Soil Microbes for Sustainable Agriculture

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Abstract

Soils are habitats for major forms of life such as microorganisms (e.g., bacteria, archaea, fungi) as well as insects, annelids, algae, and plants. Microorganisms have potential roles to play in sustainable agricultural production due to their ability to promote plant growth and enhance biotic and abiotic stress resistance, remediate contaminated soils, recycle nutrients, manage soil fertility, and weather and mineralize rocks and other abilities that result in the reduced use of fertilizers or pesticides in agriculture. Recently introduced biotechnological approaches help to modify microbes that can be used to enhance bioremediation and phytoremediation of contaminated soil that can be used for agricultural production. Sustainable agriculture is essential today to meet our long-term agricultural needs by using natural resources without degrading the environment. Here, we discuss the structure and diversity of soil microorganisms and their potential role in nutrient recycling, remediation of heavy metal from contaminated environments, plant growth promotion, stress tolerance, phytohormone production, etc. for sustainable agriculture to feed future generations.

Keywords

Heavy metal contamination · Nutrient recycling · Plant growth · Soil microbes

Abbreviations

DNA	Deoxyribonucleic acid
RNA	Ribonucleic acid
DPANN	Diapherotrites, Parvarchaeota, Aenigmarchaeota, Nanoarchaeota, Nanohaloarchaea
EM	Ectomycorrhiza
BNF	Biological nitrogen fixation
PSOs	Phosphorus-solubilizing organisms
PGPB	Plant growth-promoting bacteria
IAA	Indole-3-acetic acid
PIN	PIN-FORMED protein
GA3	Gibberellins
EPS	Exopolysaccharide

10.1 Introduction

Soils are heterogeneous habitats that support microbial populations of enormous size and diversity. Soils are home to a vast diversity of bacteria, archaea, fungi, insects, annelids, and other invertebrates as well as plants and algae. Soils provide food or nutrients to all organisms either living above or below the ground and also play critical roles in buffering and filtering freshwater ecosystem. Moreover, soil microbes such as bacteria, archaea, fungi, and cyanobacteria play diverse and often crucial roles in ecosystem services. The vast metabolic diversity of soil microbes means that their activities drive or contribute to the cycling of all major elements (e.g., C, N, P), and this cycling affects the structure and the functions of the soil ecosystem as well as the ability of soil to provide environmental services to people (Aislabie and Deslippe 2013; Meena et al. 2015d).

Agriculture faces the great challenge of providing food using limited natural resources to an ever-growing human population in the face of climate change. This great challenge cannot be faced without sustainable development (Altieri et al. 2017; Kumar et al. 2017b) that meets the needs of the present without compromising the ability of future generations to meet their own needs (ONU 1992). Sustainable agriculture is a set of strategies, especially management, which improve or maintain the quality and quantity of the food supply without compromising the environment or productivity of crops over the long term. Sustainable agriculture is essential today as it endeavors to meet our long-term agricultural needs by using specialized cultivation techniques that strive to fully utilize natural resources, something that conventional agriculture fails to achieve. This principle is environment-friendly and ensures safe and healthy agricultural products (Manzano-Agugliaro and Cañero 2010; Nuijten et al. 2016; Gázquez et al. 2016; Zapata-Sierra and Manzano-Agugliaro 2017; Yadav et al. 2018b). In sustainable agriculture, microorganisms have potential roles due to their ability to promote plant growth and stress resistance, remediate soil contaminated with heavy metals, recycle nutrients, manage soil fertility over long term, and promote the mineralization of rocks and their abilities to reduce fertilizers or pesticidal use in agriculture. The objective of this chapter is to discuss soil microbes, their function, and potential scope to use them in agricultural sustainability.

10.2 Soil Microbial Diversity

Although the size of an individual soil microorganism is very small, they have very significant effects on the physical, chemical, and biological processes in soil that are directly and indirectly critical for the growth and development of a plant and animal. Bacteria and archaea are single-celled organisms that often take the form of rods, cocci, or spirals, and a few may also form branching filaments, such as the actinomycetales. Bacterial DNA lies free within the cytoplasm since they do not have a membrane-bound nucleus. Their genome usually comprises a single circular chromosome and 2–7 smaller DNA elements known as plasmids. The genome size of bacteria is about 4000–6000 kbp and encodes 3000–4000 proteins. Bacteria usually have cell wall composed of a protein, carbohydrate, and lipid. Like other organisms, bacteria and archaea require carbon to synthesize the building blocks of the cell and require energy to drive the reactions involved in cell synthesis and metabolism. Some bacteria require oxygen to grow while other bacteria and many archaea use alternative electron acceptors, including nitrate and sulfate. For such type of anaerobic organisms' oxygen may be toxic. On the basis of energy requirement, microbes can be classified into two types: autotrophs or heterotrophs. Sunlight (photoautotrophs) and the oxidation of reduced inorganic compounds (e.g., Fe^{2+}, ammonia, or nitrite; chemoautotrophs) are the main sources of energy for autotrophic microbes to fix carbon dioxide to produce carbohydrate, fat, and protein, whereas heterotrophs use organic carbon compounds as a source of carbon and energy.

Archaea were known as extremophiles due to their abundance in harsh environments, but now it is found that they are ubiquitous in nature and widespread in many environments, including soil. Morphologically archaea and bacteria are similar, but phylogenetic analyses of 16S ribosomal RNA gene sequences revealed that the living organisms can be divided into three domains, with archaea being more closely related to eukaryotes than the bacteria (Woese et al. 1990).

Fungi, as eukaryotes, are more closely related to plant and animal than to bacteria or archaea. A membrane-bound nucleus with single or multiple chromosomes and membrane-bound organelles such as mitochondria are present in fungi. Glucans and chitin are the main components of the fungal cell wall. Fungi are heterotrophic organisms and their usual nutritional strategy is saprophytic, meaning that they feed on decaying matter. Fungi can be single-celled organisms known as yeast, while many grow in the form of a threadlike structure known as hyphae. These are commonly 2–10 μm in diameter and may be either septate or nonseptate.

Different factors like climate, vegetation, physical and chemical properties of the soil, crop cultivation, etc., influence the number of soil organisms, their diversity, biomass, and metabolic activity. For example, species diversity of soil microorganism differs totally between arid desert and humid forest, acid soils, and alkaline soils.

Initially, only cultivatable bacterial and fungal soil diversity was studied, but it represents less than 10% of the soil bacterial community. Thus, scientists were looking for other approaches. During the 1980s Norman Pace and his colleagues realized that naturally occurring microbes could be identified without culturing them (Hugenholtz et al. 1998). The extraction of DNA from soil to the amplification and sequencing of ribosomal RNA using appropriate primers followed by phylogenetic analysis helped to identify microbial species from soil. Thus, more diverse organisms could be studied by recently introduced molecular techniques. For example, sequencing of 16S rRNA and other housekeeping genes allows speculation about an organism's characteristic and identification of their closest cultivatable relative. Physiological properties of microbes can also be inferred from phylogenetic conclusions; for example, all cyanobacteria form a monophyletic group, as do many sulfate-reducing bacteria, halophiles, and methanogenic archaea (Aislabie and Deslippe 2013; Ashoka et al. 2017; Kakraliya et al. 2018).

10.2.1 Soil Bacterial Phyla

Amplification and sequencing of 16S rRNA genes from soil bacteria found at least 32 bacterium phylum-level groups, and the dominant phyla were *Proteobacteria*, *Acidobacteria*, *Actinobacteria*, *Verrucomicrobia*, *Bacteroidetes*, *Chloroflexi*, *Planctomycetes*, *Gemmatimonadetes*, and *Firmicutes*, which together represent an average of 92% of soil libraries (Janssen 2006). Although 52 bacterial phyla were described by Rappé and Giovannoni (2003), and 24 were recognized by Bergey's Manual (Garrity et al. 2004), soils seem to be dominated by only the abovementioned nine bacterial phyla. Interestingly, although the number of phyla in soil is low, species diversity is high compared with other environments (Nemergut et al. 2011; Meena and Meena 2017). *Proteobacteria* and *Acidobacteria* are the most abundant soil bacterial phyla. Different members of *Proteobacteria* make up an average of 39% of libraries derived from soil bacterial communities. The phylum *Proteobacteria* can is classified within the classes *α-Proteobacteria*, *β-Proteobacteria*, *γ-Proteobacteria*, and *δ-Proteobacteria* (Janssen 2006). Members of α, β, and γ subphyla are more prevalent in rhizosphere soils where nutrient availability is high (Fierer et al. 2007). The number of *β*- and *γ-Proteobacteria* in soil can be increased by adding low-molecular-weight carbon sources (Goldfarb et al. 2011; Eilers et al. 2012; Yadav et al. 2018a).

Agrobacterium, *Alcaligenes*, *Arthrobacter*, *Bacillus*, *Flavobacterium*, *Micromonospora*, *Nocardia*, *Pseudomonas*, and *Streptomyces* are the dominant bacterial genera in soil among the cultivatable species (Alexander 1977), but these nine genera together make up only 2.5–3.2% of soil bacteria. Of these, *Pseudomonas* spp. are the most abundant in soil bacterial communities, contributing 1.6% of the cloned sequences from soils (Janssen 2006; Meena and Yadav 2015).

Heterotrophic, autotrophic, and methanotrophic bacteria are found in *β-Proteobacteria*; important genera are *Burkholderia*, *Alcaligenes*, and *Acidovorax*. *Burkholderia* species might play important roles in soil by participation in carbon turnover, nitrogen fixation, plant growth promotion, mineral weathering, and live hyphae degradation (de Boer et al. 2004; Uroz et al. 2007; Kumar et al. 2018b). The ammonia oxidizer *Nitrosospira*, the iron oxidizer *Thiobacillus*, and the phototroph *Rhodocyclus* are important autotrophs in *β-Proteobacteria* in soil.

Heterotrophic, lithotrophic, and phototrophic bacteria are found in *γ-Proteobacteria* in the soil. *Pseudomonas* and *Xanthomonas* are the best-known heterotrophic genera in *γ-Proteobacteria*. *Pseudomonas* species can use a wide range of nutrients; most grow on more than 50 different substrates, a few even on over 100 substrates. Sugar, amino acid, fatty acid, alcohol, and hydrocarbon can be utilized by *Pseudomonas* species.

