GRSP (Cissé et al., 2020).

Beside GRSP, biosurfactants are considered to play an important role in carbon sequestration. Biosurfactants influence on the characteristic of adsorbed layers around bubbles or droplets. Hydrophobins are globular and cysteine-rich proteins secreted by fungi filamentous that shows a surface active features (Penfold and Thomas, 2019). They are produced by many fungi, for instance: *Sodiomyces alkalinus* (Kuvarina et al., 2022), *Penicillum islandicum* (Kulkarni et al., 2020), *Beauveria bassiana* (Moonjely et al., 2018), *Aspergillus nidulans, Trichoderma reseei* (Winandy et al., 2018), and *Trichoderma virens* (Taylor et al., 2021). Hydrophobins, similarly to GRSP, show the ability to formulate a microaggregates. Therefore, since hydrophobins contain both hydrophilic and hydrophobic amino acid residues, they show an amphiphilic features (Winandy et al., 2018). Hydrophobins may assemble at hydrophilic particle surface in the soil what gives them a hydrophobic ability. Such phenomenon would be desirable in dry periods, when the hydrophobic nature of hydrophobins can stabilize air channels in soil aggregates. This stabilization is connected with a preventing of capillary transport of water (Mathias et al., 2009). In turn, chaplins are a bacterial structural protein. Chaplins consist a hydrophobic cell-surface proteins (biosurfactant) produced by *Streptomyces coelicolor* (Tenconi et al., 2020), *Actinobacteria* (Rasul et al., 2022). Chaplins are believed to work as a hydrophobins in the soil. Although, they are supposed to be present in the soil in smaller aggregate scales (Dokouhaki et al., 2021).

Hydrophobin-related soil proteins (HRSP) as well as chaplins similarly to GRSP improve the aggregate stability. The aggregate formulation is believed to play a significant role in carbon sequestration and CO_2 remediation. It has been noticed that it is positively correlated with increase in SOC. Therefore, Nautiyal et al. (2019) indicated that this correlation improves soil prevention to erosion and causes a further increases soil aggregate formulation. However, it is still not clearly known what the interaction with soil organic matter turnover is. The efforts connected with identification of those interactions are deepen by an heterogenous soil medium and biodiversity of microorganisms in the soil. The lacks in the knowledge of the mechanisms and interactions between glomalins, hydrophobins, chaplins, and soil organic matter exclude to a proper identification and understanding of their impact on soil-based carbon sequestration and CO_2 remediation. Thus, it will be of a high value for a future CO_2 remediation management and climate change.

3 Plant-microbial linkages underpin carbon sequestration

Plants through a photosynthesis are crucial for soil-based carbon sequestration. A plant growth and productivity are a bottleneck for the effective CO_2 remediation. The booted plant development is believed to augment carbon sequestration. It has been previously noticed that microbes may positively influence on the plant growth (Kumar et al., 2020). There are many mechanisms of microorganisms-plant interactions either positive symbiotic and nonsymbiotic either negative (e.g., competition) (Liu et al., 2020). It has been reported that plant growth-promoting bacteria (PGPB) show an especially beneficial effect on soil and crop productivity (Ramakrishna et al., 2019). Thus, PGPB may be effectively used for remediation of marginal soil quality improving their properties and carbon storage (Ramakrishna et al., 2020). The mechanisms of plant growing promotion by PGPB are sought in facilitating the micro- and macronutrient uptake and modulating of plant enzymes, but also by induct abiotic plant cell tolerance, e.g., to salinity (del Carmen Orozco-Mosqueda et al., 2020) or drought (Ramakrishna et al., 2019). The production of organic acids or stimulation of proton pomp ATPase causes that soil pH is falling down, and in consequence, nutrients are better solubilized improving their availability to plant cells. Therefore, *Rhizobium* and *Bradyrhizobium* (N-fixing PGPB) are able to make the symbiosis with leguminous plants by creating of nodules on root. This symbiosis allows for the conversion of nitrogen to ammonia which leguminous plants use as a

N source (Ramakrishna et al., 2019). PGPB plays a biostimulating and biocontrolling functions as they are able to secret substances that inhibit growth of phytopathogens (Pellegrini et al., 2020) but also are consider as a biofertilizers and biopesticides (Riaz et al., 2021). It has been reported that *Psuedomonas fluorescens* belonging to PGPB improves C/N ratio under higher CO_2 (Zayed et al., 2020). Therefore, PGPB is considered to limit microbial respiration under elevated CO_2 which in turn may drive CO_2 remediation. Otherwise, there exist fear that increasing temperature may accelerate microbial degradation followed by higher CO_2 emissions and soil C losses (Wen et al., 2019). Wen et al. have already suggested that warming climate may accelerate C mineralization and SOC losses in drained peat soils. In turn, it has been reported that *Bacillus subtilis*, a well-known PGPB by a carbonic anhydrase (CA), may be effectively involved in C sequestration. The CA is considered to covert CO_2 into immobilized $CaCO_3$ (Maheshwari et al., 2019). PGPB may influence on the soil aggregates and carbon fixation in the soil by production of extracellular polymeric substance (EPS). However, the plant-microbial interactions for C fixation may be site-specific, and it has been noticed that some PGPB may drive plants to a higher CO_2 sequestration (Starr et al., 2021).

4 Conclusions

Soil microorganisms play a crucial role in soil organic matter transformations and belowground C-cycle. Their occurrence and activity consist an important agent that affects the soil-based C-storage. Soil microorganisms in direct and indirect way may influence on SOC stock. The production of specific substances contributes to the controlling of carbon storage. AMF and some bacteria by production of GRSP, HRSP, and chaplins improve the soil aggregate stability and indirectly accelerate CO_2 remediation. In turn, PGPB through improve plant growth, and in results, it enhances photosynthesis inducing higher SOC stock. The bioaugmentation would to be an efficient technique in boosting C storage in the soil. However, phytopathogens in the soil may significantly reduce plant yields and contribute to the reduction of carbon fixation. Therefore, an increased soil organic matter mineralization conducted by microorganisms may highly limit SOC storage and increase CO_2 re-emission to the atmosphere. Microbial contribution to the soil may be seriously affected by progressing climate change. The lowering biodiversity, enzymatic inhibitions, and changes in substrate preference pose a threat to the efficient storage of C in the soil.

Acknowledgments

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CHAPTER 6

Omics-based bioengineering: Emerging strategies for sustainable agriculture development and future perspectives

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Abbreviations

2D-GE	two-dimensional gel electrophoresis
BCA	bio control agent
cDNA	complementary DNA
CRISPR/Cas 9 &13	clustered regularly interspaced short palindromic repeats? CRISPR associated protein 9 & 13
DNA	deoxynucleic acid
EU	European Union
GC-MS	gas chromatography mass spectrometry
GMO	genetically modified
GUI	graphical user interface
HTP	high through put
IRGSP	International Rice Genome Sequencing Project
LC-MS	liquid chromatography mass spectrometry
LC-MS	liquid chromatography-mass spectrometry
MAS	marker assisted selection
miRNA	micro RNA
mRNA	messenger RNA
NGS	next generation sequencing
ORF	open reading frame
PCA	Plant Cell Atlas
PCR	polymerase chain reaction
PGPR	plant growth promoting rhizobacteria
PTM	posttranslational modifications
QTL	quantitative trait locus
RGB	R Genome Browser
RNA	ribonucleic acid
SAGE	serial analysis of gene expression
SDS-PAGE	sodium dodecyl sulfate-polyacrylamide gel electrophoresis
SWATH/ DIA-MS	sequential window acquisition of all theoretical mass spectra
WGS	whole genome shotgun
YAC	yeast artificial chromosome

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Units

Da	Dalton
Mb	megabytes

1 Introduction

Human beings depend on agriculture for food, fiber, fuel, and other commodities. Civilizations flourished around fertile land and sources of water (Gomiero, 2016). Farmers proved to be the most consequential link between civilization and the natural world. As cultures progressed and populations increased, the need for advancement in agricultural techniques became more apparent. This led to the upgrade of farming tools such as sickle and harrow to more efficient and large-scale ploughs. Eventually, large farm machinery such as tractors and field cultivators was adopted to manage the scale of demand. Even if agriculture industry had many machineries and manpower, still food production has not flourished. The major reasons that affected crop production are the overuse and consequent depletion of natural resources due to over population, crop loss due to climatic change, and the resultant biotic stress to crop varieties due to pest attack and plant disease. The new advancement in agriculture was the Green Revolution that made India, self-sufficient in food grains along with the creation of new pesticides, insecticides, fertilizers, extra nutrient supplements, weedicides, etc. But this revolution affected Indian population badly as it caused environmental pollution, soil erosion, genetic disorders, mutations, pest resistance, deadly diseases, and also significant decline in soil health (Herdt, 2006). The influence of biotechnology modified the genetic makeup of plants and animals that have high demand on market. Techniques of genetic engineering and tissue culture presented larger yield and optimized the nutritional value of products. The embryo rescue and somatic hybridization much helped the farmers as the whole plant/organism raised from a single embryo or tissue. The journey of advancement in agriculture continued through the invention of biotechniques such as marker-aided genetic analysis and marker-aided selection for specific gene identification and its tracing through generations. The recent era now being focused on to omics technology in the field of crop breeding and crop improvement (Herdt, 2006). Owing to word "omics," it simply means "the study of" such as "Genomics" means "the study of genome" so the field of specific study is added in front of the respective omics technology (Keusch, 2006). The different branches include genomics, proteomics, transcriptomics, metabolomics, phenomics, ionomics, and fluxomics (Yuan et al., 2008). Sometimes, the researchers handle this technology in an integrated way so that creative and promising revolutions occurred and being occurring in the selected area of research. This chapter discusses the major omics technologies, its advancement, and future development that prospects the sustainability in the field of agriculture (Fig. 1).

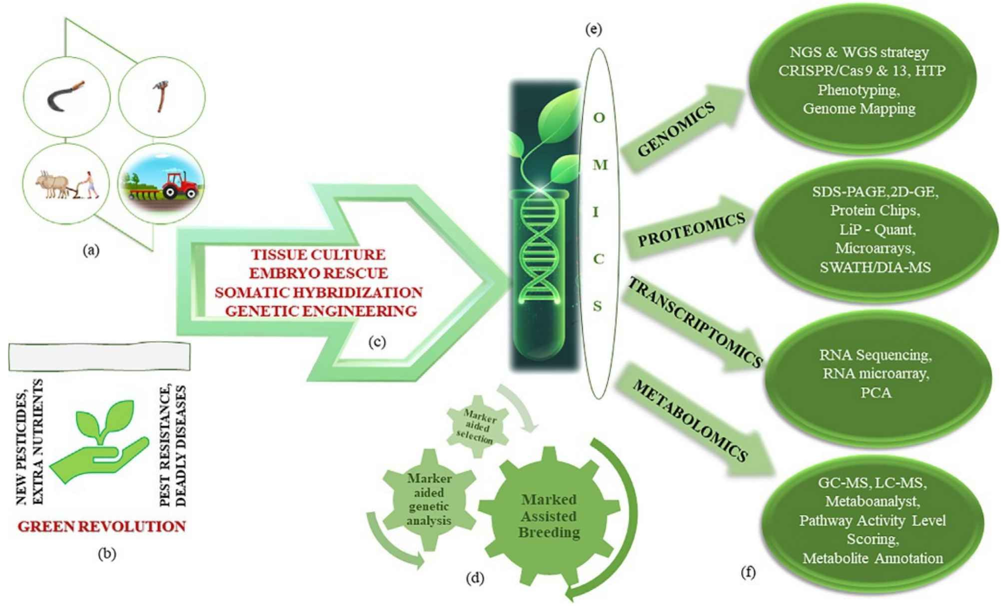

Fig. 1 Schematic representation showing the progression of agricultural techniques from traditional to modern era. (a) The traditional methods of farming which lead to (b) Green Revolution. Following that (c) new biotechnological techniques enriched the crop quality. (d) MAS techniques along with (e) omics technology opened new phase of crop improvement at the molecular level (f) showed the interaction of four omics branches along with recent advancements for sustainable agriculture.

2 Sustainable agriculture and its prospects

Climate change, high rate of biodiversity loss, soil degradation, pollution, resource depletion, rising production costs, and industrialization are just few issues that pose a threat to ability of agriculture to meet needs of society. How will agriculture be sustainable is a recent question to be asked by the people as everyone is directly or indirectly dependant on agricultural prosperity. Agriculture maintains ecological balance between humankind and environment by providing raw materials, food, fresh air, profit, etc. Traditional farming included inorganic resource utility. But it has caused slow degradation of available resources and caused adverse residual effect. Unsafe agricultural practices and economically unviable condition led to low profitability. It paved the way for organic farming which depends fully on organic sources with healthier and eco-friendly approaches. But the production rate reduced due to resistant pest attack, long term duration, increased market value of raw materials, etc. To increase the productivity of economical plants, modern biotechnological techniques, bioinformatics, omics approaches, sequencing techniques, etc., are applied for tracing out the candidate genes and mutation associated with specific traits in agricultural crops. Even the plant microbe interactions are used to shape new methods of crop protection like commercial microbial fertilizer or biopesticides using biocontrol agent (BCA) and plant growth-promoting rhizobacteria (PGPR) for disease control technology (Montesinos et al., 2002). In the field of plant improvement and better environment management, the plant genomics, transcriptomics, metabolomics, and proteomics data are needed. For that data mining research, visualization, efficient data storage mechanism, and algorithms are the major challenges faced. For dealing this problem, the emerging branches of bioinformatics and computational biology helped much as they handle large biological data and the results of different scientific studies with their practical application. Both are interrelated branches that can bring a variety of applications in the field of crop improvement.

3 Major branches in omics technology

3.1 Genomics

Genome is the total genetic composition of an organism, and its molecular analysis is called as genomics. Simply, genomics is the study of genome. This omics study helps to find out all gene location with respect to the ORF and spatial relation, its functions, and expression profiles and also can establish evolutionary relationship between different organisms. While considering plants, high phenotypic diversity prevails from thallophytes to monocots and dicots due to the size, content, and structure of nuclear genome. Owing to the history of plant genomics, one-gene-one phenotype was considered firstly. After that researchers are tried to consider many genes that contribute specific phenotype. Now, we are considering network of genes that controls complex phenotypes and also their evolutionary significance, lineages, etc. (Borevitz and Ecker, 2004). Due to the compactness, the first plant genome sequence was done with *Arabidopsis thaliana* (130Mb) by BAC-based approach. Certain chromosome inversions, ploidy, translocations, gene duplications, etc., have been studied at that time. After that genome sequencing was done with rice variety Nipponbare in connection with IRGSP using a clone-by-clone shotgun strategy and a physical map of rice genome created using YAC. Many annotations and databases emerged include miropeats for tandem repeat prediction and integrated rice genome explorer for integrating map and sequence information (Sasaki and Burr, 2000). Following this maize, sorghum genomes were sequenced, and it led to the marking of wide acceptance of molecular genetics. The whole genome shotgun (WGS) strategy yielded a fragmented genome assembly of black cotton wood *Populas tricocarpa* (Bolger et al., 2014). The sequencing of the grape vine genome is enabled to find out grape development, genetic factors affecting its quality, and best genotypes (Velasco et al., 2007). The genome sequencing is paved a way for the broad vision of functional genomics. The gene expression analysis is applied in the study of plant responses (abiotic stress tolerance) with the help of different techniques like cDNA-AFLP, SAGE, microarrays, real-time PCR, etc., in order to increase crop tolerance to stress (Pérez-Torres et al., 2018). Marker identification and marker-assisted selection (MAS) are used for the indirect selection of marker gene of a desired trait. Markers include morphological, cytological, and DNA-based markers, and among this, DNA-based markers found easy and fast detection with least pleiotropic effect and thus enable the manual selection of individuals for further propagation. Numerous markers mapped the desired gene by QTL analysis and thus helped to link the complex phenotypes to specific regions of chromosomes. This can estimate the effect and location of genetic elements that control any trait like high crop yield, disease and stress resistance, efficient nutrient uptake, etc. The plant breeding techniques started with cross breeding and mutation breeding. The backcross requirement in both techniques made it time wasting so that plant breeders look for transgenic approach. As foreign DNA is randomly got integrated to plant genome, it is easy to introduce many traits from different organisms. But its commercialization required high cost and so plant breeders again look forward to another technique which is much cost effective and free from backcrossing. Thus, breeding by genome editing paved the way for a modern era of cost-effective breeding technique (Gao, 2021) as it can improve crop varieties with addition of desirable traits along with deletion of unwanted by reducing the input costs.

3.1.1 Advancements and future development in genomics

The user-friendly GUI databases are being developed to obtain appropriate information of particular plant species. Some of the examples are PlantTribes2.0, TropGENE-DB, FlagDB database, CATMA database, PlantGDB, WAICENT, ILDIS, PaDIL, tfGDR, etc. The complete plant genome availability of biofuel feedstock breeding, insect resistance from *Bacillus thuringiensis*, nutrient gene transfer, drought resistance, etc., is made possible by using agricultural bioinformatics by utilizing these databases (Agarwal and Narayan, 2015).

The automated phenotyping platforms are emerged trying to link the genomic resources with phenotypes using HTP approaches. This allows to measure multiple phenotypes related to growth, stress, etc. A study on two pea varieties conducted to examine the cold response strategy by analyzing photosystem 2 and shoot biomass, thus provided a good tool for selection of parameters. By this study, they developed a new software for automated RGB imaging and validated the results (Humplík et al., 2015).

Tools, like Homologous Recombinitin (HR), Zinc Finger Nucleases (ZFN), TALEN, PRP, etc., are site directed nucleases with which genome editing begun. Thereafter CRISPR/Cas 9 system, Cisgenesis, RNAi, mutagenesis, etc., CRISPR is an excellent alternative to these site-directed nucleases. The crop using site directed nucleases takes around 10 years to develop resistance, whereas by CRISPR/Cas, it take short duration and will yield stress free crops. Using this technique, researchers demonstrated genetic resistance to parasitic weeds in tomato and edited CCD8 gene that negatively affected tomato morphology (Bari et al., 2019). Using CRISPR/Cas, base editing can be done which is a valuable tool in agriculture as they are not responsible for much genetic diversity. Adenine base editors along with cytosine base editors made the conversion of single nucleotide easily and effectively (Kim, 2018).

The study on improvement of warm season grasses was carried out by somatic embryogenesis which rely scope on the plant regeneration, mass production, genetic transformation, etc. As the somatic cells are dedifferentiating to new totipotent stem cells, a whole plant can be generated from this technique (Muguerza et al., 2022).

In vitro plant regeneration and callus induction were performed in a grass species called *Cenchrus ciliaris* L. through somatic embryogenesis and shoot organogenesis using three explants and four genotypes. The regenerated plant from mature seed and shoot apex derived callus along with growth supplements reported in this study can be used for *Agrobacterium* mediated transformation (AMT) using the same grass species as a future perspective (Shashi and Bhat, 2021). Even if AMT has great significance in plant transformation, it has some drawback due to the plant innate defense mechanisms. To overcome the plant defense, a new strategy developed by expressing a type III secretion system (T3SS) from *Pseudomonas syringae* strain and thus delivering its effectors AvrPto, AvrPtoB, or HopAO1. The study also suggests that histone H2A-1 plant protein is delivered by T3SS expressing *A. tumifaciens* (Raman et al., 2022).

In the advanced field of crop improvement, the resequencing of crops and finding the homology indicate the great contribution of bioinformatics. The role of genetic effects in structural variations was studied owing to the genotype to phenotype relationships in cotton variety and developed two genomes and annotations of *G. hirsutum* (NDM8) and *G. barbadense* (Pima90) of high quality. Resequencing of *G. hirsutum* accessions showed large-scale variations in A-subgenome and D-subgenome during breeding suggesting a way to cotton crop improvement (Ma et al., 2021).

3.2 Proteomics

The genomic era had witnessed many advances in particular whole functional genome studies. The postgenomic era gave rise to a new technology called proteomics, which elucidated the complete protein study. Proteins carryout most of the functions within a cell. They are synthesized during translational process and will provide valuable information of biological processes. In a cell, total protein set refers to proteome and is highly dynamic in nature due to the influence of environmental stimulus. This study can be applied in the field of agriculture to understand the nutritional value and the yield and to know how different factors have been affected by stress (Salekdeh and Komatsu, 2007). The structural proteomics mainly concentrates on structure of proteins and its applications in the field of organelle composition, subproteome isolation, and protein complexes. Owing to functional proteomics, the stability and functional integrity of protein molecules are much concentrated and are applied in the areas like yeast genomics, affinity, mouse knockouts, etc. Protein expression profiling normally done to identify the protein in an organism specifically at the time of stimulus response. This technique can be applied to study disease mechanisms, signal transduction pathways for pathway analysis, and even in medical microbiology, forensics, etc. Protein network map can be constructed to understand the interactions of different proteins in a living system. Some proteome maps of several crops like rice, barley, maize, soyabean, etc., were constructed using 2-DE and thus detected several proteins and related metabolism (Salekdeh and Komatsu, 2007). Abiotic stress proteome analysis was also an advancement in the field of crop management. Several studies were conducted in different stresses of salt, drought, cold, heat, etc., and identified the specific expression of responsive proteins and their regulation. PTM analysis can be performed by this omics field as the genomics cannot give any data on posttranslational modifications. It includes phosphorylation, glycosylation, proteolysis, methylation, etc., that can change the protein activity and thereby respond differently to different stresses. Protein-protein interactions called as interactomics can be explored as it provides valuable information on stress signal transduction and various cell responses. The powerful tools used in the interactomics include yeast two hybrid, co-precipitation, phage display, etc. (Salekdeh and Komatsu, 2007).

Proteome mining is being done for drug discovery, target identification, differential display, etc., and high throughput proteome analysis of crops provides wide scope on identification of active candidates against pest and stress tolerances.

3.2.1 Advancements and future development in proteomics

In the field of proteome mining, proteomics screening assays help the cultivators to select high quality breeding lines and can discard the wrong ones. In a study on wheat flour, thousands of wheat genotypes are screened using LC-MS quantitative shotgun method. To detect the expected storage protein and associated enzymes, powerful data mining tools available online can be utilized. Thus, we can integrate the proteomics study along with bioinformatics using tools like KEGG, UniProtKB, AgriGO, REVIGO, and pathway tools (Vincent et al., 2022).

In the recent study on structural proteomics in pea aphid, comparative proteomic analysis of four aphid cuticular structures (stylets, antennae, wings, and legs) for the receptor identification on viruses within the aphid vector was carried out and identified plant virus receptor candidates by comparative CP profiling, surface proteome composition, phylogeny, and stylus expression profiles. The surface cuticle specificities, chemoreception, sensory system, etc., are contributed by this study (Deshoux et al., 2020).

In the interactomics study on *Oryza sativa*, grain size regulators involved in various signaling pathways have been identified. The interactions between certain proteins and BR signaling pathways are explored. The qGL3-dependent network is constructed to lay a foundation to check how the BR signaling affects the grain size and length (Gao et al., 2022).

Cataloging proteins using omics technology is a great achievement as there was lack of knowledge regarding the cellular and physiological functions of different proteins in eukaryotic cells. Ubiquitin is an important protein present in all eukaryotic cells which helps in the transportation, synthesis of other proteins, and destruction of defective proteins. Ubiquitin itself forms the ubiquitin chain types with Lys residues called K63 polyubiquitin. In a study, this K63 ubiquitination is used to identify many proteins and ubiquitin conjugating enzymes (E2s). By sensor-based proteomics, K63 polyubiquitination networks in plant cells and its roles in plant functioning are revealed (Romero-Barrios et al., 2020).

The branch proteomics studied the salinity tolerance of wheat and maize, salt responsive proteins, and defense biomarkers. For salt tolerance, there should be protective cell structure during salt stresses. Ethylene activates ribosomal proteins in wheat and revealed differentially expressed proteins (DEP) in roots and shoots. Also differently accumulated proteins (DAP) that are associated with different metabolisms are categorized in chloroplast of wheat seedling leaves. Thus, it will be an efficient tool of selection instead of phenotype-based selection (Kumar et al., 2022).

The systematic mapping of target proteins and metabolites from different plant sources was being done, and their physical interactions are detected by ligand-detected NMR and tandem affinity purification (TAP). SWATH/DIA-MS approach is used for proteome quantification recently done in Arabidopsis and detected different protein groups (Venegas-Molina et al., 2021). LiP-Quant approach is used to deal with complex data, and new algorithms are being discovered with the help of machine learning. Thus, this technology can identify the targets of novel candidates of research interest (Piazza et al., 2020).

3.3 Transcriptomics

The advent of technologies such as microarray and bulk RNA-sequencing has provided a better understanding of transcriptional regulation of gene expression, in both animals as well as plants (Giacomello, 2021). The process of transcription in plants is similar to the process of transcription in humans. For a protein to be expressed, it is vital that transcription process occurs. The plant genome contains the genetic code for 36,795 proteins, from which RNA transcripts are expressed during transcription. In short, transcripts are the RNA copies of the genes. Hence, transcriptomes are considered as the lower-level organization of plants, as they correlate more to the genome than to the phenotype (Fig. 2). The branch of omics that is concerned with RNA transcripts is known as transcriptomics (Giacomello, 2021). Transcriptomics can be used to find biomarkers and understand the mutational changes that occur at the cellular level.

3.3.1 Advancements and future development in transcriptomics

The potential of transcriptomics is yet to be fully explored, as currently, there is a limitation caused by the unavailability of independent plant transcriptomic

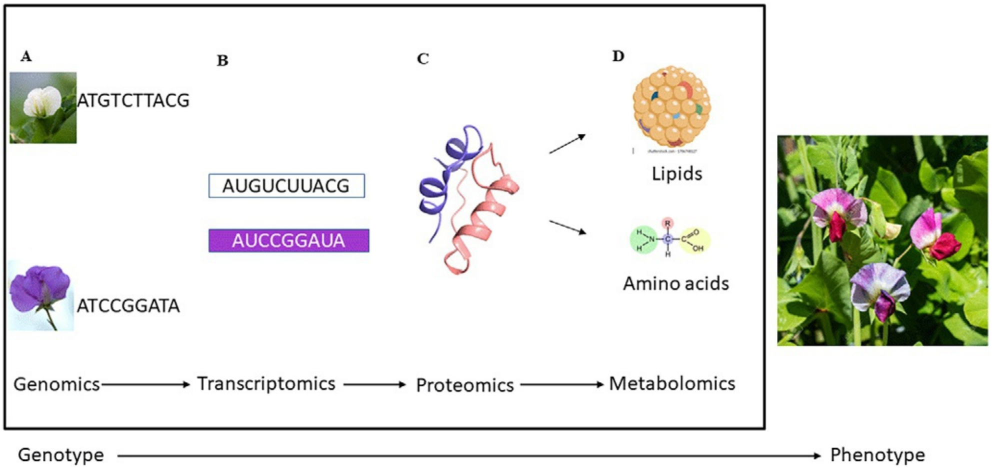

Fig. 2 Illustration showing a comparative timeline of (A) genomics, (B) transcriptomics, (C) proteomics, and (D) metabolomics, with the central dogma. The illustration also shows the proximity of each omics with genotype and the phenotype.

databases. However, in 2019, the Plant Cell Atlas was established, with the aim of comprehensively describing the state of various plant cell types and to integrate the high-resolution multiomics information (Giacomello, 2021). In a lot of cases, transcriptomics has been used along with other omics as well (Majumdar and Keller, 2021).

Over the period of past 5 years, there has been a lot of significant contributions through transcriptomics. One such example is where the effect of different agricultural products, such as corn stover and rice straw, on the liver of dairy cows was studied using the multiomics approach involving transcriptomics and metabolomics (Sun et al., 2018).

Transcriptomics analysis in sea buckthorn has been able to identify candidate genes that can be used to engineer plants that show resistance to drought stress (Ye et al., 2018). The scope is not just limited to environmental stresses but also in increasing the yield of specific crops and vegetables. Studies conducted on cucumber cell line "6547" have provided insight about the regulatory mechanism behind corolla opening in cucumber. In this study, the transcriptome, both mRNA and miRNA, was analyzed at the corolla development stage of both super and normal ovaries. From the four developmental stages, the maximum number of differentially expressed miRNAs were identified at the yellow bud stage. In cucumber super ovary, three miRNAs were found to be responsible for corolla opening: miRNA_157-CsCuRX, miRNA_411-CsGH3.6, and miRNA_161/297/257-CsHD-Zip.This provided more knowledge on how to improve the quality of the flowering plants and to produce fruits of high commodity value (Song et al., 2022). The endophytic bacteria, *Bacillus aryabhattai,* have shown to influence growth in the *Arabidopsis* and *Nicotiana tabacum* species through its interaction with the plants. This has been established through analysis on these specimens using RNA-seq. During the interaction, transcriptomics analysis identified about 363 differentially expressed transcripts, in which 268 were upregulated, and 95 differentially expressed transcripts were downregulated. The highly differentiated transcript was identified as cinnamyl alcohol dehydrogenase, while zinc finger type family protein C-x8-C-x5-C-x3-H was the most repressed transcript (Xu et al., 2022). Ever since transcriptomics has been in place, a lot of improvements have been made with respect to the crop quality and agricultural productivity. One such pairwise study on two different rice varieties identified the differentially expressed genes under different conditions of low nitrogen, full nitrogen, and 1 h after the transfer from low nitrogen condition to full nitrogen condition. Effective uptake of nitrogen by the *Pokkali indica* rice variety over *Bengal japonica* rice variety under low N conditions was proved through transcriptomics analysis (Subudhi et al., 2020). Most of the crop losses all over the world happen due to biotic stress. The usual strategy taken in that situation is to improve the host plant defense against the biotic stressors. Such approach will ensure that crop yield losses are prevented, and there would be sustainable food production. Transcriptomics has helped understand the stress tolerance in model and nonmodel crops (Malathi et al., 2022).

The takeaway message is that transcriptomics has significantly improved the level of understanding about the biochemical mechanisms that occur in different organisms. These findings have then helped design strategies to improve crop yield and build resistance against pests and diseases, improving the production volume and quality of agricultural by-products and design sustainable agricultural practices.

3.4 Metabolomics

Metabolites are small molecules that weigh less than 1200 Da and are expressed within the system, which mean the specific plant, in this context. The metabolites are much closer to the phenotype when it comes to the organization level in plants (Fig. 2). The study which deals with the understanding of the metabolites expressed under any given condition is known as metabolomics. When it comes to plants, metabolomics has been able to uncover the metabolism changes that happens during development, in response to biotic and abiotic stimuli (Castro-Moretti et al., 2020). Metabolomics approach is broadly classified into two types, namely targeted metabolomics and nontargeted metabolomics. Targeted metabolomics uses a finite list of compounds for the analysis, whereas nontargeted metabolomics uncovers the undefined and unknown compounds. Large qualitative data sets can be generated from volatilized samples using the gas chromatography-mass spectrometry technique, while small quantitative data sets, that do not need much processing, can be generated using the liquid chromatography-tandem mass spectrometry technique (Castro-Moretti et al., 2020).

3.4.1 Advancements and future development in metabolomics

Over the past 20 years, metabolomics has emerged as a field with lot of potential, as research labs all over the world spent time generating metabolite profiles. Nuclear magnetic resonance (NMR) has been widely used in unearthing the metabolites from the specimens. The large-scale generation of metabolites further enriched the metabolite pathway databases such as NIEST, KEGG, and GOLM. Over time, newer techniques came into existence, such as the advent of the free Web-tool MetaboAnalyst, and the offline software, named METLIN. Few tools that help with metabolome data preprocessing include Met-Align, MET-COFEA, ChromaTOF, and MET-XAlign (Sharma et al., 2021).

According to recent studies, food scarcity is on the rise, due to the increase in global population. By 2050, humans are expected to be 10 billion in total, on the planet. On one side, we see an increase in the abiotic stresses, caused by anthropogenic activities that include mining, industrial land and water pollution, and burning of fossil fuels. On the other hand, biotic stresses are also on the rise, due to the emergence of mutated and highly-resistant virulent pathogens that affect plants. Plant metabolomics was used to study the time dependent metabolic changes in response to *Phytophthora capsica* infection (Mashabela et al., 2022). Few studies uncovered the genes and metabolites in *Brassica napus*, expressed under stress caused by soil salinity, giving a clearer view of the mechanism behind salt stress (Wang et al., 2022). Plant growth regulation and quality improvement are other aspects where metabolomics has fared well. The effect of laxogenin C on seed germination and seedling growth of tomato was explored through metabolite studies (Deng et al., 2022). Plant root metabolites help in understanding the relationship between the plant and the microbes, thus opening the possibility of altering the root microbiota through metabolite-mediated alteration. The alteration would help in designing and cultivating plants that are resistant to environmental stress. However, with respect to metabolomics, the limitations might arise while trying to overcome the endogenous regulation of metabolites (Hong et al., 2022). Nevertheless, metabolomics has offered insightful workflows to understand nutrient use efficiency for nitrogen uptake, so that plant engineering can yield crops with high yield (Elrys et al., 2022). A lot of in silico approaches are available for metabolomic studies. For example, based on grouped metabolites, pathway activity level scoring is used to predict the pathway activity levels. Tools such as network annotation propagation (NAP), SIRIUS, NetID, and MolNetEnhancer are used to annotate the unknown metabolites that come from mass spectral networks. There are few challenges caused by large functional and chemical diversity of specialized metabolites, technical errors, presence of isomers, etc. Also, it can be agreed that a complete database of all the metabolites present in each plant is not present. There is also the limitation posed by the lack of all the relevant compounds because the existing relevant compounds belong to small spectrum of plant diversity (Singh et al., 2022). This should not pose a threat to the scope of metabolomics as there are still of lot of studies waiting to be done. The takeaway is that metabolomics provides a lot more information than any other omics, as it is directly translating to the phenotype, and the scope is at a high level (Fig. 3).

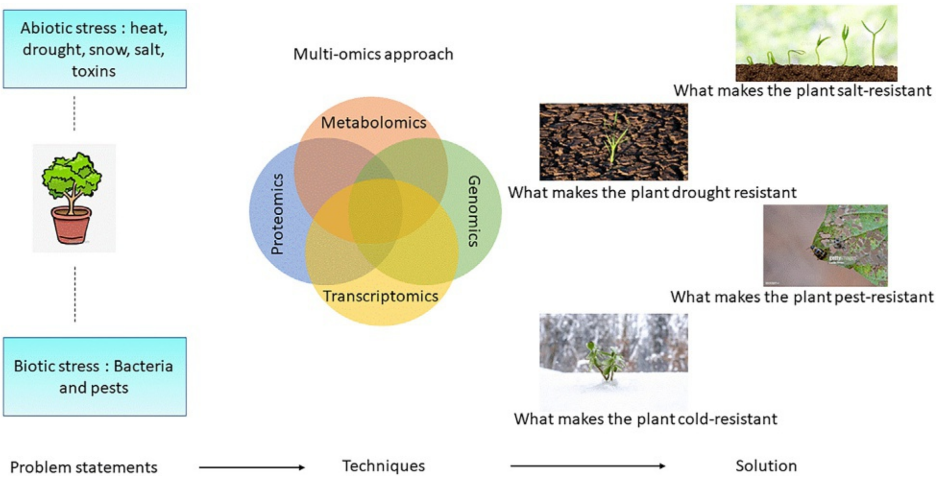

Fig. 3 Illustration showing how multiomics focuses on answering problems faced due to plant stresses.

4 Genomics social acceptability and legislative prospects in addressing food security

The current environmental conditions and the population size of the humans have increased the gap between the production of food and the distribution of food. Resource distribution is a major factor causing this gap. It will make more sense if regions with high population and low crop productivity are studied. Research in that direction can help with improving crop varieties, design agronomic practices, and build proper machinery for farm activities. Multiomics, or the study of multiple approaches, is the best method, in terms of producing fruitful research to address the food security concerns. Sequencing is getting cheaper day by day, due to extensive efforts toward building sequencers with the ability to produce more reads faster and with high efficiency (Varshney et al., 2021). Another notable fast-growing contribution is the advent of pangenomics, where sequencing is done on multiple plant genomes, which has helped to understand the adaptive diversity of the plants. Combined, all the current technologies are able to go through the different layers of the central dogma and help in the analysis of global genetic diversity, or in other words, variome (Varshney et al., 2021). The idea is to retrieve as much information as possible and then use the information to develop solutions with respect to food security. One of the approaches, differential evolution-based optimal contributions selection, was used to model genetic upgrades in wheat, making them highly tolerant to heat, increasing the grain yield and resistant to diseases. This study shows an assurance that the wheat yields would be protected for the next 60 years of global warming (Varshney et al., 2021).

While there has been a lot of encouraging developments due to multiomics, there are still two factions of agricultural biotechnology—adopters and nonadopters. The adopters grow GM crops on a commercial scale, while nonadopters stick to the traditional non-GMO agricultural practices. The pressure to adopt GM crops is there, applied on the nonadopter countries, by reconsidering their current GM-related policies (Spök et al., 2022). This comes from the fact that most of these nonadopter countries are reliant on the adopter countries for agricultural products. These include countries such as Japan, the EU, Norway, New Zealand, and Switzerland. Japan is now more liberal when it comes to GM-related policies, while Switzerland and Norway are currently working on liberalizing the current rules and regulations. New Zealand and the European Union are still struggling, due to the challenging high court decisions. However, the most powerful claim is that genome-edited crops would reduce the burden faced by the environment, due to agriculture. Climate change is an urgency, which means one does not have the luxury to continue with the carte-blanche pro-con debates, as how it was during the past three decades. There are decisions which need to be made as soon as possible, in the most sustainable way as possible (Spök et al., 2022).

5 Conclusion

Traditional agricultural practices and the Green Revolution led to the emergence of plant breeding techniques such as cross breeding, mutation breeding, transgenic breeding, genome edited breeding with CRISPR system, and so on. Later on, omics technologies such as genomics, proteomics, transcriptomics, and metabolomics evolved as a result of next generation sequencing. Each study revealed the molecular level importance and was applied in various fields including pharmaceuticals, forensics, and agriculture. Integrating multiomics with plant systems elucidated several gene functions and networks in different conditions. Thus, crop improvement became possible as the physiological and environmental stresses were resolved by the multiomics approach. Gene level, transcript level, protein level, metabolite level screening, and isolation will peep into the expression profiling of various disease mechanisms and also in signal transduction. Multiomics, various databases, and bioinformatics thus help to create a biological network over all the living organisms. The evolution of pangenomics and optimal contribution selection accelerated plant breeding with high quality crops. The application of these techniques in nonmodel plants is now increasing in order to study the diversity and new interaction patterns within them. When more explored, agriculture will become more sustainable and economical as almost every gene of every crop will be in our fingertips, so that we can manipulate and exploit their genome for our interested phenotypes.

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CHAPTER 7

Microbial contributions in restoring degraded biosphere habitats: Comparing natural and engineered approaches

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1 Introduction

The biosphere, also known as the ecosphere, is the earth's dynamic biological epidermis. It is the natural setting in which living things can be found. However, anthropogenic activity has deteriorated the biosphere's habitat. Urbanization is the primary cause of global ecological deterioration, and anthropogenic activities have consistently disrupted the earth's ecosystems. Climate change, population growth, and deforestation all lead to environmental problems, such as carbon loss, biodiversity loss, and erosion, which all create new problems for people. The massive effects are also caused by common actions such as ploughing, grazing, overfishing, hunting, diverting rivers, building cities, and overusing water. There is no effective management system for rainwater harvesting, chemical fertilizer guidelines, or other anthropogenic activities (Folke et al., 2011; Mooney et al., 2009; Coban et al., 2022). According to the report, the terrestrial biosphere habitat had harvested a significant portion of its preexisting carbon pool (Lal et al., 2012). Heavy metals such as copper (Cu), lead (Pb), zinc (Zn), cadmium (Cd), and pesticides (DDT, Dieldrin, Heptachlor, Chlordane, Endosulfan, and Dicofol) have a negative impact on farming (plants and soil) as well as human health by inhibiting enzymes, causing oxidative damage, and inhibiting neurotransmission (Takaijudin and Yusof, 2021; Alengebawy et al., 2021). Microbes in the biosphere habitat can help to restore a degraded area by providing stabilization, pollution management, aesthetic improvement, and toxic material removal (Singh et al., 2015). Also, the different microorganisms in the soil keep the soil healthy, which is an important part of keeping ecosystems going by cycling carbon and nutrients (Singh and Gupta, 2018). Soil activities such as the nutrition cycle, structural development, and plant interactions, which are guided by microbes, are critical for restoring biodiversity and ecosystem function (Harris, 2009). Nitrogen (N) fixing bacteria are essential for the growth and maintenance

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of productive soil microbial communities because they provide N through biological nitrogen fixation (Seneviratne et al., 2011). Several rhizobacteria, including *Azobacter* sp., *Bacillus subtillis, Rhizobium* sp., *Rhodospirillum rubrum,* and *Pseudomonas fluorescens*, can produce gibberellins, cytokinins, or both for plant development (Gupta et al., 2015). Contaminations caused by hydrocarbons and heavy metals can be eliminated by using biosurfactants produced by bacteria, yeast, and fungi. Biosurfactants are a type of chemical that works on surfaces. They have a low molecular weight and are very stable, nontoxic, and good for the environment (Sonowal et al., 2022). Phosphate solubilizing microbes in the soil convert inaccessible phosphate into an accessible form for plants via *Achromobacter* sp., *Burkholderia* sp., *Bacillus* sp., *Micrococcus* sp., *Agrobacterium* sp., *Erwinia* sp., *Pseudomonas* sp., *Flavobacterium* sp., and *Rhizobium* sp. (Mitra et al., 2020). It has also been observed that indigenous microbial communities from the genera *Pseudomonas* sp*., Bacillus* sp*., Alcaligenes* sp*., Acinetobacter* sp*., Escherichia* sp*., Micrococcus* sp*., Gordonia* sp*., Moraxella* sp*., Rhodococcus* sp*., Pandoraea* sp*., Streptomyces* sp., and *Sphingobium* sp., either independently or in a mixture, are involved in the degradation of xenobiotics and also play an important part in the bioremediation of severely polluted soils. Even though using indigenous microorganisms to cure such contaminated areas is advantageous, the bioavailability of hydrocarbons renders these indigenous microorganisms ineffective. However, the use of genetically modified microorganisms derived from native or wild-type strains will play a significant role in determining the overall performance of in situ bioremediation programs, as well as their active role in pollution prevention (Sangwan and Dukare, 2018; Adetunji and Anani, 2021). GMOs such as *Caulobacter crescentus* JS4022/p723-6 are used to remove heavy metals such as cadmium, while *Escherichia coli* DH5 is used to remove uranium and chromium (Rebello et al., 2021). Some biosurfactant-producing strains and their metabolites (biosurfactant) are used in oil reservoirs to recover unextractable crude oil at aged or lower oil levels; this process is known as the microbial enhanced oil recovery (MEOR) process (Sen, 2008). In addition, recombinant strain *Rhodococcus erythropolis* (RH) articulating ammonia monooxygenase (AMO) and hydroxylamine oxidase (HAO) genes, which are used in the removal of organic matter and nitrogen in landfill leachate, was developed (Bai and Tian, 2022). On the other hand, human impacts on biosphere habitat are irreversible (Williams, 2000). Restoration is the process of helping a degraded, damaged, or destroyed environment to return to its previous good condition. Restoring damaged biosphere habitat is important to stop biodiversity loss and increasing demand for ecosystem services (Bullock et al., 2011). Restoration techniques seek to reverse these effects and return an ecosystem's biotic composition and functioning to predamage levels (Araújo et al., 2013). Restoration could make cities more liveable by controlling desertification and deforestation, halting biodiversity loss, cleaning the air, and improving people's lives and interactions with nature. Many bacteria, fungi, and viruses are essential for repairing the ecosystem (Singh et al., 2019; Ducklow, 2008). As pollution in the environment worsens, microbial bioremediation has emerged as an effective, low-cost, and environment-friendly method (Tran et al., 2021). As a result, this chapter focuses on the negative effects of habitat degradation, and we need to learn more about soil microbes and how they aid in ecosystem restoration and function.

2 The cause and consequences of biosphere habitat degradation

2.1 Terrestrial habitat

In terrestrial habitats, land degradation is a widespread issue that results in the loss of soil fertility and productivity, and has worsened in recent decades due to population growth. Deforestation, inadequate farming methods with a lot of chemical fertilizers, offensive irrigation systems, and industrialization have all caused the soil to become less fertile and the land to get worse (Rashid et al., 2016; Cachada et al., 2018). Extensive chemical fertilizers have been used for mass agriculture production in the last few decades (Rey Benayas and Bullock, 2012; Migheli, 2017). Extensive usage of conventional phosphorus (P) leads to waterway eutrophication and accumulates hazardous elements, including selenium (Se) and arsenic (As) (Alori et al., 2017). Also increased common pesticides, including chlordane, dichlorodiphenyldichloroethylene (DDE), dichlorodiphenyltrichloroethane (DDTs), hexa-cyclochlorohexanes (HCHs), and dichlorodiphenyldichloroethane (DDD) (POP). Atrazine, a herbicide commonly used in crops such as maize, significantly contributes to environmental contamination. Atrazine is a chemical that could mess with the way hormones work, and if it gets into the environment, it could hurt the growth of amphibians. The hydrophobic fungicides hexachlorobenzene (HCB) and pentachlorophenol (PCP) rapidly bioaccumulate in soil and water. They have toxicological effects on fish, birds, and human milk (Pascal-Lorber and Laurent, 2011; Wang et al., 2022). Other things, from simple inorganic ions to complex organic compounds, can also make soils polluted (Cachada et al., 2018). Examples of organic pollutants are chlorinated phenols, azo dyes, chemicals that mess with hormones, polychlorinated biphenyls, pesticides, and polyaromatic hydrocarbons. The inorganic contaminants mostly come from hazardous heavy metals, for instance, chromium (Cr), arsenic (As), cadmium (Cd), mercury (Hg), and lead (Pb) (Clarke et al., 2008). Contrary to organic pollutants, trace elements are persistent in the environment and nonbiodegradable; therefore, they are effectively preserved in soils perpetually. The rising quantities of these trans-elements in the soil have increased the number of harmful environmental pollutants, which have become a major global problem (Hartemink, 2016; Tang et al., 2019). On the other hand, heavy metals in soil environments stress microorganisms more than plants or animals (Giller et al., 1998). Heavy metals may arrive in the food chain after being absorbed by plants, which means people may be exposed to them (Zwolak et al., 2019). Land serves as the last destination for waste disposal and usage; therefore, Cd produced from various sources finally makes its way to the soil, where it can be bioaccumulated in food crops (Khan et al., 2017). Soil polluted with radionuclides, notably 137Cs, and 90Sr, poses a long-term radiation risk to human health via the food chain

(Zhu and Shaw, 2000). Further, atmospheric mercury depletion events (AMDEs) in the polar regions have also been reported. Pollution from Hg in the tundra area has caused a lot of worries (Poissant et al., 2008). Also, mining often uses up the topsoil and plants, hurts the biodiversity of the soil, and makes the environment very harsh, which stops natural reforestation and soil regeneration (Wang, 2017).

2.2 Aquatic habitat

Over half of all bacteria on earth live in aquatic habitat, which includes the oceans, lakes, rivers, glaciers, wetlands, groundwater, etc., which cover about 3/4 of the planet's surface (Sandrin et al., 2009; Huang et al., 2019). Emerging contaminants in lakes, rivers, glaciers, wetlands, groundwater, and the ocean pose serious environmental and health risks (Sanganyado and Kajau, 2022). The seas and oceans are the most important biomes in the biosphere. However, more and more habitats in these biomes are being damaged. Fischer et al. (2016) found that rivers and effluents are the primary sources of microplastics from land. Still, factory trash is dumped into the water ecosystem without proper waste management, and untreated dirt is dumped into the water. This causes the number of heavy metals in marine environments to rise. In addition, cotton textiles, metal industries, dye, paints, pulp and paper, varnishes, rayon, distilleries, rubber, tanneries, steel plants, thermal power plants, mining industries, and galvanization of iron products are involved in the increasing levels of heavy metals in aquatic environments (Paul, 2017). The hydrocarbon contamination (mainly crude oil) frequently occurred due to oil leakage during oil transportation from the wellhead to storage tanks and also in the form of commercial transportation from one place to another through ships, abandoned oil wells, and refinery sites, with improperly disposed of motor oil polluting groundwater, and the ocean. Many ingredients of petroleum crude are intractable and highly poisonous due to the existence of carcinogenic, hemotoxic, and teratogenic materials like PAHs and BTEX (Varjani, 2017). Marine oil spill catastrophes lead to massive contamination of the marine environment, which could cause negative impacts on fish, invertebrate ecosystems, seabird populations, marine mammals, and phytoplankton (Chenhao and Yupeng, 2021; Jha and Dahiya, 2022). Additives used in the typical plastic industry include polybrominated diphenyl ethers (PBDEs), phthalates, nonylphenol, bisphenol A (BPA), and antioxidants. PBDE has been found in the tissues of many marine creatures, including bivalves, fish, and other marine animals (Hermabessiere et al., 2017). Micro- and nano-sized pieces of plastic can get stuck in the intestines and cause damage to the gut lining, illness, and even death. Changes in immune responses, oxidative stress, neurotoxicity, disruption of the endocrine system, changes in reproduction, embryotoxicity, genomic uncertainty, and transgenerational toxicity are all caused by microplastics (Alimba and Faggio, 2019). Also, pharmaceuticals and personal care products (PPCPs) are considered to be incipient contaminants because they contain a variety of organic compounds, perfluorinated compounds (PFCs), industrial additives and agents, disinfectant by-products, surfactants, gasoline additives, transformation products (TPs), illegal drugs, flame retardants, and pesticides. PPCPs have a big chance of building up in living things and could make aquatic animals sick. For example, chlorophyta and diatoms are more vulnerable and sensitive to PPCP contamination. PFCs have moderate water solubility, are nonvolatile, and are thermally stable; they are found in polar bears, fish, birds, oysters, crabs, and mussels (Fernández-Sanjuan et al., 2010; Xin et al., 2021; la Farré et al., 2008).

3 Significance of microbes/microbial biomass in the restoration of degraded biosphere habitats

Microbes are omnipresent, with massive and efficient genetic pools in the biosphere. Their presence constantly changes the environment where they can live and helps ecosystems stay healthy (Gupta et al., 2017; Singh et al., 2015). Microbes live in different ranges and act differently based on organic matter, texture, pH, moisture content, temperature, soil aeration, and other environmental factors (Chen et al., 2003). Microbes like protozoa, fungi, algae, bacteria, and some nematodes have multifunctional contributions in maintaining soil productivity by improving physical characteristics such as aeration, porosity, structure, and water infiltration by establishing a stabilizing soil aggregate with biological function to avoid plant disease (Rashid et al., 2016). As inoculants, bacteria, actinomycetes, fungi, and yeasts could augment plant growth primarily by potassium and phosphate solubilization, organic matter breakdown, biocontrol action, siderophores synthesis, exopolysaccharide secretion, etc. (Naik et al., 2019). Native microbes also take care of several ecosystem-level tasks, such as breaking down carbon-based waste, making humic compounds, cycling nutrients, fixing nitrogen, and getting rid of xenobiotics (Paz-Ferreiro and Fu, 2016) and restoration of ecosystem (Fig. 1). Bacteria make about 20% of the atmosphere's oxygen, 70% of its methane, 50% of its carbon, and 75% of its nitrogen. They also take out much nitrogen from the air. The nematode community and soil enzymes currently present in the soils are highly sensitive to slight physicochemical changes (García-Ruiz et al., 2009). Microorganisms in the marine environment are regarded as the most important primary producers. They fix carbon dioxide into organic matter through photosynthesis. In exchange, they make about 70% of the oxygen the world needs. More than half of all primary production and nutrient cycling on Earth is done by marine microbes (Sandrin et al., 2009; Das and Dash, 2014). The varied contributions of soil microorganisms to a range of ecological functions are shown in Table 1.

3.1 Types of microbes included in the restoration of degraded biosphere habitats

Different bacterial and fungal inoculum types could restore degraded land's fertility in various ways. Microfauna, macrofauna, microflora, and mesofauna are living organism categories in soil biosphere habitats (Rashid et al., 2016; Hartemink, 2016). Many microorganisms attempting to restore the biosphere's environment are described in Table 2.

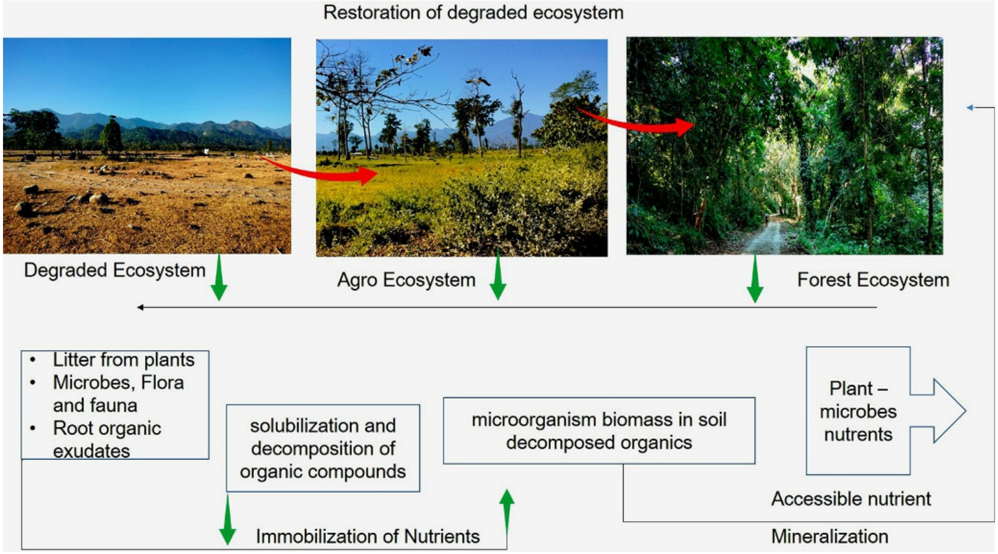

Fig. 1 Illustration showing the contribution of soil microbe biomass/microbes to agro- and forest ecosystems as a source of nutrients available to plants.

Table 1 Soil microorganisms' impact on numerous ecosystem processes.

Ecosystem process	Types of microbes involved	Mechanism of restoration	References
Carbon cycle	Bacteria and fungi	Breakdown of soluble and insoluble organic matter and convert them into readily available/ utilizable forms for plants	van der Heijden et al. (2008)
Nitrogen cycle	Nitrogen-fixing bacteria, rhizobia, mycorrhizal fungi, bacteria, fungi, archaea, denitrifying bacteria, actinomycetes	Plant nitrogen acquisition, transfer of N from organic matters and leaf litter to host plant, enhanced N availability in soil, nitrogen fixation, nutrient uptake, enhanced leaching because of nitrification, nitrogen loss, denitrification	van der Heijden et al. (2008), Naik et al. (2019), Ma et al. (2022)
Phosphorus cycle	PGPR P-solubilizing bacteria	Breakdown of phosphorous by phytohormone production, plant adaptation to salt stress, and sanitization	Satyaprakash et al. (2017), Billah et al. (2019)
Regulation of plant diversity	Arbuscular mycorrhizal fungi, PGPR	Plant nutrition, plant development, reduce stress, soil structure, and fertility	Ahanger et al. (2014), Chen et al. (2018), Nelson (2004)

Table 2 Microorganisms involved in biosphere habitat restoration.

Microbes	Process/mechanism involved	Type of habitat restored	References
Scenedesmus bijugatus, Anabaena sp., *Chlorella vulgaris, Phormidium tenue, Aulosira fertilissima, Synechococcus elongatus,* and *Nostoc linckia*	Metabolize DDT to DDD and DDE by bio-accumulation and transformation pesticides	Restoration of aquatic habitat that is destroyed by various pesticides	Mondal et al. (2019)
Pichia guilliermondii, Saccharomyces cerevisiae, Rhodotorula mucilage, Rhodotorula pilimanae, Hansenula polymorpha, and *Yarrowia lipolytica*	It is used to bio-transform Cr (VI) to Cr (III) and as pigments in dyes, paints, and inks	Restoration of terrestrial and aquatic habitat	Medfu Tarekegn et al. (2020)
Penicillium sp., *Bacillus megaterium, Aspergillus niger,* and *Bacillus subtilis*	Biosorption of Cr, Cd, and Pb	Restoration of the polluted environment in both aquatic and terrestrial habitats	Medfu Tarekegn et al. (2020), Mondal et al. (2017)
Bjerkandera adusta, Pleurotus sp., *Phanerochaete chrysosporium,* and *Trametes versicolor*	Clean up the hydrocarbon contaminations by using ligninolytic enzymes, like peroxidases and laccases	Restoration of terrestrial habitat by degrading PAH present in the soil	Bhattacharjee et al. (2020), Wang et al. (2009)
Thalassiosira pseudonana, Ditylum birghtwellii, Skeletonema costatum (Diatoms)	Removal of heavy metal contaminations via integration or adsorption, synthesized high amounts of antioxidants (phytochelatins)	Restoration of aquatic habitat by response to copper (Cu) and cadmium (Cd) stress	Kiran Marella et al. (2020)
Bacillus amylolyticus, Bacillus firmus, Pseudomonas putida, and *Psuedomona fluorescence*	Degradation of LDPE microplastic with the enzyme coded by the Alk-B gene (alkane hydroxylase)	Restoration of marine ecosystem	Jeyavani et al. (2021)
Chlamydomonas reinhardtii and *Chlamydomonas sorokiniana*	Degrades PhACs, which include antibiotics, tranquilizers, diuretics, and psychiatric drugs	Restore aquatic habitat with wastewater treatment plants	Mondal et al. (2019)
Pseudomonas aeruginosa, Pseudomonas putida, Burkholderia mallei, Burkholderia pseudomallei, Burkholderia thailandensis	Produces rhamnolipid biosurfactant type, which enhances total oil biodegradation in the oil spill area	Restoration of marine habitat by oil spill bioremediation	Patel et al. (2018)

3.1.1 Nitrogen-fixing bacteria

Nitrogen-fixing bacteria are essential for tree growth and ecosystem health because they make N through a biological process (Seneviratne et al., 2011). Nitrogen-fixing organisms are biofertilizers composed of microbial inoculants capable of fixing atmospheric nitrogen. N-fixing bacteria are classified into free-living bacteria such as *Bradyrhizobium* sp., *Azotobacter* sp., and *Azospirillium* sp., blue-green algae, and symbionts such as *Rhizobium* sp., *Frankia* sp., and *Azolla* sp. (Bhat et al., 2015; Naik et al., 2019). In addition, major N_2-fixing marine cyanobacteria are also fixing nitrogen, including *Trichodesmium* spp., *Calothrix* spp., UCYN-A (nitrogen fixation in the daytime), and *Crocosphaera* sp. UCYN-B (nitrogen fixation in the nighttime) (Zehr, 2011).

3.1.2 Arbuscular mycorrhizal fungi

In degraded ecosystems, arbuscular mycorrhizal (AM) fungi play vital roles in plant growth and recovery by reducing environmental challenges such as salt, dehydration, heavy metal toxicity, and soil compaction, which enable some plants to thrive under challenging circumstances (Liang et al., 2016; Wang, 2017). For example, Glomeromycota is a group of fungi that has helped plants grow in heavy metal-contaminated soils. Glomalin in hyphae and soils, an insoluble glycoprotein produced by AM fungus, is known to sequester the potentially toxic elements (PTEs) like Cu, Cd, and Pb and is thought to be useful for bio stabilization and soil remediation (Khan, 2005; Willis et al., 2012). At low phosphorus levels in taconite mine tailings, AMF inoculum boosted the growth of the natural grass *Panicum virgatum* (White et al., 2017).

3.1.3 Plant growth-promoting rhizobacteria

Plant growth-promoting rhizobacteria (PGPR) are an important group of root-colonizing bacteria that live in the rhizosphere and bulk soil of plants. PGPR are free-living soil bacteria that help plants grow by making them more resistant to biotic and abiotic stress, and giving them more food. The rhizosphere, a crucial natural soil location for plant-microbe relations (Basu et al., 2021; Prasad et al., 2015). Several rhizobacteria that promote plant growth are *Azobacter* sp., *Rhodospirillum rubrum*, *Bacillus subtillis*, *Pantoea agglomerans*, *Rhizobium* sp., *Paenibacillus polymyxa*, *Pseudomonas fluorescens*, and can generate gibberellins or cytokinins or together for plant development (Gupta et al., 2015). In addition, PGPR produces siderophores, organic acids, phytohormones, and stress-induced metabolites like prolines, osmotic solutes, and antioxidant enzymes, as well as regulates the functions of significant genes are responsible for stress responsive that give plants resilience under stressful situations (Subiramani et al., 2020). PGPR reduces abiotic stress by altering phytohormone metabolism (Khan et al., 2020). *Paenibacillus polymyxa* is a PGPR with *Arabidopsis thaliana* for drought resistance (Singh et al., 2019). *Bacillus subtilis* promotes the production of phytohormones, stress-response genes, and stress-related metabolites, which improves plant stress tolerance (Hashem et al., 2019).

Allelochemicals, which are by-products of PGPR, make plants less susceptible to attack by pathogens (Kumar et al., 2017). PGPR strains, including *Psuedomonas reactants, Burkholderia phytofirmans, Mesorhizobium* sp., *Psuedomonas libanensis, Bacillus pumilus, Azotobacter* sp., and *Variovorax paradoxus* are shown to have the potential to bioremediate heavy metals from polluted soils (Majeed et al., 2018).

3.1.4 Microbes mediated bioremediation

Bacteria produce siderophores, which increase mobility and decrease metal bioavailability. The resistance strategies bacteria use to combat metal toxicity include heavy metal efflux, impermeability, metal complexation, exopolysaccharide sequestration, detoxification, and volatilization via enzymes. Rhizobacteria can maintain soil pH, suppress soil-borne pathogens, and destroy organic and inorganic pollutants by rhizodegradation, transformation, and volatilization in the environment (Bandyopadhyay, 2021; Ojuederie and Babalola, 2017; Thavamani et al., 2017). Many bacterial species from the genera *Bacillus* sp., *Pseudomonas* sp., *Rhodococcus* sp., *Acidovorax* sp., *Alcaligenes* sp., *Escherichia* sp., and *Mycobacterium* sp. are identified as efficient strains for the bioremediation of heavy metals and PAHs (Yang et al., 2020; Sharma, 2021). Recent research has suggested that bacterial strains can degrade LDPE, including *Aneurinibacillus* sp., *Brevibacillus* sp., *Bacillus cereus*, and *Pseudomonas aeruginosa* (for instance, laccase enzyme from *Rhodococcus ruber*, potentially impairs LDPE) (Maroof et al., 2021). Microalgae species like *Chlorella* sp., *Scenedesmus* sp., and *Aphanocapsa* sp. can break down harmful dyes into carbon and nitrogen sources, and then remove them from water, which reduces eutrophication in the ecosystem (Touliabah et al., 2022). Microalgae *like Ochromonas danica, Ankistrodesmus braunii, Nedesmus quadricauda* and a group of *Chlorella sorokiniana* and *Pseudomonas migulae* could degrade phenols (Ben Chekroun et al., 2014; Subashchandrabose et al., 2013). Some microalgae, including *Scenedesmus bijugatus, Phormidium tenue, Chlorella vulgaris, Nostoc linckia, Aulosira fertilissima, Anabaena* sp., and *Synechococcus elongatus* are well recognized for their conversion of DDT to DDD and DDE, respectively, by the methods of bioaccumulation and transformation (Mondal et al., 2019). Several species of *Aspergillus, Rhodococcus, Penicillium, Phanerochaete, Pseudomonas, Rhizopus, Serratia*, and *Bacillus*, are capable of decomposing PET, PS, PP, and PE (Taghavi et al., 2021).

3.1.5 Biosurfactant producing microorganisms

Microbes like bacteria, fungi, and yeast produce surface-active biomolecules known as biosurfactants, which have numerous advantages over synthetic surfactants, including a low level of toxicity, biodegradability, higher foaming, being environmentally friendly, high choosiness, and stability over life-threatening circumstances, including salinity, pH, and temperature (Shekhar et al., 2015). Biosurfactants are amphiphilic, synthesized by numerous microbes when development occurs at water-immiscible or oily substrate (Mukherjee et al., 2006). Chemically, they can be profiled as glycolipids, rhamnolipids, sophorolipids, and trehalolipid (Patel et al., 2018). A rhamnolipid biosurfactant has been exposed to be proficient of enhancing the elimination of Pb, Zn, and Cd from the soil. Gautam and Tyagi (2006) found that Cd absorption can be changed when rhamnolipid and Cd form a complex and come into contact with the cell surface. *Pseudomonas* sp., *Candida* sp., and *Bacillus* sp. biosurfactants, called rhamnolipid, surfactant, and sophorolipid, are used in oil-spill bioremediation (Markande et al., 2021). Aside from bioremediation, bacteria like *Acinetobacter anitratus, Bacillus pumilus, Micrococcus luteus,* and *Vibrio parahaemolyticus* have been used to make biosurfactants, which can be used in the process of enhanced bioremediation (Das and Dash, 2014). Pande et al. (2020) found that biosurfactants made from the *Bacillus subtilis* MTCC 1427 strain made it easier to get rid of the chlorinated pesticide endosulfan. The biosurfactant synthesized by strain *Candida antarctica* by using the *n*-undecane as carbon source could encourage emulsification activity and *n*-alkanes biodegradation (Ward, 2010). Biosurfactants are biodegradable and could be used as long-term replacements for chemical surfactants in many industrial developments, such as making emulsions, lubrication, stabilizing dispersions, wetting, fixing dyes, foaming, softening, and bioremediation of organic or inorganic polluted spots (Reis et al., 2013). Sophorolipids, rhamnolipids, and surfactin, as well as those extracted from *Torulopsis bombicola, Pseudomonas aeruginosa*, and *Bacillus subtilis*, are evaluated using metals-contaminated sediment containing 3300 mg/kg Zn and 110 mg/kg Cu. About 18% of the Zn and 65% of the Cu are abolished by the selected biosurfactant after washing with 0.5% of rhamnolipid, although 60% of the Zn and 25% of the Cu are eliminated by using 4% of sophorolipids (Srivastava et al., 2021).

3.1.6 Phosphate solubilizing microorganisms

Phosphorous is one of the most important macronutrients for a plant's biological development. Mineral and organic phosphorus are the two main types of phosphorus in soil. Both are hard to get to and do not dissolve. So, many microbes in the soil could mineralize or dissolve insoluble soil phosphate to make soluble P that plants could use. Phosphate solubilizing microorganisms (PSM) inoculation is a promising method for increasing the global food supply without harming the environment (Behera et al., 2014; Alori et al., 2017). The primary way phosphorus gets dissolved by forming different kinds of organic acids. Microbes turn insoluble phosphate into a form that plants can use by making organic acids. This makes the phosphate easier for plants to take up and use. Inoculation with PSB such as *Pseudomonas* sp., *Bacillus* sp., *Rhizobium* sp., *Micrococcus* sp., *Flavobacterium* sp., *Achromobacter* sp., *Erwinia* sp., and *Agrobacterium* sp., has been shown to increase fixed phosphorus solubilization, resulting in higher crop yields (Satyaprakash et al., 2017; Saeid et al., 2018). *Arthrobacter ureafaciens, Rhodococcus erythropolis, Phyllobacterium myrsinacearum*, and *Delftia* sp. are classified as phosphate-solubilizing bacteria (PSB) after demonstrating its aptitude to solubilize a substantial amount of tricalcium phosphate in the growth medium by producing organic acids (Chen et al., 2006). The PSB strains

Enterobacter sp. UFPI B5-6, *Paenibacillus kribbensis* UFLA 03-10, *Pseudomonas* sp. UFPI B5-8A, and *Burkholderia* sp. UFLA 04-21 accumulate calcium, sulfur, boron, magnesium, phosphorus, and nitrogen (Martins da Costa et al., 2015).

