Bhoopander Giri · Rupam Kapoor
Qiang-Sheng Wu · Ajit Varma *Editors*

Structure and Functions of Pedosphere

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ISBN 978-981-16-8769-3 ISBN 978-981-16-8770-9 (eBook)
https://doi.org/10.1007/978-981-16-8770-9

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Preface

The term **Pedosphere**, derived from the Greek words pedon—soil and sphaira—sphere, was introduced in the monograph *Pedology as independent natural-scientific discipline about the Earth*. Pedosphere is the cover of the Earth where soil diversity occurs. In this sphere, the processes of soil formation remain active. Pedosphere exists at the interface of lithosphere, atmosphere, hydrosphere, and biosphere. It develops as a result of dynamic interactions between living organisms, unconsolidated regolith and consolidated bedrock, water present in the soil, on the soil and below the soil, and the air available inside the soil and above the soil. Pedosphere prevails below the vegetative cover of the biosphere and above the hydrosphere and lithosphere. It covers an insignificant thickness (in depth only one to two meters), however, enveloping the greatest density and diversity of the Life on the Earth. Indeed, pedosphere plays a fundamental role in the stable functioning of the biosphere, supporting life on the Earth and fostering favorable conditions for plants, animals, and humans as well.

Pedosphere is predicted to be a result of prolonged effects of solar radiation, atmospheric moisture, flora and fauna that prevail on the land surface, interaction of local climate, composition and structure of parent rocks, and the breakdown of minerals that ultimately leads to the formation of soil. In the pedosphere, all forms of soils possess a special type of structure and different organic and mineral components; thus, pedosphere as a whole plays very important roles in providing unique habitats for a huge diversity of life forms, developing a link between geological and biological substances circulation in the terrestrial ecosystems, making available vital mineral elements to plants and supporting human health as a lot of trace elements in the lithosphere are accessed by people through the formation of soils and utilizing such soils for food production.

Soils cover much of the Earth's land surface and support the floral and faunal species of the Earth. Soil is a multi-phase system and, therefore, functions as a medium for plant growth, storage, supply, and purification of water, and an excellent habitat for various life forms. All these functions, in turn, transform soil properties. The current state of soil properties and functions is receiving more attention as the increasing anthropogenic activities (urbanization, industrialization, intensive use of chemicals in the agricultural fields, etc.) have become major sources of soil degradation and deterioration, which indeed accelerate loss of soil fertility and productivity. Therefore, to reduce the deterioration of the soil and to control the loss of soil biological productivity and biodiversity, it is important to promote the justified and judicious use of the soil resources.

The present volume Structure and Functions of Pedosphere written by the experts of this field comprises 17 chapters and covers latest research in the field of the pedogenesis/soil-forming processes, diversity of soils, soil functions, soil proteomics, impact of anthropogenic activities on the pedosphere, plant-microbe and microbe-microbe interactions in the pedosphere, life in the pedosphere, and factors influencing the formation and functioning of soil. We believe that with the opulence of information on different aspects of soil and its sustainability, this extensive volume is a valuable resource for researchers in the area of soil science, agronomy, and agriculture, as well as academicians and students in the broad field of botany, ecology, and microbiology.

We are very much delighted and thankful to all our contributing authors for their endless support and outstanding cooperation to write altruistically these authoritative and valuable chapters. We extend our sincere thanks to all our colleagues who helped us in the preparation and compilation of this generous volume. We also thank Springer officials specially Aakanksha Tyagi, Naren Aggarwal, William Achauer, Anil Chandy, and Jayesh Kalleri for their generous support and efforts to accomplishing this wide volume. We specially thank our families for consistent support and encouragement.

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Qiang-Sheng Wu is professor at the College of Horticulture and Gardening, Yangtze University, and works as an administrative director at the Institute of Root Biology, Yangtze University. He has published two book titled *Arbuscular Mycorrhizas and Stress Tolerance of Plants* and *Arbuscular Mycorrhizal Research and Application of Horticultural Plants*. He has published more than 60 papers in international popular journals. Dr. Wu conducted 10 projects, guided 2 doctors and 18 master's students, and served as the editor of eight international journals and the member of Citrus Association in Hubei Province, and obtained the Fourth Scopus Young Researcher Award.

Ajit Varma was a Professor at the School of Life Sciences, Jawaharlal Nehru University, New Delhi, India. Presently, he is the Distinguished Scientist & Professor of Eminence of Amity Institute of Microbial Technology; Group Dy. Vice Chancellor, Ritnand Balved Education Foundation; and Vice Chairman, Amity Science, Technology & Innovation Foundation, Amity University Uttar Pradesh, India. He has published more than 314 papers in reputed journals and has been serving as an editor-in-chief of Soil Biology Series, Springer Verlag Germany. Dr. Varma is the Fellow of Alexander-von-Humboldt Society, Germany, elected Fellow of National Academy of Agricultural Sciences, and Fellow of Microbiology Society of India.

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Chapter 1
Pedogenesis and Soil Biota Interactions in the Pedosphere

Okon Godwin Okon and Ukponobong Efiong Antia

Abstract Pedogenesis can be considered as the process of soil development influenced by several climatic, physical, geological and biological factors. The process of soil formation begins with the weathering of the parent material through sequences of changes. Before the formation of soil occurs, sequences of changes have to ensue to the parent material resulting in the establishment of different layers or stratums of soil commonly referred to as soil horizons. Soil biota consists of the microorganisms, soil animals and plants living all or part of their lives in or on the soil or pedosphere. Microorganisms found in the soil include bacteria, fungi, archaea and algae, while soil animals may include protozoa, nematodes, mites, springtails, spiders, insects and earthworms. Millions of species of soil organisms exist, but only a fraction of them are culturable and properly identified. Soil organisms serve numerous roles in the pedosphere. The most critical function played by soil organisms is the regulation of biogeochemical transformations, among several other roles. The formation and turnover of soil organic matter that include mineralization and sequestration of carbon, nutrient cycling, disease transmission and prevention, pollutant degradation and improvement of soil structure are some of the functions mediated by the soil biota. The combined mass of microorganisms in the soil otherwise known as microbial biomass is reliant upon soil properties and the source(s) of C available for energy and cell metabolism. Carbon sources to the soil organisms vary in their ability to be decomposed and nutrient content. Carbon turnover, decomposition and microbial activity often lead to increases in organic matter and soil aggregation.

Keywords Bacteria · Fungi · Mycorrhizae · Microbiota · Pedogenesis · Weathering

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B. Giri et al. (eds.), *Structure and Functions of Pedosphere*,
https://doi.org/10.1007/978-981-16-8770-9_1

1.1 Introduction

Pedogenesis can also be regarded as soil formation, soil genesis and soil development. The term ‘pedogenesis’ is derived from the Greek word ‘Pedo’ which means ‘earth or soil’ and ‘genesis’ which means ‘origin or the beginning’. Pedogenesis can be considered as the process of soil development influenced by several climatic, physical, geological and biological factors (Sapkota 2020). Before the formation of soil occurs, sequences of changes have to ensue to the parent material resulting in the establishment of different layers or stratums of soil commonly referred to as soil horizons. Layers in the soil horizons can be commonly and distinctively separated using their conformation and physical properties (Sapkota 2020) such as chemistry, structure, colour and texture.

The process of soil formation begins with the weathering of the parent material through sequences of changes. Microorganisms play a pivotal role in this series by feeding on the nutrients that are released during the process of weathering resulting in the production of acids which aid the weathering process (Jenny 1994). As weathering occurs repeatedly, there is a resulting soil depth increase as a result of non-stop weathering and additional deposition of soil. Researchers have observed that an estimate of about 1/10 mm of soil is produced from weathering per year (Scalenghe et al. 2016). As deposition of soil continues, the depth deepens; the soil steadily gains the ability to support life in the form of plants beginning with the pioneer species and then with time progressing to higher plants resulting in the build-up of a plant and animal complex communities. Once these soils support the existence of higher plants, several plant activities create and deposit humus on the soil which further enriches and contributes to the deepening of the soil (Wilkinson and Humpreys 2005). Several and repeated activities of the plant and animal complex communities contribute to the maturity of the soil. With time, as a result of the continuous accumulation of humus and subsequent leaching of the soil, organic matter layers develop forming the soil profile.

1.1.1 Factors Affecting the Formation of Soil

1.1.1.1 The Parent Material

The initial solid matter that makes up the soil, referred to as the parent material, might include consolidated substances like rocks or unconsolidated particles like water deposits, volcanic ashes or organic matter. The final composition of a soil is a direct indication of the constituent of the parent material; for example, iron-containing rocks usually result in iron-rich soil with higher pH and darker colour. Usually, parent materials are collected via wind, water and volcanoes, resulting in differences in the initial composition of the rock. Parent material also influences adjacent soils that normally exhibit different soil profile due to different parent materials. Changes in the parent material during soil formation can be either abrupt or subsequent over a long period. The typical soil parent mineral materials are quartz (SiO_2), calcite($CaCO_3$), feldspar (KA_lSi3O_8) and mica (biotite) ($K(Mg, Fe)_3AlSi_3O_{10}(OH)_2$) (Donahue et al. 1977).

Most soils derive from transported materials that have been moved many miles by wind, water, ice and gravity. Silt and fine sand are moved many hundreds of miles by wind leading to the formation of loess soils (60–90% silt) in a process known as the aeolian process. Formation of loess soils is common in the midwest of North America, Northwestern Europe, Argentina and Central Asia. Clay is hardly moved by wind because it forms stable aggregates. Flowing water also facilitates the movement and settlement of materials such as the alluvial, lacustrine and marine. Alluvial materials are those moved and deposited by flowing water, while deposits of sediments in lakes are called lacustrine. Lake Bonneville and many soils around the Great Lakes of the United States are examples. Soils along the Atlantic and Gulf Coasts and in the Imperial Valley of California of the United States are called marine deposits. They are beds of ancient seas that have been revealed as the land uplifted (Sapkota 2020). Parent material moved by ice maybe deposited in the form of terminal and lateral moraines in the case of stationary glaciers. Retreating glaciers leave smoother ground moraines, and in all cases, outwash plains are left as alluvial deposits are moved downstream from the glacier (Sapkota 2020). Parent material moved by gravity can be seen at the base of steep slopes as talus cones, called colluvial material (Sapkota 2020).

1.1.1.2 Topography

The topography is characterized by the inclination (slope), elevation and orientation of the terrain. It has been well reported that topography determines the rate of precipitation or runoff and rate of formation or erosion of the surface soil profile. The topographical setting may either hasten or retard the work of climatic forces. When topography is characterized by steep slopes, it allows less rainfall to enter the soil and encourages erosion, thus leading to little mineral deposition in lower profiles. In semi-arid regions, the lower effective rainfall on steeper slopes also results in less complete vegetative cover, so there is less plant contribution to soil formation. For all of these reasons, steep slopes increase the rate of soil destruction far ahead of that of soil formation. Therefore, soils on steep terrain tend to have rather shallow, poorly developed profiles in comparison to soils on nearby, more level sites (Liu et al. 1994). Topography in the soil formation process includes factors like the geological structure of the elevation above the sea level, configuration and the slope.

The position of parent material or soil during pedogenesis influences the hydrologic cycle, transpiration and other such processes. It has been observed that soil profiles on the convex slopes are usually shallower with less distinct sublayers than the soils on the top of the concave slopes. However, organic matter of the soil at lower slopes is higher due to runoffs than the soils at higher slopes. Topography might be susceptible to changes over time by processes like soil erosion and earthquakes, which then affect the process of soil formation.

1.1.1.3 Organisms

Animal inhabitants, the human population and vegetation heavily influence the process of soil formation. In the case of effects caused by vegetation, soils present under trees tend to be more acidic and contain much less humus than those under grass. These differences are observed due to the differences in the litter produced by the two different types of vegetation. Removal or burial of soil profile by humans during construction works and the modification of organic matter by agriculture or irrigation influence the soil formation process (Sapkota 2020).

Humans impact soil formation by removing vegetation cover with erosion, waterlogging, lateritization or podzolization (according to climate and topography) as the result (Oldeman 1992). Their tillage also mixes the different soil layers, restarting the soil formation process as less weathered material is mixed with the more developed upper layers, resulting in net increased rate of mineral weathering (Karathanasis and Wells 2004). Soil organisms (animals and microorganisms) affect pedogenesis as they influence the organic matter content of soil and the texture due to their metabolic and physical activity.

Soil is the most abundant ecosystem on Earth, with microorganism being the most abundant, a great many of which have not been studied (Gans et al. 2005; Dance 2008). A population limit of about one billion cells per gram of soil is estimated; the number of species varies widely from 5.0×10^4/g to over 1.0×10^6/g of soil (Gans et al. 2005; Roesch et al. 2007). The total number of organisms and species can vary widely according to soil type, location and depth (Roesch et al. 2007).

Plants, animals, fungi, bacteria and humans affect soil formation (see soil biomantle and stonelayer). When soil animals burrow (soil macrofauna and soil mesofauna) and pore through the soil, they mix the soil and also allow gases and moisture to move about within the soil, a process called bioturbation (Meysman et al. 2006). This is the same way; plant roots penetrate soil horizons and open channels upon decomposition (Williams and Weil 2004). Plants with deep taproots can penetrate many metres through the different soil layers to bring up nutrients from deeper in the profile (Lynch 1995). Plants have fine roots that excrete organic compounds (sugars, organic acids, mucigel), slough off cells (in particular at their tip) and are easily decomposed, adding organic matter to soil, a process called rhizodeposition (Nguyen 2003). Microorganisms, such as fungi and bacteria, affect chemical exchanges between roots and soil and act as a reserve of nutrients in the rhizosphere plants (Widmer et al. 2000). The growth of roots through the soil stimulates microbial populations, stimulating in turn the activity of their predators (notably amoeba), thereby increasing the mineralization rate, and in last turn root growth, a positive feedback called the soil microbial loop (Bonkowski 2004). Out of root influence, in the bulk soil, most bacteria are in a quiescent stage, forming microaggregates. Microaggregates are mucilaginous colonies of microorganisms to which clay particles are attached, offering them a protection against desiccation and predation by soil microfauna (bacteriophagous protozoa and nematodes) (Six et al. 2004a, b). Microaggregates (20–250 μm) are ingested by soil mesofauna and macrofauna, and bacterial bodies are partly or totally digested in their guts (Saur and Ponge 1988).

1.1.1.4 Climate

Climatic conditions such as rainfall, temperature and storm patterns contribute to pedogenesis over a long period of time. The direct effect of climate on soil formation is through water and solar energy (Sapkota 2020). Water is a medium for the life cycles of various soil organisms, whereas sunlight affects the concentration of water in the soil. In desert soils, usually present around the equatorial region with high solar and water energy, the effect of climate on soil formation can be clearly seen. In the temperate regions, the soil is topical with sufficient moisture due to the humid climate (Sapkota 2020).

For all the key chemical weathering reactions, water is vital. To be effective in soil formation, water is needed to penetrate the regolith. The seasonal rainfall distribution, evaporative losses, site topography and soil permeability all work in synergy to determine how effectively precipitation can influence soil formation. The extent to which weathering of the soil goes and its formation depends greatly on how deep the water can penetrate the regolith.

Excess water penetrating through the soil profile provides conveyances of soluble and suspended materials from the higher layers (eluviation) to the lower layers (illuviation), plus clay particles and liquefied organic matter (Michalzik et al. 2001). Soluble materials may also be carried away via drainage waters from the surface. Accordingly, penetrating water fuels weathering reactions which consequently results in the differentiation of soil horizons. Similarly, water deficit or deficiency is also a key determining factor in the soil type that can be found in arid regions. Leaching of soluble salts does not occur in this kind of soils; in most cases, the excessive accumulation of the salts leads to a reduction in growth of plants (Bernstein 1975) and microorganisms (Yuan et al. 2007). It is a very common observation that soil profiles in semi-arid and arid areas also contain carbonates and certain types of expansive clays (calcrete or caliche horizons) (Schlesinger 1982; Nalbantoglu and Gucbilmez 2001). In soils of the tropical zones where through the process of deforestation the soil loses its vegetation and the soil is exposed to upward movement of water via capillary action induced by severe cases of evaporation, this water contains dissolved aluminium and iron salts implicated in the formation of the kind of soil that is not arable because of the superficial hard pan of laterite or bauxite a situation that is considered as irreversible soil degradation (lateritization, bauxitization) (Retallack 2010).

The direct impacts of climate according to Donahue et al. (1977) include:

1. A superficial build-up of lime in low rainfall areas as caliche
2. Formation of acidic soils especially in humid areas
3. Soil erosion on steep hillsides
4. Deposition of eroded materials downstream
5. Severe chemical weathering, erosion and leaching in warm and humid regions

1.1.1.5 Time

The effect of time on soil formation is not site-related as are topography and parent materials and is not also like climate and organisms that are inputs from the surrounding (flux-related). Time is an independent factor and the changes it brings are usually abrupt. Time is considered an abstract variable that shows that the evolution of soil might change without any external inputs (Sapkota 2020). The effects of time on the soil profile can be observed by the composition of the soil where the accumulation of clay and lime in the sublayers occurs due to downward translocation. The humus content in the soil horizons might also differ with ageing.

Soil texture is made up of a blend of silt, sand and clay which results in the production of peds; soil development or pedogenesis is said to have occurred when a distinct B horizon is developed (Bormann et al. 1995). The interplay of the above-mentioned soil-forming factors all depends on time for them to give any soil its characteristic features. For a soil to develop a profile, the process can take a couple of decades to a thousand or more years (Crews et al. 1995). Soil is said to constantly be in a state of change which is affected by several changing soil-forming factors (Huggett 1998), the period of time in which this change occurs seriously depends on parent material, climate, biotic activity and relief (Donahue et al. 1977).

In a situation where flooding occurs and materials are deposited, the site will show no soil development because it has just been recently deposited and there has been no ample time for such materials to develop a structure which can be regarded as a soil (Craft et al. 2002). The soil formation processes usually begin afresh as the original soil which was on the surface is completely buried. Thus, with time, such a soil will develop a profile depending on the moderations of the biota and the intensities of the climatic factors (Crews et al. 1995). When a soil is left vulnerable to the actions of erosion, that is when the soil cycle ends. However, some soil cycles are long despite soil retrogression and degradation (Crews et al. 1995; Shipitalo and Le Bayon 2004).

The factors affecting the formation of soils consistently affect the soils even in regions with a very stable landscape which have persisted for so many years (Crews et al. 1995). New materials are either being deposited above, washed or blown from the surface (Pimentel et al. 1995; He et al. 2007); this makes soil conditions really unstable because soils are constantly subjected to new and different conditions always; be it very rapid change or slow changes, they all depend on the climate, biological activity and topography (Wakatsuki and Rasyidin 1992).

Time is regarded as a key soil-forming element, and it may be studied by critically looking at the soil chronosequences, where soils of dissimilar ages but with negligible differences in other soil-forming elements can be likened (Huggett 1998). Paleosols can be regarded as soils formed during earlier soil-forming conditions.

1.1.2 Processes of Soil Formation

The soil formation process starts with a parent material. This is what determines the mineral composition and widely contributes to the chemical and physical characteristics of the soil. There are several processes or mechanisms involved in soil formation.