Other sulfate- and iron-reducing bacteria belong to the order *δ-Proteobacteria*. In soil, the sulfate reducer *Desulfovibrio* grows aerobically using lactate or ethanol as carbon source. The genus *Bdellovibrio*, a parasite of other bacteria, also belongs to the *δ-Proteobacteria*. *Helicobacter* and *Campylobacter* are genera of *ε-Proteobacteria* present in soil. Both genera are also present in the digestive tract of animals and could enter the soil with bodily waste.

Thirteen percent of soil bacterial communities belong to the phylum *Actinobacteria*, which contains three subclasses (*Actinobacteridae*, *Acidimicrobidae*, and *Rubrobacteridae*). Moreover, it also contains the subclasses *Rubrobacteridae* and *Acidimicrobidae* (Janssen 2006). *Acidobacteria* are diverse and widespread in soil, especially in acidic soil (Lauber et al. 2009). It is very challenging to cultivate *Acidobacteria* in the laboratory; thus very little is known about their metabolic capabilities. Microbes with Gram-positive cell walls belonging to the *Actinobacteria* and *Firmicutes* are abundant in soil culture collections.

Endospore-forming bacteria and lactic acid bacteria are the members of phylum *Firmicutes*. *Bacillus* and *Clostridium* are the best-known genera of endospore-forming bacteria in soil. *Bacillus* spp. can degrade many different carbon sources, including plant polysaccharides. Some species of *Bacillus* are known to be fermentative, while others fix nitrogen or are denitrifiers. The genus *Clostridium* is metabolically diverse and can ferment sugar, starch, pectin, and cellulose. *Bacillus* and other species of bacteria produce endospores for surviving long term in soil during dry periods. Lactic acid bacteria (e.g., *Lactobacillus*) are found in decaying plant materials and are often aerotolerant anaerobes.

Some members of the phyla *Gemmatimonadetes*, *Chloroflexi*, and *Planctomycetes* are poorly known because many are difficult to culture in the laboratory. Thus, their physiology, genetics, and ecology are also poorly understood. *Gemmatimonadetes* are aerobic heterotrophs that are adapted to low soil moisture conditions (de Bruyn et al. 2011; Varma et al. 2017). Aerobic heterotrophs that belong to the *Chloroflexi* can grow on oligotrophic media and can respire organohalide compounds (Davis et al. 2011).

10.2.2 Soil Archaeal Phyla

The archaea are one of the three primary domains of life (Woese et al. 1990). Archaea are unique in nature due to their presence in the environment with high temperature, extreme pH value, and saline conditions. Archaea a diverse domain of life, and members may exhibit small cells and genome and very low metabolic activity. Genome reduction plays a predominant role in archaeal evolution by which a small-genomed archaeal ancestor subsequently developed complexity via gene duplication and horizontal gene transfer (Williams et al. 2016; Dadhich and Meena 2014; Gogoi et al. 2018). Recent advances in traditional and molecular methods, used for diversity study, have opened a wide window on the diversity of archaea and have resulted in the description of economically important new lineages. Sequencing of 16S rRNA genes found 20 archaeal phyla in environmental samples, but 14 phyla do not have any known culturable representatives (Schloss et al. 2016). Described lineages of archaea are the Euryarchaeota, Thaumarchaeota, Aigarchaeota, Crenarchaeota, Korarchaeota, and DPANN (Diapherotrites, Parvarchaeota, Aenigmarchaeota, Nanoarchaeota, Nanohaloarchaea, and Asgard) (Brochier-Armanet et al. 2008; Guy and Ettema. 2011; Zaremba-Niedzwiedzka et al. 2017). Among these, Asgard is a sister group to TACK (Thaumarchaeota, Aigarchaeota, Crenarchaeota, Korarchaeota) and is considered more closely related to the original eukaryote.

Archaea are important for sustainable agriculture since they take part in ammonia oxidation and play critical roles in the global nitrogen cycle. Different members of archaea are involved in many steps of the nitrogen cycle, such as nitrate respiration and denitrification (Cabello et al. 2004; Meena et al. 2016a). Autotrophic and heterotrophic members of archaea catalyze iron and sulfur oxidation to enhance the release rate of metals and sulfur to the environment (Baker and Banfield 2003; Buragohain et al. 2017). All known methanogenic organisms belong exclusively to the archaeal domain and are generally found in oxygen-depleted environment. Archaea have a large influence in the nitrogen cycle, particularly ammonia oxidation, and the global methane cycle, but their involvement in plant phosphorus nutrition is very limited. Yadav et al. (2015) isolated twenty archaeal strains that were able to solubilize soil phosphorus. The strain IARI-WRAB2 was identified as the most efficient P-solubilizer (134.61 mg l^{-1}) followed by *Halococcus hamelinensis* strain IARI-SNS2 (112.56 mg l^{-1}). Isolated strains produced gluconic acid, citric acid, formic acid, fumaric acid, succinic acid, propionic acid, and tartaric acid to influence P availability.

10.2.3 Soil Fungal Phyla

Fungi are ancient microorganisms found in all ecological niches, including soil. Phylogenetic analysis of 192 proteins encoded by single to low-copy number genes from fungal samples suggested that there are seven phyla in the fungal kingdom. These are *Ascomycota*, *Basidiomycota*, *Blastocladiomycota*, *Cryptomycota*, *Chytridiomycota*, *Mucoromycota*, and *Zoopagomycota*. Phylogenetic analysis showed that the phylum *Cryptomycota* is the earliest diverging lineage of fungi, followed by the phyla *Chytridiomycota* and *Blastocladiomycota* (Spatafora et al. 2016). Moreover, it is assumed that there are 1.5 million to 5 million species of fungi present on Earth (Hibbett et al. 2007; Dadhich et al. 2015). *Chytridiomycota* are widely distributed and saprophytic in nature.

Rhizospheric soil influences the taxonomic and functional diversity of soil microbes, including fungi, because plant roots exude carbon compounds and excrete and adsorb nutrients from the rhizosphere. The fungal mycelium acts as a major route of carbon flow between the plant and the soil microbial community. About 1–22% of photosynthetic substances of plants are distributed to their ectomycorrhizal (EM) fungus partner (Hobbie 2006). The EM fungi release carbon from the hyphae as trehalose, mannitol, and oxalic acid. Nonetheless, mycorrhizal root tips and their vegetative mycelium also provide habitat for bacteria. Thus, fungi are important for the growth and development of plants.

10.2.4 Soil Algal Phyla

Soil algae may be unicellular or multicellular organisms, living both on the soil surface and within the soil. Most soil algae can be found growing on the soil surface or within the top millimeters of the soil. A typical abundance of algae in soil is about 10^6 cells per gram of soil. Indigenous soil algae can move from the surface to the subsurface of the soil horizon and may thus become allochthonous organisms. Algal genera known to inhabit the soil are *Chlorophycophyta*, *Euglenophycophyta*, *Rhodophycophyta*, and *Chrysophycophyta* (Aislabie and Deslippe 2013).

10.3 Nutrient Recycling and Soil Microbes

The chemical and physical recovery of substances for new use is known as recycling. Change in chemical form leading to the physical translocation of materials could also be defined as recycling. All living organisms influence their environment by chemical transformation, and oxidation and reduction by microbes is a major driver for the chemical transformation of different plant nutrients. Soil microbes play important roles in the recycling of many nutrients that are essential for life. Different nutrients like carbon, nitrogen, phosphorus, potassium, zinc, calcium, manganese, and silicon are continuously recycled by microbes. Nutrient recycling is essential because it provides the raw materials to produce amino acids, proteins, DNA, and RNA, which are the building blocks of all known forms of life. For example, weathering of minerals – the main mechanism for converting minerals to plant nutrients – is significantly influenced by microbes such as bacteria and fungi. Weathering is a process by which many plant nutrients are released from minerals. Different nutrients like calcium, magnesium, and potassium are released from weathering of silicate minerals while apatite weathering releases phosphorus in soil. Thus, mineral weathering by soil microbes plays a significant role in ion cycling and plant nutrition (Aislabie and Deslippe 2013; Meena and Yadav 2014).

10.3.1 Carbon Cycling

Carbon (C) is the key constituent of all living organisms and cycling of carbon is significantly regulated by microbes. Plants, cyanobacteria, and free-living and symbiotic lichens are primary producers and fix CO_2 to convert it to organic material. All organic materials are derived from primary producers. Autotrophic microbes can also fix CO_2 in soil. Nonliving organic materials are recycled by soilborne heterotrophic bacteria and fungi. These soil saprotrophs complete the carbon cycle by converting organic material to CO_2 during respiration. In many cases, higher animals (herbivores and carnivores) also need microbes residing in their intestinal tracts to digest particulate organic materials. The degradation of nonliving organic material to carbon dioxide is known as decomposition and is essential to obtain energy for growth. Nonetheless, mineralization of the organic compounds occurs when they are completely degraded into inorganic materials such as CO_2, ammonia, and water (Aislabie and Deslippe 2013; Layek et al. 2018).

The major agents of organic matter decomposition are fungi and bacteria, and they can also degrade complex organic molecules from the environment. Organic molecules such as organic acid, amino acid, and sugar are degraded by bacteria, especially by *Actinobacteria* and *Proteobacteria* (Eilers et al. 2012; Verma et al. 2015b). *Bacteroidetes* of bacteria help to degrade more complex carbon compound such as cellulose, lignin, and chitin, although they need relatively high amounts of available nitrogen to support the production of extracellular and transport enzymes (Treseder et al. 2011). In contrast, bacteria from low N environments are more efficient at metabolizing organic N compounds such as amino acids. Carbon mineralization in soils is positively correlated with abundance of *β-Proteobacteria* and *Bacteroidetes* while negatively correlated with *Acidobacteria* abundance (Fierer et al. 2007).