3.1.7 Microbial biofilms

Biofilms are formed when microbial colonies adhere to the surface in their exopolysaccharides. Exopolysaccharides make it possible for biofilms to resist physical, chemical, and biological challenges and to withstand environmental stress. Many recalcitrant/xenobiotic substances are exceedingly tricky to decompose, such as polyaromatic hydrocarbons (PAHs), which have prompted worries about the long-term consequences on the environment. Consequently, biofilm-based remediation is one of the most excellent solutions for PAH breakdown (Sanghvi et al., 2020). *Bacillus* biofilms, such as *Bacillus subtilis* and *Bacillus cereus*, were reported to remove Cr(III) from chrome tanning effluent successfully. Additionally, native bacterial biomass from *Staphylococcus epidermidis*, *Pseudomonas putida* CZ1, *Penicillium simplicissimum*, *Arthrobacter* sp. SUK 1205, *Stenotrophomonas* sp., *Leptothrix cholodnii* SP-6SL, *Escherichia coli*, *Shewanella oneidensis*, and *Pseudomonas* sp. Lk9, isolated from various metal-polluted locations appear to be efficient and eliminate the heavy metal from the polluted effluent (Mohapatra et al., 2019).

4 Bioengineered microorganisms

Bioengineered individual microbial species or communities have significant potential in agriculture, bioremediation, and industrial applications (Sivasubramaniam and Franks, 2016; Verma and Kuila, 2019). However, according to the United Nations Environment Programme (UNEP), native microbial strains have insufficient or slow removal potential. Therefore, genetically modified organisms (GMOs) can be used to speed up biodegradation because their changed metabolic pathways lead to the overproduction of many biomolecules/enzymes, which helps the bioremediation process (Rebello et al., 2021) shown in Fig. 2.

In the arena of bioremediation, genetic engineering act a crucial role. Capable microorganisms could be modified to improve cell membrane transport or enzymatic properties that aid in the accelerated and broad spectral breakdown of contaminants. The most well-known examples of genetically altered biological instruments are "superbugs," which help clean up oil spills and other harmful pollutants. Microbes are being created with genes to break down numerous components of complicated crude oil, and some successes have occurred (Arora, 2018). For instance, a recombinant photosynthetic bacterium *Rhodopseudomonas palustris* was bio-engineered to concurrently prompt the Hg transport mechanism to eliminate Hg^{2+} from heavy metal-contaminated water. Strain *Alcaligenes eutrophus* AE104 (pEBZ141) has been utilized to eliminate Cr from industrial wastewater. *Bacillus subtilis* 38, a UV-mutated species, is an effective multimetal sorbent

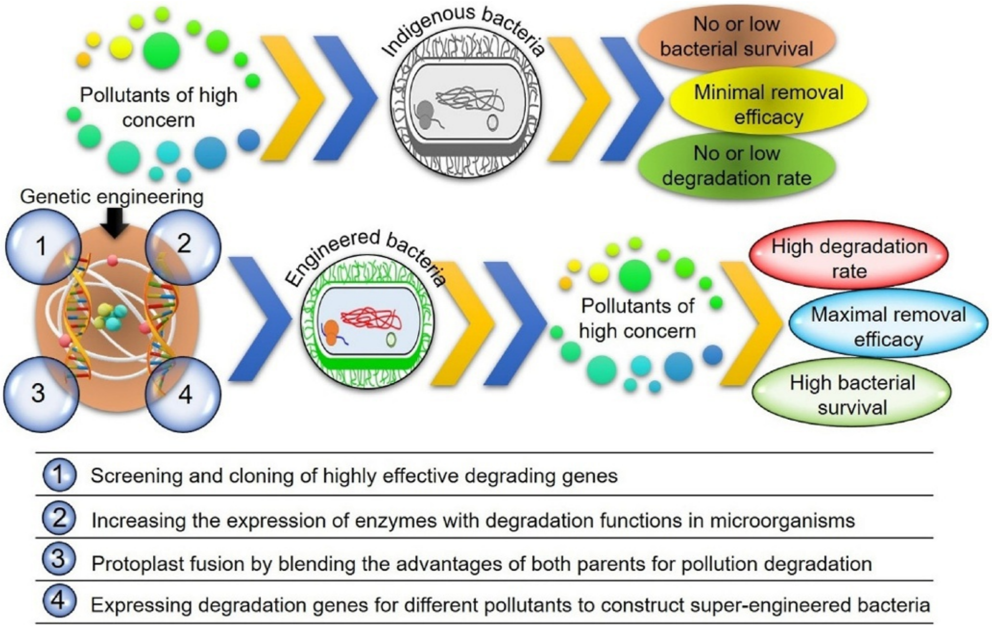

Fig. 2 Using genetically engineered microbes, induce the degradation of high-risk pollutants (Rafeeq et al., 2023). Under a Creative Commons license, https://doi.org/10.1016/j.chemosphere.2022.136751.

for Cd, Cr, Hg, and Pb (Wang et al., 2014). Different forms of PAHs are also anticipated to be reduced by genetically modified species. JS4022/p723-6H biofilms are good in retaining cadmium, and *Caulobacter crescentus* JS4022/p723-6H hexahistidine peptide found on the surface of bacterial cells acts as a whole-cell adsorbent for liquid heavy metals (Sharma et al., 2021; Xu et al., 2010). A multiplasmid-rich *Pseudomonas strain* with the ability to break down aliphatic, aromatic, polyaromatic hydrocarbons, and terpenes with the help of specific genes for removal of varies contaminations such as naphthalene, camphor, octane, hexane, and xylene (CAM plasmid), as well as decane, hexane, and octane (OCT plasmid). A complete DNT (2,4-dinitrotoluene) degradation pathway from *Burkholderia* sp. was engineered into *Pseudomonas fluorescens* ATCC 17400 (Kumar et al., 2018). *Acinetobacter baumannii* S30 pJES used for hydrocarbon biodegradation, recombinant *Rhodococcus erythropolis* eliminates organic matter and nitrogen in landfill leachate (Rebello et al., 2021). *Pseudomonas stutzeri* Rhl produces rhamnolipid, which removes H2S produced by sulfate-reducing bacteria (Zhao et al., 2016). Also, as mentioned earlier in this chapter, microbial metabolites, mainly biosurfactant surface active molecules, are used to recover trapped crude oils from marginal reservoirs. This recovery process is called the microbial-enhanced oil recovery process (MEOR). In this process, biosurfactant-producing microbial strains or specially selected consortia will be used injected into the oil reservoir, where they utilize crude oil as their sole carbon source by producing biosurfactant to decrease the surface tension and increase the bioavailability, which will enhance the oil recovery process (Sen, 2008; Quraishi et al., 2021).

5 Conclusion

Deforestation, large-scale farming, chemical fertilizers and pesticides, growing cities, and industrialization have all hurt the environment and ecosystems. These anthropogenic activities have a significant impact on habitat degradation in the biosphere. To keep the ecosystem in balance, the habitat of the biosphere depends on the biological process of nutrient cycling in the soil. As a result, restoring degraded biosphere habitats is required to save the planet. Microbes are found everywhere and play an essential role in the environment, such as keeping plants growing and the air clean so people can live. Microbial degradation is a promising way to clean the environment of organic and inorganic pollutants, which is good for the environment's long-term health. Many studies, however, have shown that native microbes are slower and cannot break down pollutants as efficiently as genetically modified organisms. Because of this, researchers must study genetically modified microbes to speed up soil health restoration and fight a wide range of contaminants. Long-term soil health could be improved by introducing potential microorganisms to boost soil fertility, biotic composition, function, and productivity, and restore degraded biosphere habitat.

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CHAPTER 8

Migration of microplastics in agriculture and marine ecosystem: Biotechnology approaches

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1 Classification of microplastics and degradation pathways in water

The classification of microplastics is closely related to the biophysical properties of the material they come from, the size of the particles themselves, and the method of their formation. The plastic particles present in the aquatic environment constitute a highly heterogeneous group, and new research methods have become the main cause of frequent changes in the classification of microplastics. Plastics are complex chemical structures in which the configuration of the arrangement of atoms determines the final properties of the material, such as strength, resistance to environmental conditions, or degradation (Crawford and Quinn, 2017).

The term "microplastic" was first introduced by the authors of a 2004 study of sediment contamination in the Plymouth area of the United Kingdom (Thomson, 2004). However, this term referred to general plastic particles and did not specify any measurable values. In 2008, the first international workshop related to the risk of plastics in the environment took place: the International Research Workshop on the Occurrence, Effects, and Fate of Microplastic Marine Debris, organized by NOAA and the University of Washington. One of the goals of this meeting was to establish the official terminology and definition of plastic particles of different structures, sizes, and densities. Within the meaning of the word "microplastic" there is a prefix "micro" suggesting that the tested fraction requires the use of optical tools. Ultimately, however, the committee decided that this name would be standardized as a term for a material not exceeding 5 mm. The lower limit of microplastics was not taken into account, so pollen and dust are also included in the microplastic group (Frias and Nash, 2019). However, in order to better understand and convey information about the particle size, Cole et al. (2011) introduced an additional division with details of particles smaller and larger than the adopted 5 mm. This classification is aimed at more precise determination of the particle size and

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uses the terms nanoplastic (<1 μm), microplastic (1 mm to 5 mm), mesoplastic (5 mm to 2.5 cm), macroplastic (2.5 cm to 1 m), and megaplastic (over 1 m) (Frias and Nash, 2019).

Another criterion for the division of microplastics is their shape. In an urban environment, in polluted waterways, the most commonly found fibers are those shed by clothes during the washing process (De Falco et al., 2018). In addition, this section also covers fishing net fibers (with different properties and structures), microgranules, films, foams, granules, and particles of various shapes. There is some risk associated with the last group, i.e., particles of different shapes, as authors from different countries may use different terminology to describe the same fraction; the result of which may be a misinterpretation of the results or conflicting data (Boucher and Friot, 2017). The classification of microplastics also results from the sources of origin, we distinguish here primary and secondary microplastics (Zeng, 2018).

2 Primary and secondary microplastics

Primary microplastics are plastics that are characterized by small size and are directly exposed to the environment, often bypassing mechanical and biological processing. These are particles that are deliberately produced at these small sizes. The most frequently described primary microplastics include granules used in the processing industry, particles of cosmetic products, components of abrasive materials, synthetic fibers, as well as tire particles or urban dust. The source of microplastic formation includes both the primary production of granules and its processing, and the average particle size ranges from 0.1 to 10 mm, with hardness of 45–95 ShA (Boucher and Friot, 2017). The content of plastics in cosmetic products ranges from 0.05% to 12%, and their size is usually 450–800 μm. This group includes makeup products, toothpaste, soaps, shower gels, and shampoos, which can contain PE, PP, PMMA, PS, and PET. The highest concentration of artificial particles is contained in face scrubs and often exceeds 17%. The production and use of plastic particles in abrasion or smoothing processes occurs widely in the construction industry (Boucher and Friot, 2017). Abrasive papers, foils, and canvases coated with aluminum oxide, silicon carbide, or aluminum zircon are a common group of microplastic sources due to their widespread use and frequent wear. The resulting microplastic usually has a size of less than 0.1 mm and a high specific density. The main sources of synthetic fibers are domestic and industrial laundries. Research has shown that the amount of particles released during washing can reach several thousand for every gram of material. The type of fabric and detergent used as well as the washing parameters (temperature, washing time, water hardness) are important here. Alkaline cleaning agents and detergents cause the production of an alkaline environment that leads to chemical damage to polyester materials through the hydrolysis of ester groups that build the structure of polyesters (Lechner et al., 2015).

The last of the discussed exemplary groups of microplastics are fragments of tires and particles formed during their production. Both the process of abrasion of the tire tread and the production cause particles of synthetic rubber, that is, Styrofoam, natural rubber, and their mixtures, with many additives (Thevenon et al., 2011). The most heterogeneous group is made of microplastics contained in urban dust. The composition of the dust is diverse and we distinguish plastic particles resulting from renovation works (drilling, grinding), the use of artificial pitches or sidewalks, and particles of varnish or facade elements (Crawford and Quinn, 2017).

Secondary microplastics are formed in the processes of degradation of larger pieces of plastic under the influence of certain factors. Typically, the secondary microplastic particles have irregular shapes and sizes despite the same source, e.g., from a PET bottle. The degradation of the material and the process of microplastic formation are conditioned by external factors and the chemical properties of the material itself. Solar radiation, mechanical friction, temperature, and water have the greatest influence on the decomposition of plastic elements (De Falco et al., 2018).

For many researchers, the shape of microplastics is the basic criterion for classifying these pollutants. Here, too, the source of microplastic is extremely important: the foil particles will have a different shape than those from tires or personal care products (Koelmans et al., 2014).

Microspheres are plastic particles less than 1 mm in diameter; often, these are 0.01 mm particles, made of polyethylene, polystyrene, and polypropylene. Microbeads are often the basic ingredients added to personal care products such as soaps, shower gels, scrubs, and toothpaste. Their size allows them to easily get into the aquatic environment, passing through filtration systems. Research shows that a single use of facial scrub may result in the release of over 94,000 microgranules of plastic into the sewage system (Crawford and Quinn, 2017).

Synthetic fibers, the source of which are thermal and chemical treatment of materials, enter the water system mainly through sewage, and to a lesser extent, through air movement and transport with the wind. The main source is commercial and industrial washing of clothes and diapers; in addition, these fibers may come from cigarette butts. It is estimated that up to 350 fibers from 1 g of fabric can be released in one wash. Subsequent tests showed that washing fleece frees more than 2000 fibers, which reduces the weight of the washed fleece by 0.7–1.3 g. In the marine environment, fishing nets are the main source of fiber and they account for the largest proportion of all fiber present there. However, they differ from the fibers from clothing in terms of structure and size, which is why they are described as a separate group. The high concentration of synthetic fibers in an area is often considered a marker of population density in a terrestrial environment. As the population increases, so does the amount of fiber in the aquatic environment. Synthetic fibers mainly belong to secondary microplastics and consist of, inter alia, PET, PS, or PA, and their diameter is less than 20 μm (Boucher and Friot, 2017).

Fibers of the fishing industry are characterized by a larger diameter and transparency, and are often made of nylon monofilaments, which makes them significantly different from fibers from clothes, carpets, or curtains. These fibers are an excellent example of secondary microplastics and the degradation of plastic structures by the water environment. Their degradation to the aquatic environment takes place during the physical use of nets and sea ropes during the abrasion process (Frias and Nash, 2019).

Pellets consist of particles from 1 to 5 mm, the source of which can be PVC, PC, or PE. Such pellets represent one of the most common pollutants in freshwater, as they are widely distributed due to industrial production processes and use. The shape resembles a disk or egg-shaped granules.

Foil is widespread due to the short period of use of the source material, such as plastic bags or packaging. It is most often a secondary microplastic with a size of 1–10 mm with the composition of, among others, PE and LDPE (Lechner et al., 2015).

Soft granules, the sources of which are, among others, car tires, include rubber or caoutchouc, and their size ranges from 0.10 to 100 μm.

Foams are classified as lightweight microplastics, and are commonly used in food containers and thermal packaging. The main ingredient is polystyrene. Its production uses styrene, a carcinogen for laboratory animals. It is classified as both primary and secondary microplastics (degradation of fishing containers). Its size is usually from 1 to 10 mm.

Fragments of epoxy resins, granules of paint coatings, adhesives, and materials used for repairing ships in shipyards, seas, and oceans. They are usually of simple composition, brittleness and a size of 0.1 to a few millimeters (De Falco et al., 2018).

3 Degradation paths of microplastics

Microplastics can enter the aquatic environment in various ways, e.g., through sewage, from soil to water courses, and also due to wind. In the marine environment, it can also be direct, e.g., due to deteriorating nets and the release of fibers into the ocean (Besseling et al., 2013). As shown by many studies, the presence of microplastics in water is a very common phenomenon, and its accumulation degree is related, among others, to the hydrodynamics of water, the proximity of large cities, or the development of a maritime economy and activities. In the case of inland waters, it is mainly related to the degree of urbanization of the area and the number of inhabitants (Thevenon et al., 2011). The microplastics detected in water contains both primary and secondary particles formed in the processes of physical abrasion, and almost 80% of all water pollution ends up in the ocean, where it creates "garbage patches" and directly and indirectly threatens the entire marine environment. Thus, up to 90% of all microplastics present in the assessments may be of land-based origin.

The greatest threat is from large industrial plants and households, where countless amounts of microplastics are produced on a daily basis, e.g., in the form of synthetic fibers, released in the washing process, which, together with water, get into the sewage system and then to sewage treatment plants (Koelmans et al., 2014). Not all wastewater treatment plants have filters that are effective enough to retain such small particles, and some of them end up in rivers or drinking water reservoirs (Murphy, 2016). The situation is similar in landfills, which are not always adapted to isolating waste from the environment. The process of slow degradation and the fragmentation caused by physical friction mean that a large part of the particles travel with the wind over long distances and can directly enter rivers. In a similar way, small particles of rubber from car tires get into the environment. Research confirms that tire particles or city dust can travel up to 12 km in the air as a result of wind or turbulence (Thevenon et al., 2011).

The cases described above concern the penetration of microplastics directly into the water system, but it is worth mentioning that the influence of agriculture is also important. In the case of compost contamination with microplastics (foil, fertilizer additives, dust), agricultural machines are able to move materials over long distances, from where they can be washed away with rain or end up in groundwater. A small part of the total marine microplastics pollution is represented by fragments from the maritime industry, which are introduced directly. Fishing, maritime transport, and, to a small extent, tourism, are involved in this. Physicochemical properties, and particle size and density determine whether this microplastic will sink to the bottom or will be affected by sea currents and will drift gradually, merging with other pollutants and creating garbage patches (De Falco et al., 2018).

4 Classification of plastic

The physicochemical properties of plastics determine their application in various industries. Strength, resistance to mechanical damage, and effective mechanical forming are important factors (selection of appropriate physical/thermal parameters to achieve desired chemical properties) (Fig. 1, Table 1).

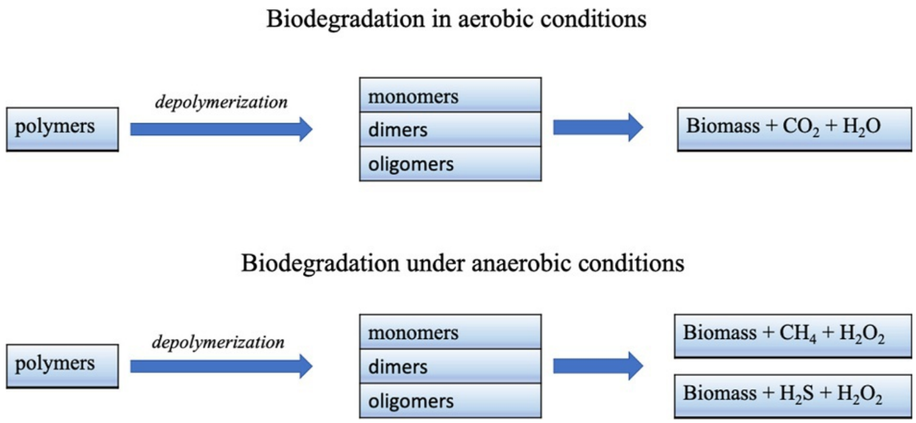

Fig. 1 Aerobic and anaerobic degradation of microplastics.

Table 1 Classification of plastics.

Abbreviations	Full name	Chemical formula	Density	Application
PET	Polyethylene terephthalate	$(C_{10}H_8O_4)_n$	1.38–1.41	– Bottles – Packaging
PE-HD	High-density-polyethylene	$(C_2H_4)_n$	0.94–0.98	– Pressure pipes – Stretch
PE-LD	Low-density-polyethylene	$(C_2H_4)_n$	0.89–0.93	– Food foils
PVC	Polyvinylchloride	$(C_2H_3Cl)_n$	1.38–1.41	– Window frames – Wire insulation
PP	Polypropylene	$(C_3H_6)_n$	0.85–0.92	– Product packing
PS	Polystyrene	$(C_8H_8)_n$	1.04–1.08	– Polystyrene pipes

4.1 Polyethylene terephthalate

Polyethylene terephthalate (PET) belongs to the class of thermoplastic polymers that are easy to form by processing methods such as pressure injection or extrusion. It is formed in the process of polycondensation of ethylene glycol and terephthalic acid and is semicrystalline. The process of thermal shaping at a temperature of 140°C gives the plastic crystallinity and resistance to abrasion. Additionally, in order to obtain better physicochemical properties, an admixture of glass fibers and carbon fibers is often used. PET materials are characterized by lightness, resistance to high temperatures and mechanical damage, a cheap production process, and a very wide range of uses in the food industry. They are most often used in the production of plastic bottles, packaging for medicines and food, or in the production of foil. The use of appropriate technology allows PET products to be reused via a recycling process; usually, this is based on the mechanical grinding of the material to a granulate fraction and its reprocessing. Clothes are made from recycled PET (sweatshirts, fleece), as are backpacks, tents, and tarpaulins. Sanitary requirements prohibit the reuse of packaging materials.

4.2 Polyethylene

Polyethylene (PE) is produced by the process of polymerization of hydrocarbons, and its physical properties are similar to that of PET (thermoplasticity, semicrystalline structure). The world production of PE for 2020 was over 110 million tons and is constantly growing. Depending on the molecular weight, there are five PE homopolymers: low-density polyethylene (PE-LD), linear low-density polyethylene (PE-LLD), high-density polyethylene (PE-HD), high-molecular-weight polyethylene (PE-HMW), and very high molecular weight (PE-UHMW). Higher molecular weight is associated with the improvement of the properties of the plastic, and such materials are characterized by increased resistance to friction, stiffness, and strength. Additionally, the molecular weight affects the electrical and dielectric properties. PE is considered a reusable material, most often used in heat-shrinkable films, as a lining for milk cartons, as well as in plastic bottles and food packaging. Additionally, it is waterproof, and resistant to petrol, alcohol, salt solutions, and acids. The most common forms of PE in mass production are PE-LD (0.910–0.925 g/cm^3, Da 40,000) and PE-HD (0.959–0.965 g/cm^3, Da 100,000–250,000). In order to improve its properties in the production of PE, glass fibers, stabilizers, and dyes are additionally used, which increases strength and resistance to UV.

4.3 Polyvinylchloride

The world production of polyvinylchloride (PVC) is in third place behind PET and PE. PVC is produced in the polymerization of vinyl chloride and its structure is amorphous. The process itself can be based on various methods, including emulsion, suspension, or mass, and the resulting products are E-PVC, S-PVC, and M-PVC, respectively. Additionally, it is classified based on density, as hard PVC and soft PVC. Products made of PVC are highly resistant to acids (including sulfuric and nitric acids), gasoline, alcohols, and oils. In addition, they are durable, and resistant to temperature changes and mechanical damage. The enrichment of the mixture with stabilizers improves the electrical properties. Many manufacturers prefer PVC because of its high fire resistance, which makes it possible to use it as a cover for cables or voltage wires. PVC is used for car gaskets, toys, bumpers, pipes, and building fittings (Crawford and Quinn, 2017).

4.4 Polypropylene

Polypropylene (PP) is a thermoplastic polymer of the polylefin family that is formed by the polymerization of propylene. Compared to PE, it is characterized by greater strength, stiffness and chemical resistance. PP can assume a semicrystalline or amorphous structure (depending on the spatial order of the CH3 groups), and it is considered one of the most versatile polymers. At a temperature of not more than 120°C, it is not affected by acids, salt solutions, or bases. PP has good electrical and dielectric properties, low absorption, and low permeability. To increase its resistance to weather conditions, it uses stabilizers to reduce oxygen degradation. In addition, spore agents, fillers (e.g., talc) and carbon black are used in the production of PP to improve its elastic properties. The use of PP is related to the properties of its individual types and is mainly based on injection, extrusion, and blow molding methods. This polymer is used to make elements of ventilation systems, food packaging, elements for washing machines, dishwashers, food processors, tar paper, sealing compounds, and sportswear. PP is a highly recyclable material; the process of its processing is similar to the recycling of other polymers.

4.5 Polystyrene

Polystyrene (PS) is a material with an amorphous structure, resulting from the polymerization of styrene, which belongs to the group of thermoplastic materials. Used and produced on a global scale in quantities exceeding 15 million tons per year in 2018, it is characterized by high hardness and stiffness, and resistance to abrasion, moisture and weather conditions. Additionally, PS has good electrical and dielectric properties. PS is relatively vulnerable to mechanical damage, cracks under mechanical loads, and is both brittle and flammable. To improve its physicochemical properties, PS copolymers and vinylcarbazole are often used in the production of PS; the enriched material shows high thermal resistance and increased toxicity. The production of PS is cheap; therefore, the scope of use of the material is very wide, including food pouches, containers for medicines, toys, plumbing fittings, elements of calculators, televisions, and many electric tools.

5 Physical and chemical factors influencing the fragmentation of microplastics

Abiotic degradation of plastic is related to the processes of hydrolysis, and photo- and thermo-oxidation, UV radiation, or mechanical stress. These processes change the properties of the material, making it more brittle or susceptible to damage. This leads to the material's airing, i.e., an increase in the surface sensitive to degradation. This is often associated with an increase in the toxicity of microplastics due to the accumulation of contaminants in fractures. In addition, the accumulation of substances can increase the specific mass of the microplastic particle, so that it sinks to the bottom, becoming more stable with regards to degradation due to the anaerobic environment, low temperature, and lack of sunlight (Rovira and Escudero, 2018).

The fragmentation of microplastics, i.e., the degradation process, takes place as a result of environmental factors such as temperature, light, water, or air, and is based on the processes of photo-oxidation, hydrolysis, mechanical friction, or oxidation. The degradability is considered to be the weakness of the material; therefore, modification of the polymers has led to the formation of a plastic with a low degradation index (Wagner et al., 2014).

Atmospheric oxidation is related to the process of oxygen catalyzing the decomposition of some polymers, including the removal of hydrogen chloride and the formation of double bonds in the structures of PVC chains. This process is limited only to surfaces exposed to atmospheric oxygen and, under favorable conditions, it can reach a depth of 1 mm into the polymer. Water currents, waves, and factors influencing the physical abrasion of the material are also important here, thanks to which the oxidation process takes place to a greater extent.

Thermal degradation is the process of degradation of plastic due to the action of temperature and consists of three successive stages: initiation, propagation, and termination. Initiation is the process of breaking down polymer chains as a result of providing a specific thermal energy and the formation of radicals (reactive molecules). In the next stage, the radicals react with the atmospheric oxygen to form peroxy radicals, which, when decomposing, generate peroxide and alkoxy radicals. This process continues uninterrupted until it is completed, in which case, either thermal energy or oxygen is lost. The temperature at which the process of thermal degradation begins is specific for each type of material (Wagner et al., 2014).

Photo-oxidative degradation is an extremely important factor influencing the decomposition of microplastics in the aquatic environment under the influence of ultraviolet radiation. The presence of chromophore groups susceptible to UV radiation in the structures of photoreactive materials leads to the breaking of chemical bonds inside these polymers, especially in the UV-B wavelength range of 280–315 nm. This significantly affects the deterioration of the mechanical properties of the material and manifests itself in increased brittleness and cracking. One can observe yellowing of the materials and their tarnishing. High resistance to UV radiation is demonstrated mainly by PVC and PTFE, as is the sensitivity of PS and PA.

The vast majority of plastics show negligible water absorption, which prevents the hydrolysis process from taking place. In the case of PA, the water absorption is higher and can result in diffusion of water into amorphous regions of the polymers where its molecules can attach to the chain, thereby breaking the chemical bonds and weakening the material (Vezzulli et al., 2013). Plastics in the environment are constantly subjected to various mechanical stresses caused by sea currents, waves, and collisions with other materials or elements of the natural environment. These stresses are most often crushing, shearing, twisting, and abrasion. All these factors contribute to the weakening of plastic structures and their physical degradation. The material strength can be determined on the basis of the tensile at break parameter in the percentage range and, in the case of brittle materials, it is usually from 4% to 8%, while linear PE obtained over 900%, which means extremely high resistance to physical tearing and deformation (Wagner et al., 2014).

6 Biodegradation in microplastics fragmentation

Plastic biodegradation is a process that occurs as a result of the action of many environmental factors with the participation of microorganisms, including bacteria and fungi. These organisms are able to derive their food and energy from nitrogen and carbon contained in polymer structures. The degree of microplastics degradation depends on the type of polymer or its size and can be up to 1000 years (Vezzulli et al., 2013). This process takes place both in aerobic and anaerobic environments, usually has a two-stage form, and its course is additionally influenced by factors such as ambient temperature, pH, and access to oxygen or sunlight. In the first stage of microplastics degradation under the influence of oxygen, moisture, light, or enzymes of microorganisms, the bonds between carbon atoms are broken, which results in fragmentation of the polymer chain. The depolymerization of the material leads to the formation of, inter alia, environmentally friendly monomers. In the second stage of biodegradation, the resulting particles can be absorbed by microorganisms and broken down to generate energy. The end products can be water, carbon dioxide, biomass, or methane (Henderson and Green, 2020).

The knowledge about the degradability of plastics is still not very large, which demonstrates the need to conduct research in this field. Currently, research is being carried out on strains of *Ideonella sakaiensis*, which show the biodegradability of PET (polyterephthalene), and *Galleria mollonella* caterpillars, which show the ability to digest PE (polyethylene) (Henderson and Green, 2020).

7 The role and fate of microplastics in water biota

The presence of microplastics has been confirmed in many places around the world, including those uninhabited by humans and having the status of national parks. In addition, research has shown the participation of microplastics in the Arctic ice caps and in the circumpolar zones. This is due to the mobility of microplastic particles in the aquatic environment and in the atmosphere, where pollution can be transferred several hundred kilometers (Tanaka et al., 2013). Huge amounts of plastic of various sizes (from millimeter-sized particles to waste more than a meter in diameter) make up the Great Pacific Garbage Patch, discovered and described by Charles Moore in 1997. Located between California and Hawaii, it has an estimated size of 1.6 million km^2 and contains approximately 129,000 tons of plastic (Zettler et al., 2013). Studies have shown that the vast majority of this waste is photodegradable plastic, which over time decomposes into dust less than 1 mm in diameter, which increases its transmission many times. Despite its origin and properties, this garbage has become a refuge and home for a large number of sea creatures, including fish, small invertebrates and flying birds. Although the concentration of microplastics in this area is very high, the negative effects of the presence of particles in the aquatic environment have also been documented elsewhere, which is becoming the subject of debate about effective methods of removing microplastics from the marine environment (Tanaka et al., 2013). The presence of rubbish clusters of various sizes and the influence of abiotic factors increase the possibility of ingestion of fragmented particles by marine organisms. In addition, these particles are characterized by a variety of shapes, colors, and sizes, which makes them attractive as food. It is also important that microplastic dust, due to the different density and buoyancy, is at different depths; surface, near-surface, and deep-sea particles have all been described. Due to the way microplastics are absorbed by marine organisms, we distinguish between accidental and deliberate consumption (Zettler et al., 2013).

Accidental ingestion most commonly affects organisms that feed through water filtration (filterers) and those that ingest microplastics present on plant parts or in other organisms, also known as passive microplastic ingestion. In the group of these animals, we distinguish mollusks, crustaceans, seabirds, and cetaceans, including whales. For some of the organisms mentioned, the microplastics contained in the intestines pose a risk related to mechanical damage and the possibility of permanent accumulation of microplastics (Collignon et al., 2012). There have been documented cases of predatory fish containing microplastics in their meat coming directly from the bodies of their victims, which indicates that humans are also at risk of being adversely affected by microplastics when consuming fish and seafood. So far, the studies have neither confirmed nor disproved such a possibility, however, this may be related to examining too small a group of individuals. Microplastic fragments have most often been found in ocean herring (*Clupea haregus*), horse mackerel (*Trachurus trachurus*), and also inside blue mussels (*Mytilus edulis*).

The deliberate consumption of microplastics is mainly related to the similarity of particles to natural food, especially in the case of omnivorous organisms. Identifying a natural prey can be very difficult in the presence of a variety of microplastic particles that shelter a potential prey (Boland and Donohue, 2003). Research has shown that for animals that are mainly driven by their eyesight during hunting, bright colors seem to be an encouragement to attack or try what an object is, due to natural evolutionary curiosity. Species with confirmed misdiagnosis of prey include *Phalaropus fulicarius* or *Puffinus gravis*. There was also a correlation between the concentration of microplastics and age in shearwaters. It turned out that higher consumption of microplastics occurs in chicks, which may be related to the regurgitation process, i.e., feeding the offspring with content transferred from the stomach to the esophagus. Additionally, it may be associated with less experience of feeding in chicks and efficiency in removing larger contaminants by the young bird (Zettler et al., 2013).

8 The effect of microplastics on living organisms

The effect of microplastics on living organisms is an extremely problematic and complex issue that must take into account the natural physiology of organisms, the effects of microplastic toxicity, mechanical damage, and the role of microplastics in organisms exposed over the long term. It is extremely difficult to determine which of the factors is the most harmful, due to the possibility of accumulation and different concentrations in specific studied regions (Le Roux et al., 2015).

Analyses so far have focused mostly on mechanical damage caused by the ingestion of microplastics, weight loss, and reduced fertility, but more and more attention is being drawn to the chemical risk associated with the high toxicity of the primary microplastic material.

The constant modification of plastics and the production of new ones means that more than 40,000 different chemical pollutants resulting from the degradation and biodegradation of plastics have been distinguished, and the pool is being increased by another six to seven substances every day. Desired material properties, such as abrasion resistance, UV resistance, or increased strength, make these particles extremely durable, which is why they are called persistent organic pollutants (POPs), and in combination with their toxicity, they have become a real threat to individual species and entire populations This led to the signing of the Stockholm Convention in 2001 and attempts to impress an enduring legislation on pollution. At that time, the division of substances into three groups was distinguished. The first annex contains substances that are strictly prohibited, the second annex, those whose use will be restricted, and the third annex includes regulations concerning direct releases into the aquatic environment. The most documented threats to organisms are phthalates, polycyclic aromatic hydrocarbons, organochlorine pesticides, bisphenols A, and brominated combustion retardants (Thevenon et al., 2011). They are often used as pesticides, insecticides, cooling liquids, pigments, or resin components (Collignon et al., 2012).

These compounds cause, inter alia, increased cracking of bird eggs, liver damage in mammals, cancer, and hormonal disorders. Microplastics act as carriers (vectors) of toxic compounds, which is favored by their high ratio of surface area to volume. Studies have shown that microplastic particles can carry several different toxins capable of causing histopathological disturbances and glycogen depletion in the tested aquatic organisms (Hirai et al., 2011).

Damage resulting from ingestion of microplastics by aquatic organisms is directly related to the species, type, and amount and size of the ingested particles. These injuries may be a temporary disturbance of physiology, long-term, chronic and increasing symptoms related, inter alia, with accumulation and, in special cases, indirectly lead to the death of the individual (Hirai et al., 2011).

One of the first reported parameters related to the swallowing of plastic particles is weight loss and the reduction in growth rate. This is due to the apparent feeling of fullness and reduced absorption of nutrients. In addition, studies conducted on invertebrates have shown that the growth rate can be reduced by 4% –20% (Le Roux et al., 2015).

Microplastic present in the digestive tract deteriorates the general condition of the body, causes ulceration, and by covering the intestinal walls, it also affects digestion. In the case of mussels, Japanese turmeric and copepods, reproductive disorders and a reduction in the number of offspring have been documented (Rochman et al., 2020).

Another disturbing effect of swallowing microplastic is its ability to remain in the tested organisms and accumulate in tissues like worms (Fig. 2). In this case, the influence of the microplastic of the finest fraction, often called nanoplastic, is considered. It has been confirmed that such fine dust has the ability to penetrate biological membranes; therefore, its transmission can take place throughout the body (Zettler et al., 2013). Many

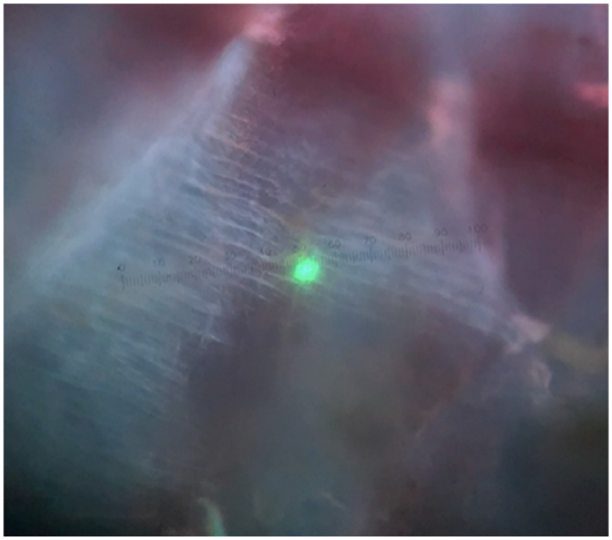

Fig. 2 Microplastic particle size 45–63 um in the muscle tissue of an earthworm (*Dendrobaena veneta*) after 30 days of exposure.

studies document the presence of fine microplastics in organs such as the eyes, brain, kidneys, liver, and also in muscle tissue (Thevenon et al., 2011). The correlation between the time necessary for the accumulation of microplastics, its concentration, type, and the species tested is not known so far, however, studies of soil organisms indicate that it may occur after about 21 days of exposure to a 1% contamination (Le Roux et al., 2015).

9 Summary

Global plastic production in 2019 exceeded 368 million tonnes, and the demand for plastics continues to grow. Low production costs and wide use of plastic mean that it is used in almost all industries. Despite the increasing number of appeals to limit the use of plastic and to produce biodegradable plastics, plastic is still the basic production material. Additional modifications aimed at improving the properties of the material are often associated with a longer period of degradation (Hirai et al., 2011).

A lot of polymer products have a very short period of use and then become useless, such as plastic cups, food packaging, foil, cutlery, or bottles. Some of them are reused, but most end up in landfills (Frias and Nash, 2019).

As a result of biotic and abiotic factors, plastics are subject to degradation, which is a direct cause of the formation of secondary microplastics. An additional threat to the natural environment are also primary microplastics, the source of which are, among others, the cosmetic industries, using polymer microgranules in toothpaste, abrasives, or soaps.

The concentration of microplastics, both on land and in the aquatic environment, increases every year, and in a highly urbanized environment its concentration may exceed the permissible standard many times. Research on the presence of microplastics most often focuses on the marine environment, where these particles pose a much greater threat to the diversity of organisms. It has been confirmed that microplastics are ingested by small organisms, due to being mistaken for food (Tanaka et al., 2013). Additionally, plastics often exhibit toxic properties, which contribute to their lethality to organisms (Rochman et al., 2020).

At least eight different types of microplastics have been classified, based on their shape, chemical composition, or morphology, including microspheres, synthetic fibers, marine net fibers, pellets, films, soft granules, or resins. In addition, the division according to the size of the particles themselves has been described, distinguishing nanoplastic, microplastic, mesoplastic, and megaplastic. This definition applies to both microplastics present in the aquatic and terrestrial environments (Frias, 2019).

The degradation of microplastics in an aqueous environment is a long-term process and depends on many factors such as temperature, light, mechanical stress, or the presence of microorganisms (Rochman et al., 2020). In addition, the efficiency of degradation is influenced by the type of polymer of which the material is composed, its size, and shape. Studies have shown that the degradation of larger plastic particles leads to the formation of a significant amount of microplastic, which can be transported by sea currents or wind over very long distances. Additionally, airing of microparticles creates fissures in which substances such as biomass and other contaminants can collect, causing the microplastic to sink to the bottom, often in silt or clay soil. The conditions there are not conducive to complete degradation; therefore, microplastics on the bottom are a real threat (Hirai et al., 2011). Most relevant to the development of research on the presence of this type of pollutant in ecosystems is the fact of the slow degradation and biodegradation of plastic in the environment and the increase in its concentration. Methods of quick detection of microplastics from soil or water and its removal are still unknown. It is recommended to conduct laboratory tests using a higher concentration of microplastics in water or soil to better visualize the effects on plant and animal organisms (Tanaka et al., 2013).

The resilient development of the economy, constant modifications of the chemical composition of waste plastics, and the lack of awareness of rational waste management are undoubtedly a global problem that may turn out to be an ecological disaster on an unprecedented scale in the future. The amount of waste deposited in uncontrolled landfills may become a problem in terms of many years of soil contamination with many microplastic fractions at the same time. The exact influence of the smallest fraction not exceeding 500 μm on plants or animals is not known, however, it has been confirmed that it is often ingested by animals inhabiting the soil, absorbed by plants, and accumulated in tissues (Hirai et al., 2011). This constitutes an additional threat panel and surely research should be directed for faster detection and removal of microplastics from both soil and aquatic environments (Collignon et al., 2012).

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CHAPTER 9

Halotolerant and halophilic bacteria present in the mangrove ecosystem: Emerging Bioengineering potentials

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1 Introduction

Mangrove ecosystems are predominantly found in the deltaic and riverine regions. They are dominant around 70%–75% of the subtropical and tropical stretches. They are found to prevent soil erosion, prevent the region from tsunami and high tides, and prevent the coastline and safeguard the residents residing in the riverine location. This region also acts as a sink where all unwanted toxins, pesticides, insecticides, agrochemicals, and other chemical discharge from the industrial belt, urban settlements, and adjacent regions get accumulated (Dutta and Bandopadhyay, 2022). Apart from aiding various ecological benefits, mangroves do have substantial commercial benefits. This region serves as the breeding grounds of varied kinds of aquatic species and nurseries for fish and other marine organisms. The marine ecosystem is the region of blending fresh and marine water, which is why this region contains a considerable number of salt-tolerating and salt-loving microbes that possess biotechnological potential (Thatoi et al., 2020). The mangrove ecosystem is both an ecologically and economically important resource. The mangrove ecosystem plays a significant role in nutrient recycling and regeneration of nutrients in its native form. As opposed to other ecosystems, the mangrove environment is distinguished by a mangrove swamp, which is brought on by elements like high tide and mudflats immersed in tidal water (Hochard et al., 2021). Additionally, the high salt concentration of mangrove water makes it ideal only for the growth of halophilic and halotolerant microorganisms.

Microbes in this region include a varied range of bacteria, algae, fungi, protozoa, and other primitive microorganisms which are found in water, rocks, shores, and other regions, and these organisms have certain ecological purposes. These are found along with other symbiotic organisms present in that region. The microbial population aids in the

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breakdown and mineralization of leaf litter leading to the productivity of the mangrove ecosystem (Mai et al., 2021). Complex interactions between these bacteria help maintain the harmony of numerous biogeochemical processes as well as the ecological balance and nutritional status. Bacteria and fungi comprise most of the biomass in tropical mangroves, and protozoa and algae are the minor players. Microorganisms that are halotolerant may survive both in the presence and in the absence of salt, whereas halophiles prefer the presence of salt. While halotolerant microorganisms create enormous volumes of organic solutes like glycerol in a salt-dependent way, halophilic microorganisms adapt by preserving osmotic equilibrium and accumulation of organoosmolytes. Microorganisms that grow, flourish, and can survive in a wide range of severe conditions such as high pH, high salinity, and varying temperature are known as poly-extremophilic halophiles. *Desulfonatronospira thiodismutans* and *Deltaproteobacteria* sp. can flourish well in higher alkaline and saline conditions in the mangrove ecosystem. *Methanopyrus kandler* and *Halorhabdus utahensis* are two well-known and severe halophiles that can thrive in high temperatures. The bioactive compounds that are produced by haloalkalothermophiles are one of the main reasons why they can survive extremes. *Halobacillus halophilus* shows strategies for dealing with extreme saline conditions in the mangrove ecosystem. The light-chloride pump that is controlled by the presence of natural light in the bacteria *Halobacterium* produces significant amounts of glycerol; an organic solute in *Dunaliella* sp. maintains a low concentration of salt in both their chloroplast and cytoplasm region. Due to their capability of the halophilic and halotolerant bacteria to adapt to high salt concentrations and high alkaline environments, these microorganisms possess enzymes and salt-tolerant genes that are extremely important and fascinating for the biotechnology research field and have found application in the pharmaceutical industry, medicine industry, and agriculture. However, extensive research has not been done in this field, and their biotechnological potential is yet to be discovered. Therefore, a thorough study and documentation of the biotechnological potential of mangrove microorganisms with salt tolerance capabilities are required. Our chapter tends to deliberate and provide insights into different biotechnological potentials of halotolerant and halophilic species isolated from the mangrove ecosystem (Fig. 1) (Thatoi et al., 2020).

1.1 Mangrove ecosystem and its importance

Mangroves are distinctive intertidal ecosystems found in tropical and subtropical areas of the world. These plants grow in swampy coastal wetlands with brackish to saline tidal waters and are distinguished as halophytic (salt-loving) trees and shrubs (Hochard et al., 2021). There are hundreds of species of algae, mollusks, crustaceans, fish, insects, reptiles, birds, and mammals in mangrove forests, making them a habitat with extraordinary biological richness (Worthington et al., 2020). The world's mangroves comprise approximately 1,50,000 km^2. The majority of the world's mangroves are found in Asia. 6.8% of the world's mangrove cover lies in South Asia. India contributes to about 45.8%

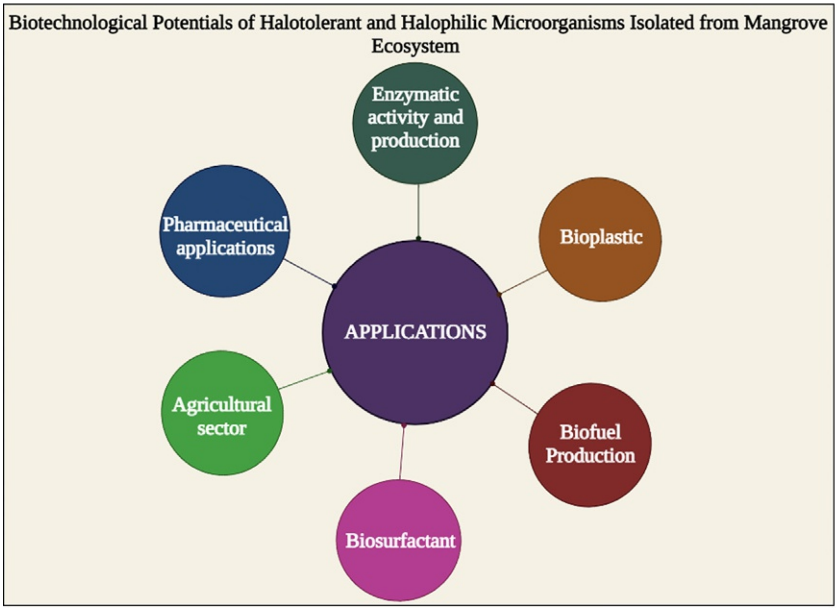

Fig. 1 Various applications of halotolerant and halophilic bacterial species isolated from the mangrove ecosystem.

of South Asia's total mangrove cover (Worthington et al., 2020). The world's largest mangrove forest is the Sundarbans spread over almost 10,000 km^2 across India and Bangladesh. The second-largest mangrove forest in the world is located at Pichavaram in Tamil Nadu, India, typically spread across 2800 km^2. Florida has the largest mangrove forest in the United States covering over 2700 km^2. On Panama's Pacific coast, near the Bay of San Miguel, are the mangroves of the Gulf of Panama covering about 2330 km^2. North-eastern Brazil houses the Bahia mangroves covering close to 2100 km^2 (including the area of land and sea). On the Pacific side of Ecuador's coastline are the Manabi mangroves spread over 1000 km^2.

Mangroves shield the coastal region from powerful storms or cyclones. They protect neighboring populated areas from erosion and the effects of storm surges during major weather events like hurricanes by acting as natural infrastructure (del Valle et al., 2020; Hochard et al., 2021). They are a wonderland for creatures that require specific environments. It is also a huge carbon storage area, which is crucial (Rahman et al., 2021).

A diverse array of plants, animals, and microorganisms can be found in the mangrove forests, especially as the terrestrial and marine habitats converge (Yeo et al., 2021). Microbes are crucial to the productivity of the mangrove ecosystem through their participation in the decomposition and mineralization of leaf litter (Mai et al., 2021). These bacteria interact in complex ways to preserve the ecological balance, nutritional condition, and harmony of many biogeochemical processes. Protozoa and algae constitute only 2% and 7%, respectively, of the total microbial biomass in tropical mangroves, whereas bacteria and fungi account for about 91% of the total microbial biomass in tropical mangroves (Fig. 2) (Mai et al., 2021).

The mangrove microbiota primarily comprises sulfate-reducing bacteria (*Desulfovibrio, Desulfococcus* sp.), N_2-fixing bacteria (*Azospirillum, Azotobacter, Rhizobium* sp.), phosphate-solubilizing bacteria (*Bacillus, Xanthobacter, Enterobacter*), many kinds of fungi, including actinomycetes and ligninolytic, cellulolytic, pectinolytic, amylolytic, and proteolytic fungi. The mangrove ecosystem is dominated by algal taxa such as *Chlorophyta*, *Cyanophyta*, *Rhodophyta*, and *Chrysophyta* (Allard et al., 2020; Mai et al., 2021).

High-throughput sequencing has recently provided a thorough understanding of the microbiota of the mangroves (Mai et al., 2021). It has been documented that bacteria in the sediments play a key role in the adaptability and succession of mangroves in intertidal areas. The depth of the soil layer, pH, salinity, and nutrient availability all have a strong correlation with soil features, including the benthic microbial population (Allard et al., 2020). Additionally, bacteria in sediments perform significant biogeochemical roles (such as those in the C, N, and S cycles), which help mangroves survive in intertidal areas (Rahman et al., 2021).

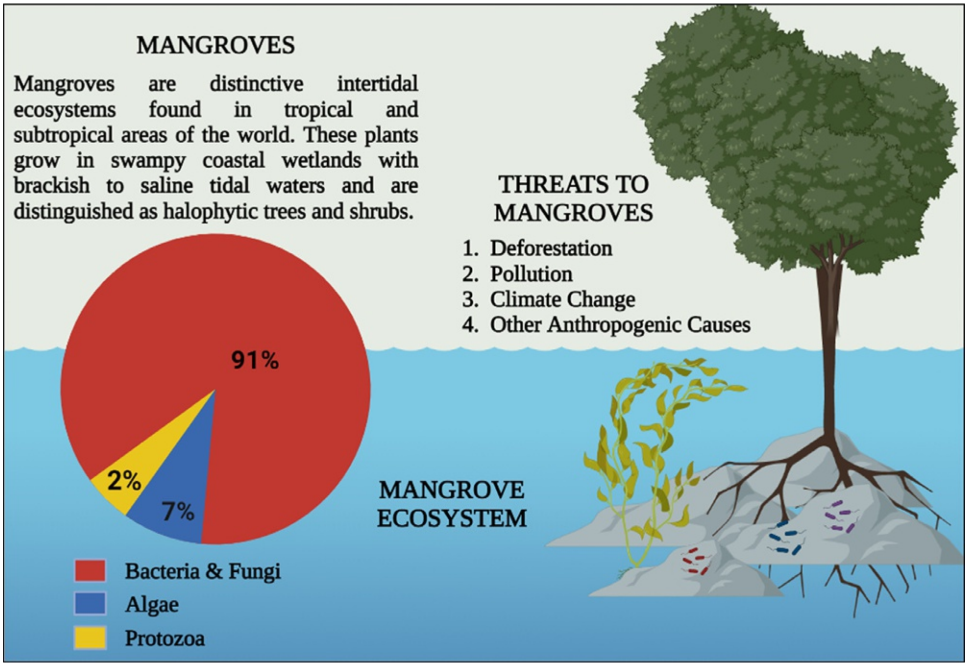

Fig. 2 Population diversity index predominantly found in mangrove forests.

1.2 Metabolites from mangroves

Mangrove microorganisms have a wide range of enzymatic activity and can use unique enzymes to catalyze a variety of biochemical activities. Particularly, halophilic bacteria have an abundance of hydrolytic enzymes (amylases, nucleases, phosphatases, and proteases) and can function in environments where the majority of proteins precipitate or become denaturized (Tavares et al., 2021). Currently, there is an economic interest in the hydrolase enzymes produced by halophilic bacteria. Erythromycin, rapamycin, tetracycline, lovastatin, and resveratrol are examples of secondary metabolites that are biosynthesized by a class of enzymes known as polyketide synthases (PKSs), which have all been identified and purified from halophilic bacteria (Santhaseelan et al., 2022). Mangroves are biochemically distinct and produce a wide range of natural compounds with distinctive bioactivity when growing in this harsh environment. They have chemically new active metabolites with various chemical structures, including alkaloids, phenolic compounds, steroids, tannins, and terpenoids (Tavares et al., 2021).

People have long used mangrove plants as traditional medicines, preferring the bioactive components from its secondary metabolites to cure a variety of illnesses. To prevent oxidative stress, mangrove secondary metabolites may be used as an antioxidant. Endophytic bacteria with the capacity to produce secondary metabolites usually dwell in the tissues of mangroves (Santhaseelan et al., 2022). Natural substances produced by microbes are significant sources of numerous medications that are being used extensively to treat a wide range of illnesses and infectious agents, including cancer, immunosuppression, bacteria, and viruses (Rahmawati et al., 2019). Actinomycetes that have been identified from mangrove ecosystems are a potentially valuable source for the development of antiinfection and antitumor drugs as well as diabetic and neurodegenerative disease therapeutics (Allard et al., 2020).

Many commercial species of marine and terrestrial organisms include young reef fish, find food, breeding grounds, and nursery sites in these forests along the land-sea interface (Worthington et al., 2020). Despite mangroves being important, they are being lost at a rate of 1%–2% per year globally, and the pace of loss has increased to 35% during the past 20 years (Worthington et al., 2020). Major threats to mangrove habitats include climate change (sea-level rise and changing rainfall patterns) and human activity (urban growth, aquaculture, mining, and overexploitation of timber, fish, crustaceans, and shellfish). Typically, habitat loss is accompanied by a decline in biodiversity. Lower biodiversity and altered ecosystem processes have been evidenced in disturbed mangrove ecosystems (Allard et al., 2020).

Mangrove endophytes are unique in that they have special characteristics that let them endure in the tough mangrove habitat. They are appealing candidates for bioprospecting due to their capacity to create novel bioactive substances and enzymes (Tavares et al., 2021). More research on mangrove endophytes is required to address their involvement in the abiotic and biotic stress tolerance of mangroves, especially in light of the endophyte-mediated enhancement of plant performance in other habitats (Santhaseelan et al., 2022). Humans should be warned that mangrove forest areas are shrinking and that resources are getting exhausted. It is time to educate the public and take appropriate action.

1.3 Halophilic and halotolerant microorganisms

Mangroves are home to millions of microorganisms such as algae, fungi, bacteria, cyanobacteria, and fungus-like protists. In turn, these microbes play an essential role in maintaining these mangroves. The widely prevalent microorganisms in these regions are *Desulfovibrio*, *Desulfotomaculum*, *Desulfosarcina*, and *Desulfococcus* sp. These microbes act as sulfur-degrading microorganisms and thrive under extreme conditions of pH, temperature, and salinity and are considered as poly-extremophilic microorganisms. Methanogenic microorganisms like *Chloronema*, *Thiopedia*, *Leucothiobacteria* sp., *Beggiotoa*, *Methanopyrus kandler*, and *Halorhabdus utahensis* are also present in mangroves and are extremely halophilic and hyperthermophilic (Holguin et al., 2001). Halotolerant microorganisms are those that can sustain themselves in the present as well as the absence of salt whereas halophiles thrive in the presence of salt. Halophilic microorganisms adapt by maintaining osmotic balance accumulation of organoosmolytes whereas halotolerant microorganisms form huge volumes of organic solutes like glycerol in a salt-dependent manner.

The mangrove ecosystem can be differentiated from other ecosystems as it is characterized by a mangrove swamp which is attributed to features such as high tide and mudflat submerged under tidal water. Furthermore, mangrove water has a high salt content and thus is suitable for the growth of only halophilic and halotolerant microorganisms (Akpan-Idiok and Solomon, 2012). According to the recent studies, Gram-negative halophilic and halotolerant bacteria are more dominant in saline environments as compared to Gram-positive halophilic and halotolerant bacteria. *Bacillus* and *Micrococcus* sp. are the most dominant among the Gram-positive halophiles in saline environments. Halotolerant and halophile microorganisms are widely distributed over hypersaline environments such as saline lakes, marshes, pans, and saline soils. They are majorly classified based on their salt prerequisites such as slight halophiles, moderate halophiles, and extreme halophiles, and grow optimally at 0.2–0.85 M, 0.85–3.4 M, and 3.4–5.1 M respectively.

Some of the halophilic and halotolerant microorganisms studied have been enlisted in Table 1.

The structured utilization of halophilic microbial diversity in the mangroves can have a profound effect in the field of biotechnology, especially in the industrial-scale manufacturing of medicines, enzymes, and biofertilizers. The unique properties of halophilic microorganisms make them suitable for use in biotechnological industries. Thus, the biotechnological potential of halophilic and halotolerant microorganisms and their application in the industry needs to be studied more extensively.

Table 1 Overview on different halophilic and halotolerant species isolated from mangrove ecosystem and their respective industrial applications.

Source organism	Compound/enzymes	Applications	Mangrove system	References
Halococcus agarilyticus, Halobacterium sp., *Haloferax mediteranei, Natrial bamagadii, Natromonas pharaonic*	L-asparaginase	Protease production for leather industries, food, and dairy industries	Sundarbans	Gaonkar and Furtado (2018)
Actinopolyspora sp.	Glycine betaine and trehalose	Antibiotic production	West coast of India	Kokare et al. (2004)
Haloarcula sp.	Polyhydroxyalkanoates (PHAs)	Amylase production, petrochemical based synthetic thermoplastic	Northern Vietnam	Van-Thuoc et al. (2012)
Bacillus sp.	PHA	Food, the textile and brewing industry	Northern Vietnam Mangrove rhizosphere of the Sundarbans	Siroosi et al. (2021)
Rhodococcus sp.	Protease	Industrial scale production of enzymes	Chanthaburi, mangrove forest, eastern Thailand	Thatoi et al. (2020)
Marinobacter sp., *Chromohalobacter canadensis, Streptomyces* sp.	Amylases, lipases, proteases	Carbon recycling in the ecosystem, the industrial scale production of enzymes	Mangrove of Guanabara Bay, Brazil Seacoast of Kozhikode, Kerala Coast of Goa Nagoa, Diu Somnath, Gujarat Triveni Sangam, Gujarat	Kumar et al. (2012)
Vigribacillus sp.	Chromate reductase	Bioremediation	Bhitarkanika mangrove	Mishra et al. (2012)

2 Biotechnological potentials and applications of halotolerant and halophilic microorganisms

2.1 Enzymatic activity and production

Enzymes are catalysts that enhance the metabolic activities of living organisms. Mangroves produce a variety of novel microbes having significant biotechnological activities. Owing to their higher yield and low production costs, microorganisms make excellent sources for the synthesis of enzymes (Corral et al., 2019). Microbial enzymes have vast applications in different sectors by virtue of their affordable manufacturing costs, environmental friendliness, lack of ethical issues, and easy characterization. It is observed that the enzymes extracted from the marine microbes are more active and effective as compared to their corresponding ones extracted from any other organism. *Bacillus* is the most effective enzyme-producing genus of all. The major commercially important hydrolytic enzymes are amylases, lipases, keratinase, cellulases, and proteases.

- Amylase—The core enzymes that play a role in carbohydrate digestion can be used in the pharmaceutical industries against digestive problems followed by other industries like textile, detergent, food processing, and chemicals. Amylase is used for the diagnosis of acute pancreatitis.
- Lipases—This enzyme functions by breaking down fat and utilizing it as a source of energy for the body. In an experiment on thermohalophilic bacteria, lipase had a specific activity of 326.6 U/mg and a molecular weight of 50 kDa. It is predominantly used in the detergent, additives (taste/flavor modification), pharmaceutical, cosmetic, oleochemical, and fat processing sectors, and also for wastewater treatment (Oren, 2010).
- Keratinase—The proteolytic enzyme that has the ability to eradicate keratin is regarded as being extremely important in many biotechnological techniques because of their resilience in handling resistant substrates and discernible stability under adverse environments. When a microbial producer is exposed to a keratinous substrate, keratinases are typically released extracellularly, however findings of cell-bound and internally generated keratinases have also been recorded. Keratinase exhibits special features that can be used in bioprocessing, including the bioconversion of keratin into usable products, the treatment of textiles, the depilation of leather, and other commercial uses (Van-Thuoc et al., 2012).
- Cellulase—Cellulases are a complex group of enzymes that catalyzes the degradation of cellulose polysaccharide by disintegrating the β-1,4-glycosidic linkages. Out of the 10 real cellulase families, there are seven distinct protein folds, making cellulases the most diversified class of enzymes that aids the single substrate hydrolysis. Cellulases can be classified into three different types, majorly endoglucanases, exocellulase, and processive endoglucanases each of which has unique structure and mechanism of action. There are numerous industrial applications of cellulase. The textile wet processing, biostoning of denim fabric, biopolishing of textile fibers, softening of clothing, and removing excess dye from fabrics, the paper industry includes a few of the key applications of cellulase in the textile industry (Santhaseelan et al., 2022).

- Protease—The protease family of enzymes plays a major role in hydrolyzing the peptide bonds into shorter polypeptides or amino acids. Proteases that are of microbial origin are highly suitable for biotechnological applications because of their high yield, minimal time consumption, fewer space constraints, sophisticated genetic manipulation, and cheaper cost (Ramezani et al., 2015). Also, proteases from microbial origin have a far fewer chance of contamination as compared to other sources.
- Chitinase—The enzyme responsible for degrading the glycosidic bonds in chitin majorly contributes to generating carbon and nitrogen for the ecosystem. Its applications include waste management in the food industry (Harris et al., 2019).

The other two worth mentioning enzymes are L-asparaginase and L-glutaminase. They function by hydrolyzing asparagine and glutamine respectively into their acids and ammonia (Banerjee et al., 2019). Both enzymes are proven to be promising in the treatment of acute lymphoblastic leukemia and tumor cells. Microorganisms are considered to be the best source due to large-scale production despite it causing immunological responses in the long run. Most of the tumor cells lack the capability to produce L-asparagine and thus it has to be supplied externally for optimum growth. When the L-asparaginase enzyme is incorporated, it prevents the production of asparagine by cleaving it into L-aspartic acid and ammonia, thus retarding the growth and sometimes selectively killing the tumor cells. Similarly, there are certain tumor cells that have the inability to produce glutamine due to their insufficient enzymatic pool. For such cells, L-glutaminase majorly contributes to preventing the further maturation of the tumor cells (Table 2) (Shirazian et al., 2016).

Table 2 Different enzymes and their application, produced by halophilic and halotolerant bacteria.

Bacterial species	Enzyme	Applications	References
Staphylococcus sp.	Amylase	Medical, detergent, and food industry	Prathiba and Jayaraman (2018)
Ochrobactrum pseudogrignonense	Lipase	Pharmaceutical and cosmetics industry	Barnard et al. (2010)
Microbacterium arborescens	Protease	Prevent contamination in fermentation	Barnard et al. (2010)
Bacillus sp.	Chitinase	Agro-industrial sectors	Halder et al. (2016)
Bacillus licheniformis	Keratinase	Biofertilizers and detergents	Javid et al. (2020)
Streptomyces sp.	Cellulase	Food, textile, and biofuel industry	Elazzazy et al. (2015)
Pseudomonas ovalis	L-asparaginase and L-glutaminase	Treatment of tumor cells and antiviral application	Amiri et al. (2016)

2.2 Pharmaceutical applications

Microbial population is extremely vital for human existence and is also regarded as a vast resource pool that can be used for the greater good of humanity. The ability of certain organisms to survive in harsh environments in comparison to the other organism on earth fascinates due to their harsh physiological characteristics, adverse growth conditions, and the synthesis of beneficial bioactive compounds. Marine sources offer excellent opportunities for creating potential therapeutic compounds since they are abundant in metabolites with antioxidant characteristics (Thatoi et al., 2020). A diverse range of plants, animals, and microorganisms can be found in mangrove forests, where terrestrial and marine habitats converge. Halophilic and halotolerant bacteria are considered as important and reliable sources for tumors having lesser side effects on the body. Many halophilic bacteria living in the mangrove ecosystem show the ability to produce various secondary metabolites that are crucial precursors for drug formation. These bacteria serve as a competent alternative to plant cells for obtaining anticancer natural products. Bacterial metabolites have been regarded as the most traditional strategy against the viability of cancer cells, despite the fact that experimental data suggests that bacterial cells have alternative ways of communicating with tumor cells than metabolites (Corral et al., 2019). In a cytotoxic assay conducted on human hepatic cell line Bel 7402, 45 halophilic bacterial strains with 14 crude extracts were examined and demonstrated IC_{50} of 500 g/mL. Five out of the total demonstrated significant activities with IC_{50} lower than 40 g/mL (Chen et al., 2010). Biosurfactants are active substances that break up surface tension and are produced at the microbial cell surface or discharged by the microbes. It has been noted recently that these biosurfactants also carry several medicinal and pharmaceutical applications. Biosurfactants derived from the halophilic bacteria *Bacillus* sp. BS3 and *Halomonas* sp. BS4 were observed to significantly (P .05) lower the survivability of mammary epithelial carcinoma cells to 24.8% and 46.8 at dosages of 0.25 and 2.5 g/mL, respectively (Donio et al., 2013). Usage of antibiotics have increased to a threatening level over the past few decades leading to the occurrence of multidrug-resistant bacteria (MDR) that has successfully decreased the effectiveness of the antibiotics against human diseases. Halophilic bacteria are considered to have potential antimicrobial effects against the pathogens. For instance, halophilic strains of the genus *Vibrio*, such as *Vibrio* sp. A1SM3-36-8, synthesize 13-*cis*-docosenamide with specific antibacterial activity against methicillin-resistant *Staphylococcus aureus* (MRSA) and cytotoxic activity against cervical adenocarcinoma (SiHa) and pneumatic cancer (A-549) (Mukherjee et al., 2019). Another study to be referred was conducted on the soil samples from Marakkanam saltern and Pichavaram mangrove forest, India where the methanolic extracts of halophilic bacteria *Bacillus* VITPS12 and *Planococcus maritimus* VITP21 were assessed to check their antioxidant and anticancer activities. Assessment of the cellular viability using the 3-(4,5-dimethylthiazol-2-yl)-2,5-diphenyltetrazolium bromide assay, and the antioxidant activity of the metabolic extracts were assessed using the DPPH (2,2, diphenyl-1 picrylhydrazyl), reduction power, and metal ion chelating assays. UV-visible spectrophotometry and 1H NMR spectroscopy have shown that the methanolic extracts include certain metabolites, such as total flavonoid and -carotene, which support their anticancer and radical scavenging properties (Prathiba and Jayaraman, 2018). The isolation of actinomycetes from mangrove ecosystems has great promise toward the development of new antiinfection and antitumor drugs as well as diabetic and neurological disease therapeutics (Hong et al., 2009). Using morphological, biochemical, and molecular detection methods and screening assays, just 3% of the compounds suppressed the protein PTP1B linked to diabetes, while 20% demonstrated efficacy against the maturation of human colon tumor 116 cells. These cases demonstrate how exactly the microorganisms at high salinities produce molecules of pharmaceutical and therapeutic importance.