1.1.2.1 Weathering Phase

The breakdown of rocks and minerals at or near the Earth's surface into products is called weathering. It results in attainment of equilibrium with the conditions found in such environment (Sapkota 2020). The products of weathering are the major source of sediments for erosion and deposition. The weathering processes can be physical, chemical or biological. Physical weathering results in the breakdown of mineral or rock material by entirely mechanical methods brought about by a variety of causes. Abrasion of large rocks occurs when some forces cause two rock surfaces to come together, causing mechanical wearing or grinding of their surfaces. Chemical weathering is the alteration of the chemical and mineralogical composition of the weathered material via chemical means. A number of different processes, including hydrolysis, oxidation, reduction, hydration, carbonation and solution, result in chemical weathering, while the disintegration of rock and mineral due to the chemical or physical agents of an organism is considered biological weathering. The organisms that can cause weathering might range from bacteria to plants to animals (Sapkota 2020).

1.1.2.2 Build-up of Materials in Soil

Forces generated from water, ice or wind encourage the build-up of decomposing organic matter materials or new mineral materials over a period of time. In the case of poorly drained soils, the organic matter accumulates since water-logging prevents it from being oxidized or broken down by soil organisms. However, in the case of well-drained soils, the accumulation of materials occurs when the root systems hold them up. Particle deposited by wind forces, water or ice equally leads to the accumulation of new materials. Some plants with the help of symbiotic bacteria fix atmospheric nitrogen and ammonia compounds into the soil as nitrates (Sapkota 2020).

1.1.2.3 Leaching

Leaching is the removal of soluble components of the soil column by water. During leaching, bases like calcium are washed down through the soil leading to the acidification by hydrogen ion substitution. Through the movement of water, wind or ice, or by the uptake of the accumulated materials by plants, new particles including clay, organic matter, clay, silt or other chemical compounds get leached and eroded or taken up by plants. This alters the parent material of the soil as well as the physical and chemical compositions of the new accumulated materials (Sapkota 2020).

1.1.2.4 Transformation

The chemical weathering of soil particles, such as silt, sand and clay minerals, as well as the change of organic materials into degradation-resistant organic matter is known as transformation. Following transformation, the clay alongside other accumulated materials is washed from the upper layer and is deposited in the lower horizons (Sapkota 2020). The soil organisms like plants and animals also contribute to the transformation of the soil by the physical and chemical breakdown of materials. The soil begins to take shape on its own through transformation, which improves water retention capacity and nutrient composition (Sapkota 2020).

1.1.2.5 Calcification

Calcification occurs when the removal of water through evapotranspiration exceeds precipitation initiating the upward movement of dissolved alkaline salts from the groundwater. Meanwhile, the movement of rainwater causes a downward movement of the salts (Sapkota 2020). Several machineries including siltation, over-pressure, erosion, and lake bed succession contribute to the formation of soil.

1.1.3 Soil Composition

Soil is the outer, loose layer that covers the surface of Earth. Soil quality and climate being the major determinants of plant distribution and growth depend not only on the chemical composition of the soil but also the topography (regional surface features) and the presence of living organisms. Plants obtain inorganic elements from the soil, which serves as a natural medium for land plants (Lumenlearning 2013). Soil consists of four major components (Lumenlearning 2013) which include inorganic minerals, air, organic matter and water.

1. Inorganic mineral matter, about 40–45% of the soil volume
2. Organic matter, about 5% of the soil volume
3. Air, about 25% of the soil volume
4. Water, about 25% of the soil volume

The amount of each of the four major components of soil is determined by the quantity of vegetation, soil compaction and presence of water in soil. A healthy and a good soil has sufficient air, water, minerals and organic material to stimulate and sustain plant life. The organic material of soil, called humus, is made up of microorganisms (dead and alive) and dead animals and plants in varying stages of decay. Humus improves soil structure, making available water and minerals to plants. The inorganic material of soil is composed of rock, slowly broken down into smaller particles that vary in size. Soil particles ranging from 0.1 to 2 mm in diameter are sand. Soil particles between 0.002 and 0.1 mm are called silt, and even smaller particles, less than 0.002 mm in diameter, are called clay. Soils with no dominant particle size, containing a mixture of sand, silt, and humus, are called loams (Lumenlearning 2013).

1.1.3.1 Physical Properties of Soil

Soils are made up of combinations of four distinct layers or horizons: O horizon, A horizon, B horizon and C horizon.

1. The O horizon has freshly decomposing organic matter (humus) at its topmost part; more decomposed vegetation is found at its base. Humus enhances soil moisture retention and enriches the soil with nutrients. Topsoil, the top layer of soil, varies considerably with an average depth of 2–3 inches. For instance, river deltas have deep layers of top soil; an example is the Mississippi River delta. Due to richness of the topsoil in organic material, a lot of microbial processes occur there, and this richness is responsible for plant production (Lumenlearning 2013).
2. The A horizon consists of a mixture of inorganic products of weathering with organic material. It is regarded as the beginning of true mineral soil. This horizon is dark in colour because of the presence of organic matter. In this area, rainwater percolates through the soil with materials carried from the surface (Lumenlearning 2013).
3. The B horizon is the subsoil. It is an accumulation of mostly fine material that has moved downward from the O and A horizon, resulting in a dense layer in the soil. In some soils, the B horizon contains nodules or a layer of calcium carbonate (Lumenlearning 2013).
4. The C horizon is the soil base. It is made up of the parent material, plus the organic and inorganic material that is broken down to form soil. The parent material may be either created in its natural place or transported from elsewhere to its present location. After the C horizon exists the bedrock (Lumenlearning 2013).

Some soils may have additional layers or lack one of these layers. The thickness of the layers is also variable, depending on the factors that influence soil formation. In general, soils that are not fully mature may have O, A and C horizons, whereas mature soils usually display all of these, plus additional layers.

1.2 Properties of Soil as a Biological System

1.2.1 Physical Structure and Distribution of Organisms in Soil

Soil, being composed of solid, liquid and gaseous phases, is a peculiar environment for living organisms. The soil is composed mainly of the solid phase; the liquid and gaseous phases vary depending on agricultural practices and climatic conditions. The soil structures, that is, the organization and arrangements of soil particles, influence the biological, chemical and physical properties of soil. Soil particles differ in their size, shape and chemical composition and may be linked with different bonds. The organization of soil structure is hierarchical because primary particles bind together to form secondary particles that can interact further to form bigger particles, such as microaggregates and macroaggregates (Oades and Waters 1991). The hierarchical organization of the solid particles creates pores of various sizes that may be filled by water or telluric gases.

The pores and their sizes influence the spatial separation of soil organisms:

1. Micro-arthropods are found to inhabit macropores.
2. Nematodes can also live in intermacroaggregate pores.
3. Protozoa, small nematodes and fungi can also be present in intramacroaggregate or intremicroaggregate pores.
4. Intramicroaggregate pores can only be occupied by bacteria and viruses (Elliott and Coleman 1988; Six et al. 2004a, b).

This spatial arrangement of organisms with pores depends on the organism size. Bacterial size is about a few micrometres, that of fungi is less than 100 μm, and that of Acari and Collembola ranges from 100 μm to 2 mm (Six et al. 2004a, b). One very important effect of the separation is the protection of some soil organisms against the predatory nature of others; bacteria may be protected from protozoa.

Living organism populations are usually higher in areas such as the rhizosphere (the soil attached to roots), the detritusphere (the soil around a plant residue) and the drilosphere (soil around biopores created by earthworms) (Coleman and Crossley 1996; Nannipieri et al. 2003). These are regarded as the microsites (hotspots), part of the less than 1% of the available space where soil organisms inhabit.

Conditions such as acidity; low water and low oxygen (O_2) availability; predation and inter- and intra-competition between organisms; and frequent disturbances (drying-rewetting and freezing-thawing cycles and the presence of toxic

Table 1.1 Some values of microbial biomass C (MBC) and microbial biomass N (MBN) in soil (redrawn from Smith and Paul 1990)

Soil	Sandy loam	Silt loam	Clay	Silt	Clay loam	Clay loam
Vegetation	Pasture	Cereal grass	Pasture	Pasture	Cereals	Wheat
MBC (kg ha^{-1})	288	288	750	800	1200	1940
MBN (kg ha^{-1})	48	48	100	309	240	385

compounds) are the reasons why soil organisms inhabit the less than 1% of the enter soil environment (Dini-Andreote and Van Elsas 2019). However, according to Smith and Paul (1990), the microbial biomass is massive, ranging from 1% to 5% of the organic matter of soil; these values, expressed as microbial biomass C or microbial biomass N, can range from 280 to 1940 kg ha^{-1} and from 40 to 385 kg ha^{-1}, respectively (Table 1.1).

1.3 Soil Biota

1.3.1 Microbial Diversity and Functions

Soil biota consists of the microorganisms, soil animals and plants living all or part of their lives in or on the soil or pedosphere (Soil Quality Institute 2001). Microorganisms found in the soil include bacteria, fungi, archaea and algae, while soil animals may include protozoa, nematodes, mites, springtails, spiders, insects and earthworms. Millions of species of soil organisms exist, but only a fraction of them are culturable and properly identified. Microorganisms are members of the soil biota but are not considered members of the soil fauna (Fortuna 2012). The soil fauna is the collection of all the microscopic and macroscopic animals in a given soil. Soil animals can be conventionally grouped by size classes: macrofauna (cm; enchytraeids, earthworms, macroarthropods), mesofauna (mm; microarthropods, mites and collembolan) and microfauna (μm; protozoa, nematodes) (Fortuna 2012).

Due to the sizes of soil organisms, the location of their habitats is usually restricted or localized. Organisms like nematodes live in the thin water films and capillary pores of aggregates while preying and feeding on other aquatic microfauna such as amoebas. Soil protozoa, although land-adapted, are members of aquatic microfauna that can dwell in water films in field moist soils. Water films are created by the adsorption of water to soil particles. Soil has a direct effect on the environmental conditions, habitat and nutrient sources available to the soil biota (Fortuna 2012).

1.3.2 Key Roles of the Soil Biota

Soil organisms serve numerous roles in the pedosphere. The most critical function played by soil organisms is the regulation of biogeochemical transformations, among several other roles. The formation and turnover of soil organic matter (OM) that include mineralization and sequestration of carbon, nutrient cycling, disease transmission and prevention, pollutant degradation and improvement of soil structure are some of the functions mediated by the soil biota (Gupta et al. 1997). The by-products of metabolic oxidation or reduction of C and N compounds in soils include GHG (Madsen 2008). Carbon (IV) oxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) constitute dominant soil GHGs. However, GHG emissions can be regulated with some soil management practices such as N fertilization and tillage which can stimulate specific microbial activities such as autotrophic nitrification, denitrification and mineralization (Greenhouse Gas Working Group 2010) by the oxidation and reduction of C and N (Fortuna 2012).

The combined mass of microorganisms in the soil otherwise known as microbial biomass is reliant on upon soil properties and the source(s) of C available for energy and cell metabolism. Carbon sources to the soil organisms vary in their ability to be decomposed and nutrient content. Carbon turnover, decomposition and microbial activity often lead to increases in organic matter and soil aggregation. Different ecosystems vary in their ability to support soil organisms and sequester carbon in organic matter. Organic carbon constitutes the chemical precursor of generation of organic matter and is the energy source for most soil organisms. Microbial degradation of plant biomass and organic matter provides access to C and other nutrients such as nitrogen and phosphorus required by many living organisms. Mineralization of organic N to ammonium (NH_4^+) and additions of N fertilizers that contain NH_4^+ stimulate nitrification a process driven by nitrifying bacteria and archaea that transform NH_4^+ to nitrate (NO_3^-) (Maier et al. 2009; van Elsas et al. 2007). Nitrate can further be denitrified by microorganisms to nitrite and nitrous oxide (N_2O).

The soil food web refers to the community of organisms that live all their lives or part of it in the pedosphere and mediate the transformation and transfer of nutrients between the living (biotic) and non-living (abiotic) components of the pedosphere through a series of conversions of energy and nutrients as one organism and/or substance is consumed by other organisms (Sylvia et al. 2005). The mesofauna (collembolan, mites) are known to shred materials into smaller pieces as their role in nutrient turnover, thereby providing higher surface area for greater access for microfauna (bacteria, fungi, mycorrhizae) for further recycling of the majority of C. Soil organisms can be part of the detrital food chain when their organic C forms part of dead materials. The detrital food chain allows the formation of new soil organic matter and the recycling of nutrients from existing organic matter. Biological systems contain fairly constant elemental ratios of carbon/nitrogen/phosphorus/sulphur (C/N/P/S). These ratios and mass balances allow scientists to monitor biochemical shifts between organisms or ecosystems (net change = input + output + internal change) (Fortuna 2012).

Most members of the soil fauna are grouped as chemoheterotrophs based on their nutritional type. They obtain C and energy by the oxidation of organic compounds (Sylvia et al. 2005). These processes of oxidation or mineralization of an organic carbon source to CO_2 by chemoheterotrophs maybe be limited in a process known as carbon sequestration. The by-products of the mineralization process by chemoheterotrophs are metabolites, heat and CO_2, a greenhouse gas (GHG). The production of CO_2 can reduce O_2 concentrations available in the soil for use by aerobic organisms. This may create anoxic sites within microaggregates, resulting in microenvironments with different amounts of nutrients and oxygen (van Elsas et al. 2007). The CO_2 generated may be converted to CH_4^+ (another GHG) via anaerobic respiration by archaea known as methanogens in microsite environments. Methane can undergo oxidation back to CO_2 in adjacent microsites. This process is carried out by methanotrophic bacteria (Fortuna 2012).

1.3.3 Microbiota Arena of Activities

The ability of microorganisms to recycle C provides direct and indirect health benefits to plants. Soils that contain larger amounts of organic matter will have higher microbial biomass and also higher rates of microbial activity. Many times the beneficial microorganisms, in their activities, outcompete the non-beneficial ones (plant pathogens). This is known as general suppression of plant pathogens (Sylvia et al. 2005). Another form of suppression observed in soils with high levels of organic matter is the specific suppression where antagonistic microorganisms have explicit means of suppressing pathogens through the production of antibiotics. Soils that exhibit such properties are termed suppressive soils. Microorganisms also interact directly with plants through symbiotic relationships that provide nutrients to plants while supplying C to the microorganism(s). Some microorganisms are known to inhabit the internal tissues of plants and provide certain benefits to their host in a symbiotic relationship. *Rhizobium*, a soil bacterium, induces the formation of root nodules on the roots of soybean plants where it lives and fixes nitrogen for the plant while using the carbon source (carbohydrates) provided by the plant (Fortuna 2012).

1.3.4 Microbiota; Arena of Activities in the Pedosphere of a Forest

Soil as an heterogeneous environment contains limited resources and multiple ecosystems of various sizes between a forest floor, the rhizosphere of a tree, an aggregate, and a single pore of an aggregate. These ecosystems contain areas or arenas of activity rich in detritus or plant matter representing approximately 10% of the total soil volume (Beare et al. 1995; Coleman and Crossley 1996). These arenas, otherwise called 'hot spots' of activity, are widely distributed in space and time. They contain a rich biodiversity of organisms that play key roles in the biogeochemical cycling and in the release of nutrients transferred from one ecosystem to another. Many organisms in a soil are redundant and serve a similar purpose (e.g. the heterotrophs involved in C cycling). Other 'keystone' organisms have greater influence on soil processes than their numbers would indicate. Nitrifiers are 'keystone' organisms that control transformations in a portion of the N cycle but constitute less than 1% of the total microbial population (Fortuna 2012).

The description below depicts soil as an arena for the diverse activities of living organisms. When leaves fall to the forest floor, they are physical breakdown by the shredding action facilitated by the members of the mesofauna (e.g. mites, collembolans). Microorganisms then take over the degradation process. With time, worms consume the decaying leaves and deposit them in the drilosphere. The deposited here are found within the soil aggregates, and with other organic materials, they replenish the supply of N, P and OM used by soil organisms. Mucilages are produced by the active microorganisms feeding on detrital leaf matter. These mucilages with other organic materials increase the size and stability of the aggregate ecosystem. In this way, soil organisms release, transform and relocate resources found in arenas of activity throughout the pedosphere through a number of biogeochemical cycles.

1.4 Soil Biota Interactions

1.4.1 Interactions Between Microbes, Plants and Fauna

Interactions between species (bacteria, fungi, plant, animal or virus) are categorized by how cells interact with other species and how they sense neighbouring cells of the same species. These interactions occur at three levels, namely, physical, biochemical and nutritional levels. Physical level of interaction is between cells occupying the same microenvironment; biochemical level of interaction relates how cells respond to molecular signals sent off from other cells, and at nutritional level, responses due to metabolic activities are referred (Van Elsas et al. 2019).

These three types of interactions can occur simultaneously (Van Elsas et al. 2019). Interactions between microbes in soils have been extensively studied in vitro but not in vivo due to the complexity and heterogeneity of soils. The importance of these interactions is what makes soil microsites habitable (Nannipieri et al. 2003). Motile organisms such as protozoans; nematodes and earthworms; fungi, with their hyphae; chain-forming organisms, (such as *Bacillus mycoides*, actinomycetes and fungi); and plant roots can move between different soil microenvironments (Van Elsas et al. 2019).

Quorum sensing (QS) is one of the most studied molecular signals between bacterial cells. According to Pietramellara et al. (2009), it involves the regulation of several bacterial processes, such as symbiosis, virulence, competence for transformation, conjugation, antibiotic production, motility, sporulation and biofilm formation. Studies have revealed that QS signals are important in the assemblage of bacterial cells with specific QS signals and exclusion cells of species with anti-QS signaling traits (Pietramellara et al. 2009).

Interactions in soil are also moderated by the release of antibiotics against organisms of different species. Positive and negative interactions are also observed among bacteria and fungi. Fungi are observed to promote the soil colonization of bacteria found on the external surface of their hyphae and using fungal exudates. Bacteria also benefit from soil fungi when they make use of monomers or oligomers produced from the breakdown of polymers, such as the cellulose of plant residues, by the activities of fungal extracellular enzymes (Pietramellara et al. 2009).

Negative interactions between bacteria and fungi are observed by the predatory action of myxobacteria on fungi, the release of antifungal compounds by bacteria and the use of bacterial cells as nutrient sources by some fungal species (Pietramellara et al. 2009). There exist several interesting interactions among microbial species in soil. Bacteria and fungi can be found down the food web as nutrient sources for eukaryotic organisms.

Bacteria in the rhizosphere of plants thrive due to the presence of the root tip exudates; because root exudates are generally C-rich compounds, bacteria have to make N from soil organic matter and share the same with the plant host (Bonkowsky and Clarholm 2012). Another interaction is that of protozoa and bacteria. Protozoa graze on bacteria, releasing ammonium N into the soil environment because the C/N ratio of protozoa cells is higher than that of bacterial cells. The released ammonium is taken up by the plant, and thus the microbial loop shifts the competition for N between plants and bacteria in favour of plants (Bonkowsky and Clarholm 2012).

The rhizosphere is the soil around the roots of plants where higher microbial activity is usually observed compared to the bulk soil because of rhizodeposition, which includes root exudates, mucilage, root debris and whole detached root cells (Samad et al. 2019). Beneficial, pathogenic and neutral microorganisms are all inhabitants of plant's rhizosphere. Among the beneficial microorganisms, the plant growth-promoting bacteria stimulate plant growth by providing nutrients and protecting plants from various abiotic and biotic stresses (among the latter, the biological control of pathogens) while also benefiting from the synthesis of organic carbon from the plant (Samad et al. 2019). Beneficial microbes at the roots of plants could invade them leading to a symbiotic relationship after a complex molecular cross-talk involving both the release of root exudates and microbial exudates. The most studied molecular cross-talks are those between rhizobia and legumes (Cooper 2007) and mycorrhizae and plants (Martin et al. 2007).