Degradation of organic matter under anaerobic conditions is only carried out by microbes who produce organic acids and gases such as hydrogen and carbon dioxide from organic compounds. Under strictly anaerobic conditions methanogenic bacteria use hydrogen to reduce the CO_2 and to produce CH_4 gas. Moreover, methanogenic bacteria can metabolize methanol, acetate, or methylamine to CH_4 and CO_2 (Aislabie and Deslippe 2013; Kumar et al. 2018a).

10.3.2 Nitrogen Cycling

Nitrogen (N) is an essential element for all living organism as it is a main constituent of protein and nucleic acids. Protein and nucleic acids are the building blocks of all living systems. Although animals obtain N from organic sources, plants get N from inorganic nitrogen sources such as ammonium and nitrate or simple amino acids (e.g., glycine). Different N pathways such as nitrogen fixation, dissimilatory nitrate reduction to ammonia (DNRA), nitrification, ammonification, and denitrification are employed by microbes. Different microbial processes of N pathways often limit ecosystem productivity as plant biomass production is significantly influenced by N (Aislabie and Deslippe 2013; Meena et al. 2018c).

Biological nitrogen fixation (BNF), the reduction of atmospheric free nitrogen gas to ammonium, is only carried out by prokaryotes. Nitrogen fixation is the only biological process through which new N enters into the biosphere, so it is critically important for ecosystem function. The ammonium produced during BNF is assimilated into amino acids and subsequently polymerized into proteins. Nitrogen-limiting conditions in soil induce nitrogen fixation by microbes. Although rhizobia (*Rhizobium*, *Mesorhizobium*) and *Frankia* are the main players for symbiotic BNF, nitrogen fixation is also carried out by free-living microbes (e.g., *Azotobacter*, *Azospirillum*, *Burkholderia*, *Clostridium*, and some methanogens). Root exudates from plants may supply some of the energy required for nitrogen fixation. Nitrogen fixation rates through symbiotic process are often two or three times higher than those of free-living soil bacteria.

Nitrification is another important process for the availability of plant N in which ammonia or ammonium ions are oxidized to nitrite and then to nitrate. The whole process of nitrification is strictly dependent on a few autotrophic bacteria and Crenarchaeota. Oxidation of ammonia to nitrite is mediated by bacteria like *Nitrosospira* and *Nitrosomonas* or the *crenarchaeum Nitrososphaera*, whereas the oxidation of nitrite to nitrate is mediated by bacteria such as *Nitrobacter* and *Nitrospira*. Nitrification also has some agricultural disadvantages because the oxidation of ammonium to nitrite changes its charge from positive to negative. This leads to nitrate leaching as the negatively charged ions do not interact strongly with soil particulates and can be readily washed into groundwater, which is an important factor for groundwater contamination.

Denitrification is a microbial respiratory process during which soluble nitrogen oxides are used as alternative electron acceptors under anaerobic conditions. Nitrate (NO_3^-), nitrite (NO_2^-), and nitric oxide (NO) are converted to greenhouse gas (GHG), i.e., nitrous oxide (N_2O) or nitrogen gas (N_2). It occurs predominantly in waterlogged soil that has become anaerobic. Complete denitrification (N_2 production) is the major biological mechanism by which fixed N returns to the atmosphere from soil and water and completes the nitrogen cycle. Denitrification creates considerable losses of fixed N from soil, thus limiting the availability of nitrogen essential for crop production. Denitrification is carried out by a diverse range of phylogenetically unrelated soil bacteria (*Proteobacteria*, *Actinobacteria*, and *Firmicutes*), fungi, and other soil eukaryotes. Many denitrifying organisms lack one or more of the enzymes involved in denitrification and are known as "incomplete" denitrifiers. For example, most fungi and approximately one-third of sequenced bacterial denitrifiers (Kobayashi et al. 1996; Philippot et al. 2011; Meena et al. 2018a) lack N_2O reductase enzymes, so their final denitrification product is N_2O. This incomplete denitrification product is a major source of GHG emissions from pastoral agriculture in New Zealand (Saggar et al. 2012). Multiple steps in the nitrogen cycle are influenced by bacteria. For example, *Rhizobium*, *Bradyrhizobium*, and *Azospirillum* have members that both fix nitrogen and denitrify. Nitrifying bacteria such as *Nitrosomonas* can also participate in denitrification.

Nelson et al. (2016) used soil metagenomic data to characterize the biogeography of microbial nitrogen metabolism traits and concluded that about 402 bacterial and 53 archaeal genera encoded nitrogen pathways. Similar trends are also found in bacteria and archaea for their relative frequency of N pathways, except for the dissimilatory nitrite reduction to ammonium pathway (DNRA), which is absent in archaea. Fungal sequences are only associated with assimilatory pathways, including ammonia assimilation, assimilatory nitrate to nitrite, and assimilatory nitrite to ammonium.

10.3.3 Phosphorus Cycling

Phosphorus (P) is not an abundant element in the environment and normally occurs as phosphate in organic and inorganic compounds. Phosphorus availability is reduced at neutral and alkaline pH due to their tendency to precipitate in the presence of divalent and trivalent cations. Microorganisms play an important role in P recycling. Physical movement of P occurs in the P cycle without alteration of the oxidation state. Microorganisms do not usually oxidize or reduce P but assimilate inorganic phosphate and mineralize organic P compounds. In many cases, P is combined with calcium, making them insoluble and unavailable for plants.

Microbes mineralize organic P to form inorganic phosphate by phosphatase enzymes produced by many bacteria and fungi. Moreover, microbes transform insoluble and immobilized inorganic P to soluble or mobile P by producing organic acids. Microbes release P not only for their own use but also for plants and other soil organisms. Mycorrhizal fungi produce oxalate to release phosphate from insoluble mineral P, which is a major strategy for enhancing P availability, allowing plants to overcome P deficiency. Several ectomycorrhizal basidiomycetous fungi have high-affinity phosphate transporters that are expressed in extraradical hyphae in response to phosphorus deficiency in their host (Plassard and Dell 2010; Meena et al. 2015e).

By polymerization, orthophosphate molecules can be linked with each other by phosphoanhydride bonds to make polyphosphate. Polyphosphate (poly-P) is an important compound for organisms to grow for longer period under adverse conditions (Mukherjee et al. 2015). Microorganisms like cyanobacteria and microalgae take up inorganic phosphorus from their growing environment and store it within their cells as poly-P granules to adapt to unfavorable conditions like salt stress, osmotic stress, UV radiation, and fluctuations of pH and temperature in the environment (Achbergerová and Nahalka 2011).

Different microalgal species like *Chlorella* sp. and *Scenedesmus* sp. and cyanobacterial species like *Aphanothece* sp., *Spirulina* sp., *Arthrospira* sp., and *Phormidium* sp. are being used in bioremediation for the removal of nutrients from wastewater (Ray et al. 2013). These microalgae and cyanobacteria could not only be used for excess P removal from wastewater and other polluted environments, but the poly-P in their cells could also be utilized in soil as slow and moderate release phosphorus as bio-fertilizers to optimize plant growth (Mukherjee et al. 2015; Datta et al. 2017b).

Moreover, the release of plant-available phosphorus from the insoluble poly-P present in the biomass of microalgae and cyanobacteria is influenced by the activity of phosphorus-solubilizing organisms (PSOs) in the soil, making the whole process very slow and steady, and thus P supply in the rhizosphere occurs according to the demand of crops. This process therefore reduces the probability of excess P supply (Ray et al. 2013) and control the loss of inorganic phosphorus as soil runoff originating from the injudicious use of inorganic fertilizers.

10.3.4 Sulfur Cycling

Sulfur (S) is present in various organic and inorganic compounds that are transformed from an oxidized state (SO_4^-) to a reduced state (H_2S) by different microorganisms. The S cycle cannot be completed without the help of microorganisms. Both sulfate and hydrogen sulfides are produced from the removal of sulfur from organic compounds under aerobic and anaerobic conditions. In both cases, bacteria play important roles. Moreover, elemental S can be produced by sulfate-reducing bacteria (Atlas 1997).

10.3.5 Iron Cycling

Iron (Fe) cycling is very important for its availability to different organisms. The cycling of Fe is completed by microorganisms by transformation of ferrous (Fe^{2+}) and ferric (Fe^{3+}) oxidation states. The ferric states are less soluble in water; hence plants cannot use Fe in this form. Thus, the conversion of the ferric state to the ferrous state by microorganisms, especially by bacteria, is very important for agricultural sustainability. Different bacterial genera such as *Thiobacillus*, *Galionella*, and *Leptothrix* oxidize iron compounds and enhance plant nutrition. A few species of these genera can deposit ferric hydroxide on their extracellular sheath. Over billions of years, this deposition can form substantial Fe deposits (Atlas 1997).

10.3.6 Calcium Cycling

Calcium (Ca) bicarbonate and calcium carbonate are two forms of calcium in nature. The bicarbonate form is readily available for plants, but carbonate is not. Different acidic compounds produced by microorganisms solubilize, precipitate, and immobilize Ca compounds that are very important for plant growth and development. Different algal genera play an important role in the precipitation of calcium as calcium carbonate in marine habitats (Atlas 1997), which is an important source of Ca.

10.3.7 Silicon Cycling

Silicon-rich shell structures are found in many algae, especially in diatoms. Algae accumulate and precipitate silicon dioxide to form their outer shells. An enormous amount, about 10 billion metric tons, of silicon dioxide is precipitated in the oceans each year by different microorganisms. After death, the shells of these microorganisms develop into deposits of silicon dioxide. Various industries mine these deposits for silicon (Atlas 1997).

10.3.8 Manganese Cycling

Manganese (Mn) is mainly found in two forms: divalent manganese, which is water soluble, and the almost insoluble tetravalent manganic ion. Manganese oxides form from manganese ions by oxidation and form nodule-like structures on bacterial sheath under aerobic conditions. Mass growth of these types of bacteria such as *Leptothrix discophora* in ocean sediments is considered a major source of Mn (Atlas 1997).