2.3 Agricultural sector

The involvement of microorganisms in agriculture is crucial. Given the existence of a high amount of salt concentrations, soil salinity is a significant issue for agricultural productivity in many fields and the occurrence of infertile soil in various regions. In saline soil, there is a presence of an excess amount of soluble salt, and in hypersaline soil there are clay particles that have a negative charge along with the positively charged Na^+ ions (Mishra et al., 2012; Thatoi et al., 2020). The saline soil's high sodium salt content, which is a result of natural or manmade processes, led to an adverse effect and the plant/crop growth gets impeded. Natural salinity is the result of salts building up over time as a result of weathering. The weathering process, which involves the breaking down of rocks and releasing soluble salts, has continuously led to salt accumulation, including calcium chloride, sodium chloride, and magnesium chloride.

The mangrove ecosystems have favored the sustenance of halophilic and halotolerant microbes over other microorganisms by releasing various exudates and nutrients into the immediate environment (Margesin and Schinner, 2001). As a result, the symbiotic relationship between plants and microorganisms was established, and also the microbial population used the components of exudates as an energy source for their survival. The halophilic and halotolerant microorganisms that are isolated from crops that thrive in the saline environment can prove to be beneficial as they have the power to stimulate growth in plants (Chathalingath et al., 2023; Etesami and Beattie, 2018) by producing phytohormones (indole acetic acids, gibberellic acids, and cytokinin), solubilizing and binding nutrients (phosphorus, potassium, zinc, and siderophores), biological nitrogen fixation, and ACC (1-aminocyclopropane-1-carboxylic acid) deaminase activity (Etesami and Beattie, 2018; Stanley et al., 2021). According to the reports, mangrove ecosystems also contain helpful bacteria for agricultural purposes. In addition to that, microorganisms isolated from the mangrove ecosystem showcase the capacity for nitrogen fixation, create ammonia, solubilization of phosphate, and help in the production of growth hormones for plants. Microorganisms, abundantly found in the mangrove plant's rhizosphere soil, have a valuable contribution to the agricultural sector (Margesin and Schinner, 2001). It is known that the rhizosphere bacteria found in the soil around plant roots promote plant growth. It has been noted that bacteria like *B. megaterium* and *Azotobacter vinelandii* promote the enhancement of the growth and health of mangrove seedlings. By using nitrogen-fixing bacteria that have the salt tolerance ability obtained from the saline environment, the fertility of both the soil from dry lands and soil that are saline in nature can be increased. Microorganisms that promote plant growth are frequently used in agriculture to increase growth and crop harvests (Kanekar and Kanekar, 2022; Yadav and Saxena, 2018). Additionally, the bacteria which has the ability to solubilize phosphate are found in mangrove soils and are known to have a lot of possible application as biofertilizers to boost growth in plants and higher income yield in saline soils. *Laguncularia racemose* and *Avicennia germinans*, two species of mangrove, growing in rhizosphere soils, include thirteen strains of bacteria that may solubilize phosphate. These thirteen bacterial strains are *Bacillus licheniformis, Vibrio proteolyticus, Bacillus atrophaeus, Bacillus amyloliquefaciens, Paenibacillus macerans, Enterobacter taylorae, Enterobacter aerogenes, Pseudomonas stutzeri, Xanthobacter agilis, Enterobacter asburiae, Chryseomonas luteola*, and *Kluyvera cryocrescens*. Succinic acid, acetic acid, isovaleric acid, and lactic acid are produced by the maximum number of bacterial species present in the mangrove habitat and are capable of solubilizing insoluble phosphates into these niches (Dutta and Bandopadhyay, 2022; Patankar et al., 2021).

2.4 Biosurfactants production

The importance and interest in industrial biotechnology give potentially difficult opportunities for this field of study. Historically, one of the most adaptable process chemicals has been surfactants (Elazzazy et al., 2015). There are several uses for biosurfactants, which are surface-active substances with the capacity to lower interfacial and surface tension. They are employed in the food industry for stability, texture and flavor enhancement, and shelf-life extension. Numerous industrial, medical, and environmental uses for biosurfactants and the halophilic bacteria that make them necessitate exposure to extremes in temperature, pressure, ionic strength, pH, and chemical solvents (Shakeri et al., 2021). Therefore, halophiles which were found in mangrove regions were *Acinetobacter* sp., *Enterobacter* sp., and *Pseudomonas putida* which grew on *n*-hexadecane. Mangrove resources have a great deal of potential for economic use in the fields of food, environmental protection, cosmetics, biopesticides, and medicines. Biosurfactants are typically used to remediate oil-contaminated soil and water (Marchant and Banat, 2012). The accelerated rehabilitation of oil-polluted saline environments could greatly benefit from halophilic bacteria that can produce biosurfactants. Several studies suggested the use of marine biotypes for the repair of hydrocarbon pollution in marine habitats or coastal areas (Gomes et al., 2018). In order to use biosurfactants for in situ microbiologically enhanced oil recovery, it is necessary to have organisms that can create and grow these substances under the current environmental circumstances. By using an enrichment-culture technique, biosurfactant-producing bacteria including *Leucobacter komagatae* and *Ochrobactrum anthropi* were identified from mangrove sediments in southern India (Gomes et al., 2018). These bacteria showed emulsifying properties similar to those of synthetic surfactants. The novel biosurfactants discovered in this research show remarkable potential for usage in commercial biotechnological processes that are cost-effective (Zhang et al., 2018). *Pseudomonas aeruginosa PBSC1*, a bacterium that produces biosurfactants, was found in the mangroves of Pichavaram, Tamil Nadu, India. (Elazzazy et al., 2015).

2.5 Bioplastics generation

It is crucial to create new kinds of biodegradable polymeric materials that can be produced responsibly and cheaply in order to solve environmental concerns about plastic pollution. Polyhydroxyalkanoates (PHAs), natural polymers made by bacteria with characteristics similar to oil-derived polypropylene/polyesters, are one class of bioplastic with a high potential for commercialization (Chiciudean et al., 2019). The goal of the work was carried out that was used to identify and characterize halotolerant bacteria that could efficiently manufacture large quantities of PHAs from inexpensive biomass (Jeon et al., 2021). Bacterial intracellularly accumulated storage compounds include polyhydroxyalkanoates (PHA), a biodegradable polymer (bioplastic). Although additional forms are possible, PHAs are primarily made up of poly-beta-hydroxybutyric (PHB) acid and poly-beta-hydroxyvaleric acid (Tavares et al., 2021). Microorganisms on the plastic surface that are able to secrete degrading enzymes are typically the cause of plastic's biodegradation (Suryawanshi et al., 2020). The majority of these enzymes, such as lipase or dehydrogenase, attack the polymer substrate after hydrolytic cleavage. As a result, the polymer is broken down into smaller molecules (such as oligomers, dimers, and monomers), which microbial metabolism eventually converts to carbon dioxide or water (Tavares et al., 2021). The halophiles also have the benefit of being easily cultivable in a straightforward, uncontaminated saline open pond. Recently, it was shown that a very halophilic archaeon that was isolated from a salty soil in Egypt accumulated PHB as intracellular granules (Suryawanshi et al., 2020).

2.6 Biofuel production

The utilization of fossil fuels at an alarming rate has led to a dire need for the search for renewable, efficient, and environment-friendly ways of fuel production. Biofuels are one such alternative that can be opted for to meet the increasing demands of the 21st century (Dutta and Bandopadhyay, 2022). Bioethanol, biobutanol, biogas, and biodiesel are the most commonly used biofuels. Recent advancements have shown that bioethanol is the most efficient biofuel of all. It is produced at a large scale in industries and has a dedicated market occupancy of more than 90% to it. Various chemical and physical techniques have been developed for the production of biofuels but the biological conversion of biomasses into biofuels has been adopted the most because of its cost-effectiveness. During biofuel production using the biological approach, there is an increase in pH and salinity, and thus microorganisms that thrive under this condition can be used for biofuel production (Barnard et al., 2010).

The enzymes that are produced by the halophiles and halotolerant microorganisms have optimal enzymatic activity at an alkaline pH and this is due to the presence of negatively charged amino acids which coat the surface of the enzyme with negative charges and as a result, the activity of these enzymes get accentuated during biofuel production (Corral et al., 2019).

Amongst biofuels, bioethanol is widely acclaimed because its production from biomasses not only makes it economically efficient but also eco-friendly. Lignocellulosic biomass comprising lignin, hemicellulose, cellulose, and starch is majorly utilized for the manufacturing process of bioethanol which involves pretreatment, enzymatic hydrolysis, fermentation, and distillation (Indira et al., 2018). Since cellulose, hemicellulose, and lignin are resistant to biodegradation, it is of utmost importance to carry out the pretreatment process under extreme pH and temperature conditions. Predominantly lime has been used for the pretreatment process but recent advancements have led to the usage of alkaline salts as a substitute. After the biomass has been hydrolyzed, it results in the formation of reducing sugars. These reducing sugars are then converted to ethanol by microbial intervention.

Recent studies have shown that *Nesterenkonia* sp. strain F, isolated from Aran-Bidgol lake in Iran, could synthesize butanol, ethanol, and acetone under both aerobic and anaerobic conditions. It was observed that *Nesterenkonia* sp. could utilize 50 g/L glucose for 72 h under anaerobic conditions to produce approximately 105 mg/L of butanol, 66 mg/L of butanol, and 291 mg/L of ethanol utilizing 50 g/L of glucose under aerobic conditions. A recent study also showed that a marine *Candida* sp. was utilized for the production of bioethanol from *Kappaphycus alvarezii* which is red algal biomass. The report demonstrated that the marine yeast could thrive in the presence of 2.5%–15% of salt concentration and produce ethanol by fermenting reduced sugars. The report further discussed that a very high salt concentration of 13% had a minimal inhibitory effect on the fermentation activity of the yeast but had an optimal activity within a range of 6.25%–11.25% salt concentration (Amiri et al., 2016).

Few studies have also shown that halotolerant and halophilic microorganisms could be used as nonfood feedstock for the production of bioethanol. It was reported that the filamentous cyanobacterium *Arthrospira platensis* could be directly converted to ethanol without the requirement of any pretreatment processes. *Arthrospira platensis* is a rich source of glycogen, thus could be utilized for the production of bioethanol. Amylase-producing *Saccharomyces cerevisiae* was also used as a source of bioethanol production earlier in this study. Utilization of the cyanobacteria yielded around an approx. of 86% of bioethanol which is the highest yield from cyanobacteria (Aikawa et al., 2013). Furthermore, various feedstocks such as starch, lignin, cellulose, hemicellulose, mannan, and many more could be utilized where these halophilic and halotolerant microorganisms would play a role in the hydrolysis process which will yield bioethanol as a resultant product. Thus, the remarkable potential of these microorganisms is being utilized and researched to develop a more sustainable, eco-friendly, and a more cost-efficient alternative.

3 Recent advancements and future prospects

The mangrove habitat is an abundant source of microorganisms. In this kind of niche habitat, both halophilic and halotolerant microorganisms predominate (Banerjee et al., 2019; Corral et al., 2019). Due to their capacity to adapt to moderate-to-moderately high salt concentrations, these microorganisms secrete significantly important enzymes and possess salt-tolerance genes that are imperatively important for biotechnological studies (Yadav and Saxena, 2018). Scientists have been attracted by microbial studies in salty environments because salt-tolerant bacteria have been used biotechnologically in medicine, industry, and agriculture (Oren, 2010). In a study by Halder et al. (2016), a critical focus was made on the isolation and characterization of halophilic organisms from the deltaic regions of Sunderban. For the physicochemical and microbiological study, soil samples were taken from four distinct locations in Sunderban. Three potential isolates were chosen after qualitative screening and their abilities to produce different bioactive compounds were further improved using various growth media. The isolates were characterized, and a phylogenetic tree was built relying on the sequencing of genes from 16S rRNA. The isolates displayed both antibiotic resistance and multiple heavy metal tolerance. The organisms were subsequently examined for extracellular polymeric substances (EPS) generation as well as different extracellular enzyme productions to investigate their potential for use in diverse biotechnological applications (Halder et al., 2016). According to a pot culture assay and a scientific study carried out by Mukherjee et al. (2019), it was observed that under physiological stress exerted by combinatorial treatment under arsenic and hypersaline conditions *Halomonas* sp. isolated from the rhizospheric section of *Avicennia marina,* which grows in the areas of Indian Sundarbans, demonstrated increased rice growth elevation. It's interesting to note that *Halomonas* sp. Exo1 turned out to be a productive producer of exopolysaccharides under abiotic stress conditions. According to this study, salt caused exopolysaccharide synthesis, which in turn raised the strain's osmotic tolerance. Arsenic also enhanced exopolysaccharide synthesis, which led to the sequestration of arsenic, demonstrating a positive feedback process. The sequestration of exopolysaccharide-mediated salt and arsenic in its purified form was explored in vivo and in vitro, and the properties based on the binding of substrate were evaluated by SEM-EDX and FT-IR investigations to comprehend the function of exopolysaccharide in the biosorption of arsenic and salt. Finally, an increase in the growth of plants observed in a pot assay, when the pure exopolysaccharide and the strain were present separately, depicted the contribution of exopolysaccharides directly to the promotion of plant development (Mukherjee et al., 2019). A study by Javid et al. (2020) demonstrated that the mangrove forests of Qeshm Island (Iran) are an excellent target for performing research on aquatic or benthic biodiversity. The isolation of 19 halotolerant and halophilic bacteria from the sediments in order to understand the microbial diversity in this region. By streaking, initial colony observation, and bacterial staining, the extracted bacterial strains were morphologically studied. The characterization of the strains was carried out with the help of several biochemical analyses, which included the Methyl Red Test (MR), KOH Test, Voges-Proskauer Test (VP), Triple Sugar Iron Test (TSI), Urease Test, S/I/M Test, Lysine Iron Agar Test (LIA), MacConkey Agar Test (Mac), Oxidase Test, Ornithine Decarboxylase Test (ODC), Antidiuretic Hormone Test (ADH), Catalase Test, and Tryptophan Deaminase Test. The severe halophilic strain which is Gram-positive in nature flourished at salt concentrations to a level of 30% NaCl, while halophilic bacteria were observed to grow best in salt concentrations of 5%–20% NaCl. Four strains of halophilic bacteria and one extremely halophilic Gram-positive bacteria were also subjected to molecular studies. Following 16S rDNA gene Sanger sequencing, a 99% bootstrap value was obtained by the phylogenetic taxonomy analysis. This analysis showed that there is a close relationship between the halophilic bacteria and the strains of the genus *Bacillus licheniformis, Bacillus, Bacillus paralicheniformis, Bacillus velezensis,* and *Bacillus* sp. With a 100% bootstrap value, the extremely halophilic strain was linked to *Planococcus plakortidis* strains (Javid et al., 2020). In a study carried out by Santhaseelan et al. (2022), the pharmaceutical industry and healthcare are expected to adopt halophilic microbial products extensively (Santhaseelan et al., 2022). The industrial interest stems from their biotechnological potential for producing suitable solutes, biopolymers, and other compounds (Van-Thuoc et al., 2012). The additional study must concentrate on their morphological characterization and mechanisms of action to realize their full clinical potential. This will enable medical professionals to predict which molecule will have the required therapeutic impact. The beneficial bacteria can also be examined for various probiotic qualities that can be useful to human nutrition and health. Future economic and environmental effects from studies on plant microbiomes and microbiomes from severe habitats are particularly promising. Therefore, a thorough study and documentation on the potential of microorganisms found in the mangrove ecosystem in the field of biotechnology showcasing the ability to tolerate high salt concentrations are required (Thatoi et al., 2020; Van-Thuoc et al., 2012).

4 Conclusion

Mangroves belong to the tropical and subtropical regions corresponding to the salt-tolerant niches of the world. Pertaining to the saline and hyper-saline physiological conditions, mangrove ecosystems harbor a variety of halotolerant and halophilic bacteria. These species of bacteria isolated and characterized from the mangrove ecosystem are potent sources of antioxidants, anticancer drugs, antidiabetic medications, and other active compounds. History testifies that halophiles and halotolerant organisms have been used time and again to manufacture solar salts derived from seawater and the production of traditional-fermented processed food items. The halophilic and halotolerant organisms sustained in hostile environmental conditions are at better position than any other organism thriving on earth, pertaining to their physiological features and production of significant bioactive molecules. Halophilic and halotolerant organisms acclimatizing optimally to the high salinity are able to secrete metabolites that have immense potential in the biotechnological sector. With recent scientific expeditions, massive exploitation of extremophiles has been observed in the development of novel biomolecules with imperative application in food technology, pharmaceuticals, fermentation industry, biomedicine, agriculture, etc. Halophilic and halotolerant organisms having high metabolic variability with low nutritional demands make them promising candidates for genetic engineering and an array of applied biotechnological applications. Furthermore, the consequent application of high throughput technology is helping us continuously decipher the molecular physiological and metabolic parameters for the efficacious production of noble bioactive leads produced by halophilic and halotolerant microorganisms isolated from swampy mangrove ecosystems. Nevertheless, some of these halotolerant and halophilic bacteria isolated from mangrove habitats are capable of fabricating huge amounts of biocompatible solutes that can be used as stress-protective agents.

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CHAPTER 10

Microbes are the natural ecological engineers in the forest ecosystem

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1 Introduction

The forest ecosystem comprises living organisms that extend skyward to tree canopies and downward to soil layers, influenced by varied biotic and abiotic processes. Forest ecosystems are open entities maintaining the energy and material cycle with neighboring biotic and abiotic components. These processes are vital for the continued survival of ecosystems (Waring and Running, 2007). Due to their high biodiversity, forests are a crucial feature of terrestrial vegetation. Forest resources provide a diverse set of services that form the basis for regional and national economies, ecological sustainability, addressing climate change, and human survival, including timber supply, climate modulation, carbon and oxygen balance, conservation of soil and water, and vegetation allocation (Chen et al., 2022). For example, the primary producers of forests can fix the carbon and act as an important carbon sink. According to Giguère-Tremblay et al. (2020), the Taiga forest can store 187–105 PgC year^{-1} in standing biomass and 198–271 PgC year^{-1} in soils (Tremblay et al., 2020). The tree is the dominant primary producer in a forest ecosystem and usually grows in various layers, each of which contributes to ecological processes. Across multiple forest ecosystems, 300–1000 trees have more than 10 cm breast height diameter per hectare and account for more than 90% of forest primary production (Baldrian, 2016). The forest microbiome highly regulates the diversity of trees in a forest ecosystem (Compant et al., 2019). The microbial community in forest ecosystems is diverse, constitutes the vast majority of Earth's biodiversity, and plays an essential role in processes that propel the forest ecosystem, such as litter decomposition, nitrogen fixation, the nutrient cycle, xenobiotic mitigation, plant diversity, and plant nutrient uptake. They occur in the phyllosphere, rhizosphere, and endosphere (Vincent et al., 2021). Fungi, archaea, and bacteria are among the organisms that constitute the plant microbiota.

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The aerial surface of the plants, i.e., the phyllosphere, is the world's most significant and unusual microbial habitat, supporting the varied community of bacteria, fungi, viruses, cyanobacteria, actinobacteria, nematodes, and protozoans (Bashir et al., 2022). The dominant phyllosphere bacterial communities are *Bacteroidetes*, *Proteobacteria*, *Firmicutes*, and *Actinobacteria*. Phyllosphere bacteria genera such as *Bacillus*, *Pseudomonas*, *Arthrobacter*, *Methylobacterium*, *Massilia*, *Sphingomonas*, and *Pantoea* are consistently reported from different plant species (Parasuraman et al., 2019). Fungi are an important phyllosphere group that can interact with plants epiphytically or endophytically, and some are best known for their pathogenesis in plant systems (Voříšková and Baldrian, 2013). Both epiphytic and endophytic phyllosphere fungi exhibit diverse roles in the residing host. They undergo varied metabolic functions, including leaf litter decomposition and carbon and nitrogen recycling. Endophytic fungi aid plants by conferring resistance to biotic (pathogens) and abiotic (drought and salinity) stresses and promote plant development (Sivakumar et al., 2020). *Alternaria alternata*, *A. tenuissima*, *Aspergillus niger, A. flavus, A. stellatus*, *Cladosporium cladosporioides*, *Fusarium equiseti*, *F. incarnatum, F. oxysporum*, *F. proliferatum, Penicillium aurantiogriseum*, *P. janthinellum, Talaromyces funiculosum, Trichoderma aureoviride*, and *T. harzianum* are common fungal species found in phyllosphere (Ripa et al., 2019). Actinobacteria, the saprophytic gram-positive bacteria that live in soil, is another phyllosphere group adapted to reside epiphytically or endophytically, in addition to bacterial and fungal diversity. They are extensively researched for their therapeutic secondary metabolites (Singh et al., 2006). In general, actinobacteria symbiotically associate with plants and secrete novel secondary metabolites with enormous implications for host-herbivore interactions. The phyllosphere actinobacteria species include *Actinoallomurus acacia*, *A. coprocola*, *A. oryzae*, *Actinoplane missouriensis*, *Actinomadura glauciflava*, *Amycolatopsis tolypomycina*, *Jishengella endophytica*, *Kribbella* sp., *Microbispora* sp., *Micromonospora* sp., *Microbispora mesophila*, *Nocardia alba*, *Nocardioides* sp., *Nonomuraea rubra*, *Planotetraspora* sp., *Pseudonocardia* sp., and *Streptomyces* sp. (Yadav, 2017; Sivakumar et al., 2020). The plant physiology and the environmental conditions determine the diversity of phyllosphere actinobacteria. Studies revealed that phyllosphere actinomycetes diversity is high in tropical and temperate ecosystems (Sivakumar et al., 2020; Rossmann et al., 2017). Interactions between phyllosphere microbial communities and plants, as well as differences in their distinct environmental factors, alter the integration of these microbial communities and contribute to disparities in their abundance and structure in individual plant species. The phyllosphere's microbial communities enhance the development processes of plants, such as nitrogen fixation, pathogen defense, metabolite modification, and phytohormone biosynthesis. According to metagenomic and metaproteomic studies, phyllosphere microbiota can synthesize proteins that aid in the preservation and absorption via porins and ABC transporters and stress tolerance, including reactive oxygen species (ROS), methanotrophy, and nutrition cycling (Rossmann et al., 2017).

The rhizosphere microbiome, known as the forest plants' second genome, contains bacteria, algae, fungi, oomycetes, viruses, archaea, and nematodes that dwell in the limited zone surrounded and impacted by plant roots. Most rhizosphere microbiome members, also known as mutualistic microbes, form a complex food web that is symbiotically connected and consumes many plant nutrients (Mendes et al., 2013). They enhance plant health by boosting food availability, increasing stress tolerance, and secreting plant hormones. In addition to those microbes, harmful microbes such as soil-borne pathogens coexist in the rhizosphere, limiting the developmental processes of plants and decreasing agricultural productivity (Li et al., 2021).

Every plant contains a secret microbial world. Numerous bacteria and fungi live within them, without harming their hosts (Mercado-Blanco, 2015). Those diverse groups are called endophytes and play a vital role in maintaining plant health. Endophytes are found in all or almost all plants, and in most situations, endophytes become seed infected and continue to assist plant development and health when seeds mature (White et al., 2019). Endophytes primarily colonize the plant body through the roots, although they can enter the leaves, stems, flowers, or cotyledons. Most endophytes are found in soil, and plant colonization appears to begin in the rhizosphere (Mercado-Blanco, 2015). Endophytic bacteria may invade all organs of plants. For example, they can infect roots by a wound or direct penetration and then spread to other areas via apoplast or symplast routes (Goodwin, 2022). The diversity and composition are determined by the plant, the plant organ and its physical state, the plant's stage of development, and the environment (Compant et al., 2021). The interaction of endophytic fungi with plants has been widely examined in various geographical and climatic settings. They are found in all known plant species, as well as mosses, ferns, and lichens. Endophytic fungi mainly belong to the Ascomycotina group or their monosporic fungi and certain Zygomycotina, Basidiomycotina, and Oomycotina taxa that can create diverse bioactive compounds, boost host development and resilience to environmental challenges, and promote waste rot (Sun and Guo, 2012).

The plant-microbe relationships are widespread and can vary from symbiotic to parasitic or pathogenic (Lugtenberg, 2015). Plant-associated microorganisms are becoming recognized as vital in regulating plant phenotypes and influencing plant-herbivore interactions (Biere and Bennett, 2013). Microorganisms mediate plant-herbivore interactions in two ways. First, plant pathogens and symbionts alter the suitability of host plants as a resource for herbivorous organisms by altering their physiology, abundance, biochemistry, phenology, and morphology, which in turn affects herbivore population, performance, dynamic, and community structure. Second, herbivorous-microbe symbionts or pathogens influence their herbivorous hosts' capacity to absorb food plants, significantly impacting their performance and specialty on various food plants (Biere and Bennett, 2013). In addition, microbes alter plant-producing signals, affecting the herbivorous insects' oviposition and feeding behavior. In general, vector-borne pathogenic

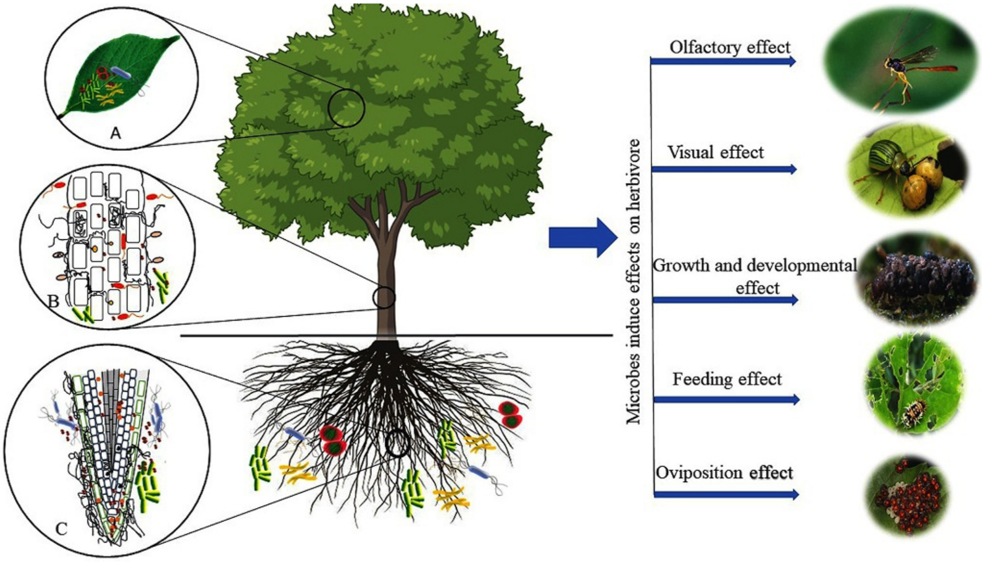

Fig. 1 Plant-microbes-herbivore interaction. (A) Phylosphere microbiome, (B) Endosphere microbiome, (C) Rhizosphere microbiome.

microorganisms can alter the plant signals and the behavior of herbivorous vectors in a way that predicts increased microbial infection, which means that pathogens can control both host plants and vectors and that beneficial and pathogenic plant-related microbes can also be found in their host plants. Microbes and plant interaction also alter herbivorous insects' foraging and oviposition behavior (Grunseich et al., 2019). Plant feedback control against herbivores and microbial boosting of nutrient availability in the soil can impact the whole plant microbiome by directly or indirectly modifying soil conditions by secreting secondary metabolites. This feedback control is a major driver of the aboveground community's reaction to herbivores (Fig. 1).

2 Forest biome

Forests are landscape segments in which trees dominate biological and environmental conditions and processes on a local or regional scale. They are massive, typically long-lived annual plants with a thick wooden trunks and a dense root system (Northcote and Hartman, 2004). Forests are located worldwide and are the planet's most impactful terrestrial ecosystem. As per Food and Agriculture Organization (FAO), forests encompass 31% total land area of the world, or around 4.06 billion hectares, with half of the world's forests located in five nations and two-thirds located in 10 countries (*Global Forest Resources*

Assessment, 2020). According to Pan et al. (2013), forests contain around 80% of the world's plant biomass and contribute to 75% of total primary production (Pan et al., 2013). Forests have significant ecological and economic contributions through their varied products and ecosystem services, both locally and globally, and play an essential role in societal transition that conserves nature while also improving human well-being and generating income, particularly for rural people (Brockerhoff et al., 2017). Forests are critical sources of greenhouse gas emissions and carbon sinks, with carbon loss through respiration stabilized by primary producers exceeding 7%–25%, but they also impact other components and the geochemical cycle of the climate (Baldrian, 2016). Forests absorb billions of tons of carbon dioxide permanently stored in their biomass (FAO, 2022). As per FAO, the total carbon stored in the forests was estimated as 662 Gt in 2020, at an average of 163 t per ha. In 2020, live biomass accounted for approximately 45% of forest carbon stock, soil organic matter accounted for 45%, and dead wood and litter accounted for 10%. The worldwide forest carbon stock fell between 1990 and 2020, while forest carbon stock per ha grew, owing to better forest management. Between 2011 and 2020, net emissions from land use, land use change, and forestry were 4.1 Gt CO_2 or nearly 10% of the total anthropogenic CO_2 emissions. However, the terrestrial sink (mainly forests) has been much more extensive than emissions from land-use change, sequestering 11.4 Gt of CO_2 each year, accounting for up to 29% of annual anthropogenic CO_2 emissions from 2011 to 2020. The tropical and subtropical areas account for 78% of total emissions and 54% of total removals (*The State of the World's Forests*, 2022).

Forests alleviate the effects of climate change, preserve biological diversity, and serve as a potent source of bioenergy (Adams et al., 2019; *The State of the World's Forests*, 2022). There are four sorts of forests in general: temperate, tropical, subtropical, and boreal (WWF, 2019). Furthermore, the forest may be divided into two types: primary forest (comprised of natural tree species with no apparent signs of human activity, and no major distribution in biological processes) and planted forest (focused on production and conservation) (Carle and Holmgren, 2003). Temperate forests of North America, North Asia, Western and Eastern Europe, and Oceania are composed of deciduous, broad-leaved, and coniferous evergreen trees. The temperate forest has a mild climate, which implies that temperature and rainfall patterns vary from seasons 3 to 4. The yearly temperature ranges between 30°C and 40°C, while the annual rainfall ranges between 500 and 4000 mm (WWF, 2019). The temperate forests that receive enough precipitation (2000–8000 mm) are considered as rainforests. Temperate rainforests are found in Valdivian forests of southwestern South America, the Pacific Northwest of North America, New Zealand, Tasmania, Southwestern Japan, the Northeastern Atlantic, and the Eastern Black Sea region (Adams et al., 2019). Tropical forests are found within 28 degrees of the equator, primarily in Central America, Asia, Africa, South America, Australia, Mexico, and several Pacific islands. It rains more than 200 cm yearly in some locations, making them exceedingly damp. Temperatures vary from 20°C to 35°C

(WWF, 2019). The boreal forest, also known as taiga, covers huge areas of both North America and Asia, occupying a transition zone between temperate forest and tundra. Plant richness is significantly lower than in temperate forests, with coniferous species dominating the tree population. The boreal forest has the most living biomass, which is assumed to be a net carbon sink (DeAngelis, 2008).

Forests are composed of intricate biotic and abiotic components. All of these components comprise a forest ecosystem, and they are linked to one another via interdependent food chains. Particularly, the tree's bark supports a variety of insect and microbiological ecosystems (Fig. 2). Forests support 80% of amphibian species, 75% of birds, and 68% of mammal species, while tropical forests support 60% of all vascular plant species. Among the vascular plants, bamboo is an important component of the forest ecology, spreading extensively across the forest canopy to aid in forest protection and regeneration (Fig. 2C). More than 700 million acres of forest (18% of the total forest area) are officially protected. Nonetheless, deforestation and forest degradation threaten forest biodiversity (Fig.3) (*The State of the World's Forests*, 2022). Trees share overlapping habitats in every forest biome with various microbial interactions, which may be pathogenic, mutualistic symbiosis, commensal, or endophytic. Many of these microorganisms significantly affect the ecology and development of the forest biome and are critical to maintaining fundamental ecosystem functions. Also, forest ecosystems' microorganisms facilitate bidirectional nutrient exchange between plants and soil. Microbial communities perform essential ecosystem tasks by transmitting and mobilizing nutrients from organic matter and minerals to plants, promoting plant health (Uroz et al., 2016; Dukunde et al., 2019) (Fig. 2).

Fig. 2 Tree bark harbors insect and microbial ecosystem (A). Tree and plant share overlapping habitat (B). Bamboo is an important component of ecosystem (C).

Fig. 3 Degraded forest ecosystem of Ultapani forest, Assam (A)–(C).

3 Forest microbiome

Bacteria, fungi, protozoans, and archaea dominate the forest microbiome, found in the living tree wood, foliage, ground vegetation, bark surface, roots, the rhizosphere, soil, deadwood, invertebrates, wetlands, litter, rock surfaces, and the atmosphere (Baldrian, 2016).

Bacteria are a significant, albeit understudied, component of the microbial community of the forest ecosystem, which play a critical function in this habitat. Bacterial populations in forest soils are affected by nutrient availability and biotic interactions and play an essential role in the soil's carbon, nitrogen, and phosphorus cycle processes. They facilitate the detritus cycle enhancing nutrient recycling in the forest ecosystem (Lladó et al., 2017). For example, *Enterobacter*, *Clostridium*, *Klebsiella*, *Pactobacterium*, *Serratia*, and *Citrobacter* encode enzymes such as cellulase, pectinases, proteases, xylanases, polygalacturonases, mannanases, pectate lyase, and CMCases essential for degradation of the cell wall (Joko et al., 2014; Hamann et al., 2015). Furthermore, different species of bacteria are responsible for nitrogen fixation in forest ecosystems and other ecosystem processes, such as mineral weathering, which releases inorganic nutrients (Lladó et al., 2017). The most important nitrogen-fixing bacteria include *Azotobacter*, *Azospirillum*, *Bacillus*, *Bradyrhizobium*, *Microbacterium*, *Clostridium*, *Klebsiella*, *Rhizobium*, *Pseudomonas*, *Enterobacter*, *Serratia*, *Burkholderia*, and *Beijerinckia* (Wagner, 2011). Actinobacteria release low-molecular-weight organic solutes and solubilize inorganic phosphate. *Bacillus mucilaginous*, *B. edaphicus*, and *B. circulans* are the most effective potassium solubilizers (Saeed et al., 2021). Many endophytic bacteria arise in the rhizosphere environment, attracting microorganisms due to root exudates and rhizosphere deposits. Stem and leaf surfaces also create exudates that attract bacteria (Hardoim et al., 2015).

Certain bacteria species are plant pathogens that can cause plant diseases. Although bacterial infections in trees are often less severe than fungal diseases. Plant pathogenic bacteria (PPB) are widely distributed. It is believed that 150 species of the 7100 identified bacteria are responsible for various plant diseases. However, there are specific examples of bacterial diseases that can be fatal. Example of such pathogenic bacteria include *Dickeya*, *Liberibacter*, *Erwinia*, *Pectobacterium*, *Candidatus*, *Pantoea*, *Agrobacterium*, *Pseudomonas*, *Ralsonia*, *Burkholderia*, *Acidovorax*, *Xanthomonas*, *Clavibacter*, *Streptomyces*, *Xylella*, *Spiroplasma*, *Phytoplasma*, *Brenneria*, and *Xylophilus* (Aguilar-Marcelino et al., 2020).

Even though bacterial cells are less abundant in plant tissues than fungi, they are an essential component of the plant microbiome. They are abundant in the rhizosphere but less so in the endosphere and phyllosphere. Plant microbial communities have been found to contain members of the majority of known bacterial species. However, the diversity of bacteria in plant microbiomes is often smaller than in surrounding soil, and some selection mechanisms appear to be in play, driving the makeup of plant-associated bacterial communities (Asiegbu and Kovalchuk, 2021). Most bacteria have a basic form with a single spherical, rod-shaped, or spiral shape (Fritz et al., 2008). Because they have flagella, many bacterial species can move actively (Kearns, 2010). Bacterial cells may form various aggregates of varying complexity in some instances. There are instances of Actinobacteria with more complicated morphology. *Streptomyces species*, for example, exhibit filamentous development that results in the creation of pseudo hyphae and, in certain circumstances, further differentiation of those hypha-like structures into the substrate and aerial mycelium (Kearns, 2010).

In forest ecosystems, another group of microbes, i.e., fungi, play critical roles by interacting with plants in mutualistic, saprotrophic, and pathogenic ways (Zeilinger et al., 2016). Their interactions with trees, the primary structural component of forests, can influence the carbon and nitrogen cycles and biodiversity maintenance. Mycorrhizal fungi can improve plant nutrient absorption and access to organically bound nutrients. Although most tropical forest trees generate arbuscular mycorrhizas, a significant majority (e.g., dipterocarps and certain Leguminosae) form ectomycorrhizas; yet, the differences in their effects on tropical tree performance have received little attention. Fungi act as recycling agents in forest ecosystems, breaking down organic material, which is quite complex, such as lignin, and making it accessible for plant development, resulting in positive feedback mediated by such fungi. Finally, as infections, fungi can impact patterns of tree death in tropical forests, which has ramifications for tree growth and nutrient cycling and has also attracted attention as a possibility for explaining high tropical tree diversity under the auspices of the Janzen-Connell effect (Jia et al., 2020; Bauman et al., 2022). The diversity of fungi in tropical forests is significant due to variations in forest microhabitats and suitable climatic conditions (Romero et al., 2021). The wide variety of lifestyles is linked with a similarly broad fungal morphological spectrum ranging from tiny yeasts to giant mushroom-forming fungi, implying a plethora of ecological interactions, some of which we know nothing about (such as endophytes) (Tomao et al., 2020).

Fungi diversification is critical to ensuring the supply of many ecosystem services essential to forest ecosystem function and human well-being. Forest fungus diversity and richness support the variety and abundance of other taxonomic groupings (Rudawska et al., 2022). Wildlife relies heavily on forest fungus for sustenance. Furthermore, being the primary resource of socio-economic activities centered on the harvesting of mushrooms for recreational and commercial purposes, it provides essential measures and cultural ecosystem services (Martínez de Aragón et al., 2011). Furthermore, soil fungus mycelium is a significant source of food for other soil organisms, such as collembolan species and fungal mycoparasites (Hedĕnec et al., 2013).

Viruses are essential components of all ecosystems, but their ecological role needs to be better understood. Their role in forest ecosystems varies greatly and is heavily influenced by host-virus combinations (French and Holmes, 2020). Since viruses lack their metabolism, they always indirectly impact the environment, and their infections are rarely fatal to forest trees (*Understanding Emerging and Re-emerging Infectious Diseases,* 2007). Some viruses are thought to be potent modulators of insect, herbivore, and fungal populations and play a role in biocontrol agents (Dietzgen et al., 2016; Wagemans et al., 2022). Bacteriophages are the most ubiquitous creatures on the planet, and they may influence the general dynamics of microbial ecosystems, even in forests. For example, the number of bacteriophages in the soil system may be high. They can affect bacterial mortality, resulting in dramatic changes in the makeup of the soil's microflora (Wang et al., 2022). Viruses may also influence the pathogenicity of microflora. For instance, mycoviruses reduced the pathogenicity of *Cryphonectria parasitica* (chestnut blight fungus) (Hillman and Suzuki, 2004). Simultaneously, many viruses are enigmatic and appear to have little effect on host fitness. Most of plant viruses are positive-sense RNA viruses, e.g., Bromoviridae, Tombusviridae, Potyviridae, Endornaviridae, Secoviridae, Closteroviridae, Betaflexiviridae, Mitoviridae, and Virgaviridae (Gergerich and Dolja, 2006; Asiegbu and Kovalchuk, 2021). Other plant virus families include Rhabdoviridae (negative-sense RNA), Geminiviridae, Secoviridae (ssDNA), and Caulimoviridae (dsDNA) (Asiegbu and Kovalchuk, 2021). Some species of Partitiviridae are found in plants and fungi (Mata et al., 2020). They induce chronic and often asymptomatic infections in both the circumstances. Interestingly, the basidiomycete *Helicobasidium purpureum* and its host plant *Beta vulgaris* are both infected with partitiviruses that are remarkably similar. The presence of both fungal and plant-infecting partitiviruses in the genera *Alphapartitivirus* and *Betapartitivirus* shows that partitiviruses can occasionally transmit between plant and fungal hosts. Intimate relationships between plants and pathogenic, endophytic, or symbiotic fungi may provide a possible channel for viral transmission (Roossinck, 2019).

4 Phyllosphere forest microbiome

The phyllosphere is the aerial or aboveground section of the plant that includes the floral and vegetative foliar components. The leaves are the most prominent and serve as a unique niche for microbial diversity (Thapa and Prasanna, 2018). Phyllosphere nomenclature has evolved significantly during the previous two decades. Morris elucidated the phyllosphere as the microenvironment extending from the leaf surface outward to the outer edge of the boundary layer surrounding the leaf and inward into the leaf tissues. On the other hand, Doan and Leveau divided the phyllosphere into two tightly related yet distinct niches, namely "phylloplane" and "phytotelmata," to contain both the leaf surface landscape and the leaf surface waterscape (Doan and Leveau, 2015). The phyllosphere is composed of various aboveground surfaces of plants and is estimated to cover an area of 4108 km^2, nearly equal to the entire Earth's surface (Parasuraman et al., 2019). Despite multiple abiotic influences, the phyllosphere is occupied by a rich array of microorganisms, including several species of filamentous fungi, yeasts, algae, bacteria, and less commonly, protozoa and nematodes, each with their own set of traits and activities (Vorholt, 2012). Significant contributions to the global nitrogen and carbon cycles, bioremediation of xenobiotics, plant growth-promoting characteristics, biocontrol agents against diseases, and other activities are the outcome of the actions of the individuals present in this global niche (Thapa and Prasanna, 2018). Bacteria are the most common microbes in this ecosystem, with an average population of 106–108 cells per cm^2. However, the abundance of epiphytic bacteria varies depending on the plant species and its surrounding environment owing to phyllosphere physical and nutritional circumstances. Broad-leaf plants generally have more bacteria than grasses or waxy broad-leaf plants (Sivakumar et al., 2020). Most phyllosphere bacteria accumulate within biofilms, especially at the junction of epidermal cells, in depressions created along the vein and at the base of the trichome, where they are usually trapped within extracellular polymeric substances (EPS) (Vorholt, 2012). These extracellular polymeric materials are responsible for assembling biofilms into groups of microorganisms, influencing spatial organization, interacting between microorganisms, and acting as a glue between pathogenicity and virulence factors of the cells (Karygianni et al., 2020). EPS can also accumulate other nutrients and molecules. The presence of extracellular enzymes in the EPS matrix aids in the establishment of extracellular digestion (Costa et al., 2018). Phyllobacteria communities are generally dominated by α and γ-proteobacteria, and bacteroidetes, while β-proteobacteria and firmicutes may also be part of this community (Kembel et al., 2014). The core of phyllosphere communities appears to be composed of a few bacterial species, most notably *Pseudomonas*, *Sphingomonas*, *Methylobacterium*, *Bacillus*, *Massilia*, *Arthrobacter*, and *Pantoea* (Bulgarelli et al., 2013). Kembel et al. (2014) discovered roughly 400 bacterial species dominated by bacteroidetes; α-, β-, and γ-proteobacteria; and actinobacteria (Kembel et al., 2014).

According to Redford et al. (2010), Bacteroidetes and β-proteobacteria are more prevalent in gymnosperms, but Actinobacteria and γ-proteobacteria are more prevalent in angiosperms (Redford et al., 2010). Phylogenetic diversity exists among phyllobacteria from various tree species. On the other hand, their metaproteome is successfully integrated regarding the features of survival on the leaf surface, i.e., they share a standard set of critical functional proteins necessary for survival (Rosado et al., 2018). Several species of *Phyllobacteria*, *Actinoallomurus acacia*, *Pseudonocardia halophobica*, *Actinomadura glauciflava, Microbispora mesophila, Amycolatopsis tolypomycina, Actinoplane missouriensis, Streptomyces javensis, Actinoallomurus coprocola, Jishengella endophytica, Kribbella* sp., *Micromonospora* sp., *Microbispora* sp., *Pseudonocardia* sp., *Nonomuraea rubra, Nocardioides* sp., *Nonomuraea* sp., *Nocardia alba, Pseudonocardia endophytica, Planotetraspora* sp., *Streptomyces* sp., and *Actinoallomurus oryzae* have been found on plants such as *Oryza sativa, Triticum aestivum, Lobelia clavatum, Elaeagnus angustifolia, Xylocarpus granatum, Acacia auriculiformis, Aquilaria crassna,* and *Lupinus termis*, from arid, semiarid, and mangrove environments (Sivakumar et al., 2020). Phyllosphere fungi are an essential component of the forest microbial community; they comprise epiphytic fungi that live on the leaf surface and endophytic fungi that dwell asymptomatically within the leaf and they play a vital part in the operation of the high species diversity and ecosystems (Roy and Banerjee, 2018). Endophytic and epiphytic fungi inhabit two distinct microenvironments in the phyllosphere: endophytic fungi dwell within the tissues of the host plant leaves, whereas epiphytic fungi live on the surface of the plant leaves and rely on nutrients either from the surrounding atmosphere or compounds emitted by the host plant (Kumar et al., 2017). As a result, the plant is likely to have more control over the colonization of interior tissue fungus than the outside surface (Yao et al., 2019). Filamentous fungus is thought to be temporary leaf surface dwellers, primarily present as diseases, whereas fast sporulating species and yeast occupy this environment more actively (Lindow and Brandl, 2003). Osono observed in 2008 that the phyllosphere fungus in the plant *Camellia japonica* includes endophytic *Colletotrichum gloeosporioides* and *C. acutatum*, as well as epiphytic *Pestalotiopsis* sp., *Aureobasidium pullulans, Phoma* sp., and *Ramichloridium* sp. (Osono, 2008). However, the number and variety of fungi vary according to plant species and eco-climatic circumstances. Furthermore, seasonal and leaf age-dependent changes exist in the epiphytic and endophytic phyllosphere fungal assembly; for example, *Geniculosporium* sp. varies with leaf age, while *Cladosporium cladosporioides* varies with both season and leaf age of the plant *Camellia japonica* (Osono, 2008). Li et al. (2022) recently reported an evergreen broad-leaved forest dynamic plot in southern China, with Ascomycota dominating. The five main classes in the core microbiome are Sordariomycetes, (Sporocadaceae), Eurotiomycetes (Onygenales incertae sedis), Dothideomycetes (Dissoconiaceae, Dothioraceae, Aureobasidiaceae, Mycosphaerellaceae, Teratosphaeriaceae), Agaricomycetes, and Tremellomycetes (Li et al., 2022).

5 Endosphere forest microbiome

A diverse microbial community and microorganisms populate the plant's interior either mutually or pathogenically. They serve a significant role in the development and health of forest plants and nutrient cycling (Compant et al., 2021). Endophytes are derived from the Greek words endo (inside) and phyton (plant) (Waghunde et al., 2021). Endophytic microorganisms are therefore defined as a group of organisms that colonize inside the tissues of plants as fungi or bacteria that may or may not affect the plant. Endophytic microbes are often found in all forest plants (Goodwin, 2022). Stomata (natural openings) are the most common routes for endophytic microbes into the plant body, but they eventually extend throughout all plant tissue, including roots, leaves, stems, flowers, and cotyledons (Adeleke and Babalola, 2022). Most endophytic bacteria naturally dwell in soil and can infect plant roots by wounds or direct penetration, developing biotrophically in the apoplast and subsequently invading stems by passing through the vascular system or apoplast of the stem and spreading to leaves, flowers, and seeds (Goodwin, 2022). They can also infect other tissues directly by infiltrating the leaf surface through stromata, wounds, or direct penetration (Gudesblat et al., 2009). *Methylobacterium*, *Pseudomonas*, *Colobacter, Irwinia, Acidovorex, Crisiobacterium, Penibesilas, Sphingomonas, Korinebacterium, Acinetobacterium, Devosia*, and *Brevundimonas* are common endophytic bacterial species found in most plants (Adeleke and Babalola, 2022). Many variables influence the richness of endophytic bacteria, including the physiology of plants, soil pH, soil type, and environmental circumstances (Afzal et al., 2019). It has been reported that the most significant diversity and the number of bacteria are found in the roots of woody plants, followed by the stem and finally the leaves. However, there is substantial variance among herbaceous angiosperms (Goodwin, 2022).

Endophytic fungi have piqued researchers' interest because they not only provide novel sources of cytotoxic chemicals such as antibacterial and anticarcinogenic substances but also impacts plant development by creating growth hormones, enhancing nutrition through two-way nutrient transfer and protecting plants from pathogens (Fadiji and Babalola, 2020). In addition, they protect the plant against harsh environmental circumstances, such as enhanced drought resistance, heavy metals tolerance (Zn, Cu, and Pb), and successfully competed with saprobic fungi (Alam et al., 2021). Endophytic fungi are highly biodiverse and multifaceted microbial communities that appear to be omnipresent. The endophytic fungus has been found in practically all plants, including species established in the Arctic and Antarctic areas, deserts, seas, and tropical rainforests (Wen et al., 2022). Transmission of fungal endophytes to the host tissue follows vertical and horizontal pathways. Vertical transmission of endophytic fungus occurs by seeds from the mother plant to the offspring, referred to as "real endophytes." Horizontal transmission occurs through spores in the soil or air (Rana et al., 2019). The reported endophytic fungal genera include *Acremonium, Alternaria, Aspergillus, Berkleasmium, Chaetomium,* *Cladosporium, Claviceps, Colletotrichum, Cryptococcus, Curvularia, Fusarium, Geomyces, Glomus, Leptospora, Metarhizium, Microdochium, Neotyphodium, Ophiognomonia, Phaecilomyces, Penicillium, Phaeomoniella, Phyllosticta, Piriformospora, Rhizoctonia, Rhizopus, Rhodotorula, Talaromyces, Trichoderma, Wallemia*, and *Xylaria* (Rana et al., 2019; Adeleke and Babalola, 2022).

6 Rhizosphere forest microbiome

The rhizosphere microbiome is also referred to as the second genome of forest plants comprising bacteria, algae, fungi, oomycetes, viruses, protozoa, archaea, and nematodes (Li et al., 2021). It is a narrow zone surrounded and impacted by plant roots. It is a hot spot for different species where plant roots interact with diverse bacteria and is regarded as one of the most complex ecosystems on Earth (Mendes et al., 2013). Most species of the rhizosphere microbiome are part of a complex food web that feeds on the considerable quantity of exudates generated by plant roots (Li et al., 2021). These rhizosphere microbial communities have potential roles linked to probiotics, and plant protection, garnering scientific community's attention (Li et al., 2021). Nevertheless, information on how the rhizosphere microbial populations impact plant development and resistance is limited (Li et al., 2021; Mahmud et al., 2021). Through chemotaxis, the rhizosphere microbiome responds to plant root exudates, influencing the rhizosphere population and eventually changing its response to plant age and seasonal change (Feng et al., 2021). Although the rhizosphere vegetation biomass varies widely, its mass and gross primary productivity frequently contribute more than 20% of the ecosystem's total net primary output. Rhizosphere vegetation niches are varied, as is usual for the plant halobionts, and are analogous to the corresponding environments associated with trees (Hassani et al., 2018). Rhizosphere vegetation, like trees, is often seasonally changing and dependent on the temperature and precipitation regime (Slaughter et al., 2015). Furthermore, the floral composition of deciduous forests changes during the year as light precipitation changes, and distinct cohorts of plants are presented before tree leaf emergence and throughout the shaded summer. That microbial vegetation development also heavily depends on forest successional age, with very young and highly ancient stands housing more plants (Baldrian, 2016). The seasonality of ground vegetation activities has been shown to influence the seasonality of related microbial populations (Davey et al., 2012). Symbiotic and endophytic species in annual plants are predicted to be replaced by saprotrophs following the senescence and dieback of their plant hosts. It should also be emphasized that ground vegetation has a relatively small impact on overall photosynthetic output compared to trees (Baldrian, 2016). Two forms of microbiota may be found in the rhizosphere: beneficial microbiota and pathogenic microbiota, and they release a variety of chemicals that can be useful or toxic to the soil (Mendes et al., 2013). In the forest rhizosphere, several trophic fungus species have been found, which can be classified as mycorrhizal, endophytic, or pathogenic (Frąc et al., 2018). Fungi are vital in establishing the forest's rhizosphere microbiome and microbial biomass. Furthermore, fungal diversity considerably impacts the effectiveness and dynamics of forest ecosystems (Izquierdo et al., 2021). Plant roots develop symbiotic relationships with most arbuscular mycorrhizae or ericoid mycorrhiza fungi, which frequently coexist in the soil alongside ectomycorrhizal tree symbionts (Baldrian, 2016). In 2015, van der Heijden et al. found that over 50,000 fungal species might form mycorrhizal associations with roughly 250,000 plant species, concluding that virtually all terrestrial plants have symbiotic relationships with mycorrhizal fungi (van der Heijden et al., 2015). Basidiomycota, Ascomycota, Chytridiomycota, Glomerromycota, and Zygomycota are the most common fungal species in the rhizosphere.

Bacterial species in the rhizosphere microbiome have been shown to play critical roles in nutrient absorption, stress resistance, and disease reduction. The most important bacterial populations are plant growth-promoting (PGPR) bacteria, nitrogen-fixing bacteria, and pathogenic bacteria. PGPRs are mainly present freely in the soil. Still, they are symbiotically associated with completing critical tasks such as enhancing fertilizer efficiency, rhizodegradation, regulating plant growth and development, and reducing abiotic and biotic stress (Bhattacharyya and Jha, 2012). The known bacterial divisions include Bradyrhizobium, Burkholderia, and Mesorhizobium, which primarily operate as plant growth promoters and nitrogen fixers in the forest biome (Chaudhary et al., 2021).

Plants are constantly assailed by hundreds of microbial communities, including commensals, pathogens, and symbionts, particularly in the rhizosphere (Ling et al., 2022). Plant pathogens and N-fixers are concentrated in the rhizosphere because their reproduction and function rely on organic matter supplied by the plant host (Backer et al., 2018). Although the rhizosphere is a dynamic environment in which the microbiome develops rapidly in location and time, evidence is mounting that plants shape the rhizosphere microbiome to their advantage and skillfully use the microbial functional repertoire (Ling et al., 2022) (Table 1).

7 Microbes enhance plant-herbivore interaction

Plant-herbivore interactions shape the ecology of natural ecosystems and the evolutionary paths of interacting species (Becerra, 2007). Herbivore-plant-host relationships are the product of a complex evolutionary interplay (Bruce, 2015). Herbivores get their energy primarily from primary producers, which are plants. Herbivory harms plants by limiting growth and reproduction. In addition to directly affecting plants through

Table 1 Plant microbe interaction in forest ecosystem.

Microorganism		Occurrence	Interaction	Function	Reference
Bacteria	*Pseudomonas syringae*	Phyllosphere	Epiphytic	Pathogenic and also acts as a plant growth-promotor bacteria, and biocontrol agents	Xin et al. (2018), Passera (2019)
	Pseudomonas sp.	Rhizosphere	Endophytic	Antagonastic against fusariumsolanii, and plant growth promotor	Yasin et al. (2021)
	Paneibacillus sp.	Rhizosphere	Endophytic	Antagonastic against fusariumsolanii, and promote growth of plant	Yasin et al. (2021)
	Azotobacter spp.	Phyllosphere, and Rhizosphere		Nitrogen fixation, and promote the growth of plant	Rico et al. (2014), Alwan and Hussein (2019)
	Pantoea agglomerans	Phyllo sphere, Endosphere and Rhizosphere	Epiphytic and endophytic	Biocontrol, bioremediation, and promote the plant growth	Dutkiewicz et al. (2016)
	Erwinia phyllosphaerae sp.	Phyllo sphere	Endophytic	Solubilize phosphate, and produce auxin	Pan et al. (2022)
	Beijerinckia sp.	Phyllo sphere and Rhizosphere		Nitrogen fixation, and promote plant growth	Pan et al. (2022)
	Bacillus thuringiensis	Phyllosphere	Endophytic	Insecticidal activity	Argôlo-Filho and Loguercio (2013)
	Rhodococcus cerastii	Phyllosphere, and Rhizosphere	Endophytic	Biodegradation, and bioremediation	Ivshina et al. (2021)
	Syntrophobacter spp.	Rhizosphere		Litter decomposition	Qu and Sun (2021)
Fungi	*Dothideomycetes*	Phyllosphere, Endosphere, and Rhizosphere	Endophytic	Biocontrol agents, and degrade lignin	Gouli et al. (2021)

Continued

Table 1 Plant microbe interaction in forest ecosystem—cont'd

Microorganism		Occurrence	Interaction	Function	Reference
	Cephalosporium diospyri	Phyllosphere	Endophytic	Case persimmon wilt	Crandall and Baker (1950)
	Aureobasidium pullulans		Epiphytic	Antimicrobial, and biocontrol agents	Bozoudi and Tsaltas (2018)
	Penicillium chrysogenum	Rhizosphere, and endosphere	Endophytic	Antimicrobial	Tiwari and Ganesen (2019)
	Penicillium halotolerans	Rhizosphere	Endophytic	Biodegradation, and nutrients recycling	Park et al. (2019)
	Epicoccum purpurascens	Phyllosphere	Epiphytic	Biocontrol agents, and induce the shoot growth	Koutb and Ali (2010)
	Truncatella conorum-piceae	Endosphere	Endophytic	Decomposed of plant material	Koutb and Ali (2010)
	Rhizosphaera kalkhoffii	Endosphere	Endophytic	Can cause severe defoliation, and death of branches	Monteiro et al. (2022)
	Gymnopilus spectabilis	Phyllosphere	Saprophytes	Litter decomposing	Pérez-Izquierdo et al. (2021)
	Colletotrichum higginsianum	Phyllosphere	Endophytic	Cause anthracnose diseases	Yan et al. (2018)
	Colletotrichum linicola	Phyllosphere, and endosphere	Endophytic	Cause plant disease	Vasić et al. (2014)
	Fusarium solani	Rhizosphere	Endophytic	Cause root rot disease	Yasin et al. (2021)
	Trichoderma harzianum	Rhizosphere	Endophytic	Antagonization, promote plant growth, uptake, and use efficiency of macronutrients, and oligo/micronutrients	Vukelić et al. (2021)
Virus	*Rosellinia necatrix mega birnavirus* 1			Control white root rot disease *Rosellinia necatrix*	Kanematsu et al. (2014)
	Cryphonectria hypovirus 1			Infect the chestnut blight fungus *Cryphonectria parasitica,* and act as a biological control agent	Rigling et al. (2018)

tissue loss, it also indirectly impacts other species via impacts on the shear host plant. Plant-herbivorous interaction refers to the formation of interactions when the plant's underlying defenses prevent pest invasion (Mitchell et al., 2016). Plants exhibit adaptable defense mechanisms that effectively discourage herbivory in most arthropod species. A compatible relationship happens when the pest is either not identified by the plant or has acquired the mechanism to avoid or defeat plant defenses (Kant et al., 2015; Rioja et al., 2017). Plant defenses are ineffective in these conditions, allowing the pest to flourish and reproduce successfully. This plant-herbivore defensive interaction frequently stimulates the resistance mechanism in plants, which can minimize future herbivory and boost plant fitness (Kaplan et al., 2008; Rashid War et al., 2018). In addition, induced resistance across tissues can result in resistance to herbivores (Barber et al., 2012).

Plants are often mutualistically associated with microbes, which dwell endophytically or ectophytically in the phyllosphere and rhizosphere. Beneficial plant microbiota, specifically PGPR, nitrogen-fixing rhizobia, arbuscular mycorrhizal fungi, phyllospheric, and rhizospheric endophytes, are known to influence plant-herbivore interactions (Grunseich et al., 2019). These microorganisms stimulate plant defense signaling pathways by partially or reprogramming the metabolic pathways involved in the defense signaling process to activate certain defense-regulated phytohormones like salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) (Singh et al., 2016). The plant defense process entails reprogramming the defensive response in plants, engineered mainly by the rhizosphere microbiome. Jasmonic acid created systematic resistance via a range of signaling pathways, while salicylic acid established systemic acquired resistance in plants by interacting with pathogenesis-related proteins (Veselova et al., 2014). In addition, to combat herbivores, these phytohormones involve phytoalexin production, deposition of callose, cell wall thickening or strengthening, metabolite formation, and pathogenesis-related protein synthesis (Chekwube Enebe and Oluranti Babalola, 2019). Bacillus, Enterobacterium, Macrobacterium, Pseudomonas, Rhizobium, Serratia, Streptomyces, Erwinia, Xanthomonas, and PGPR have been found to increase the plant's defensive response via systemic acquired resistance against a wide range of herbivores. Systematic acquired resistance increases direct plant defenses, such as the synthesis of resistant chemicals, and indirect defenses, such as the synthesis of compounds or food incentives that attract natural enemies to kill herbivores (Grunseich et al., 2019). For example, the leaf beetle *Cassida rubiginosa* (thistle tortoise) feeds the *Phoma destructive*-infected plant, eventually diminishing its pupal weight, ovaries, growth rate, survival rate, and feeding (Kruess, 2002). Apriyanto and Potter (1990) reported that striped cucumber beetles ate more, and *Spodoptera frugiperda* ate less on systemic leaves of infected plants (*Cucumis sativus* infected with Tobacco necrosis virus) (Apriyanto and Potter, 1990). *Pseudomonas syringa*, TMV, *Alternaria brassicae*, and *Uromyces rumicis* enhanced the plant's ability to produce potent biochemical compounds that influenced herbivores such as *Manduca sexta, Helicoverpa zea, Phaedon cochleariae*, and *Gastrophysa viridula* to reduce growth and development rates, oviposition, pupal weights, gregariousness, food conversion efficiency, fecundity, and increased mortality (Stout et al., 2006). Even though pathogenic bacteria can alter plant development and architecture, they can also cause local and systemic changes in morphological features such as leaf toughness (through changes in lignin content), trichome density and type, leaf thickness, and leaf color. Changes in these characteristics may impact subsequent attackers; for example, the yellowing of certain virus-infected plants boosts their visual attraction to some herbivores, while the folding and pocketing of some viral-infected leaves might provide refuge (Stout et al., 2006; War et al., 2012) (Table 2).

Table. 2 Plant-microbes host interaction.

Microbes	Associated plant	Effective against host	Effect on host body	Reference
Phoma destructive	*Cirsium arvense*	*Cassida rubiginosa*	Growth of larvae, weight of larvae, and pupae were reduced, and increased mortality rate	Kruess (2002)
Puccinia carduorum	*Salix x cuspidata*	*Gastrophysa viridula, Phaedon cochleariae,* and *Cassida rubiginosa*	Weight of larvae decreased, and mortality increased	Simon and Hilker (2005)
Uromyces rumicis	*Rumex crispus,* and *Rumex obtusifolius*	*Gastrophysa viridula*	Reduced growth, and development rates	Hatcher et al. (1994)
Pseudomonas syringae		*Cicadellidae, Creontiades pallidifer, Aleurodicus dispersus etc*	Reduced growth, and development rates	Zhang et al. (2017)
Tobacco necrosis virus	*Cucumis sativus*	*Spodoptera frugiperda*	Reduced growth, and development rates	Apriyanto and Potter (1990)
Cucumber mosaic virus	*Cucurbita pepo*	*Myzus persicae,* and *Anasa tristis*	Negatively effect on gustatory cause, growth, and oviposition	Mauck et al. (2010)
Alternaria brassicae	*Brassica oleracea*	*Phaedon cochleariae*	Reduced weight of pupal, and negatively effect on oviposition	Rostas and Hilker (2002)

8 Conclusion

A forest is a stable and sustainable niche for diverse organisms. Microorganisms are naturally symbiotically associated in plants' phyllosphere, rhizosphere, and endosphere regions in a forest ecosystem. This interaction is crucial for sustaining an ecosystem's productivity, functionality, and sustainability. Various bioactive chemicals are produced due to plant-microbe interaction, assisting the plant in combating herbivore attraction by triggering the plant's secondary defensive signaling pathways. Several studies have focused on insect and invertebrate herbivores, but the processes and extent of plant-microbe-herbivore interaction are still in their infancy. More in-depth research is needed to understand the impact of plant-microbe-herbivore interactions on ecosystems. Microorganism inoculation into plants is projected to dramatically accelerate the restoration of forest plant variety after insect herbivore devastation. This technology may be utilized in agriculture as an alternative to chemical pesticides, fertilizers, and weedicides, considerably improving crop productivity and protection. They will be future eco-friendly environmental tools, given their long-term viability and effectiveness.

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Authors' contributions

B.G.: first draft, data compilation; N.F.: editing, proofreading; H.S.: prepare design, concept, final draft, and all the figures.