Generally, rhizodeposition selects for certain species of microorganisms, giving a decrease in microbial diversity when moving from the bulk soil to the rhizospheric region of the soil (Samad et al. 2019). Microbial diversity, even at the rhizosphere, is greatly affected by the type of soil. The study of the denaturing gradient gel electrophoresis (DGGE) profiles of the rhizosphere soil of *Carex arenaria*, a non-mycorrhizal plant species, reveals different patterns of diversity with different types of soil (De Ridder-Duine et al. 2005). The use of metagenomics sequencing confirmed that soil types could impose a larger selective pressure on plant-associated bacterial communities than plant species themselves (Yech et al. 2017; Schlaeppi et al. 2014). Interestingly, the effect of soil type is not as impactful on the endosphere (the interior of roots colonized by endophytes) as on rhizosphere (Escudero-Martinez and Bulgarelli 2019). According to Fizpatrick et al. (2018), 40% of the variation in microbial diversity depended on the host species in the endosphere but only 17% in the rhizosphere soil when 30 angiosperms were grown in a garden soil (Fizpatrick et al. 2018).

1.4.2 Interactions Between Endophytes and Plants

An endophyte is an endosymbiont, often a bacterium or fungus that lives within a plant for at least part of its life without causing apparent disease. Endophytes are ubiquitous and have been found in all the species of plants studied to date even though most of these endophyte-plant relationships are not well understood. Many economically important forage and turf grasses (e.g., *Festuca* spp., *Lolium* spp.) exhibit improved abilities to tolerate abiotic stresses such as drought, as well as improve their resistance to insect and mammalian herbivores when found in association with fungal endophytes (*Neotyphodium* spp.) (Lumenlearning 2013).

Endophyte transmission for one plant to another is possible, and it is done either vertically (directly from parent to offspring) or horizontally (from individual to unrelated individual). Vertically transmitted fungal endophytes are asexual and transmit via fungal hyphae penetrating the host's seeds (e.g., *Neotyphodium*). Since their reproductive fitness is intimately tied to that of their host plant, these fungi are often mutualistic. On the other hand, horizontal transmissions of fungal endophytes are sexual and done through the spreading of fungal spores by wind of insect vectors. Horizontally transmitted endophytes are often closely related to pathogenic fungi, even though they are not pathogens (Lumenlearning 2013). Endophytes present lots of benefits for the host plants. They prevent pathogenic organisms from colonizing them by their own extensive colonization of the plant tissue; they create a 'barrier effect', where the local endophytes outcompete and prevent the activities of pathogenic organisms. Beneficial actions of endophytes may involve the production of certain chemicals capable of inhibiting the growth of competitors and pathogenic organisms. Some bacterial endophytes have proven to increase plant growth, help plants survive drought and heat and prevent plant diseases. However, the presence of fungal endophytes can cause higher rates of water loss in leaves (Lumenlearning 2013).

Endophytes produce a wide range of compounds, some of which are very important in combating pathogens and even cancers in animals and humans. One remarkable endophyte with medicinal benefits to humans is *Pestalotiopsis microspora*, an endophytic fungus of *Taxus wallichiana* (Himalayan yew), which was found to produce taxol. This fungus was discovered by Gary Strobel. Researches on endophytes are currently intensified for their roles in agriculture and biofuel production and commercially viable enzymes. Certain crop plants are inoculated with endophytes intentionally to provide increased disease or parasite resistance, while others may possess metabolic processes that convert cellulose and other carbon sources into 'myco-diesel' hydrocarbons and hydrocarbon derivatives. *Piriformospora indica* is an interesting endophytic fungus of the order Sebacinales. The fungus is capable of colonizing roots of plants and forming symbiotic relationship with every possible plant on earth. *P. indica* has also been shown to increase both crop yield and plant defence of a variety of crops (barley, tomato, maize, etc.) against root pathogens (Lumenlearning 2013).

The general belief is that there may be many useful endophytes, but information on them are masked due to dearth of research information and destruction of areas of biodiversity due to deforestation; thus many useful endophytes for curing disease might be permanently lost for medicinal use before they are discovered. Studies of plants grown at different climates or at increased carbon (IV) oxide levels have different distributions of endophytic species. This is an indication of the effect of climate change on plant endophytes and their interactions with plants (Lumenlearning 2013).

1.4.3 Interactions Between Mycorrhizal Fungi and Plant Root

Mycorrhizae is a term used to describe the association of some plants with fungi. This is a symbiotic association that gives both access to certain nutrients in the soil and protect against disease, predation and toxicities. Conditions such as low nutrient concentration, low diffusion rate or low soil moisture lead the development of nutrient depletion zone in the soil. When this happens, most plants rely on fungi to facilitate the uptake of minerals from the soil through the formation of mycorrhizae. In these associations, the fungi are actually integrated into the physical structure of the root (Lumenlearning 2013).

Through mycorrhization, the plant obtains phosphate and other minerals, such as zinc and copper, from the soil, while nutrients, such as sugars, from the plant root are made available to fungi. Mycorrhizae do increase the surface area of the plant root system as fungal hyphae spread beyond the nutrient depletion zone. Fungi can obtain up to 20% of the total carbon accessed by plants. The long, thin hyphae of fungi grow into small soil pores with ease to access phosphorus otherwise unavailable to the plant. The beneficial effect on the plant is best observed in poor soils. Mycorrhizae also function as a physical barrier to pathogens, inducing generalized host defence mechanisms through production of antibiotic compounds by the fungi. Fungi have also been found to have a protective role for plants rooted in soils with high metal concentrations, such as acidic and contaminated soils (Lumenlearning 2013).

Two types of mycorrhizae have been described: ectomycorrhizae and endomycorrhizae. Ectomycorrhizae form an extensive dense sheath around the roots, called a mantle. Hyphae from the fungi extend from the mantle into the soil, which increases the surface area for water and mineral absorption. This type of mycorrhizae is found in forest trees, especially conifers, birches and oaks. Endomycorrhizae are also called arbuscular mycorrhizae. Here the fungal mycelium is embedded within the root tissue. Endomycorrhizae are found in the roots of more than 80% of terrestrial plants (Lumenlearning 2013).

1.4.4 Interactions Between Soil Bacteria and Plant Root

Plants cannot obtain adequate amount of nitrogen for their optimal growth and general metabolism from the soil, so they form symbiotic relationships with rhizobia that can fix it as ammonia. Nitrogen being an important macronutrient is vital for nucleic acid and protein synthesis. Atmospheric nitrogen, which is the diatomic molecule N_2 or dinitrogen, is the largest pool of nitrogen in terrestrial ecosystems, and it is very unavailable to plant in this state. Plants do not have the necessary enzymes to convert this N_2 into biologically useful forms.

Plants, however, depend on nitrogen which can be 'fixed' by microorganisms. Nitrogen can be converted to ammonia (NH_3) through biological, physical or chemical processes, but the biological nitrogen fixation (BNF) is exclusively done by prokaryotes, such as soil bacteria or cyanobacteria. Biological nitrogen fixation contributes about 65% of the nitrogen used in agriculture.

The NH_3 resulting from fixation is transported into plant tissue and incorporated into amino acids, proteins and nucleic acid during biosynthesis. Many legume seeds, such as soybeans and peanuts, contain high levels of protein and are among the most important agricultural sources of protein in the world (Lumenlearning 2013).

1.5 Conclusion and Future Perspective

The pedosphere happens to be a very varied environment uniquely designed to support life, with its limited resources which is spread out in different sizes and shapes of the diverse ecosystems. The pedosphere houses numerous soil biota. Microorganisms found in the soil include bacteria, fungi, archaea and algae, while soil animals may include protozoa, nematodes, mites, springtails, spiders, insects and earthworms. Millions of species of soil organisms exist, but only a fraction of them are culturable and properly identified. Soil organisms serve numerous roles in the pedosphere. The most critical function played by soil organisms is the regulation of biogeochemical transformations, among several other roles. The formation and turnover of soil organic matter that include mineralization and sequestration of carbon, nutrient cycling, disease transmission and prevention, pollutant degradation and improvement of soil structure are some of the functions mediated by the soil biota.

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Chapter 2
Intermicrobial Interactions in the Pedosphere and Their Importance

Lebin Thomas and Ishwar Singh

Abstract Microbial biodiversity of the pedosphere is intricately associated with pedogenesis and subsequent maintenance of soil structure. In soil, microorganisms interact among themselves and with other factors and can get inhibited (antagonism) or benefited (synergism) from such interactions. The antagonistic interactions that are of common occurrence in soil environment are effected with an interference competition encompassing different chemical mediators, inhibitors, or physical interactions to obtain increased access to soil resources or niche. Besides, microbes positively interact in a synergism for rendering highly valuable ecosystem functions of releasing carbon compounds, increasing water and nutrient availability in the soil, organic matter decomposition, and mobilization of nutrients. During synergistic interactions, there could be metabolic interdependence among microbes where one protects and promotes efficient substrate utilization, growth, and reproduction in the other with the production of different bioactive compounds. Further, during interactions microbes utilize small diffusible molecules of quorum sensing systems for regulating production of virulence factors or biofilm formation. The microbial interactions contribute to the distribution of soil aggregates and structure with their decomposition activities, biodegrading of different pollutants, and secretion of polymeric substances. Further, multimicrobial interactions enhance bacterial nodulation activity and physiological development in plants. Furthermore, the interacting microbes have the potential applications in the biological control of pre- and post-harvest problems of microbial contamination and development of chemicals of pharmaceutical importance.

Keywords Antagonism · Biofilms · Chemical mediators · Microbial interactions · Pedosphere · Synergism

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B. Giri et al. (eds.), *Structure and Functions of Pedosphere*,
https://doi.org/10.1007/978-981-16-8770-9_2

2.1 Introduction

Pedosphere, an outermost soil layer of the Earth, refuges a vast biodiversity that is predominated by different microorganisms. These microbes not only interact among themselves but also with other biotic and abiotic factors of the soil and play an irreplaceable role in the overall health of the soil. Dynamic microbial interactions that may be neutral, beneficial, and harmful lead to development of specific and variable niches and activities under the influence of factors such as nutrient availability, organic matter, physical conditions, and litter and woody habitats in rhizosphere as well as bulk soil (Urbanová et al. 2015; Kuzyakov and Blagodatskaya 2015). Accordingly, these factors significantly modify the abundance of microbial communities at different soil profiles, where microbes adapt to be involved in mineral bio-weathering, soil formation, decomposition, and nutrient cycling (Zhu et al. 2014; Lladó et al. 2017). The microbial utilization of chemicals from the bedrock as an energy source and as a part of metabolic activities, nutrient mobilization, and biofilm matrix production initiates the soil formation process (Flemming et al. 2016).

The secretion of chemical mediators is an important aspect of any microbe–microbe interaction that can affect microbial partner and their specific microenvironment, which involves shared metabolism, cooperative quorum sensing systems, and combined colonization of niches (Scherlach and Hertweck 2018). The relationships among microbes typically correlate with differences in niche preference, competition for the same substrates, extracellular enzymes, toxin production, and environmental modification (Faust and Raes 2012). The acquisition and acclimatization of nutrient resources and a suitable soil niche are often accompanied with antagonistic interactions among microbes. During this competitive interaction, microbes inhibit one another with diverse chemical mediators such as antibiotics, enzymes, siderophores, bacteriocins, volatile compounds, and inhibitors or disruptive physical interactions to obtain increased access to resources or space (Lugtenberg et al. 2017). Different bacteria can interact among each other with quorum sensing diffusible molecules for controlling important traits like production of virulence factors or biofilm formation (Fuqua et al. 1996), whereas fungi rapidly utilize organic compounds to exert a selection pressure on bacteria for these nutrients and further can attack with their defensive production of antibacterial compounds, detoxification, efflux of antibiotics, exudation of strong organic acids, and altering gene expression of bacteria (Gadd 1999; Duffy et al. 2003).

In contrast to antagonism, microorganisms in soil interact with each other for achieving synergism as endo-/ectosymbionts and helpers. Bacterial endosymbionts produce bioactive compounds; promote efficient substrate utilization, growth, and sporulation; and elicit asexual reproduction and protection from oxidative stress in their host fungi (Pakvaz and Soltani 2016; Pawlowska et al. 2018). Further, microbial endosymbionts have relatively smaller genome size, which facilitates nutritive interdependence and sharing of primary metabolites with their hosts that provide advantages in co-inhabiting of ecological niches together, particularly where there is a limitation of nutrients (Bonfante and Desirò 2017). The ectosymbiotic bacteria present on or in vicinity of fungal hyphae increase their host nutrient availability, growth, metabolism, fitness, and asexual reproduction (Frey-Klett et al. 2007; Oh et al. 2018). Helper bacteria facilitate establishment of mycorrhizal symbioses and promote fungal pre-symbiotic survival in the rhizosphere (Rigamonte et al. 2010). Similarly, mycorrhizal fungi provide a favorable and protective habitat to many soil microflora with the creation of habitable pore space and by increasing the availability of soil nutrients and organic matter in the rhizosphere (Andrade et al. 1998; Rashid et al. 2016). Further, the development of mushrooms involves a wide variety of interactions particularly mutualism among bacteria and fungi in soils and substrates (Carrasco and Preston 2020).

The interactions among microorganisms expedite mediation of a wide range of essential soil processes, including the restoration of degraded lands, maintenance of soil structure, decomposition of simple and recalcitrant organic matter, enhancement of soil fertility, biodegradation of different pollutants, and stabilization of water-stable soil macro- and micro-aggregates (Lladó et al. 2017; Khanpour-Alikelayeh and Partovinia 2021). Besides, at the root–soil interface, the microbial interactions can culminate into a tripartite symbiosis among plants–mycorrhiza–rhizobia, where the bacterial root nodulation can be dependent on mycorrhiza formation, as these could co-exist in the form of root symbionts (Barea et al. 2005). This symbiosis can alleviate water-deficit damage and enhance the bioavailability of nutrients and tolerance in plants. Moreover, the wide range of chemicals associated with microbial interactive activities have provided with the perspectives for their application in sustainable agriculture and post-harvest control (Kanchiswamy et al. 2015), along with obtaining beneficial drugs having potent biological activities (Guttenberger et al. 2017).

2.2 Microbial Diversity in Pedosphere

Pedosphere harbors a very rich microbial diversity. However, in the soil spatial variations of pH, temperature, moisture, composition, organic matter, nutrient availability, and biotic interactions create specific and variable microbial niches that determine the microbial abundance and activity in the soil (Kuzyakov and Blagodatskaya 2015). For instance, rhizosphere, where both microorganisms and their products interact dynamically with plant roots, supports high levels of microbial activity. The rhizospheric microbiome has a prominence of mycorrhizal fungi that interact symbiotically with most of the land plants (Kluber et al. 2011; Singh and Giri 2017). In most soils, there is an abundance of bacteria belonging to the phyla *Acidobacteria*, *Actinobacteria*, *Proteobacteria*, *Bacteroidetes*, and *Firmicutes* (Lauber et al. 2009). On the continental scale, biogeographical patterns of soil bacterial community composition indicate their ecological strategies for obtaining nutrients and organic matter in different niches. The abundance of *Acidobacteria* and *Alphaproteobacteria* in acidic soils negatively correlates with the carbon availability. This is indicative of these to be slow-growing oligotrophs (those present in areas of less nutrient and carbon) that have adapted to resource limitations, though these can show a high metabolic versatility (Jones et al. 2009; García-Fraile et al. 2016; Lladó et al. 2016). However, the members of *Bacteroidetes* and *Actinobacteria* become abundant with increasing soil pH, and these are potent decomposers of cellulose and other biopolymers (Lauber et al. 2009; López-Mondéjar et al. 2016).

An alteration of microbial community structure is known to occur within soil profiles that can be similar for soils from different landscape positions. In forest soils, bacterial communities are typically modified by nutrient availability and biotic interactions and accordingly inhabit multiple habitats of bulk soil, rhizosphere, litter, and woody habitats (Lladó et al. 2017). The characterization of microbial community composition and diversity with depth of different soil profiles has indicated a high bacterial diversity in the top 10 cm (organic horizon), while there is an exponential decrease of relative microbial biomass and soil carbon concentrations with depth (mineral soil horizon) (Eilers et al. 2012). With an increasing soil depth in all profiles, there is a significant, yet a similar effect on the microbial community composition, particularly of a decline in the relative abundance of *Bacteroidetes* with depth, and of a relative abundance in Verrucomicrobia among 10 and 50 cm, which might be from their preference for an oligotrophic environment or specific microniches. Typically, members of *Acidobacteria*, *Proteobacteria*, and *Actinobacteria* are abundant in organic and mineral horizons, while communities of *Firmicutes* and *Chlorofexi* can constitute a larger proportion in the recalcitrant carbon substrate- and inorganic nutrient-containing mineral horizons (Eilers et al. 2010; Baldrian et al. 2012; Uroz et al. 2013). The litter habitat, an important carbon source, is frequently dominated with a diverse fungal community, though bacteria belonging to *Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, and *Proteobacteria* are also involved in its decomposition (Eichorst and Kuske 2012; Kim et al. 2014). Some bacteria as *Betaproteobacteria* present in nutrient deprived soils are involved in efficient mineral weathering that supply an important reservoir of inorganic nutrients (Leveau et al. 2010; Collignon et al. 2011). Moreover, there can be differences among microbial communities prior and subsequent to bio-weathering of a region. For example, the weathered sites of Arctic glacier moraines contain phylogenetically diverse bacterial communities of chiefly *Alphaproteobacteria*, *Cyanobacteria*, *Acidobacteriaceae*, and *Acetobacteraceae*, while the vegetated regions show the presence of bacterial community typical of developed soils, including *Actinomycetales*, *Verrucomicrobiales*, *Gemmatimonadales*, *Burkholderiales*, and *Rhizobiales* (Mapelli et al. 2011).

Like bacteria, a substantial decrease of fungal activity, biomass, and diversity also occurs with soil depth. This vertical distribution of the fungal community is in accordance with soil stratification, where saprotrophic fungi are abundant at the carbon-mineralized region of forest surface, while the mycorrhizal fungi that mobilize nitrogen become profuse with soil depth (O'Brien et al. 2005; Lindahl et al. 2013). For the temperate and boreal forest soils, the abundant and diverse saprotrophic and mycorrhizal fungal communities are typically dominated with the

Basidiomycota (58%) and *Ascomycota* (27%), while the others are *Mucoromycotina* (7.9%), *Glomeromycota* (3.4%), and *Chitridiomycota* (2.2%) (Voříšková et al. 2014). However, with increasing soil depth, the species abundances of *Ascomycota* decrease (42% to 15%), while that of *Basidiomycota* increase (48–71%). This distinct vertical stratification of microbial communities is because of accumulation and decomposition of litter with higher chemical heterogeneity of nutrients on the soil surface and a decreased organic matter with increasing soil depth that decreases microbial biomass and rates of respiration and extracellular enzymatic activities (Baldrian et al. 2013). Equally, the anaerobic soils have complex interactions of multiple functional microbial groups. In these soils, as in rice terrace paddies, mutualistic interactions among bacteria belonging to sulfate-reducing, nitrogen-fixing, iron(III)-reducing, and methane-oxidizing groups involved in methane generation are abundant, depending on the critical availability of sulfate, total nitrogen, total iron, and total organic carbon, respectively (Sun et al. 2018).