10.4 Microbes for Remediation of Heavy Metal Contamination

Industrialization and modern agricultural practices are putting increasing negative pressure on agricultural soil and water by releasing large quantities of hazardous waste, heavy metals, and organic contaminants that are a serious problem not only for agriculture but also for human health. Trace amount of different heavy metals like lead (Pb), cadmium (Cd), mercury (Hg), chromium (Cr), zinc (Zn), uranium (Ur), selenium (Se), silver (Ag), gold (Au), nickel (Ni), and arsenic (As) is useful for plants, but upon excess uptake they reduce plant growth by imposing negative effects on plant photosynthesis, plant mineral nutrition, and the activities of essential enzymes (Gadd 2010; Yadav et al. 2017c). The presence of high concentrations of heavy metals in soil enhances absorption and accumulation of heavy metals by plant that enter the human body through the food chain (Sadon et al. 2012; Meena et al. 2015c). Metals in soil can be classified into five major geochemical forms: (i) exchangeable, (ii) bound as carbonates, (iii) bound as Fe and Mn oxides, (iv) bound to organic matter, and (v) residual metal. Microbes play an important role for the remediation of contaminated soils and are thus an important avenue for sustainable agriculture.

10.4.1 Sources of Heavy Metals

Pedogenetic processes of weathering of parent materials and anthropogenic sources are the main source of heavy metals in the environment, although the most significant natural sources are weathering of minerals, erosion, and volcanic activity. The anthropogenic source depends upon human activities such as mining, smelting, electroplating, pesticide and phosphate fertilizer discharge, application of biosolids (e.g., livestock manures, composts, and municipal sewage sludge), and atmospheric deposition (Dixit et al. 2015 and references therein). However, modern agricultural practices such as nonjudicial use of agrochemicals (pesticides, fertilizers, etc.), long-term application of urban sewage sludge, disposal of industrial waste, waste incineration, and vehicle exhaust are the main sources of heavy metals in agricultural soil.

10.4.2 Dominating Microbial Populations in Heavy Metal-Contaminated Soil

Soil is the major sink for heavy metal contamination, and one kilogram of soil can contain 1 to 100,000 mg of heavy metal (Gadd 2010). Soil microbes, especially rhizospheric microorganisms, play an important role for heavy metal detoxification in contaminated soil. Heavy metal detoxification in the rhizosphere occurs by a range of microorganism including prokaryotes and eukaryotes. Bacterial population structure in heavy metal-contaminated soil was studied by Pires et al. (2017), who concluded that *Firmicutes*, *Proteobacteria*, and *Actinobacteria* are dominating in soil and that the dominant genera were *Bacillus*, *Pseudomonas*, and *Arthrobacter*. Nodule formation and nitrogenase activity of rhizobia are sensitive to heavy metal. Symbiotically effective and heavy metal-tolerant rhizobial strains were found in contaminated soil and improve the quality of contaminated soil (Checcucci et al. 2017; Dhakal et al. 2015). Though *Ascomycota* and *Basidiomycota* are the predominant fungi in heavy metal-contaminated soil, arbuscular mycorrhizal fungi are dominant in nutrient-poor heavy metal-contaminated soil. A list of microbes involved in heavy metal remediation is given in Table 10.1.

Table 10.1 List of microorganisms involved in remediation of heavy metals from contaminated soil

Microorganism	Strain	Functions	References
Bacteria	*Achromobacter* sp. AO22	Volatilizes Hg^{2+} by *MerA* reductase to Hg^0	Kiyono and Pan-Hou (2006), Ng et al. (2009)
	Bacillus subtilis	Removes ferrous (Fe) by active bioaccumulation involving displacement of other ions Generates enzymes to bind metals into less harmful complexes that are stored within the cell	Holan et al. (1994)
	Bacillus licheniformis	Removes metals (Cd, Cr) by bioaccumulation	Zouboulis et al. (2004)
	Deinococcus radiodurans	Removes heavy metals through transformation	Brim et al. (2000)
	Desulfovibrio desulfuricans	Removes metals (Cu, Cr, Ni) by physical adsorption and metabolic processes	Kim et al. (2015)
	Escherichia coli	Expresses different proteins and peptides and activates different molecular mechanisms for the remediation of Zn, Cu, As, Cd, and Hg from soil	Murtaza et al. (2002), Kostal et al. (2004), Kang et al. (2007)
	Enterobacter cloacae	Bioremediation of heavy metals (Pb, Cd, Ni) occurs by antioxidant enzyme activity, flocculant production, and protein expression	Kang et al. (2015)
	Klebsiella pneumonia M426	Volatilizes Hg (II) to Hg (0) by a reductase enzyme and removes mercury as insoluble Hg through the formation of volatile thiols	Essa et al. (2002)
	Kocuria rhizophila	Remove metals by adsorption (Cd, Cr)	Haq et al. (2016)
	Micrococcus luteus	Cells are able to absorb metals (Cu, Pb), probably by passive physical mechanisms involving cell walls as well as cytoplasmic mechanisms	Puyen et al. (2012)
	Pseudomonas fluorescens	The biosorption of nickel ions (Ni) occurs in free cells or immobilized cells Produces low-molecular-weight cystine-rich proteins called metallothioneins for removing Hg and Cr from contaminated soils	Lopez et al. (2002), Gupta and Diwan (2017)
	Sulfate-reducing bacteria	Biosorption of arsenic occurs in free or immobilized cells	Teclu et al. (2008)

(continued)

Table 10.1 (continued)

Microorganism	Strain	Functions	References
Fungi			
	Aspergillus niger	Capable of accumulating heavy metals (Au, Cu) within their structure	Dursun et al. (2003)
	Botrytis cinereus	Pb (II) ions accumulated by biosorption	Akar et al. (2005)
	Penicillium chrysogenum; Penicillium spinulosum	Remove metals (Zn, Pb) by biosorption	Nemec et al. (1977), Tobin et al. (1984), Townsley et al. (1986), Niu et al. (1993)
	Phanerochaete chrysosporium	Removes metals (Pb, Cu, Zn) by biosorption	Iqbal and Edyvean (2004)
	Pleurotus platypus	Removes metals (Pb) by biosorption	Das et al. (2010)
	Rhizopus arrhizus	Take up heavy metals (Ag, Hg, Zn, Cd, Pb) using electrostatic attraction to charged functional groups	Tobin et al. (1984)
	Rhizopus oryzae	Removes Cu by adsorption	Fu et al. (2012)
	Saccharomyces cerevisiae	Heavy metals [Zn (II) and Cd (II)] removed through an ion exchange mechanism	Chen and Wang (2007), Talos et al. (2009)
Algae/ cyanobacteria	*Asparagopsis armata*	Removes metals (Cd, Ni, Zn, Cu) by biosorption	Yang et al. (2015)
	Codium vermilara	Removes metals (Cd, Ni, Zn, Cu, and Pb) by biosorption	Yang et al. (2015)
	Lessonia nigrescens	Adsorption of metals by electrostatic interaction	Hansen et al. (2006)
	Sargassum muticum	Used as biosorbent for Sb	Ungureanu et al. (2015)
	Spirogyra spp.	Binding of heavy metal (Pb) onto the cell surface and to cytoplasmic ligands, phytochelatins, metallothioneins, and other intracellular molecules	Gupta and Rastogi (2008)
	Spirulina spp.	Remove heavy metals (Cr, Cu, Mn, and Zn) by adsorption, phytosorption, and affinity to negatively charged cell wall components	Mane and Bhosle (2012), Coelho et al. (2015)

10.4.3 Microbial Mechanisms for Heavy Metal Tolerance

Some traditional/conventional techniques such as adsorption processes, chemical oxidation/reduction, reverse osmosis, and sludge filtration have been used for the removal of heavy metals from the environment. However, they have some limitations like high reagent requirement, and in a few cases these methods are not sensitive enough to recover the heavy metal ions, which may behave unpredictably. Bioremediation is an avenue for the removal of heavy metal ions from polluted environment using the activities of algae, bacteria, fungi, or plants. Bioremediation using microorganisms is sustainable because they help to restore the natural state of the polluted environment with long-term environmental benefit and cost-effectiveness.

Detoxification of heavy metals by microorganisms can occur naturally or through the addition of electron acceptors, nutrients, or other factors. Microorganisms use several techniques (Fig. 10.1) for heavy metal detoxification, such as biosorption, adsorption, and compartmentalization of heavy metals into intracellular molecules. Metal binding, vacuolar compartmentalization, and volatilization are important strategies that microorganisms use to detoxify heavy metals.

The valence transformation of heavy metals is a key mechanism for detoxification, especially for those metals whose toxicity depends on valence state. For example, mercury-resistant bacteria use organomercurial lyase to convert methyl mercury to Hg (II), which is one hundred times less toxic than methyl mercury (Wu et al. 2010; Meena et al. 2016b). Chromium-resistant bacteria convert Cr (VI) to Cr (II), which is less toxic and less mobile. Metal binding is another important mechanism of microbes that occurs through different chelators such as metallothioneins, phytochelatins, and metal-binding peptides. Chelators bind to the metal to facilitate microbial absorption and transport of metal ions.

Microorganisms can remove volatile heavy metals from contaminated environment. Heavy metals like mercury (Hg) and selenium (Se), which have volatile state, can be volatilized by microorganisms. By using the *MerA* enzyme, mercury-resistant bacteria reduce Hg^{2+} to the volatile elemental form Hg (0). Se (V) is also reduced to elemental Se (0) to remediate the contaminated environment (Wu et al. 2010). Microorganisms employ biosorption, bioaccumulation, biotransformation, and biomineralization to survive in the metal-polluted environment (Gadd 2000; Lin and Lin 2005; Varma et al. 2017a). Adsorption means the physical binding of ions and molecules onto a surface. Microorganisms carry different functional groups, like –SH, –OH, and –COOH, on their cell surface that absorbs metals from the polluted environment. Microbes also secrete chelating agents or disrupt particular transporter system to reduce metal ion accumulation in the cell. They also bind metal ions intracellularly to molecules such as thionein and change the distribution pattern of metal ions in the vacuole and mitochondria (Siddiquee et al. 2015; Yadav et al. 2017a).