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CHAPTER 11

Use of microbial enzymes to degrade pesticide residues in agroecosystems-sustainable practices

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1 Introduction

The agricultural use of pesticides is continually increasing due to the need for food security. According to the FAOSTAT (2022), the total pesticide use worldwide has increased by about 75% between 1999 and 2019. Unfortunately, their application usually causes their accumulation along with their metabolites in food and different environmental compartments (Ramadan et al., 2016). Thus, the need to eliminate them from both aqueous and terrestrial environments is of great importance to reduce their threat to living organisms, including humans (Kaur Gill et al., 2021). Biological processes offer a potential solution for the eco-friendly and cost-effective elimination of contaminants from different environments through biodegradation, which involves different metabolic pathways (Salah-Tazdaït and Tazdaït, 2019; Tazdaït and Salah-Tazdaït, 2021). Among all organisms, bacteria are the best candidate to be applied in pesticide degradation because of their diversity in terms of biochemical processes involved in which the pesticides usually serve as electron and/or carbon donors (Kumari et al., 2020; Salah-Tazdaït et al., 2018; Tazdaït et al., 2013a). Many bacterial species from diverse environments are also known to use pesticides as phosphorous (Munir et al., 2016), nitrogen (Salah-Tazdaït et al., 2018), and sulfur (Singh and Walker, 2006) sources. Organothiophosphates, for instance, have widely been proved to be entirely or partially degraded by several bacterial and fungal strains. Prominent examples include *Xanthomonas* sp. 4R3-M1, *Pseudomonas* sp. 4H1-M3, and *Rhizobium* sp. 4H1-M1 (Rayu et al., 2017), *Bacillus paramycoides* NDZ (Ren et al., 2020), *Pseudomonas putida*, *Pseudomonas aeruginosa* ACP2, and *Pseudomonas azotoformans* ACP1 (Singh et al., 2020), *Sphingobium* sp. K22212 and Cam5-1 (Ahn et al., 2018), *Klebsiella pneumoniae* CP19 and *Bacillus cereus* CP6 (Elshikh et al., 2022), *Aspergillus niger* MK640786 (Hamad, 2020), and *Trichoderma viride*, *Rhizopus stolonifer*, *Fusarium graminearum*, *Penicillium digitatum*, and *Bispora antennata* (Mostafa et al., 2022). In soil, microorganisms' growth may be influenced by different

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changeable abiotic factors, including pH, temperature, humidity, and nutrient availability, which may hamper their inherent ability to transform pesticides. Microorganisms can also lose partially or totally their degradative abilities for pesticides through spontaneous mutations. Microbial enzymes are of considerable significance in the pesticide microbial degradation process. Their application for pesticide removal from contaminated media is gaining significant interest nowadays. In fact, many studies have been devoted to the use of either refined free or immobilized microbial enzymes for detoxifying soils contaminated by pesticide residues. The advantages of using purified microbial enzymes over whole-cell systems include, among others: (1) high reaction specificity, (2) possible use in environmental conditions that may not favor efficient microbial growth, (3) no toxic byproducts formation, and (4) large-scale production in cost-effective bioprocesses (Kumar et al., 2019). However, some drawbacks can limit their use in real environmental conditions. For instance, various environmental factors can hamper the catalytic activity of enzymes through reversible or irreversible inhibition. In addition, the extracellular proteases secreted by indigenous microorganisms present in the environment to be detoxified can also enormously alter the enzymes dealing with the pesticides degradation (Rao et al., 2010).

This chapter describes research works concerned with the use of microbial enzymes for pesticides's biotreatment in agroecosystems.

2 The major groups of pesticides applied in agriculture: Mode of action and toxicity

2.1 Mode of action

The pesticides act through different modes of action (Fig. 1).

2.1.1 Fungicides

In agriculture, fungicides are applied to combat fungi liable to cause pathogenic damage to cultivated crops and plants. Fungicides affect the respiratory process, the biosynthesis of chitin, melanins, sterols, and nucleic acids, and act on microtubules.

- Fungicides affecting the respiratory process

  These fungicides act on the oxidative catabolism of carbohydrates and lipids.

  - Multisite fungicides:

    Mineral fungicides (copper, sulfur) and synthetic fungicides (dithiocarbamates, quinones, and hydroxyquinones) block enzymes or coenzymes with thiol groups (Bodourian et al., 2022; Malandrakis et al., 2020).

  - Single-site fungicides:
    - ○ Mitochondrial complex II inhibitors: Carboxamides act on coenzyme Q reductase (Guo et al., 2019).

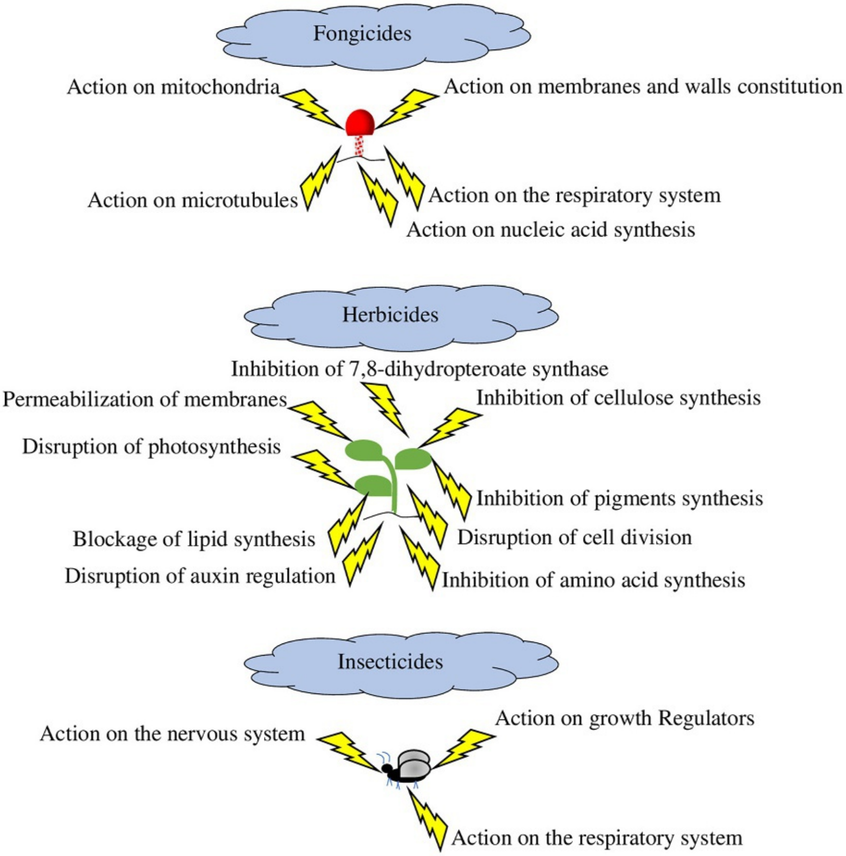

Fig. 1 Modes of action of pesticides.

    - ○ Mitochondrial complex III inhibitors: Cyazofamid acts on the site of coenzyme Q situated on the inner face of the organelle membrane (Qi). Strobilurins, imidazolinones, and oxazolidinediones act on the site of coenzyme Q located on the membrane outer face of the organelle(Qo) (Esser et al., 2014).
    - ○ Fungicides affecting the bioavailability of ATP: Silthiofam prevents the transfer of ATP from mitochondria to the cytoplasm. Fluazinam and meptyldinocap affect oxidative phosphorylation of the respiratory chain by permeabilizing mitochondrial membranes to protons (Earley et al., 2012).
- Fungicides affecting biosynthesis
  - – Fungicides affecting the constitution of the walls: The organophosphate family inhibits chitin synthase (Gikas et al., 2022).
  - – Fungicides affecting the constitution of membranes: Demethylase inhibitors (DMI) (family of imidazoles, pyridines, pyrimidines, and triazoles) inhibit

  C 14 demethylase. Amines (morpholines and piperidines) inhibit C 8-7 isomerase and/or C 14 reductase. Hydroxyanilides inhibit C 4 demethylase (Debieu and Leroux, 2015; Krauß et al., 2021; Leroux and Walker, 2011).
  - Fungicides affecting nucleic acid synthesis: In this category are the fungicides that inhibit RNA biosynthesis, either by inhibiting RNA polymerase I (phenylamides) or by inhibiting adenosine deaminase I (hydroxypyrimidines). There are also some products that block DNA synthesis (isoxazoles) (Bhagavatham et al., 2021; Gent et al., 2008; Zia et al., 2020).
  - Fungicides affecting amino acid biosynthesis: Cyprodinil, mepanipyrim, and pyrimethanil inhibit the biosynthesis of methionine (Lamberth, 2012).
  - Fungicides affecting carbohydrate biosynthesis: Dicarboximides and fludioxonil disrupt osmoregulation, causing a cytoplasmic accumulation of polyols (inositol, glycerol, mannitol) (Sang et al., 2017).
- Fungicides acting on microtubules

The families of benzamides, carbamates, and benzimidazoles bind to ß tubulin, preventing the polymerization of α with ß tubulin. Phenylureas also act on microtubules, but the target is unknown (Matsuzaki et al., 2020).

2.1.2 Herbicides

Herbicides are substances responsible for slowing the growth or destroying target plants called weeds. Weeds are considered crop enemies because they compete with the crop itself for the organic and mineral resources of the soil, water, space, and light. This definition also includes volunteer crops (canola, potatoes, sunflowers, etc.) that are undesirable, i.e., in subsequent crops. Herbicides act in the soil on the roots or the leaves. They have different sites of action on plants:

- photosynthesis disruptors.
- cell membrane permeabilizers.
- growth disruptors: inhibition of cell division, disruption of elongation, and cellulose anabolism inhibitors.
- amino acid anabolism inhibitors.
- lipid anabolism inhibitors.
- pigment synthesis inhibitors.
  - Permeabilization of membranes
    Nitrophenols or oxynils permeabilize plant membranes to H+ ions, blocking ATP synthesis and pH regulation (Rodríguez, 2014).
  - Inhibition of cellulose synthesis
    Isoxaben and dichlobenil inhibit the synthesis of cellulose (Tegg et al., 2013).
  - Disruption of cell division
    Dinitroanilines, benzamides, and pyridines bind to α-tubulin, preventing its polymerization into microtubules (Délye et al., 2004).

- Inhibition of pigments synthesis

  Inhibition of protoporphyrinogen oxidase by: triazolinones, phenylpyrazoles, *N*-phenylphthalimides, oxadiazoles, and diphenyl ethers (Hao et al., 2011).

- Disruption of photosynthesis

It occurs at the level of two targets:

- PS I: the family of bipyridiles compete with ferredoxin and are reduced by the PsaC protein, creating superoxide ions and hydrogen peroxide (Fuerst and Norman, 1991).
- PS II: benzothiadiazole, phenylcarbamates, hydroxybenzonitriles, phenyl-pyridazines, pyridazinones, triazines, triazinones, uracils, and substituted urea block the transfer of electrons, inducing oxygen reactive species production (Rutherford and Krieger-Liszkay, 2001).

  - Blockage of lipid synthesis

    Aryloxyphenoxypropionates and cyclohexane-diones inhibit acetyl-coenzyme A carboxylase, involving fatty acid synthesis. Benzofuran and thiocarbamate families can block elongases (Dayan, 2019).

  - Inhibition of amino acid synthesis

- Acetolactate synthase and acetohydroxyacid-synthetase inhibitors: sulfonylureas (chlorsulfuron, flazasulfuron), propoxycarbazone, imidazolinones (imazamox), and triazolopyrimidines (florasulam, metosulam) act on these enzymes, inhibiting the synthesis of valine, leucine, and isoleucine (Galili et al., 2021).
- Aromatic amino acid synthesis inhibitors: Glyphosate inhibit enolpyruvylshikimate-3-phosphate synthase (Devkota and Johnson, 2016).

  - Disruption of auxin regulation

    Phenoxyalkanoic, benzoic, picolinic, and quinoline carboxylic acids cause growth disturbances (Zinkgraf et al., 2017).

  - Inhibition of 7,8-dihydropteroate synthase (DHP)

    Asulam inhibits DHP, which takes part in the anabolism of folic acid. This acid is involved in the synthesis of purine and pyrimidine bases and certain amino acids (Vadlamani et al., 2022).

2.1.3 Insecticides

Insecticides are active substances that kill insects, their larvae, and/or their eggs. Synthetic organic insecticides are carbon molecules synthesized and different from inorganic or mineral insecticides. Among organic insecticides, three prominent families stand out: organophosphates, a group that has existed since 1944, many molecules of which have been removed from the market because they have proven to be toxic; carbamates, an important group, also includes many fungicides and herbicides; finally, synthetic pyrethroids, which are less toxic than organophosphates and carbamates and are used at low doses.

- Insect growth regulators
  - Molt disruptors: Pyriproxyfen disturbs the reproductive physiology of the insect. Molting inhibitors (buprofezin) block the hydroxylation of ecdysone and interrupt

  the larval development of the insect. Molt triggers (tebufenozide and halofenozide) are ecdysone agonists (Retnakaran et al., 2001).
  - Chitin inhibitors: Benzophenyl ureas, buprofezin, and tebufenozide inhibit the production of chitin (Gogi et al., 2021).
- Action on the nervous system
  - Action on the axonal nerve impulses transmission: The organochlorine family binds to the sodium channels and disrupts its functioning (Field et al., 2017).
  - Action on synapses and neuromediators: Organophosphates and carbamates act at the level of cholinergic synapses by inhibiting the functioning of acetylcholinesterase (Colovic et al., 2013). Phenylpyrazoles (fipronil) inhibit GABAergic synapses (Wei et al., 2017). Pyridine-azomethrins (pymetrozine) trigger serotonin release from serotonergic neurons (Zhao et al., 2022).
- Action on the respiratory system

The families of quinazolines (fenazaquin), pyridazinones (pyridaben), and pyrazoles (tebufenpyrad and fenpyroximate) are inhibitors of site I of the mitochondrial chain (coenzyme Q oxidoreductase) while hydramethylnon inhibits the complex cytochrome bc1 (Bajda et al., 2017; Joo and Keum, 2018; Singh, 2014).

2.2 Toxicity

The penetration of pesticides into the body can be done by several routes: by voluntary ingestion or not, by inhalation, or by skin contact. There are two types of exposure: primary exposure and secondary exposure. In primary exposure, the persons concerned are directly handling the products. Secondary exposure concerns the entire population through contact with residues emanating from pesticides used in food and the environment (Kalyabina et al., 2021). The health effects of pesticides depend on the type of poisoning (acute or chronic).

2.2.1 Acute poisoning

Acute effects related to pesticide poisoning occur immediately or within a few hours of significant exposure.

- Acute poisoning by insecticides
  - Organophosphates and carbamates: These products have good skin penetration and are toxic by the respiratory route (high volatility). They are digestive, respiratory, cardiac, and muscular, with increased secretions, contracted pupils, impaired consciousness, or even the onset of a coma. Depending on the dose absorbed by the body, the intoxicated person recovers with or without sequelae (polyneuropathy) or dies (Vale and Bradberry, 2017). Organophosphates are the only pesticides with an antidote: pralidoxime (Eddleston et al., 2009).
  - Synthetic pyrethroids: Symptoms of irritation and local neurological disorders are observed (Ramchandra and Victor, 2019).

  - Organochlorines: They are powerful enzyme inducers and can therefore influence the degradation of other substances, such as alcohol and drugs, and lead to overdose phenomena (Jayaraj et al., 2016).
  - Methyl Bromide: It can lead to impaired consciousness up to coma and death (Lecailtel et al., 2015).
- Acute poisoning by fungicides
  - Dithiocarbamates are mucocutaneous irritants (Zakharov et al., 2016).
  - Copper sulfate: It causes irritations of the skin and mucous membranes, metal fever, vomiting, and diarrhea, with possible kidney and red blood cell damage (Cohen, 2000; Perestrelo et al., 2021).
- Acute poisoning by herbicides
  - Amides: They cause burns when projecting a concentrated solution (Lushchak et al., 2018).
  - Quaternary ammoniums: They cause irritations of the skin, eyes, and mucous membranes, pharyngeal pain, digestive disorders, liver and kidney blockage, and pulmonary fibrosis with paraquat (Hrubec et al., 2021).
  - Sodium chlorate causes hemolysis and methemoglobinemia, with renal and hepatic damage (Ali et al., 2017).
  - Substituted urea: They cause nervous system depression, digestive disorders, methemoglobinemia, and irritations of the skin and eyes (Weerasinghe et al., 2019).
  - Triazines cause the central nervous system to depress in case of massive intake (Lushchak et al., 2018).

2.2.2 Chronic poisoning

Chronic poisoning occurs after multiple exposures to small amounts of pesticides. The delay before the onset of symptoms can sometimes be very long. Exposure to pesticides, like rotenone, would increase the risk of Parkinson's illness by 70% (Sherer et al., 2003). The danger of certain pesticides on reproductive function has been taken seriously into consideration following the dramatic consequences linked to the use of dibromochloropropane (DBCP); there are several tens of thousands of male agricultural workers whose infertility has been related to DBCP exposure (Hwang et al., 2013). There is an increased threat of the occurrence of innate anomalies of the digestive tract in women residing in areas of aerial spraying of malathion (N'Go et al., 2013). Preconception exposure to chlorophenoxy and triazine results in a moderate increase in early miscarriages, while exposure to glyphosate or thiocarbamate is associated with late miscarriages (Goodman et al., 2014; Naidoo et al., 2011; Shirangi et al., 2011). Furthermore, there is a significant association between prematurity and maternal serum concentration of dichlorodiphenyldichloroethylene (DDE), one of the biologically active metabolites of dichlorodiphenyltrichloroethane (DDT) (Garced et al., 2012).

3 Biochemical aspects of the biodegradation of pesticides in soil

The bioremediation approach, which involves the combination of fundamental metabolic reactions and engineering techniques, has gained significant attention not only because of its low energy consumption but also because of the large availability and diversity of microorganisms whose degradative potential makes it possible for the detoxification of virtually every hazardous compound. Thus, the bioremediation technique is considered more practical than classical physicochemical remedy techniques such as adsorption, incineration, photodegradation, coagulation, etc. Besides, the bioremediation approach offers, in some cases, the valuable advantage of converting hazardous compounds, including pesticides, into their simple inorganic constituents (H_2O, Cl^-, CO_2, SO_4^{2-}, NH_3, PO_4^{3-}) (Birolli et al., 2019; Cycoń et al., 2013; Kaur and Goyal, 2019; Tazdaït et al., 2013a). Pesticides biodegradation is accomplished by a large metabolically diverse bacteria, including Alphaproteobacteria (*Agrobacterium radiobacter* J14a, *Sphingomonas* sp. SRS2, etc.) (Sørensen et al., 2013; Struthers et al., 1998), Betaproteobacteria (*Alcaligenes faecalis* CGMCC 17553, *Achromobacter* sp. LZ35, *Neisseria subflava*, etc.) (Anusha et al., 2009; Xia et al., 2017; Yang et al., 2019), Gammaproteobacteria (*Stenotrophomonas maltophilia* OG2, *Pseudomonas stutzeri*, *Proteus*, *Klebsiella pneumoniae* BPBA052, etc.) (Ozdal et al., 2017; Salah-Tazdaït et al., 2018; Tang et al., 2019), and also by fungal (*Penicillium, Trichoderma*, and *Aspergillus*) (Correa et al., 2023) and yeast (*Candida pseudolambica*) (Ebadi et al., 2022) isolates.

The microbial biodegradation of xenobiotics profoundly depends on their concentrations in the media. It is assumed that the biodegradation of a given contaminant takes place only if its concentration is above a certain concentration called minimum substrate concentration (S_{min}). In this case, the contaminant would serve as a substrate to sustain microbial growth (Becker and Seagren, 2010).

Depending on the extent of their biodegradation, the pesticides usually serve for energy production, reducing power, and cellular growth in the case of their complete degradation (Mineralization). In contrast, in the presence of growth substrates, either simple substrates, such as glucose, acetate, citrate, etc., or complex ones, such as molasses, whey, and date syrup, they usually undergo minor changes in their chemical structure (Biotransformation) (Salah-Tazdaït et al., 2018; Tazdaït et al., 2013b, 2015). Nevertheless, in the case of a mixture of appropriate microorganisms, the secondary substrates can serve as electron and energy sources. Besides, two situations exist depending on the relation of biodegradation to growth. In the first situation, the pesticide is driven into the primary metabolism and usually serves as a growth substrate or primary substrate (carbon, nitrogen, sulfur, phosphorous, or energy sources). For example, chlorpyrifos has been reported to serve the growth of a strain pertaining to the genus *Cupriavidus* (*Cupriavidus nantongensis* X1^T). The strain could use chlorpyrifos as a unique source of carbon, thanks to an organophosphorus hydrolase which initiates the degradation of the pesticide by yielding two metabolites, namely diethylthiophosphate and trichloropyridin-olate (Shi et al., 2019). In the second situation, the pesticide is degraded cometabolically, called secondary substrate or cometabolic substrate. The yielded compounds are not further degraded by the microorganisms that generate them unless other microorganisms in the environment can use them as growth substrates. This, for instance, has been observed during the biodegradation of parathion by *Bacillus* sp. isolated from a silty loam soil and grown in the presence of peptone-yeast extract used as a growth substrate. The author reported that the biodegradation of parathion by the strain resulted in the liberation of two metabolites (diethylthiophosphate and *p*-nitrophenol) and that the pure-cultured strain in soil exhibited no significant parathion hydrolysis (Nelson, 1982) (Fig. 2).

It is generally admitted that the more the xenobiotic is in a reduced state, the more likely it serves as an electron donor and/or carbon source during the microbial primary metabolism.

On the other hand, during biotransformation reactions, pesticide metabolites are produced that are usually equally or more toxic than the parent pesticides. For instance, during biotic or abiotic oxidation of malathion, one metabolite in particular, malaoxon, is formed and exhibits higher toxicity levels than the parent molecule (Gupta and Crissman, 2013; Tazdaït et al., 2015). Thus, special care should be taken to identify pesticide metabolites during biodegradation processes to confirm the success of the bioremediation approach.

Besides, similarly to other xenobiotics, the pesticides can exhibit an inhibitory effect on their own biodegradation or microbial growth in either single or mixed cultures (Tazdaït et al., 2015). This inhibitory phenomenon is usually best described by the Haldane model.

The bacteria and fungi involved in the biodegradation of pesticides act by generating various intracellularly or extracellularly located enzymes, including hydrolases (esterases, phosphotriesterases, organophosphorus hydrolase (OpdA and OpdB), carboxylesterases), oxygenases, transferases such as glutathione *S*-transferase, and oxidoreductases such as oxygenases (mono or dioxygenases), laccases, and peroxidases whose encoding genes can have either chromosomal or plasmidic localization. Among these enzymes, hydrolases have been deeply researched and have been demonstrated to efficiently degrade a variety of xenobiotics, especially organophosphorus pesticides, owing to their diverse substrate specificity range (Singh and Walker, 2006). Bacteria, through dehalogenases, also play important roles in the cleanup of organohalide-pesticides (Sarma and Joshi, 2020). Table 1 gives some examples of microbial enzymes related to the degradation of pesticides from different classes.

The application of microbial enzymes for pesticide removal from contaminated soils, including those under agricultural exploitation, is of significant interest nowadays. Several studies have dealt with the use of microbial enzymes for decontaminating natural or agricultural soils from pesticide residues. Although, most of them have been performed on soils that are artificially contaminated with pesticides and supplemented with mediator

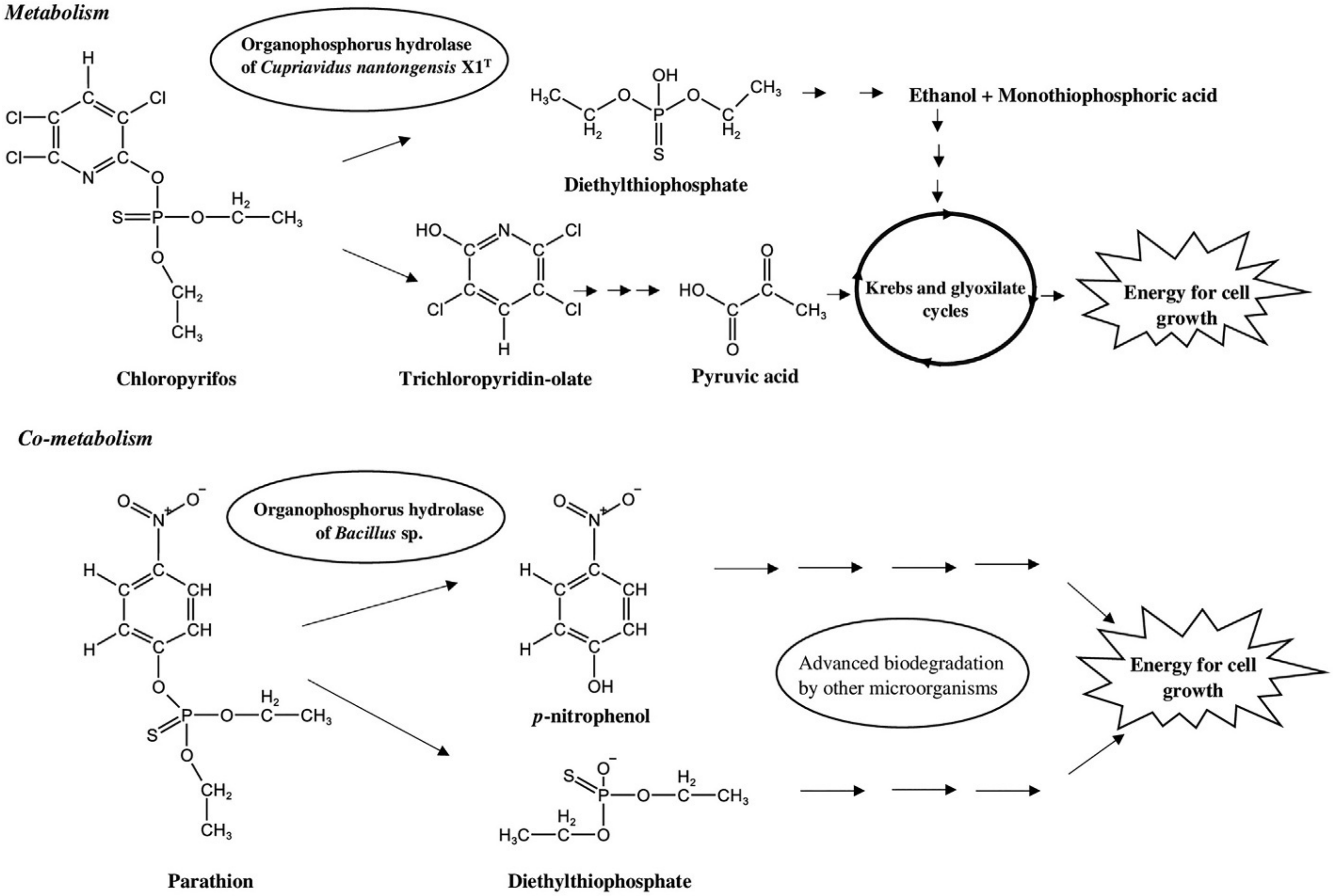

Fig. 2 Schematic showing classification of pesticides bioremediation reactions according to the relationship between biodegradation and growth. Note that successive *arrows* designate multiple metabolic reactions.

Table 1 Examples of pesticides degradation by microbial enzymes.

Enzyme class	Enzymatic activity	Microorganism	Location	Pesticide	Result (removal percent)	Product	References
Hydrolases							
Organophosphorus hydrolase	28.59[a] (PF) and 33.41[a] (QP)	*Kosakinia oryzae* VITPSCQ3	/	Profenofos (PF)	82 after 48 h	Diethyl phosphate and 4-bromo, 2-chlorophenol	Dash and Osborne (2020)
				Quinalphos (QP)	92 after 48 h	Diethyl phosphate and quinoxalin-2(1*H*)-one	
Organophosphate degrading enzyme (OpdB)	/	*Pseudomonas* sp. *BF1-3*	/	Chlorpyrifos	97 after 9 days	3,5,6-Trichloro-2-pyridinol	Barman et al. (2014)
Organophosphate degrading enzyme (OpdA)	/	*Agrobacterium radiobacter* P230	/	Diazinon, parathion, coumaphos, phosmet, fenthion, etc.	/	/	Horne et al. (2002)
Phosphotriesterase	/	*Bacillus* sp. *CBMAI 1833*	/	Methyl parathion	>99 after 6 h	*p*-nitrophenol	Alvarenga et al. (2018)
		Bacillus cereus P5CNB			83 after 6 h		
Mutant phosphotriesterase (Sso-3M) immobilized on regenerated cellulose membrane	6.4[b]	*Sulfolobus sulfataricu*	/	Paraoxon-ethyl	89 at 1.7 min residence time	/	Vitola et al. (2021)

Continued

Table 1 Examples of pesticides degradation by microbial enzymes—cont'd

Enzyme class	Enzymatic activity	Microorganism	Location	Pesticide	Result (removal percent)	Product	References
Organophosphorus hydrolase	0.73[b]	*Enterobacter aerogenes* CP2 and *Streptococcus pyogenes* CP11	Cytosol	Chlorpyrifos	77 after 48 h 74 after 48 h	Diethylthiophosphoric acid	Lourthuraj et al. (2022)
Esterase	/	*Bacillus subtilis* 1D	Extracellular	Cypermethrin	95 after 15 days	3-(2,2-Dichloro ethenyl)-2,2-dimethyl-cyclopropanecarboxylate and cyclododecylamine	Gangola et al. (2018)
Carboxylesterase	1685.71[b]	*Escherichia coli* IES-02	/	Malathion	81 after 20 min	Monocarboxylic acid and dicarboxylic acid	Sirajuddin et al. (2020)
Oxidoreductases							
Laccase	/	*Bacillus subtilis* 1D	Cytosol	Cypermethrin	95 after 15 days	/	Gangola et al. (2018)
Thermo-alkali stable laccase	1089.70[b] (di-methoxy phenol used as a growth substrate)	*Pseudomonas* sp. S2	Extracellular	Dichlorophos, chlorpyrifos, profenovos, and monocrotophos	45.99 after 6 h 80.56 after 6 h 75.45 after 6 h 81.84 after 6 h	/	Chauhan and Jha (2018)
Manganese peroxidase	0.12[a]	*Pleurotus ostreatus*	/	Triclosan	>90 after 4 days	/	Maadani Mallak et al. (2020)

CYP 450 monooxygenase	0.31[b]	*Pseudomonas aeruginosa* PS-4	/	Propiconazole	100 after 3 days	1,2,4-Triazole, 2,4-dichlorobenzoic acid, and 1-chlorobenzene	Satapute and Kaliwal (2016)
Transferase							
Glutathione *S*-transferase	/	*Klebsiella jilinsis 2N3*	/	Chlorimuron-ethyl	42.91	2-Amino-4-chloro-6-methoxypyrimidine and *o*-sulfonate benzoic imide	Zhang et al. (2020)
Lyase							
Enolase (phosphopyruvate hydratase)	111.1[b]	*Microbacterium esteraromaticum* MM1		Fenamiphos	/	/	Logeshwaran et al. (2020)

/, not provided.

[a] Enzyme activity (U/mL).

[b] Specific enzyme activity (U/mg of protein).

compounds in the case of laccase systems. Enzymatic treatment of pesticides-contaminated soils involving fungal enzymes such as peroxidases and laccases has gained considerable interest. Hence, in a study by Zhao and Yi (2010), the authors investigated the influence of soil pH and soil oxygen concentration on the enzymatic treatment of a woodland soil contaminated by DDT (1,1,1-trichloro-2,2-bis (4-chlorophenyl) ethane). The enzyme tested was a laccase produced by the white rot fungi *Panus conchatus*. It was evidenced that high concentrations of oxygen in soil and acidic pH values (2.5–4.5) positively affected the efficacy of laccase. In another study, the combined use of laccase and the fungus (*Flammulina velutipes*) that produced it was more effective in remediating DDT-contaminated woodland soil than the separate use of them. This coremediation approach efficiently transformed DDT with a maximum degradation rate of 66.82% (Fan et al., 2013). An optimization approach has been successfully applied to enhance the performance of hexahistidine-containing organophosphorus hydrolase (His6-OPH)/poly-L-glutamic acid (PLE50) complex immobilized on natural zeolite in degrading chlorpyrifos in soil. His6-OPH was produced by a recombinant *Escherichia coli* SG13009[pREP4] system harboring a plasmid encoding the enzyme. The results obtained under optimized conditions showed complete degradation of chlorpyrifos (100 mg/kg) within 72 h in different soil types (sand, chestnut soil, gray forest soil, and chernozem) (Senko et al., 2017).

In the case study reported by Scott et al. (2011), a commercial bacterial phosphotriesterase (EC 3.1.8.1) able to degrade a broad range of organophosphorus insecticides (malathion, dichlorvos, methyl parathion, ethyl parathion, diazinon, chlorpyrifos, etc.) was successfully applied, in Australia, to remediate a soil planted with almond trees treated with diazinon (2 L/ha). The enzyme preparation applied at 1 kg/ha resulted in 77% diazinon degradation after only 1 h of enzymatic treatment. Nevertheless, no increase in the diazinon removal rate was observed after 7 days of treatment, possibly due, as suggested by the authors, to the irreversible adsorption of a part of diazinon on the soil particles. On the other hand, the enzyme exhibited no toxic effects on different organisms, including bacteria, rate, *Scenedesmus subspicatus*, *Daphnia magna*, and *Brachydanio rerio*.

Remediating pesticide-contaminated soils by enzymes produced by fungi and bacteria is more difficult than that in aqueous media. This is because enzymes tend to adsorb either organic or mineral compounds of soil, thus seriously hindering the assessment of their performance and activity.

4 Engineered and intrinsic in situ bioremediation

Biocatalysts, extremely effective for the degradation of organophosphates, have been intensively explored. Indeed, many enzymes can effectively hydrolyze organophosphates.

4.1 Organophosphate hydrolases

Organophosphate hydrolases (OPHs) pertain to the aryltriphosphate dialkylphosphohydrolases (EC 3.1.8.1) and the amidohydrolases superfamily. These enzymes were originally isolated from *Sphingobium fuliginis* ATCC 27551 and *Brevundimonas diminuta* MG. Another closely related enzyme (OpdA) was obtained from the bacterium *Agrobacterium radiobacter* P230 (Eddleston et al., 2020; Wales and Reeves, 2012). Considerable work has been made to characterize and engineer these enzymes. The most notable works are outlined below.

4.1.1 OPH of Brevundimonas diminuta

This 35 kDa enzyme could degrade a broad range of organophosphorus insecticides, with catalytic efficiencies ($kcat/K_M$) reaching $3.8 \times 10^7 M^{-1} s^{-1}$ for paraoxon (Meier et al., 2013).

4.1.2 OPH of Sphingobium fuliginis

S. fuliginis (ATCC 27551) has been obtained from rice paddy water and could breakdown diazinon, parathion, and many other organophosphates. The manufacture of organophosphates decontamination solutions has been considered using recombinant OPH (Azam et al., 2019).

4.1.3 OPH of Agrobacterium radiobacter (OpdA)

The bacterial strain *A. radiobacter* P230 expressing the OpdA enzyme can hydrolyze organophosphates insecticides. The structure of OpdA has been resolved and has made it possible to highlight similarities with the mechanism of certain metallophosphoesterases. Protein engineering has been used to improve the degradation of organophosphate insecticides. As reported by Jackson et al. (2009), a rational approach allowed the discerning of residues related to the stereospecificity of the enzyme, allowing to obtain a variant showing improvements in the catalytic activity of 480 times and 8 times, respectively, for the Z and E stereoisomers of chlorfenvinphos.

Since OPHs are effective biocatalysts, their use for decontamination has been considered, and immobilization strategies have been studied. Trityl-agarose was used for immobilization, thus maintaining the ability of the enzyme to hydrolyze organophosphates insecticides. Moreover, the thermostability of the enzyme when immobilized was improved six times in comparison to the free configuration at 55°C (Blatchford et al., 2012). Other instances of OPH immobilized on amyloid fibril nanostructures and nonwoven polyester textiles have been described (Gao et al., 2014).

4.2 Organophosphate acid anhydrolases (OPAA) and prolidases

An isolate originating from a moderately halophilic bacterium belonging to the *Alteromonas*, capable of hydrolyzing a certain number of organophosphates, has been described. The OPAA-2 enzyme was purified from this isolate and characterized as a 60 kDa polypeptide. The enzyme can breakdown DFP (diisopropyl fluorophosphate) and phosphofluoridate-type chemical compounds such as soman and sarin (Štěpánková et al., 2013).

4.3 Paraoxonase

A human enzyme called paraoxonase (PON1, EC 3.1.8.1.) is of great importance. After the first reports indicating the capacity of an esterase, isolated from mammalian serum, to breakdown paraoxon, many studies have been conducted. PON1 can hydrolyze a broad spectrum of OP insecticides. PONs from rabbit and human sera have been purified and differ only in the terminal protein sequence. However, human PON1 remains challenging to purify from plasma, and its heterologous expression does not allow high yields (Carr et al., 2015). However, adenovirus and baculovirus infections of the *Trichoplusia ni* (Hubnet, 1803) larva resulted in the large-scale production of a recombinant system (HuPON1) (Otto et al., 2010).

5 Genetically engineered enzymes for pesticides biodegradation

Bacillus diminuta phosphotriesterase is a good candidate, which can be enhanced with enzyme engineering strategies for catalytic decontamination of organophosphates. Protein engineering strategies to improve the activity of OPH have been carried out. A mutagenesis approach, for example, has made it possible to obtain improved variants against diisopropylfluorophosphate (DFP), allowing for the first time to increase the hydrolysis of phosphorus-halide bonds. Other approaches have also made it possible to improve the efficacy toward paraoxon (Bigley and Raushel, 2019).

Protein engineering strategies were therefore considered to improve the ability of *Sphingobium fuliginis* OPH to discriminate between the enantiomers of certain organophosphates. A variant capable of hydrolyzing a chromogenic analogue of the most toxic stereoisomer of the nerve agent soman was produced approximately threefold more efficiently than the wild form of the enzyme. Other mutagenesis work has made it possible to generate variants with improved activities for malathion and DFP (Iyer and Iken, 2015).

The enzyme diisopropylfluorophosphate fluorohydrolase (DFPase, EC 3.1.8.2), isolated from *Loligo vulgaris*, has driven a special attention of researchers. This enzyme, derived from a squid, effectively hydrolyzes DFP and tabun. The heterologous generation of the enzyme was carried out with *Escherichia coli* used as a system of expression. The enzyme produced is stable for 1 year at 4°C (Farnoosh and Latifi, 2014; Hartleib and Rüterjans, 2001).

Enzyme engineering has been used to obtain more efficient PON variants. Mammalian PON1 is more effective for cyclosarin and soman detoxification than OPH and DFPase isolated from *Bacillus diminuta* and *Loligo vulgaris*, respectively. PON1 variants were enhanced 10–380-fold for the degradation of chlorpyrifos-oxon, cyclosarin, DFP, parathion, and soman (Amitai et al., 2006). Paraoxonase PON3 was also purified and then modified by directed evolution. Thus, the catalytic efficiency of recombinant PON3 mutants was increased up to 240 times for paraoxon. PON3 activity and stability were further modulated by combining gene shuffling and mutagenesis based on phylogenetic analyses (Aharoni et al., 2004; Khersonsky et al., 2009).

Another enzyme called methylparathion hydrolase (MPH, EC 3.1.8.1), an aryldialkylphosphatase, belongs to the metallo-lactamase family (Dong et al., 2005). A recombinant MPH expressed in *Escherichia coli* has been characterized and is active on methylparathion and other insecticides such as dichlorvos or malathion (Yang et al., 2008). Random mutagenesis of MPH from *Pseudomonas stutzeri* improved the degradation of chlorpyrifos by five times (Xie et al., 2014). Another MPH, OPHC2, has been identified in the C2-1 strain of *Pseudomonas pseudoalcaligenes* and the SMSP-1 strain of *Stenotrophomonas* sp. (Shen et al., 2010; Wu, 2004). An OPHC2 analog enzyme, named *Po*OPH from *Pseudomonas oleovorans*, has been discovered. This enzyme exhibits lactonase arylesterase and lactonase activities and also OPH promiscuity activity. A variant of *Po*OPH$_{M2}$ was constructed, and its activity enhanced 106-fold and 7-fold against ethylparaoxon and methylparathion, respectively (Luo et al., 2014).

Among the enzymes capable of degrading organophosphates, phosphotriesterase-like lactonases (PLL) compose a promising class of proteins close to bacterial phosphotriesterases. PLLs are natural lactonases which catalyze the hydrolysis of *N*-acyl-homoserine lactones (AHL) implicated in the quorum sensing system in several bacteria (Bzdrenga et al., 2017). PLLs have been obtained from different microorganisms, including hyperthermophilic bacteria or archaea. These enzymes demonstrate significant stability to pH, temperature, detergents, and solvents, exhibiting good prospects for decontaminating organophosphates using extracellular enzymes (Kallnik et al., 2014; Zhang et al., 2012). Particular attention was paid to the enzyme SsoPox isolated from the hyperthermophilic archaea *Sulfolobus solfataricus* discovered in the solfatara of Vesuvius and has a gene homologous to that coding for the PTE of *Bacillus diminuta*. The corresponding enzyme was produced, and its phosphotriesterase activity, although weak, was demonstrated. Among the degraded substrates is paraoxon, which is why this enzyme has been named: *Sulfolobus solftataricus* Paraoxonase. SsoPox effectively hydrolyzes some lactones, such as *N*-acyl homoserine lactones, which are molecules known for their involvement in bacterial quorum sensing. Due to its hyperthermophilic origins, the enzyme exhibits extreme temperature stability; it is active from 10°C to 100°C, with high resistance to denaturation by temperature (106°C) and urea. It is also tolerant to solvents and sterilization and has a long shelf life. Additionally, SsoPox is active over a broad pH range between 5.0 and 9.0 (Merone et al., 2005). From his observations, the idea arose to combine the incredible structural stability of this enzyme with the catalytic efficiency of *Bacillus diminuta* PTE by transferring its active site into the SsoPox structure. Indeed, high stability generally confers increased mutation tolerance. Hyperthermophilic structures are usually good candidates for evolution, and their high stability allows them to minimize certain mutations' deleterious impact. A wide variety of mutations can thus be generated without drastically affecting the protein's functionality. Furthermore, substrate promiscuity was determined as a possible origin for functional divergences that could be inception for evolutionary strategies (Khersonsky et al., 2006). Mesophilic phosphotriesterases are suggested to have probably derived from PLLs. Therefore, their respective structures and sequences were compared, allowing the determination of residues implicated in improving phosphotriesterase activity. A mutational database listing potentially useful substitutions for phosphotriesterase activity has been generated. This database, associated with in silicostructural analysis, was applied as a strategy for engineering on SsoPox for organophosphate degradation. Variants showing improvements in activity for certain pesticides and an extended field of action have been obtained (Jacquet et al., 2017). According to Elias et al. (2008), R223H and Y97W mutations also affect phosphotriesterase activity. The replacement of residue W263 was also studied. This residue is located in the active site and is involved in the conformational flexibility of the enzyme, playing a significant role in its substrate promiscuity. Mutagenesis by saturation was applied at this position by using degenerate primers. It was found that two subsets of mutations stand out, favoring either lactonase or phosphotriesterase activity. For the latter, the W263F, W263L, and W263M variants are particularly interesting. SsoPox and its variants are active on a broad range of organophosphates. The activity of SsoPox stimulated by anionic detergents at room temperature has also been reported, which is extremely interesting for decontamination using extracellular enzymes (Hiblot et al., 2012).

6 Conclusion

There has been a tremendous research effort focusing on using pesticide-degrading microorganisms for remediating agricultural soils. Nowadays, efforts are being dedicated to using microbial enzymes because this strategy has proven its effectiveness in terms of rapidity and specificity in treating soils contaminated by pesticides. However, their use on a large scale meets some serious challenges, chiefly their cost-ineffective production. This drawback could be significantly overcome by using byproducts (whey, molasses, wheat straw, citrus pulp, etc.) from the agro-industrial sector. These complex compounds are very low cost, even gratuitous, and richly composed of nutritive elements that can support both microbial growth and enzyme production. Additionally, developing genetically engineered enzymes through mutagenesis approaches with new or improved properties and using metabolic engineering methods could also reduce industrial enzyme production costs. The optimization of the composition of the growth medium by mathematical procedures could also significantly improve enzyme production.

Besides, the discovery and characterization of novel microbial strains able to produce more effective pesticides-degrading enzymes should be encouraged and further financed by governments worldwide, especially in agricultural countries suffering from acute soil contamination with pesticide residues.

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CHAPTER 12

Chemical-assisted biological methods for in situ remediation of petroleum hydrocarbon-contaminated soils

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1 Introduction

Petroleum, or crude oil, is a fossil fuel and is classified as a nonrenewable source of energy. All over the world, petroleum is known as the most valuable energy source that is extracted from natural underground reservoirs (Asghar et al., 2016). Huge annual petroleum consumption by the major countries of the world like the United States, China, and Japan have shown the severe dependence of the world on petroleum (IEA, 2021). Furthermore, in developing countries, such as Iran, the economy and industrial growth also still rely severely on petroleum and other petroleum-derived product revenues (Solaymani, 2021). Fig. 1 also represents the world's total energy supply by source in 1973 and 2019, which was reported by the International Energy Agency (IEA) in September 2021. This statistical information shows that petroleum had been one of the main sources of energy for almost 49 past years, and it has been predicted that this trend will continue till 2050 (IEA, 2021). Hence, most countries with remarkable proven petroleum reserves attempt to produce more crude oil to maintain and improve their position in the global oil market and provide the energy required for their infrastructures of urbanization and industrialization. However, the exploration, exploitation, refining, transportation, storage, and consummation of petroleum and its by-products pose unavoidable risks to the environment (Asghar et al., 2016). The environmental issues related to fossil fuel consumption have caused serious problems and concerns for the governments, oil and gas companies, and environmentalists.

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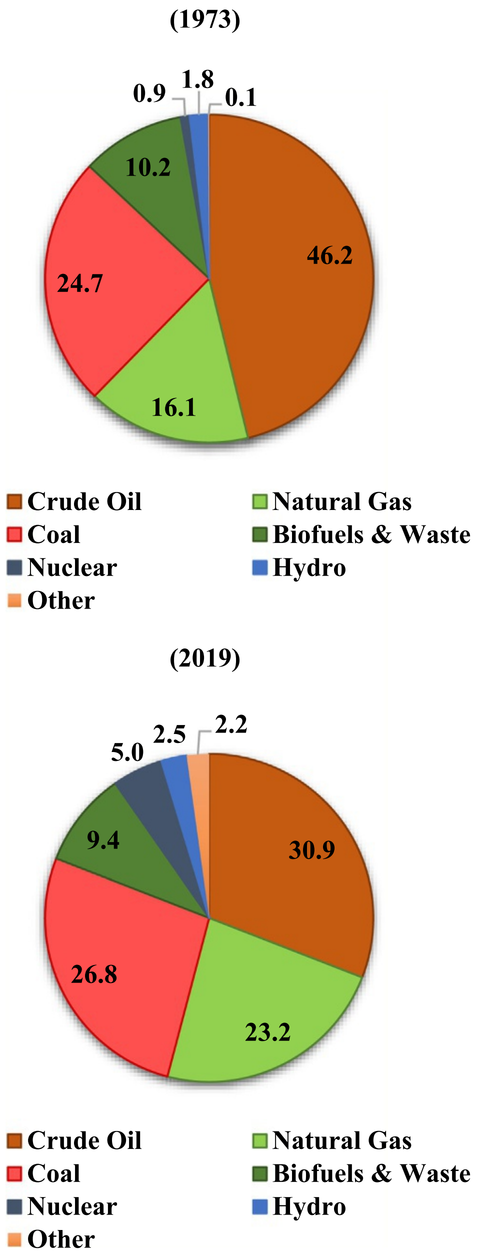

Fig. 1 Percentage share of world's total energy supply by source (IEA, 2021).

1.1 Petroleum composition

Petroleum is a complicated mixture of hydrocarbon and nonhydrocarbon-containing compounds. Hydrocarbons are compounds that contain only elements of carbon and hydrogen and include an extensive array of linear, branched, cyclic, and aromatic components with a wide range of molecular weights (MW) from extremely light, i.e., C_1 with a MW of 16 g/mol, to very heavy, i.e., $\sim C_{80}$ with MW up to 1000 g/mol. Nonhydrocarbon-containing compounds, like resins and asphaltenes, have further elements, such as nitrogen, sulfur, oxygen, and some heavy metals. Asphaltenes are mostly considered to be the heaviest fraction of petroleum (Brown et al., 2017).

Almost all components of petroleum include the aliphatic hydrocarbons (the organic components with carbon and hydrogen joined together in straight, branched chains, or nonaromatic rings such as alkanes, alkenes, and alkynes), naphthenic acids, monoaromatic hydrocarbons (benzene, toluene, ethylbenzene, and xylenes), and polycyclic aromatic hydrocarbons are known as toxic components (Ruberg et al., 2021). However, monoaromatic and polycyclic aromatic hydrocarbons are considered as highly toxic, mutagenic, and carcinogenic components in nature (Ziółkowska and Wyszkowski, 2010). These components are not very mobile in soil, barely soluble in water, and usually resistant to physical, chemical, or biological degradation. Specific concentrations of these components in nature can be sources of severe contamination and an immediate threat to all living organisms dwelling in a polluted region (Henry, 1998; Ziółkowska and Wyszkowski, 2010). The results of the toxicity assessment of petroleum components show that the accumulation and durability of these components in the environment can bring about the detrimental effects in aquatic and terrestrial ecosystems, enter the food chain, retain for decades and affect plants, animals, and finally humans. Depending on the exposure to petroleum and its by-products, either directly or indirectly, human health is severely affected by these types of contaminations. The irritation of the skin and eyes, breathing and neurologic problems, and physical/physiological effects on mental health, genetic, immune, and endocrine systems are known as the main effects of these pollutants on human health (Kuppusamy et al., 2020).

It should be mentioned that petroleum-based products have various physical, chemical, and toxic properties dependent on the refinement process and additives. Hence, identification of the toxicity of specific petroleum components is essential as it will enable people to diagnose potential ecological threats connected with petroleum products exploitation (Ziółkowska and Wyszkowski, 2010).

1.2 Types of petroleum pollution

As stated in the previous section, generally petroleum has a toxic nature and in regions where petroleum development is widespread, air, water, and soil resources can become polluted with its wastes and by-products.

1.2.1 Air pollution

A variety of air pollutants are released throughout the petroleum development processes, i.e., exploration, exploitation, refining, transportation, storage, and consummation of petroleum. These contaminants are released from a number of sources, such as venting, flaring, vehicles, engines, etc. Nitrogen oxides (NO_2, NO_3), sulfur oxides (SO_2, SO_3), and carbon dioxide (CO_2), which are emitted by fossil fuel combustion, and volatile hydrocarbon compounds such as toluene, xylene, and methane (CH_4) are the most common air pollutants during the petroleum development processes (Sadatshojaie and Rahimpour, 2020). These pollutants, especially CO_2 and CH_4, pose a remarkable risk to the environment and living conditions. They are the leading cause of acid rain, the depletion of ozone, and global warming (Yoro and Daramola, 2020).

1.2.2 Water pollution

Illegal oily sewage discharge, petroleum spill accidents during fuel transportation by ships, and offshore petroleum drilling platforms are the main sources of petroleum pollutants released into aquatic ecosystems (Han et al., 2019). The considerable amount of petroleum pollutants that is released from these sources can decrease the production and diversity of marine plants and animals. The toxic mixtures available in oily sewage can cause ecological disturbances, including the aquatic community structure and food chain alteration. They can also influence groundwater or drinking water. Furthermore, a large amount of petroleum spilled on the surface of the sea may cause fires and safety problems for shipping (Han et al., 2019; Medeiros et al., 2022).

1.2.3 Soil pollution

Common sources of contamination of the shallow subsurface environment, i.e., soil and groundwater, are pipeline leaks, poor storage, leaking underground and aboveground storage tanks, leakage from refinery equipment, petrochemical industry effluent discharge, oil wells integrity failures, and natural seepage of petroleum (Essaid et al., 2015). The released petroleum kills or inhibits numerous microbial species, thus changing the functionality of the microbial community and consequently the terrestrial ecosystem. Plants exposed to petroleum hydrocarbons are influenced by direct toxicity, access prevention to light, and the incapability to gain nutrients and water due to oil limiting their movement through the soil matrix, all of which severely diminish the productivity of plant (Truskewycz et al., 2019). Petroleum hydrocarbons are also accessible for crop uptake in agricultural soils, consequently representing a potential route of human exposure and a risk to human health (Grifoni et al., 2020).

1.3 Necessity of petroleum-contaminated soils remediation

The contamination of each source, i.e., air, water, and soil, can affect the other due to the material circulation in the environment. In other words, air pollution can greatly hurt the soil and water resources. When we contaminate our air, we are also contaminating the precipitation that falls into water bodies and soils (Kaitala et al., 1992). Water contamination can also contribute to soil contamination and vice versa. Therefore, all of the mentioned types of petroleum contamination are important and should be considered in basic and applied research to find a proper solution for pollution entering the environment prevention or early remediation.

Meanwhile, soil is one of the resources which plays a vital role in the Earth's ecosystem (Fitzsimons and Miller, 2010). Soil functions, known as general soil capabilities that are important for various environmental, agricultural, and urban applications, are highly influenced by contaminants especially petroleum-based ones (Kuppusamy et al., 2020), as discussed formerly. Soil pollution with petroleum components is a serious issue all over the world since more than 90% of environmental petroleum pollutants' burden is stored in the soil. Therefore, soil is the main sink of petroleum pollutants in the environment (Kuppusamy et al., 2020; Sui et al., 2021).

The fate and transport of petroleum pollutants in the soil is also a complex process. Fig. 2 displays the simple conceptual model of petroleum release in the soil. If released petroleum has adequate quantities, there is a potential to penetrate into the subsurface. Nevertheless, the penetration rate and its extent depend on other factors such as the properties of soil, i.e., porosity, pore size, heterogeneity, and the amount of moisture as well as the physical properties of pollutants, i.e., viscosity, density, and surface tension (Brown et al., 2017). In subsurface, petroleum is distinct from the aqueous and gas phases and commonly named nonaqueous phase liquid (NAPL). In the soil porous media, three mobile fluid phases can coexist and simultaneous flow of water, NAPL, and air, i.e.,

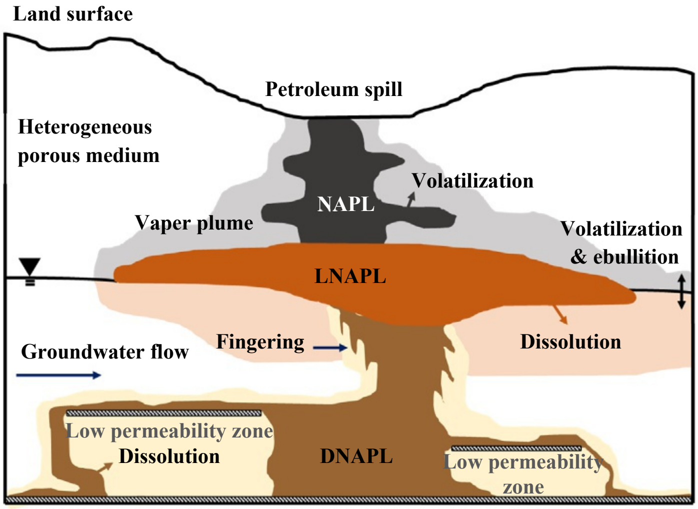

Fig. 2 The fate of petroleum in the shallow subsurface environment.

multicomponent multiphase flow, may happen. This part of the soil is also known as the unsaturated zone (Fagerlund, 2006). It should be noted that the chemical constituents of NAPL may also be present as volatilized components in the gas phase, i.e., air.

NAPL will infiltrate into the soil to the extent that its head is inadequate to prevail pore entry pressures. In this situation, more migration stops. As such, the NAPL volume traveling declines as immobile residual NAPL is trapped and left behind due to capillary forces in the column of soil. If NAPL overcomes the resistive forces, then it will steepen through the column of soil until it reaches the water table. The NAPL with a lower density than water, named light nonaqueous phase liquid (LNAPL), will float on the water table and may reach the surface water. Hydrocarbon dissolution from the LNAPL into the groundwater may also occur and cause pollution plumes that are transported to sensitive receptors (Brown et al., 2017). In the case of NAPL denser than water, named dense nonaqueous phase liquid (DNAPL), the contaminants can infiltrate as a separate immiscible phase below the water table, thus reaching deep into the groundwater or saturated zone of the soil. It should be mentioned that geological heterogeneity greatly affects the path of migration and entrapment of DNAPL. The principal movement of DNAPL will be vertically downward owing to its density, nonetheless, some lateral spreading will happen as it meets lower permeability strata (Rivett et al., 2006).

Along with all the stated consequences of the petroleum presence in the soil environment, it is also a serious risk for the groundwater resources which in turn poses a threat to the supply of drinking water. As mentioned, migrating NAPL abandons a trail of immobile residual NAPL ganglia and adsorbed droplets on soil grains behind its path of migration and creates long-term sources of drastic groundwater contamination. Because of the low solubility of NAPLs in water, they dissolve slowly through contact with flowing groundwater. Consequently, migration of the dissolved-phase toxic plume can occur over a long period of time, posing a lasting risk to ecological safety and human health (Huo et al., 2020; Ramezanzadeh et al., 2020).

On the basis of the above points, it is essential to clean the soil from detrimental petroleum substances to protect life from their deadly effects. Many countries are developing their own plans to deal with the soil pollution done by petroleum. They have established petroleum spill working teams with the assistance of environmental research organizations to assess and remediate affected regions. The leading countries in this field are Denmark, United Kingdom, France, Austria, Norway, and Germany (World Population Review, 2022). So far, several soil clean-up strategies have been proposed to remove petroleum from contaminated soil. Although some of these methodologies are known to be efficacious, they are not always admitted by the community or at times have been examined just in the laboratory and not on a field scale. Generally, petroleum-contaminated soil remediation requires a fast, environmentally friendly, and cost-effective approach.

2 In situ remediation technologies

Every polluted region has its own features in terms of properties of soil and pollutant, soil stratification, hydrology, current land use, land use and contamination history, proprietorship, social and economic requirements, etc. Therefore, each new soil remediation case needs a particular approach in which the treatment strategy will be tailored to the needs and requirements of the site (Ok et al., 2020). Generally, to specify which treatment technology to use on a petroleum-contaminated site, a step-by-step approach is needed as illustrated in Fig. 3. In this proposed framework, one or more technology sets for remediation of the contaminated site are selected based on different criteria.

Various technologies have been proposed for controlling risks and remediating a polluted site. Generally, remediation can occur either on excavated soil or extracted water (ex-situ remediation) or in soil and water in the subsurface (in situ remediation) (Ossai et al., 2020). In ex-situ treatment approaches, the soil may be treated by applying chemical, biological, physical, or thermal processes in mobile installations on-site, and then the treated material is sent back to the original location. Off-site treatment may be used as well. It indicates that the excavated soil is sent to specialized soil treatment centers. In this way, all contaminated soil is rapidly taken away from the polluted site (Ok et al., 2020). In situ remediation technologies also include the application of chemical,

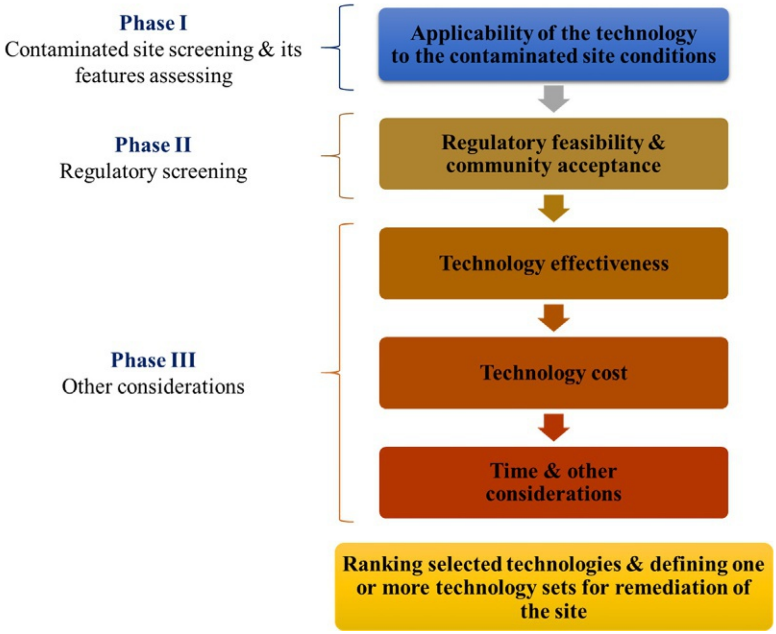

Fig. 3 Framework for the selection of remediation technology.

biological, physical, or thermal processes in the subsurface to degrade, eliminate, or immobilize pollutants without removing the bulk soil (U.S. EPA, 2006).

In general, since no soil is excavated, in situ remediation is less disruptive, more environmentally friendly, and usually less costly due to the simpler procedures than ex-situ methods. In situ treatment techniques expose workers and the surrounding public to the lowest amount of pollutants. Furthermore, in situ methods can be implemented even to soil located directly beneath buildings or at working factory sites, where excavation is troublesome. These types of remedial technologies are also more effective for addressing deep contamination (Reddy, 2010; U.S. EPA, 2006). Due to the stated advantages, in situ technologies are more considered in research and field implementation. This chapter also focuses on applying chemical-assisted biological strategy as a promising in situ remedial method. Therefore, this section is devoted to perusing the topical in situ treatment techniques suggested in the literature.

The in situ remedial technologies are commonly classified into three main categories based on the principal mechanisms by which the treatment is attained:

- Physical/chemical treatment technologies
- Biological treatment technologies
- Thermal treatment technologies

The key property of the in situ remedial technologies is the fluids or other designed reactants delivery into the subsurface using trenches and horizontal or vertical drains and wells. The capability to control and proctor the delivery of these fluids is vital for the usefulness of in situ remedial technologies in remediating the contaminated zone (Reddy, 2010; U.S. EPA, 2006). According to the subsurface environments and pollutant properties, each in situ treatment technology has both advantages and restrictions in its capability to efficiently deliver, control, and recover administered fluids and/or reactants and pollutants. Each of the mentioned technologies is discussed in the following sections.

2.1 Physical/chemical treatment technologies

This group of in situ remediation technologies is the most diverse as well as widely used group of remediation methods. This in situ remediation technologies category comprises soil vapor extraction (Cao et al., 2021), solidification/stabilization (Ma et al., 2018), chemical oxidation (Chen et al., 2016), electrokinetic separation (Prakash et al., 2021), and soil-flushing (Senevirathna et al., 2021).

2.1.1 Soil vapor extraction

In situ soil vapor extraction is a relatively simple physical treatment process wherein a vacuum is used to bring a controlled subsurface airflow to eliminate volatile and semivolatile organic compounds from the unsaturated zone to the surface. The operational process of this remedial method typically includes attaching vacuum blowers to the extraction wells that are mostly made with slashed polyvinyl chloride to impel airflow through the soil matrix. Concrete, geomembrane, asphalt, or any other covers with low permeability are frequently placed over the surface of the soil to avoid short-circuiting of airflow and to increment the influence radius of the extraction wells. The polluted air is transported to the surface and allowed to pass through a vapor/liquid separator to get rid of any humidity before the air treatment. Air treatment is generally conducted via adsorption using activated carbon or, for the case of more concentrated waste streams, via thermal oxidation or condensation treatment systems. Moreover, the generated stream of water by the vapor/liquid separator may need treatment. Substitution air can be supplied into the subsurface medium by injecting air through a blower or via permitting air to flow into inactive injection wells. It should be noted that vertical wells are widely considered in soil vapor extraction process design once the pollution and/or the water table is present at a shallow depth. However, horizontal wells or trenches have been defined as a better choice for lateral flow and formation access (Kuppusamy et al., 2020; U.S. EPA, 2006).

2.1.2 Solidification/stabilization

In situ solidification/stabilization technique is used to limit the spread of many forms of organic and inorganic pollutants in unsaturated and saturated media through solidifying and/or stabilizing the contaminated soil (Désilets and Charette, 2017). Solidification is a process that changes polluted media into a homogeneous solid substance with robust structural integrity via its encapsulation with the aim of altering its physical properties. In the stabilization process, the hazard potential of contaminated soil is decreased by restricting contaminants' solubility, mobility, and/or toxicity (Abdulhamid et al., 2021). In other words, the stabilization process relies on the lessening of contaminants' solubility, mobility, or toxicity via physical or chemical reactions with the pollutants, instead of the pollutants matrix (e.g., soil or sediment), as is conducted in solidification (Désilets and Charette, 2017). The operational process of the in situ solidification/stabilization generally includes mixing a binding/stabilizing agent with polluted soils via an auger or the high-pressure injection of a solubilized binding/stabilizing agent to force the binder into the polluted soil pore spaces (Désilets and Charette, 2017; U.S. EPA, 2006). If volatile components are existing or it is probable to produce toxic gases during the solidification/stabilization process, a gas emissions gathering and treatment system may also be needed (Désilets and Charette, 2017).

2.1.3 Chemical oxidation

In situ chemical oxidation technology relies on the oxidative power of particular chemicals. This remediation technology can be applied to unsaturated and saturated media and many different organic and inorganic pollutants (ITRC, 2005). The process of chemical oxidation generally contains reduction/oxidation reactions, namely redox, that chemically alter dangerous pollutants to harmless or less toxic substances that are more stable, less mobile, or inert. The redox reactions comprise the transition of electrons from one chemical to another, in which one reactant is oxidized, i.e., loses electrons, and another is reduced, i.e., obtains electrons (U.S. EPA, 2006). Various kinds of oxidants have been introduced for the remediation of petroleum-polluted soil, including potassium or sodium permanganate, hydrogen peroxide, Fenton's reagent, sodium persulfate, peroxymonosulfate, and ozone (Lim et al., 2016). These oxidants are usually injected or mechanically mixed into the target zone to promote destructive abiotic degradation reactions. It should be noted that the delivery system type considered in the design of the chemical oxidation process highly hinges on the pollutants' depth, the physical state of oxidants (gas, liquid, and solid), and their rate of decomposition (U.S. EPA, 2006).

2.1.4 Electrokinetic separation

In situ electrokinetic remediation is the process of applying a weak direct electrical current to the subsurface to detach and extract organic pollutants, heavy metals, and radionuclides from unsaturated and saturated soil, sediment, and sludge (Ramalingam, 2013; U.S. EPA, 2006). The electrical current is exerted across a pair of electrodes that have been placed in the ground on each side of the mass of polluted soil. Throughout electromigration, chemical components with positive charge migrate toward the cathode, negatively charged ones move toward the anode, and then they are pumped out. The transport mechanism of electromigration does not need the pore water's advective flow for the movement of chemical species. However, in porous media with fine grains, the applied electrical current also causes electro-osmosis. This transport mechanism is an electrically induced pore water hydraulic flow between the electrodes, which can transfer neutrally charged species. Another transport mechanism during electrokinetic remediation is electrophoresis which can move suspended, micelles, and charged colloids (Saini et al., 2021; U.S. EPA, 2006). The physical and chemical processes involved in this remediation technique can be electrolysis, adsorption-desorption, diffusion, precipitation-dissolution, and oxidation-reduction based on the designed procedure. The field implementation of this remediation technique needs electrodes, a power supply, wells, pumps, and treatment units to treat the produced polluted water (Ramalingam, 2013).

2.1.5 Soil flushing

In situ flushing has been known as an innovative approach for the treatment of polluted unsaturated and saturated soil. This remediation technique can treat soil polluted with organic and inorganic contaminants. However, its performance is more effective for pollutants with low solubility, such as petroleum hydrocarbons. The process of this remediation method includes the injection of a predesigned aqueous solution, usually via vertical wells, into the target polluted region. This injected solution then flows through the polluted zone. The pollutants are mobilized via solubilization, emulsification, or other physicochemical interactions with the flushing agent. After passage through the polluted region, the effluent is gathered and pumped to the surface for discharge, recirculation, or on-site further treatment and reinjection (Strbak, 2000). The injected aqueous solution frequently contains acidic or basic solutions, reducing agents, chelating agents, surfactants, cosolvents, or any other solution designed and prepared in groundwater (Strbak, 2000; U.S. EPA, 2006). By enhancing the pollutants' solubility or mobility at the source, in situ soil flushing can offer a faster and more effective way for in situ remediation of the soil (Huo et al., 2020).