2.3 Microbial Interactions in Pedogenesis

The pedosphere of the Earth is constantly involved in soil formation. The rocks on the crust of the Earth are frequently exposed to various physical, chemical, and biological agents that modify their structure. Consequently, the weathering or rock decomposition and erosion occur, which are fundamental for the development of soil (pedogenesis) and productive growth of crops (Anderson 2019). During biological weathering, living biota (microorganisms, plants, and animals) wield mechanical forces and metabolites that alter the minerals in rocks. In the initial stage of bio-weathering, different chemolithoautotrophic microbes utilize chemicals from the bedrock as an energy source for making their food. The oxidation of minerals by these microbes for procurement of electrons causes alteration of the primary mineral structure with a liberation of many crucial nutrients (Frings and Buss 2019). Different microbial communities with their metabolic activities yield the soil developing materials of relatively non-weathered minerals or organic matter along with an increased nitrogen concentration (Zhu et al. 2014). Among those microbial communities involved in the complex procedure of bio-weathering, lithobionts have prominence in regulation of initial rock weathering, soil stability, and the hydrological and nutrient cycles (Pointing and Belnap 2012). These communities frequently include *Cyanobacteria*, free living nitrogen-fixing bacteria, algae, fungi, and complex lichens, which could inhabit the surface (epilithic), underside (hypolithic), and inside (endolithic) of rocks and are adapted to severe environmental conditions of high radiation and desiccation (DiRuggiero et al. 2013; Warke 2013). This microbe-mediated rock weathering subsequently expedites the establishment and growth of non-vascular plants, amplification of organic matter and nitrogen accumulation, formation of a superficial original soil, and maintenance of nutrients.

Being an initial rock colonizer, the photoautotrophic blue-green cryptoendolithic *Cyanobacteria* induce weathering of silica and substratum alkalization (Büdel et al.

2004). During photosynthesis, the *Cyanobacteria* accumulate and secrete hydroxyl (OH^-) ions into the pores of sandstones, causing carbonate precipitation within their colonization zones. This bio-alkalization prevents the cementing of silica grains and results in a sequential exfoliation of upper rock layer, where sandstone flakes and detaches from the rock surface (DiRuggiero et al. 2013). Different iron-oxidizing bacterial communities, dominated with *Alphaproteobacteria* and pioneer *Cyanobacteria* colonizers, are known to prime bio-weathering of the lithoid substrate in the bare Arctic glacier moraines for an accelerated soil development and plant establishment (Mapelli et al. 2011). Another prominent constituent of lithobiontic communities is lichens that inhabit the rocks and facilitate their weathering. The amalgamation of fungal hyphal penetration and algal nitrogen fixation within the expanding and contracting lichen thallus result in an enhanced release of organic acids (as oxalic acid), which solubilize the mineral substrate and chelate metallic cations (Seneviratne and Indrasena 2006). The lichen *Verrucaria rubrocincta* while colonizing endolithic habitats actively degrades the substrate and does bio-mineralization as it produces precipitated microcrystalline calcite (micrite), which has a reflective property that efficiently shields them from the detrimental radiation and further preserves moisture (Garvie et al. 2008).

Further, several bacterial communities form a biofilm matrix of hydrated extracellular polymeric substances (EPS) in which micro-habits are developed as a survival mechanism on solid mineral surfaces that are open to the atmosphere (Gorbushina 2007). The biofilms are stabilized by a three-dimensional adherence among adjacent soil or dust and extracellular polymers of lipids, nucleic acids, proteins, and polysaccharides. This accretion functions as evaporation barriers to enhance water retention and enable cells to metabolize dissolved colloidal and solid biopolymer and is important in weathering by varnishing and protecting the weathered areas (Flemming et al. 2016; Wieler et al. 2019).

2.4 Microbial Antagonistic Interactions in Soil

Microbial antagonism or competition is a chief interaction that occurs in the soil due to differential abilities of microorganisms to access and decompose labile and recalcitrant compounds for organic energy and for production of chemically and physically diverse inhibitors. The antagonism prevailing at the soil environment typically is for resource nutrient acquisition and assimilation, accompanied with an interference in which microbes inhibit one another with different chemical mediators, inhibitors, or physical interactions to obtain increased access to resources or space (Lugtenberg et al. 2017). The characteristic microbial antagonistic interactions occurring at soil are depicted in Fig. 2.1.

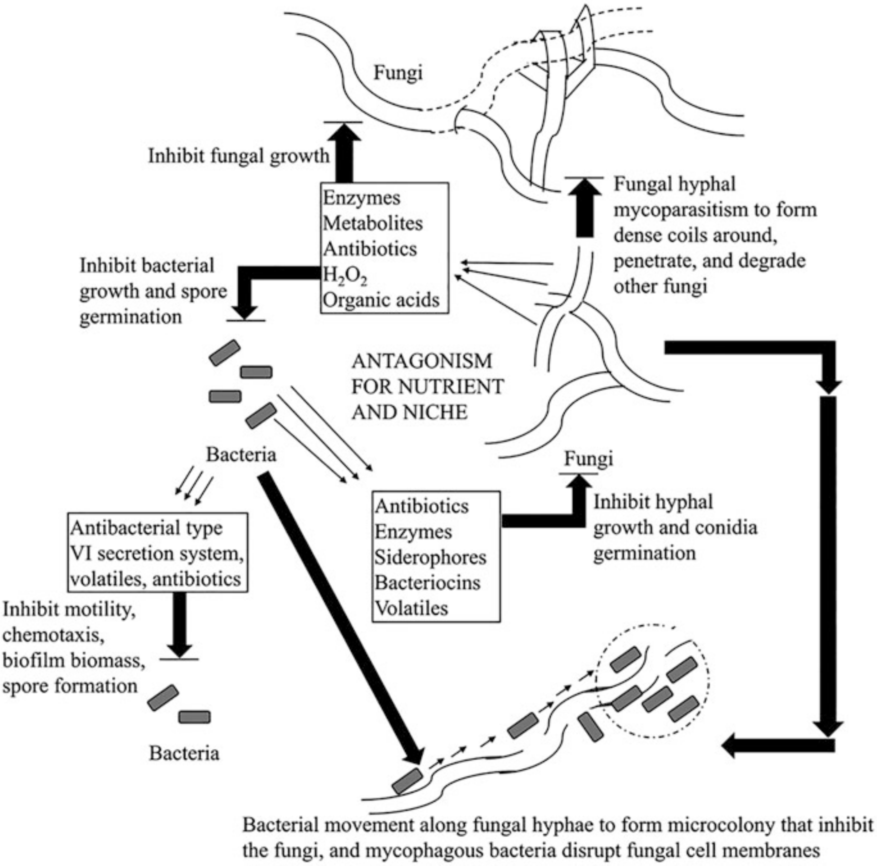

Fig. 2.1 A schematic representation of the various antagonistic microbe–microbe interactions occurring in soil for accessing similar nutrients and niche

2.4.1 Chemical Mediators as Molecular Weapons

Microbes during antagonistic interactions in the soil produce diverse molecular weapons in the form of chemical mediators that include antibiotics, enzymes, siderophores, bacteriocins, and volatile organic compounds (VOC). The Gram-negative rhizospheric bacteria produce 2,3-deepoxy-2,3-didehydro-rhizoxin, phenazine-1-carboxylic acid, phenazine-1-carboxamide, 2,4-diacetylphloroglucinol, pyrrolnitrin, 2-hexyl-5-propyl resorcinol, and cyclic lipopeptide viscosinamide as antibiotics to attack fungal pathogens (Johansson and Wright 2003; Haas and Défago 2005). The Gram-positive bacterium *Bacillus amyloliquefaciens* can produce antibiotic groups of surfactins, iturins, and fengycins (Torres et al. 2017). Similarly, many fungi produce antibiotics such as sulfamethoxazole, sulfadiazine, thiabendazole and fenbendazole, and β–lactam antibiotics like penicillin and cephalosporin C exhibiting anti–bacterial and anti–fungal properties (Martín 2020). The negative relationships among bacteria and fungi correlate with differences in niche preference, competition for the same substrates, extracellular enzymes, toxin production, and environmental modification (Faust and Raes 2012). Fungi produce actual sources of energy and carbon in the form of water-soluble sugars and phenolic compounds with their extracellular enzymatic activities on lignocellulose. These carbon sources being suitable growth substrates for other microorganisms including bacteria cause an intense competition, which can deprive the fungus of energy for decreased lignocellulose degradation (De Boer et al. 2005). This is observed among members of bacteria, *Deltaproteobacteria*, *Firmicutes*, and *Spirochaetes* with fungal *Ascomycota* (Zhao et al. 2021).

There is an extensive involvement of VOC in the antagonistic interactions among different microbes including pathogen inhibition and induction of soil fungistasis. These volatiles are a group of low-molecular-weight inhibitors that can diffuse from the air-filled pores of soil, which increases the distance of their antagonistic interactions (Effmert et al. 2012). The antimicrobial VOC ammonia can modify antibiotic resistance of a physically distanced bacterium, while cyanide ion is a potent inhibitor of copper-containing cytochrome c oxidase metalloenzymes (Lugtenberg et al. 2017). The colonization of soil by fungi can be negatively affected with the emitted fungistatic volatiles of bacterial communities, as sulfur dioxide, dimethyl disulfide, benzene (1-methylethyl), benzaldehyde, dimethyl trisulfide, and benzofuran (Li et al. 2020). The bacterium *Pseudomonas donghuensis* strain SVBP6 displays a broad range and diffusible antifungal activity. It produces a soluble tropolonoid compound, 7-hydroxytropolone, which has an inhibitory effect on the phytopathogenic fungus *Macrophomina phaseolina* (Muzio et al. 2020). The secreted VOC of *Pseudomonas donghuensis* P482 including dimethyl sulfide, S-methyl thioacetate, methyl thiocyanate, dimethyl trisulfide, hydrogen cyanide, and 1-undecan has potent antifungal (*Rhizoctonia solani* and *Fusarium culmorum*) and antioomycete (*Pythium ultimum*), but not antibacterial activities (Ossowicki et al. 2017). The bacterial VOC can affect motility of other bacteria in the soil. The biofilms formed by the soil bacteria can induce defenses with VOC and prevent the growth of pathogens, particularly in the extremely competitive environment of rhizosphere. The bacterium *Bacillus subtilis* can secrete 2,3-butanedione and glyoxylic acid that decrease the swarming and cause downregulation of genes related to chemotaxis and motility of *Escherichia coli*, *Burkholderia glumae*, *Pseudomonas aeruginosa*, and *Paenibacillus polymyxa* (Kim et al. 2013). Moreover, inside biofilms, it produces 3-methyl-1-butanol and 1-butanol to protect an occupied niche from the invasion of other competing bacteria by causing their reduced development and extracellular matrix gene expression (Hou et al. 2021). The VOC produced from the soil microbial community can suppress pathogens. Volatiles emitted from a broad range of agricultural soils are known to suppress the growth in pathogenic fungi *Rhizoctonia solani* and *Fusarium oxysporum*, and the oomycete *Pythium intermedium*, which is linked to various soil properties and microbial community composition (Van Agtmaal et al. 2018).

Several microbes, such as *Trichoderma*, can affect pathogen growth and/or activities with the production of extracellular enzymes cellulases, chitinases, β-1,3-glucanases, lipases, and proteases that hydrolyze the polymeric fungal cell wall cellulose, chitin, hemicellulose, and protein (Lugtenberg et al. 2017). The fungus *Bjerkandera adusta* degrades polycyclic aromatic compound and reduces the growth of pathogenic *Fusarium oxysporum* f. sp. *conglutinans* in a strong mycoparasitism that involves a direct penetration of *Fusarium* hyphae, along with increased activity of superoxide dismutase, catalase, peroxidase, and phenylalanine ammonia lyase (Feng et al. 2021). The different chemical mediators involved in microbe–microbe antagonistic interactions in the soil are given in Table 2.1.

2.4.2 Interactions for Obtaining Nutrients

The soil bacterial group of pseudomonads produce an arsenal of factors that inhibit the growth of other microbes. These are mostly diffusible compounds with antibacterial, antifungal, entomotoxic, nematotoxic, and phytotoxic properties (Gross and Loper 2009). The soil bacteria *Pseudomonas fluorescens* WCS365 and *Pseudomonas chlororaphis* PCL1391 are known to effectively compete for the same niche and root exudate nutrients with fungus *Fusarium oxysporum* f. sp. *radicis-lycopersici*, during which the bacteria negatively affect infection of the tomato roots by the fungus (Bolwerk et al. 2003). The bacteria produce an antifungal metabolite phenazine-1-carbox-amide that suppresses the fungal hyphal growth and branching as well as the colonization and infecting ability of the fungus. This chemotaxis with the subsequent colonization and slowing the growth of hyphae brings the bacteria near to the compounds such as amino acids, organic acids, and sugars secreted by the fungus. Moreover, strain WCS365 can reduce the ability of *Fusarium* dissemination by affecting the formation of microconidia and their germination, particularly at low nutrient availability (Kamilova et al. 2008). The acidification caused from the production of gluconic acid by *Pseudomonas fluorescens* BBc6R8 is known to impair the biosynthesis of the diffusible lactone antibiotic γ-actinorhodin in *Streptomyces coelicolor* (Galet et al. 2014). In a bacterial interspecies interaction, *Pseudomonas putida* and *Pseudomonas protegens* can secrete antibiotic molecule 2,4-diacetylphloroglucinol that inhibit biofilm gene expression in the soil bacterium *Bacillus subtilis* along with reducing bacterial biofilm biomass and spore formation (Powers et al. 2015).

The bioavailability of iron, which is essential in many biological processes, remains low in aerobic environments of soil. However, in a factor that determines the effect of microbial competition, certain microbes can detect and utilize the iron-chelating siderophores (xenosiderophores) produced from other microbes. *Pseudomonas fluorescens* BBc6R8 can both stimulate and antagonize the growth of ectomycorrhizal fungus *Laccaria bicolor* S238N and further inhibit the actinomycete *Streptomyces ambofaciens* ATCC23877. This antagonistic activity is pronounced in iron-limited conditions of soil with the bacterial production of

Table 2.1 The antagonistic effects of different chemical mediators involved in microbe–microbe interactions occurring at soil

Microbial antagonistic interaction	Mechanism	Chemical mediators involved	Reference
Trichoderma atroviride inhibited the mycelial growth of *Phytophthora infestans*	The hyphae had morphological and ultrastructural damages, including cell deformation, collapse, and degradation of cytoplasmic organelles	Volatile organic compounds (VOC) emitted were 3-methyl-1-butanol, 6-pentyl-2-pyrone, 2-methyl-1-propanol, and acetoin	Elsherbiny et al. (2020)
Chromobacterium vaccinii had growth inhibition on fungi *Trichoderma* sp., *Phoma* sp., and *Colletotrichum* sp.	Fungi had extensive morphological abnormalities of swollen hyphal cells, vacuolar depositions, and cell wall alterations	VOC of dimethyl disulfide, dimethyl trisulfide, indole, 1-octanol, and octanoic acid	Ebadzadsahrai et al. (2020)
Paenibacillus sp. EJP73 inhibited fungus *Lactarius rufus*	Affected hyphal radial growth	Bacterial soluble metabolites and volatile 2,5-diisopropylpyrazine	Aspray et al. (2013)
Pseudomonas protegens CHA0 inhibited *Azospirillum brasilense* Sp7	*Pseudomonas* produce lethality on *Azospirillum* cells	Antibacterial type VI secretion system, diffusible metabolites, inhibitory effects mostly mediated with siderophores, Gac/Rsm-regulated antibiotic	Maroniche et al. (2018)
Bacillus subtilis IBFCBF–4 with *Fusarium oxysporum* f. sp. *niveum*	*Bacillus* cause abnormal swelling and increased branching to the hyphae and suppress the mycelial growth of fungi	Volatile and non-volatile compounds, biosynthesis of iturin A, bacillomycin, fengycin, surfactin, bacilysin, tasA, and mersacidin	Zhu et al. (2020)
Pseudomonas sp. COR52 and A2W4.9 with fungi *Rhizoctonia solani* AG2–2 and *Pythium myriotylum* CMR1	The fungal hyphal distortion and/or disintegration resulting in complete lysis	Bacteria produce viscosin group of cyclic lipopeptides pseudodesmin and viscosinamide	Oni et al. (2020)
Burkholderia sp. HQB–1 with fungi *Fusarium oxysporum*, *Colletotrichum gloeosporioides*, *Botrytis cinerea*, and *Curvularia fallax*	Bacterium showed antifungal activities with the inhibition of mycelial growth, inhibiting RNA synthesis and DNA binding, interfering with redox balance, and inducing the generation of reactive oxygen species	The antifungal metabolite phenazine-1-carboxylic acid	Zhizhou et al. (2020)

(continued)

Table 2.1 (continued)

Microbial antagonistic interaction	Mechanism	Chemical mediators involved	Reference
Lactococcus and *Streptococcus* species with methicillin-resistant *Staphylococcus aureus*, *Streptococcus pneumoniae*, Enterococci, and *Clostridium difficile*	*Lactococcus* and *Streptococcus* prevent the growth of drug-resistant bacterial strains	Production of bacteriocin nisin that has anti-biofilm properties	Shin et al. 2016
Fungus *Aspergillus fumigatus* with the bacterium *Streptomyces rapamycinicus*	Inhibition of bacterial spore germination	Activation of fungal metabolite fumigermin synthesis that requires the polyketide synthase FgnA	Stroe et al. (2020)
Rhizoctonia solani with bacteria *Serratia proteamaculans* and *Serratia plymuthica*	Fungal growth inhibition, hyphal rearrangements with increased frequency of septa and branching, swollen mycelium and dolipore septa, cell wall thickening	Transcriptional regulation of fungal gene expression related to xenobiotic degradation, toxin and antioxidant production, energy, carbohydrate and lipid metabolism, depletion of ergosterol in fungal membrane	Gkarmiri et al. (2015)
Bacteria *Serratia marcescens* with *Mucor irregularis*	Fungal hyphae inhibition, an increasing permeability of fungal cell membrane	Bacteria invade and reside within fungal hyphae with the involvement of red pigment prodigiosin, upregulation of genes encoding the type VI secretion system and an outer membrane associated murein lipoprotein	Hazarika et al. (2020)
Bacillus subtilis 3610 with *Pseudomonas chlororaphis* PCL1606	The extracellular matrix protects *Bacillus* colonies from infiltration of *Pseudomonas* that otherwise would increase fluidity and loss of *Bacillus* colony structure	Sporulation of *Bacillus* mediated with histidine kinases KinA and KinB along with type VI secretion system of *Pseudomonas*	Molina-Santiago et al. (2019)

secondary metabolites of siderophores and the biosurfactant viscosin (Deveau et al. 2016). *Pseudomonas fluorescens* BBc6R8 produces siderophores pyoverdine and enantiopyochelin, while *Streptomyces ambofaciens* ATCC 23877 synthesizes desferrioxamines B and E and coelichelin siderophores typically. But when interacting together, *Pseudomonas fluorescens* BBc6R8 does not produce these siderophores and utilizes the ferrioxamines and ferricoelichelin of *Streptomyces ambofaciens* ATCC 23877 as xenosiderophores, with the involvement of a TonB-dependent receptor FoxA (Galet et al. 2015). While synthesis of the iron-scavenging pyoverdine has another consequence for competitive dynamics in soil among the communities of *Pseudomonas* bacteria, those which are non- and low producers have genes for multiple pyoverdine receptors that can exploit compatible heterologous pyoverdines from other community members, thereby potentiating antagonistic co-evolution and diversification in natural bacterial communities (Butaitė et al. 2017), whereas the effect of the two broad-spectrum antibiotics rifampicin and kanamycin on the fungus *Mucor hiemalis* is associated with high diversity of bacteria indicated of altered community composition from initially dominating *Alphaproteobacteria* to dominance of *Gammaproteobacteria*. Further, this caused morphological and behavioral changes in *Mucor hiemalis*, as it showed fast hyphal extension penetrating air–water interfaces of soil, with altered pigmentation and volatile emission that was beneficial for resource utilization (Schulz-Bohm et al. 2017).