In brief, microorganisms use cell wall-associated binding, intracellular accumulation, metal chelators, extracellular polymeric reactions with transformation, extracellular mobilization or immobilization of metal ions, and volatilization of metal

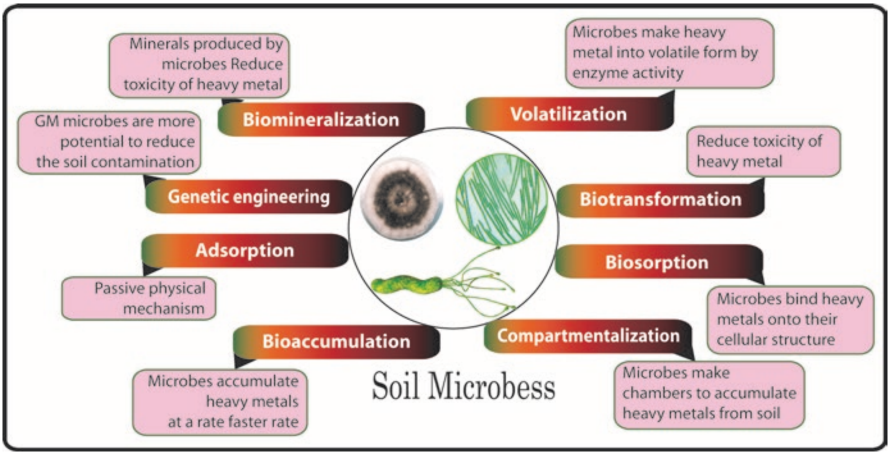

Fig. 10.1 Mechanisms of soil microbes for heavy metal detoxification from contaminated environments

ions to reduce the active concentration of metal ions present in the polluted environment. The high load of heavy metals in nutrient-poor soil is not a problem for arbuscular mycorrhizal fungi and other microbes because they bind metal ions on their external cell surface or transport them into the cells for compartmentalization (Ehrlich 1997).

Metal speciation, toxicity, mobility, dissolution, and deterioration are significantly influenced by microbes (Gadd 2010). Interaction of metals and microbes is a complex phenomenon that depends on physicochemical properties of the soil, type and concentration of metal species, metabolic activity of microbes, and the diversity of microbes. Behaviors of soil metals like for its mobility, biological activity, availability, and chemical nature are dependent on the ability of metals to react with organic compounds such as low-molecular-weight organic acid, carbohydrate, and enzyme secreted by microorganism (Patel et al. 2008; Meena et al. 2015a). However, bioavailability and accumulation of heavy metals are heavily influenced by the type and texture of soil, the physicochemical properties of the soil, plant genotype, and soil-plant-microbe interaction as well as agronomic practices such as fertilizer application, water management, and crop rotation system.

10.4.4 Microorganisms Use Heavy Metal for Their Own Growth and Development

Metals like Cu, Zn, Co, and Fe are essential for survival and growth of microbes, but the same metals also exhibit toxicity at higher concentration and may inactivate protein molecules (Oorts et al. 2006; Samanovic et al. 2012; Meena and Lal 2018). Although no biological function was observed for Al, Cd, and Hg, upon accumulation in microbial cell they may affect enzyme selectivity, interfere with cellular function, damage DNA structure, and may result in cell death (Belyaeva et al. 2012).

Nickel (Ni) is not only a primary nutrient for microbes but also plays essential roles in many microbial cellular processes. When Ni enters into the cell, it incorporated into several microbial enzymes like urease, NiFe hydrogenase, acetyl-CoA decarbonylases/synthase, methyl coenzyme Ni reductase, etc. (Mulrooney and Hausinger 2003), but Ni is toxic to bacteria at higher concentration. Therefore, different species of bacteria have developed different strategies to regulate the level of intracellular Ni to overcome this problem. For instance, *Bradyrhizobium japonicum HypB* has been shown to be able to bind up to 18 Ni ions per dimer and exhibits GTPase activity (Fu et al. 1995; Eitinger and Mandrand-Berthelot 2000; Mulrooney and Hausinger 2003). The Cu, Mo, and Mn ions bound predominantly with Fe to siderophores, resulting in an 84- to 100-fold increase in siderophore production (Balogh et al. 2003; Bellenger et al. 2007). Cobalt (Co) is essential for a broad range of physiological and biochemical functions of microbes (Jayakumar et al. 2008; Okamoto and Eltis 2011). For example, nodulation and nitrogen fixation in soybean has been found increased when Co is applied (Das et al. 2000; Meena et al. 2014). Moreover, rhizobial inoculation along with Co application significantly increased the total uptake of N, P, K, and Co by summer groundnut (Almeida et al. 2007; Kumar et al. 2017a).

10.5 Genetic Modification of Microorganisms for Sustainable Agriculture

The zone of soil around roots that is influenced by root activity is known as the rhizosphere. The intimacy of this interface between plants and their environment is essential for the acquisition of water and nutrient and for beneficial interaction with soilborne microorganism but also increases the vulnerability of plant to a range of biotic and abiotic stresses. Plant growth-promoting bacteria (PGPB), commonly known as rhizobacteria, have been engineered to enhance the production of stress-induced hormones, antibiotics, antifreeze proteins, trehalose, and lytic enzymes for enhancing plant growth and stress tolerance. Introduced PGPR must be established and maintain biologically active population for their success in competition with the already-adapted indigenous microbes. Genes involved in growth promotion have proven effective for strain improvement. Thus, attempts have been made to modify the timing or level of their expression or by transferring and expressing them in alternate hosts for enhancing plant growth and development (Ryan et al. 2009; Ram and Meena 2014).

10.5.1 Genetically Modified Microbes Enhance Plant Growth and Stress Tolerance

A number of attempts have been made to overexpress plant chitinase for enhancing plant protection against pathogenic fungi. Many researchers have reported that these approaches achieve tolerance in plants to different stresses, which along with increased crop yield is a major goal for sustainable agriculture. The endo-chitinases *CHIT33* and *CHIT42* from mycoparasite fungi were introduced into tobacco plants. Genetically modified tobacco plants expressing fungal *CHIT33* and *CHIT42* were resistant not only to a wide range of fungal and bacterial pathogens but also to biotic stresses such as salinity and heavy metal stress (Dana et al. 2006). Genetic modification of *E. coli* by the expression of the *chiA* gene caused rapid and extensive bursting of the hyphal tip of *Sclerotium rolfsii* and effectively reduced its ability to cause disease in beans (Shapira et al. 1989). Genetically modified *Pseudomonas* sp. containing and expressing the *chiA* gene from *Serratia marcescens* effectively controlled *Fusarium oxysporum* and *Gaeumannomyces graminis* (Sundheim et al. 1988). *Pseudomonas fluorescens* strain BL915 was modified by Ligon et al. (2000) to enhance the production of the antifungal compound pyrrolnitrin by introducing the *gacA* gene, and it was found that the synthesis of pyrrolnitrin in the modified strain of *Pseudomonas* constitutively expressed from a multicopy plasmid produced about 2.5-fold more pyrrolnitrin than the parental strain.

Pretreatment of the soil with the engineered strain effectively decontaminates the soil and reduces disease incidence (Timms-Wilson et al. 2000). An engineered derivative of *P. fluorescens* strain 5-2/4 expressing an integrated cassette carrying the DAPG biosynthesis operon showed increased control of *P. ultimum* (Alsanius et al. 2002). Recombinant bacterial strains (EG2424 and EG2348) were developed to enhance the efficiency of a biopesticide. The modified EG2424 strain was developed by conjugation of *Bacillus thuringiensis* strain *kurstaki* and *B. thuringiensis* strain *tenebrionis*, which were more active against European corn borer, Colorado potato beetle, and *Leptinotarsa decemlineata* (Sanahuja et al. 2011 and references therein). To extend the *B. thuringiensis* host range and efficiency, Wang et al. (2008) constructed a new strain by introducing the *cry3Aa7* gene into the UV17 strain, which produces *Cry1Aa*, *Cry1Ac*, *Cry1Ca*, and *Cry2Ab*. The new strain was toxic to both Lepidoptera and Coleoptera insects. Moreover, Liu et al. (2010) reported the construction of strain BIOT185 from the original strains HBF-1 and BTO 185 that express *Cry8ca2* and *Cry8Ea1*. The new strain is toxic toward scarab insect such as *Anomala corpulenta*.

10.5.2 Genetic Modification of Microbes for Enhancing Heavy Metal Remediation from Contaminated Environments

Microorganisms are modified by genetic engineering approaches for enhancing specific characteristics, such as enhancing the ability to degrade a wide range of contaminants for the bioremediation of soil, water, and activated sludge. Modified strains can survive and remain active in the environment. Plant-associated degradation of pollutants in soil by genetic modification of endophytic and rhizospheric bacteria is an important avenue for the remediation of contaminated soil (Dixit et al. 2015 and references therein). Therefore, modified strains can be used as bioremediators for the reclamation of polluted soil and water. Additionally, microbial biosensors have been designed to quantify the degree of contamination at the contaminated site quickly and accurately. A number of biosensors for determining the concentration of Hg, Ni, Cu, and As have been developed. Strains of *E. coli* and *Moraxella* sp. have been modified to enhance chelation on the cell surface and showed 25 times more accumulation of Cd and Hg compared to a wild-type strain (Bae et al. 2001, 2003; Meena et al. 2017a). The environmental plasmid *pTP6* (containing *merR1TPAGB1* and *merR2B2D2E* gene clusters) was introduced into *Cupriavidus metallidurans* strain MSR33; this modification enhanced Hg biodegradation with the synthesis of organomercurial compounds. *Deinococcus radiodurans* bacterial strain with chromium-reducing ability has been modified to enhance toluene degradation by transferring the *tod* and *xyl* operons of *P. putida* into them. The transgenic approach has been used to introduce the trehalose biosynthetic gene(s) into plants or into plant growth-promoting bacteria, but it has been much simpler to use genetically manipulated PGPB to achieve the same end because a single engineered bacterial strain may effectively protect a large number of different crop plants (Glick 2012 and references therein).