2.2 Biological treatment technologies

Biological treatment techniques have been known as the most cost-effective and eco-friendly technologies. The biological technique generally includes the use of microorganisms or vegetation which can alter hazardous materials into materials that may be less dangerous than the original mixtures (Yuniati, 2018). The most common types of in situ biological treatments are bioventing (Tzovolou and Tsakiroglou, 2018), biosparging (Bell et al., 2022), phytoremediation (Iyer et al., 2021), and natural attenuation (Varjani and Upasani, 2019).

2.2.1 Bioventing

In situ bioventing includes the gas injection into the unsaturated region to augment the intrinsic ability of Indigenous microflora for the biodegradation of an organic or inorganic pollutant. The used gas may retain the subsurface medium, aerobic or anaerobic, or make available a substrate that allows the cometabolic degradation to happen (U.S. EPA, 2006). In aerobic bioventing, oxygen is supplied to polluted unsaturated soils via air injection wells to facilitate aerobic microbial degradation. The microorganisms oxidize the pollutants to obtain energy and necessity carbon for growth, by using the supplied oxygen (Chakrabartty and Harun-Or-Rashid, 2021). While aerobic bioventing is effective for breaking down a wide variety of hydrocarbons, the chlorinated mixtures are not efficiently treated aerobically. The present microbes may directly and anaerobically degrade these pollutants by reductive dechlorination or cometabolic ways. Anaerobic reductive dechlorination is one of the biological mechanisms, generally defined by sequential chlorine ion removal from a molecule. Microbes gain energy from this process. In some other conditions, microbes, by obtaining the required energy and carbon from other mixtures (cometabolites), incidentally degrade pollutants. In these processes, a similar type of system for gas delivery as aerobic bioventing is needed. However, rather than air injection, nitrogen, electron donors, e.g., hydrogen and carbon dioxide, as well as an appropriate gaseous substrate to help cometabolic reactions with the objective compounds are applied. Nitrogen is used to move the oxygen in the soil, and the electron donor gas is used to ease microbial dechlorination (Bala et al., 2022; U.S. EPA, 2006).

2.2.2 Biosparging

This in situ remediation method is very similar to the bioventing remediation process, in which a gas is injected into the subsurface environment to stimulate microbial activities and facilitate the removal of contaminants from polluted sites. Nevertheless, unlike bioventing, the gas which is mostly air and gaseous nutrients is injected into the saturated region of the soil (Maitra, 2018). Biosparging can decrease concentrations of dissolved and residual petroleum constituents in the saturated zone as well as any other toxic chemical compounds in this region that are biodegradable under aerobic conditions. Generally, the purpose of biosparging process is to improve the bioavailability of pollutants, promote biodegradation of contaminants, and diminish the volatile and semivolatile organic compounds' volatilization (Turgeon et al., 2019).

2.2.3 Phytoremediation

Phytoremediation utilizes plants and associated microbes to extract, decompose, contain, or immobilize various organic and inorganic contaminants in unsaturated and saturated media. However, phytoremediation is recommended for the treatment of large regions of shallow pollution. Phytoremediation is also best applied to pollution with low and moderate levels, since high levels of pollutants may be toxic to plants and prevent their growth. Hence, this remediation method is suggested to use in combination with other methods or as an ultimate clean-up step in contaminated site remediation (U.S. EPA, 2006). During this remediation method, the plant roots may uptake contaminants and accumulate it in their tissues (phytoextraction) which may necessitate the plant to be harvested and appropriately disposed of (Arthur et al., 2005). Furthermore, the contaminants may break down via metabolic processes within the plant or in the soil medium via the effects of enzymes and other substances generated by the plant tissues (with the exception of the roots). This mechanism is named phytodegradation (U.S. EPA, 2006). Degradation of contaminants may also happen in the soil surrounding the plant roots because of the enhancement of the microbial activity by roots. This mechanism is also called rhizodegradation (Arthur et al., 2005). Phytovolatilization and phytostabilization are also other mechanisms of contaminant removal. Phytovolatilization is usually introduced as the pollutant uptake into a plant and its transpiration to the atmosphere. Phytostabilization is defined as a mechanism that prevents pollutants from moving within the root region, i.e., the soil surrounding the plant roots (U.S. EPA, 2006).

2.2.4 Natural attenuation

Natural attenuation includes different physical, chemical, or biological processes that, under specific situations, operate without human involvement to decrease organic and inorganic contaminants' volume, toxicity, mobility, or concentration (Jørgensen, 2011). This remediation approach has been applied mainly to saturated media, but similar principles can be used in unsaturated regions. Since natural attenuation is a passive process in which the decrease in the concentration of toxic compounds depends only on natural mechanisms, persistent sources of pollution should be addressed before applying this method. Also, a comprehensive description of subsurface situations on the site, comprising an explanation of the extent of pollution and the development of a site conceptual model, is essential. The existing microbial species, pH conditions, redox potential, geochemistry, and mineralogy should be assessed as part of the characterization of the site. If this evaluation phase shows that favorable situations may exist to support natural attenuation, then microbial respiration and the products of chemical reaction, degradation products, and the rate of diminishing concentrations of objective compounds over time should be investigated. Eventually, monitoring the performance at the field scale is a vital part of any natural attenuation effort. The monitoring system should be provided based on the site situations to allow recognition of any variations in the assumptions utilized to choose natural attenuation. If monitoring shows that natural attenuation is not meeting the project's objectives, then a preapproved site remedial plan should be considered for implementation (U.S. EPA, 2006).

2.3 Thermal treatment technologies

Thermal treatment technologies are mostly grouped into five techniques including electrical resistance heating (Han et al., 2021), conductive heating (LaChance et al., 2004), steam injection and extraction (xue Liu et al., 2021), radio-frequency heating (Guan et al., 2021), and vitrification (Hansen and Timmerman, 2019). Excepting the vitrification, all of these remedial techniques depend on the application of heat to the subsurface to augment the removal efficiency of frequently volatile and semivolatile pollutants (U.S. EPA, 2006).

2.3.1 Electrical resistance heating

This type of in situ thermal remediation technology includes passing an electrical current via the moisture of the soil between an array of electrodes. The soil resistance produces heat greater than 100°C, due to the electrical energy in the soil pore spaces. Thus, steam and mobile pollutants are produced and recovered mostly via vacuum extraction, then processed at the surface (Ding et al., 2019). Electrical resistance heating has been recommended for the enhancement of the volatile and semivolatile pollutant removal in unsaturated soils. But it can be used in saturated media as well. It has also been used to augment the removal of a wide range of petroleum compounds (Beyke and Fleming, 2005; Gauglitz et al., 1994). In this remediation approach, electrodes can be considered as wells that are equipped to deliver electrical power at nominated depths and operate as vapor/liquid recovery wells. Electrical resistance heating systems can be deployed to any depth. If the electrical resistance heating system is installed only in the unsaturated region, water may be added to the electrodes to retain the humidity of the soil and, consequently, the electricity flow (U.S. EPA, 2006).

2.3.2 Conductive heating

Conductive heating utilizes either a group of vertical heater/vacuum wells or surface heater blankets once the objective zone is in nearly 6 in. of the surface of the ground (U.S. EPA, 2006). The heater wells usually operate at the range of 400–800°C due to the dominance of radiation and conductive heat transfer. However, this method can be used at low (<100°C), moderate (~100°C), and higher (>100°C) temperature ranges to remove a wide variety of contaminations. In this in situ remediation approach, the target zones are heated through thermal conduction and convection. Around each heater well, remarkable temperature gradients are created. Conductive heating commonly removes the pollutants via various mechanisms such as steam stripping, coboiling, thermal desorption, thermal oxidation and pyrolysis, and thermally boosted bioremediation and hydrolysis (Ding et al., 2019). Previous experiences show that this remediation method acts best in the unsaturated regions; nevertheless, it does find use in saturated regions with low hydraulic conductivity (Sun et al., 2020; U.S. EPA, 2006).

2.3.3 Steam injection and extraction

Steam injection and extraction is an in situ remediation technology in which the injection of steam into the subsurface is conducted and combined with the extraction of fluids (Ding et al., 2019). In this remediation method, steam gives up its vaporization of latent heat to the soil, once it is injected into the subsurface. The steam condenses into a hot water phase, due to the loss of heat, travels radially into the soil medium, and translocates air and water in front of it. Continual injection of steam ultimately causes the soil adjacent to the well to attain steam temperatures and generate a steam front that initiates to propagate away from the well (U.S. EPA, 2006). Hence, this process creates three different zones with an increment of interval from the injection well, called a steam zone, a changeable temperature zone comprising water, and an ambient temperature zone comprising cool fluids. The mechanisms of contaminant removal differ in each created zone. For instance, stripping and coboiling are dominant in the steam zone. Viscosity reduction and hydraulic displacement have been introduced as the main removal mechanisms in the changeable temperature zone. The ambient temperature water movement may displace contaminants as well (Ding et al., 2019). Finally, the migrating steam and liquids are extracted using multiphase extraction wells and treated at the surface. Steam injection and extraction remediation method has been applied in both unsaturated and saturated media to remove mainly NAPL contamination (Azizan et al., 2016).

2.3.4 Radio-frequency heating

Radio-frequency heating utilizes electromagnetic waves ranging from 500 kHz to 500 MHz. The electromagnetic heating rule contains the electromagnetic energy conversion into thermal energy via the interaction among the electromagnetic field and atoms/molecules existing in the irradiated material. This interaction severely relies both on the nature of the material and on the frequency of radiation. Conduction losses, dielectric losses, and more infrequent magnetic losses can cause heating (Bientinesi et al., 2015). However, radio-frequency heating mostly heats soil via dielectric heating, and low MHz frequencies are normally used during this process (Ding et al., 2019). The radio-frequency heating remedial method has been recommended for volatile pollution in tight and unsaturated soils which cannot be effectively heated by means of steam due to mass transfer restrictions. Radio-frequency heating energy is rendered into the subsurface through an array of electrodes, installed at predetermined and discrete locations and depths. This remediation method can be joined with a system of vapor extraction or multiphase extraction to extract the contaminants (Ecologia, 2011).

2.3.5 Vitrification

In situ vitrification is another thermal method that commonly uses electrodes and electrical resistance to heat a contaminated soil matrix at high temperatures, i.e., 1400–2000°C, to produce stable and inert glass and crystalline solids in unsaturated and saturated media (Trifunović, 2021). Passing electrical current generates heat, which is distributed to the surface of soils. When the soil melts, the electrodes sink into the ground, which augments the distribution depth of heat. Once the electric current stops, the melted soils cool and vitrify by encapsulating and immobilizing the pollutants in the vitreous material. The treatment of inorganic and organic pollution is possible simultaneously during the in situ vitrification. The various inorganic or radioactive pollutants present in the soil matrix can be vitrified frequently. However, organic pollutants are generally destroyed through pyrolysis or volatilized during the heating process of the in situ vitrification. The gases released during this process are gathered in the waste gas gathering hood for additional treatment on the surface. The solid products in this remediation method are frequently leach-resistant, chemically stable, and have features similar to igneous rocks or basalt (Thibodeau et al., 2019).

The points mentioned earlier are a short review of the principles of various in situ remediation technologies, which have been suggested and investigated in the literature. Each of the described remediation methods, which has been categorized in physical/chemical, biological, and thermal technologies, also has its own advantages and disadvantages. However, Table 1 summarizes the general advantages and disadvantages of the three main groups. Biological treatment technologies owing to their environmentally friendly and cost-saving features as well as ease of use have been preferred by several environmental researchers and specialists (Bala et al., 2022; Iyer et al., 2021). However, biological treatment technologies cannot lonely answer the needs of petroleum-contaminated soil remediation projects at the field scale, due to the lack of ability of living organisms and plants to efficiently break down petroleum constituents into less harmful compounds and a very long time of remediation, typically from several months to several years (Zhen et al., 2021). Hence, biological treatment technologies are commonly

Table 1 Comparison of in situ soil remediation technologies.

Remediation technology	Advantages	Disadvantages
Physical/chemical	• Simple operational equipment • Low energy consumption and cost-effective • Relatively short remediation period	• Risk of secondary contamination • Sensitive to subsurface heterogeneity
Biological	• Low cost and investment • Low environmental and secondary contamination risk • Easy operation	• Not appropriate for remediation of high-concentration contaminants, especially petroleum ones • Very long remediation period
Thermal	• High efficiency especially for petroleum pollution • Less sensitive to subsurface heterogeneity • Short remediation period	• Risk of the destruction of the soil's physical, chemical, and biological properties • Risk of the destruction of the soil's organic matter • Soil shrinkage • High energy consumption • Very high remediation costs and investment in a short time frame, especially when the size of the treatment volume is large

recommended to use in conjugation with other remediation techniques or as a final clean-up step in petroleum-contaminated site remediation (U.S. EPA, 2006). Thermal treatment technologies have been also recognized as high removal efficiency techniques with short remediation periods (Ding et al., 2019). Nevertheless, they have severe destructive effects on the environment as well as high costs, which make them less preferable for usage (Vidonish et al., 2016). Physical/chemical treatment technologies are also usually cost-effective and can be accomplished in short times, in comparison with biological remediation technologies. Their operational equipment is easily accessible and is not engineering or highly energy-intensive (FRTR, 2020). Physical/chemical treatment technologies have also a remarkably less environmental risk in comparison with thermal technologies. Therefore, the physical/chemical treatment technologies are the reasonable and preferable choice for the in situ petroleum-contaminated soil remediation in combination with biological techniques.

Among the physical/chemical treatment techniques, the in situ soil flushing process has been recognized to be a promising technology for the treatment of petroleum-contaminated soils and consequently has attracted great attention in recent years (Chattopadhyay and Karthick, 2017; Karthick et al., 2019; Longpré-Girard et al., 2016; Senevirathna et al., 2021; Wu et al., 2016). However, one of the open questions and the main challenges for the field usage of this remediation process is the design of suitable flushing/invading agents with high contaminant removal efficiency as well as a minimum side effect on the environment and low risk of secondary contamination. By comparing various recent literature works, it can be found that the development and application of novel technologies and chemicals as flushing/invading agents for petroleum-contaminated soil treatment are highly interesting topics to be investigated for further details.

3 In situ biological treatment

Biological treatment technologies were formerly introduced. Their main mechanisms of contaminant removal were described. Finally, in situ biological treatment techniques were compared with other common in situ technologies. This section is allocated to review the accomplished works of each of the mentioned methods of in situ biological remediation of petroleum hydrocarbon-contaminated soils. The keynotes in related research are described and the main drawbacks of the biological treatment technologies for petroleum pollutant removal as well as the need for auxiliary remediation methods are further highlighted.

3.1 Bioventing/biosparging

As stated previously, bioventing and biosparging involve usually the process of providing oxygen or other nutrients to intensify microbial activity and, subsequently, enhance bioremediation (Brown and Ulrich, 2014). A typical schematic of the process of these remediation technologies in an unsaturated medium is shown in Fig. 4. Bioventing and biosparging technologies mostly depend on the Indigenous oleophilic microbes present in the unsaturated and saturated media to break down the petroleum constituents. These indigenous microorganisms are supplied with nutrients and low-pressure oxygen through an injection well (Macaulay and Rees, 2014). The results of a pilot-scale study done by Bulman et al. (1993) show that bioventing technology was able to reduce the total hydrocarbon concentration by 10%–30% to a depth of 3 m during a 6-month period. They achieved an additional 30% reduction in the concentration of total hydrocarbon to a depth of 3.5 m by venting with nutrients and after a subsequent 6 months. Their main objective to perform this pilot test was to approve the nutrient supply effectiveness during the bioventing treatment of diesel fuel-contaminated medium with a concentration of 1500 mg/kg. Another pilot test was performed by Werner et al. (1997) to remediate a polluted zone near six underground storage tanks holding jet fuel. The hydrocarbon pollution was detected due to the fuel leakage from a depth of about 1.2 m to approximately 2.7 m with an average concentration of 1250 mg/kg. Their results show that the used bioventing technology was able to nearly fully treat the contaminated site after 15 months. Sperry et al. (2001) also conducted a biosparging field trial. They

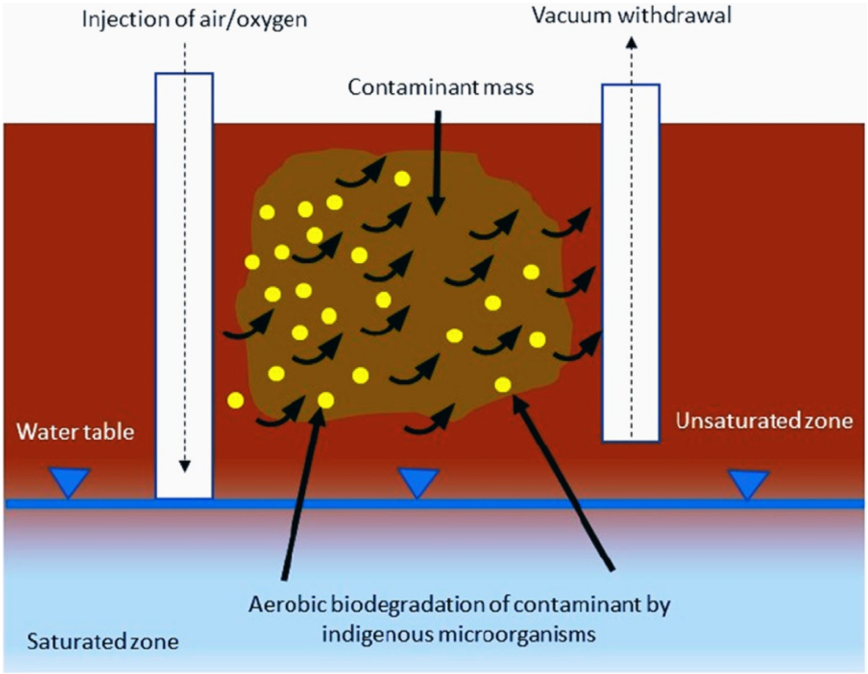

Fig. 4 Schematic of bioventing remediation process (Sales da Silva et al., 2020).

reported that the oxygen injection for nearly a 9-month period effectively diminished benzene concentrations in groundwater by several orders of magnitude at the intermediate and deep regions. The maximum initial average groundwater benzene concentration measured at the monitoring wells in this field trial was in the range of 1500–2500 μg/L. In addition to pilot and field-scale trials, numerous laboratory-scale investigations have also been carried out. For instance, Thomé et al. (2014) evaluated the bioventing performance through a number of experiments that were accomplished in bioreactors using soil polluted with 4% of the mixture of diesel and biodiesel. Their results confirm 85% of pollutant degradation after 60 days. They also proved that the airflow intensities and intervals have no remarkable influence on the bioventing performance. Nearly, the same investigations have also been reported in recent publications (Safdari et al., 2018; Xiao and Zytner, 2019). Most of these studies confirm that these remediation technologies are too slow, especially in degrading heavy petroleum hydrocarbons even when oxygen and nutrients are supplied. This may be due to the result of the absence of other auxiliary natural oil-degradation processes such as evaporation in both the unsaturated and saturated zones (Macaulay and Rees, 2014). The studies performed also indicate that low-permeability soils may yield some difficulties for these remediation technologies owing to a restricted ability to distribute air through the subsurface or limited ability to deliver oxygen gas to the polluted soil (Sharma, 2019).

3.2 Phytoremediation

A schematic of the phytoremediation process to break down, transfer, deactivate, and immobilize petroleum hydrocarbons is illustrated in Fig. 5. In this plant-based remediation approach, plants should be selected in such a way that they have maximum propagation, growth, development, and specific root area. Moreover, the selected plants should be native and well-suited to the soil conditions of the region. Their growth period should be extended under pollution conditions (Medina et al., 2003). Most studies propose grasses and legumes with good potential for phytoremediation owing to their widespread fibrous root systems. The grasses' root system has the highest specific surface area compared to other plant types and penetrates the soil to a depth of nearly 3 m (Medina et al., 2003; Minai-Tehrani et al., 2006). Various studies have also been allocated to evaluate other plants' ability and the pertinent parameters to remove petroleum hydrocarbon pollutants from soil media. For instance, Diab (2008) studied the ability of three types of plant species to remediate desert soils contaminated with 2.2%–2.3% crude oil. The results indicate that *Vicia faba*, *Zea mays*, and *Triticum aestivuml* plants were able to degrade contaminants up to 62.4%, 19.9%, and 17.6%, respectively. Zhang et al. (2010) also investigated the phytoremediation of petroleum-contaminated soil using Pharbitis nil L. and its related microbial community. They observed that the soil samples planted with Pharbitis nil L. had remarkably fewer residual petroleum hydrocarbons than unvegetated soils. However, based on their obtained results, the saturated, i.e., lighter, hydrocarbons had a noticeable reduction compared with other components. They stated that

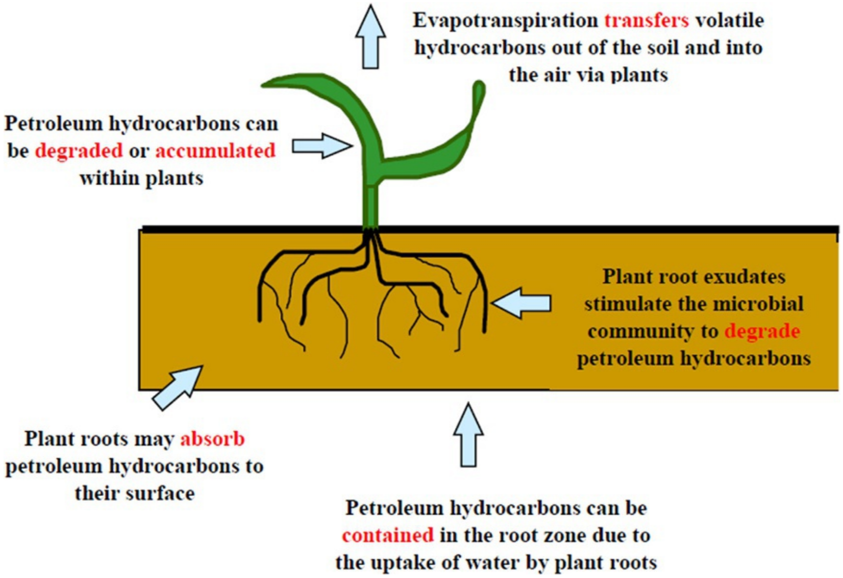

Fig. 5 Schematic of phytoremediation process (Frick et al., 1999).

phytoremediation of petroleum-contaminated soil efficiency significantly depends on the concentration of petroleum pollution in soil. For their case study, the effect of remediation by Pharbitis nil L. was best for the petroleum pollution concentration of less than 1%. They stated that when the petroleum pollution concentration is high, for instance, more than 4%, the propagation of plant biomass and correlative rhizosphere microorganisms are inhibited. Consequently, petroleum hydrocarbon biodegradation is also prevented. The same general conclusions for the phytoremediation of petroleum-contaminated soils have been also confirmed by several recent research works (Hussain et al., 2022; Kong et al., 2018; Wang et al., 2021). Although phytoremediation is currently considered to be the cheapest and most welcomed remediation technology by society, it takes a long time to clean up polluted soils, in some cases several years. Furthermore, this remediation technology is also affected by seasons (Stepanova et al., 2022).

3.3 Natural attenuation

As stated previously, natural attenuation is a combination of natural processes, without any human intervention that results in a decrease in toxicity, mobility, mass, volume, and/or concentration of contaminants (Declercq et al., 2012). Fig. 6 displays the conceptualization of natural attenuation processes at a petroleum hydrocarbon-polluted site. The natural processes are mostly biological degradation, volatilization, dispersion, dilution, and sorption of the pollutant onto the organic matter and clay minerals in the soil. In this remediation method, long-term monitoring is an absolute need since the pollutant plume must not reach humans or aquatic wildlife habitats (Mulligan and Yong, 2004).

Microorganisms are responsible for the biological degradation of petroleum components (Balba et al., 1998). Several investigations have been performed on the treatment of petroleum hydrocarbon-contaminated soil by various microorganisms (Nwankwegu and Onwosi, 2017; Polyak et al., 2018; Safdari et al., 2018; Wu et al., 2017). The effective microorganisms for the biodegradation of petroleum hydrocarbons based on the accomplished works are the ones from genera *Pseudomonas*, *Flavobacterium*, *Acinetobacter*, *Achromobacter*, *Mycobacterium*, *Rhodococcus*, *Alcaligenes*, *Bacillus*, *Mucor*, *Aspergillus*, *Penicillium*, and *Candida* (Nwankwegu and Onwosi, 2017; Polyak et al., 2018; Wu et al., 2017). Natural attenuation treatment strategy is frequently suggested to use for benzene, toluene, ethyl benzene, and xylene as well as chlorinated hydrocarbon removal from contaminated soils (Mulligan and Yong, 2004). A 480-day field study on the natural biodegradation of hydrocarbon-polluted clayey soil conducted by Chaîneau et al. (2003) shows 56% removal of hydrocarbon without adding any nutrients to the soil. Beckley and Geoffery (2011) investigated the impact of natural attenuation on the bioremediation of waste engine oil-polluted soil. They used polluted soil samples with waste engine oil concentration in a range of 0%–10% w/w oil in the soil. They observed that by natural attenuation the total hydrocarbons decreased by nearly 30% after 9 months. The

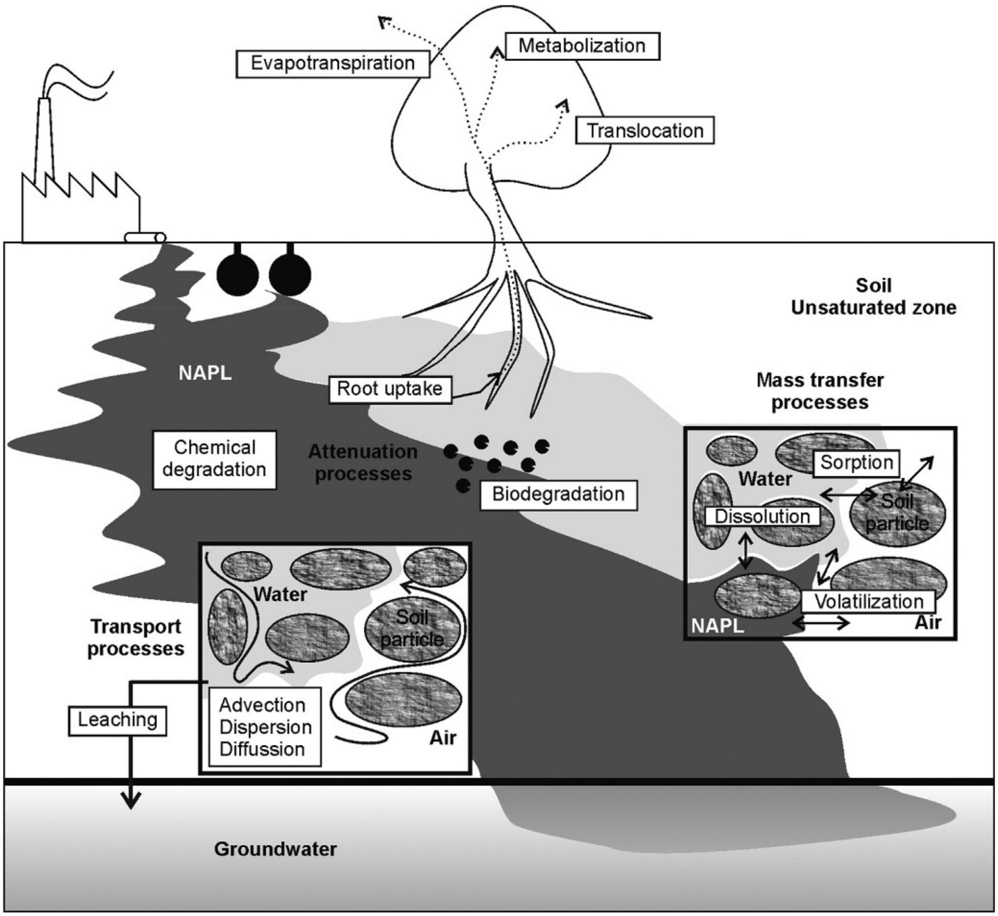

Fig. 6 Schematic of natural attenuation process (Balseiro-Romero et al., 2018).

reduction of total hydrocarbons for the case with higher waste engine oil concentration was much lower. Though natural attenuation may be applied at many sites, it infrequently can be used as an only remediation process since nonengineered biodegradation processes are extremely slow. Furthermore, natural attenuation is subject to hydrological alterations; hence, it can take considerable periods of time (Mulligan and Yong, 2004).

4 Chemical-assisted biological methods

Owing to the potential toxicity, mutagenicity, carcinogenicity, and capability to be bioaccumulated in the food chain of petroleum hydrocarbon contaminants, the treatment of soil polluted with these types of contaminants requires a fast and effective approach. As previously discussed, in situ biological treatment technologies have limited ability to treat soil contaminated with petroleum hydrocarbons. In situ flushing of soil using suitable chemicals has gained much attention to accelerate the treatment of contaminated soils with petroleum hydrocarbons and enhance bioremediation efficiency (Cheng et al., 2018; Sakhaei and Riazi, 2022). In this section, advances in using chemicals, i.e., surfactants and nanomaterials, as novel and effective flushing/invading agents during in situ soil flushing are stated and discussed. The pollutant removal mechanisms during in situ soil flushing using these chemicals and their influence on improving bioremediation processes are highlighted.

4.1 Surfactant-assisted biological remediation

Surfactants or "surface-active" substances are organic amphiphilic molecules with a lipophobic head and a lipophilic tail (Holmberg et al., 2014). If the surfactant is in the water or an oil phase, the corresponding terms "hydrophilic" and "hydrophobic" are used. The hydrophilic group of surfactants may either have a negative or positive charge, or no charge. Based on the charge of the hydrophilic head, the chemical surfactants have been categorized as anionic, cationic, amphoteric (when surfactant has both positive and negative charges), and nonionic surfactant (Farn, 2008). The hydrophilic head usually is a sulfate group, a sulfonate group, a carboxylate group, a quaternary ammonium group, sucrose, a polypeptide, or polyoxyethylene. The hydrophobic group is usually paraffin, olefins, alcohols, alkyl benzenes, or alkylphenols (Paria, 2008). The opposite forces within the same molecule generate two phenomena: adsorption and aggregation. The adsorption consists of the migration of the surfactant to gas/liquid, solid/liquid, or liquid/liquid interfaces. The surfactant molecules orientate to diminish the contact between the lipophilic group and the polar solvent. This behavior results in a change in the interface properties. In polar solvents, for example, water, the second phenomenon for lessening the contact between the lipophilic groups and water is the aggregation of surfactant molecules in the bulk solution with the hydrophilic heads orientated toward the aqueous solution. This process is known as micellization and the molecular assemblies are micelles (Domínguez et al., 1997). The micelles can present spherical, cylindrical, lamellar, or layer shapes (see Fig. 7) and can be formed at a different surfactant concentration, whereby is named "critical micellar concentration" or CMC (Farn, 2008). At this CMC, the system presents the lowest interfacial tension and, above the CMC, there are no variations of properties, for example, surface and interfacial tension, adsorption, and detergency (Paria and Khilar, 2004). The value of the CMC can be specified by a change in the physicochemical characteristics of the surfactant solution as the surfactant concentration rises (Haq et al., 2017) and relies on the type, structure, and composition of the surfactant. Likewise, CMC depends on factors of solution such as ionic strength, temperature, and the presence of organic additives (Morán et al., 2004; Perger and Bešter-Rogač, 2007).

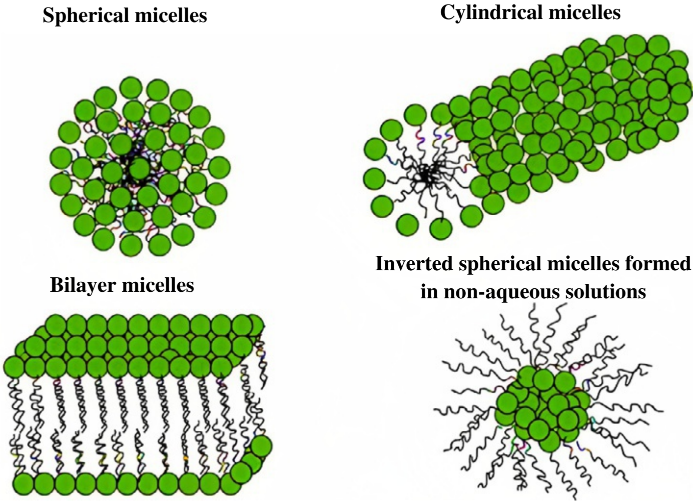

Fig. 7 Different micelles shapes (Lugo, 2010).

Considering that surfactants may modify both the bulk solution and interfaces, surfactants present a wide range of properties such as detergency power (Cheng et al., 2020; Ferri and Stebe, 2000; Lynn and Nguyen, 2005), surface and interfacial tension reducing (Myers, 2020; Wade et al., 1978; Zhao et al., 2007), emulsification (Li et al., 2021; Lin and Chen, 2006), lubrication (Briscoe et al., 2006; Kamada et al., 2011), wetting control (Ivanova and Starov, 2011; Lee et al., 2008), anticorrosion ability (Ganjoo and Kumar, 2022; Malik et al., 2011), solubility (Fountain et al., 1991; Mishra et al., 2009), and adsorption (Somasundaran and Zhang, 2006; Zhang and Somasundaran, 2006). Indeed, in 1949 Griffin noticed that there was a relationship among the chemical nature of surfactants and their properties as surface agents, which was named hydrophilic-lipophilic balance (HLB). HLB is based on an experimental method and refers to the assignment of a determined number of HLB (between 1 and 20) related to the balance between the size and strength of the hydrophilic and lipophilic group of surfactant molecules (Pasquali et al., 2008). HLB is known as an indicator of the solubilization behavior of surfactants (Park et al., 2010). Surfactants with abilities to clean contaminated soil usually show HLB values between 12 and 16 (Lakatos-Szabo and Lakatos, 1999; Liu et al., 2006; Parnian and Ayatollahi, 2008). However, two surfactants may present the same HLB but exhibit different solubility characteristics, whereby HLB is only an indicator of the chemical nature of a surfactant (Gadhave, 2014). This lack of precision is because the HLB does not consider the effect of various physicochemical variables of the system such as surfactant concentration, presence of alcohol or electrolytes, and temperature (Salager and Antón, 1998).

4.1.1 In situ soil flushing with surfactants

The primary application of the surfactants was their use as soaps and detergents for cleaning purposes approximately 2000 years ago (Behler et al., 2001). Likewise, natural and synthetic surfactants have been used for cosmetics and personal care products (Bhalekar et al., 2017; Datir et al., 2021; Lourith and Kanlayavattanakul, 2009), the dyeing of textiles (Baliarsingh et al., 2013; Kumar and Tyagi, 2014; Proffitt and Thomas Patterson, 1988), as lubricants, antibacterial and static discharges in fibers (Alila et al., 2005; El-Nahhal et al., 2017, 2018), paints and coating products (Holmberg, 1996; Parikh, 1995), mining (Kovshov and Kovshov, 2017; Rohana and Ushaa, 2013), and enhanced oil recovery (Atta et al., 2021; Bera et al., 2013; Massarweh and Abushaikha, 2020), among others applications. Moreover, surfactants are also used for enhancing the solubility and biodegradability of petroleum hydrocarbons in unsaturated and saturated soil media. Mobilization and solubilization of petroleum contaminants are the primary mechanisms involved in the in situ surfactant remediation of petroleum hydrocarbon-contaminated soils, as illustrated in Fig. 8. The mobilization effect is defined as the capability of surfactants to improve the migration of petroleum pollutants in a porous medium. The hydrophobic groups of surfactant monomers have a tendency to attach to petroleum pollutants, while the hydrophilic groups tend to expose to the aqueous solution. Consequently, NAPL and adsorbed petroleum contaminants will be surrounded by surfactant monomers. The interfacial tension reduces as a result of surfactant monomers accumulation at the interface of oil-water. Adsorbed surfactants decrease the surface-free energy per unit area needed to generate a new surface, based on the thermodynamic terms. Consequently, NAPL prefers to disperse in the aqueous solution, which is the basis for the formation of oil-in-water (O/W) emulsions. Simultaneously, the hydrophobic groups of surfactant monomers adsorbed on the surface of the petroleum-polluted solid and gradually penetrated along the interface of oil/solid. Hence, a hydrophilic adsorption layer is formed. It alters the wettability of the solid surface; consequently, petroleum contaminants are stretched and fell off under the hydraulic action (Liu et al., 2021). On the other hand, solubilization of petroleum contaminants is caused by the micelles formation of surfactant from CMC, which traps the contaminants onto the hydrophobic cores of micelles by means of hydrophobic forces, and as a consequence, increases their solubility in the aqueous solution (Chu and So, 2001). Although solubilization starts at the CMC point, higher removal efficiencies have been reported at concentrations more than the CMC value (Rathankumar et al., 2022). Finally, the mobilized and dissolved pollutants in the aqueous phase may be removed by biotic/abiotic routes and/or extraction wells (Mao et al., 2015).

In general, surfactants for in situ soil flushing should have good contaminants solubilization and less adsorption onto the soil. Similarly, to implement efficient surfactant remediation of petroleum hydrocarbon-contaminated soils is necessary that the surfactant presents low toxicity, high biodegradability, and is cost-effective (Mao et al., 2015). On

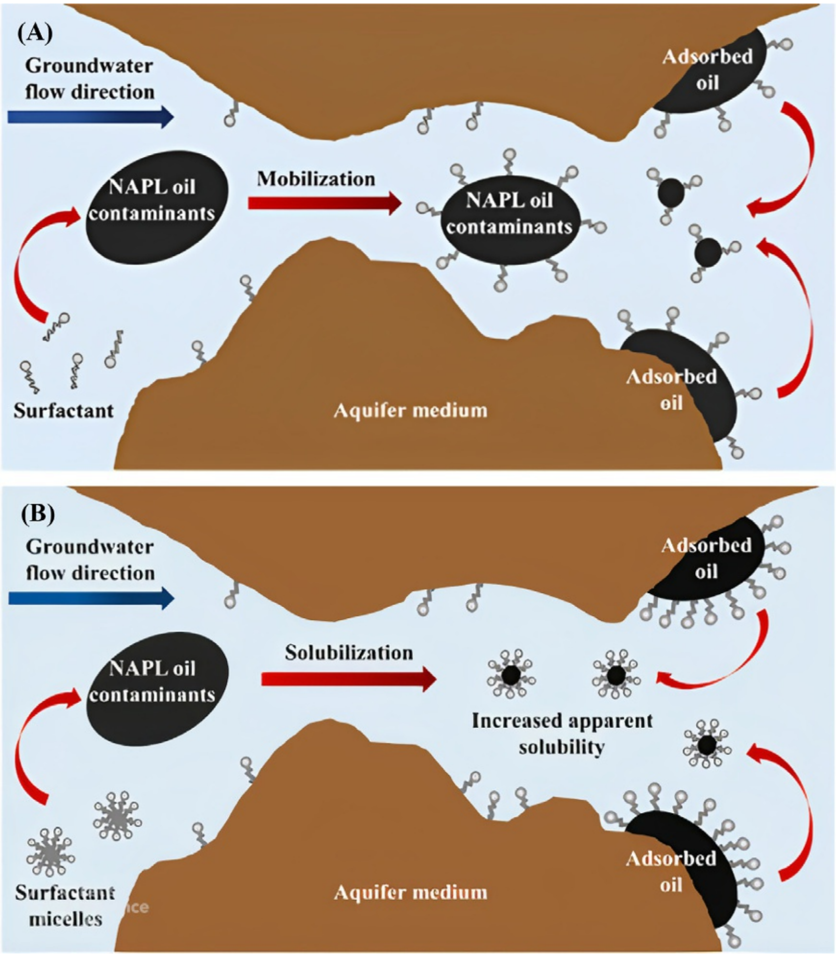

Fig. 8 Schematic of (A) mobilization and (B) micellar solubilization of NAPL during in situ soil flushing with surfactant (Liu et al., 2021).

the other hand, biosurfactants have increased attention in the environmental remediation area (Bezza and Nkhalambayausi-Chirwa, 2015). Biosurfactants provide different benefits over synthetic surfactants including biodegradability, biocompatibility, and good performance over extreme environmental conditions (e.g., high or low temperature, pH, and salinity) (Kuyukina et al., 2005; Mulligan et al., 2001). Furthermore, biosurfactants can be more cost-effective than chemical surfactants because of their low CMC (Varjani et al., 2015). Several microbial species have been recognized to generate biosurfactants, and the chemical structure of these surface active compounds varies widely. Indeed, the hydrophilic head of biosurfactant can be a carbohydrate, amino acid, peptide, phosphate, carboxylic group, or alcohol, while the hydrophobic tail consists of fatty acids, hydroxy fatty acids, or α-alkyl-β-hydroxy fatty acids (Mohanty et al., 2013). However, the biotechnological processes for biosurfactant synthesis may present high production costs.

4.1.2 Improvement of biological processes and their challenges

One of the difficulties of petroleum hydrocarbon biodegradation is the low availability of pollutants for microbial attack. Surfactants can ameliorate the bioavailability of petroleum hydrocarbons through the solubilization of these contaminants onto the micelles. In other words, surfactants emulsify the petroleum hydrocarbons facilitating access to the microbes (Jabbar et al., 2022). Owing to these beneficial characteristics, several studies have been focused on surfactant-assisted biological methods for the remediation of petroleum hydrocarbon-polluted soils (Cheng et al., 2018; Shin et al., 2006). Surfactant-assisted bioremediation of petroleum hydrocarbons is controlled by several factors, containing the selection of an appropriate surfactant and the dose applied for removing the contaminant, the selection of the suitable microbial culture, toxicity, and biodegradability of the surfactant in the soil.

Typically, nonionic surfactants have shown an adequate performance for soil treatment than cationic or anionic surfactants (Wang and Keller, 2008) because the cationic surfactants are usually adsorbed into the soil particles (Zhu et al., 2003) while anionic ones can be precipitated in soil (Jafvert, 1991). The most common nonionic surfactants studied for soil remediation are Triton X-100, Igepal CA-630 (octylphenoxy polyoxyethylene ethanol), Tween 80 (polyoxyethylene sorbitan monooleate with 20 ethylene oxides units) and Tergitol NP-10 (nonylphenol ethoxylate with 10 ethylene oxides units). More ethylene oxide units of surfactant increase the hydrophilicity and, consequently, rise the HLB number. Indeed, the HLB value of the surfactant can affect the oil distribution in the system through emulsification and micellar solubilization. Mohanty and Mukherji (2012) and Song and Bielefeldt (2012) suggested the usage of nonionic surfactants with mid-range HLB values for bioremediation of petroleum hydrocarbon-polluted soils and indicated an inhibitor effect of surfactants with low and very high HLB values. However, Torres et al. (2005) showed the adequate bioremediation of diesel from aged soils using nonionic surfactants with low HLB value, which was ascribed to the formation of the water-in-oil (W/O) emulsion. This behavior corroborates that although HLB is an indicator of the chemical nature of surfactant, other existing parameters affect the bioremediation of petroleum hydrocarbon-polluted soils.

The surfactant type also affects the micelles' structure and the solubilization of hydrophobic substances in the micelles. Typically, for similar hydrophobic chain lengths, nonionic surfactants have demonstrated higher solubilization. Though, micelle water partition coefficients in mixed surfactants can impact the success of petroleum hydrocarbon remediation (Mohanty et al., 2013). The implementation of mixed surfactants makes a micelle system, which causes lower CMC values than the singular surfactant system, and consequently, a lower interfacial tension can be obtained. The structural heterogeneity of surfactants promotes the capture of different molecules of petroleum hydrocarbons inside the micelle, which improves the bioavailability of the microorganism (Rehman et al., 2021). Similarly, the shape of micelles impacts the success of petroleum hydrocarbon remediation using surfactant-assisted biological methods. Lanzon and Brown (2013) studied the sorption of a nonionic surfactant Brij30 on the bacteria *Burkholderia* sp. in the form of hemimicelles. The results suggested that the hemimicelles formation rather than monomers on the bacterial cell surfaces enhances the bioavailability of petroleum hydrocarbons.

On the other hand, administering an appropriate dose of surfactant impacts both the success of petroleum hydrocarbon remediation and the cost of the process. At a high dose, surfactants may harm the microbes responsible for the petroleum hydrocarbon degradation and be less cost-effective. In addition, a high dose of surfactant may imply a negative impact on petroleum hydrocarbon degradation due to the accumulation of intermediate species in the environment, which in turn may be toxic. The intermediates species may be acidic and may cause a drop in pH in the system. This situation could difficult the viability of the application of surfactant-assisted microorganisms as an environmental solution for petroleum hydrocarbon spills. Likewise, the use of determined surfactants may change the microbial structure system and, consequently, these microorganisms tend to degrade the surfactant instead of the petroleum hydrocarbons (González et al., 2011). Thus, the eventual degradation of surfactants by natural microorganisms could be a more sustainable and showy option for the remediation of petroleum hydrocarbon-polluted soils.

Another factor that influences the success of the treatment of petroleum hydrocarbon-contaminated soils is the selection of microorganism culture and, consequently, the interactions between the surfactant and the microorganisms. The uptake of petroleum hydrocarbons is favored by an increase in the cell surface hydrophobicity of microorganisms. The influence of surfactants to alter the cell surface hydrophobicity of microbes has been studied using zeta potential measurements. Mohanty and Mukherji (2012) determined the effect of Triton X-100 during the degradation of two compositionally distinct NAPLs by a culture of *Burkholderia multivorans* (NG1). The values of zeta potential evidenced that surfaces of NG1 were less negative in presence of surfactant Triton X-100 during the degradation of NAPL 1 and 2. The decrease of negative charges of the NG1 surface may facilitate the interaction with negatively charged NAPL droplets owing to the existence of less repulsive charges between them. Accordingly, the alteration in the cell surface charge may favor the uptake of petroleum hydrocarbons by microorganisms. Hence, the successful implementation of surfactant-assisted biological methods for the treatment of petroleum hydrocarbon-polluted soils has many technical challenges and relies on several factors related to the surfactant, contaminants, soil, and microbial culture.

4.2 Nanomaterials-assisted biological remediations

Nanotechnology is the science and engineering area focused on designing, characterization, producing, and applying materials at a nanometric scale, between 1 and 100 nm. Although in nature there are several examples of materials with sizes lower than 100 nm, such as molecules of the human body, it was recently that nanotechnology became relevant to the scientific community for its potential for technological innovation. The current interest in nanotechnology is dated from 1996 in a panel of the World Technology Evaluation Center, which highlighted the new properties and behavior of nanostructures. This disruptive behavior is due to the particles with the nanometric size having properties that may differ from the same material with the dimension of solid volumetric (Poole and Owens, 2003) like their high surface-to-volume ratio.

The significant elements of nanotechnology are nanomaterials. The nanoscale materials are substances with at least one dimension in the range of 1–100 nm. Based on the classification of nanoscale, there are zero-dimensional nanomaterials, which are characterized by having three dimensions in the nanometric regime including nanoparticles (see Fig. 9). One-dimensional nanomaterials with one dimension in the nanoscale range are

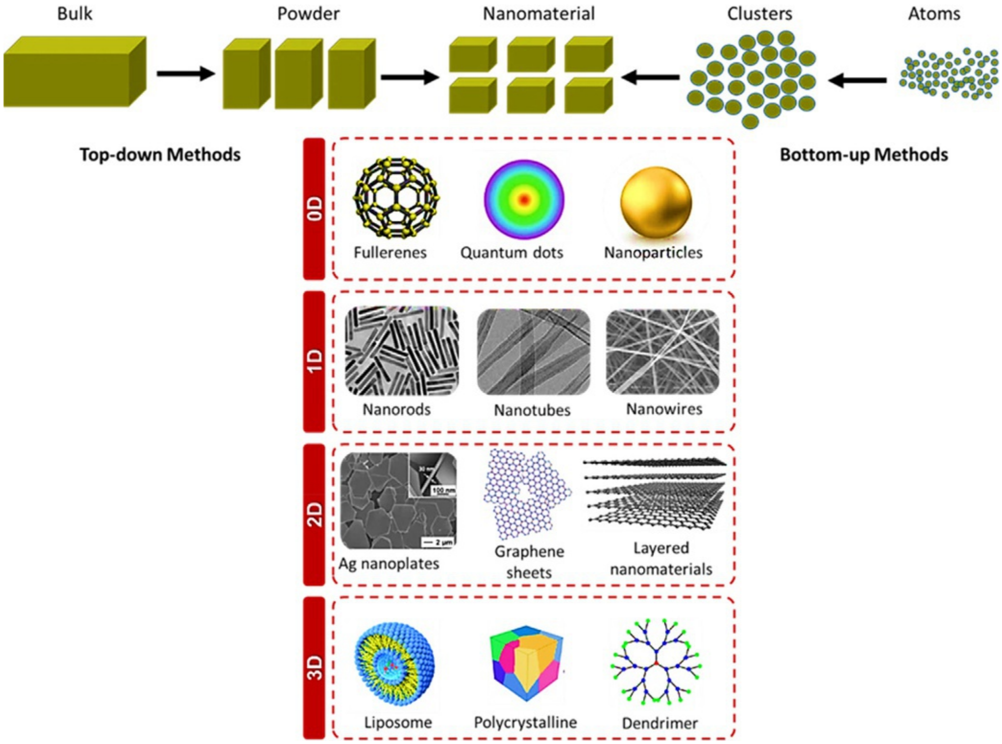

Fig. 9 Classification of nanomaterials based on their dimensionality and a schematic representation of the top-down and bottom-up approaches for the fabrication of nanomaterials (Alkaç et al., 2021).

nanorods or nanotubes, and two-dimensional materials are characterized by having two dimensions between 1 and 100 nm like nanofilms, nanolayers, and nanocoatings (Vollath, 2008). Nanocomposites consist of multiphase material where at least one of the components has a dimension less than 100 nm. This nanoscale phase is dispersed in another phase obtaining a combination of the individual features of these components (Omanović-Mikličanin et al., 2020). The manipulation of nanomaterial features is possible by controlling their size. Decreasing the particle size of nanomaterials increases the functional groups on the surface (Kröger et al., 2021). Likewise, the coordination number for surface atoms is lower than the internal atoms, which favors their mobility and reactivity with the other species. Surface-to-volume ratio of a nanoparticle can be 35%–45% times higher than a larger particle (Jamkhande et al., 2019).

Based on their morphology, size, and features, the nanomaterials may be carbon-based nanomaterials (Zhang et al., 2013), metal nanoparticles (Dreizin, 2009), semiconductor nanomaterials (Kumar, 2010), polymeric nanomaterials (Kobayashi and Müllen, 2015), and lipid-based nanomaterials (García-Pinel et al., 2019). Carbon-based nanomaterials including fullerenes and carbon nanotubes have shown high sensitivity for tailored manipulation, electric and conductive properties, and high strength (Mauter and Elimelech, 2008). Metal nanoparticles are prepared from divalent and trivalent ions and are characterized by their high surface-to-volume ratio and high adsorption of different contaminants from soil and water (Narayan et al., 2019). Also, polymeric nanomaterials can be obtained from various types of natural and synthetic polymers, which have demonstrated high reactivity, safety for biological applications, and good biodegradability (Han et al., 2018). Lipid-based nanomaterials are usually spherical vesicles consisting of ionizable lipids, which are positively charged at low pH and are neutral at physiological pH. The biocompatibility and biodegradability nature as well as the ease of scale up production are known as the main advantages of lipid nanomaterials (Editorial, 2021).

All the properties rely on the size and shape of nanomaterials, which may be controlled during synthesis processes. The synthesis of nanomaterials can be performed following different kinds of methods: biological, physical, and chemical approaches. The microorganisms such as bacteria, fungi, algae, biological templates (e.g., DNA and proteins), plants, and plant extracts have been used for nanoparticle preparation (Das et al., 2017). Usually, the methodology to prepare nanoparticles is classified as "top-down" or physical methods and "bottom-up" or chemical methods, as shown in Fig. 9. In the "top-down" approach a larger material is pulverized for obtaining nanometric particles by mechanical milling techniques, photons, heat, and ions, among others. In the "top-down" method, nanoparticles are prepared by nucleation through chemical combinations of atoms or ions (Arole and Munde, 2014). Among chemical methods are including sol-gel method, coprecipitation, thermal decomposition, solvothermal, sonochemical, pyrolysis, chemical vapor deposition, microemulsions, microwave-assisted methods, and ion exchange. The selection of an adequate technique depends on the size, type, and desired properties of the nanomaterial (Kolahalam et al., 2019).

4.2.1 In situ soil flushing with nanomaterials

In general, nanoremediation includes the usage of nanomaterials to remove pollutants in the soil, water, and air. Nanomaterials have been used as adsorbents, catalysts, and membranes (Anjum et al., 2019). Several types of nanomaterials have been applied for nanoremediation, for instance, metal oxides, zeolites, carbon nanotubes, and magnetic nanoparticles, among others (Alazaiza et al., 2021). Also, nanomaterials supported by clay minerals, zeolites, activated carbon, and biochar have enhanced the reactivity and adsorption capacity of the nanomaterials for removing different contaminants (Mandal et al., 2018). Nanomaterials may penetrate a contaminated area where microparticles cannot reach and can chemically decrease or aid catalytic reactions to destroy or transform determined contaminants (Rizwan et al., 2014).

The mechanisms recognized behind the nanoremediation in different media of soil, water, and air are mostly adsorption, photodegradation, heterogeneous catalysis, and electro-nanoremediation (Mukhopadhyay et al., 2022). The adsorption process is a surface phenomenon in which the contaminant is collected at the adsorbent in the solid-liquid interface. The nature of the bonding or type of interactions depends on the nature of the adsorbate (contaminant) and adsorbent (e.g., the nanomaterial). The adsorption can be categorized as physical adsorption and chemical adsorption. Physical adsorption contains interactions such as Van der Waals forces, hydrogen bonding, or electrostatic attraction and is considered a reversible process. In contrast, the chemisorption is produced by chemical reactions among the adsorbate and adsorbent by covalent bonding and is irreversible (Dąbrowski, 2001). A good adsorbent is characterized by a high adsorption capacity to remove the contaminants, high selectivity for specific contaminants, and should be reusable and recyclable. Thus, the contaminants should be readily removed from the surface of the adsorbent to regenerate and reuse the adsorbent. Also, the adsorbent should present a fast mass transport of contaminants, resulting in lower costs of removing process (Sahoo and Prelot, 2020).

Likewise, the photocatalytic process has been demonstrated to be an effective and inexpensive method for eliminating contaminants such as petroleum hydrocarbons from the soil. Photocatalysis is a photoreaction that is accelerated by the attendance of a catalyst (Wankhade Atul et al., 2013). Zhang et al. (2008) investigated the photocatalytic degradation of phenanthrene, pyrene, and benzo [a] pyrene on soil in the presence of TiO_2 nanoparticles of 20 nm using an ultraviolet (UV) light source at a temperature of 30°C. The results indicated that catalyst TiO_2 augmented the photodegradation of petroleum hydrocarbons significantly. Similarly, the authors showed that in acidic or alkaline situations the photocatalytic degradation rates of petroleum hydrocarbons were higher than in neutral conditions. This behavior corroborates the synergistic effect between the presence of a nanoparticulated catalyst of TiO_2 and UV irradiation. Other authors, indicated that doping of TiO_2 nanoparticles with metal ions can enhance the catalytic performance of these nanomaterials under visible light irradiation (Khairy and Zakaria, 2014).

On the other hand, a heterogeneous catalyst is a substance that continually creates active sites due to its reactants being under reaction situations (Schlögl, 2015). Most of the heterogeneous catalysts are composed of nanoparticles of an active phase such as a metal, which is dispersed on cheaper high-surface area support like a porous oxide (Zaera, 2012). The heterogeneous catalysts may be easily removed but do not present fast kinetics of the reaction, which has generated major interest in developing nanomaterials to accelerate the reaction rate. In addition, electrokinetic and electrodialytic methods consist of the application of a low-level direct current for the transport of different types of contaminants and the induction of electrochemical reactions (e.g., electrolysis and electrodeposition) (Gomes et al., 2015). Gomes et al. (2014) verified that the simultaneous use of electroremediation and nanoscale zero-valent iron or nanoiron (nZVI) has a high capability for removing pesticide (Molinate) from the soil and, additionally, cause its degradation by the action of nanoparticles. The combination of electroremediation with the use of nZVI enhanced the transport of these particles even in soils with low permeability fine grain.

The first implementation of nanomaterials for in situ treatment of contaminated soils was reported approximately 20 years ago and demonstrated the capacity of nanomaterials to remain active in the soil for up to 56 days. However, the nanoremediation in the soil has been limited by the high cost of the nanomaterials and a lower efficiency to remove some contaminants under in situ conditions (Mukhopadhyay et al., 2022). Various approaches have been focused on the reuse and regeneration of nanomaterials for reducing costs such as magnetic nanoparticles. Magnetic nanoparticles are developed from magnetic elements such as cobalt, iron, nickel, and oxides like chromium di-oxide (CrO_2), cobalt ferrite (Fe_2CoO_4), maghemite (Fe_2O_3, γ-Fe_2O_3), and magnetite (Fe_2O_4) (Sharma et al., 2015). Magnetic nanomaterials have shown abilities as adsorbents or catalysts in removing different contaminants from the soil. These particles are characterized by a facile separation by means of a magnet and metal ion adsorption (Fei et al., 2022). Additionally, the usage of magnetic nanoparticles did not alter the composition of the soil. nZVI has been used widely for in situ soil remediation due to the fast kinetics, lower cost/benefit ratio, and nontoxic impact on the environment (Mondal et al., 2021). These nanoparticles have been used as a reducing agent to treat contaminated soils with polychlorinated biphenyls (Lowry and Johnson, 2004), pesticides (Elliott et al., 2009), and polycyclic aromatic hydrocarbons (Chang et al., 2005), among others. The simple schematic of in situ treatment of contaminated soil using nZVI is shown in Fig. 10. Recently, green iron nanoparticles were developed for the removal of petroleum hydrocarbons from water and soil. Murgueitio et al. (2018) showed that iron nanoparticles prepared using the extract of mortiño berry reached a removal of 81.9% of petroleum hydrocarbons after 32 h of exposure to the nanomaterial. The behavior of green zero-valent iron nanoparticles was attributed to their high surface area, high reactivity, and faster kinetics compared with conventional bioremediation processes.

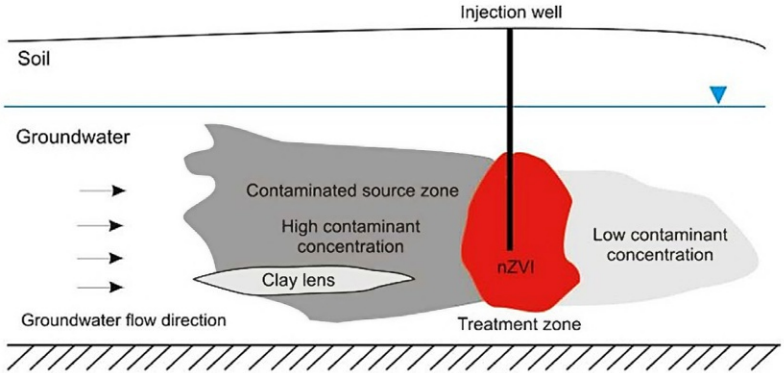

Fig. 10 Schematic of in situ groundwater remediation using nZVI (Laumann, 2013).

Although the application of nanoparticles as adsorbents or catalysts in removing contaminants from the soil has been important, the use of these nanomaterials in conjugation with surfactants to improve their mentioned mechanisms of contaminant removal during in situ soil flushing is the emerging field of study (Almahfood and Bai, 2018; Rezk and Allam, 2019). Few studies have been allocated to this subject in the field of in situ soil treatment. However, the conducted studies show that the presence of nanoparticles in flushing agents, for example, silica nanoparticles, can improve the mass transfer and the dissolution of petroleum hydrocarbons (Ramezanzadeh et al., 2020).

4.2.2 Improvement of biological processes and their challenges

Nano-bioremediation is defined as the removal of a contaminant using simultaneously nanoparticles and a biological method for quickening the removal and/or degradation rate of contaminants (Cecchin et al., 2017). Several recent studies have demonstrated that nano-bioremediation reduced the toxicity of contaminants to microorganisms. Nanomaterials have a quantum effect, which implies lower activation energy to allow a chemical reaction. Thus, nanomaterials increase the efficiency of microorganisms in eliminating organic pollutants from the soil, reducing remediation time and costs (Rizwan et al., 2014). On the other hand, plants present some advantages compared with microorganisms. Plants are simpler to cultivate than other organisms which need controlled conditions or a continuous nutrient supply for their production. Likewise, plants can produce various molecules involved in transforming contaminants such as glutathione, flavonoids, reactive oxygen species, and bioactive molecules (Vázquez-Núñez et al., 2020). Similarly, numerous studies have demonstrated the effect of nanomaterials on plants resulting in production systems with lower costs, energy, and wastes (Fraceto et al., 2016; Servin and White, 2016). Le et al. (2015) studied the degradation of polychlorinated biphenyl (Aroclor 1248) using bimetallic nanoparticles Pd(nFe) and the subsequent biodegradation with *Burkholderia xenovorans*. Aroclor 1248 was dechlorinated using bimetallic nanoparticles with mostly innocuous products. The resulting biphenyl was biodegraded by means of *Burkholderia xenovorans*. The toxicity of the residual polychlorinated biphenyl decreased from 33.8×10^5 μg/g to 9.5×10^5 μg/g. Other works focused their research on the synergistic effect of nanomaterials and plants on removing pollutants from the soil such as Le et al. (2019), who used bimetallic nZVI for removing hexabromocyclododecane (HBCD) considering the effect of humic acid present in the soil and tobacco plant. The percentage of removal using nZVI with the plant was 41% compared with 13%, 15%, and 27% obtained by systems consisting of only plant, plant with humic acid, and plant with nanoparticles and humic acid. The humic acid presence influenced the bioaccumulation of HBCD stereoisomers in the plant.

Besides the positive effects of nano-bioremediation on contaminated soils with petroleum hydrocarbons and other types of contaminants, nanomaterials could alter the soil horizons, soil physicochemical features, and the living organisms there. Many of the applied nanomaterials are not biodegradable and stay in the environment (soil, water, and air). These materials can modify the soil medium through sedimentation, adsorption by microorganisms, adhesion to the surface, dissolution, and transformation. The biodegradation degree depends on factors like the chemical nature of nanomaterials and particle size. Likewise, correlated soil factors must be considered to understand the complex interactions of a nano-bioremediation process such as organic composition and heterogeneity of the soil (Daryaee et al., 2021a,b; Pachapur et al., 2016). For example, Layet et al. (2017) demonstrated that the fraction of clay in the soil enhanced the CeO_2 nanoparticles retention and reduced the Ce adsorption, whereas organic matter increased the Ce uptake. However, in a low-level of organic matter the addition of the organic citrate coating enhanced the phytoavailability of the cerium resulting in smaller aggregates, which facilitated the transport of the nanoparticles to the roots of the *Festuca arundinacea* and *Solanum lycopersicum* L. Similarly, some investigations have reported negative effects of nanomaterials on plants such as a decrease in the growth of the plant and roots, productivity, and production of enzymes, among others (Pérez-Hernández et al., 2020).

The usage of nanomaterials for environmental applications has shown both positive and negative effects on the abundance and diversity of micro, meso, and macrofauna. García-Segura et al. (2018) studied the impact of soil fauna polluted with petroleum hydrocarbons from noncontaminated soil to moderately and highly contaminated soil. The results indicated that mesofauna density was remarkably higher in moderate soil contaminated than in the control soil. Similarly, macrofauna presented a high density in the most contaminated area but not was significant. Additionally, mesofauna was more sensitive to petroleum hydrocarbons due to the stronger changes from noncontaminated soil to highly polluted soil. Several species were more sensitive to hydrocarbons like naphthalene and fluorine, positively for termites, ants, and earthworms, and had negative effects on snails and acari. Indeed, Dendooven et al. (2011) showed that epigeic earthworms can accelerate the elimination of petroleum hydrocarbons and their degradation products from the soil. Larger numbers of earthworms were needed, which could be expensive at a larger scale. This finding could be a new pathway for studying biological candidates for the degradation of petroleum hydrocarbons in the soil. However, these effects depend on variables such as type of living organisms, methods of application, doses of nanoparticles, and physicochemical characteristics of the soil. Consequently, this behavior suggests the necessity of a tailored design of nanomaterials depending on the system nanomaterial-contaminant-living organism-soil and an eventual modification that enhanced their performance for specific contaminant removal with a minimal environmental impact.

5 Research findings and gaps

Petroleum, as a key part of global energy, plays an essential role in the process of national and international economic development. Nevertheless, soil and groundwater pollution arising from petroleum exploitation, transportation, processing, and storage pose unavoidable risks to the environment. Petroleum components are mostly known as carcinogenic, mutagenic, and teratogenic toxic materials, and the polluted media with these contaminations need a fast and effective remediation strategy. In situ biological treatment techniques despite their cost-effective and social acceptance features have limited ability to remediate soil polluted with petroleum hydrocarbons. In situ soil flushing using appropriate chemicals has gained much attention to accelerate the treatment of petroleum hydrocarbon-contaminated soils and enhance bioremediation efficiency, which is known as chemical-assisted biological methods. Among proposed chemicals, surfactants and nanomaterials owing to their specific properties have great potential for the treatment of petroleum hydrocarbon-polluted soils. Although several kinds of research have been allocated to the application of such chemicals for in situ soil treatment, critical gaps in the current gained knowledge exist. Some of the important ones are highlighted in the following:

- The design of subsurface remediation processes using surfactants requires more biodegradable molecules, with lower toxicity and lower CMC for being considered a viable environmental technology. These factors have increased the demand for bio-based surfactants and chemical surfactants-assisted biological methods, which eventually may replace the use of a singular chemical surfactant system. Likewise, the high production costs of bio-based surfactants should be mitigated by using renewable bioresources as raw substances for the production of these species. On the other hand, considering the mentioned variables that may affect removing petroleum hydrocarbons using surfactant-assisted biological methods, field tests are severely recommended before scaling the usage of this technology on a larger scale.
- Although the works focused on the application of nanobioremediation for pollutant removal from the soil have gained attention in the last years, the mechanisms and

interactions between nanomaterials, contaminants, living organisms, and soil as well as methods of application are not fully understood. Furthermore, it is necessary to know the transport route and nanomaterials transformation under field conditions to design better materials with lower environmental impacts. The mobility and destination of nanomaterials, when deposited in the soil, have not been investigated deeply. The mineral and organic composition as well as the soil heterogeneity must be considered to recognize the mechanisms behind the mobility and fate of the nanomaterials.