2.4.3 Microbial Physical Interaction

Microorganisms while interacting come in different degrees of physical contact during antagonism in the soil. The bacterium *Serratia marcescens* has a remarkable capacity to move along and inhibit the mycelia of several zygomycetes and basidiomycetes. During this, bacterium forms microcolonies, which grow and coalesce into a biofilm over fungal mycelium (Hover et al. 2016). Moreover, there are certain mycophagous soil bacteria, as *Collimonas* spp. that obtain access to organic nutrients present in living fungal hyphae with rapid adherence to fungal (*Rhizoctonia solani*, *Mucor hiemalis*, *Trichoderma harzianum*) hyphae, production of antifungal volatiles, and disrupting the integrity and causing leakage of fungal membranes during the mycophagy (Garbeva et al. 2014a; Ballhausen et al. 2015). *Trichoderma harzianum* displays a hyphal mycoparasitism on fungal root pathogen *Sclerotinia sclerotiorum*, in which mycelium of *Trichoderma* forms dense hyphal coils to hold, degrade, and penetrate the *Sclerotinia* cell wall (Inbar et al. 1996).

Further, *Trichoderma guizhouense* has the potential to antagonize *Fusarium oxysporum* f. sp. *cubense* with aerial hyphae that destroy the host with hydrogen peroxide (H_2O_2). *Trichoderma* protects itself from the H_2O_2 that it produces to combat other host fungi by upregulating a gene cluster comprising two polyketide synthases, whose products trigazaphilones function as a complementary antioxidant mechanism for the protection (Pang et al. 2020). Moreover, the strains of *Pseudomonas* produce lethality on *Azospirillum brasilense* cells when in direct contact with an antibacterial type 6 secretion system, which is a bacterial nanomachine that introduces effectors into cells for host manipulation and inter-bacterial competition (Bernal et al. 2018; Maroniche et al. 2018).

2.5 Microbial Synergistic Interactions in Soil

Bacteria and fungi can positively interact to enhance the nutrient availability in the soil, thereby providing highly valuable ecosystem functions (Fig. 2.2). During this, the organic compounds exuded from bacteria can enhance the hyphal growth of AM fungi, which itself release carbon products that provide energy for different soil microorganisms (Andrade et al. 1997; Barea et al. 2005), while a co-inoculation of fungi and bacteria can increase the water and nutrient availability in the soil with mechanisms of organic matter decomposition, nitrogen fixation, and the solubilization and mobilization of phosphorus, potassium, and iron (Meena et al. 2010; Bandara et al. 2017). The various mechanisms of microbial synergistic interactions are given in Table 2.2.

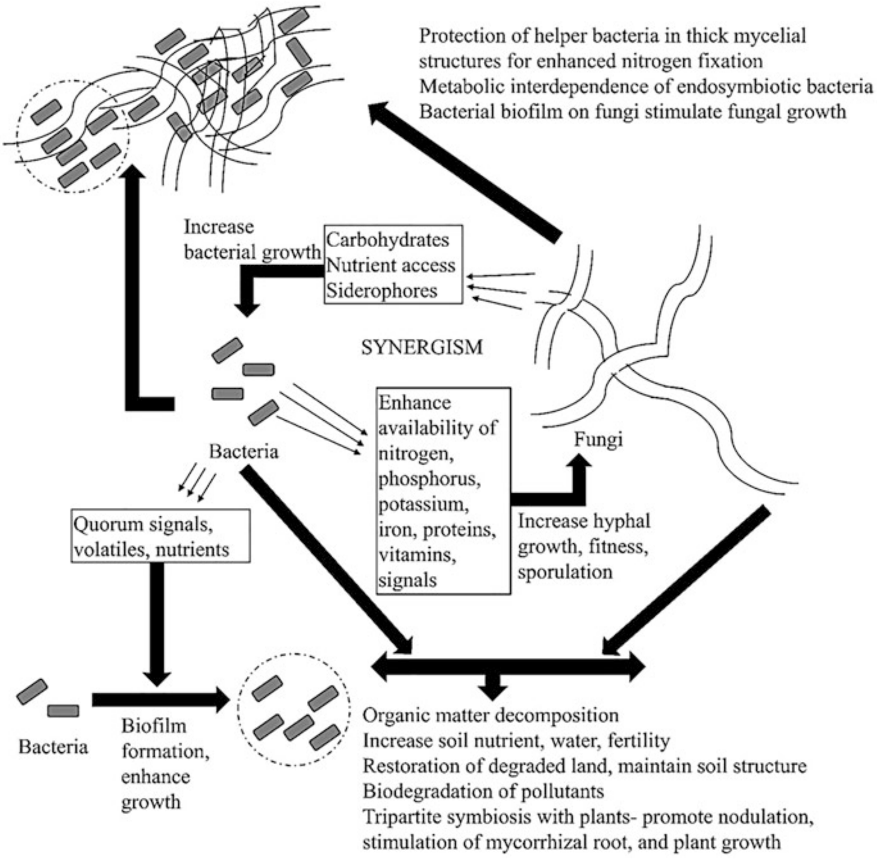

Fig. 2.2 A schematic representation of the various synergistic microbe–microbe interactions occurring in soil for accessing nutrients, stimulating microbial colonization, and enhancing plant growth

Table 2.2 The various mechanisms of synergistic interactions among microbes in the soil

Interacting microbes	Beneficial effects	Mechanism	Reference
Arbuscular mycorrhizal fungi (AMF) hyphae with other soil microflora (bacteria, actinomycetes, anaerobes, P solubilizers, and non-AM fungi)	Enhance water-stable soil aggregate (WSA) stability individually and additively in concert	AMF affect microorganism numbers indirectly by providing a favorable and protective habitat with the creation of habitable pore space in the WSA	Andrade et al. (1998)
Bacillus subtilis NEB4, *Bacillus subtilis* NEB5, and *Bacillus thuringiensis* NEB17 with *Bradyrhizobium japonicum*	Enhanced soybean nodulation of *Bradyrhizobium* with increases in nodule number, nodule weight, shoot weight, root weight, total biomass, total nitrogen, and grain yield	*Bacillus* produces flavonoid inducible activators that cause increased biological and economic yields with positive effects on signaling among *Bradyrhizobium* and soybean plants	Bai et al. (2003)
Pseudomonas fluorescens 2137 with *Bradyrhizobium japonicum*	Increased the growth, colonization, and nodulation of *Bradyrhizobium japonicum* A1017 on soybean roots	The production of growth-promoting substances with acetylene reduction activity that stimulate the growth of *Bradyrhizobium*	Chebotar et al. (2001)
Bacillus thuringiensis with *Bradyrhizobium japonicum*	Enhance nodulation and nitrogen fixation of *Bradyrhizobium* on soybean roots	Production of siderophores and auxins by *Bacillus*	Lucas García et al. (2004)
AMF with *Burkholderia* sp., *Herbaspirillum*, or *Azospirillum*	Fungi augment the ability of free living N fixation of bacteria in the soil	Increasing the supply of plant-derived carbon, provides the carbon and P required by nitrogenase enzymes for an enhanced nitrogen fixation among bacteria	Nasto et al. (2014); Reis et al. (2015)
Brevibacillus brevis with AMF *Glomus mosseae*	Enhanced AMF development that increased Cd tolerance in *Trifolium repens*	Production of indole acetic acid by *Brevibacillus* enhanced root growth, nodule production, and AMF intra- and extra-radical development	Vivas et al. (2005)
Pseudomonas monteilii HR13 with AMF	Stimulation of mycorrhizal establishment on *Acacia* species	Bacteria production of phenolic compounds, as hypaphorine, increased the aggressiveness of the fungal symbiont that promoted mycorrhizal establishment	Duponnois and Plenchette (2003)
Curtobacterium citreum BE with AMF *Rhizophagus*	Co-inoculation enhanced mycorrhizal colonization and the growth and dry	Increased mineral nutrition, higher Ca/Mg ratio,	Bourles et al. (2020)

(continued)

Table 2.2 (continued)

Interacting microbes	Beneficial effects	Mechanism	Reference
neocaledonicus and *Claroideoglomus etunicatum*	weight of *Tetraria comosa*	and lower metal movement	
AMF *Rhizophagus irregularis* with phosphate solubilizing bacteria (PSB) *Pseudomonas alcaligenes*	Enhanced the mineralization of soil phytate in the hyphosphere of AMF host plant *Medicago sativa*	Higher soil acid phosphatase activity and mobilization of the solubilized P	Zhang et al. (2014a)
Endophyte *Aspergillus terreus* with symbiotic yeast *Meyerozyma caribbica*	The yeast enhances the adaptation of *Aspergillus* to thermal as well as osmotic stress	The yeast induces the expression of global regulator genes involved in lovastatin biosynthesis and those involved in growth and development	Arora et al. (2021)
Streptomyces AcH 505 with necrotrophic fungus *Heterobasidion abietinum* 331	Enhanced colonization of Norway spruce roots with *Heterobasidion*	A fungal metabolite of 5-formylsalicylic acid was increased in the presence of *Streptomyces*	Keilhofer et al. (2018)
Foliar endophyte *Pestalotiopsis aff. neglecta*, with endohyphal bacterium *Luteibacter* sp.	Enhances growth of endophyte and tomato	The IAA production is enhanced with an L-tryptophan-dependent pathway	Hoffman et al. (2013)
Ustilago maydis associated with an intracellular bacterium *Bacillus pumilus*	Fungus grew in nitrogen-free media	Symbiotic bacterium provides the fungus the ammonium, product of N2 fixation, while the fungus provides carbon compounds and some amino acids to the metabolism of the bacterium	Ruiz-Herrera et al. (2015)
Tricholoma matsutake with bacteria *Dietzia*, *Ewingella*, *Pseudomonas*, *Paenibacillus*, *Rhodococcus*	For successful generation of the fruiting bodies and promote the growth of the fungus	Bacteria suppressed other molds and functioned as a biocontrol agent	Oh et al. (2018)
AMF species (*Glomus multisubtensum* and *Rhizophagus intraradices*) with bacteria *Klebsiella variicola*	Increases growth and tuber inulin of *Helianthus tuberosus*	*Klebsiella* showed phosphate-solubilizing ability and produced high organic acids and indole-3-acetic acid. The AMF subsequently took available phosphorus and transported to plant roots	Nacoon et al. (2020)
Fungus *Agaricus bisporus* with bacteria *Actinobacteria*,	Enhances the initiation of *Agaricus* fructification	The native bacteria consume fungal mycelium secreted VOC of	Chen et al. (2013)

(continued)

Table 2.2 (continued)

Interacting microbes	Beneficial effects	Mechanism	Reference
Firmicutes, *Proteobacteria*		1-Octen-3-ol and ethylene that stimulate fructification	
Fungus *Pleurotus eryngii* with bacteria *Pseudomonas* sp. P7014	Stimulate the development of the fungal mycelia	Bacteria produce the phytohormone IAA	Kang and Cho (2014)
Pseudomonas fluorescens FAP2 with *Bacillus licheniformis* B642	Formation of a mixed biofilm in wheat rhizosphere and rhizoplane	Production of IAA, siderophore, and ammonia, phosphate solubilization, production of EPS, alginate, cell surface hydrophobicity, and swarming motility	Ansari and Ahmad (2019)

2.5.1 Nutrient Supply

The sharing of a common micro-habitat at the rhizosphere allows several microbes including the arbuscular mycorrhizal fungi (AMF), rhizobia, and plant growth-promoting rhizobacteria (PGPR) to interact during their functioning or root colonization. In these multiple symbioses, activities could occur as the AMF can promote rhizobial and PGPR population, which can enhance AMF formation and functioning, while PGPR can enhance rhizobial root nodulation on legume roots (Leij 1998). There are different bacterial and fungal species that enhance the soil fertility by increasing the availability of nitrogen, phosphorus, potassium, and iron with an increased soil organic matter and production of organic acids that mobilize these nutrients into the rhizosphere (Rashid et al. 2016). Bacteria *Bradyrhizobium japonicum* UCM B-6018 and *Rhizobium leguminosarum* can enhance the soil fertility with nitrogen, phosphorus, potassium, iron, and organic matter (Tytova et al. 2013), whereas bacteria *Achromobacter* spp., *Azotobacter chroococcum*, *Azospirillum* spp., *Bacillus* spp., *Burkholderia* spp., *Pseudomonas alcaligenes*, *Pseudomonas aeruginosa*, and *Streptomyces* spp. can specifically enhance the availability of phosphorus in the soil (Yadav et al. 2014). Among fungi, *Rhizophagus intraradices*, *Glomus aggregatum*, *Glomus viscosum*, *Claroideoglomus etunicatum*, and *Claroideoglomus claroideum* enhance the soil with nitrogen, phosphorus, and potassium availability (Zhang et al. 2014b).

The microbial diazotrophs present in the bulk soil that metabolically fix atmospheric nitrogen to ammonia are free living organisms and include members of *Cyanobacteria*, *Proteobacteria*, *Archaea*, and *Firmicutes* (Orr et al. 2011; Miao et al. 2020). The requirement of ATP to fix atmospheric nitrogen is met by oxidizing organic molecules, which are obtained from other organisms (for free-living bacteria), photosynthesis (for photosynthetic microbes), or host plants (for associative and symbiotic nitrogen fixer) (Rashid et al. 2016). However, in degraded lands the microbial nitrogen fixation is affected from nutrient limited conditions, loss of fertility, and reduced water holding capacity of soils that reduce the growth of bacteria and association with their hosts (Zahran 1999). Besides, fungi can indirectly affect nitrogen fixation with different bacteria present in their mycelia that form a symbiotic association. The inorganic or organic phosphorus in most productive or degraded agricultural soils is typically present in immobilized or unavailable form, particularly as highly reactive inorganic form develops complexes with iron, aluminum, and calcium causing their adsorption or precipitation in the soil (Fonte et al. 2014). This adsorbed or sparingly soluble phosphorus of the native and inherited soil or finely ground rock can be mineralized (enzymatic hydrolysis), solubilized, and mobilized by phosphorus-mobilizing microbes either directly or indirectly (Divjot et al. 2021). Under direct mechanisms, these microbes secrete enzymes such as phosphatases or phytases or carry out acidolysis specifically for releasing bound phosphorous. Acidolysis-mediated phosphorous solubilization involves acidification of soil due to proton extrusion and production of low-molecular-weight organic acid anions (succinic, citric, gluconic, α-ketogluconic and oxalic acids) by microbes that release phosphorus on soil adsorption sites and chelate the cations bound to phosphorus with their hydroxyl and carboxyl groups (Jones and Oburger 2011), while indirect mechanisms of microbial phosphorus solubilization mainly involve lowering of soil pH with formation of carbonic acid from released CO_2 during respiration and from the release of protons when NH^{4+} is assimilated, along with the removal and assimilation of phosphorus (Illmer and Schinner 1995).

Similarly, the availability of the potassium also remains low in soil due to its limited concentration. The most of it occurs in bound state within phyllosilicates of silt and clay fractions, while some exists in soil solution or on movable sites (Sparks and Huang 1985). Microbes increase the availability of potassium in soil through acidolysis and complex formation (Parmar and Sindhu 2013). Different neutrophilic lithotrophic bacteria including *Bradyrhizobium japonicum*, *Cupriavidus necator*, *Ralstonia solanacearum*, *Dechloromonas agitata*, and *Nocardioides* sp. can utilize structural ferrous (Fe^{2+}) as an electron donor within potassium-containing biotite mineral for oxidation (Shelobolina et al. 2016). An inoculation of *Bacillus edaphicus* NBT causes potassium mobilization from minerals of mica, biotite, kaolinite, and smectite, during which there is an increased production of citric, oxalic, tartaric, succinic, and α-ketogluconic acid, along with chelation of silicon ions (Sheng and He 2006), while species of AMF – *Funneliformis* and *Rhizoglomus* – and *Aspergillus* can solubilize K accompanied with the release of organic acid anions of citrate, malate, and oxalate (Teotia et al. 2016). Another element required for fertile soil is iron, which is typically sparingly available as the Fe^{2+} gets oxidized to ferric (Fe^{3+}) ions that form insoluble compounds (Ma 2005). For this iron-limited condition, bacteria can interact with soil and solubilize iron from mineral or organic compounds with the synthesis of siderophores, which are low-molecular-mass organic compounds that have high affinity to chelate and form complexes with Fe^{3+} on the cell membrane (Kramer et al. 2020). The Fe^{3+} in this complex is then reduced to Fe^{2+}, which gets released from the siderophore into the cell, thereby solubilizing iron. Additionally, co-inoculation of different microbes is beneficial in recovering the degraded soils. For instance, different combinations of *Bacillus megaterium* and

AMF (Armada et al. 2014), *Pseudomonas putida* and AMF (*Rhizophagus intraradices*) (Ortiz et al. 2015), *Azospirillum brasilense* and *Pantoea dispersa* (Mengual et al. 2014), and *Pseudomonas* sp. R81 and *Piriformospora indica* (Kumar et al. 2012) could enhance the soil nutrients of nitrogen, phosphorus, and potassium. The fungi from *Ascomycota* and *Basidiomycota* can alleviate bacterial iron limitation by providing an access to iron with the provision of fungal siderophores, as ferrichrome and coprogen (Pierce et al. 2020).

The AMF in moderately degraded soils can provide a favorable environment for other microbes. It particularly provides the carbon and phosphorus required by nitrogenase enzymes for an enhanced nitrogen fixation among bacteria that form an association with their host plant (Nasto et al. 2014). The extra-radical hyphae of AMF are known to have the potential of protecting nitrogen-fixing bacteria, as *Burkholderia* sp., inside their thick mycelial structures for sheltering the enzyme complex from oxygen and fixing the atmospheric nitrogen in this structure (Bianciotto et al. 1996; Minerdi et al. 2001). By increasing the supply of carbon, these fungi can further augment the ability of other free-living nitrogen-fixing bacteria, as *Herbaspirillum* and *Azospirillum*, which consequently enhances the nitrogenous compounds in soil surrounding them or the mycorrhizosphere (Baldani et al. 2000; Reis et al. 2015). The bacterial fixation of atmospheric nitrogen and release of extracellular polysaccharides and other bioactive compounds positively influence soil fertility and the growth and persistence of associated soil microorganisms while decreasing soil pathogens and enhancing crop growth (Seneviratne et al. 2008; Singh 2014).

A metabolic interdependence of bacteria and host fungi is observed in *Rhizopus microsporus* that harbors endosymbiotic bacteria *Burkholderia rhizoxinica* and *Burkholderia endofungorum*, as the bacterial cells within the fungal cytosol are responsible for the biosynthesis of the macrocyclic polyketide metabolite rhizoxin (Partida-Martinez and Hertweck 2005; Partida-Martinez et al. 2007). There is a highly specific alliance among *Rhizopus microsporus* and *Burkholderia rhizoxinica* for the synthesis of the highly potent phytotoxin rhizoxin, during which a type 2 secretion system of the bacterial endosymbiont releases chitinolytic enzymes (chitinase, chitosanase) and chitin-binding proteins that are essential for bacteria to enter fungal hyphae (Moebius et al. 2014). Besides, a group of transcription activator-type effectors from *Burkholderia rhizoxinica* is essential for the establishment of the symbiosis, for it induces host sporulation and invokes a protective intracellular survival inside the fungus (Richter et al. 2020). The genome sequence of an endobacterium *Candidatus Glomeribacter gigasporarum*, which occurs in the cytoplasm of AMF *Gigaspora margarita*, has indicated a reduced genome that had a convergent evolution for intracellular interaction, where it depends on the AMF host for carbon, nitrogen, and phosphorus supply (Ghignone et al. 2012). This aerobic endosymbiotic bacterium has type II and type III secretion systems and contributes to AMF host fitness with the production of vitamin B12 and antibiotic- and toxin-resistant molecules, increasing sporulation, bioenergetic capacity, and ATP production, along with eliciting mechanisms to detect branching factor of strigolactones and detoxifying reactive oxygen species (Salvioli et al. 2016).