10.5.3 Biosensor Development and Genetic Modification of Microbes

Biosensors are analytical devices which are used to convert change in biological reaction into an electrical signal output and are made of a combination of a biological component, transducer, and electronic reader. It may use the concept of a general microbial bioassay, based upon estimation of the reduction in light transmittance (Rubban et al. 2015; Yadav et al. 2017b). Bacterial luminescence properties are also used in the biosensor development. For example, the bioluminescent bacterium *Vibrio fischeri* has been used to develop biosensors (Belkin 2006). Genetically modified *E. coli* strain Hb101 containing the *luxCDABE* gene cluster and the cyanobacterium *Synechocystis* PCC6803 carrying the *luc* gene from the firefly *Photinus pyralis* were also used to develop biosensors (Belkin 2006).

Genetically modified microbial biosensors were used for metal pollutant detection. For example, the *zra*P and *cus*C promoters of *E. coli* XL1 fused with *rfp* and *gfp* reporter genes were used to detect Cu and Zn at 5.10 mg l^{-1} and 2.59 mg l^{-1}, respectively (Ravikumar et al. 2012). *E. coli* modified by the introduction of the *merR* and *luxCDABE* genes was able to detect mercury (II) at a concentration of 1 μg l^{-1} (Ivask et al. 2007) and 3×10^{-3}μg l^{-1} (Ivask et al. 2009). The specificity of genetically modified microbial biosensors is very high for certain group of metals. For example, a genetically modified *Ralstonia eutropha* strain AE2515 was developed (Tibazarwa et al. 2001) by introducing the *cnrYXH* regulatory genes in the upstream region of *luxCDABE* for detecting Ni and Co. This biosensor worked very well for detecting Ni and Co but failed to detect Zn, Cr (III and V), Mn, Cd (II), and Cu (II) ions.

10.5.4 Genetically Modified Microbes for the Remediation of Organic Xenobiotic Contaminated Soil

Genetically engineered microbes are used to the transformation of organic xenobiotics to overcome the limitations of traditional methods of bioremediation. Genetic engineering techniques were used by different companies and academia during the 1990s to exploit microbial metabolism for the bioremediation of xenobiotics (Zwillich 2000), but they were hampered due to regulatory challenges involved in genetic engineering research. However, increased degradation of 3,4-chlorotoluene and 3-chlorotoluene was observed by Abril et al. (1989) and Brinkmann and Reineke (1992) in genetically modified *Pseudomonas* sp. Although the radiation-tolerant genetically modified microbe *Deinococcus radiodurans* was developed for toluene degradation, it was not used for bioremediation purpose in the field due to potential risks and regulatory challenges (Lang and Wullbrandt 1999; Ezezika and Singer 2010; Mitran et al. 2018).

With the advent of the latest biotechnological techniques such as genetic modification of bacterial strains using natural gene transfer, recombinant DNA technologies can be used to produce specific enzymes that promote the degradation of toxic organic substances (Chakraborty and Das 2016; Pandotra et al. 2018; Meena et al. 2017b). Moreover, the application of genetic engineering approaches to plant-associated endophytic and rhizospheric bacteria can enhance the degradation of toxic compounds in the contaminated site by phytoremediation (Fasani et al. 2017). Enzymes found in four *Pseudomonas* strains clearly showed oil biodegradation capabilities (Gao et al. 2017; Chebbi et al. 2017).

Agent Orange, one of the toxic herbicides and defoliants used in Vietnam War by the US military, is a mixture of phenyl herbicide including 2,4-dichlorophenoxyacetic acid (2,4-D) and 2,4,5-trichlorophenoxyacetic acid (2,4,5-T) and is closely linked to increased incidence of cancer (Ezezika and Singer 2010). A recombinant strain of *Burkholderia cepacia* was shown to be very effective for the degradation of Agent Orange (Chauhan et al. 2008). In artificially contaminated soil, the genetically modified endophytic *P. putida* strain VM1441 (pNAH7) increased naphthalene degradation rates up to 40% compared to uninoculated plants and protected pea plants against the toxic effect of naphthalene (Germaine et al. 2009). The genetically modified endophyte *B. cepacia* G4 increased toluene tolerance in the yellow lupine plant and reduced phytovolatilization of toluene by 70% (Taghavi et al. 2005).

10.5.5 Genetically Modified Microbial Strains and Rhizosphere Competence

Ecological fitness of PGPR strain is essential for evaluating the potential risks associated with the release of modified strain into the environment. With this view, De Leij et al. (1998) introduced modified *P. fluorescens* SBW25 into the pea and wheat rhizosphere and did not find any negative metabolic burden on indigenous rhizosphere bacteria. To observe strain performance and competitiveness on crop species, the same modified strain was co-inoculated on three different crops such as on barley, pea, and navy bean under controlled conditions. The wild-type strain Q8r1-96 outcompeted Z30-97 on barley, but both strains maintained similar population densities on navy bean. Surprisingly, the engineered strain displaced the wild type on pea (Ryan et al. 2009 and references therein), suggesting that the crop species modulates strain competitiveness and must be considered when assessing the potential fate and the risk posed by the release of recombinant strains into the environment.

10.5.6 Future Research Orientations for Genetic Modification

The plant rhizosphere can be modified using different approaches, such as selection of crop species and varieties, introduction of microorganisms or soil amendments, and by genetic modification of plant and microbial activities. The emergence of molecular techniques now allows the direct manipulation of genes that influence rhizosphere functions present either in the plant or in the rhizospheric microbes. Genomics has given rise to metagenomics, which allows mass sequencing to aid the rapid exploration of microbial diversity of the rhizosphere. Though there are a number of encouraging avenues in rhizosphere modification, it remains a challenge due to the lack of understanding of the complex chemical and biological interactions among plants and microbes in the rhizosphere. Fundamental issues like microbial abundance and diversity in the soil remain unresolved (Ryan et al. 2009 and references therein).

Social acceptance regarding genetically modified organisms is also a major issue. These issues are relatively small in Canada, China, Japan, and the USA but are very great in Europe, even among members of the scientific community. However, the demands of an ever-increasing population are closely related to a risk of reduction of arable surface area (for instance, in fertile river deltas, urban areas, or lowlands). Also, environmental pollution through industrial waste and use of agrochemicals are major concerns for sustainable agriculture. To address these issues, safe alternatives such as nonpolluting solutions, novel natural biocontrol agents, and possibly genetically modified options are important. The scientific community should put more and continuous emphasis in this positive direction. Thus, the public of the future may benefit from safe, sustainable, and environmentally sound agricultural practices.

10.6 Bacteria Improve Plant Growth and Crop Yield

Microorganisms use a range of mechanisms, including N_2 fixation by the nitrogenase enzyme, nitrate reductase activity, siderophore production, phytohormone synthesis, etc., for enhancing plant growth and development both under normal and in stress environments (Fig. 10.2). To preserve ecological diversity and use sustainable agriculture to restore crop productivity, a new concept was raised using "environmentally friendly" N_2-fixing bacteria as a mode of increasing crop yield (Okon and Labandera-Gonzálezb 1994). Both nitrogen-fixing bacteria and free-living rhizospheric bacteria (e.g., *Pseudomonas*, *Bacillus*, *Azotobacter*, *Azospirillum*) are involved in growth promotion and yield increment of legumes, cereals, and other crops.

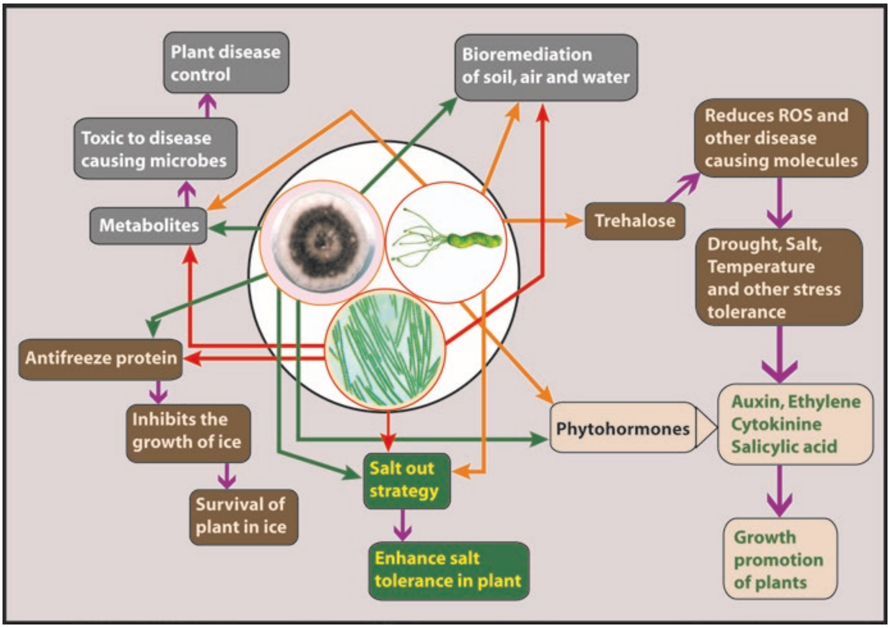

Fig. 10.2 Roles of soil microbes on plant growth and enhancement of stress tolerance

10.6.1 Phytohormones Produced by Microbes

Microbes are significant sources of major plant hormones: auxin, cytokinin, gibberellin, abscisic acid, and ethylene; nowadays, many microbial sources of phytohormones have been identified. Phytohormones of microbial origin can alter plant physiology and are able to cause diverse outcomes ranging from pathogenesis to promotion of plant growth (Spaepen 2015). Microbes that produced different phytohormones which played critical roles in growth and developments of plants are mentioned in Table 10.2. Data on auxin production is most widely available. These phytohormones have potential for agricultural uses, and the microbial production of plant hormones may have a bright future in sustainable agriculture.