- Contaminants should be easily eliminated from the surface of the nanomaterial to regenerate and reuse the nanomaterial as an adsorbent. Synthesis of nanomaterials in high yields and low cost has gained interest worldwide. This situation has produced reusable and recyclable nanomaterials taking advantage, for example, of their magnetic properties. Another option for producing nanomaterials at lower costs has been the synthesis from agricultural and industrial wastes. Other key characteristics that should be considered for the optimal production of nanomaterials are the chemical nature, morphology, and mean particle size of the material, which influences the specific surface area. Also, synthesis can include the functionalization by the conjugation of active molecules or functional groups that interacts with the media.
- Living organisms (microorganisms or plants) play an important role in the removal of a specific contaminant, and its selection depends on the availability, determined controlled conditions, a possible nutrient supply, secondary products during the degradation, costs, and energy of production. For determining the optimal conditions of the system nanomaterial-contaminant-living organism-soil, laboratory experiments under artificial substrates, natural soil, and field conditions should be carried out to maximize the efficiency of the removal of contaminants and to minimize the impact on the environment.

Finally, considering that the soil is the basis of numerous ecosystem processes, the scientific community should increase their attention to the effect of novel remediation technology such as bio-based surfactants and nanomaterials as well as other effective remediation strategies on endemic living organisms.

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CHAPTER 13

Review of the effects of oil pollutants on physicochemical and biological soil properties

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1 Soil and its importance in the environment

Soil is one of the most important natural and limited resources of the earth and considered the most vital component of the environment after the weather. Soil has vital importance and plays a key role in climate change, land erosion, food security, and ecosystem processes (Tahoori and Parvin, 2016). Soil is the central part of the earth's ecosystems and is the intermediary between the bedrock and the earth's surface (Fig. 1). Therefore, it is an important and effective factor in the formation and emergence of any soil ecosystem.

There are many definitions for soil. Here it is enough to present two universally accepted definitions of soil. Soil is developed as a result of biological, chemical, and physical processes comprising the weathering of rocks and the decay of vegetation. Organic materials such as clay, silt, sand, and gravel particles are the main components of soil that are mixed in such a way that provides a growing environment for plants. Soil profiles comprising layers more or less parallel to the surface of the earth have been a result of the interaction between climate, parent materials, topography, and living organisms over a long period. The difference between soil and parent material is due to its morphology, properties, and characteristics (Houghton and Charman, 1986). The Council of Europe also provides a similar definition of soil with a slight change: soil is an integral part of the earth's ecosystems, which is located between the surface of the earth and the parent rocks. Soil is classified into several consecutive horizontal layers with particular biological, chemical, and physical properties. From the point of view of the history of soil use and the environment and ecology, the concept of soil includes porous sedimentary rocks and other permeable materials and their accompanying water and groundwater sources (Hannam and Boer, 2002). Soil is a natural dynamic body that is formed due to soil forming factors and processes and contains mineral and organic materials that cover the outer crust of the earth, and plants are able to grow on it. Soil is one of the important and valuable resources of nature, from which almost 95% of human food is supplied. In other

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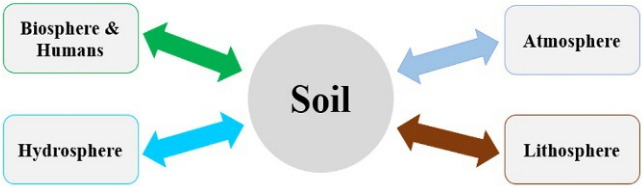

Fig. 1 Soil is at the center of ecosystems.

words, soil is the basis and source of production and storage of raw materials, which plays the main role in regulating and maintaining the life of living beings. Therefore, it plays a vital role in the life of humans and other organisms, and without healthy soil, life will not exist.

2 Soil pollution

Soil as a natural resource, global capital, and bed of life plays essential roles in the establishment and growth of human societies as well as other living organisms, and it is actually the origin and a part of the human and other animal beings' food chain. Therefore, any contamination in the soil may enter the food chain and get transferred to the human body. Soils have a special ability called self-healing and are considered nature's cleaners. In addition to being nutritious, there is another property called soil purification, which is due to its physical and chemical properties. Self-purification power of the soil is less than that of air and water due to its low exchange rate. For this reason, soil contamination is the most important type of environmental pollution. Soil is the most important and most widespread substance that cleans water and recycles waste, but it has a limited capacity (Ghazban, 2011). Solid, liquid, and even gas hazardous materials that are mixed with natural soil cause soil pollution. Soil pollution can harm humans, animals, and plants. Damage to plants is caused by contaminated soils very easily and through the growth of plants in polluted soils and absorption of soil pollutants (Zahedifar et al., 2016, 2019). Swallowing, inhaling, and skin contact with contaminated soil are the ways that pollutants enter human and animal bodies. Sometimes, using plants or the meat of animals that have been exposed to soil pollution can be harmful to humans. In some cases, working in contaminated soil can be harmful to human health (Dabiri, 2013). The concentration of many toxic materials and pollutants that are added to the soil may increase and eventually become a serious threat to the environment. Some toxic materials remain in the soil for centuries. Even though harmful organic materials such as carbon, oxygen, hydrogen, phosphorus, nitrogen, and sulfur decompose in the soil and eventually become recycled elements, as long as they are being decomposed, they are still considered harmful to the environment (Ghazban, 2011). Chemical soil and environmental contaminants that are potentially hazardous are either organic or inorganic compounds. Fig. 2 illustrates a

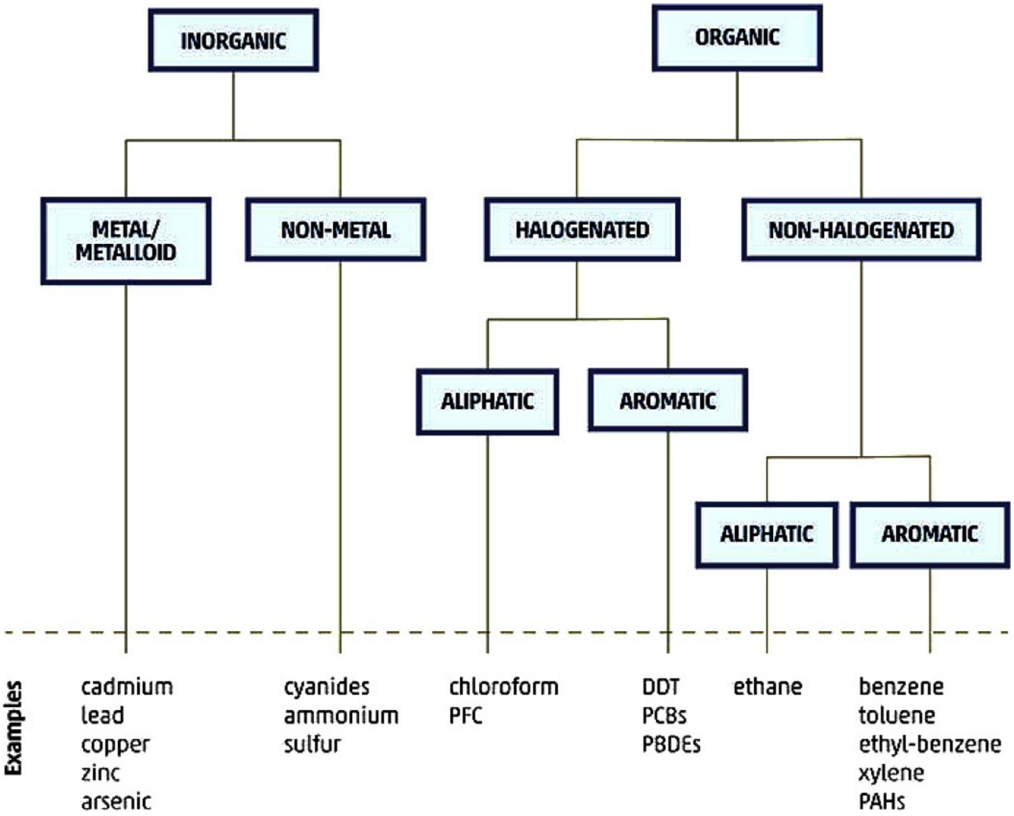

Fig. 2 Systematic classification of IUPAC for the main pollutants in soils. *(After Swartjes, F. A., 2010. Introduction to contaminated site management. In: Dealing with Contaminated Sites: From Theory Towards Practical Application. Springer Netherlands, Dordrecht, pp. 3–89.)*

systematic classification of some of the most common pollutants in soil environments considering their chemical characteristics.

Soil as a substrate for production of the food, humans' necessity, is of great value and importance; however, it sometimes is neglected, that is, direct and indirect addition of pollutants to soil cause undesirable changes where, in some cases, the balance in the soil is disturbed and the soil faces a challenge called pollution (Frick et al., 1999). In other words, pollution is any change in the characteristics of water, soil, air, and food that adversely affect environment, human activity, other living organisms, and the ecosystem (Chen et al., 2015). Pollution-induced soil degradation can become an iterative cycle of degradation (Fig. 3) that can ultimately lead to the loss of ecosystem services. Loss of soil productivity, reduction of biodiversity, crop yield and water quality, contamination of food products, and loss of marketability are of the main quantifiable economic losses resulting from soil pollution (Fig. 4).

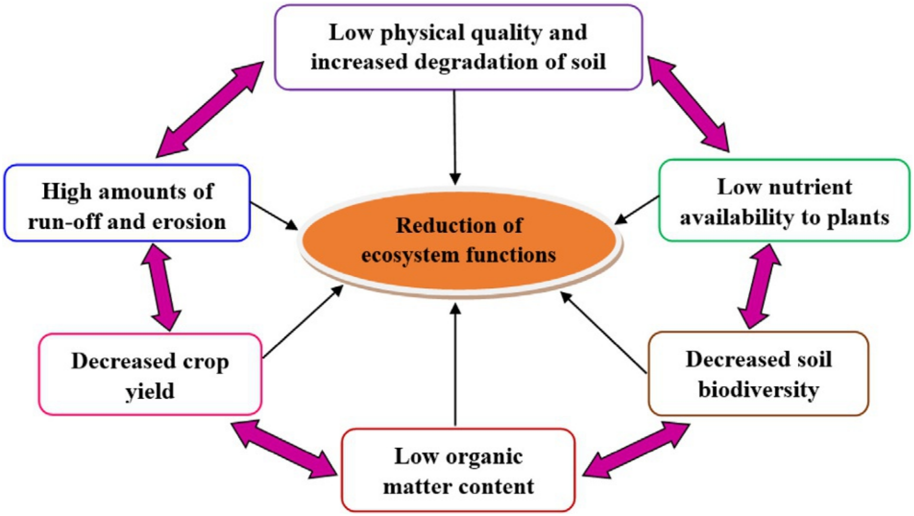

Fig. 3 Pollution results in a chain of degradation processes in soil, jeopardizing soil's ability to provide key ecosystem services. *(After https://www.fao.org.)*

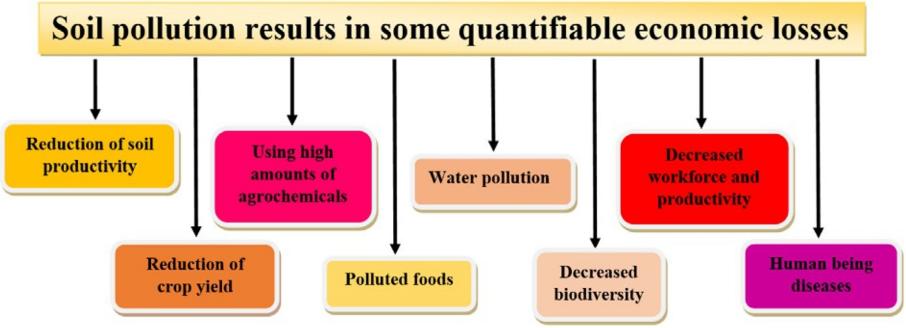

Fig. 4 The main quantifiable economic losses resulting from soil pollution. *(After https://www.fao.org.)*

3 Oil pollution and the most common and the most used oil products

Oil pollution is an unavoidable consequence of rapid population growth and industrialization process in oil-rich countries (Roshanghiyas and Bagheri Puor, 2019). The term total petroleum hydrocarbons, TPHs, is used to describe a large family of several hundreds of chemical compounds of crude oil origin. TPHs is a mixture of chemicals; but all of them are mainly composed of hydrogen and carbon, and hence they are called hydrocarbons (Suja et al., 2014). The most common petroleum pollutants in the soil include crude oil, kerosene, gasoline, polycyclic aromatic hydrocarbons (PAHs), chlorinated solvents, toluene, benzene compounds, xylene (BTEX), ethylbenzene, etc. (Das and Chandran, 2011; Karthick et al., 2019; Momeni et al., 2018). Fig. 5 shows charts of crude oil distillation and its derivatives.

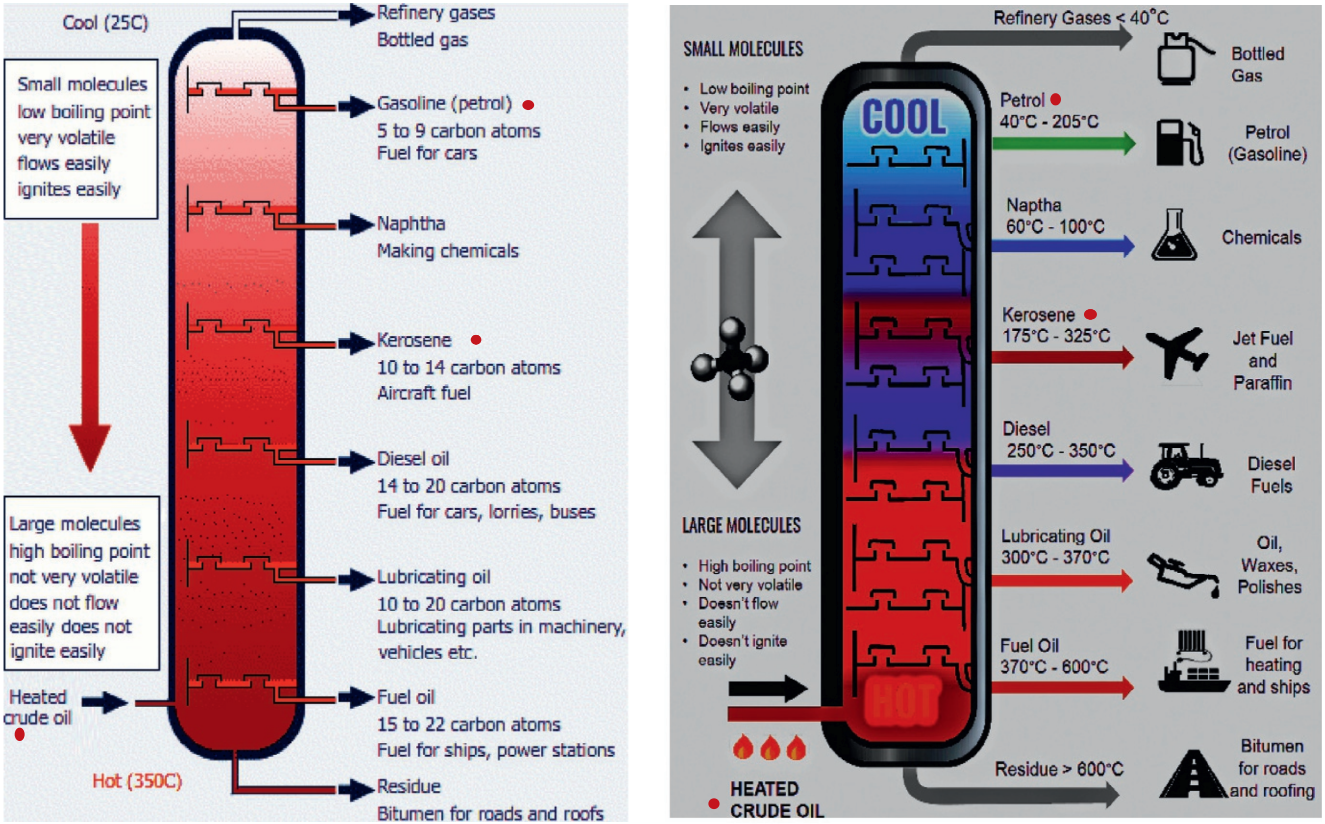

Fig. 5 Diagram of crude oil distillation and its derivatives. *(source: (Left) environbusiness.com; (Right) enerpac.com.)*

Today, crude oil and its derivatives are the important source of energy for daily life and industry (Das and Chandran, 2011). Crude oil is an unrefined liquid containing carbon and hydrogen in the form of saturated (alkanes) and unsaturated (alkynes) hydrocarbons, alkenes, and aromatic hydrocarbons. It has been estimated that more than 5–10 million tons of oil enter the oceans every year. Extraction, purification and processing, transportation, and use of oil increase the risk of environmental pollution with accidental spills, especially in oil-producing countries (Tahhan et al., 2011). Today, due to the large use of petroleum compounds all over the world, the pollution caused by these compounds is very widespread in the world. So far, oil companies around the world have drilled more than 3,600,000 wells. There are about 6000 oil production wells in America alone; the number of oil wells in Western Europe is about 6000, the number of known oil and gas basins in the world is more than 22,000, and the Ahvaz oil field in Iran also has 464 oil wells. Accumulation of petroleum hydrocarbons, one of the most widespread groups of environmental organic pollutants, in the soil can harm the environment and human health (Rezaee, 2005; Najafi Asfad and Darabinia, 2012). In addition to crude oil, gasoline is also one of the most commonly used and useful petroleum products in the world (Abdollahinejad et al., 2019). Gasoline is a petroleum compound with medium mass, boiling point between 175°C and 355°C and has more than 200 petroleum hydrocarbon compounds with the mass range of C_{10}-C_{28} alkanes and usually contains 30% alkane, 45% cycloalkane, and 24% aromatic compounds (Abdollahinejad et al., 2019). Also, the United States Coast Guard's emergency response notification system has listed kerosene as an environmental pollutant due to the presence of some toxic compounds, e.g., polyaromatic hydrocarbons, benzene, toluene, and xylene (Mojarrad et al., 2017). On the other hand, kerosene mainly has 9–16 carbon atoms and more than 80% of alkane materials and compounds (Nouri et al., 2013b), and due to having compounds such as alkanes, cyclic alkanes, olefins with the approximate chain length of 9–20 carbons (Mojarrad et al., 2017), it can be considered as a general petroleum compound. In addition, this hydrocarbon substance is often used as a solvent, hydrocarbon fuel, and heating agent in factories and homes. It is also used in rural areas for various purposes (Nouri et al., 2012). Contamination of soil with oil pollutants, especially the cases of its widespread use that were mentioned earlier, is relatively common in the world, and it is necessary to identify and investigate the behavior of soil in the face of this problem and manage it (Kamel et al., 2018; Daryaee, 2020).

4 Origin and types of petroleum products' pollution and their transport within soil

Oil pollutants penetrate the soil in various places such as oil storage tanks and refineries, petrochemical production facilities and dilapidated industrial factories. Tanker accidents, bombing, spreading and leakage of petroleum products and its derivatives from storage tanks, damaged transmission pipes, discharge from onshore and offshore facilities, and natural leakage are other sources of oil pollution in the soils that necessitate a special attention to soil pollution as well (Hassanshahian, 2014; Hassanshahian et al., 2014; Falciglia and Vagliasindi, 2015; Momeni et al., 2018).

Normally, petroleum hydrocarbons transfer to the environment (air, water, and soil) and the entire aquatic and terrestrial ecosystems through production, refining, storage operations, transportation, and consumption. The most general and important route of petroleum hydrocarbons' transferring and entrance into the soil is summarized in Fig. 6 (Ambaye et al., 2022). It should be noted that the hydrophobic nature of different petroleum hydrocarbons remarkably affect their attraction and adsorption rate toward soil, water, and air environments, but as shown in Table 1, the amount of their adsorption depends on their characteristics and nature of the environment. In other words, the interactions of pollution with the investigated environments are different.

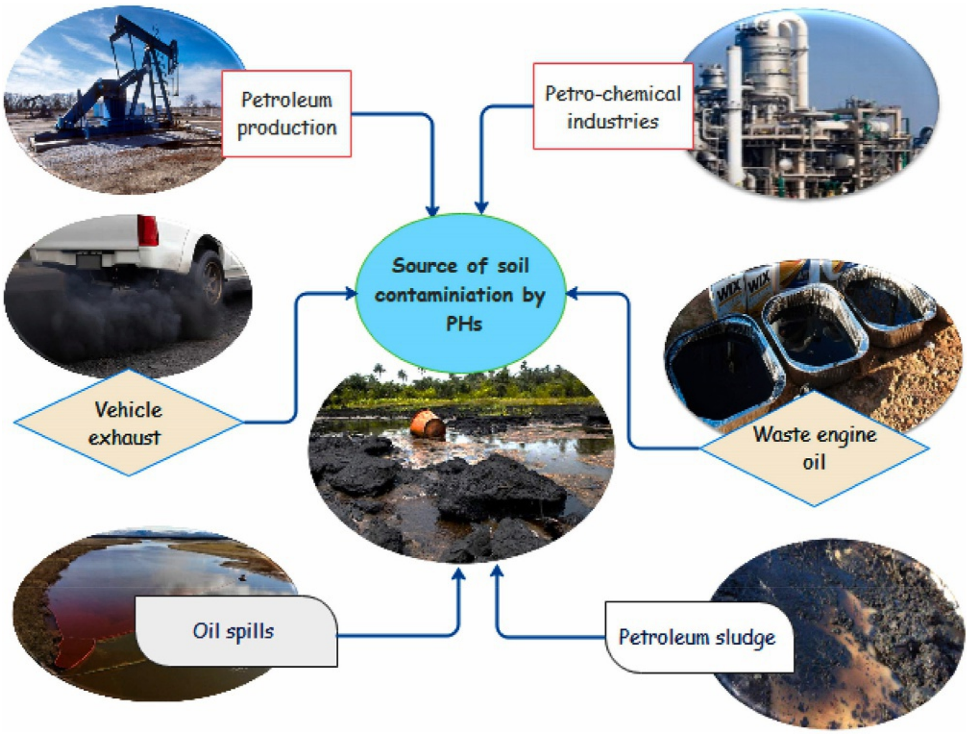

Fig. 6 Sources of soil contamination by petroleum hydrocarbons. *(After Ambaye, T.G., Chebbi, A., Formicola, F., Prasad, S., Gomez, F.H., Franzetti, A., Vaccari, M., 2022. Remediation of soil polluted with petroleum hydrocarbons, and their reuse for agriculture: recent progress, challenges, and perspectives. Chemosphere, 133572.)*

Table 1 Distribution of petroleum hydrocarbons in aquatic (water) and terrestrial (soil and air) ecosystems.

	Adsorption (%)		
Petroleum hydrocarbons (PHs)	**Adsorbed in gas**	**Adsorbed in water**	**Adsorbed in soil**
Acenaphthene	0	0	100
Acenaphthylene	0	0	100
2-Methylnaphthalene	0	0	100
Naphthalene	0.5	0	99
o-Xylene	1	11	88
Ethylbenzene	5	13	83.5
p-Xylene	1	4	95
m-Xylene	1	5	94
Toluene	3	12	87
Benzene	6	18	76

After https://slidetodoc.com/contaminated-land-dealing-with-hydrocarbon-contamination-remediation-options.

Oil pollution is divided into the following two groups in terms of distribution and level of pollution in nature:

(1) In situ pollution caused by oil tanker accidents, destruction or explosion of an oil terminal, oil piers, and transmission lines.

(2) Diffuse pollution caused by the application of petroleum mulches and other petroleum products in large areas (Seyed Alikhani et al., 2011).

The density of nonaqueous phase liquids (NAPLs) or petroleum pollutants has a great impact on their behavior in the soil environment (Nouri et al., 2013a). Petroleum pollutants are divided into the following two general categories based on their density compared to water (Delleur, 2006):

(1) LNAPLs: NAPLs that have a lower density than water and are often placed as pollution in the upper layers of porous environments such as aquifers. The leakage of LNAPLs under the influence of capillary and gravity forces lead to their vertical movement. In unsaturated soils, they fill soil pores. If the amount of leakage is high, the liquid phase will reach the surface of the water and accumulate there, and from there it will move along with the underground water slowly and remain floating on the surface due to their lower density than water (Delleur, 2006).

(2) DNAPLs: NAPLs that have a higher density than water. In this situation, most of the contaminants reaches lower levels of water (Abdul et al., 1990). After the penetration of NAPLs into the soil, a part of them evaporates, a part is decomposed by soil living organisms, a part is retained by the capillary force of the soil, and a part is transferred to the porous environment of the soil in the form of immiscible mixing (Jarsjö et al., 1994). Therefore, it is necessary to recognize their effects on the environment (Nouri et al., 2013a). Regarding the distribution and transfer process of organic materials or hydrocarbons in the soil, it should be mentioned that the transfer can be done in saturated or unsaturated soils. Factors such as gravity and capillarity are effective in transfer of materials in such a way that when a large volume of material is put on the earth surface, its vertical movement is due to the force of gravity. During this process, the pollutant first occupies the contact points of the soil particles and then it occupies the small pore spaces between the particles. After that, the vertical and horizontal movements within the soil profile are carried out under the influence of gravity and capillarity (Abdul et al., 1990; Rezaei et al., 2022). The extent and spread of oil pollution mainly depends on soil hydrology characteristics such as porosity, permeability, soil type, the amount of soil water, as well as the concentration and type of pollution. It should be noted that during the leakage of hydrocarbon compounds, there is a possibility of evaporation of some of its volatile compounds. Hence, people who are in contaminated areas and sites can be exposed to contamination by inhaling toxic fumes. In addition, some petroleum compounds are removed from the leakage environment due to the presence of surface water. However, those compounds that penetrate into the soil remain in the environment for a long period of time depending on their chemical and physical characteristics. Different mechanisms and several factors are effective in the movement of oil pollutants and their degradation in soil and ground water. Absorption of oil products by soil particles is one of the most important processes affecting their fate in soil environment. This process has a very important role in the movement of hydrocarbons in the soil and it affects other processes, especially biological and chemical processes (Daryaee, 2020).

5 Necessity and importance of studying oil pollution and oil-contaminated soils

Oil pollution is an unavoidable consequence of the fast growth of population and the process of industrialization in oil-rich countries (Roshanghiyas and Bagheri Puor, 2019) where wide areas of the countries may expose to soil pollution by petroleum products and water may contain all kinds of oil pollutants. Therefore, research is necessary in this field. It should be noted that today soil contamination with petroleum materials (TPHs) is one of the most major and important problems that seriously threaten the environment, human health, and other living organisms (Alharbi et al., 2018; Ren et al., 2018; Abdollahinejad et al., 2019; Karthick et al., 2019; Ossai et al., 2020). In other words, oil pollution decreases productivity of the soil and makes it unusable for agriculture, the penetration of pollution into ground water and entering it pollutes water, and on the other hand, in some cases, it also results in air pollution and negative effects on respiration (Hassanshahian et al., 2014). Land pollution and soil erosion resulted from the presence of these pollutants in the soil is one of the most important problems facing the current and future generations of mankind. Therefore, a comprehensive investigation of

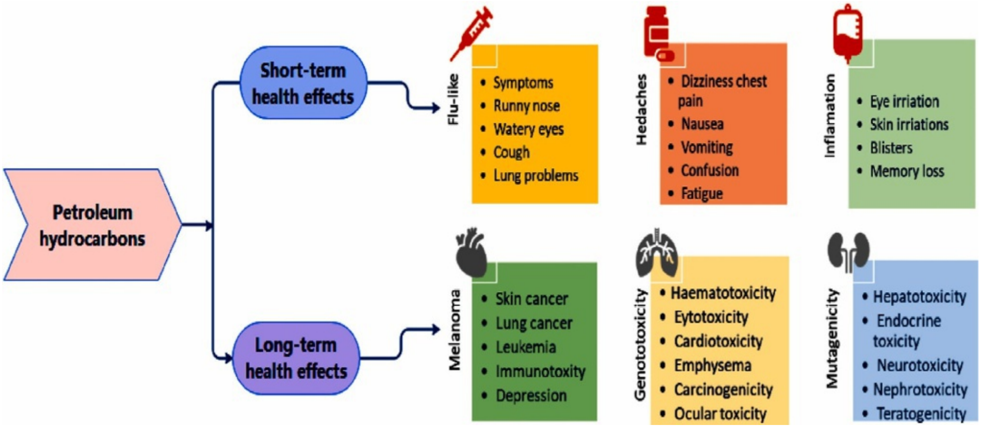

Fig. 7 The effects of petroleum hydrocarbon on human health. *(After Ossai, I.C., Ahmed, A., Hassan, A., Hamid, F.S., 2020. Remediation of soil and water contaminated with petroleum hydrocarbon: a review. Environ. Technol. Innov. 17, 100526.)*

the factors affecting it is a priority in most countries of the world (Mohammadi et al., 2015). Some materials in oil are known as carcinogens and mutagens. Accumulation of these oil compounds in the environment is a serious threat to human health, organisms, and living ecosystems due to their toxicity (Kim et al., 2013). Consequently, it has caused a broad range of toxicological effects on the animal and human health. For instance, hemotoxicity, mutagenicity, ocular toxicity, genotoxicity, hepatotoxicity, carcinogenicity, cardiotoxicity, cytotoxicity, nephrotoxicity, neurotoxicity, immunotoxicity, and teratogenicity, as illustrated in Fig. 7 (Zheng et al., 2014; Azeez et al., 2015; Ossai et al., 2020; Premnath et al., 2021).

Furthermore, oil pollution is a serious threat to agriculture and crop production, and oil-contaminated soils are unusable for industrial or recreational purposes (Issoufi et al., 2006). Oil contamination of soils reduces soil permeability, which has negative effects on the plants and soil microorganisms (Merkl et al., 2005; Robertson et al., 2007). Aromatic hydrocarbon compounds are one of the most persistent oil organic pollutants, which are carcinogenic and mutagenic, enter the body via the food chain, and are dangerous for human and animal health (Zhang et al., 2010).

6 Necessity and importance of studying soil properties

The leakage of petroleum pollutants in the environment cannot be ignored (Alharbi et al., 2018; Ren et al., 2018; Karthick et al., 2019; Ossai et al., 2020). In addition, the spillage of crude oil and its derivatives is one of the most key factors that change the engineering characteristics and behavior of soils (Akinwumi et al., 2014). Considering that, the release of oil materials in the soil results in a change in the resistance parameters and their behavior, so it is very important to study the physical, mechanical, geotechnical, chemical, and biological characteristics of the soil contaminated with oil derivatives. It should be noted that different soils in terms of their texture and structure show different behaviors in response to oil pollutions and the differences are mainly due to different reactions between different types of soil and types of oil pollution (Rajabi et al., 2017). As a result of leakage of oil pollutants into the soil, in addition to the negative environmental effects such as contamination of ground water resources (Alharbi et al., 2018; Ren et al., 2018; Karthick et al., 2019; Ossai et al., 2020), it causes changes in the physical and geotechnical characteristics of the contaminated soil. These changes in granular soils are changes in physical characteristics and in fine-grained soils, are changes in soil structure. Therefore, studying the effect of oil pollution on soils of different textures provides more extensive information (Roshanghiyas and Bagheri Puor, 2019; Daryaee et al., 2021a). It can be seen that any kind of remediation of such soils requires a quantitative evaluation of the physical, mechanical, chemical, and biological properties of the soil in the presence of these pollutants because remediation of the petroleum contaminated soil is very necessary for the proper protection of water and soil resources (Nouri et al., 2013b; Daryaee et al., 2021b). In general, for the appropriate use of such soils, it is necessary to study their physical, mechanical, chemical, and biological characteristics and behavior more and more precisely. The complexity of the soil environment and the many diverse features of its components (living organisms, organic and mineral compounds, type of minerals, porosity and permeability, transferability of pollutants in soil, building and soil compaction) are all the causes of different behavior and reactions of contaminated soils against petroleum pollutants and their absorption rate and ease of movement in the soil. Studying these characteristics and identifying how they interact with pollutants provide the basis for correct and scientific management of such soils (Minai et al., 2006; Asadi and Heidari, 2016). In addition, due to the development of pollution, the cleaning of polluted areas has become a necessity. In some cases, to reduce or remove pollution, instead of using noncontaminated soil, oil-contaminated soil is moved from its place and used in road construction or for parking cars. But in most cases they have to remediate contaminated soils, and after removing or reducing pollution, the soils are used for secondary and regional purposes (Alsanad et al., 1995; Asadi and Heidari, 2016). The need for comprehensive studies in natural conditions on petroleum compounds exposed to the environment is quite tangible, that is, the effects of petroleum materials in the soil should be further investigated through these real results. If there is a need to modify these lands, there should be enough information about their characteristics in the soil and operations and how to deal with them. Nowadays, soil pollution with petroleum materials, especially petroleum-intensive materials, is increasing and this issue can be harmful and limited from the environmental point of view and based on the type of land use. Therefore, before any action, it is necessary to check the effect of these materials on different characteristics of the soils in order to increase the necessary knowledge and information about these contaminated soils. Information regarding the effect of petroleum materials on various biological, physical, and chemical characteristics of the soils and other related characteristics is needed to make the necessary decisions for different uses of oil-contaminated soils. Especially, it should be used in the management and improvement of these soils as well as in the conditions of using petroleum materials to protect soil erosion by water and wind (Daryaee et al., 2021a).

7 Effects of oil pollutions on soil properties

Exploitation of oil fields increases the possibility of leakage of oil pollutants into the surrounding soil. In addition to environmental damages and consequences, this phenomenon also causes destructive changes in the mechanical, physical, chemical, and biological properties of the soils that may result in destruction of buildings and reduction of soil permeability that consequently increases the potential of runoff production and soil erosion. This type of soil degradation is a global problem that constantly changes the soil in different areas and in different ways. It is worth mentioning that these changes mainly take place in the structural characteristics of the soils, which results in changes in compatibility of the soils. As mentioned, the number of known oil and gas basins in the world is more than 22,000 basins (Rezaee, 2005; Najafi Asfad and Darabinia, 2012). All over the world, especially in oil-rich countries and critical regions, oil pollutants create many environmental problems (Alharbi et al., 2018; Ren et al., 2018; Karthick et al., 2019; Ossai et al., 2020). Since organic pollutants have high stability in the soil; therefore, their gradual accumulation in the soil over time causes changes in the primary characteristics of the soils and consequently the natural functions of the soil are negatively influenced and agricultural products decreases (Liang et al., 2012). Different researchers have investigated the topics of soil pollution. Investigators reported that the fine-textured soils are more affected by pollution than the coarse-textured soils. For instance, Fine et al. (1997) introduced a parameter called the sensitivity index varying from 0 to 1 in various types of soil. Other investigators reported that the sensitivity index of 0.01–0.1 and 0.6–0.9 for the coarse-textured and fine-textured soils, respectively (Fretwell et al., 1998). When soil is contaminated with chemicals, the physical and chemical interactions occur between the soil and the chemicals, which cause changes in the structure, physical and mechanical soil attributes (Meegoda and Rajapakse, 1993; Beytolahpour and Raeesi Estabragh, 2016). The structure of soils depends on the type of clay minerals, physical and chemical properties of fluid between soil particles e.g., temperature, ion type, electrolyte concentration, dielectric constant, dispersion, and anion absorption. The amount of physical and chemical interactions in the soil can be expressed by the spread of double layer. A decrease in the thickness of the double layer creates a flocculated structure; whereas, an increase in the thickness of this layer creates a dispersed structure (Moore and Mitchell, 1974; Beytolahpour and Raeesi Estabragh, 2016). It has also been shown that van der Waals gravity plays an important role in the compressibility behavior of contaminated soils including settlement, shear strength, permeability, and swelling potential (Moore and Mitchell, 1974). In fact, soil clay is considered the most important part of the soil structure due to its high load and specific surface area compared to sand and silt (McKenzie, 2003). Therefore, the effect of soil particle distribution on soil structure depends more on the amount of soil clay. Clays due to their electrostatic properties and high specific surface area are physically and chemically active and play key roles in joining soil particles and forming soil aggregates. After organic matter, it is one of the most key factors in the formation and stability of soil structure (Rengasamy et al., 1984; Taghizadeh Ghassab et al., 2017). The subject of environmental problems is the result of chemical and physical reactions occurring between the pollutant and the soil and change the behavior of the soil, and the soil behavior is generally interpreted with the physical, mechanical, chemical, and biological characteristics of the soil (Chen et al., 2015; Daryaee, 2020). Among these characteristics are resistance, permeability, and compressibility, etc., which cause the initial balance between soil characteristics to be disturbed (Sabour et al., 2018). Studying and investigating the effect of petroleum materials on various soil properties, including physical, mechanical, chemical, and biological characteristics, in addition to environmental and agricultural issues, can help researchers to investigate the behavior of soil in the presence of petroleum compounds and expressing the reduction of soil resistance in the presence of the large amounts of these compounds. As shown in Fig. 8, soil health is affected by many properties, all of which are affected by each other and are related together.

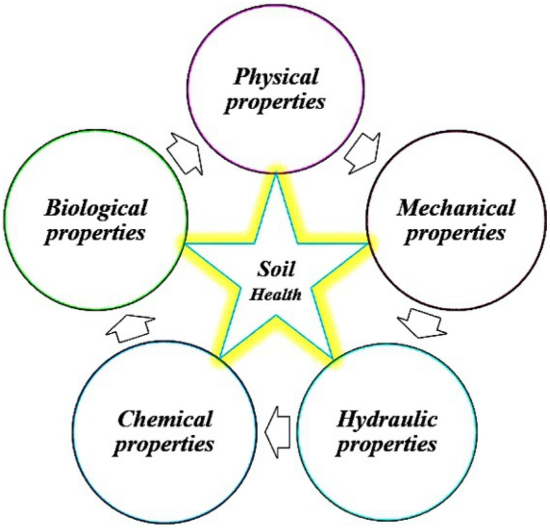

Fig. 8 Schematic view of soil properties and their relations.

7.1 Physical properties

Addition of petroleum hydrocarbons as a coating on the surfaces of soil colloids or in the soil matrix results in the creation of a phenomenon called water repellency in the oil-polluted soils. Research related to this issue has shown that two centimeters of the soil surface have the highest amount of water repellency (Doerr and Thomas, 2000). Surface layer of the soil is the connection between the pedosphere and the atmosphere and therefore has a major impact on the processes related to these two parts. Moreover, studies have shown that soil contamination with oil pollutants and heavy metals causes a strong increase in soil water repellency. In hydrocarbon-contaminated soils, soil water repellency usually appears after a long period of drought and, as a result, the moisture content of the field decreases (Takawira et al., 2014). Water repellency is one of the basic problems of soils contaminated with petroleum materials, which can affect water distribution by reducing infiltration, increasing surface runoff, soil erosion, and preferential flow (Kamel et al., 2018). Soil water repellency shows a condition in which the soil shows resistance to the water infiltration into the soil during periods of several minutes to several hours or even more (Dekker et al., 2001). This phenomenon is generally occurred due to the presence of organic compounds such as waxes, tannins, fatty acids, and gums (Roy and McGill, 2000; Amjadian et al., 2018; Gavili et al., 2018; Moradi-Choghamarani et al., 2019). In other words, these compounds result in water repellency due to the presence of water insoluble components. It caused the desired organic compound to be placed on the surface of the soil particles and by increasing the contact angle between the water and the interface between the soil and the air (soil surface), preventing the water from entering the soil and absorbing it. According to the viscosity of compounds and organic pollutants and the desired soil texture, the amount and intensity of water repellency will also be different (Leelamanie et al., 2013; Kamel et al., 2018). In most of the researches related to the investigation of the effect of petroleum pollutants on soil water repellency, the results showed that the presence of petroleum pollutants in the soil causes severe water repellency in the soil (Buczko and Bens, 2006; Takawira et al., 2014). Also, in another study, it was estimated that by increasing the amount of clay in the soil, the intensity of water repellency decreases (Harper and Gilkes, 1994). On the other hand, the coarser the texture of the soil becomes, due to having a lower specific surface area, it is more easily exposed to hydrophobic materials and more water repellency is created (Kamel et al., 2018).

One of the main effects of water repellency is the reduction of water infiltration capacity into the soil, increase of surface runoff, reduction of soil and water connection, reduction of soil wettability, nonuniform soil wetting, effect on three-dimensional distribution, and the increase of soil moisture dynamics. Preferential flow, which is one of the other consequences of water repellency, causes the rapid leaching of nutrients in the soil, reduction in plant growth, increase in floods caused by heavy rains, and the intensification of water erosion (Wallis et al., 1990; Karimian et al., 2016). Due to the importance and effects of soil water repellency on plant growth, soil erosion, and the surface hydrological cycle, this issue has received increased attention in recent decades. Wettability is another index of soil water repellency. It is the capability of a liquid to contact a solid surface (or spread over a surface) and is derived from intermolecular forces. The balance between cohesion and adhesion forces determines the degree of wetting. Wetting, in other words, is the tendency to obtain the maximum contact surface for a liquid with a solid surface (Fig. 9). The amount of contact of a drop of liquid with a solid surface is effective in determining the degree of wetting. The closer the contact angle is to 180 degrees, the water repellency increases and the wettability decreases. Therefore, the contact angle that is the angle between a drop of liquid and a solid surface is a quantitative index of the wettability of the solid by the liquid. Contact angles of smaller and larger than 90 degrees indicate that the solid surface is hydrophilic and hydrophobic, respectively. At zero angle, the surface gets completely wet; in other words, the 90-degree angle is the boundary between hydrophilicity and hydrophobicity. The maximum and the minimum contact angles of a droplet with a surface are called as the advancing and receding angles, respectively (Chow, 1998; Jafari Horastani et al., 2022). According to Chow's theory (1998), different liquids are subdivided in terms of contact angle or solid surfaces (Table 2).

The studies that have been conducted so far in relation to the effect of oil pollution on the physical, mechanical, and resistance properties of soils which show that some soil characteristics such as permeability, internal friction angle, Atterberg limits, and other

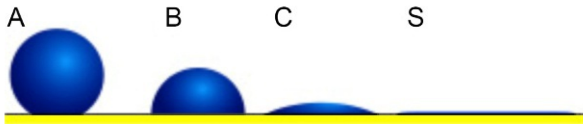

Fig. 9 Wetting ability of different fluids: A and S with a large and a small contact angle show fluids with very little and high wetting ability, respectively.

Table 2 Effect of contact angle on degree of wettability and strength of double interaction (Chow, 1998).

Wettability (after Fig. 9)	Contact angle	Degree of wetting	Interaction strength	
			Solid-liquid	Liquid-liquid
S	$\Theta = 0^{o}$	Perfect wetting	Strong	Weak
C	$0 < \Theta < 90^{o}$	High wetting	Strong	Strong
			Weak	Weak
B	$90^{o} \leq \Theta < 180^{o}$	Low wetting	Weak	Strong
A	$\Theta = 180^{o}$	Nonwetting	Weak	Strong

resistance characteristics of contaminated soils are different from those of the natural soils (Estabragh et al., 2011, 2016). Most of the studies have been related to the effect of soil pollution on soil permeability, which is very important in agriculture and has a very important role and is highly related to other physical and mechanical characteristics of soil (Antony et al., 2016; Moghaddas et al., 2018). Investigators reported that addition of organic pollutants depending on their type would have different impacts on aggregate stability of the soils. Water repellency is a key feature in soil stability, and as the intensity of water repellency increases, the stability of the soil structure increases. This is because of the fact that the hydrophobic layer is like a coating on the soil particles that protects soil particles against the force of water and the wind and can control erosion to some extent by reducing the erodibility of the soil. In terms of the effect of organic matter type on the stability of soil particles, it has also been shown that the presence of aromatic acids in petroleum compounds in the oil-contaminated soils causes soil particles to come together and consequently increase the stability of soil aggregates (Zolfaghari and Hajabbasi, 2008; Besalatpour et al., 2013; Hosseini et al., 2015). In other research works, it has been stated that hydrophobic compounds have caused the formation of clay-humin complexes in the long term and as a result increased the soil stability (Piccolo and Mbagwu, 1999). Also, it was reported that the presence and increase of organic-aromatic pollutants in the soil causes the stability of soil aggregates and then the amount of dispersible clay decreases (Dexter et al., 2008). Daryaee and Moosavi (2022) researched with the aim of investigating the effect of 0%, 1.5%, 3%, and 4.5% kerosene on De Leenheer and De Boodt index (DDI) in clay loam soil found that the application of different levels of this oil material caused a significant decrease in DDI compared to that of control. They concluded that the use of different levels of kerosene in the soil caused a decrease in the stability of the soil structure compared to that of control. Furthermore, in another research, Daryaee et al. (2021b) evaluated the influence of addition of 0%, 1.5%, 3%, and 4.5% levels of crude oil, gasoline, and kerosene on some physical and mechanical properties of different calcareous soils of sandy loam, loamy sand, and clay loam texture classes. They found that application of different levels of oil treatments caused a significant increase in dynamic (water droplet penetration time) and static (soil-water contact angle) water repellency, and the maximum values of both properties were observed in the soils treated by crude oil (except for the dynamic water repellency which was obtained in the gasoline-treated clay loam soils). They also reported that the addition of all oil treatments caused a significant increase in the mean weight (MWD) and geometric mean (GMD) diameter of soil aggregates obtained from the wet and dry sieving methods. Although, the trend of changes in the MWD and GMD in the loamy sand soil in the dry method was not similar to that of the others. The maximum value of the dry MWD and GMD was observed in the gasoline-treated soils, and the maximum wet MWD and GMD were observed in the gasoline-treated clay soils and the crude oil-treated sandy soils (Daryaee et al., 2022a). Furthermore, they found that the effect of applying different levels of oil treatments on the amount of spontaneously and mechanically dispersible clay had relatively the same trends. This means that low levels of the applied oil treatments significantly increased the mentioned properties, whereas higher levels of oil treatments significantly decreased them. The maximum amount of spontaneously dispersible clay was observed in the kerosene-treated clay soils and the gasoline-treated sandy soils; whereas, the maximum amount of mechanically dispersible clay was observed in the kerosene-treated clay loam and loamy sand and the gasoline-treated sandy loam soils (Daryaee et al., 2022b).

7.2 Mechanical properties

Oil pollution penetrates downwards in the soil layers with the help of its own weight. The mobility and dynamics of crude oil and its derivatives in the soil depend on the viscosity of the pollutant, the amount of pollution leakage, and the infiltrability of the contaminated soil. When the oil pollutant penetrates into the soil layers, if the ground water level is low enough, the pollutant moves in the unsaturated soil area before reaching the ground water and absorbs on the soil colloids. Oil pollutants absorbed by soil particles cause changes in the geotechnical characteristics of the soil such as the plastic and liquid limits (Fig. 10) (Rahman et al., 2010; Rajabi and Sharifipour, 2019).

The review of the references showed that, in general, with the increase of natural organic carbon in the soil, the plastic and liquid limits increased, and the plasticity index remained almost constant. In most of the references, it is also reported that this increase is linear in the case of the plastic limit and is nonlinear for the liquid limit (Asadi and Heidari, 2016; Moradi, 2013). In another research, it is mentioned that if the soil has less

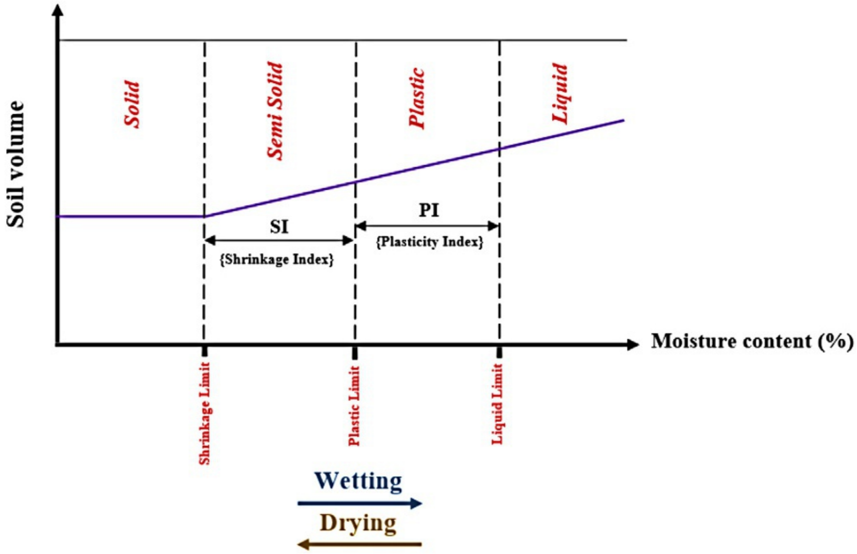

Fig. 10 Atterberg limits and the soil volume changes against moisture changes.

than 10% clay, it shows plastic behavior if it has some organic matter (Keller and Dexter, 2012). In general, different results have been reported for the effect of organic pollutants on the soil's mechanical properties. So far, many studies have been done for evaluating the effects of oil pollution on the resistance and mechanical characteristics of fine- and coarse-textured soils and, in some cases, different results have been obtained. These differences are mainly due to the different reactions that different types of soils show against different types of pollution (Daryaee, 2020). Among the studies conducted for evaluating the effect of oil contamination on the attributes of fine-textured soil, some investigators stated that the Atterberg limits and plasticity index increased (Akinwumi et al., 2014; Adeoye et al., 2015). While in contrast to the other researchers, by conducting experiments on oil-contaminated soils, they concluded that with increasing the level of contamination, the Atterberg limits decrease. In a research related to the effect of gasoline on the plasticity of fine-textured soils, it was found that contamination with this petroleum product caused the decrease in soil plasticity because the pollutant surrounds the clay particles and prevents the effect of water on the clay particles. Some investigators have investigated the effect of oil pollutions on the Atterberg limits and compaction characteristics of soil, but as it was mentioned, their research studies have not reached the same results particularly in the fine-textured soils. For this reason, it is difficult to describe the effect of crude oil pollution on clay soil in a general and comprehensive way, and it needs an extensive comprehensive research (Daryaee, 2020). Some researchers stated that due to the nonpolarity of crude oil molecules and the other petroleum pollutants and the thinning of the thickness of the spread double layer in the presence of these compounds, adding crude oil to the soil causes a decrease in the plastic and liquid limits and the plasticity index of contaminated soils. Roshanghiyas and Bagheri Puor (2019) stated that with increase in the amount of oil pollution, the liquid limit, the plastic limit, and the plasticity index decrease, and this decrease in the plasticity index is far more, and the more clayey the texture of the soil, the lower this amount is. The results of the experiments in relation to the optimal moisture content for compaction (OMCC) and the maximum specific mass of dry soil showed that with increase in the amount of oil pollutants, the OMCC decreases, and the maximum specific mass of dry soil increases. This may contribute to the fact that crude oil is hydrophobic, and it spreads around the soil particles like a membrane and does not allow the water to react with the soil particles. However, with low soil moisture conditions, the friction force between the particles increases and the effect of compression energy on the particles decreases. Therefore, the maximum dry specific mass decreases and the empty space between the particles increases. On the other hand, when water is added to the soil, it acts as a lubricator and causes the soil to become softer and more compressible, and the maximum specific mass of the dry surface of the soil increases (Roshanghiyas and Bagheri Puor, 2019). Furthermore, a research was conducted to investigate the effect of adding different organic pollutants (with a dielectric constant lower than water) such as crude oil, kerosene, gasoline, and other petroleum materials on the shear strength of the soil. Its results showed that the presence of these organic pollutants in the soil has caused the soil particles to stick together and fill the pores, thus reducing the permeability and having a remarkable effect on the shear strength of the soil as an important mechanical property of the soil. Results also indicated that at low levels of the studied pollutants, the shear resistance increases and, as it approaches, the saturated conditions decrease. It should be noted that in most of the references, the change in shear strength has been reported as about 3%, and the drier the soil, the higher the shear strength (Khamehchiyan et al., 2007; Ur-Rehman et al., 2007; Hasanloorad and Khabbazi, 2018; Roshanghiyas and Bagheri Puor, 2019). The results of another research showed that addition of crude oil causes a decrease in permeability and shear resistance in sandy soil (Alsanad et al., 1995). Some investigators also reported that the permeability of some types of soils (clay with high plastic properties, poorly grained sand, and sand with a large amount of silt) decreases due to the addition of crude oil (Khamehchiyan et al., 2007). They also concluded that the effect of this pollutant on the shear strength of sandy and clay soils was different. Researchers also investigated the effect of gasoline and crude oil pollution on the shear strength of sandy soils and showed that by increasing this pollution to 4%, the shear resistance increases and then with a further increase in pollution, the shear strength decreases by 10% (Adeoye et al., 2015; George et al., 2015). A reduction in the shear strength of oil-contaminated soil in unsaturated sandy soil was also reported by Shin and Das (2001). A research was conducted by Daryaee et al. (2021a) to evaluate the impacts of 0%, 1.5%, 3% and 4.5% of crude oil, gasoline, and kerosene on some physical and mechanical properties of texturally different soils. The results revealed that application of different levels of oil treatments resulted in a significant increase in the Atterberg limits, penetration, and shear resistances in both clay loam and sandy loam textures and a significant decrease in the loamy sand texture compared to that of control (Daryaee et al., 2021a). Furthermore, the application of petroleum products led to a significant reduction in OMCC (proctor) in both the clay loam and sandy loam textures; whereas, their application resulted in a significant increase in OMCC of the loamy sand texture. While the studied petroleum materials led to a significant increase in the maximum bulk density (ρb_{max}) of the sandy loam and loamy sand textures compared to that of control, a significant reduction was observed in the OMCC of clay loam texture (Daryaee, 2020).

7.3 Hydraulic properties

Soil water repellency and the formation of water-repellent layers, especially in the surface layers of the soil, cause irreparable damage to the quality of the soils which requires a lot of time and money to correct and improve it (DeBano, 1971). As mentioned, water repellency causes nonuniform distribution of moisture in the soil and nonuniform wetting of soil and creation of preferential flows. It also decreases the infiltration capacity of soil, the continuity of soil water, and soil wetting ability. In turn, water repellency increases the surface runoff, flooding after normal or heavy rains and intensification of erosion (Wallis et al., 1990). A research shows that the adverse consequences of soil water disposal in hydrological and geomorphological fields, where millions of dollars are spent annually all over the world to reduce the risks caused by sudden floods (Imeson et al., 1992). Karimian et al. (2016) reported that with the increase in water repellency due to the blockage and filling of the pores with water-repellent organic materials and the swelling and thickening of the soil particles, the penetration of water into the soil and the hydraulic conductivity decreased significantly. Daryaee (2020) also stated that the presence of inorganic and organic particles in hydrophobic organic materials might cause blockage of soil pores, especially in the surface layers of the soil, which can reduce the amount of water penetration into the soil and hydraulic conductivity of soil. On the other hand, the study of Nieber et al. (2000) showed that the hydrophobic soils treated with octadelcy tricholorosilane solution had more saturated hydraulic conductivity compared to the hydrophilic soils. Furthermore, Noormehanad and Tabatabai (2014) during their research on hydraulic conductivity in hydrophobic soils reported that the lowest hydraulic conductivity was observed in the hydrophobic treatment and the highest was obtained in the treatment with the maximum amount of water repellency. On the other hand, it should be stated that the differences in observations and results obtained from various experiments by different people are not only due to environmental factors and various conditions during the experiments but also due to the duration and passage of time and different reactions between different soils that depend on different types of pollution and organic matter treatments. Micromorphological studies carried out by Asadi and Heidari (2016) to study the particle size and the formation of sand and silt grains have proven this process well that solid oil stains with black to light brown color cause the soil particles to stick together and flatten. This indicates that with increase in petroleum materials, the formation of granular soil aggregates and soil porosity increased (Ratnaweera and Meegoda, 2006). This confirms the increasing trend of soil hydraulic conductivity due to the addition of organic pollutants.

The main direct consequences of water repellency is its impacts on the soil moisture retention curve, SMRC (DeBano, 1981). Soil moisture retention curve is one of its important characteristics, which is used in irrigation, drainage, and erosion (Rezaei and Neyshabouri, 2002). This curve has a special importance in soil physics because it shows the effect of soil texture and structure, porosity, pore size distribution, and surface absorption on soil water retention (Darbandi et al., 2006). Oil pollution is effective on the shape, slope, and coefficients of the curve equations of SMRC (Kamel et al., 2018). It should be noted that the SMRC in low suctions is more influenced by soil structure and in high suctions it is more influenced by soil texture (Sillers et al., 2001). Oil pollution causes water retention. In the oil-contaminated soils, in all textures, due to the reduction of macropores, in low suctions, it decreases and due to the increase of micropores, in high suctions, it increases. Of course, it should be noted that this increase and decrease in water retention are different in the soils of different texture and structure (Kamel et al., 2018). The reason for the increase in water retention in higher suctions is the change in pore size distribution, the decrease in the size of large and medium pores due to their blockage (Kamel et al., 2018). The presence of organic anions as a dispersion agent in crude oil, which has a destructive effect like sodium, and also due to the increase of soil organic matter and carbon, causes a change in the apparent specific mass of the soil (Bachmann and van der Ploeg, 2002; Rawls et al., 2003; Dexter, 2004a, b; Kamel et al., 2018). Following the mentioned changes, the soil moisture at field capacity conditions and the amount of water available to the plant increase due to the expansion of micropores. But it should be noted that although water repellency increases the amount of water available to the plant, the reduction of coarse soil permeability can lead to unfavorable conditions for hydraulic conductivity and plant growth (Kamel et al., 2018). The greatest effect of oil pollution on the shape, slope, and coefficients of the SMRC can be seen at higher levels of pollution and at low suctions, but at higher suctions, the shape of the SMRC becomes closer to each other, and in general, oil pollution has a definite effect on the pore distribution (Kamel et al., 2018). Daryaee (2020) also evaluated the impact of 0%, 1.5%, 3%, and 4.5% levels of crude oil, gasoline, and kerosene on some physical and mechanical properties of different calcareous soils. She stated that application of different levels of oil treatments caused a significant increase in the saturated hydraulic conductivity in the loamy sand and sandy loam textures compared to that of control, whereas with respect to clay loam texture, a significant decrease was obtained. She also found that, in general, the best model for fitting and predicting the SMRC based on the evaluation criteria of coefficient of determination (R^2) and Akaike information criterion (AIC) in 71.30% of cases was the Kosugi model (Eq. 1) (Kosugi, 1999). Therefore, the coefficients of Kosugi's model (Kosugi, 1999) were used to perform statistical analysis. It was found that application of the above-mentioned levels of petroleum materials in the desired petroleum treated soils caused a significant increase in saturated moisture content and the standard deviation of suction distribution and a decrease in residual moisture content and the middle suction of the SMRC compared to the control. She also stated that soil hydraulic characteristics including SMRC are influenced by soil water repellency. This means that with increasing soil water repellency, the amount of water retention in the soil increases, as well as the volume percentage of moisture in a specific suction is more than the hydrophilic soil. Furthermore, the shapes of SMRC are different in the hydrophilic soil and in the soils of different degrees of water repellency.

$$\frac{2(\theta(h)-\theta_r)}{\theta_s-\theta_r} = \operatorname{erfc}\left(\frac{\ln\left(\frac{h}{h_m}\right)}{\sigma\sqrt{2}}\right) \tag{1}$$

where θ_s, θ_r, h_m, and σ are saturated moisture content, residual moisture content, middle suction, and standard deviation of suction distribution, respectively.

Rawls et al. (2003) also stated that soil organic carbon affects soil water retention through changes in apparent specific gravity and soil texture. de Jong (1983) stated that soil organic carbon increases volumetric moisture content in all suctions. Furthermore, Noormehanad and Tabatabai (2014) found that sewage sludge as a hydrophobic organic substance increased the percentage of saturated soil moisture content. Karimian et al. (2016) also reported that the lowest saturated moisture content was related to the non-hydrophobic treatment, which was related to the low organic matter of the treatment. They also pointed out that the amount of residual moisture content increased with increase of soil water repellency. Furthermore, the amount of saturated and residual moisture contents and the difference in the amount of volumetric moisture content in the wet and dry conditions was greater in low suctions, indicating the greater effect of organic matter that protects the large soil pores to change into the small pores. Also, Bauters et al. (2000) stated that the amount of air suction in hydrophilic soils is half of that in hydrophobic soils. Daryaee and Moosavi (2020) studied the hydraulic conductivity and the suction of penetration front of crude oil as the two important physical parameters in the process of absorption of this pollutant and its penetration into the soil in five different types of soil textures including sandy, loamy, sandy loam, loamy sand, and sandy clay. Their results showed that the greater the amount of sand in the soils, the greater the hydraulic conductivity of the soil to transport oil in the soil and the lower the suction of penetration front of the crude oil in the soil. The highest hydraulic conductivity and the lowest suction of the penetration front were observed in the sandy texture, and the lowest hydraulic conductivity and the highest suction of the penetration front were also observed in the sandy clay loam texture. Daryaee and Moosavi (2021) conducted a study to determine soil saturated hydraulic conductivity through different infiltration models (Kostiakov and Philip) and the relation between the flux of oil entering the soil and the inverse of the depth of the wetting front in soils of different textures including loamy sand, sandy clay loam, and sandy clay. They found that the highest value of hydraulic conductivity was observed in the sandy loam soil and the lowest value was observed in sandy clay loam soil. Furthermore, in all three soils, the highest value of the estimated hydraulic conductivity was obtained using the Kostiakov's equation. On the other hand, a lot of similarity was observed between the results of Philip's equation and the relationship between the flux and the inverse of the wetting front depth in all of the studied soils.

7.4 Chemical properties

Mineral compounds, organic materials, and environmental factors (Fig. 11) affect soil chemistry, followed by soil chemical properties. Petroleum substances themselves are a type and part of organic substances. The origin of crude oil is actually the organic substances obtained from the remains of living plants and animals, which have been accumulated over thousands of years in the layers of the earth and are converted into crude oil

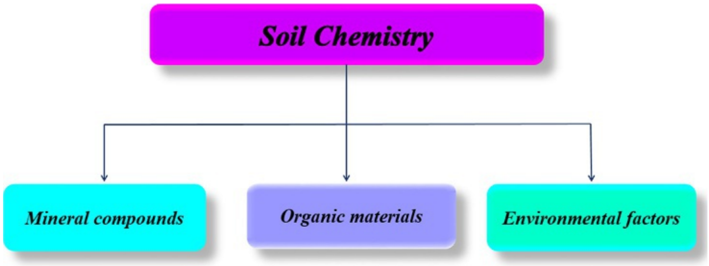

Fig. 11 Factors affecting soil chemistry and chemical properties.

under pressure and heat. In other words, during a series of reactions of bacterial decomposition and corruption, condensation, and polymerization, organic materials turn into a very thick hydrocarbon material called Kerogen, which is the primary material in the structure of crude oil (Rezaee, 2011).

Researches have shown that the increase in oil pollution resulted in a remarkable decrease in soil agricultural capacity, salinity, concentrations of potassium, sodium, magnesium, and calcium. Whereas, oil pollution increased nitrogen and organic matter due to the nature of the polluting compounds, which are a source of carbon and nitrogen and will increase these elements in the soil (Shahrezaei and Hajabbasi, 2019). Among the chemical changes, due to the contamination of soil by petroleum materials, it was reported that soil organic matter, cadmium pollution, apparent density (Onweremadu and Duruigbo, 2007), electrical conductivity (Ayotamuno et al., 2006; Besalatpour et al., 2008), and sulfides (Udo and Fayemi, 1975) increased. Whereas, the total nitrogen and nitrate (Mathew and Obbard, 2001; Weigand et al., 2001; Agbogidi et al., 2007), available phosphorus and soil pH (Mathew and Obbard, 2001; Weigand et al., 2001; Achuba and Peretiemo-Clarke, 2008; Bona et al., 2011) decreased. Shukry et al. (2013) stated that increasing the level of applied crude oil, MDA compounds, or unsaturated fatty acids in jojoba plant leaves decreased the concentration of sodium, magnesium, and calcium elements in the shoot and increased potassium concentration in the shoot. They also reported that in the roots, the amount of calcium and sodium increased, but the amount of potassium and magnesium decreased. In addition, with the increase in the concentration of crude oil, the amount of heavy metals such as copper, manganese, lead, and cadmium in the aerial and root organs and the concentration of iron in the shoot of jojoba plant increased. In the mentioned study, a decrease in copper in the soil after harvesting was also found following an increase in the level of contamination. An increase in the concentration of potassium in bean plants cultivated in soil contaminated with petroleum materials has also been observed with increasing pollution (Lale et al., 2014). The creation of unfavorable conditions for plant growth follows the increase in the concentration of crude oil due to the decrease in the level of nutrients or the increase in the concentration of some elements such as iron to the toxic concentration (Udo and Fayemi, 1975; Mansoorpoor, 2015). Ogbuehi et al. (2011) and Essiett et al. (2011) also concluded that increasing the level of engine oil and crude oil caused an increase in the concentration of zinc in the plant. Other investigators reported that reduction of nitrogen concentration in the plant by adding petroleum derivatives to the soil is due to: (1) increase in soil carbon compared to nitrogen; (2) reduction of ammonia and nitrification processes in the soil; (3) growth of fungi and bacteria population; and (4) reduction of available nitrogen for the plant (Iwanow et al., 1994; Amadi et al., 1996; Rimovsky et al., 1998; Mansoorpoor, 2015).

7.5 Biological properties

7.5.1 Biological activity and functional diversity

There are various types of living organisms in the soil environment (Fig. 12). Petroleum hydrocarbons have very low concentrations of mineral compounds. As a result, when

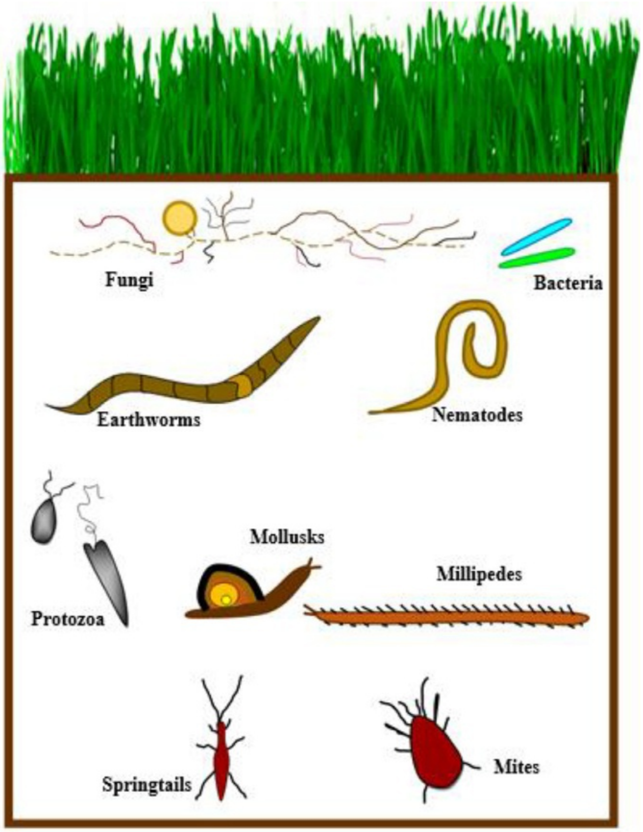

Fig. 12 Schematic view of soil living organisms (www.terrabiotec.com).

they enter the soil, the ratio of carbon to nitrogen (C/N) and carbon to phosphorus (C/P) increases to a certain extent. As a result, the growth of microorganisms is limited in these conditions. Regulating and adjusting the C/N ratio and C/P ratio depends on the form of boosters such as urea, ammonium sulfate, potassium hydrogen phosphate, etc., which stimulate and increase the biological decomposition of crude oil and other specific hydrocarbons (Dibble and Bartha, 1979).