The interactions among typically stationary, spore-producing *Streptomyces venezuelae* and different fungi (*Saccharomyces cerevisiae*, *Candida albicans*, *Candida parapsilosis*, *Zygosaccharomyces florentinus*, *Saccharomyces castellii*, *Debaryomyces hansenii*) triggered an exploratory mode of *Streptomyces* development (Jones et al. 2017). This is promoted with the fungal consumption of the existing glucose supply and respiration, as *Streptomyces* initiate exploratory growth to colonize the soil environments with more readily available nutrients. The growth is further enhanced with a *Streptomyces*-produced VOC of trimethylamine that signals this exploratory behavior to other physically separated streptomycetes. Furthermore, the VOC benzonitrile and dimethyldisulfide emitted by rhizobacteria *Collimonas pratensis* Ter91 (β-Proteobacteria) and *Serratia plymuthica* PRI-2C strain (γ-Proteobacteria) can stimulate growth and gene expression of the phylogenetically distinct *Pseudomonas fluorescens* Pf0-1 (Garbeva et al. 2014b). The expressed genes were of catalase (protecting the cell damage by reactive oxygen species), sulfotransferase (catalyze addition of a sulfo group from a donor to an acceptor alcohol or amine), chemotaxis sensory transducer genes (of chemoattractants for facilitating movement toward an environment with nutrient input), and diguanylate cyclase (gives a spreader type phenotype).

The development of edible fungal mushrooms involves a wide variety of interactions including mutualism among bacteria and fungi in soils and substrates (Carrasco and Preston 2020). Different bacterial communities of the phyla *Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, *Chloroflexi*, and *Proteobacteria* benefit edible ascomycetes such as morels (*Morchella* spp.) or truffles (*Geopora*, *Choiromyces*, *Leucangium*). The bacteria-mediated benefits that increase the growth and development of fungi include degradation of cellulose, chitin, and organic compounds into available carbon sources, enhancing the availability of metal ions of iron and manganese with maintenance of acidic soil pH, reduction, and siderophore production and denitrification in the presence of fungal exudates (Berlemont and Martiny 2015; Liu et al. 2017). The *Actinobacteria* members can enhance the nutrition for their associated truffle (*Tuber magnatum*), as *Curtobacterium flaccumfaciens* and *Rhodococcus* sp. solubilize phosphate and iron that have limited availability in the grounds (Pavić et al. 2013). Besides, these bacteria decompose chitin, pectin, lipids, and proteins, exhibit urease activity, and inhibit the truffle pathogen *Verticillium leptobactrum*. For the growth and fructification of edible Basidiomycetes *Agaricus bisporus* and *Pleurotus ostreatus*, the soil microbes promote sequential and synergistic degradation of the lignocellulosic biomass and produce fermented substrates composting from agricultural residues (Vajna et al. 2010; Vieira and Pecchia 2018). This involves members of bacterial phyla *Firmicutes*, *Proteobacteria*, *Actinobacteria*, *Bacteroidetes*, and *Thermi* that degrade cellulose, metabolize nitrogen and sulfur, release ammonia, produce hormones, inhibit the growth of parasites, and soften the substrate that facilitates substrate colonization of the fungus (Zhou et al. 2017; Carrasco et al. 2019). Additionally, the extracellular capsules or slime layers of certain bacteria can provide nutrients for fungal succession in intimate biophysical and metabolic interactions, which allow for their interdependent development and co-evolution (Zhao et al. 2021). Therefore, these can be utilized for inoculation, particularly in degraded soils to enhance plant yield, reduce chemical usage, and develop a sustainable fertilizer management in agro-ecosystems.

2.5.2 Endosymbiotic Microbial Interaction

Fungi belonging to phyla *Ascomycota*, *Basidiomycota*, and *Mucoromycota* are known to harbor obligate or facultative endosymbiotic bacteria in the rhizosphere (Bastías et al. 2020). The bacteria are associated with fungi, which could be in the rhizosphere (*Diversispora epigaea*, *Gigaspora margarita*, *Laccaria bicolor*, *Piriformospora indica*, *Suillus variegatus*), on plant leaves (the species of *Microdiplodia*, *Pestalotiopsis*), as plant pathogens (*Rhizopus microsporus*, *Rhizoctonia solani*), or saprotrophs (*Mortierella elongata*). The lack of certain enzymes for the biosynthesis of biomolecules and catabolism of nutrients, along with the requirement of nutrient supply, makes the endosymbiotic bacteria to become dependent on their fungal hosts (Ghignone et al. 2012; Sun et al. 2019). However, these endosymbionts positively affect diverse activities in their fungal hosts including promoting efficient substrate utilization, growth, sporulation, and protection from oxidative stress (Vannini et al. 2016; Pawlowska et al. 2018).

Besides, the obligate endosymbiotic bacteria can further elicit asexual reproduction in their hosts and are vertically transmitted along the fungal reproduction to colonize their asexual spores (Bianciotto et al. 2004; Partida-Martinez et al. 2007). A beta-proteobacterium *Burkholderia* can regulate asexual proliferation of sporangiospores and modify sexual reproduction of host fungus *Rhizopus microsporus* in a heritable mutualism by mediating the control of a *ras2* gene that encodes a GTPase required for fungal reproductive development (Mondo et al. 2017). The various benefits to fungal hosts tend to be more with obligate than facultative bacterial endosymbionts, and with an increased dependency, these have a high metabolic demand of respiration rates (Uehling et al. 2017; Bastías et al. 2020).

2.5.3 Ectosymbiotic Microbial Interaction

In addition, there are ectosymbiotic bacteria that are present on or near fungal hyphae. These bacteria can have positive effects on the fungi including increasing nutrient availability, enhancement of fungal growth, metabolism and fitness, and stimulating asexual reproduction (Frey-Klett et al. 2007; Oh et al. 2018). The sporocarps of *Suillus grevillei* contain species of *Pseudomonas*, *Bacillus*, and *Streptomyces*, among which *Pseudomonas putida* caused enhancement of fungal growth with the production of volatile metabolites and siderophores (Varesel et al. 1996). The AMF and PGPR (rhizobia and pseudomonads) are known to have direct physical interactions. The bacteria *Pseudomonas fluorescens* WCS 365 and *Rhizobium leguminosarum* strains B556 and 3841 are effective colonizers, as these adhere to spores and hyphae of AMF *Gigaspora margarita*, mediated with the production of an extracellular material containing cellulose (Bianciotto et al. 1996), whereas a coexisting cultivable bacteria *Curtobacterium* sp. TN4W-19 promotes the mycelial growth of fungus, *Stereum* sp. strain TN4F (Kamei et al. 2012).

The ectobacterial strains of *Pseudomonas* sp. TN3W-8 and *Enterobacter* sp. TN3W-14 enhanced the fungal growth of *Phlebia brevispora* TN3F (Harry-asobara and Kamei 2018). Further, in a mutualistic interaction, *Bacillus subtilis* supplies thiamine to the growing fungal mycelia of *Aspergillus nidulans* and then travels and proliferates within the fungal provided space (Abeysinghe et al. 2020). Furthermore, phosphate solubilizing bacteria (PSB) can be transported in a thick water film on the extra-radical hyphae of AMF toward organic phosphorus patches to enhance mineralization, though this requires an energy source in the form of hyphal exudates (Jiang et al. 2021). The bacterial adhesion rate on the fungal surface can be increased with rhamnolipid that modifies the physicochemical properties of both bacteria and fungi, which could be an essential initial mechanism in promoting bacterial mobilization for soil bioremediation (Hamzah et al. 2020). Additionally, ectomycorrhizal fungi enhance the absorption of soil moisture, total carbon or nitrogen, and nutrients and reduce the bulk density and heavy metals of soil (Yu et al. 2020).

2.5.4 Helper–Bacteria

Another important microbial interaction involves the mycorrhiza–helper–bacteria (MHB) which facilitate establishment of ecto- and endo-mycorrhizal symbioses including stimulation of mycelial growth and enhancement of mycorrhizal formation in the rhizosphere (Frey-Klett et al. 1997). The MHB are known to belong in the phyla of *Proteobacteria* (*Agrobacterium*, *Azospirillum*, *Azotobacter*, *Burkholderia*, *Bradyrhizobium*, *Enterobacter*, *Pseudomonas*, *Klebsiella*, *Rhizobium*), *Firmicutes* (*Bacillus*, *Brevibacillus*, *Paenibacillus*), and *Actinomycetes* (*Rhodococcus*, *Streptomyces*, *Arthrobacter*) (Rigamonte et al. 2010). The MHB can supply nutrition to the fungus with nitrogen fixation or mineral solubilization and can challenge other bacteria that inhibit mycorrhiza formation. These promote fungal pre-symbiotic survival, regulation of the actin cytoskeleton organization, hyphal growth in soil, and establishment of symbiosis; alter fungal anabolism and catabolism to increase lipid synthesis required for higher growth rates; solubilize inorganic phosphate; inhibit the growth of fungal root pathogens; and produce antimicrobial metabolites (Dowling and O'Gara 1994; Frey-Klett et al. 2007).

Several MHB are known to be mainly fungus-specific. The metabolite auxofuran of MHB *Streptomyces* sp. AcH505 can promote the growth and mycorrhiza formation of *Amanita muscaria* on *Picea abies* but inhibit the development of *Hebeloma cylindrosporum* and other pathogenic fungi (Riedlinger et al. 2006). However, this beneficial effect of MHB could further be non-specific to a fungus. For instance, *Paenibacillus* sp. EJP73 that is an MHB for *Lactarius rufus* microcosm can enhance mycorrhiza formation of *Laccaria bicolor* (Aspray et al. 2006). The MHB secrete different substances that facilitate the establishment of the fungal mycorrhiza to their hosts. For example, MHB *Pseudomonas monteilii* HR13 can stimulate the establishment of ectomycorrhizal (*Pisolithus* and *Scleroderma*) and endomycorrhizal (*Glomus intraradices*) fungi on *Acacia* species by secreting phenolic compounds such as hypaphorine, which increase the aggressiveness of the fungal symbiont for mycorrhizal colonization (Duponnois and Plenchette 2003). Fluorescent pseudomonads including *Pseudomonas fluorescens* isolated from Douglas fir–*Laccaria bicolor* mycorrhizae and mycorrhizosphere preferentially utilized the fungal mycelium-located trehalose carbohydrate, suggesting capability of fungus to have trehalose-mediated selection on the neighboring fluorescent pseudomonads (Frey et al. 1997).

2.5.5 Quorum Sensing and Biofilm Formation

Bacteria interact with one another by quorum sensing (QS) systems that involve the use of small diffusible molecules for controlling important traits like production of virulence factors or biofilm formation. In LuxI–LuxR-type, one of the most utilized QS system in bacteria, members of the LuxI protein family produce signals in the form of diffusible fatty acyl-homoserine lactones (AHL) that are detected with LuxR-type transcription factor receptors (Fuqua et al. 1996). The different LuxI homologs can use S-adenosylmethionine and fatty acyl-acyl carrier protein as the substrates for fatty acyl–HSL synthesis (Moré et al. 1996). Though many *Proteobacteria* members possess LuxI–LuxR-type QS system that detects AHL signals, the photoheterotroph *Rhodopseudomonas palustris* produces and detects an aryl-homoserine lactone of p-coumaroyl-homoserine lactone. The LuxI homolog BraI of *Bradyrhizobium* produces a small signal molecule of cinnamoyl–homoserine lactone, which is detected by the BraR of *Rhodopseudomonas palustris* to elicit QS (Ahlgren et al. 2011). While *Photorhabdus asymbiotica* utilizes the LuxR homolog, PauR to sense dialkylresorcinols and cyclohexanediones than the AHL as signals (Brameyer et al. 2015). The filamentous fungi as *Aspergillus niger*, *Aspergillus nidulans*, and *Fusarium graminearum* are known to secrete small diffusible QS molecules of farnesol, tyrosol, phenylethanol, and tryptophol. These signals are essential in fungal morphogenesis, germination of macroconidia, initiating apoptosis, pathogenicity, controlling cell population, and biofilm development (Mehmood et al. 2019). The QS molecules of yeasts, particularly *Saccharomyces cerevisiae*, are 2-phenylethanol, tyrosol, and tryptophol, while that for *Candida albicans* are farnesol and tyrosol, which function in cell–to–cell communication and development of hyphal form (Jagtap et al. 2020).

The bacterial, EPS, VOC, and high-nutrient input are able to induce the formation of biofilms. The excreted EPS forms a scaffold matrix which mediates surface associations, maintains biofilm cohesiveness, and provides competitive advantages of enhanced fitness during desiccation, increased survival in environmental stress, and elevated opportunities for horizontal gene movement (Lennon and Lehmkuhl 2016; Costa et al. 2018). The VOC ammonia can induce biofilm formation in *Bacillus licheniformis*, *Bacillus subtilis*, and *Staphylococcus aureus*, while soluble indole was shown to increase biofilm formation in *Vibrio cholera* (Mueller et al. 2009; Létoffé et al. 2014). There is a higher diversity and evenness indices of soil with biofilms, where species of *Bacillus* and *Paenibacillus* constitute the main biofilm-forming bacteria in the soil stimulated with increased provision of labile nutrients, enhanced EPS production, and development of microaggregates (Wu et al. 2019). Bacterial interactions within the biofilms influence their development. The matrix production in *Bacillus subtilis* is influenced with interspecific interactions with close relatives, which results in an increased expression of matrix genes via the activation of a sensor histidine kinase, and altering of other unrelated subpopulations (Shank et al. 2011). The bacterial biofilms contain micro-meter-sized cell aggregates that further affect local soil physicochemical properties including bio-clogging in the soil pores which influences water permeability, development of connection among minerals, and formation of soil microaggregates with strengthened internal cohesion (Pintelon et al. 2012; Lin et al. 2016). The microbial biofilms adhere to different biotic and abiotic surfaces with a secreted exopolymeric matrix, which provide plant growth promotion and stress management and an environment for the synthesis and entrapment of nanoparticles that could be beneficial toward biocontrol and crop management as an eco-friendly method to practice sustainable agriculture (Bhatia et al. 2021).

2.6 Importance of Microbe–Microbe Interactions

Microorganisms are involved in mediating a wide range of essential soil processes, including the restoration of degraded lands, recycling of nutrients, nitrogen fixation, and the decomposition of dead organic matter, while functioning as decomposers, symbionts, or pathogens (Lladó et al. 2017). Additionally, microbial interactions result in the secretion of pharmaceutically relevant chemicals.

2.6.1 Maintenance of Soil Structure

The soil structure is constituted of individual particles of sand, silt, and clay that are aggregated in different sizes together with organic, inorganic, or chemical factors. It has fundamental importance in soil functions, management of crops, root growth, and agricultural ecosystem sustainability (Rillig et al. 2002). However, anthropogenic activities of extensive land use, deforestation, urbanization, improper agricultural practices, and industrialization are causing degradation of land, including loss of soil fertility and productivity (Khaledian et al. 2017). This necessitates the requirement of different sustainable nutrient management systems for establishing the fertility of degraded soils. One possibility that can be explored is the integrated management of microbial inocula and organic fertilizers.

Bacteria and fungi are important binding agents that form and stabilize water-stable soil macroaggregates of >250 μm (Leifheit et al. 2015). Bacteria contribute to soil structure typically with their decomposition activities and secretion of slimy polymeric substances including negatively charged polysaccharides of polyuronic and amino acids. Bacteria decompose organic materials into small organo-mineral products that in combination with their slimy secretions adhere soil particles into macroaagregates (Degens 1997; Stevens et al. 2014). Further, various soil fungi can stabilize soil aggregates with the extra-radical hyphae of their mycelium through direct (entrapment of soil particles within the hyphal mass) and indirect (exudation of glomalin, hydrophobins and related proteins, mucilage, and polysaccharides to the soil) mechanisms (Peng et al. 2013; Espeland et al. 2013). The hydrophobic glomalin protein protects the mycelium from drought and other microbes, and with their adhesive character, these can stabilize soil aggregates together with decomposed hyphae, minerals, and organic matter (Rillig et al. 2002). Fungal exudation of hydrophobic compounds increases the hydrophobicity of soil organic matter that forms more water-stable aggregates and avoid breakage at dry condition (Hallett et al. 2009). Fungi can increase the soil organic carbon, which is positively related to mean diameter of aggregates that further enhance soil structure (Xu et al. 2015). Additionally, restoration of soil structure can be achieved with a combined application of bacterial and fungal inocula with organic amendments. The AMF *Rhizophagus irregularis* can increase and stabilize the soil aggregation, when used in combination with organic residues (Leifheit et al. 2015).

Microbial community can affect the distribution of soil aggregates in the rhizosphere with their interactions. The carbohydrates and fatty acids derived from microbes along with their biomass are a considerable source of soil organic matter that increases with density (Ludwig et al. 2015). However, the relative contribution of microbial residue decreases with depth, as the organic matter and total nitrogen are maximum at the topsoil, which then typically decrease to 24% and 16% of the maximum values, respectively, at 90–100 cm subsoil (Sradnick et al. 2014). The accumulated organic compounds of fungal mycelium provide a suitable substrate for the growth of other bacteria and fungi that become important in the formation of soil aggregates. For instance, within the fruiting bodies of *Agaricus lilaceps*, the interacting bacterial species of *Pseudomonas fluorescens* and *Stenotrophomonas maltophilia* can bind more soil than other individually present bacteria (Espeland et al. 2013).

2.6.2 Benefits to Plants

Rhizobia and PGPR share common microhabitats in the root–soil interface, which facilitates them to interact during root colonization. There occurs a beneficial co-operative effect among these microbes. An important symbiotic multimicrobial interaction occurs among AMF and rhizobia that enhances the bacterial nodulation activity in legumes. This culminates into a tripartite symbiosis among legume–mycorrhiza–rhizobia, where the bacterial root nodulation can be dependent on the mycorrhiza formation, as the rhizobia could co-exist with AMF in the form of root symbionts or as free living in the rhizosphere (Barea et al. 2005). During this co-existence, the phosphorus demand for nodule formation and that of other nutrients such as Zn, Cu, Mo, Ca, etc. for the infectivity and the symbiotic effectiveness of rhizobia are provided by the AMF, which can further protect from drought-induced nodule senescence (Ruiz-Lozano et al. 2001), while nitrogen, which is fixed by the rhizobia, is crucial for formation, functioning, and cell wall chitin synthesis of AMF and maintaining proper physiological condition including high carbon dioxide fixation rate of plants (Smith et al. 1979). The PSB and AMF can further be involved in phosphorus solubilization and mobilization, respectively, with their interactions on organic phosphorus mineralization, particularly in the root-free soil (hyphosphere). The phosphate solubilized by PSB might not reach plant root surface as it is sparingly diffusible. But this solubilized phosphate could be taken by the mycelium of AMF to be supplied for the plants, thereby functioning as a bridge among roots and surrounding soil microhabitats beyond phosphate depletion zone at the rhizosphere (Barea et al. 2005). The interactive effects of AMF *Rhizophagus irregularis* and PSB *Pseudomonas alcaligenes* enhanced the mineralization of soil phytate in the hyphosphere of AMF host plant *Medicago sativa*, with a higher soil acid phosphatase activity (Zhang et al. 2014a). The strains of *Rhizobium meliloti* can increase AMF *Glomus mosseae* colonization unit and succinate dehydrogenase activity, along with nitrate reductase activity and nutrient acquisition ability in AMF plants where the number of lateral roots and their branching gets increased (Tobar et al. 1996; Barea et al. 1996).