10.6.2 IAA Produced by Bacteria Enhances Plant Growth Even Under Saline Conditions

Indole-3-acetic acid (IAA) or auxin is a plant hormone that has roles in growth, development, and behavioral processes in the plant life cycle. Auxin is involved in all developmental stages, from the cellular level to whole-plant development, and is regulated in different pathways in the plant body. In the plant cell, auxin biosynthesis occurs in a two-step biochemical reaction from the amino acid tryptophan via the products of the gene families TAA1/TAR and YUCCA (Cheng et al. 2006; Stepanova et al. 2008). Auxin may also be converted reversibly to other forms by many other enzymes. However, after biosynthesis auxin is moved from cell to cell via different carrier proteins, among which the PIN family and the ABCB family are the most studied (Zazimalova et al. 2010). These carriers facilitate compartmentalization of auxin in plant cells/tissues in a coordinated way and thereby take part in the development of the plant. Although excess amounts of auxin have negative effects on plants, judicious application ensures optimal growth. The IAA is not only produced in plants but also by microbes, especially by bacteria. Soil is one of the major sources from which many IAA-producing bacteria have been identified, and mining is still continuing. These beneficial bacteria are very much essential for sustainable agriculture. The effect of the rhizospheric bacteria *Azotobacter chroococcum*, two strains of *P. fluorescens*, and *B. subtilis* on the growth and yield of onion was assessed by Colo et al. (2014). The result showed that *B. subtilis* was the best producer of IAA, whereas *P. fluorescens* strains were better at producing siderophores and solubilizing phosphates. The *B. subtilis* and *Azotobacter chroococcum* variants produced the highest onion yield. The IAA-producing bacterial strains with growth-promoting traits were isolated by Khiangte and Lalfakzuala (2017).

Salt is a major limiting factor for seed germination and seedling growth due to its toxic effects. This effect can be alleviated by employing phytohormone-producing

Table 10.2 Phytohormone-producing microbes and their functions

Name of strains	Functions	References
Auxin-producing microbes		
B. megaterium ST2-1	Enhanced root and shoot growth and chlorophyll content of plants under controlled conditions through the production of auxin	Mohite (2013)
P. putida GR12-2	Enhanced root growth of canola through the production of auxin	Patten and Glick (2002)
Aspergillus niger BHUAS01; *Penicillium citrinum* BHUPC01	Increased chickpea (*Cicer arietinum*) growth by producing auxin	Yadav et al. (2011)
B. cereus A-139	Increased growth of lateral root in *Arabidopsis* and mungbean by producing auxin	So et al. (2009)
Enterobacter cloacae MSR1	The length of the primary roots, the number of secondary roots, and root dry weight of *Pisum sativum* and the root growth of alfalfa were significantly increased by inoculation with bacteria producing auxin	Ashraf et al. (2016)
B. amyloliquefaciens FZB42	Inoculated plants showed higher root dry weight and increased accumulation of N, P, and K	Mohite (2013)
P. stutzeri P3	Capable of producing IAA in vitro and enhance plant growth	Lata et al. (2006)
P. fluorescens AK1 and AK2	Bacterial inoculation increased root growth in rice due to the production of auxin	Karnwal (2009)
B. subtilis PRBS-1 and AP-3	IAA-producing bacterium, stimulated outgrowth of roots in soybean	Araújo et al. (2005)
Erwinia herbicola 299R	Produced significant amount of indole-3-acetic acid (IAA) in artificial media	Brandl and Lindow (1998)
Cytokinin-producing bacteria		
B subtilis IB-22	Stimulates amino acid deposition in wheat roots due to the production of cytokinin	Kudoyarova et al. (2014)
P. fluorescens G20-18	Acts as a biocontrol agent against *P. syringae* in *Arabidopsis* due to the production of cytokinin	Großkinsky et al. (2016)
B. licheniformis Am2; *B. subtilis* BC1; *P. aeruginosa* E2	Cytokinin-producing strain capable of accelerating cell division in cucumber	Hussain and Hasnain (2009)
Rhizobium fredii USDA 205; *Bradyrhizobium japonicum*	Has potential for stimulating cortical cell division in legume roots due to the production of cytokinin	Dawn and Barbara (1989)

Salicylic acid-producing strains		
B. licheniformis MML2501	Inhibited mycelial growth of fungal pathogens. Can be used in crop protection through systemic resistance induced by the production of salicylic acid	Shanmugam and Narayanasamy (2009)
P. fluorescens WCS374r	Induced systemic resistance in rice against the leaf blast pathogen *Magnaporthe oryzae* and also in radish due to the production of salicylic acid	Ran et al. (2005); de Vleesschauwer et al. (2008)
P. fluorescens CHA0; *P. aeruginosa* 7NSK2	Produced salicylic acid in association with grapevine that confers a systemic resistance against *Botrytis cinerea*	Verhagen et al. (2011)
Azospirillum brasilense Cd; *Azospirillum lipoferum* USA 5b	Improved growth of leaf and root of rice due to secretion of gibberellins	Fabricio et al. (2001)
Photorhabdus temperata M1021	Increased plant length, chlorophyll content, and fresh and dry biomass of rice through secretion of gibberellins	Ullah et al. (2014)

bacteria. The bacterial strain *P. aurantiaca* TSAU22 produces the phytohormone IAA and can alleviate salt stress (Egamberdieva 2009). This strain increased seed germination (from 54% to 90%) and seedling growth of cotton. Dormancy of wheat induced by salinity can be broken by the IAA-producing bacteria *P. aurantiaca* TSAU22, *P. extremorientalis* TSAU6, and *P. extremorientalis* TSAU20 (Egamberdieva 2009; Dhakal et al. 2016). Root growth of wheat seedlings was increased up to 25% under nonsaline conditions, while under saline conditions root growth was increased up to 52%. Amelioration of salt effects on seedling growth of soybean was also reported (Jabborova et al. 2013). The IAA-producing bacterial strain *P. putida* TSAU1 significantly increased soybean seedling root growth up to 29% under nonsaline condition and up to 86% at 100 mM NaCl. The IAA-producing *Kocuriatur fanensis* strain 2M4 was tested on groundnut (*Arachis hypogaea* L.) under nonsaline condition and found that total plant length and fresh biomass were increased by 18 and 30%, respectively. In saline soil the tested isolate restored the increased total plant length and fresh biomass of groundnut seedlings up to 17 and 13%, respectively (Goswami et al. 2014). Growth promotion activity of IAA-producing bacterial isolates was also reported in tomato and barley (Gajendramurthy et al. 2017).

10.6.3 The Involvement of Bacterial Gibberellins (GA_3) in Plant Growth and Yield Promotion

Gibberellins (GAs) are a large group of natural biomolecules, tetracyclic diterpenoid acids which are involved in physiological and developmental processes of plants. These processes include seed germination, seedling emergence, the growth of the stem and leaf, floral induction, and the growth of the flower and fruit (Pharis and King 1985; Sponsel 2003; King and Evans 2003). However, gibberellins are produced not only by higher plants and fungi but also by bacteria (Gutiérrez-Mañero et al. 2001; MacMillan 2002; Datta et al. 2017a). Historically, the physicochemical characterization of bacterial gibberellin was first done by Atzorn et al. (1988) in *Sinorhizobium meliloti* and demonstrated the presence of four gibberellins: GA1, GA4, GA9, and GA20. There is no known direct role for gibberellin in fungi and bacteria; rather they can be considered as secondary metabolites that induce reactions in host plants that are beneficial to them. Chemical synthesis of GA and other hormones is complicated and the products are costly and of low purity, but GA obtained from microbes may overcome these shortcomings. The final products obtained through this method not only possess higher bioactivity and purity, but are also produced at much lower cost, which is highly desirable for sustainable agriculture. Several studies have been conducted to find and characterize GA-producing bacteria and examine their growth-promoting activities in plants.

Microbes dwelling in root nodules of legume plants sometimes modify the hormonal levels within the nodule by producing GA or gibberellin-like substances, thereby affecting plant cell metabolism (Cassán 2003). Dobert et al. (1992) observed a significant internode elongation in lima bean when inoculated with a specific *Bradyrhizobium* sp. (strain 127E14) that was not seen in plants inoculated with other compatible *Bradyrhizobium* species. Joo et al. (2009) identified *Burkholderia* sp. KCTC 11096BP as a gibberellin-producing bacterium. The gibberellin-producing bacterium *B. cereus* MJ-1 caused a 1.38-fold increase in fresh weight (fw) and a 1.28-fold fresh weight gaining roots of pepper plant (Joo et al. 2006).

GA-producing bacteria also increase the growth and nutritional quality of leafy vegetables. Radhakrishnan and In-Jung (2016) demonstrated a significant increase in shoot length, shoot fresh weight, and leaf width of lettuce when the plants are associated with the bacterial strain *B. methylotrophicus* strain EK2. Gibberellin produced by this bacterium is responsible for enhanced growth of lettuce. Endophytic GA-producing bacteria also increase plant growth. The endophytic bacterium *B. amyloliquefaciens* RWL-1 produced GA in rice plants and regulated a few other endogenous phytohormones (Shahzad et al. 2016). The endophytic bacterium *B. subtilis* LKM-BK promotes seedling growth of cocoa (Ishak et al. 2016) and *Sphingomonas* sp. LK11 promotes growth of tomato plants (Khan et al. 2014; Kumar et al. 2015; Meena et al. 2018b).

Microbes can play a significant role in plant growth and development. It is unlikely that plant growth acceleration by rhizobacteria is a result of the combined action of several mechanisms; phytohormone production by microbes has a direct positive influence on the growth and yield of important crop plants (Arkhipova et al. 2005; Idris et al. 2007; Sihag et al. 2015). Therefore, use of these plant growth-promoting bacteria can reduce the indiscriminate use of fertilizer in the field. Their judicious application will enhance sustainable agriculture.