7.5.2 Microbial population and species diversity

Kerosene pollution has remarkable effects on the microbial population of the soil ecosystem that is important in terms of designing biodegradation strategies in the polluted areas. Nseabasi and Antai (2012) investigated the effect of kerosene pollution in four fields cultivated with different plants in Nigeria. Their results showed that oil pollution has a decreasing effect on the quantity of heterotrophic bacteria and an increasing effect on the quantity of decomposing bacteria. The interpretation of these researchers regarding these results was that the stress of kerosene on the soil microbial population leads to the selection of bacterial groups that are able to use kerosene as a carbon source, and therefore, the sensitive heterotrophic bacterial population is destroyed. As a result, the decomposing bacteria overcome the entire microbial population. Xu and Obbard (2003) conducted a series of simulated laboratory studies with desert soil samples contaminated with kerosene in China for a period of 180 days. They concluded that with the increase of the soil incubation period, the microbial, enzyme, and decomposition indicators in the soil showed a significant increase. They attributed this increase to the adaptation of the microbial community to oil pollution over time. Keshavarz et al. (2019) stated that with increase of oil levels, the mean microbial respiration increased. Labud et al. (2007) also reported that contrary to the idea that the toxicity of petroleum compounds reduces the activity of microorganisms, observations showed that the increase of petroleum compounds in the soil increased the microbial respiration. Another investigator showed that due to hydrophobicity of petroleum compounds, drought stress is created around the roots (Merkl et al., 2005). Pezeshki et al. (2000) concluded that in the oil-contaminated soils, due to the presence of a layer of oil that covers the surface of the soil, the flow of oxygen into the soil is limited, which in turn causes anaerobic conditions for the roots. Furthermore, Kiarostami et al. (2014) showed that oil pollution increased the population of soil anaerobic microbes around the sunflower and corn root systems.

8 Effects of oil pollution on plant growth and yield

Crude oil creates unfavorable conditions for plant growth (Omosun et al., 2008). Oil pollutants usually reduce the efficiency of plant growth and development, especially in the early stages of growth (Al-Yemeni et al., 2010). Planting in soils contaminated with petroleum materials faces limitations because plants grown in the oil-contaminated soils usually face a combination of drought stress, lack of nutrients, and chemical toxicity (Gerhardt et al., 2009). Oil is a physical barrier that prevents the entry of water and oxygen into the soil and plant and then causes stress in the plant (Ogbo et al., 2010). Plants suffer damages as a result of oil pollution, including chlorosis, necrosis, reduced growth, and disturbances in growth parameters (Almansoory et al., 2015). In oil-contaminated soils, the leaves turn red and the stems turn almost yellow and brown (Agamuthu et al., 2010; Almansoory et al., 2015). The yellowing of plants may be due to chemical stress in tissue and cell surfaces (Meudec et al., 2007). One of the first symptoms of poisoning caused by crude oil hydrocarbons on plants is the growth reduction (Chaineau et al., 1997). A decrease in biomass production and plant growth occurs in the oil-contaminated soil (Adam and Duncan, 2002). This decrease may be a result of the inherent toxicity of petroleum materials (Cheema et al., 2010). In the soils contaminated with oil, a decrease in germination, yield, and number of plant leaves has been observed (Minoui et al., 2015). Regarding the reduction of germination percentage in oil-polluted soils, Adam and Duncan (2002) reported that the germination rate decreases even in low concentrations of pollution. The volatile part of oil plays an important role in delaying seed germination and reducing the germination percentage. Also, the remaining oil in the soil causes a more negative effect because it physically prevents the transfer of oxygen and water between the seeds and the surrounding environment and causes disruption in germination (Adam and Duncan, 2002). Similar results were reported by Kiarostami et al. (2014) such that the germination and yield of corn decreased by 50% and 92%, respectively, in 2% and 4% crude oil pollution conditions. The significant decrease in the growth of corn can be related to the immobility and less availability of nitrogen and phosphorus or the toxicity of iron and manganese in the soil. Of course, the presence of oil in the soil can have a different effect than what has been stated so far. For example, in some cases, it has been reported that with degradation of the petroleum hydrocarbons in the soil, organic materials are produced and the growth of plants may increase due to increase in organic matter that supplies nutrients to the plant and improves the physical conditions of the soil (Udo and Fayemi, 1975).

The absorption of toxic oil molecules in the contaminated soils can change the structure and permeability of the plasma membrane, in such a way that some oil compounds dissolve the membrane and as a result disrupt the root function and plant mechanism (Penã-Castro et al., 2006). Due to its direct connection with the soil, the roots of plants are most affected by the environment and soil content, and in the presence of any type of unfavorable conditions, such as salinity, drought, waterlogged conditions, and the presence of pollutants and toxins in the soil, the roots are the most accessible part of the plant for damage. The response of plant roots in dealing with toxins or pollutants in the contaminated soils includes their removal, decomposition, and inactivation (Kiarostami et al., 2014). Increased oil pollution in the soil resulted in a significant decrease in the function of the plant's aerial organs and decreased the fresh and dry weight and also the length of aerial organs, which is probably caused by the toxicity of the petroleum hydrocarbon compounds (Shahrezaei and Hajabbasi, 2019). One of the first signs of plant poisoning in oil-contaminated soils is the growth inhibition and then growth reduction. The hydrophobic property of petroleum compounds changes the behavior of the soil and causes heterogeneity of water distribution in the soil. This problem causes a water shortage in the soil and creates dry conditions in it, and the ability of plants to access water and food is reduced (Bengough, 2003). As a result, plant growth and production are reduced. The reduction of plant growth, especially the roots, has been reported in the studies of some researchers (Merkl et al., 2004). On the other hand, an increase in the oil pollution causes an increase in the root length. While, in relation to the fresh and dry weight, as in aerial organs, an increase in oil pollution of the soil causes a decrease in the two mentioned parameters (Shahrezaei and Hajabbasi, 2019), and it seems that the root gets out of the contaminated environment by increasing its length. In this connection, Merkl et al. (2004) reported that in soils contaminated with crude oil, the root growth of tropical plants of *Centrosema brasilianum* and *Calopogonium mucunoides* increased as compared to their stem. They found that this issue is a kind of defense response and the plant's strategy in facing the lack of access to nutrients in the contaminated soil since increasing root growth increases soil nitrogen absorption (Marschner, 1995). Therefore, increasing the length of plant roots in order to provide water and nutrients is one of the mechanisms of plants against some stresses such as oil pollution. Contamination of 7.5% of crude oil with Bermuda grass also caused a significant decrease of 31%–33% of biomass at different levels of nutrient treatments (Basumatary and Bordoloi, 2016). This yield reduction may be due to the toxicity of petroleum products (Cheema et al., 2010). It also has been reported that, with increasing contamination, the average percentage of root colonization decreases significantly (Keshavarz et al., 2019). Some researchers reported that the reduction of root colonization is a strategy to limit the additional absorption of contamination through fungal roots (Hovsepyan and Greipsson, 2004). Udo and Fayemi (1975) observed visible symptoms of toxicity including yellowing of leaves, loss of plant water, stunted growth, and death of maize seedlings when the soil was contaminated with 0%–10.6% of oil. The range of changes varies with the difference in the type and concentration of the pollutant compounds and also depending on the plant species. In general, various plant species have different strategies against pollutants due to their different morphological and physiological characteristics.

Barrutia et al. (2011) showed that after 2 months of growth in soil contaminated with petroleum materials, the number of photosynthetic pigments (chlorophyll and carotenoid) of white clover plant decreased significantly. But in the case of *Lolium* plant, no significant difference was seen between the plants grown in the contaminated and noncontaminated soils in this regard. In the study of the biochemical and physiological responses of rice plants to two hydrocarbons, phenanthrene and pyrene, Li et al. (2008) observed that the high level of pollution resulted in a 29% decrease in chlorophyll content. Also, Saraeian et al. (2015) concluded that chlorophyll of the control plants and the plants grown on oil sludge-treated soil were not significantly different. But they reported that with the increase in soil pollution, the amount of plant chlorophyll decreased significantly, i.e., the amount of total chlorophyll in the plants grown on the oil sludge-treated soils was 26%–37% lower than that of the control. Proline can be considered as a nonenzymatic antioxidant that causes free oxygen radicals.

Proline, like a strong antioxidant, has the ability to prevent cell death against environmental stress (Chen and Dickman, 2005). Proline accumulation in plants under stress is related to the reduction of damage in cell membranes and proteins. Proline synthesis is involved in reducing the cytoplasmic osmotic potential and maintaining the NADP/NADPH+ ratio. In addition, proline acts as an osmolyte, scavenger of radicals, stabilizer of macromolecules, and a part of the cell wall. The importance of proline accumulation in maintaining the water status of the plant is greater than the importance of other organic materials. In other words, proline acts as the most common osmolyte accumulated in stress conditions. As a chemical protector, proline stabilizes the natural form of proteins and prevents the natural form of enzyme compounds from collapsing, and it is a metal chelator, prevents lipid peroxidation, and preserves membrane integrity (Hayat et al., 2012). It has been reported that with the increase in the amount of oil in the soil, the amount of proline in the plant increased significantly i.e.,the amount of proline in the plants grown in the treatment of 40% and 80% sludge was two and three times that of the control, respectively (Saraeian et al., 2015). Furthermore, it has been reported that bean plants grown in soil contaminated with hydrocarbons accumulated high amounts of proline (Malallah et al., 1996).

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CHAPTER 14

Insights into economically important endophytic and rhizospheric bacteria of true mangroves of Indian Sundarbans using high throughput mapping

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1 Introduction

1.1 Indian Sundarbans

The Sundarbans are bestowed with the honor of being designated as the world's largest contiguous mangrove in addition to being a Ramsar site as on February 1, 2019. The total geographical area coverage of the mangroves spans over 20,400 km^2, and in 1987, it was classified as a UNESCO World Heritage Site. The nomenclature of the ecoregion is possibly derived from the mangrove *Heritiera fomes* (Vernacular: Sundari) that dominates the mangrove landscape (Bera et al., 2022). The Indian Sundarbans are a key biodiversity hotspot that constitute a very important premise for the genesis of a substantially productive and biologically enriched ecosystem, which forms a shelter and a feeding ground for a broad variety of species including one-third of the global number of mangrove tree species with more than 200 additional species of plants, 400 fish species, 300 avian species, 35 types of reptilians, and 42 mammalian species. It also consists of innumerable benthic invertebrates, bacteria, fungi, etc. (Duraiappah et al., 2005; Donato et al., 2011; Carugati et al., 2018; Gopal and Chauhan, 2006; Choudhury et al., 2001). The Sundarbans hold a string of deltaic chains with conglomeration of several fragmented islands, a portion of which stretches into Bangladesh, extending over Khulna Division over an area of 6017 km^2 (Bera et al., 2022). The mangroves assume a critical role in worldwide climate regulation, sequestering approximately 1000 tons of carbon per hectare, thus being one of the most carbon-rich ecosystems worldwide. Indian Sundarbans also exert a buffering effect against frequent tropical cyclones, tsunamis, and storms that would otherwise extend their rampage to the urban peripheries. They provide an essential array of goods and services, e.g., acting as an exemplary source of seafood, preliminarily based on shrimp cultivation, for both subsistence and consumption via national and global seafood trade

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and yielding commercially valuable products such as firewood and timber, making a significant contribution to the way of life and security of the indigenous coastal communities. The Sundarbans aid in controlling wave energy, limiting shore degradation, and retention of terrestrial deposits and recycling nutrients, thus supporting clear offshore waters. This essentially enhances the degree of photosynthesis among the phytoplankton. It also augments the robust nature and growing capacity of reef fish communities, coral reefs, and seagrass beds (Bochove et al., 2014; Ghosh et al., 2015; Chaudhuri et al., 2019).

1.2 Genesis of saline stress and its implications in the ecosystem

There are several reasons currently plaguing the very sustenance of this substantially dynamic ecosystem, and innumerable factors are responsible for the significant degradation of the coastline biosphere in the recent past including overexploitation of local resources due to a dearth of sufficient alternative supplementary livelihoods, climate change, elevation of surface water temperature, rise in sea level, and shore erosion. Due to the rising sea level and withdrawal of freshwater supply, the distorted soil salinity level is another emerging factor severely impacting the indigenous flora and fauna as well as the natural vegetation often accompanied by habitat loss and thus deteriorating, if not obliterating, the chances of having a sustained livelihood for the local inhabitants.

A plethora of factors cumulatively contribute to the disturbed zonation of differential salinity profiles throughout the Sundarbans, which in turn adversely impacts the native flora and fauna in the Indian Sundarbans (Goodbred and Kuehl, 2000; Hanebuth et al., 2013; Syvitski et al., 2009). Ecological factors like tectonic upliftment of the Bengal basin, subsidence by sediment compaction, varying freshwater inputs, oscillating pre- and post-monsoon rainfall, intermittent cyclones, funicular movement of saline groundwater, and human interferences such as unchecked urbanization, damming on the lower Gangetic plane, urban sewage and industrial waste disposal without adequate treatment leads to modification of hydrological balance, and nutrient dynamics (Stanley and Hait, 2000; Mitra et al., 2009; Zaman et al., 2014; Ghosh et al., 2015; Nath et al., 2021). The eastern and western parts of the deltaic chain are hyposaline due to the availability of meltwater inputs derived from Bidyadhari, Matla, or Hariabhanga rivers streaming from the Himalayas whereas the central portion is deprived of and disconnected from such inflowing freshwater dilution, leading to hypersalinity of the Matla river, which is further detached from the Bidyadhari and Ganga-Bhagirathi-Hooghly river system due to increased siltation and clogging (Mitra, 2019). All these factors cumulatively lead to an inconducive environmental condition for the continued persistence of the native mangroves. These also lead to an unfavorable and suboptimal environment for maintaining agricultural practices, which strong-arms the farmers to adopt cultivation of high-yielding varieties of crops, postgreen revolution, which in turn necessitates supplementary inputs of nitrogenous fertilizers and organophosphate pesticides and herbicides (Nath et al., 2021).

Agricultural run-off from such products often accumulates in the low-lying watershed, drainage basin, and mudflat areas of the biosphere reserve, thus reinforcing the vicious cycle perturbing the soil salinity profiles.

Mangroves, like any other terrestrial plants, are heavily dependent upon synergistic associations with microbial communities, which translate into mutually beneficial interactions. In such communities, the bacteria can be primarily classified according to their mode of occurrence into three basic categories: epiphytic, rhizospheric, and endophytic (Afzal et al., 2019).

1.3 Rhizosphere

Bacterial communities of immense diversity are supported by the soil (Turner et al., 2013; Weinert et al., 2011). The constitution of communities of soil microbes is greatly influenced by multiple abiotic factors, including the pH of the soil, with existing literature validating the fact that Acidobacteria dominate under conditions that are acidic, whereas Proteobacteria, Actinobacteria, and Firmicutes predominate in alkaline or neutral soils (Turner et al., 2013; Griffiths et al., 2011). There is a strong influence of plants on rhizosphere microbiota (Turner et al., 2013; Tkacz et al., 2015; Lundberg et al., 2012; Bulgarelli et al., 2012), which is substantially different from that of bulk soil. The total diversity of the microbes in the rhizospheric region is generally less than that in soil, which may be attributed to the high selectivity exercised by the plants in this region (Turner et al., 2013; Tkacz et al., 2015) and is evident, particularly in the endosphere and the rhizoplane. The existence of strain-specific selection between *Arabidopsis thaliana* and *Pseudomonas* in the microbiota associated with the former's root system suggests that there is partial control of the selection of microorganisms, which will colonize the rhizosphere by plant genes (Haney et al., 2015). In a similar fashion, repetitive phytocultivation in the same exact soil can lead to formation of a suppressive soil in which excessive amount of microbiota suppresses pathogenic growth (Mendes et al., 2011); for instance, through the increased microbial abundance of peptide antibiotics producing *Gammaproteobacteria* (Mendes et al., 2011). Leguminous plants like *Medicago truncatula*, pea, cereals like barley, and *Lotus japonicus* also exert strong effects on rhizosphere (Turner et al., 2013; Tkacz et al., 2015; Zgadzaj et al., 2016; Bulgarelli et al., 2015), and stringent selections of the microbes is usually found in the root-associated microbiota.

1.4 Endosphere and endophytes

A range of biochemical compounds like oligopeptides, polysaccharides, vitamins, nucleic acids including purines and pyrimidines, enzymes, different macronutrients and micronutrients, mucilage, free oxygen, and water present in the root exudates serve to establish a chemotactic gradient for migration and settlement of a potential endophytic population. These chemical elicitors have an apparent discriminatory power to selectively encourage the propagation and thus colonization of a certain microbial population while suppressing the others, especially under unfavorable conditions such as nutrient deficiency (Bais et al., 2006). This phenomenon is termed rhizoengineering (Jha et al., 2014). For instance, organic acids' secretion may drastically lower the soil pH while mucilage-derived nutrients attract a large and diverse population of beneficial microbes thus playing an instrumental role in shaping the rhizospheric and finally the endophytic microbiome (Kloepper, 1992; Dakora and Phillips, 1996). Competitive efficiency of the beneficial microbes contributes equally to establishing a substantial rhizospheric population and augment their endophytic colonization potential, e.g., some bacteria produce secondary metabolites (including antibiotics), which provide them with an upper-hand in such an environment enabling them to establish their rhizocompetence (Duffy and Defago, 1999; Slininger and Shea-Wilbur, 1995; Walker et al., 2003).

Populations of beneficial plant growth promoting bacteria often undertake one- or two-component signaling pathways to reciprocate the plant signals such as the GacS/GacA-regulatory system, which is absolutely critical and necessary for the synthesis of enzymes, which are extracellular in nature and secondary metabolites for enhancing colonization efficiency (Heeb and Haas, 2001). Other two-component systems reported in similar functions include the ColR/ColS apparatus, which regulates the methyltransferase/WapQ operon in *Pseudomonas fluorescens* (De Weert et al., 2006).

Endophytes can be defined as microorganisms, which could inhabit the internal plant organs and tissues both intra- and intercellularly, including all the aerial, subaerial, and underground parts, either transiently or permanently without eliciting any apparent pathogenicity and developing a mutualistic association with their host (Liu et al., 2017; Compant et al., 2021). Endophytic bacteria can afford to share a close proximity due to their residence within the plant host and thereby directly deploy their advantageous effects such as improving nutrient acquisition from soil, thus promoting host plant growth, and aiding the host in biotic and abiotic stress tolerance via synthesis of antioxidants along with other important metabolites for countering the detrimental effects of the stressors. Cross-talk between the plethora of signaling pathways of plant-endophyte interactions further aids in mediating allelopathic effects against a diverse range of competitive plant species, as studied in case of perennial ryegrass hosting endophytic strains of *Neotyphodium lolii,* which suppress the growth of white clover (Sutherland et al., 1999). In exchange, the endophytic communities receive a consistent supply of nutrients and a guarded conservatory niche unperturbed by the oscillating ecological circumstances that can otherwise affect the rhizospheric and epiphytic microbial consortia (Liu et al., 2017; Afzal et al., 2019).

1.5 High-throughput technologies

A specific region of DNA in the microbial population is utilized as a marker for phylogenetic and diversity mapping of constituent microbes in metabarcoding approaches (Kwei et al., 2011; Groendahl et al., 2017). For prokaryotic DNA, the most commonly used molecular marker is the small subunit (SSU) ribosomal RNA gene 16S (Franzen et al., 2015; Preetha et al., 2012), which is perhaps the most widely used in the study of microbiome diversities across studies ranging from the clinical laboratory to field settings (Jovel et al., 2016; Godoy-Vitorino et al., 2018; Perkerson et al., 2010; Scheldeman et al., 1999; Burgess et al., 2017; Cheneby et al., 2000). Based on target amplification of the V3 and V4 regions, 16S sequencing has found wide usage in the taxonomy-based characterization of microbiomes across different ecosystems and environmental conditions (Jovel et al., 2016; Godoy-Vitorino et al., 2018; Perkerson et al., 2010; Scheldeman et al., 1999). In the instance of bioprospecting of bacterial candidates, metabarcoding using 16S rRNA has been employed with success in the identification of *Nostoc* spp., *Arthrospira* spp., *Geobacillus* spp., and *Streptomyces* spp. (Cheneby et al., 2000; Alanagreh et al., 2017; Lafontaine and Tollervey, 2001), to name a few.

Thus, metabarcoding offers a holistic, overarching view of community structure, diversity, constituent members, and taxonomic positions of myriad organisms between and within ecosystems (Preetha et al., 2012; Monard et al., 2013). Using metabarcoding eases the characterization and identification of bacterial consortia with potential for prospective bioproducts in a cursory glance that is preliminary in nature.

Even though metabarcoding is fast and its cost-effectiveness champions its usage, it is crippled considerably by the limited resolution it offers and can hardly be utilized to discriminate between closely related strains or species. These challenges stem from its polymerase chain reaction (PCR)-based short read sequencing associated with guanine-cytosine (GC) content bias and the errors that creep into operational taxonomic units (OTUs) assignment (Carruthers et al., 2018). Although some improvement has been made in picking of OTUs, metabarcoding is relatively limited to the level of genera (Preetha et al., 2012; Walter et al., 2017; Nolla-Ardevol et al., 2015; Krohn-Molt et al., 2013). Metabarcoding fails to establish the involvement of individual microbes at the molecular level in the ecosystem as it targets only a single section of metagenome, leading to several genes remaining untapped; hence, their structural and functional roles in the microbial community remain unearthed. Taking into consideration the complexity of communities of bacterial members, methods with broader coverage are essential for a comprehensive description of the complex communities toward elucidation of the existence of novel drugs and bioprospecting.

2 Data acquisition and analysis

2.1 Sample collection

The maximum population density of the Mangroves under study at specific sites (shown in Fig. 1) was used as a determinative factor for the choice of sampling site. Three plants with robust growth patterns were identified within the community, which were at least 2 m apart from one another. Rhizospheric soil samples and the roots of the plant specimens were collected from a depth considered appropriate beneath the base of the muddy

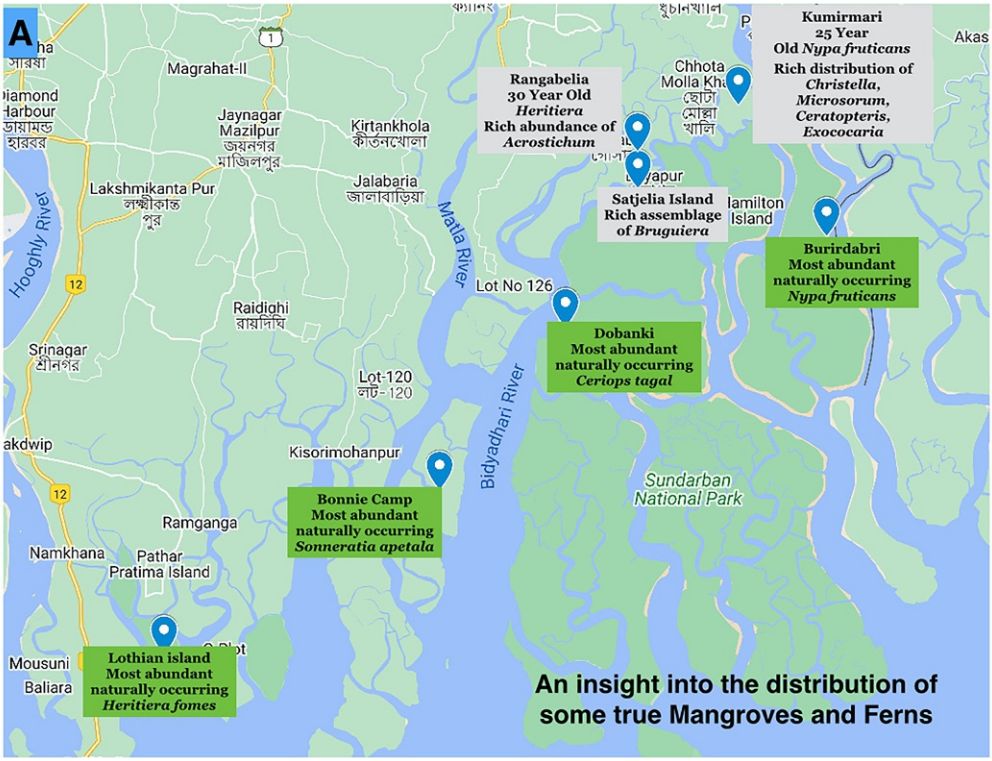

Fig. 1 An insight into the distribution of some true mangroves and ferns in the Indian Sundarbans. The map indicates a few sites with a rich distribution of naturally occurring mangroves and the most abundant ones are listed under the indicated site.

swamp that is less susceptible to the semidiurnal inundation of tides. The respective samples were then pooled to obtain the rhizospheric and endophytic assemblages. Sample collection was performed by wearing protective gear including mask on the face and gloves on the hands to reduce any remote chance of contamination during the collection procedure of the samples. The soil and root samples were secured in sterile zip-lock packets and kept inside an icebox at 4°C to preserve them against any decay or loss of biological sterility.

2.2 Sample preparation

For the Illumina sequencing pipeline, genomic DNA was isolated from the rhizosphere as well as homogenized root samples, utilizing an in-house protocol that has been duly standardized. DNA quality was quantified using QUBIT, while its quantity was assessed on an agarose gel with the final assessment being done by Nanodrop. The preparation of the library was performed using the V3–V4 regions of the 16S rRNA library, a protocol standardized by Illumina. The library was then quantified and validated using quantitative PCR and Agilent Bioanalyzer (DNA 1000 chip). The generated library, consisting of V3–V4 amplicons, was finally sequenced on the Illumina MiSeq using 300 × 2 PE chemistry.

For the Nanopore sequencing pipeline, samples were thawed first, and then DNA was isolated using NUCLEObond AXG20 (Machery—Nagel), and the concentration of DNA was measured using the Qubit 3.0 DNA broad range kit (Thermo Fisher). Following this, the standard protocols (Jain et al., 2015) for Barcoding, adaptor ligation, clean-up, and library preparation, and sequencing were performed using the Sequencing kit (Oxford Nanopore Technologies, SQK-LSK 109) and computational analysis was performed using the protocol described in (Das et al., 2020).

2.3 Bioinformatic analyses

The FASTQC toolkit (http://www.bioinformatics.babraham.ac.uk/projects/fastqc) was employed to perform the quality control (QC) of the obtained raw reads. After QC processing, paired end reads were clustered into operational taxonomic units (OTUs) by using the QIIME2 (Quantitative Insights into Microbial Ecology) software (http://qiime2.org/) (Bolyen et al., 2019) to identify the constituent members of the microbial community under scrutiny. The reads that passed QC validation were uploaded to the MetaG server (http://www.bioinformatics.uni-muenster.de/tools/metag/index.hbi?) for analysis to classify abundant bacteria to Genus-level. The obtained Genus-level abundance data of the rhizosphere bacterial communities of *Excoecaria agallocha* Linn., *Heritiera fomes* Buch.-Ham., *Ceriops tagal* (Perr.) C.B.Rob, and *Nypa fruticans* Wurmb. and endophytic communities of *Heritiera fomes* Buch.-Ham., *C. tagal* (Perr.) C.B.Rob, and *N. fruticans* Wurmb., were compared using Venny v2.1.0 (https://bioinfogp.cnb.csic.es/tools/venny/) to identify species-specific and core rhizospheric and endophytic bacterial assemblages. The top five most abundant bacteria at each of the sampling sites are shown in Fig. 2. Finally, the obtained core rhizospheric bacterial assemblage and the core endophytic bacterial assemblages were compared using Venny v2.1.0 to obtain the core set, shown in Fig. 3. The relative abundances of the members constituting the core set across the analyzed plants have been used to generate a heatmap using the web-based tool, Morpheus (https://software.broadinstitute.org/morpheus), shown in Fig. 4.

3 Insights into the potential functions and roles of abundant bacterial members

Typically, metagenomic-based high-throughput data analysis focuses solely on the elucidation of the taxonomy abundance, but the use of artificial intelligence methods and enrichment analysis has enabled us to predict the roles of the important members that are harbored by the plants in the their rhizospheric and endophytic niches. The box plots

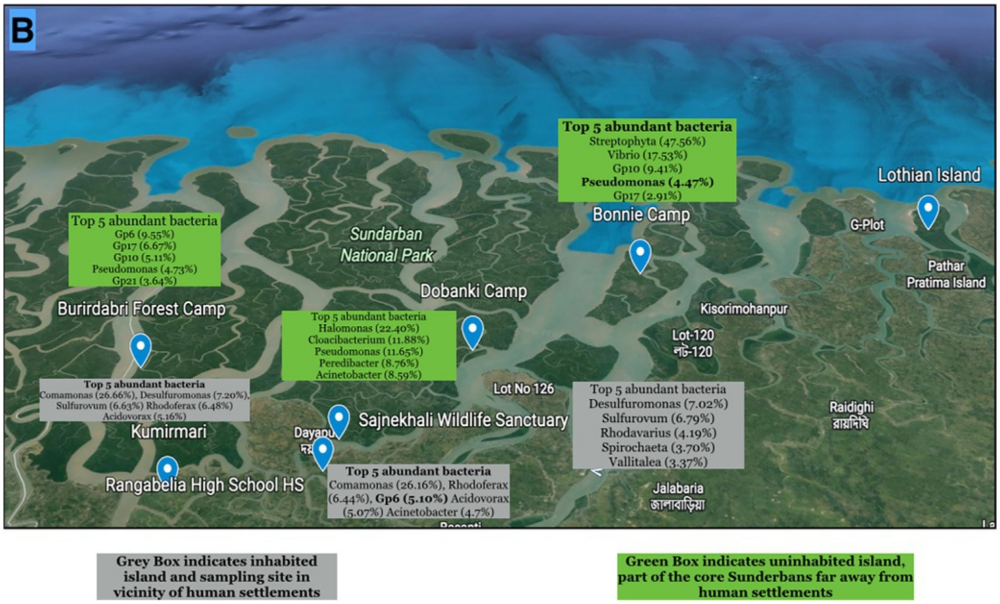

Fig. 2 The top five most abundant bacterial genera across both rhizospheric and endophytic bacterial assemblages at each of the sampling sites. The value in brackets indicates relative percentage abundance of the indicated bacterial genus.

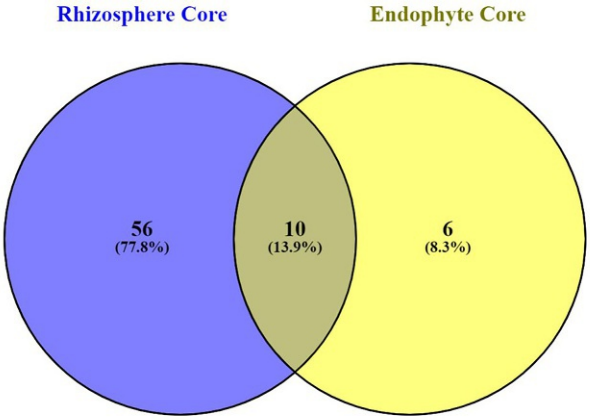

Fig. 3 Venn analysis between rhizospheric and endophytic bacterial core assemblages. 56 bacterial genera are unique to the rhizospheric core, 6 bacterial genera are unique to the endophytic core, and 10 bacterial genera are common across both datasets, which is being considered as core set.

shown in Fig. 5 depict the relative contribution of rhizospheric and endophytic samples to the top functions in terms of abundance, while Fig. 6 shows the comparative heatmap of core predicted functional pathways across the analyzed samples. This section shall throw light on the most abundant and beneficial bacteria that we have been able to unearth from the niches.

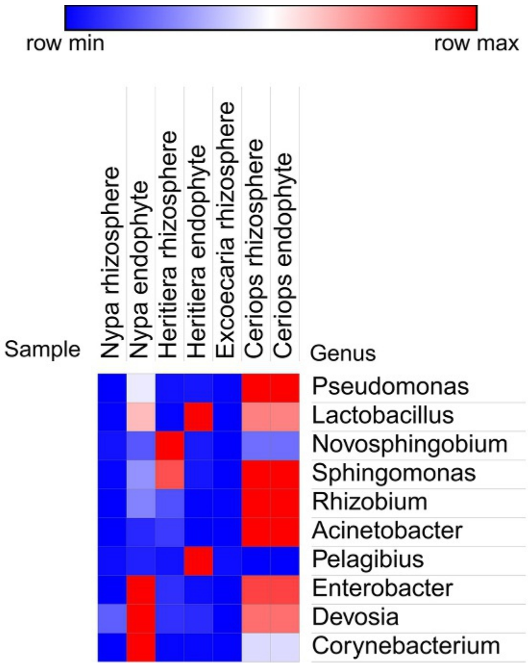

Fig. 4 Heatmap of relative abundances of genera constituting the core set across all analyzed rhizospheric and endophytic samples.

3.1 Acinetobacter

Acinetobacter members have been garnering increasing attention from the scientific fraternity in recent years for their potential to act as causative agents of nosocomial infections of varying severity (Bergogne-Berezin and Towner, 1996; Knapp et al., 2006; Winn and Koneman, 2006; Peleg et al., 2008; Towner, 2006; Vanbroekhoven et al., 2004; Weinstein, 1998). In addition, their proficiency in developing extreme (XDR) and multidrug drug resistance (MDR) (Bergogne-Berezin, 1995; Jain and Danziger, 2004; Peleg et al., 2007; Prashanth and Badrinath, 2005), their ability to produce verotoxins (VA) (Grupper et al., 2007), and their role in enhanced removal of biological phosphorus from wastewater (Carr et al., 2001; Ghigliazza et al., 1998; Nicholls and Osborn, 1979) add to the scientific interest. Studies have shown that *Acinetobacter* is capable of being utilized as a potential hydrocarbon bioremediation agent (Mandri and Lin, 2007; Margesin et al., 2003; Zanaroli et al., 2010; Reyes-Sosa et al., 2018) and *Acinetobacter baylyi* ADP1 has exhibited significant competence for natural transformation independent of the origin of DNA, thereby granting it a potential to be an important tool in biotechnological applications (Barbe et al., 2004; Chen et al., 2008; Vallenet et al., 2008; Vanbroekhoven et al., 2004). The possible applications of *Acinetobacter* in biologically important functions are summarized in (Doughari et al., 2011).

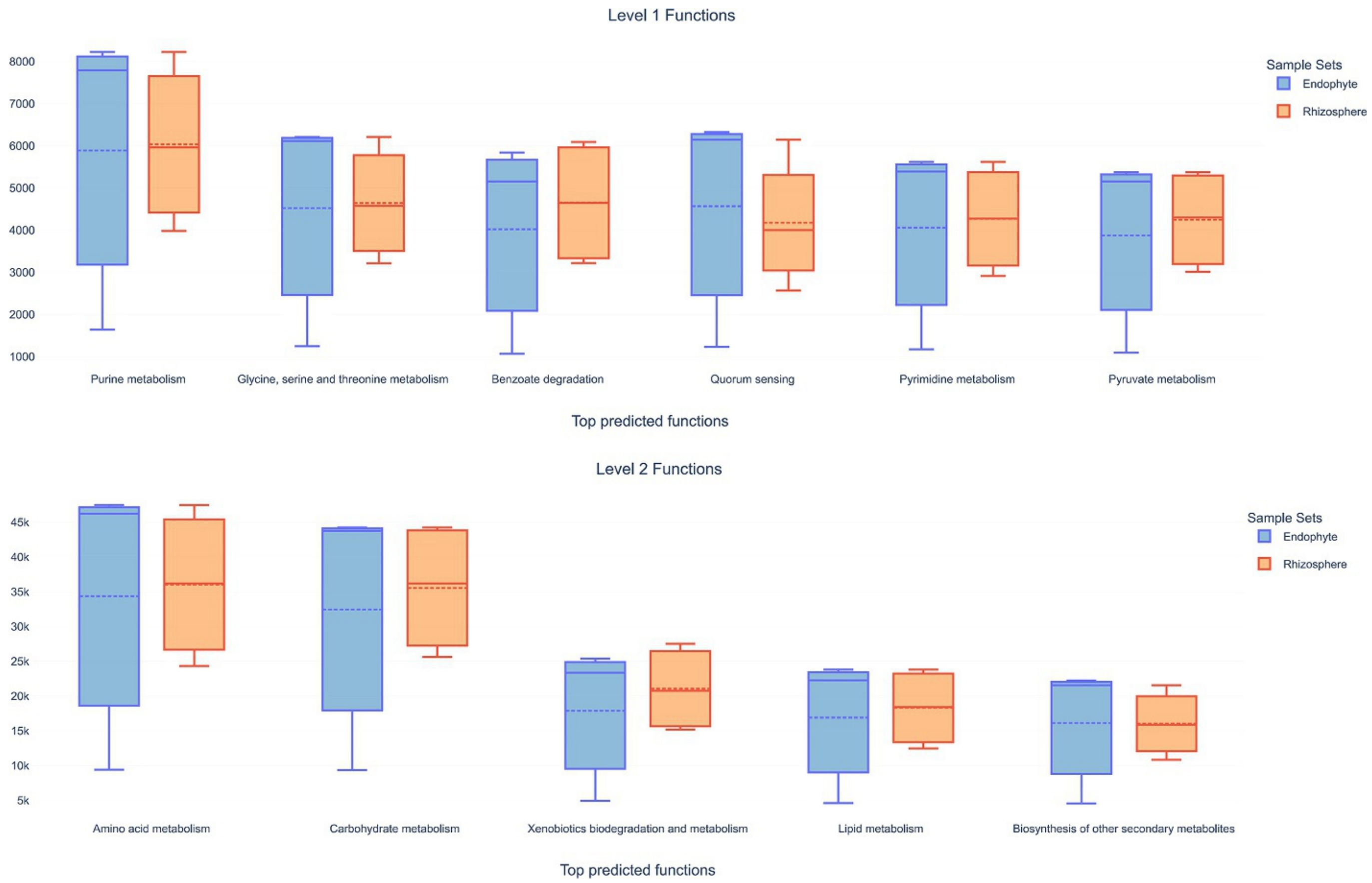

Fig. 5 Relative contribution in terms of abundance of the rhizospheric and endophytic sample sets to top predicted functions of the core set.

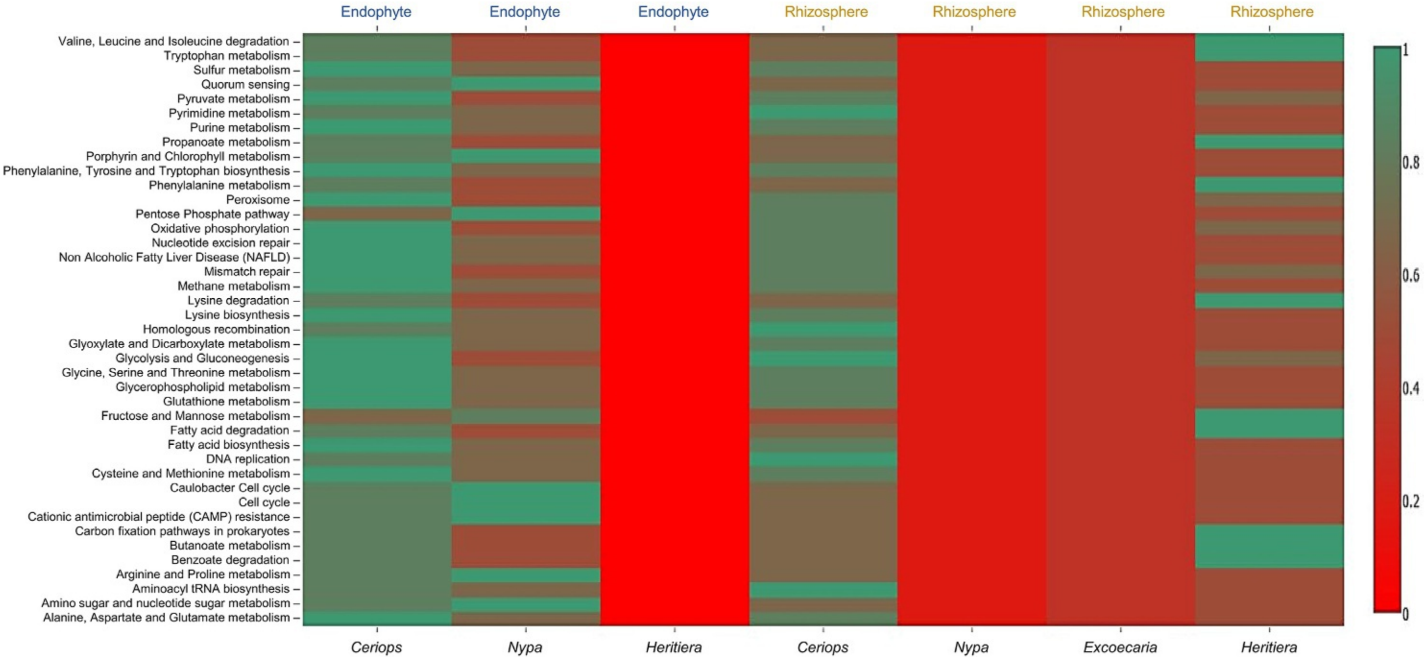

Fig. 6 Heatmap of core predicted functions across the rhizospheric and endophytic datasets.

3.2 Sphingomonas

The genus *Sphingomonas* possesses members with multifaceted functions of which the most significant is bioremediation of environmental contaminations including polycyclic aromatic hydrocarbon (PAH) biodegradation (Xu et al., 2016; Muangchinda et al., 2015; Yingjie et al., 2019; Kleinsteuber et al., 2006; Leys et al., 2004). They produce highly beneficial biopolymers and exosaccharides like gellan gum (Palumbo et al., 2020; Costa et al., 2018; Stevens et al., 2016) and sphingan (Huang et al., 2022; Li et al., 2022; Chang et al., 2022) and studies have shed light on an interesting role of this genus in the biodegradation of compounds that are organometallic in nature (Ruan et al., 2018a; Ruan et al., 2018b; Koutinas et al., 2019). Some members of this genus have been associated with plant growth-promoting activities when subjected to abiotic stressors such as increased salinity, water scarcity, and heavy metal contamination in soil (Khan et al., 2014; Khan et al., 2017; Kim et al., 2013; Pan et al., 2016; Bilal et al., 2018; Khan et al., 2016). This role can be justified by their ability to produce phytohormones such as gibberellins and indole acetic acid (IAA) (Khan et al., 2014). The fact that *Sphingomonas* members perform such diverse ecologically important functions via the secretion of secondary metabolites confers significant economic value to them, as they are amenable to bioengineering for utilization in various environmental cleanup strategies. A comprehensive overview of the suitability of this genus for bioprospecting has been provided by (Asaf et al., 2020).

3.3 Novosphingobium

Bacteria belonging to the genus *Novosphingobium* have widespread natural distribution and have been isolated from diverse environments such as seawater (Huo et al., 2015), soil contaminated with toxic chemicals (Chaudhary and Kim, 2016; Niharika et al., 2013), plant rhizospheres (Kampfer et al., 2015), hot springs (Xian et al., 2019), activated sludge (Chen et al., 2014), and freshwater (Liu et al., 2021), indicating excellent environmental adaptability. Some isolates have been found to biodegrade mono-, poly-, and heterocyclic aromatic hydrocarbons (D'argenio et al., 2014; Liu et al., 2005; Sohn et al., 2004; Yuan et al., 2009), for instance, fluoranthene, bisphenol A, phenol, polychlorophenols, phenanthrene, and benzo(*a*)pyrene. This makes them a great candidate as potential bioremediators of polluted soil and water. A few bacteria have exhibited suitability for their employment as plant growth-promoting rhizobacteria (PGPR) based on their capabilities of alleviating salt stress conditions (Vives-Peris et al., 2018), and producing acetoin, IAA (Krishnan et al., 2017), and siderophore (Zhang et al., 2016). In other avenues, *Novosphingobium rosa* Ikeda-3 isolated from winery wastewater produces two different exopolysaccharides (one floating and the other precipitating) when grown under aerobic conditions in a medium containing sucrose as the only source of carbon (Matsuyama et al., 2003). Thus, genus *Novosphingobium* has been an object of extensive attention for its potential applications in environmental management strategies and in the field of agriculture.

3.4 Pseudomonas

This genus harbors one of the most notorious members of the ESKAPE group of pathogens (*Pseudomonas aeruginosa*), but there have been reports of other members who have exhibited bright prospects as potential biofertilizers. Reports have shown that the usage of *Pseudomonas* sp. as a biofertilizer in *Lactuca sativa* L. resulted in a significant increase in carotenoid and chlorophyll content under different levels of salinity duress, which resulted in soil fertility enrichment via the production of proteins, hormones, and prolines (Azarmi-Atajan and Sayyari-Zohan, 2020). Pseudomonads have been harnessed as agents of biocontrol and bioremediation, with a prime example being the success achieved by *P. protegens* and *P. fluorescens* in crop protection and pest control, where they have been hypothesized to act as antagonist and/or competitors to plant pathogens (Kupferschmied et al., 2013). The ability of members of this genus to catabolize a myriad array of compounds have been utilized for detoxification and biodegradation of heavy metals, pesticides, oil spill hydrocarbons, and many other pollutants (Wasi et al., 2013).

3.5 Rhizobium

Across the different varieties of soils, rhizobial bacteria are ubiquitous members of the rhizospheric community, independent of the presence or absence of a leguminous plant (Jones et al., 2016). Perhaps the most important and predominant role of *Rhizobium* involves biological nitrogen fixation via the establishment of symbiotic cross-talk mediated by flavonoids and lipo-chitooligosaccharides (LCO) (synthesized by the mutualistic rhizobia) with the roots of leguminous plants, whereby it converts atmospheric nitrogen into the relatively bioavailable form of ammonia, with the enzyme nitrogenase (Shiferaw et al., 2004). Multiple strains of *Rhizobium* are also capable of solubilizing tricalcium and dicalcium phosphates and hydroxylapatite (Abd-Alla, 1994). Selected strains of the diazotrophic symbionts have been shown to possess abiotic stress tolerance functionalities including improved associative nitrogen fixation under varying soil characteristics, climatic conditions, nutrient availability, availability of water, salinity, and in the presence of xenobiotics and toxins, implicating their potential utility in forest and agricultural soils under inconducive conditions and reclamation of land (Bouizgarne et al., 2015). Additionally, traits of plant growth promotion in rhizobia, including siderophore release, phytohormone synthesis, production of ACC deaminase, and the release of volatile compounds like 2,3-butanediol and acetoin, may aid the growth of legumes while reducing metal toxicity (Hao et al., 2014). In due course of biofilm formation and quorum sensing, the exopolysaccharides (EPSs) layer synthesized by a select strain of *Rhizobium* consisting of glucose, mannose, and mannuronic acid, enhances uptake of water and minerals by plant roots via modulation of soil characteristics (Kaci et al., 2005).

3.6 Enterobacter

Enterobacter members are part of the ESKAPE group of pathogens (*Enterococcus faecium*, *Staphylococcus aureus*, *Klebsiella pneumoniae*, *Acinetobacter baumannii*, *P. aeruginosa*, and *Enterobacter* spp.) with Priority 1: Critical designation (Rice, 2008; Tacconelli et al., 2018), which is one of the leading causes of resistant nosocomial infections (Akbari et al., 2016; Paauw et al., 2009; Morand et al., 2009; Allerberger et al., 1996; Boucher et al., 2009; Canton et al., 2002; Davin-Regli et al., 1996; Davin-Regli et al., 1997; De Champs et al., 1989; Wenger et al., 1997; Wu et al., 2018). In addition, the *Enterobacter* members are naturally occurring commensals of the animal and human gut microbiomes. Among these, a few species have been found to be involved in hospital-acquired outbreaks and infections (Akbari et al., 2016; Bertrand et al., 2003; Chow et al., 1991; Paauw et al., 2009; Morand et al., 2009; Sanders Jr. and Sanders, 1997). The *Enterobacter* genus is associated with diverse environmental habitats, as reviewed in (Davin-Regli et al., 2019). These bacteria have been recovered from water and soil and are endophytes or considered phytopathogens for numerous plant species (Singh et al., 2018). Some species have been associated with bioprocessing approaches (Brenner et al., 1986), including generation of microbial fuel cells (MFC) where the significant benefit of a faster start-up and the development of an electroactive biofilm indicate *Enterobacter aerogenes* as a prime candidate to be used as a biocatalyst for MFC applications (Zhuang et al., 2011).

3.7 Devosia

First isolated from a soil rich in riboflavin (Foster, 1944; Nakagawa et al., 1996), *Devosia* have since been isolated from an extremely varied range of environments, including marine sediments (Pang et al., 2022; Zhang et al., 2021), nodules of legumes (Rivas et al., 2003; Bautista et al., 2010), soils contaminated with hydrocarbon pesticides like hexachlorocyclohexane (Kumar et al., 2008; Verma et al., 2009; Ryu et al., 2008), cerebrospinal fluid samples from humans (Nicholson et al., 2015), and horse blood (Kampfer et al., 2021). A study analyzing the genomes of 27 strains of the genus *Devosia* (Talwar et al., 2020) brought to light the open pangenome represented by unique genes, which suggest that over the course of evolution, this genus acquired bioremediation capabilities (Hassan et al., 2015a) in order to survive the environmental insults that they were subjected to across diverse habitats. A recent study shows that *Devosia* are capable of plant growth promotion, which can be utilized to improve the productivity of the rice crop (Chhetri et al., 2022). Apart from roles in nitrogen fixation and nitrification (Yu et al., 2022), perhaps the most widely known functional attribute of *Devosia* is the ability to degrade mycotoxins, especially Deoxynivalenol (DON, or also known as vomitoxin) (Hao et al., 2022), which is produced by *Fusarium* spp. and is the most abundant mycotoxin contaminant of cereal grains (Yan et al., 2020; He et al., 2016; Lyu et al., 2018). The gradual accumulation of vomitoxin in the levels of food chain is a threat to global food safety and human health, causing immune suppression, disturbances in appetite, vomiting, and nausea (Payros et al., 2016; Streit et al., 2012; Hassan et al., 2015b). Thus, the question of how to effectively reduce human exposure to DON gains prime importance. An increasing number of studies have sought to elucidate the molecular pathway of the biotransformation of DON (Hassan et al., 2017; He et al., 2015; Carere et al., 2018; Gao et al., 2021), and *Devosia* has shown the brightest prospect in tackling DON contamination by even ameliorating the toxic effects of the mycotoxin in mouse studies (Guo et al., 2020; Zhao et al., 2016).

3.8 Corynebacterium

Corynebacterium is a genus consisting of members who are predominantly pathogens, with a notable exception being *Corynebacterium glutamicum*. With an increasing number of reports of newer pathogenic members being characterized (McMullen et al., 2017; Hacker et al., 2016; Souza et al., 2019; Diop et al., 2018; Jamir et al., 2022; Jaen-Luchoro et al., 2022), a handful of reports exist that document the potential of *Corynebacterium* to be employed as a bio-agent. An interesting study showed that cell extracts of *C. glutamicum* can enhance the efficiency of colonization by *Pseudomonas chlororaphis*, a plant growth-promoting rhizobacterium in rice (Bowya and Balachandar, 2020b; Bowya and Balachandar, 2020a). C. glutamicum has already been harnessed as a microbial cell factory for production of various compounds like indole (Mindt et al., 2022; Ferrer et al., 2022), isomaltulose (Hu et al., 2022), γ-aminobutyrate (GABA) (Son et al., 2022), phenylalanine (Kataoka et al., 2022), and ectoine (Jiang et al., 2022).

3.9 Lactobacillus

Lactobacillus or lactic acid bacteria (LAB) can be isolated from a diverse range of environments including gut of domestic monogastric animals (e.g., pigs) and birds (e.g., poultry), thereby establishing viable bioprospecting opportunities for the isolation of probiotic strains from fecal samples (Robledo-Cardona et al., 2018). They are industrially suitable microorganisms due to their classification under GRAS (Generally Recognized As Safe) category for human and animal usages and have been traditionally considered as probiotics (Reddy et al., 2012). They are frequently utilized as starter cultures for fermentation of dairy, meat, and other food industries (Puspita et al., 2022). One of the predominant metabolic products yielded by them includes stereospecific L form of lactic acid via fermentation of molasses by *Saccharolytic* LAB or a relatively cost-effective fermentation of alternative starchy substrates by amylolytic LAB, as opposed to a racemic mixture obtained from full-fledged chemical syntheses (Reddy et al., 2012). LAB have multiple utilities as energy and food for humans, serving as microfactories for production of food preservatives, additives and aromatic compounds, as industrial feedstock for synthetic products, in the synthesis of polylactate as biodegradable plastic, etc. (Puspita et al., 2022; Reddy et al., 2012). Recent evidence elucidates an interesting utility of Lactobacilli as microbial consortia in production of biohydrogen via dark fermentation in vinasse-based medium constituting complex or pure carbon sources under varied conditions of H_2 partial pressure (Sydney et al., 2018). The ability of Lactobacillus to degrade intestinal oxalate is being increasingly explored as a probiotic approach for cure of kidney stones (Sreeja et al., 2018). Additionally, antioxidant potential and immunomodulatory activities of lactobacilli such as antimutagenic and anticarcinogenic properties, hypercholesterolemic functionalities, antagonization of intestinal pathogens, induction of B and T cell proliferation, enhanced mononuclear cell phagocytotic activity, Natural Killer (NK) cell tumoricidal activities mediated by intact bacterial cells, or LAB components such as peptidoglycan, teichoic acid, and exopolysaccharide substantiate the probiotic efficacy of LAB for augmenting host immune response (Liu et al., 2011).

From our analysis, we were also able to predict the nature of interaction between the major members occupying the respective niches, shown in Fig. 7. Unidirectional (red

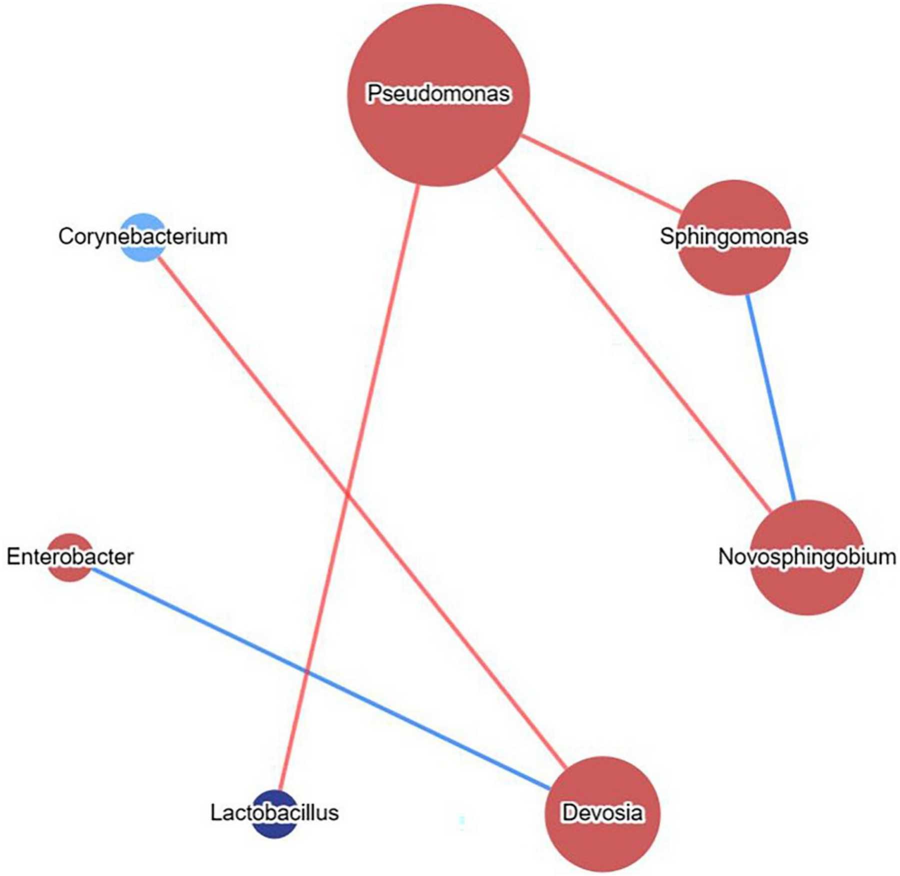

Fig. 7 Function driven correlation network or co-contribution network of interactions present among the major members of the core set. The *red lines* denote unidirectional interaction while the *blue lines* indicate bidirectional interaction between the interacting genera. The size of the node represents a visual cue toward the predicted relative importance of that genus toward this correlation network.

lines) and bidirectional (blue lines) interactions were seen in the generated network. This indicates a complex sensory signaling pathway active among the major members of the core set, which probably contributes to the core niche holobiont.

4 Conclusion and future prospects

We are yet to unearth the true potential of the bacterial communities that are prevalent in the rhizospheric and endophytic niches of the mangroves of the Indian Sundarbans. Their role in the maintenance of the biogeochemical cycles and the food chain and food web of the region is still at the nascent stage of elucidation though we know that perturbations in these assemblages affect not only the mangrove plants but also the surrounding ichthyofauna, crustaceans, and other stakeholders of the ecosystem including human beings. The impact of climate change has directly reduced the habitat of a majority of the true mangroves and replantation programs and restoration practices can only work better, if proper insights into the function and dynamics of the bacterial members are properly mapped. We believe that a combination of metatranscriptomics and metaproteomics could help us unravel the gray areas since using metagenomics we have been able to understand the abundance and specificity of the bacterial members.

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CHAPTER 15

The rhizosphere microbiome: A key modulator of plant health and their role in secondary metabolites production

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1 Introduction

The soil has a critical role in the biosphere, the soil is one of the most complicated and least known matrices. Nutrient cycling, carbon storage, water maintenance, maintaining terrestrial diversity, biotic control, and the conversion of possibly harmful compounds and elements are the major ecological roles of soil (Haygarth and Ritz, 2009). The soil microbiota is an essential part of soil ecosystems, and it plays an important role in terrestrial ecological functions, particularly the control of carbon and nutrient cycles. Plant roots get benefits from the diverse microbial population of bulk soil, especially specific bacterial species residing in the rhizosphere. The rhizosphere is considered a relatively small area of nutritionally rich soils that occupy plant roots and are influenced by microbial activity and root exudates (Slimane and El-hafid, 2021).

Plant-microbe interaction is a multifaceted, interactive, and constant process that dates to the beginning of plant colonization on earth, resulting in an assemblage of host and nonhost species and formulating a distinct ecological component known as a "holobiont." Plants are consistently invaded both by beneficial and pathogenic microorganisms, primarily bacteria and fungi, in both natural and agricultural ecosystems (Dolatabadian, 2020). The interaction between plants and microbes is considered an important element of the terrestrial environment. There are four types of interactions between plants and microbes, which include mutualism, competition, commensalism, and parasitism. Among them, the most well-known types of interaction are commensalism and mutualism, where either single or both species get a benefit (Wu et al., 2009). The rhizosphere comprises one of the most complex systems on the planet; it is a place for various organisms like nematodes, fungi, and bacteria, and compared to bulk soil, the rhizosphere has greater microbial abundance and activity but lesser diversification. Plants have been known to put selection pressures mostly on the rhizosphere microbial community, and community-level analysis has

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revealed unique microbial diversity linked to various plant species. This suggests that plant-emanated compounds show a distinct role in the rhizosphere microbiome assemblage (Gray and Smith, 2005). The relationships among plants and microbes occur in two ways: negative interaction, which causes the development of disease in plants, and positive interaction, which acts as a growth stimulator. The microbiota in the rhizosphere and phyllosphere is vibrant and is affected by a diverse range of biotic and abiotic factors, which include soil physicochemical characteristics, plant biological activities, signaling molecules between plants and microbes, and external factors, which include environmental conditions (Parasuraman et al., 2019a).

The term rhizosphere to describe the part of the soil where microorganism-facilitated operations are influenced by the root system. This consortium of microorganisms is considered the root microbiome, and recent research suggests that certain pathogens may be disrupted by an additional line of defense, an emerging defensive system barrier, the plant microbiome, which can be divided into the phyllosphere microbiome, the endosphere microbiome, and the rhizosphere microbiome. The rhizosphere microbiome consists of bacteria, fungi, and oomycetes and is therefore directly connected to plant health and growth (Li et al., 2021). Plant growth-stimulating phytohormones are produced by rhizosphere bacteria and phyllosphere colonizing epiphytes. The experiment was conducted by Boiero et al. (2007) in which they assessed the phytohormone synthesis of *Bradyrhizobium japonicum* cultivated in pure culture. They discovered that the three strains are capable of synthesizing the five main plant hormones differently: auxins, cytokinins, gibberellic acid (GA3), abscisic acid, and ethylene. This is significant because it has a significant role in promoting plant growth. In comparison to years of research on the human microbiome, the study of the plant microbiome is relatively new. So far, the data show that plant microbiomes are as important as human microbiomes. Plants are constantly interacting with their surroundings, so communication and interactions with microbes are crucial to their survival (Podila et al., 2009). Plants are known to synthesize a variety of chemical compounds known as plant bioactive compounds, synthesized by the plant via metabolic pathways that branch off from the metabolic pathways of primary metabolites. Albrecht Kossel, Nobel laureate in physiology and medicine in 1910, was the first person to define the term secondary metabolite. The plant's secondary metabolites have been shown to have a range of biological effects, offering a scientific foundation for the utilization of herbal ingredients in the traditional system of medicine. They are antibiotic, antifungal, and antiviral, and thus capable of protecting plants from pathogenic organisms (Hussein and El-Anssary, 2019). Plant secondary metabolites perform various functions such as defense from pathogens, pests, herbivores, stress responses, and facilitating organismal interactions. Plant microbiomes, on the other hand, play a direct or indirect role in many of the above-said processes, by improving plant metabolism. The plant can influence its microbiome by eliciting the various metabolites; thus, microbiome, in turn, can influence the metabolic profile of the host plant (Pang et al., 2021).

2 The microbiome of the rhizosphere

The soil in the rhizosphere region promotes the development of microbial inhabitants, which are referred to as mesotrophic. The rhizosphere region is alienated into three different areas: endorhizosphere, which considers the region of the root cortex, endodermis, and apoplastic space of cells, rhizoplane considers as the root area, and the ectorhizosphere considers as the area, which stretches from the rhizoplane to bulk soil. The relations among plants and microbes can occur in three distinct regions phyllosphere, endosphere, and rhizosphere. The phyllosphere region is the above-ground region of plants, while the endosphere region is the internal transport system. The "rhizosphere" is defined as the region of soil that is specifically influenced by or allied with plant roots and plant-formed material (Bhattacharyya and Jha, 2012). It is the narrow soil region influenced by plant roots. This region is considered as one of the prime locations for microbial colonization, which has a strong interaction with the plant. Therefore, the rhizosphere microbiome gained attention from scientists and researchers for study. The research shows that the microbial inhabitants in that region play an important role in maintaining plant health; they also promote plant nutrient uptake and defense against pathogens (Dutta and Bora, 2019). The rhizosphere contains up to 10^{11} microbial cells/g of root and more than 30,000 species of prokaryotes (Berendsen et al., 2012). The assembly and pattern of root exudate impact microbial activity and inhabitants, which influence the nematodes and microarthropods that live in this environment. There are shows advantageous and detrimental relations between rhizosphere species and plants that disturb the function of root and plant development (Kennedy and de Luna, 2005). The term microbiome is defined as the consortia of microorganisms also known as microbiota and is associated with animals, humans, and plants. The impact and role of microbes in influencing the host immune system and fitness have received increased attention in recent years. Environmental factors including temperature, pH, and the availability of nutrients influence the composition of microbiota in a host. The excessive use of chemical fertilizers in agriculture, and the rise of new antibiotic and pesticide-tolerance strains in both agriculture and medicine, can have an impact on the host's ability to cooperate properly with the microbiota (Taghinasab and Jabaji, 2020). The rhizosphere microbes also show a significant role in crop production and reduce the need for chemical fertilizers, which also helps to achieve high-productive yields (Dazzo and Ganter, 2009). The microbes and the compounds that they secrete act as valuable biostimulants, which play an important role in maintaining plant stress responses. It has been shown that treating the plant with plant growth-promoting rhizobacteria (PGPR) is an active approach to stimulating crop growth (Backer et al., 2018). Most soil microflora is carbon deficient (Garbeva et al., 2011). As plants secrete up to 40% of their photosynthesis product into the rhizosphere, the rhizosphere has more complex microbial population abundances than the nearby bulk soil. It is defined as the rhizosphere effect (Bais et al., 2006). Therefore, the management of the rhizosphere microbiome provides a new way to balance crop yield, nutrient reliability, and environmental impact (Sarma et al., 2019a). The rhizosphere management strategies include increasing the efficiency of roots, the nutrient acquisition process of the rhizosphere, and utilization by crops rather than depending only on chemical fertilizers (Zhang et al., 2010). Rhizosphere engineering has long-term applications in crop growth, particularly population engineering. Plants are known as one of the key modulators of the rhizosphere likewise, microbes can design to reconfigure the rhizosphere. The plant microbiomes have significant functions related to the production of probiotics and plant protection, which has piqued the interest of the research community; however, the data on how rhizosphere microbial communities impact plant development and resistance is limited. Conventional culture-dependent methods, as well as emerging technologies such as next-generation sequencing (NGS) and meta-omics technology, have all been useful for describing microbial accumulations. According to research, plants disturb and employ the advantageous microbial community in the soil in reply to pathogenic microorganism invasion deprived of eliciting a robust immune response to support their development and suitability (Li et al., 2021). The microbes enhance crop yields, resistance to pests, and help to tolerance the stress (Siddharthan et al., 2022) (Fig. 1).

The rhizosphere organisms that have proven their positive role in plant development and strength mostly include nitrogen-fixing prokaryotes, mycorrhizal fungi, plant growth-promoting rhizobacteria (PGPR), biocontrol microorganisms, mycoparasite fungi, and protozoa (Backer et al., 2018) (Table 1).