The chief mechanism of nodule formation enhancement with PGPR co-inoculation is implicated to be from their production of plant hormones and different metabolites. A co-inoculation of *Pseudomonas fluorescens* 2137 enhanced the production of growth-promoting acetylene reduction activity, which increased the growth, colonization, and nodulation of *Bradyrhizobium japonicum* A1017 on *Glycine max* (soybean) roots (Chebotar et al. 2001). Different soil bacterial strains of *Pseudomonas fluorescens*, *Pseudomonas putida*, and *Aeromonas hydrophila* increased nodulation and the weights of nodules formed by *Bradyrhizobium japonicum* 110 on soybean root that enhanced plant growth (Polonenko et al. 1987). Similarly, a co-inoculation of PGPR strains of *Serratia proteamaculans* 1–102 and *Serratia liquefaciens* 2–68 at an optimal dose increased nodule number, rate, and nitrogen fixation of *Bradyrhizobium japonicum* on soybean (Bai et al. 2002). Bacterium *Bacillus thuringiensis* that enhance nodulation and nitrogen fixation of *Bradyrhizobium japonicum* on soybean roots could produce siderophores that promoted the production of fluorescent phytoalexins, which then induce the nodulation genes of *Bradyrhizobium*. Further, *Bacillus thuringiensis* can produce auxins, whose hormonal effect on the root surface positively affects nodulation with an increased root surface that makes contact with the soil (Lucas García et al. 2004). The AMF *Rhizophagus irregularis* or *Funneliformis mosseae* along with *Pseudomonas fluorescens* can alleviate water-deficit damage and enhance tolerance in plants by enhancing accumulation of more ascorbate peroxidase and glutathione peroxidase and decreasing severe water deficiency induced by hydrogen peroxide and malondialdehyde (Aalipour et al. 2020).

Inoculation of beneficial microbial groups in soil can enhance plant development, nutrient uptake, nitrogen fixation, and quality of root system due to an increase in the bioavailability of plant nutrients (Requena et al. 1997). A mixed inoculation of the PGPR *Bradyrhizobium japonicum* with AMF *Glomus intraradices* increased the concentration of diosgenin in *Trigonella foenum–graecum*, particularly in drought stress conditions. This was due to increase in ACC deaminase activity, leaf proline concentration, phosphorous in roots, and metabolite production, along with decreased peroxidase activity (Irankhah et al. 2021). Moreover, the species-specific interaction among bacteria and AMF could have beneficial or detrimental effects on the plants. An inoculation of *Bacillus amyloliquefaciens* exerted an enhanced AMF symbiosis with increased number of arbuscules, concentration of glomalin, and root length in *Triticum aestivum*, while *Bacillus subtilis* decreased fungal symbiosis and glomalin (Wilkes et al. 2020). A co-inoculation of *Rhizobium* and phosphate-solubilizing *Pseudomonas striata* or *Bacillus polymyxa* enhanced the chickpea grain yield (Alagawadi and Gaur 1988). A combined microbial inocula consisting of *Rhizobium meliloti*, AM fungus *Glomus mosseae*, and a phosphate-solubilizing rhizobacterium *Enterobacter* sp. could enhance the accumulation of nitrogen and phosphorus in *Medicago sativa* (alfalfa) roots. This occurred from an enhanced nitrogen fixation and release of phosphate ions, either from the added rock phosphate or from the indigenous phosphate (Toro et al. 1998). There was an enhanced Cd tolerance observed in *Trifolium repens* after a co-inoculation with native microorganisms of *Brevibacillus brevis* and *Glomus mosseae*, as these strains were more efficient for nutrient uptake, immobilizing metals, and decreasing their translocation to the shoot (Vivas et al. 2005). The indole acetic acid hormone produced by *Brevibacillus brevis* further enhanced root growth, nodule production, and AM fungal intra- and extra-radical development, while dehydrogenase, phosphatase, and β-glucosidase activities were indicative of microbial metabolism and soil fertility.

2.6.3 Decomposition of Organic Matter

Bacteria and fungi are chief decomposers of simple as well as recalcitrant organic matter in the terrestrial ecosystem and thus play crucial role of bringing entrapped nutritive elements back in the biological cycle. Constructive interactions among bacteria and fungi have been reported in relation to lignocellulose substrate degradation within soil where functioning of lignocellulose-degrading basidiomycetes is benefited in the presence of bacteria with regard to nitrogen supply and detoxification of mycotoxic compounds (De Boer and van der Wal 2008). Bacterial co-inoculation with fungi (*Heterobasidion annosum*, *Resinicium bicolor*, or *Hypholoma fasciculare*) could increase the degradation of spruce wood blocks as bacteria promote fungal growth and enzymatic activity (Murray and Woodward 2003).

Decomposition of macrophytes is affected with the interactions of bacteria and fungi that are influenced by material composition and environmental conditions. During decomposition of macrophyte *Zizania latifolia*, *Hydrilla verticillata*, and *Nymphoides peltata* leaf litters, there is an increase of bacterial diversity of *Gammaproteobacteria*, *Bacteroidetes*, *Deltaproteobacteria*, *Firmicutes*, and *Spirochaetes* that had co-occurrence with *Basidiomycota* and *Ascomycota* fungi, according to different macrophyte species (Zhao et al. 2021). In this, the positive bacteria–fungi interaction prevailed, particularly of phosphate solubilizers *Flavobacterium* sp. and lignocellulose-decomposing *Basidiomycota*, in the presence of *Hydrilla verticillata* nutrients, which accelerated the decomposition and re-circulation of leaf litter. Additionally, the bacterial positive effects on fungal activity include increasing accessibility of substrates to the fungus with production of cellulase and pectinase enzymes, decomposing toxic solutes, and enhancing the nitrogen availability for fungal growth (Johnston et al. 2016).

2.6.4 Biodegradation of Soil Pollutants

Different microbial groups are known to interact with each other for achieving synergism toward biodegrading different pollutants (Khanpour-Alikelayeh and Partovinia 2021). A consortium of fungus *Fomitopsis pinicola* and the bacterium *Ralstonia pickettii* could synergistically degrade the toxic and recalcitrant organochlorine pesticide 1,1,1-trichloro-2,2-bis(4-chlorophenyl) ethane (DDT) to less toxic metabolite of 1-chloro-2,2-bis(4-chlorophenyl) ethylene (DDMU). During this synergistic degradation, the fungus modified the DDT to metabolite 1,1-dichloro-2,2-bis (4-chlorophenyl) ethane (DDD) with reductive dechlorination, while the bacterium modified this accumulated DDD to 1,1-dichloro-2,2-bis(4-chlorophenyl) ethylene (DDE) with dehydrogenation, followed by reductive de-chlorination of DDE to DDMU (Purnomo et al. 2020a). The biodegradation ability of the harmful azo group textile dye of methyl orange by fungus *Gloeophyllum trabeum* can be enhanced in the presence of bacterium *Pseudomonas aeruginosa*. This involves the formation of various non-toxic metabolites with mechanisms of desulfonylation, demethylation, and hydroxylation (Purnomo et al. 2020b), while the *Aspergillus ochraceus* NCIM–1146 and *Pseudomonas* sp. SUK1 association, with their synergetic reactions, enhanced decolorization and detoxification of azo dye Rubine GFL and textile effluent. This was accompanied with an induction of laccase, veratryl alcohol oxidase, azo reductase, and NADH–DCIP reductase in the consortium, along with production of aromatic amines (Lade et al. 2012).

A defined fungal–bacterial co-culture of *Penicillium* sp.–*Serratia marcescens*, respectively, can enhance the biodegradation of polycyclic aromatic hydrocarbon (PAH) benzo[a]pyrene with inducible hydroxylases to produce complex mixtures of conjugated derivatives (Machín-Ramírez et al. 2010). Similarly, a defined mixed bacterial culture of *Pseudomonas* sp. with *Actinobacteria* strains of *Rhodococcus* sp. and *Gordonia* sp. efficiently biodegraded a mixture of low- and high-molecular-weight PAH of naphthalene, phenanthrene, and pyrene with their synergistic bioemulsifying activities (Isaac et al. 2015). A consortium of fungus *Acremonium* sp. with bacterium *Bacillus subtilis* utilized an increased dehydrogenase activity as an effective strategy toward the bioaugmentation of crude oil-contaminated soil (Ma et al. 2015). A synergistic effect was observed between two yeast (*Sarocladium* sp. and *Cryptococcus* sp.) isolates for an increased oil and pyrene degradation. This included enhanced surfactant production, emulsification activity, and cell surface hydrophobicity and a reduction of surface tension (Kamyabi et al. 2017). The application of an efficient fungal (*Mortierella* LEJ702)–bacterial (*Arthrobacter globiformis* D47, *Variovorax* SRS16) consortia increased bioremediation of pesticide diuron with mineralization in a polluted soil, which was facilitated by transport of bacteria by fungal hyphae (Ellegaard-Jensen et al. 2014). The bacterial (*Halophilic* sp. JAS4, *Klebsiella pneumoniae* JAS8, *Enterobacter asburiae* JAS5, *Enterobacter cloacae* JAS7) and fungal (*Botryosphaeria laricina* JAS6, *Aspergillus tamarii* JAS9, and *Lasiodiplodia* sp. JAS12) consortium could degrade the contaminated organochlorine insecticide endosulfan in agricultural soils utilizing solid material formulation of sawdust, soil, fly ash, molasses, and nutrients (Abraham and Silambarasan 2014).

2.6.5 Biocontrol and Drug Development

The antagonistic microbial interactions have applications in the biocontrol of plant diseases that occur at various stages of food and feed production (Thakur and Singh 2018). The antagonistic potential of soil microbes is used in the biocontrol of various plant diseases as wilt in cucumber and lettuce (Inbar et al. 1996), foot and root rot in tomato (Bolwerk et al. 2003), banana wilt diseases (Zhizhou et al. 2020), *Fusarium* wilt of watermelon (Zhu et al. 2020), wilt in *Brassica napus* (Feng et al. 2021), etc. The wide range of activities associated with VOC including signaling, controlling, and inhibiting microbial activity and growth, drug resistance, affecting biofilm formation, eliciting induced systemic tolerance of plants to different abiotic and biotic stresses, and promoting plant growth have provided with the perspectives for their application in sustainable agriculture and post-harvest control (Kanchiswamy et al. 2015).

Beneficial drugs can be obtained that emanate during symbiotic and antagonistic interactions of microbes. For instance, the redox family of phenazine antibiotics produced by *Pseudomonas* and related bacteria in biofilms with other microbes possess antibacterial, antihypertensive, antiparasitic, antimalarial, neuroprotectant, radical scavenging, and anti-cancer biological activities (Guttenberger et al. 2017; Krishnaiah et al. 2018). Further, the antimitotic ability of rhizoxin of *Rhizopus microsporus* with endosymbiotic bacteria *Burkholderia rhizoxinica* and *Burkholderia endofungorum* to bind rice β-tubulin for inhibition of mitosis and cell cycle arrest has attracted considerable interest as a potential antitumor drug (Scherlach et al. 2006). An interaction of *Penicillium fuscum* with *Penicillium camembertii* or *Penicillium clavigerum* yielded unique macrolides of berkeleylactones along with the known antibiotic macrolide, patulin, and citrinin. These new macrolides were found inhibitory to methicillin-resistant *Staphylococcus aureus* strains, *Bacillus anthracis*, *Streptococcus pyogenes*, *Candida albicans*, and *Candida glabrata* (Stierle et al. 2017). The fungus *Fusarium tricinctum* after interacting with bacterium *Bacillus subtilis* 168 trpC2 produces important secondary metabolites, of which lateropyrone and Enniatins B1 display antibacterial activity against *Staphylococcus aureus*, *Streptococcus pneumoniae*, and *Enterococcus faecalis* (Ola et al. 2013). In another study, *Streptomyces lividans* caused *Fusarium tricinctum* to enhance the production of new naphthoquinone dimers of fusatricinones, new lateropyrone derivative of dihydrolateropyrone, and cryptic compounds of zearalenone, (−)–citreoisocoumarin, macrocarpon C, and hydroxy-2-(2-hydroxypropyl)-5-methylchromone. Among upregulated products were the antibiotically active compound lateropyrone; the depsipeptides enniatins B, B1, and A1; and the lipopeptide fusaristatin A (Moussa et al. 2019). The fungus *Penicillium* sp. DT-F29 produces prenylated 2,5-diketopiperazines that have bromodomain-containing protein 4 (BRD4) inhibitory activities, when in contact with bacterium *Bacillus* sp. B31 (Yu et al. 2017). These diketopiperazines can be used to circumvent the physical and metabolic properties of peptides during identification of drugs.

The quorum sensing inhibitors that affect bacterial biofilms have potential broad range anti-microbial activity and can be helpful in the treatment of infections caused by multidrug-resistant pathogens (Khalid and Keller 2021). This can involve an interference with quorum sensing signal production with the inhibition of autoinducer-2 synthesis, quinolone signal-molecule synthesis, peptide autoinducer synthesis, and N-acyl-homoserine lactone synthesis (Fleitas Martínez et al. 2019). The fungal secondary metabolite ambuic acid is known to inhibit the production of quorum sensing-mediated gelatinase and the cyclic peptide quormones of *Staphylococcus aureus* and *Listeria innocua* (Nakayama et al. 2009). Thus, it has the potential to be utilized as a lead compound of drugs that target the quorum sensing among Gram-positive bacteria. Similarly, 2,4-di-tert-butylphenol, a quorum sensing inhibitor produced from fungus *Daldinia eschscholtzii*, can prevent the adhesion and invasion of *Pseudomonas aeruginosa* to the A549 lung alveolar carcinoma cells in combination with ampicillin (Mishra et al. 2020). This suggests its potential to be exploited as an individual drug or in combination with antibiotics as an anti-virulence and anti-biofilm agent, particularly for combating infections from the multidrug resistant *Pseudomonas aeruginosa*. Another fungus *Usnea longissima* has the capability to exert production of unique drug molecules as acetone soluble metabolites of organic acids and fatty acids for controlling biofilm formation, quorum sensing, and production of virulence factors (pyocyanin, protease, elastase, rhamnolipids, extracellular polysaccharides) in *Pseudomonas aeruginosa* PAO1 (Bajpai et al. 2020).

Furthermore, bacteria are known to produce heat-stable bacteriocins as colicins, microcins, lantibiotics, pediocin, carnobacteriocin, enterolisin, caseicin, etc. that are structurally and functionally diverse antimicrobial peptides, which inhibit other specific bacterial strains (Simons et al. 2020). Moreover, these bacteriocins in their purified form have applications in food technology for extending the duration of food preservation, treating pathogen disease, cancer therapy, and maintaining human health, thereby becoming a potential drug candidate to treat multiple drug resistance pathogens (Yang et al. 2014). The cytotoxins etoposide and ivermectin are potent inducers of novel antifungal compounds and cysteine protease inhibitors secreted from *Streptomyces albus* J1074, which are implicated in cancer therapy (Xu et al. 2017). Thus, microbial interaction-mediated induction of secondary metabolite production is one of the important resources for new drugs. The microbial interactions lead to the production of various secondary metabolites, which can be used to identify potent antimicrobials of bacteria and fungi. Therefore, an exploration on the synthesis, mode of action, and functions of various natural molecules emanating from microbial interactions could facilitate the detection of new and useful pharmaceutical drugs.

2.7 Conclusion and Future Prospects

The vigorous environment of soil supports diversity, interaction, and multiple functions of enormous communities of organisms. Within this, the microbial interactions facilitate soil formation and many processes of nutrient mobilization, decomposition of organic matter, biodegradation, maintaining plant growth, and productivity. An alteration of microbial community structure could occur within soil profiles that are typically modified with nutrient availability and biotic interactions. There are diverse molecular weapons that microbes produce during their interactions in the soil, while some physically interact for either promoting or inhibiting the growth of one another and affecting nutrient availability. The microbe–microbe interactions have importance in essential soil functions, management of crops, biodegradation of different pollutants, biological control of pre- and post-harvest problems for sustainable agriculture, and development of drugs with multiple biological activities.

However, a vast proportion of microbial diversity in the soil, with their structure, functioning, and genetic capacity, is yet to be known. Most studies on microbial distributions are from the near-surface horizons, while those communities of the whole soil profile remain much less known. Further, harmful anthropogenic inputs can alter the relative abundance, diversity, and functional characteristics of microbial communities. These microbial communities could have vital functions in mediating many ecosystem processes at different environmental conditions. Despite an ability of lignocellulose degradation, the community dynamics of several soil bacteria and their plausible interactions involved in recalcitrant wood biopolymer decomposition remains largely unexplored than those of the fungal decay. Additionally, different soil fertility enhancement and aggregation mechanisms of microbial interactions are underdeveloped, which would require new field-based studies, whereas little is known about the molecular mechanisms underlying different interspecies microbial interactions. An application of symbiotically interacting bacterial and fungal inocula with crops and organic fertilizers is an emerging tool for restoring degraded lands, which requires adequate selection for the mixed cultures as an important factor. Increasing the knowledge on microbial processes occurring in the soil ecosystem would allow for an enhanced management of agricultural practices and conservation.

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Chapter 3
Role of Soil Biology on Soil Health for Sustainable Agricultural Production

J. C. Tarafdar

Abstract For tenable agriculture production and soil health maintenance, microbial and faunal activity is very important which helps to maintain ecology in soil with minimal effect on environment. Soil biology can find a good balance between the requirement of food production and the protection of the ecological system within the environment. Good and healthy soil can undergo a number of ecosystem services; the most notable are soil nutrient cycling, water quality, and productivity management, helping decomposition and pulling out greenhouse gases from the atmosphere. Soil microorganism's diversity and activity are the major component of soil health which is intimately associated with the sustainable agriculture. Beneficial microorganisms intensify the water use efficiency and nutrient availability to plants, besides phytohormone production, soil nutrient cycling, and plant resistance to environmental stresses. In general, organic farming and proper tillage practice improve soil health by increasing the abundance, diversity, and activity of microorganisms. Soil biological properties answer faster and may be better indicator than physical and chemical properties of soil although the biological components in soil occupy only 0.5% volume of soil and normally contribute up to 10% of soil organic matter. Soil quality is considered as the major linkage between the agricultural conservation management practices and sustainable agriculture. Improvisation of soil biology needs to grip of various interactions; the notable are soil biological community and diversity, plant species, soil type, climate, as well as soil management practices. The biological properties in the soil can be improved by addition of crop residues, animal manure, root and cover crops, green manure, compost, and other sources as well as cropping systems and crop rotation. Moreover, to promote the soil biological properties, balanced fertilization is very important. The introduction of beneficial organisms such as nitrogen-fixing bacteria, phosphorus solubilizing and mobilizing organisms, blue green algae, mycorrhizae, etc. was found to enhance the soil health, plant nutrient uptake, aggregation, soil structure, porosity, and heavy metal tolerance.