10.6.4 Trehalose Biosynthesis in Plants from Microbial Origin Confers Stress Tolerance

Trehalose is a nonreducing disaccharide composed of two glucose units; it is an α-D-glucopyranosyl-(1→1)-α-D-glucopyranoside. It is also known as mycose and has been identified in many organisms: bacteria, yeast, fungi, higher and lower plants, insects, and other invertebrates. It is an energy source, protein or membrane protectant, and osmolyte (Elbein et al. 2003). Initially it was considered a rare sugar, but later was discovered in many organisms. Trehalose is multifunctional, and some functions are specific to certain species (Iordachescu and Imai 2008). It appears to act as an energy source for microbes and also protects them from dehydration (Crowe et al. 1992; Drennan et al. 1993; Elbein et al. 2003). Trehalose produced by microbes can protect the plant from different stress conditions to varying degrees. Trehalose produced by the desiccation-sensitive bacterial strain *P. putida* KT2440 can protect pepper and tomato plants from drought (Vilchez et al. 2016; Sofi et al. 2018). Research found that the products of the *otsAB* genes are responsible for trehalose production in the bacterial strain *P. putida* KT2440. Increased level of trehalose is known as an osmoprotectant under several different abiotic stresses, including high salt, drought, and unfavorable temperature. Trehalose-producing microbes are resistant to both acid and high temperature. Trehalose can form a vitreous phase during dehydration to protect biomolecules from damage by drought and salt (Glick 2012). A few approaches have been developed to increase the concentration of trehalose in plants. Firstly, some growth-promoting bacteria in association with plants are capable of producing ACC deaminase and trehalose naturally, which can protect plants from stresses. Cyanobacteria can also produce and accumulate trehalose under stress conditions. During salt stress, cyanobacterial strain can produce trehalose and other compatible solutes that confer different degrees of salt resistance (Sakamoto et al. 2009; Klahn and Hagemann 2011). Application of such approach in the agricultural field is helpful for increasing productivity and an effective tool for sustainable agriculture.

10.7 Cyanobacterial Salt Stress Tolerance Modulation

Cyanobacteria are photosynthetic, unicellular, aquatic, free-living, and often colonial organisms. Their cell can be large enough to see with the naked eye (cell size range 0.5–40 μm) and they have been present on this planet for 3.5 billion years. They are frequently known as "blue-green algae" as they are aquatic and photosynthetic. Cyanobacteria are relatives of other bacteria (prokaryotes), but some of them later became incorporated into eukaryotic entities through evolutionary processes when they took up residence inside the plant cell as chloroplast through endosymbiosis. Cyanobacteria are agriculturally important as they are capable of surviving and thriving under extreme conditions such as desiccation, high temperature, extreme pH, and high salinity.

Some cyanobacteria are nitrogen fixers and play an important role in plant growth and development. Cyanobacteria that are capable to fixing the atmospheric nitrogen can be used as valuable biological input for improving soil texture, conserving soil moisture, scavenging the toxic sodium cation from the soil, and also for improving the soil properties. There is a symbiotic relationship between rice plants, the fern *Azolla*, and the cyanobacterium *Anabaena*. There is a direct symbiotic relationship between *Anabaena* and the fern, where *Anabaena* colonizes the fern leaves and the latter one fixes atmospheric nitrogen. The fern thus provides an inexpensive natural fertilizer to the rice when it dies at the end of the season (Vaishampayan et al. 2001; Verma et al. 2015). Culture filtrates of the cyanobacterial strains *Calothrix ghosei*, *Hapalosiphon intricatus*, and *Nostoc* sp. isolated from wheat rhizosphere enhanced germination, length of radicle, and coleoptile of wheat (Karthikeyan et al. 2009). Besides rice, their influence on other crop plants, e.g., wheat, tomato, pulse, and vegetable, is also documented (Kaushik and Venkataraman 1979; Karthikeyan et al. 2007). Cyanobacterial strains also improve soil health. Chamizo et al. (2018) conducted an experiment using non-nitrogen-fixing (*Phormidium ambiguum*) and nitrogen-fixing (*Scytonema javanicum*) cyanobacterial species on different textured soils to examine cyanobacterial biocrust development and thereby change in the physicochemical properties of soil. Electron microscopy analysis found a contrasting structure of the biocrust induced by these two cyanobacteria. The strain *S. javanicum* increased the total organic C and total N content, while *P. ambiguum* increased the total exopolysaccharide (EPS) content and soil penetration resistance. On the whole, the improvement in soil fertility and stability supports the viability of using cyanobacteria to restore degraded arid soils. Cyanobacterial inoculum could also supplement up to 20% nitrogen for rice cultivation in saline soil (Aziz and Hashem 2003; Meena et al. 2017c).

Salt is a major limiting factor for plant growth and crop production. To mitigate the salt problem while keeping natural resources undisturbed, microbial inoculation is an eco-friendly alternative to synthetic and hazardous chemical. Cyanobacteria can improve the growth and yield of crops and can be used as an effective tool for management/restoration of soil fertility. Certain cyanobacterial strain also improves the physicochemical properties of the saline soil by enriching them with carbon, nitrogen, and available phosphorus. Traditionally, chemically synthesized agents like gypsum, sulfur, or excessive irrigation are applied to reduce salinity, but they are not cost-effective or environmentally friendly. Salt-affected soils are less productive and impermeable to water. Due to poor hydraulic conductivity and aeration, saline soil becomes poor and less fertile (Singh et al. 2016; Verma et al. 2015a). Cyanobacteria can be used to treat alkaline soils, and soil fertility can be improved by subsequent cultivation of cereals, sugarcane, and horticultural crops. Cyanobacteria use the “salt-out strategy” to address the changing salt concentrations. At high salt concentration, cyanobacteria synthesize and accumulate osmoprotective compounds, maintain low internal concentration of inorganic ions, and express a set of salt stress protein. Moreover, under different abiotic stress conditions, cyanobacterial cells showed rapid expression of several stress-regulated proteins and modified protein synthesis program. To maintain low intracellular salt concentration, inorganic solutes like disaccharides (sucrose, trehalose, and glucosylglycerol), quaternary amines (glycine betaine), and free amino acids (glutamine) are produced in the cell which in turn minimize the osmotic stress on the cell. These compatible solutes help cyanobacteria to survive in saline desert soils (Oren 2000). The most important ecophysiological features of cyanobacteria are their ability to slow their growth rate over a wide temperature range and their tolerance to desiccation, freezing, and salinity stress, which makes them dominant in these environments. They have the ability to tolerate very low water potential and extracellular mucopolysaccharides slow down the flow of liquid water during freezing.

Saline soils typically have high pH values, large amount of carbonate, and high exchangeable sodium. Cyanobacteria produce biofilm and conserve organic C, N, and P and soil moisture, and convert the sodium clays into calcium clays (Singh et al. 2016; Meena et al. 2015b). They add organic matter and N to saline soils, which help to bind the soil particles together, thus improving soil permeability and aeration (Maqubela et al. 2009). Excretion of polysaccharide and lipid by cyanobacteria improves the physicochemical quality of saline and alkaline soils. Cyanobacterial species such as *Anabaena oscillarioides*, *A. aphanizomenoides*, and *Microcystis aeruginosa* exhibited salt tolerance ranging from 7 to 15 g l^{-1} (Coutinho and Seeliger 1984; Moisander et al. 2002). There is a positive correlation between NaCl tolerance and exopolysaccharide (EPS) production in some cyanobacteria (Ozturk and Aslim 2010). The EPS produced by cyanobacteria are believed to protect bacterial cell from desiccation, heavy metals, or other environmental stresses, including salt stress. Elevated level of exopolysaccharide increases protection. The cyanobacterial strain *Synechocystis* sp. BASO444 produces large amounts of EPS (500 mg l^{-1}) and showed high tolerance against salinity (Ozturk and Aslim 2010).

10.8 Conclusion

Although the size of an individual soil microorganism is very small, it has a very significant effect on the physical, chemical, and biological process in the soil that is directly and indirectly critical for the growth and development of plants and animals. Soil microbes play important roles in the cycling of many nutrients that are essential for life. Different nutrients like carbon, nitrogen, phosphorus, potassium, zinc, calcium, manganese, and silicon are continuously recycled by microbes. Nutrient recycling is not only essential for plants but also for other forms of life because it provides the materials to produce amino acids, proteins, DNA, and RNA, those that are essential for all living system.

Industrialization and modern agricultural practices are putting increasing negative pressures on agricultural soil and water by releasing large quantities of hazardous waste, heavy metals, and organic contaminants that are a serious problem not only for agriculture but also for human health. Trace amount of different heavy metals like lead (Pb), cadmium (Cd), mercury (Hg), chromium (Cr), zinc (Zn), uranium (Ur), selenium (Se), silver (Ag), gold (Au), nickel (Ni), and arsenic (As) is useful for plants, but upon excess uptake they reduce plant growth by imposing negative effects on plant photosynthesis, plant mineral nutrition, and the activities of essential enzymes. Bioremediation is an avenue for the removal of heavy metal ions from polluted environment using the activities of algae, bacteria, fungi, or plants. Bioremediation using microorganisms is sustainable because they help to recover the natural state of the polluted environment with long-term environmental benefit and cost-effectiveness. Detoxification of heavy metals by microorganisms can occur naturally or through the addition of microbial strains from nature or developed by genetic modification. Microorganisms use biosorption, adsorption, compartmentalization of heavy metals into intracellular molecules, metal binding, vacuolar compartmentalization, extracellular mobilization, or immobilization of metal ions to reduce active concentration of metal ions present in polluted environments.

Genes responsible for growth promotion have been proven effective tool for strain improvement through modifying their expression timing and level or by transferring and expressing them in alternative hosts for enhancing plant growth and improving the fitness of the modified strain. Microorganisms modified by genetic engineering have enhanced specific characteristics, such as the ability to degrade a wide range of contaminants for the bioremediation of soil, water, and activated sludge, enhancing the biotic and abiotic stress tolerance of plants, enhanced phytohormone production, etc. Modified strain can survive and remain active in harsh environment. Plant-associated degradation of pollutants in soil by genetic modification of endophytic and rhizospheric bacteria is an important means for the remediation of contaminated soil. Microorganisms use a range of mechanisms, including N_2 fixation by the nitrogenase enzyme, nitrate reductase activity, siderophore production, and phytohormone synthesis for enhancing plant development and growth both under normal and stress environments. Auxin, cytokinin, gibberellin, abscisic acid, and ethylene are major plant hormones, and more phytohormones have also been identified. Diverse microbial species have the ability to produce phytohormones, and these are now being widely used in agriculture for enhancing plant growth and stress tolerance.

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