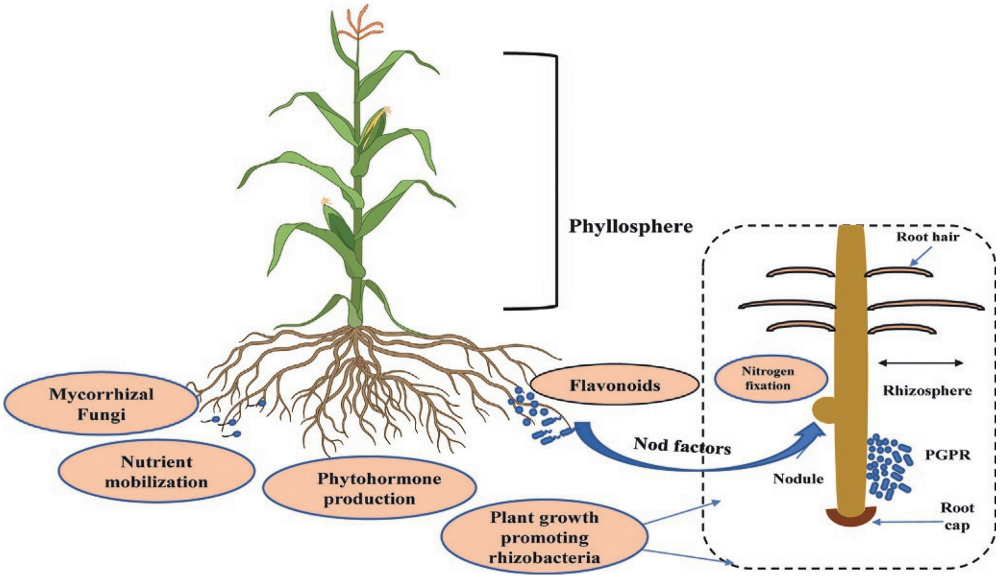

Fig. 1 The schematic representation indicate the rhizosphere region and their associate microbiome.

Table 1 Plant probiotic bacteria associated with rhizosphere microbiome and their role to promote plant health.

S. no.	Rhizosphere microbiome	Plant probiotic bacteria	Role	References
1	Plant growth-promoting rhizobacteria (PGPR)	• Plant growth-promoting rhizobacteria • Non-pathogenic pseudomonas and bacillus • Azotobacter	• To promote nutrient accessibility in soil • Help plant nutrient acceptance and integration • Supporting the nitrogen cycle	Woo and Pepe (2018)
2	Mycorrhizal fungi	• *Gigaspora* • *Funneliformis/rhizophagus* • *Laccaria* • *Trichoderma* sp.	• Carbon exchange • Promote water and nutrient absorption • Help plants during environmental and biotic stress	Pringle et al. (2009), Rouphael et al. (2015), and Woo et al. (2014)
3	Plant probiotic bacteria involved in nitrogen fixation	• *Azospirillum* • *Azotobacter* • *Azorhizobium* • *Bacillus* • *Rhodospirillum* • *Clostridium*	• Biological nitrogen fixation	Menendez and Garcia-Fraile (2017)
4	Plant probiotic bacteria involved in the production of plant hormones	• *Azotobacter* • *Bacillus* • *Paraburkholderia* • *Acinetobacter* • *Alcaligenes*	• Promote the production of plant hormones like auxin, gibberellin, ethylene, and cytokinin	Bashan and Holguin (1997), Khan et al. (2017), and Sawana et al. (2014)
5	Microparasitic fungi and biocontrol agents	• *Trichoderma atroviride* • *Trichoderma virens* • *Trichoderma reesei* • *Trichoderma asperellum* • *Trichoderma harzianum*	• Biocontrol agent • Promote plant growth, protection, and immune system • Help in the synthesis of secondary metabolites	Herrera-Estrella (2014), Singh et al. (2014), and Speckbacher and Zeilinger (2018)

2.1 Nitrogen-fixing prokaryotes

Nitrogen-fixing bacteria are known for their symbiotic association and most nitrogen fixation is done by prokaryotes. They are recognized to form a symbiotic association with nearly all major groups of plants and with some fungi. The most of nitrogen fixation is done by nodulated plants, which include both legume and actinorhizal. Cyanobacteria are the endosymbionts of all non-nodulated nitrogen-fixing symbioses (Singh et al., 2014). The nitrogen-fixing prokaryotes have the nifH gene, which encodes the protein ferritin. The nifH gene acts as a genetic-based marker for nitrogen-fixing prokaryotes (Li et al., 2022). Biologically, nitrogen fixation is achieved by an enzyme called nitrogenase. The enzyme nitrogenase has a high oxygen affinity; therefore, nitrogen fixation is carried out more efficiently in an anaerobic environment. In the case of anaerobic bacteria, it does not have any limitation, but it obliviously causes problems in obligately aerobic and diazotrophic for example *A. vinelandii*. This problem can be solved by the consumption of dioxygen by terminal oxidases that help to maintain the low intercellular concentration of oxygen that allows the nitrogenase to work efficiently (Holyoake et al., 2015). Nitrogen fixation is most significantly achieved by *Rhizobium* species they are free-living gram-negative soil bacteria that depend on dead and decomposed material to obtain nourishment. They infected plants via root hair under stress conditions, the root of legumes plants secrete some flavonoids and isoflavonoids by sensing these chemicals they are attached to the root. That induces the expression of several other genes which responsible for the formation of root nodule, which responsible for the formation of lipo-oligosaccharide nod factors (Bending, 2003). The primary product of biological nitrogen fixation is ammonia, but ammonia is toxic to plant cells to encounter this problem, ammonia is quickly converted into proteins or other organic compounds such as ureides. This is done by either the active bacterium or its mutual host (leguminous plants are the hosts in the case of root-nodule-based nitrogen fixation) or by another microorganism (Liou and Madsen, 2008). Furthermore, the enrichment of composts with phosphate, potassium-solubilizing microorganisms, and nitrogen-fixing bacteria is now one of the most feasible ways to promote the nutritive value of the compost product. It is done by inoculating the compost heap with *Azotobacter chroococcum* tends to increase the nitrogen content by fixing atmospheric N_2 (Bhattacharjya et al., 2021). The nitrogen-fixing *Bacillus* species are used as microbial biofertilizers. *Bacillus* spp. can survive in different soil types, they have stress-resistant endospores, and they can tolerate adverse environmental conditions (Singh et al., 2020). According to a recent report, *Hydrogenobacter* sp. can fix nitrogen at 70°C, which is the reported maximum temperature in bacteria for nitrogen fixation (Chen et al., 2021) (Fig. 2).

2.2 Mycorrhizal fungi

Mycorrhizal fungi comprise roughly 10% of entirely known fungal species, including virtually all Glomeromycota and significant proportions of the *Ascomycota* and *Basidiomycota* (Lewis, 2016). Mycorrhizal fungi are a prominent part of the plant microbiome. Two

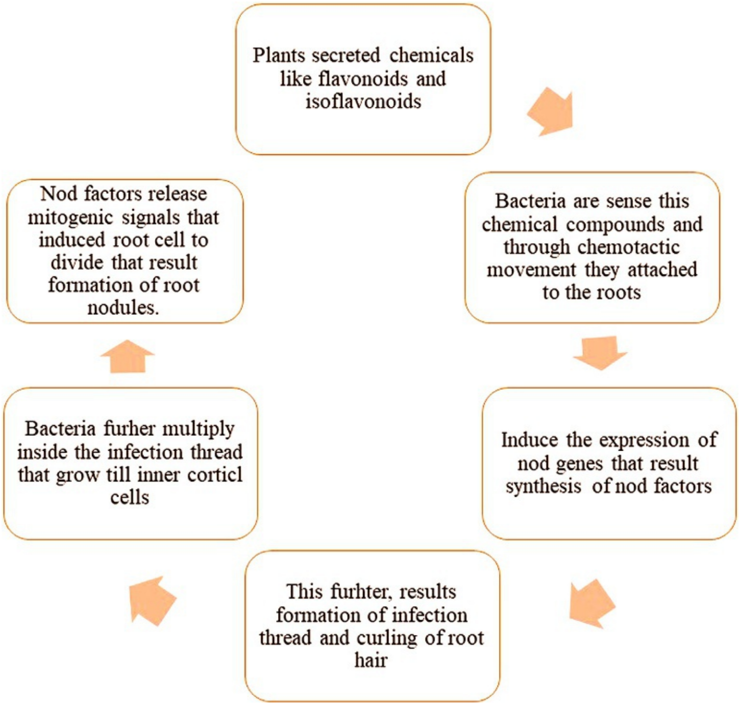

Fig. 2 The process of root nodule formation.

types of mycorrhizal fungi recognized to form symbioses with plant roots include arbuscular mycorrhizal (AM) fungi and ectomycorrhizal (EM) fungi (Averill et al., 2019). Mycorrhizal fungi are commonly found in most plants near the rhizosphere region and can form relationships with all gymnosperms, as well as more than 83% of dicotyledonous and 79% of monocotyledonous plants (Kennedy and de Luna, 2005). The current research study revealed the inoculation of arbuscular mycorrhizal fungi (AMF) into several medicinal plants to explore their effects on the phytochemical component in seeds, fruits, leaves, shoots, and roots along with biomass. Most of the studies confirmed that AMF could increase plant biomass and improve the formation of several active compounds in plants (Zhao et al., 2022). The study was carried out by inoculating eight species of AMF on *Salvia miltiorrhiza* Bge to evaluate the effect on plant growth and production of phytochemicals under greenhouse conditions. The study concludes that the rate of mycorrhiza production and root biomass effectively increased. Specifically, after treatment with AMF, phenolic acid production was also impacted (Wu et al., 2021). Although, the primary functional process by AMF promote plant growth is the absorption of inorganic phosphate from the soil, there is growing proof that AM fungi also shows a crucial role in plant nitrogen uptake. Extra radical mycelium nitrogen uptake can account for even more than 30% of total plant nitrogen uptake. AM fungi's extra radical hyphae can take up and assimilate both organic and inorganic forms of nitrogen from the soil, as well as translocate nitrogen to the plant (Pérez-Tienda et al., 2011). Mycorrhizal fungi help plants to absorb nutrients. The hyphae of mycorrhizal fungi are known to possess a large area of soil beyond the nutrient-depleted region that forms throughout the roots. The external hyphae of EM fungi increase in surface area on average 60-fold. Because of their small diameter, fungal hyphae can efficiently extract nutrients from the soil (Johnson and Gehring, 2007). The hyphae of AM Fungi form a branched structure within the cell, which is known as arbuscules, and they are known to form colonies only in the area of the root cortex, which is assumed to serve as the functional place for nutrient exchange (Balestrini et al., 2015). The colonization of AMF boosts nutrient availability and plant growth. The impacts are particularly advantageous for plants grown in nutrient-deprived soil in terms of yield and yield-related components. Furthermore, mycorrhizal plant species alter molecular and biochemical pathways, which increases the formation of phytochemicals in different parts of the plants (Kumar et al., 2021) (Fig. 3).

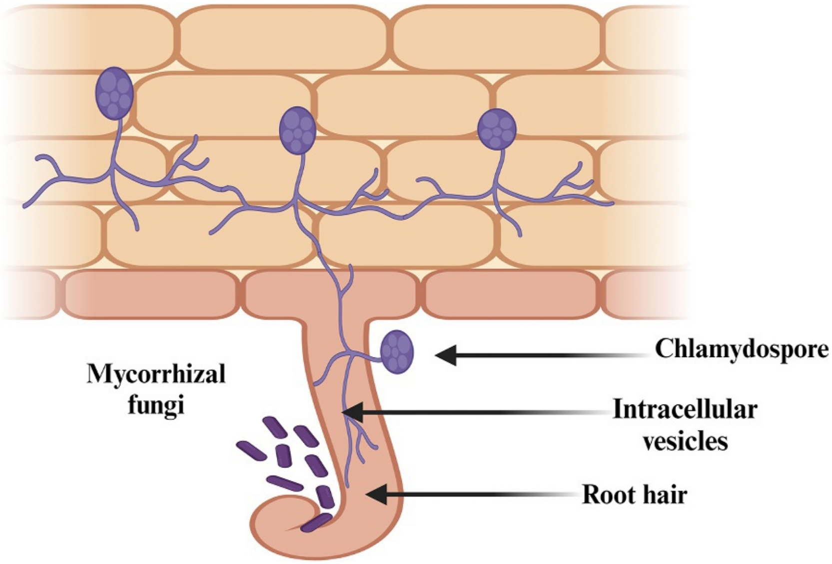

Fig. 3 Schematic representation of attachment of arbuscular mycorrhizal (AM) fungi on root hair. (Created with BioRender.com).

2.3 Plant growth-promoting rhizobacteria (PGPR)

Plant growth-promoting rhizobacteria are a type of soil bacteria that colonize near or on the superficial region of the root and they have a very significant role in promoting plant health and development by producing and secreting several regulative substances in the rhizosphere (Ahemad and Kibret, 2014). The extracellular and intracellular plant growth-promoting rhizobacteria are the two main types of plant growth-promoting bacteria (Vedamurthy et al., 2021). The microbiome of the rhizosphere performs an important role in agriculture practices because of a rich variety of root exudates and plant cell debris that brings up diverse and exclusive forms of bacterial colonization. They are recognized to perform a variety of function, which includes nutrient absorption and assimilation, helping to promote the texture of the soil, and controlling and secreting extracellular molecules such as hormones, bioactive compounds, antibiotics, and several signal molecules, these all have a role to promote plant growth (Backer et al., 2018). The plant growth-promoting rhizobacteria are classified based on the function they performed they act as (i) biofertilizers that help to increase nutrient availability to plants, (ii) rhizoremediators that degrade the organic matter, (iii) phytostimulation, which acts as plant growth promotors generally via synthesis of phytohormones, and (iv) biopesticides by controlling the diseases (Antoun and Prévost, 2005; Somers et al., 2004). The research is carried out on PGPRs to investigate their mode of action to develop a better strain for biofertilizers. The PGPRs are known to be promoting plant growth by modulating the whole microbial community. The general mechanism of action of PGPRs includes both direct as well as indirect action. The direct action includes nitrogen fixation, stimulating the production of phytohormones, and solubilizing the minerals like iron and phosphorus, while indirect action of PGPRs includes biocontrol activity, which includes the synthesis of antibiotics and extracellular enzymes (Bhattacharyya and Jha, 2012). The plant growth-promoting activity of PGPRs includes the synthesis of hydrogen cyanide and ammonia (NH_3). Due to its substantial toxicity against plant pathogens, hydrogen cyanide (HCN) is commonly utilized as a biological control in agroecosystems; however, HCN is also utilized in metal ion chelation and therefore, is indirectly involved in phosphate availability (Singh et al., 2019). Fungal-derived PGPM is widely used but is underappreciated in the literature. The most well-known example of mycorrhizal fungi such as *Gigaspora*, *Funneliformis*, or *Rhizophagus* (Glomus), and *Laccaria*, which are root obligate biotrophs capable of establishing mutualistic interactions with more than 80% of vascular plant species. They take part in carbon exchange and increase the plant's capability to uptake water and nutrients, thus mitigating the adverse effects of abiotic and biotic stresses (Woo and Pepe, 2018).

2.4 Biocontrol microorganism

The most effective and long-term operation strategy for protecting plants and crops is the biocontrol of pests and plant pathogens. Biological control includes biocontrol microbes, which are currently identified as an essential method for plant disease control in sustainable agriculture. There are several biological control options available. However, further research on this topic will need comprehensive knowledge of the multifaceted relationships between plants, the environment, and pathogens since it could easily fail, if plants are already under the pressure of disease (Syed Ab Rahman et al., 2018). The primary biocontrol agents are fungi and bacteria, which can protect plants from pathogens via both direct and indirect mechanisms (Albert et al., 2022). Microbial biocontrol agents are used in a variety of ways. Without directly interacting with the pathogen of interest, microbial biocontrol agents interrelate with plants by triggering resistance in them. While some microbial biocontrol agents influence pathogen growth conditions through nutrient competition or other mechanisms. Antagonists have different mechanisms they directly interfere with the pathogen via hyperparasitism and antibiosis (Köhl et al., 2019). The other type of mechanism of action of bacterial biocontrol agents includes inhibition of quorum sensing in the pathogen and the inhibition of the signaling pathway in the pathogen, which helps for initiation of virulence. Examples of such quorum-sensing inhibitors include lactonases, pectinases, and chitinases (Bonaterra et al., 2022). Some bacteria will act as biocontrol agents by producing antimicrobial and insecticidal metabolites. Examples of such bacteria are *Streptomyces tanaschiensis*, *Bacillus subtilis SPB1*, and *Pseudomonas chlororaphis O6*, etc., and metabolites include flavensomycin, biosurfactant, pyrrolnitrin, phenazines, hydrogen cyanide, cyclic lipopeptides, etc. (Lee et al., 2022; Sarma et al., 2019b). Pathogen control through sustainable agriculture practices (such as the use of biological adversaries) has recently been commercialized, and a variety of experimental methods are now being developed. Through a close association with living plant cells, biotrophic pathogens grow, procreate, and acquire nutrients from live plant tissue. *Cladosporium fulvum*, the causal mediator of tomato leaf mold, and *Ustilago maydis*, the causative agent of corn smut, are two examples (Figueroa-López et al., 2016).

2.5 Mycoparasite fungi

Mycoparasitism is referred to as the more usual type of antagonism, and involves physical interaction with the host mycelium. The process of mycoparasitism entails the tropical growth of biocontrol fungal mycelium toward the pathogen, which is followed by comprehensive coiling and the exudation of numerous hydrolytic enzymes, resulting in the pathogen cell wall or membrane dissolution. The procedure of mycoparasitism is categorized into four stages. In the first step, growth of chemotropic fungal mycelium to the phytopathogenic fungi, followed by identification. The further steps include the attachment of phytopathogenic fungi and deterioration of the cell wall, followed by penetration of the host fungal cell (Ram et al., 2018). Mycoparasites fungi, or fungi that feed on other fungi, are responsible for the production of volatile and non-volatile secondary metabolites. During mycoparasitism, several bioactive compounds are generated their role is to enervate the host and assist the parasitism. Moreover, there is scientific proof that certain secondary metabolites behave as communication molecules. Many fungal mycoparasites have a valuable impact on plants, and some of their secondary metabolites boost plant growth and protection (Speckbacher and Zeilinger, 2018). Mycoparasitic and antagonistic fungi are currently being researched as a biological option or as an alternative to chemical fertilizers for the regulation of fungal pathogens. Selection of the strain and genetic mutation has resulted in some fungi that are efficient as fungicides under certain cultural conditions. *Trichoderma* species the most well-known biocontrol fungi has an antifungal mechanism that involves the action of chitinases and glucanases, which are enzymes to degrade fungal cell walls (Lorito et al., 1998). The *Trichoderma* genus is a necrotrophic mycoparasite. Their mechanisms of action are prey sensing and chemotaxis, physical attack to host by coiling around hyphae, adhesion to host, etc. The last stage of mycoparasitic interaction is cell wall degradation and death of the host. The *T. lignorum* strain can protect citrus seedlings from the pathogen *Rhizoctonia solani*. They will act against *R. solani* through necrotrophic mycoparasitism (Tyśkiewicz et al., 2022). *Coniothyrium minitans* is another example of a mycoparasitic biological control agent. They can synthesize antibacterial and antifungal substances. *C. minitans* is one of the biological control agents of the pathogenic fungi *Sclerotinia sclerotiorum*. *C. minitans* will produce antifungal substances like macrosphelide A to inhibit hyphal growth in *S. sclerotiorum* thereby ensuring the protection of crops from sclerotinia diseases. The antibacterial substances from *C. minitans* will inhibit the growth of *Xanthomonas* and *Clavibacter* (Zhao et al., 2020).

3 Phyllosphere microbiome

The research on plant microbiomes has primarily focused on the rhizosphere, such as the mutually beneficial relationship between plant roots as well as bacteria and fungi, along with the dynamics of soil-borne pathogens. With the recent addition of genomic and molecular technologies, plant microbiome research has increased rapidly over the past decade or so, from the rhizosphere to the phyllosphere and endosphere (Zhu et al., 2022). The phyllosphere is the above-ground section of a plant that is inhabited by a diversity of microbes, including both epiphytic (organisms that grow on the surface of a plant) and endophytic (organisms that reside within the plant) (Vorholt, 2012). The plant phyllosphere microbiome has been found to perform a crucial part in the adjustment of the host plant to different environmental stress factors by increasing resistance to cold, heat, drought, and salinity. Another study on the plant phyllosphere microbiome has revealed that both environmental and biotic factors perform a crucial role in the development of phyllosphere microbiomes (al Ashhab et al., 2021). According to molecular research, the dominant bacterial inhabitants of the phyllosphere are alpha-, beta-, and gammaproteobacteria, as well as firmicutes. The phyllosphere is composed of four main phyla of bacteria, which include *Proteobacteria*, *Firmicutes*, *Bacteroides*, and *Actinobacteria* (Sivakumar et al., 2020). The phyllosphere includes above-ground region of the plant, which includes the caulosphere (the surface of the stem), asthenosphere (the exterior region of the flower), carposphere (the surface of fruits), and phylloplane (the exterior region of leaves). The association between the plant and the phyllosphere microbiome demonstrated that there is a mutually beneficial relationship observed between them in which microbial communities undertake many beneficial activities involved to assist the plant's growth and development, which includes nitrogen fixation, defense from pathogenic microorganisms, moderation of metabolite via a biocatalysis mechanism, and phytohormone synthesis. According to the reports, the degree of nitrogen fixation by the phyllosphere microbial community and the degree of microbial nitrogen fixation is more in the phyllosphere (Parasuraman et al., 2019b). Furthermore, the phyllosphere microbiome participates in the biosynthesis of plant hormones such as indole-3-acetic acid (IAA), auxins, and cytokinin, which promotes plant growth and development by promoting elongation, cell proliferation, tissue differentiation, and apical dominance. Still, the role of phyllosphere microorganisms in the production of plant hormones is not fully understood (Sivakumar et al., 2020). In recent agriculture practices, chemical fertilizer is an essential component to provide nutrients for crop development because they are not readily accessible in the soil or from other organic sources. They have some inherited side effects which include reduced crop productivity, the disparity in soil nutrients, and interruptions in the plant-microbe relationship. In this case, an alternate solution to chemical fertilizers that effectively gives nutrients to the plants and, importantly, does not disturb the plant-microbe relations is required. In this respect, advantageous microbiota in the plant phyllosphere is a substitute solution (Kumar et al., 2016).

4 Endosphere microbiome

The plant endosphere is inhabited by complex microbial communities and microorganisms known as endophytes, which live in the plant interior for at least part of their lives. Endophytes have recently gained a lot of attention due to the growing awareness of the significance of host-associated microbiota in the performance and functioning of their host (Compant et al., 2021). Endophytes are microorganisms that can form colonies in plants and microbes, and they can be easily isolated from any microbial or plant-growing medium. The endophytes serve as the hub for potent bioactive secondary metabolites, which have antimicrobial, insecticidal, anticancer, and other bioactive properties (Gouda et al., 2016). Endophytes are considered an important aspect of sustainable agriculture they play a vital function in the modulation of their host plant's primary and secondary metabolism. Endophytes have direct and long-lasting interaction with the host thereby they can escape from harsh environmental conditions. Endophytes assist plants in different ways such as in acquiring nutrients from the soil, nitrogen fixation, phosphate accessibility, phytohormone, and antimicrobial production, according to recent research findings. There is a tremendous opportunity to create and develop novel products such as endophytes-based microbial formulations and elicitors to promote plant growth, and secondary metabolites (Pandey et al., 2022). Over 1 million endophytic fungal species are believed to exist in nature. Schultz divided fungal endophytes into three groups: (a) mycorrhizal fungi, (b) balansicaeous or pasture endophytic fungi, and (c) non-pasture endophytic fungi. Endophytic fungi produce bioactive compounds that are dissimilar from those produced by their host plants, and these compounds are essential for improving the ability to adapt to both fungal endophytes and their host plants, including resistance to both environmental and biotic stresses. Furthermore, such compounds can stimulate the formation of a plethora of very well and unique secondary metabolites, which humans can exploit and apply as important medicinal resources (Jia et al., 2016). Very few studies reported the benefits of endophytes as well as their biologically active compound and it has become clear in recent decades that the degree of discovery of active novel chemical entities is decreasing. Whereas plant sources are being widely researched for the discovery of novel bioactive molecules for a wide range of medicinal causes, endophytic microorganisms have a crucial role in the discovery of bioactive compounds with an extensive range of applications in the health and pharmaceutical industry (Lam, 2007).

5 The concept of plant probiotics by comparing the concept of human probiotics

The term probiotic means "for life"; it is defined as the consortia of bacteria that have a beneficial effect on humans and animals (George Kerry et al., 2018). Havenaar and Huis In't Veld state that a probiotic is a viable single- or mixed-culture of bacteria that supports the host by enhancing the characteristics of the indigenous flora once implemented in an animal or man (Havenaar and Huis In't Veld, 1992). In higher eukaryotes, the overall fitness of organisms does not only depend on their genes and adaptability, but also on the bacteria that live in and on them. These microbes can be beneficial, harmful, or neutral, but all of them play a significant role in the host's survival in its environment. The microbiota is the microbes that are associated with an organism and make up the microbiome (Spence and Bais, 2013). The human gut is a distinctive reserve of a diverse group of microbes that comprise the human-microbiome biological entity. Over 100–1000 microbial species are part of the human gut microbiome and mainly help in regulating the host's internal environment, playing a crucial part to maintain host health. This amazing synergetic relationship has sparked a lot of interest in this field. These organisms play an important role in defense function, eupepsia, catabolism, and anabolism, as well as brain-gut responses. Probiotics may help to reduce disruptions in the intestinal microbiota. The study shows that the diversity of gut microbiota is significantly influenced due to several biological processes. Other factors, such as an unbalanced diet, poor physical activity, and smoking, cause rapid changes in microbial composition. Probiotics have an important role in preserving the optimal composition of the intestinal microbiota (Trush et al., 2020).

The word plant probiotic bacteria was coined by Haas and Keel to describe a consortium of microorganisms that fulfill three major criteria the first is effectiveness and competitiveness in niche colonialization, they can mediate induced systemic resistance (ISR) in their hosts, and the occurrence of direct antagonistic traits on pathogenic organisms. Subgroups of this plant probiotic bacteria are mostly observed in soils and the rhizosphere is known as plant growth-promoting rhizobacteria (PGPR), which was proposed previously (Menendez and Garcia-Fraile, 2017). Based on their interaction with the host plant, the plant probiotic bacteria are classified into two types. The first type is free-living rhizobacteria, which are found outside of plant cells and help plant growth by secreting the metabolite, which is released in the rhizosphere region. The second group of bacteria is the endophytes, which are found inside plant tissue or in cells and directly exchange metabolites with the host plant (Gray and Smith, 2005; Hardoim et al., 2015). Some of the plant probiotic bacteria can integrate their physiology and even undergo bacterial differentiation within plant cells leading to the development of specialized structures. Rhizobia are known mutualistic symbiotic bacteria that form symbiotic relationships with leguminous plants, and promote nitrogen fixation in specialized root structures known as root nodules (Suzaki and Kawaguchi, 2014). Most plant probiotic bacteria commonly bacterial endophytes can synthesize plant phytochemicals, which are organic molecules involved in a variety of processes throughout the various stages of plant development and growth. The diverse range of beneficial bacteria can produce them and use them as plant growth promotion traits (Costacurta and Vanderleyden, 1995). Bacillus, Pseudomonas, Acinetobacter, Alcaligenes, Arthrobacter, and Serratia are the major genera of plant growth-promoting probiotic bacteria. They support the host plant by synthesizing the phytochemicals, antibiotics, and lytic enzymes, nitrogen fixation, solubilizing soil mineral nutrients, and support the host plant from any disease (Rahman et al., 2018).

6 Rhizosphere engineering is a key approach to the regeneration of the soil microbiome

The rhizosphere region is considered an intensive network of the root system, soil, and a diversified group of microbes, fungi, protozoa, and archaea. Crop development and yield are directly affected by rhizosphere conditions. Plant growth and yield are stimulated by nutrient-rich rhizosphere environments, and vice-versa. Excess cultivation depletes utmost soils, which must be replenished either before or at the time of the next crop.

Most fertilizers used as the primary basis for crop nutrients are chemical fertilizers, but uncontrolled and excessive uses of chemical fertilizers caused a significant threat to agricultural sustainability and ecosystem stability (Berendsen et al., 2012). Rhizosphere engineering provides a unique opportunity to reengineer the synthetic microbial populations to promote plant health, resistance to disease, and stress tolerance and regulation (Dries et al., 2021). The recent concept of "rhizosphere engineering" suggested the inoculation of efficient beneficial microbes to resemble the organized biological systems in native soils, thereby enhancing the rehabilitation of efficient, valuable microbes, which is correlated with the fruitfulness of the soil and regenerating the natural microbial community depleted by crop domestication. These treatments may help to support plant health, growth, and protect from various environmental stresses (Woo and Pepe, 2018). Manipulation of the microbiome is one of the key approaches for reassembling the rhizosphere. The ability to manage and manipulate the entire rhizosphere microbiome is limited due to the complexity of the microbiome; though, the furthermost straightforward and most sustainable method to modify the microbiome is through the addition of artificially multiplied microbial species. Several biofertilizers, which contain one or more species of fungi or bacteria have been industrially synthesized and are now readily accessible for improving plant growth and sustainability (Kumar and Dubey, 2020). Microbiome engineering entails recognizing and cultivating prospective plant growth-promoting microbes. In depth investigation/selection of the several components, assessment of microorganism compatibility, determining the causes and consequences in the native agricultural ecosystem, formulation development, distribution strategy, and technical assistance (Berendsen et al., 2012; Berg et al., 2014; Kong et al., 2018; Yakhin et al., 2017). According to recent studies, the development of plant and metabolite content seems to be reliant on multifaceted relationships with the biotic environment, such as metabolic correlations with connected microbes in the rhizosphere region, phyllosphere, and endosphere. Thus, restructuring the phytobiome could be a long-term strategy for manipulating the metabolic performance of plants while reducing the use of synthetic fertilizers. Plants naturally gather microorganism communities that repopulate plant surfaces as well as the endosphere and are closely linked to shifts in plant performance. As a result, reassembling the phytobiome may result in unexpected and unwanted changes in the plant-soil system. Second, because of the numerous players involved, determining how microorganisms induce a specific plant phenotype necessitates a comprehensive understanding of those complex relationships (Wang et al., 2022).

7 Plant-microbe interactions in secondary metabolite production

Plants coexist with a diverse range of microorganisms, both beneficial and detrimental. The overall health of plants and efficiency relies on effective communication with microbiota. Metabolites exuded from roots are the primary means of communication, mainly diverse secondary metabolites. The metabolites alter the configuration and functional composition of the plant-linked microbiota (Koprivova and Kopriva, 2022). Plant-microbial interactions can be categorized as either positive (symbiotic or non-symbiotic) or negative (competition or parasitism relations). Zestful changes in the genome, metabolic activity, and signaling systems of the symbiotic cohorts were also seen in symbiotic interactions. Wide range of environmental factor impacts plants. Indeed, organisms such as fungi, bacteria, and viruses can modify plant function, growth, and reproduction in both symbiotic and asymbiotic interactions. Plants and microorganisms, communicate through diverse chemical signaling pathways. At the rhizosphere level, microbes can induce molecules known as elicitors, which affect plant cell receptors. The elicitor molecules and their activities differ depending on the microbes and stimulate distinct biochemical reactions in plants, like a synthesis of secondary metabolite elicitors are microbial compounds that stimulate morphological changes in plants, and elicitation refers to signaling pathways in plants that incorporate elicitor signals. (Chamkhi et al., 2021). The secondary metabolism pathway in plants is defined as the small molecular products of metabolism that are not required for the organism's survival. The secondary metabolites are plant-defensive compounds produced by various secondary metabolism pathways in nature (Yang et al., 2018). The research of plant-based herbal remedies is mainly based on the characterization of bioactive molecules derived from different medicinal plants. The plant secondary metabolites are organic compounds confined to certain taxa in the plant kingdom and they are not involved directly to promote plant growth and development, but they are known to carry out a variety of other vital roles (Kumar et al., 2021). Secondary metabolite formation is the outcome of thousands of years of plant-microorganism interaction, and more than 100,000 metabolites are thought to perform a significant role in the plant defense system (Wink, 2008). Plant growth-promoting rhizobacteria not only produce phytohormones, but also regulate the plant's endogenous phytohormone level (Taghinasab and Jabaji, 2020). According to the studies on seeds of *S. miltiorrhiza*, core microbiomes on seeds have a role in the biosynthesis and metabolism of terpenoids and other bioactive molecules (Chen et al., 2018). The *Paraburkholderia fungorum* BRRh-4 and *Bacillus amyloliquefaciens* B Chi1 help to improve the production of anthocyanin in strawberry fruits. Similarly, plant probiotics improve the production of carotenoids. In strawberry fruits, strain *P. fungorum BRRh-4* has a role in eliciting the production of flavonoids (Rahman et al., 2018). Numerous bacterial species can produce plant secondary metabolites like cytokinin, gibberellins, abscisic acid, and indole-3-acetic acid. Examples of such bacteria are *Rhizobium phaseoli*, *Bacillus pumilus*, *B. macroides*, and *Acinetobacter calcoaceticus* (Kang et al., 2019). More than 75% of crop plants have a symbiotic interaction with AMF. AMF colonization enhances the production of secondary metabolites like flavonoids, triterpenoids, glycosylates, apocarotenoids, cyclohexanone derivatives, and phenolic compounds. The *Rhizophagus intraradices* promote the formation of phenolic compounds and terpenoids in *Mentha* *spicata* (Kumar et al., 2021). Some Trichoderma strains help plants to fight against pathogens by producing secondary metabolites (Vinale et al., 2008). Plant bioactive compounds are commonly divided based on their chemical structure. Several complex molecule groups such as phenolics, flavonoids, terpenes, steroids, and alkaloids, have been linked to the activation and reinforcement of plant defense (Bourgaud et al., 2001). They contain bioactive compounds and rich in phytochemicals that can regulate metabolic activities and thus, promote better health (Galanakis and Drago, 2022). Plants produce some important kinds of bioactive molecules: phenolics, terpenes, and nitrogen/sulfur-containing molecules, which refer as alkaloids. Terpenes' basic unit is 5-C isoterpenoid, which is toxic and repellent to herbivores. Amino acids are the primary source of nitrogen and sulfur-containing compounds. The shikimic acid pathway is responsible for the production of phenolics, which provides the defensive ability to plants (Fig. 4 represents the biosynthesis pathway of production of plant secondary metabolites). Plant secondary metabolites have been classified using a variety of criteria due to their diverse array of plant immunity. Among the criteria are widely accepted precursors, an essential role, and a mechanism of action. Classification is based on the method of production and accumulation of plant secondary metabolites that have a role in plant defense (Zaynab et al., 2018). Plant secondary metabolites play an important role in adapting to various environmental factors that limit plant growth and biosynthesis of secondary metabolites.

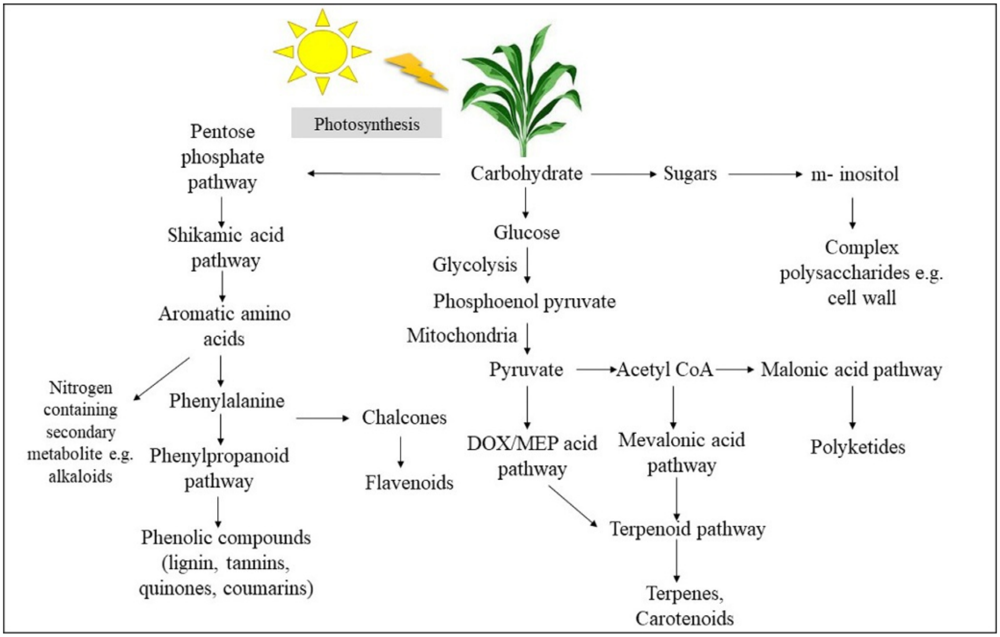

Fig. 4 The biosynthesis pathways involved in the production of plant secondary metabolites.

Secondary metabolism precisely maintains plant growth and development by acting as an essential source of phytochemicals that protect plants from environmental constraints (Bhattacharya, 2019).

8 Conclusion and future aspects

Through the current literature, it is supported that plan-microbe interaction is a constant and interactive process that goes on for many years. The plant and microbe interactions are positive as well as negative. The positive interaction is considered a symbiotic relationship that can benefit plants as well as hosts. The negative interaction includes pathogens, which are harmful to plants. The rhizosphere is considered the region of soil that is associated with or affected by plant roots and this region is specifically considered as one of the prime locations for the colonization of microorganisms. This consortium of microorganisms is considered as the microbiome/microbiota like human gut microbiota. This plant-associated microbiome is known as the plant probiotic bacteria, and it plays a very significant role in maintaining plant health and growth. The study suggests that the molecules secreted by plant probiotic bacteria are biostimulants and they have an important role in the plant's growth, protection, and production of secondary metabolites. They also support the plant during various biotic and environmental stresses. The secondary metabolite is a metabolic intermediate or product that is required for plant growth, they are potent source of bioactive compounds, and current research proves that these bioactive compounds have many health-beneficial properties. The overuse of chemical fertilizers, pesticides, and herbicides during agricultural practices affects the soil composition and alters the microbiome of the rhizosphere. Therefore, rhizosphere engineering is considered the future aspect of reassembling the microbiome composition. This includes the inoculant of plant growth-promoting rhizobacteria that can reprogram the altered microbiome composition; therefore, the future development of commercial inoculants is considered the emerging area of sustainable agriculture.

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CHAPTER 16

Endophytic bacteria: Bioactive compounds and their therapeutic importance

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1 Introduction

Since ancient times, medicinal herbs have been widely used for human welfare, and their metabolites have acted as an essential stockpile for plant-based therapeutic drugs. During the evolutionary period, the recombination of genes and the host has a linear positive association between medicinal plants and endophytes in synthesizing metabolites (Cai et al., 2004). Surprisingly, in recent years, microorganisms associated with plants, instead of actual plants, have proven to provide materials and products with considerable medicinal promise. Endophytes are an endosymbiotic species of bacteria that grow inter- and/or intracellular sites in the leaf segments, petioles, stem and roots, buds, fruit, seeds, and panicles of weeds as dead and hollow hyaline cells of plants (Specian et al., 2012). These organisms complete all or a portion of their life cycles inside their hosts, usually without developing disease symptoms. They interact with their hosts in various intricate ways, including antagonism, mutualism, and occasionally parasitism (Nair and Padmavathy, 2014). Endophytes have been shown to promote nutrient uptake and host plant growth and development. They may raise plants' resistance to insects and other pests and increase their capacity to withstand various biotic and abiotic stresses. They synthesize phytohormones and other bioactive substances with potential biotech applications (Joseph and Priya, 2011). In every plant researched, researchers have found evidence of one or more types of endophytes (Strobel and Daisy, 2003).

2 Endophytic bacteria

The prevalence of endophytic bacteria within a species of plant varies greatly. It is influenced by several factors, including the host species and their genetic background, host growth conditions, and environmental factors (Dudeja and Giri, 2014). Endophytic

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bacteria are normally isolated from all plant compartments, including seeds, and colonize the intercellular space. Endogenous bacteria have been found in dicotyledonous and monocotyledonous plants, including woody plant species like pears and oak and herbaceous plants like sugar beet and corn. Endophytes have been linked to more than 200 genera from 16 phyla of bacterial species. Most endophytes belong to the phyla *Actinobacteria*, *Firmicutes*, and *Proteobacteria* (Golinska et al., 2015). The diversity of endophytic bacteria ranges from gram-negative to gram-positive bacteria such as *Achromobacter*, *Agrobacterium*, *Acinetobacter*, *Brevibacterium*, *Bacillus*, *Microbacterium*, *Pseudomonas*, *Xanthomonas*, etc. (Sun et al., 2013). A single genus, *Streptomyces*, has been estimated to be responsible for 76% of the bioactive metabolites produced by endophytic bacteria, which are varied and function as antibacterial and anticancer substances (Berdy, 2012). Alkaloids, benzoquinones, flavonoids, steroids, phenols, terpenoids, and xanthones are a few of the structurally distinct, bioactive natural metabolites primarily found in bacterial endophytes and have a great deal of potential for the development of novel treatments (Tan and Zou, 2001). They are highly efficient manufacturers of cytotoxic, immunosuppressive, antioxidant, antiviral, antifungal, and antibacterial metabolites, as now more than 200 bacterial species have been introduced as endophytes (Golinska et al., 2015; Nisa et al., 2022).

3 The therapeutic potential of endophytic bacteria

Much scientific evidence suggests that endophytic bacteria are the basin of unique bioactive substances like alkaloids, methoxyphenols, xanthones, depsipeptide, bicyclic lactones, butenolides, butyrolactones, benzopyran derivatives, cytochalasin-related compounds, diketopiperazine, depsidoenes, ergosterol, isofuranonaphthalenone, maleimide-bearing compounds, and cyclic pentapeptides. These recognized compounds have been characterized by good therapeutic properties such as antidiabetic antioxidant, antimicrobial, anti-inflammatory, antiviral, anticancer, neuroprotective, and hepatoprotective properties, which are important to sustainable health care and a healthy lifestyle (Kumar et al., 2022) (Fig. 1). Here, we have addressed the research demonstrating that endophytes serve as repositories for new bioactive substances with prospective therapeutic applications. Various endophytic bacteria have produced a variety of natural drugs that have been identified and purified. Table 1 summarizes these compounds' medicinal potential and their respective sources.

4 Biocontrol potential of endophytic bacteria

The use of a biological agent or microorganisms to control the growth of an insect or pest is known as biocontrol. Biological control is another name for this process. To get pest-free fields, biocontrol is employed. To minimize the harmful impacts of plant diseases and promote plant disease resistance, biological control is defined as the utilization of

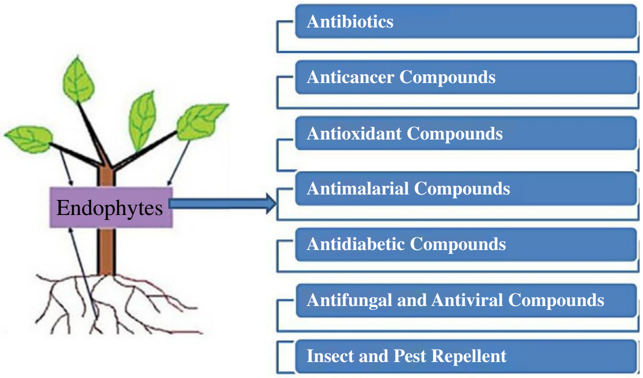

Fig. 1 Therapeutic application of bacterial endophytes.

Table 1 Endophytic bacterium their antibiotics and reported activities.

Name of endophytic bacteria	Source of endophytic bacteria	Types of chemicals produced	Antibiotics isolated	References
Pseudomonas viridiflava	*Lactuca sativa*	Lipopeptides	Ecomycin	Miller et al. (1998)
Streptomyces sp.	*Kennedia nigriscans*	Peptide	Munumbicin	Castillo et al. (2002, 2006)
Pseudomonas syringae	*Nicotiana benthamiana*	Lipopeptides	Pseudomycins	Harrison et al. (1991)
Streptomyces sp.	*Greevilea pteridifolia*	Peptide with quinoxaline rings	Kakadumycin	Castillo et al. (2003)
Streptomyces sp.	*Kennedelia candel*	Pentacyclicindolosesquiterpine	Xiamycin	Ding et al. (2011)

beneficial organisms and their products, such as metabolites and genes. The main goals of biological treatment are to lower insect populations and generate pest-free crops. It is a long-term and self-sustaining solution for invasive plant management. The biological organisms utilized in this procedure are used to control pests, including mosquitoes, bacteria, and grazing animals, and to inhibit the spread of weeds. Endophytic bacteria can decrease or stop some pathogenic organisms from causing harm. They appear to affect their plant host significantly through methods related to those identified in bacteria which are found in the rhizosphere (Ryan et al., 2008).

5 Antifungal properties

Studies on the bioactivity of the bacterial endophytes isolated from medicinal plants have revealed the presence of several bioactive chemicals with various known and unknown activities, including several powerful antifungal drugs. For instance, the growth of the disease-causing fungi *Phytophtora* sp., *Rhizoctonia* sp., and *Sclerotium* sp. was inhibited by a *Bacillus* strain discovered in the stems of the Indian conventional medicinal plant *Bacopa monnieri* L. (Jasim et al., 2016). Additionally, this bacterium can suppress pathogenic species such as *B. subtilis*, *Escherichia coli*, *Salmonella enterica*, *Klebsiella pneumonia*, and *Staphylococcus aureus*. *Ralstonia solanacearum*, which causes wilt disease in tomatoes, is significantly inhibited by two unidentified isolates of endophytic bacteria from healthy tomato plants (Purnawati, 2014). Additionally, it is demonstrated that endophytic *Bacillus* sp. isolated from yearly crops functions as a possible biocontrol agent for the fungus that causes cacao's black pod rot (Melnick et al., 2008). Like this, endophytic bacteria *Rhodococcus* sp. isolated from *Arabidopsis thaliana* (L.) reduced symptoms of the fungus *Ceratocystis fimbriata*'s black rot disease in sweet potato leaves (*Impomeoa batatas* (L.) Lam.) (Hong et al., 2016). Bacteria endophytes isolated from *Andrographis paniculata* Nees. displayed various actions concerning clinical and fish pathogens (Arunachalam and Gayathri, 2010). *Pythium aphanidermatum*, *Rhizoctonia solani*, *Sclerotium rolfsii*, and the plant-pathogenic fungi that were successfully inhibited by the lipopeptide "pumilacidin," which was formed by the bacteria *Bacillus pumilus*, isolated from the South American woody shrub cassava (de Melo et al., 2009).

6 Antibiotics produced by endophytic bacteria

Alarming growth is seen in the global population, and numerous new health problems are emerging. One reason to be concerned is the rise in drug-resistant microorganisms. The universal fight against the escalating issue of antibiotic ineffectiveness depends on research into antibiotics and other microbial natural compounds. The natural medicinal compounds produced by endophytic bacteria have numerous prospective applications in the pharmaceutical sector. Due to their close and nonharmful relationship with plants, endophytic bacteria have gained enormous interest in the past few years in creating a range of antimicrobial substances with unique mechanisms of action (Strobel and Daisy, 2003). Numerous endophytic bacteria-derived secondary metabolites have proven therapeutic applications (Gunatilaka, 2006). *Pseudomonas entomophila*, *Bacillus tequilensis*, *Pseudomonas hibiscicola*, *Chryseobacterium indologenes*, and four endophytic isolates from *Aloe barbadensis* Miller, possess a wide range of antimicrobial actions against disease-causing microorganisms such as *Salmonella typhimurium, S. aureus*, *S. pyogenes*, and *Klebsiella pneumonia* (Akinsanya et al., 2015). Ecomycins, Munumbicins, Pseudomycins, and Xiamycins are natural compounds produced from EB that have antibacterial, antiplasmodial, and antimycotic properties. A number of these natural compounds have even been said to have antiviral capabilities, including those that can combat HIV. Endophytes are considered a fantastic source of bioactive natural compounds. Many bacterial endophytes produced different antibiotics, representing among the most promising new antibiotics sources that have not yet been fully explored.

Interestingly, powerful antibiotics such as iturin, fengycin, and surfactin were discovered among the various bioactive components of the bacterial strain. Another *Bacillus* endophytic strain isolated from the ancient eastern medicinal herb *A. paniculata* Nees was recognized for its broad-spectrum antibacterial activities (Roy et al., 2016). The bacterial pathogens *Aeromonas caviae*, *B. cereus*, *B. subtilis*, *Proteus vulgaris*, *P. Aeruginosa*, and *Vibrio parahaemolyticus* were all inhibited by this strain. Three different anti-infective metabolites were found in the extracts, one of which was a derivative of the anti-infective compound anthracene *Streptomyces* sp. NRRL 30562. A new class of bioactive compounds known as munumbicins was isolated from medicinal plant *Kennedia nigriscans* stem tissues (Castillo et al., 2002). Munumbicins are effective against bacteria that cause disease in humans and plants, including strains resistant to antibiotics. *Mycobacterium tuberculosis* having multidrug resistance was successfully treated with *munumbicin B*. Surprisingly, each munumbicin particle proved effective against *Plasmodium falciparum*, the malaria-causing parasite with the highest pathogenicity level. Opportunistic human pathogens *Burkholderia cepacia* complex, which causes significant infections in immune-compromised persons, were inhibited by bacterial endophytes isolated from the medicinal plant *E. purpurea* (Chiellini et al., 2017). Methicillin-resistant *S. aureus* has been inhibited by the bacterial endophytes *Bacillus amyloliquefaciens* isolated from *Curcuma zanthorrhiza* Rox. (Indrawati et al., 2018). Some of the new antibiotics generated by endophytic bacteria include Ecomycins, Munumbicins, Pseudomycins, and Kakadumycins. Ecomycins are known to be produced by *Pseudomonas viridiflava*, an endophytic bacterium (Miller et al., 1998). Interestingly, anti-HIV activity is demonstrated by Xiamycin-A (Ding et al., 2010). Ding et al. (2011) published the results of three novel indolosesquiterpenes: xiamycin B, sespenine, and indosespene, and in addition to the known Xiamycin-A, from the Streptomyces sp. HKI0595 culture broth, a bacterial endophyte of the common mangrove tree, *Kandelia candle*. According to their research, these Xiamycins were effective against various bacteria, including methicillin-resistant and vancomycin-resistant *Enterococcus faecalis*, and *S. aureus*. Many natural compounds produced by bacterial endophytes isolated from turmeric are antibacterial, inhibiting the growth of various bacterial pathogens (Christina et al., 2013). Potential endophytic bacteria and their novel antibiotic compounds are listed in Table 1.

7 Anticancer properties of endophytic bacteria

The abnormal cells inside the body are known to be cancer or tumors; the cells inside the body are uncontrolled inside the body. Cancer disease is just not only in humans or animals but also it is possible in any other living organism. Lungs, prostate, brain, breast tumors, etc., are common types of cancer. The leading cause of mortality globally is cancer, accounting for over 8.2 million deaths. According to a report by the World Health Organization (WHO), death due to chronic disease will increase by 70% more by the year 2030. The natural compounds obtained from the endophytic bacteria are a significant source of anticancer agents and play a massive role in medicines related to anticancer drugs (Schulz et al., 2002). The first anti-tumoral EPS, a naturally occurring substance with excellent therapeutic efficacy for treating cancer as a novel anticancer agent, was identified in Bacillus (Chen et al., 2013). From the Brazilian medicinal herb *Lychnophora ericoides*, actinobacterial endophytic isolates, primarily *Streptomyces*, have shown efficacy against human cancer cell lines in addition to bacteria and yeast, demonstrating its potential cytotoxicity (Conti et al., 2016). Thirty-nine percent of extracts of bacterial endophytes showed tremendous cytotoxic activity against various carcinoma cell lines. The Acinetobacter extracted showed crucial anticancer properties by reducing cancer or tumor cell lines of cancer cells by 50%. *Acinetobacter*, *Bacillus subtitles*, *Pantoea* sp., etc., are some bacterial endophytes isolated and extracted from plants with huge anticancer potential. Several bioactive substances found in *C. macowanii* leaves, including augustine, crinamine, lycorine, pretazettine, and galanthamine, have been linked to anticancer activity (Fennell and van Staden, 2001). *Acinetobacter guillouiae* crude extract of endophyte, the only sample analyzed, was influential in combating UMG87 glioma cells and may be a successful therapy for brain cancer; cells were decreased by 31% at 100 g/mL and by 53% at 3.13 g/mL (Nair and van Staden, 2013).

The anticancer action of crude endophytes extracts from *Bacillus safensis*, *Arthrobacter pascens*, *Enterobacter asburiae*, *Pseudomonas palleroniana*, and *P. cichorii* has never before been reported, as far as we are aware. The only sample tested that demonstrated anticancer activity against UMG87 glioblastoma cells was *A. guillouiae* crude endophyte extract, which showed a 31% cell decline at 100 g/mL and a 53% cell decline at 3.13 g/mL, suggesting that it may be a valuable anticancer drug for brain cancer. With a 50% cell decrease at 100 g/mL, crude extracts of *B. safensis* demonstrated remarkable effectiveness on A549 lung cancer cells. Colon, hepatocellular, and breast carcinoma were all responsive to crude extracts of the sea sponge-isolated from bacterial endophyte *B. safensis* (Ferdous et al., 2018). There is evidence that *Pseudomonas* species produce anticancer substances and act against various cancer cell types in human types (Michelsen et al., 2015). At a 100 g/mL concentration, *P. putida* crude endophyte extracts reduced A549 lung cancer cells by 47%. Fluorouracil, an anticancer medication, and a bioactive aromatic molecule may be produced by *P. putida* TJ151 (Asif et al., 2016). The *P. putida* L-methioninase enzyme has demonstrated anticancer action against leukemia cell lines in the liver, HepG2, breast, MCF-7, prostate, and colon (Selim et al., 2016). Methioninase obtained from *P. putida* and 5-fluorouracil prevents tumor development, which accounts for the exhibited activity (Yoshioka et al., 1998). At a 100 g/mL concentration, raw endophyte extracts from *Raoultella ornithinolytica* reduced A549 lung cancer cells by 43%. Human endometrioid ovarian cancer line, breast adenocarcinoma line, and HeLa cell line have all been exposed to the protein complex of *R. ornithinolytica*, which has demonstrated anticancer properties (Fiołka et al., 2013, 2015). Crude endophytic extract of *A. pascens*, *E. asburiae*, *Pseudomonas* sp., and *P. palleroniana* did not exhibit any

Table 2 Endophytic bacteria with anticancer properties.

Name of endophytic bacteria	Source of endophytic bacteria	Host plant family	References
Bacillus polympeal	*Lilium lancifolium*	Liliaceae	Weselowski et al. (2016)
Bacillus	*Malus domestica*	Rosaceae	Xiao et al. (2017)
B. licheniformis	*Prosecco*	Vitaceae	Baldan et al. (2015)
B. pseudomycoides	*Perennial ryegrass*	Poaceae	Berdy (2012)
Bacillus dentriformis	*Aquilaria malaccensis*	Thymelaeaceae	Ryu et al. (2005)
Acinetobacter guillouiae	*Sugar beet*	Amaranthaceae	Sebola et al. (2019)
Bacillus subtills	*Glycine max*	Fabaceae	Shweta et al. (2013)
Pantoea sp.	*Saccharum officinarum*	Poaceae	Uche-Okereafor et al. (2019)

observable cancer activity against A549 lung cancer cells. They are purifying and evaluating the crude endophyte extracts of *B. safensis*, *P. putida*, *P. palleroniana*, and *R. ornithinolytica* for their anticancer properties against different cancer cell lines. An endophytic bacterial strain, EML-CAP3 isolated from *C. annuum* L. leaf, exhibited strong antiangiogenic properties. Lipophilic peptides produced by this endophytic bacterial strain inhibited the increase of human umbilical vein endothelial cells and showed antiangiogenic potential in tumor development (Jung et al., 2014). Details of endophytic bacteria and their anticancer compounds are listed in Table 2.

8 Antioxidant properties of endophytic bacteria

Common sources of natural antioxidants include fruits, vegetables, and medicinal herbs. Nevertheless, it has been claimed that endophyte metabolites could serve as a source of new natural antioxidants. Antioxidants block the body's free radicals, scavenge them, or promote their decomposition. Excessive free radical generation from exogenous or endogenous sources may contribute to several diseases, including autoimmune disorders, cancer, and neurodegenerative and cardiovascular diseases (Pham Huy et al., 2008). Consequently, investigating natural sources of chemicals with antioxidative action has increased in recent years. In a more recent investigation, secondary metabolites discovered in endophytic *Pseudomonas aeruginosa* isolated from *Anredera cordifolia* leaf extract showed pharmaceutically significant antioxidant properties. These secondary metabolites comprised 15 volatile constituents, including diisooctyl (Ngidi et al., 2020). Endophytic bacteria bacillus isolated from *Carica papaya* L. leaves can generate secondary metabolites. They had a 68.5% free radical scavenging activity and up to 69 mg gallic acid/g total phenolic content (Adiwibawa Prasetya et al., 2019). A possible antioxidant supplement may be obtained from the crude extract of the endophytic bacterium *Methylobacterium*

Table 3 Endophytic bacteria with antioxidant properties.

Name of endophytic bacteria	Source of endophytic bacteria	Host plant family	References
Methylobacterium radiotolerens	*Arachis hypogaea*	*Fabaceae*	Dourado and Cesar (2015)
Chryseo bacterium	*Solanum lycopersium*	*Solanaceae*	Montero-Calasanz et al. (2014)
Micrococcus	*Cyperus conglomerates*	*Cyperaceae*	Lafi et al. (2016)
Aeromonar	*Glycine max*	*Fabaceae*	Akinsanya et al. (2015)
Cedecea	*Arugula*	*Brassicaceae*	Akinsanya et al. (2015)
Klebsiella	*Noble dendrobium*	*Orchidaceae*	Kifle and Laing (2016)
Bacillus atrophaeus	*Glycyrrhiza uralensis*	Fabaceae	Mohamad et al. (2018)
Lysinbacillus	*Zea mays*	*Poaceae*	Diale et al. (2018)
B. licheniformis	*Z. mays*	*Poaceae*	Aljuraifani et al. (2019)
Bacillus thuringiensis, *B. anthracis*, and *B. cereus*	*Berberis lycium*	*Berberidaceae*	Nisa et al. (2022)

radiotolerans, which was isolated from the seeds of the medicinal plant Combretum erythrophyllum (Photolo et al., 2020). *Paenibacillus polymyxa* EJS-3 bacteria isolated from the Chinese medicinal plant *Stemona japonica* exhibited antioxidant properties. Exopolysaccharide (EPS) from this bacterial species was produced in vitro, and both the raw and the refined EPS showed potent scavenging action against hydroxyl radicals and superoxide. Although *Berberis lycium* is a significant medicinal plant, there is limited information available on the recovery and assessment of the therapeutic potential of its endophytic bacteria. *Bacillus thuringiensis* (SBL3), *B. anthracis* (SBL4), and *B. cereus* (LBL6) crude extract isolated from their host *Berberis lycium* exhibited good antioxidant activity for 43%, 45%, and 56%, respectively, at a concentration of 1000 g/mL (Nisha et al., 2022). Table 3 provides information on endophytic bacteria with antioxidant properties.

9 Antimalarial properties of endophytic bacteria

More than 3.3 billion people worldwide are still suffering from the danger of transmission, and it is considered one of the significant causes of death and morbidity (Ateba et al., 2018). Ninety-one countries reported 445,000 malaria fatalities and 216 million new incidents in 2016. Most malaria cases are found in subtropical and tropical areas of the world, particularly in Southeast Asia and sub-Saharan Africa, where *Plasmodium falciparum* is responsible for 80% of all cases (Ateba et al., 2018). In addition, gancidin W, isolated from an endophytic bacteria *Streptomyces* sp. hosted by *Shorea ovalis*, demonstrated antimalarial activity against *Plasmodium berghei* PZZ1/100 in vivo, resulting in about 80% parasite growth reduction in male ICR mice to strain at 6.25 and 3.125 g/kg.b.wt. (Zin et al., 2017). Using the microculture radioisotope approach, isofuranonaphthalenone isolated from *Nodulisporium* sp., which inhabits *Antidesma ghaesembilla*, has also demonstrated an inhibitory effect against the "multidrug-resistant *P. falciparum* K1 strain" (Prabpai et al., 2015). Endophytic *Streptomyces* strain SUK8, SUK10, and SUK27 isolated from three Malaysian plants, *Scindapsus hederaceus*, *Shorea ovalis*, and *Zingiber spectabilis*, have the new antimalarial compounds against *Plasmodium berghei* PZZ1/100 (Baba et al., 2015).

10 Antidiabetic properties of endophytic bacteria

Diabetes mellitus (DM) is caused by either improper glucose metabolism associated with lower blood insulin levels or insulin resistance in the target organs. This disease affects several people worldwide, and between 1980 and 2014 there were 422 million more patients than in 1980. Its prevalence is anticipated to increase from 171 million in 2000 to 366 million in 2030 (Shaw et al., 2010). The most common type of diabetes mellitus is type 2, affecting around 90%–95% of DM patients. Such people experience a slowdown in the pancreas' ability to release insulin in response to a meal, which causes the postprandial increase of blood sugar after eating. Diabetes can be regulated by synthetic antidiabetic drugs and allopathic hypoglycemic agents, which control the activity of some metabolic enzymes, including amylases. But it has been estimated that existing synthetic antidiabetic drugs and allopathic hypoglycemic agents have several limitations and allergic reactions. Hence, there is a constant need for discovery. Therefore, there is a continuous need to discover the development of safe new lead biomolecules and more effective antidiabetic compounds to combat diabetes mellitus and prevent the side effect caused by existing synthetic antidiabetic drugs and allopathic hypoglycemic agents.

The diverse applications of active molecules to treat diabetes mellitus and other chronic illnesses, cheap production costs, and structural variety of natural product drugs have reignited interest in this field. Secondary metabolites produced by bacterial endophytes in medicinal plants, such as alkaloids, flavonoids, steroids, terpenoids, etc., are recognized to have a variety of biological functions. Moreover, due to their natural origin, metabolites derived from plants are increasingly preferred for therapeutic applications worldwide. Natural products, especially those of plant origin, are the premise for discovering prospective chemical substances and will play an important role in upcoming drug development. In addition, many florae provide large amounts of bioactive chemicals, which may occur without undesirable elements and their potent pharmacological effects. Over the centuries, many floras have been used, especially in developing countries, in the fight against diabetes in order to reduce the financial burden of conventional medicines for humans. Based on earlier research, it can be claimed that endophytic bacteria are a fantastic source of chemicals that may be used to cure diabetes. *Exiguobacterium indicum*, an Endophytic bacterium from *Murraya koenigii* (L.) Spreng leaves, chloroform extract significantly reduced blood sugar levels in unaltered rats and prevent diabetes in streptozotocin-induced diabetic rats (Habbu et al., 2014). *Tinospora crisp* entophytic actinomycetes isolates revealed a unique species that share 92% of its DNA, with *Streptomyces olivochromogenes* exhibiting antidiabetic properties (Pujiyanto et al., 2012; Chigurupati et al., 2021) Endophytic bacteria *Cronobacter sakazakii* isolated from *Durio zibethinus* leaves recently revealed α-glucosidase- and α-amylase-inhibiting action and have remarkable potential in creating antidiabetic bioactive chemicals.

11 Anti-inflammatory potential of endophytic bacteria

The wide range of activity of compounds originating from endophytes also includes anti-inflammatory effects; Streptomyces sp. LJK109, isolated from *Alpinia galangal* root, tends to produce 3-methylcarbazoles, the primary anti-inflammatory component, and inhibits macrophage development of the inflammatory mediators TNF-, IL-1, IL-6, IL-10, and PGE2, in a dose-dependent manner (Taechowisan et al., 2012). Using both in vivo and in vitro tests, Urumbil and Anilkumar (2021) showed the ethyl acetate extract of *Bacillus subtilis* strain-MG 692780 from *Emilia sonchifolia* (Linn.). The injection of the bacterial extract significantly decreased the inflammations in mice brought on by formalin and carrageenan.

12 Future perspective in therapeutic applications of endophytic bacteria

Endophytic bacteria are a major source of bioactive compounds due to their diverse metabolic capabilities and mutualistic relationship with the host plant, which chemically enhances the host plant's response to environmental challenges (Jasim et al., 2016). In actuality, endophytic biosynthetic adaptability produces a high metabolite variety that may be investigated to develop therapeutics to combat plant and human pathogens. Endophyte subculturing and storage significantly impact the output of endophytic therapeutic substances (El-Sayed et al., 2020). As a result, finding potential microorganisms must go on, and a coculturing system has to be set up for better endophyte exploration. It is desired and necessary to continue the development of in vitro plant-endophytes models in order to shed light on the use of new resources in these sectors. Biotechnological techniques like in vitro modification, genome mining, and functional genomics should be used to identify new compounds with significant medicinal potential against human diseases and to increase the productivity of a therapeutic drug from endophytic bacteria.

13 Conclusion

Bacterial endophytes are the most prominent group of the wide range of species that occur in different environments and can produce diverse bioactive compounds, which are beneficial for developing new drugs. It is vital to look for new treatments because many germs have evolved to be resistant to the available antibiotics. Understanding endophytes' physiology, metabolic processes, defensive function, production of secondary metabolites, and motivating professionals in biomedical research to contribute to endophyte-related research requires a great deal of work. In conclusion, endophytic bacteria hold tremendous potential for bioprospecting and may 1 day provide a source of novel medicines and antibiotics. Since endophytic bacteria can produce novel and advantageous bioactive substances, there are very few studies investigating the therapeutic potential of endophytic bacteria. Therefore, the present situation demands considerable research to examine underutilized, underused, and overlooked endophytic microorganisms. In order to effectively explore endophytic bacteria in the exploration of new therapeutic substances, it is essential to establish a network of scientists from fields, including ethnobotany, chemistry, microbiology, molecular biology, pharmacology, taxonomy, and bioinformatics.

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Progress in Biochemistry and Biotechnology

BIOTECHNOLOGY OF EMERGING MICROBES

Prospects for Agriculture and Environment

Our planet is facing unprecedented challenges pertaining to agriculture, food security, and environmental issues. Rapid growth in industrialization, increase in population, erosion of soil, degradation of agricultural lands, deforestation, accumulation of recalcitrant chemicals, global warming, and fossil fuels are some of the major causes of this phenomenon. Although no one can precisely predict the future, it is unanimously accepted that we must do something to prevent such a catastrophic future. Although different environmental engineering strategies have been developed, only a few address the relationship between carbon dioxide accumulation, biosphere, and ecosystem safety. Biotechnology and bioengineering of microbes are sustainable alternatives to address these challenges due to their rapidly increasing potential for the development of living systems.

Biotechnology of Emerging Microbes brings together the ideas and latest developments of leading biotechnologists and bioengineers. The book covers various aspects of microbe-mediated rhizosphere, biosphere, and environmental and ecosystem biotechnology and focuses on the restoration and management of the rhizosphere, the biosphere, and the ecosystem with microbes for a sustainable future.

This book is designed to provide information on various technical and application details of microorganisms and their products in light of biotechnology and bioengineering approaches. The book provides up-to-date knowledge to beginners, researchers, students, scientists, engineers, and industry stakeholders, who can support the management of ecosystems through the use of microbes.

Key Features

- Provides various technical and application details of microorganisms and their products in light of biotechnology and bioengineering approaches
- Brings together the ideas and latest developments of leading biotechnologists and bioengineers
- Covers various aspects of microbe-mediated rhizosphere, biosphere, and environmental and ecosystem biotechnology

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