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B. Giri et al. (eds.), *Structure and Functions of Pedosphere*,
https://doi.org/10.1007/978-981-16-8770-9_3

Keywords Soil health · Soil biology · Soil organisms · Management · Organic farming · Indicators

3.1 Introduction

The fundamental for plant growth is depending on the biological activity of soil. The living forms of soil are the soil organisms which include megafaunna, macrofaunna, mesofaunna, microfauna, and microflora. Soil biology is responsible in carrying out the crucial life processes in soil. Soil health depends on the capacity of the soil to ascertain environmental quality, sustain biological productivity, and keep going health of all living beings. In general, biotic and abiotic components of an ecosystem interrelate with each other for proper functioning of all processes. The fundamental of plant growth depends on the biological activity of the soil that includes nitrogen, phosphorus, and sulfur cycles which are responsible for bioavailability of nutrients and the deposition of organic carbon responsible to provide soil structure that is responsible in reducing soil erosion and improving water movement and retention. Soil organisms are contributing enough in sustaining soil health, fertility, and agricultural productivity. The important roles on soil health and water dynamics are played by soil organisms starting from nutrient cycling to nutrient retention. They are capable to release stored nutrient of plant and animal tissues and convert them into forms usable by plants. The organisms are also capable to breakdown the soil organic matter and release inorganic nutrients that may then be used by the plants. Soil fertility contains three interrelated components, i.e., physical fertility, chemical fertility, and biological fertility. Besides soil fertility, soil microorganisms play essential roles in the nutrient cycles that are fundamental to life on this planet. There may be hundreds of millions to billions of microbes in a single gram of soil. The most numerous microbes in soil are the bacteria, followed in decreasing numerical order by the actinomycetes, the fungi, soil algae, and soil protozoa. Soil biological properties retaliate quickly and have suggested better indicators than soil physical and chemical properties which alter only after drastic change in soil quality (Nannipieri et al. 1990). The health of the soil can be defined as the position of the soil being in sound physical, chemical, and biological condition, having the capability to sustain the growth and development of land plants. Although the living component of soil speaks for a small fraction (<0.05% dry weight), it is absolutely essential to many soil functions and to maintain overall soil quality. The main functions of them toward the sustainable agricultural production are nutrient cycling, pest and pathogen protection, water availability, production growth factors, and formation of stable aggregates to increase water infiltration and reduce risks of soil erosion.

3.2 Characteristics of a Healthy Soil

A healthy soil is one where the soil organic matter level matches with the land use and soil structure. Moreover, it maintained the level of soil organic matter. The soil also conserves the nutrient storage capacity and minimizes the off-site nutrient loss. As far as possible, the nutrient additions match the removal and losses. The water infiltration, storage, and supply also meet the land use needs. There will be no constraints to water use as well as drainage is minimized where there is a risk of dry land, salinity, or acidification. The biological function of the soil is always improved with resilient and diverse biological community. The soil should have optimum biological functioning with the key function of biota that regulates nutrient recycling with non-appearance of disease expression. A healthy soil can accommodate the active and diverse populations of beneficial organisms with minimum plant pest population. The soil must support the plant growth under different land use requirements and sustain resource condition and ecosystem services. It also helps to increase the environmental and community health with the fit for purpose as well as profitable while conserving soil resources and reducing the environmental impact. A healthy soil is rebound more quickly under unfavorable soil conditions.

3.3 Soil Organisms

Soil is a natural media for biological diversity. Organisms present in the soil are interacting with one another and with plants and small animals forming a web of biological activity. The food web of soil includes beetles, springtails, mites, worms, spiders, ants, nematodes, fungi, bacteria, and other organisms. Their function is to improve the entry and storage of water, resistance to erosion, plant nutrition, and breakdown of organic matter. They make balances to the soil food web through population control, mobility, acclimatization, and survival. The organisms in the soil bestow a wide range of essential services to the sustainable function of all ecosystems. Generally, they are the primary driving agents of nutrient cycling, regulating the dynamics of soil organic matter, soil carbon sequestration, and greenhouse gas emission, modifying soil physical structure and water regimes, enhancing the amount and efficiency of nutrient acquisition by the vegetation, and enhancing plant health. This assistance not only is essential to the functioning of natural ecosystems but constitutes an important resource for the sustainable management of agricultural systems.

Soil is also an excellent culture media for the growth and development of various microorganisms. It is now believed to be dynamic for a living system that provides shelters for many animal types, from invertebrates such as worms and insects up to mammals like rabbits, moles, foxes, and badgers. Soil is a more or less homogeneous system which has resulted from the decomposition of plant and animal remains although it contains mineral particles, plant and animal residues, living systems,

Table 3.1 Expected microorganisms in a fertile soil

Organism	Population (million)
Bacteria	1–100
Actinomycetes	0.1–1.0
Fungi	0.1–1.0
Algae	0.01–0.1
Protozoa	0.01–0.1

Adopted from Mehra (2004)

water, and gases. Soil microorganisms are very important because they affect soil structure and fertility. It can be classified as bacteria, actinomycetes, fungi, algae, and protozoa. Soil is a dynamic habitat and gives mechanical support to plants from which they extract nutrients. Although they constitute only <0.5% (w/w) of the soil mass, they have a major impact on soil properties and processes. In general, 60–80% of the total soil metabolism is due to the microflora (2 mm in diameter). Macrofauna includes vertebrates such as snakes, lizards, mice, rabbits, moles, etc. that primarily dig within the soil for food or shelter and invertebrates that include snails, earthworms, and soil arthropods such as ants, termites, millipedes, centipedes, caterpillars, beetle larvae and adults, fly and wasp larvae, spiders, scorpions, crickets, and cockroaches which live in and feed in or upon the soil, the surface litter, and their components. Soil macrofauna are important regulators of decomposition, nutrient cycling, and soil organic matter dynamics and pathways of water movement as a consequence of their feeding and burrowing activities. The mesofauna (0.1–2 mm in diameter) in soil includes mainly micro-arthropods, such as pseudo-scorpions, springtails, mites, and the worm-like enchytraeids. They have limited burrowing ability and generally live within soil pores, feeding on organic materials, microflora, microfauna, and other invertebrates. Nematodes are tiny filiform roundworms that are common in soils everywhere. The microfauna (nematode, protozoa, rotifers, etc.) are capable of digesting just about any organic substance and some inorganic substances (such as TNT and synthetic rubber). These organisms are often essential links in the food chain between primary producers and larger species. The population of microorganisms per gram of fertile soil is presented as Table 3.1.

Soil organisms are accountable for cycling of C, N, and other nutrients required by plants, strengthening soil structure, relocating and decomposing organic material, preserving soil quality and health, and expanding soil aeration and penetrability as well as involved in disease transmission and control. The major functions of soils performed by the soil organisms are to tie up plant roots, supply water to plant roots, deliver air for plant roots, supply nutrients for plant growth, etc. They can influence also both biotic and abiotic factors and edaphic parameters. Overall, they play the key role in ecosystem functioning. Microbial diversity reports the complexity and variability at different levels of biological organization. It bound the genetic variability within taxa (species) and the number (richness) and relative abundance (evenness) of taxa and functional groups (guilds) in communities. Important aspects of diversity at the ecosystem level are the range of processes, complexity of interactions, and number of trophic levels. To maintain the activity of earthworm in summer, irrigation is the best way. It also helps to increase in springtail, mite, and protozoa population as well as encourage to improve the soil microbial biomass content. The ecosystem services delivered by soil biota are nutrient cycling and regulation of water flow and storage, biological regulation of soil sediment movement, maintenance of soil structure, as well as improved carbon sequestration in soil.

3.4 Decomposition of Organic Material

Soil organic matter is a primary food source that stores energy and nutrients which are used by both plants and soil microbes. It is a product of biological decomposition and a primary food source for soil microbes. Bacteria and fungi act as primary decomposers; they have the ability to break down organic material releasing useful nutrients. Bacteria generally utilize carbon sources that are easy to break down (like fresh plant material and plant exudates, which are sugars and other metabolites leaked from the roots); on the other hand, soil fungi generally can break down tougher sources like cellulose, hemicellulose, and lignin. Organic matter is a primary driver of soil productivity and is the foundation of functional soil biology. It is mainly composed of carbon, hydrogen and oxygen but also has small amounts of nutrients such as nitrogen, phosphorous, sulfur, potassium, calcium and magnesium contained within organic residues. Soil organic matter also exists as four distinct fractions which vary widely in size, composition and turnover times in the soil. They are living organisms (<5%), fresh residue (<10%), solubilized organic matter or humus (33–50%) and decomposing organic matter or active fraction (33–50%). Organic matter decomposition is a biological process that includes the physical breakdown and biochemical transformation of complex organic molecules of dead material into simpler organic and inorganic molecules (Juma 1998). It is a part of the nutrient cycle and is essential for recycling the finite matter that occupies physical space in the biosphere. Three major reactions occur during decomposition process. (1) Assimilation is the conversion of substrate materials into protoplasmic materials, for example, organic carbon to microbial carbon and protein to microbial protein. (2) Mineralization is the conversion of organic substance to inorganic form, for example, essential elements are released (N, P, S etc.). (3) Immobilization is when inorganic nitrogen from the soil is converted to microbial protein.

Microorganisms have the major role to decompose the organic carbon fraction like cellulose, lignin, hemicelluloses, chitin and lipids present in soil organic matter. Organic matter decomposition is primarily a microbiological process, and its actual rate and extent are influenced by environmental variables, including soil temperature, moisture, oxygen, nitrogen content, the quality and quantity of available carbon substrates, as well as soil management. Decomposition is carried out by heterotrophic microflora and microfauna comprising bacteria, fungi, actinomycetes and protozoa. Besides the microflora and microfauna, many species of mesofauna such as earthworms also play an important role in the initial breakdown of organic residues. Organic matter decomposition serves three functions for the micro flora:

Table 3.2 Functions of decomposers

Name of decomposer	Functions
Nematode, protozoa, collembola, mites, acari, earthworms, molluscs, and termites	Physical decomposition
Mycorrhizae, polysaccharide producing fungi and bacteria, bioturbating invertebrates, plant roots	Maintenance of soil structure and regulation of soil hydrological structure
Microorganisms and plant roots, invertebrate aggregates	Gas exchange and carbon sequestration
Mostly microorganisms	Soil detoxification
Microorganisms and plant roots, saprophytic and litter feeding invertebrates	Nutrient cycling and decomposition of organic matter
Mycorrhizae, other fungi, and other microorganisms	Suppression of pests, parasites, and diseases
Rhizobia, mycorrhizae, actinomycetes, diazotrophic bacteria, and various other microorganisms	Symbiotic and asymbiotic relationships
Plant roots, rhizobia, mycorrhizae, actinomycetes, pathogens, biocontrol agents, soil biota	Plant growth control

(1) providing energy for growth, (2) supplying carbon for the formation of cell material, and (3) providing other nutrient and elements needed for cell growth. The functions of different members of decomposers are shown in Table 3.2.

The decomposition of organic matter is mainly an enzymatic process. Normally, enzymes are produced by microbial cells, irrespective of the substrate in the environment. It may metabolize its substrate within or outside the cell. They may categorize as intracellular or extracellular enzymes. Extracellular enzymes are essential for the decomposition of polysaccharides because the microbial cell is impenetrable to the large polysaccharide molecules. Monosaccharides, such as glucose, are metabolized by intracellular enzymes. Organic residues added to the soil are first broken down into their basic components by extracellular enzymes; and the basic components are subsequently utilized by intracellular enzymes. The optimum condition for better organic matter decomposition in soil depends on adequate water supply, sufficient supply of nitrogen, optimum soil pH, better aeration, warm climate, and a fine state of mechanical disintegration. The important products released during decomposition are carbon dioxide (CO_2), energy, water, plant nutrients, and resynthesized organic carbon compounds. The business of decomposition takes place in five different steps; they are fragmentation, leaching, catabolism, humification, and mineralization. Decomposition will take place in both aerobic and anaerobic condition. The products such as CO_2, NH_4, NO_3, H_2PO_4, SO_4, H_2O, and essential plant nutrients like Ca, Mg, Fe, Cu, Zn, etc. are formed during aerobic decomposition, and CH_4; organic acids like lactic, propionic, and butyric; NH_4; various amine residues ($R\text{-}NH_2$); H_2S; ethylene ($CH_2{=}CH_2$); and humic substances are formed during anaerobic decomposition. Organic matter decomposition serves three functions for the microflora: (1) providing energy for growth, (2) supplying carbon for the formation of cell material, and (3) providing other nutrient and elements needed for cell growth.

3.5 Nutrient Cycling

Soil biology is known for the cycles of carbon, water, and nutrients. Carbon, nitrogen, phosphorus, and many other nutrients are stored, transformed, and cycled through soil. Decomposition by soil organisms is at the center of the transformation and cycling of nutrients through the environment. The foremost operator of nutrient cycling in soil is the soil biology. The active carbon makes use of soil bacteria, which are directly available for use by microbes. Much of this active carbon begins as plant exudates. These exudates excreted from plant roots are a primary food source and are utilized by soil bacteria directly along the plant roots. As the bacteria die, they mineralize and release nitrogen contained in their bodies, thus cycling nutrients. The microbes themselves constitute a considerable amount of nutrient cycling in their own biomass. The microbial biomass or the number of microbes a soil sustains can be 2–5% of the total organic matter in a soil. However, this fraction is self-motivated and living. This fraction also contains considerable amounts of essential plant nutrients. Biologically significant amounts of nitrogen, sulfur, and phosphorus are mineralized into plant available forms and released for uptake when microbes expire.

Protozoa are predators. They play a key role in nutrient cycling by just doing what they do. They feed on the soil bacteria. Soil bacteria have a carbon-to-nitrogen ratio of about 5:1, while protozoa have a ratio closer to 10:1. As the protozoa feed on the bacteria, they consume more nitrogen than they need. The excess is excreted and utilized by plants, and the cycling process continues. In general, on an average 16 mineral and non-mineral nutrients are necessary for plant growth. Plant takes non-mineral nutrients such as carbon, hydrogen, and oxygen from air and water. On the other hand, mineral nutrients are pinned up from the soil which can be classified as macronutrients (N, P, K), secondary nutrients (Ca, Mg, S), and micronutrients (B, Cl, Cu, Fe, Mn, Mo, Zn). The root interception by plants mainly helps to absorb nutrients from soil along mass flow and diffusion. Mass flow is answerable for the majority of the nutrient uptake. The primary pools for meeting the short-term crop needs are from crop available and exchangeable pools. The main processes occurring in nutrient cycles are mineralization, immobilization, sorption, precipitation, weathering, and losses. Relative contributions of root interception, mass flow, and diffusion for transport of different nutrients are shown below (Table 3.3).

Table 3.3 Relative contributions of root interception, mass flow, and diffusion in nutrient transport to corn roots

Nutrient	Root interception	Mass flow	Diffusion
N	1	99	0
P	2	4	94
K	2	20	78
Ca	21	79	0
Mg	9	91	0
S	4	94	2

3.6 Soil Aggregation

Soil aggregation is the arrangement of primary soil particles like sand, silt, and clay around the soil organic matter with uninterrupted particle associations. The particles of different sizes held together by both the attraction of soil particles and the binding of organic matter between soil particles. Soil aggregation refers to a soil's ability to hold particles together. It was supported by soil biology by simply decomposing organic material and developing organic matter. As organic matter increases in soil, the ability to form soil aggregates increases. Soil fungi aid in this process by helping the soil physically hold particles together. Arbuscular mycorrhizal fungi coat their hyphae with a compound called glomalin. Glomalin serves as a protective coating to prevent nutrient and water loss as they are transported to the plant. Glomalin also serves as soil glue and helps stabilize soil aggregates. These processes, along with many others, improve soil structure and help soil resist disruptions like wind and water. Soil organic matter plays a key role in forming and stabilizing soil structure, enhancing soil physical properties, and nutrient recycling (Beare et al. 1994; Martens 2000). Soil aggregate, the basic unit of soil structure, mediates many physical and chemical processes in soils (Six et al. 2000; Albalasmeh et al. 2013), such as soil compaction, soil nutrient recycling, soil erosion, root penetration, and crop yield. Aggregate stability is frequently used as an indicator of soil structure (Xie et al. 2015) because better soil structure and higher aggregate stability are vital to improve soil fertility, soil sustainability, and productivity (Zhang et al. 2016). Soil organic carbon guides the aggregate stability and soil structure (Onweremadu et al. 2007). The level of stability is different among the different sizes of aggregation. In general, organic carbon in the microaggregate is more strongly bound than it is in the macroaggregate (Gershenson et al. 2009). The distribution of organic matter of different cropping systems varies according to the quantity and quality of the crop residue present as well as the environmental condition. The changes in soil aggregates are responsible to the cropping system, transformation of soil organic matter, and the active habit of microorganisms. The important indicators for soil aggregate stability are soil mean weight diameter (MWD), geometric mean diameter (GMD), fractal dimension (D), percentage of aggregate destruction (PAD), and water-stable aggregate stability rate (WSAR). Fungi and bacteria are responsible for the formation of water-stable soil aggregates. Fungal hyphae can physically bind soil mineral and organic particles together. Normally, both fungi and bacteria can secrete polysaccharide mucilages that are sticky and glue the soil particles together into aggregates. This aggregate can prevent slaking and dispersion of soil and make the aggregate stable against water for several months. With the adoption of suitable management practices, soil aggregation might be improved. The important practices are lower the agro-ecosystem disturbances, improve in soil fertility, increase in organic inputs, increase plant cover, use of high biomass production crops, the return of crop residues, etc. The increasing root length density and use of extensive fibrous roots crop help to build highest level of macroaggregation. For improving soil structure, increase in diversity, quantity, and activity of soil flora and fauna is important.

3.7 Nutrient Availability

It is positively impacted by microbial activity. Fungi play an important role for nutrient availability. The interrelated factors responsible for nutrient availability are the parental rock material, particle size, humus and water content, pH, aeration, temperature, root surface area, the rhizoflora, and mycorrhizal development. Mycorrhizal fungi form mutualistic relationships with plants and utilize carbon from plant roots. In exchange, the fungus helps solubilize phosphorus and other nutrients, making them available for plant use. This process essentially extends the reach of plant roots, increasing their ability to tap nutrients. Some soil bacteria form symbiotic relationships with plants to increase nutrient availability. Rhizobium bacteria infect the root hairs of specific legume species. In exchange for carbon, this bacterium fixes atmospheric nitrogen. This nitrogen is available for the plant itself to use. However, once the plant dies, the excess nitrogen is released and available for subsequent plant use. Moreover, nutrients contained in the processed biosolids are slowly released, as those from organic manures, and are stored for a longer time in the soil, thereby ensuring a positive residual effect on plant root development and growth leading to higher crop yields (Abou El-Magd et al. 2005). In general, bacteria are decomposers by eating dead plant material and organic waste; subsequently they release nutrients that other organisms could not access. So, they help to change the nutrients from inaccessible to usable forms. The process is especially essential in the nitrogen cycle. Fungi are very helpful candidate in nutrient cycling as they have the ability to breakdown nutrients that other organisms cannot. They also can attach themselves to plant roots. Fungi get carbohydrates from the plants; instead it helps the plant by supplying its needed nutrients. Further fungi can get food by being parasites and attaching themselves to plants or other organisms for selfish reasons. Nutrient availability has an effect of growth rate and carrying capacity. In general, growth rate increases over nutrient availability which is generally transported to roots by diffusion, a slow process, when they have limited mobility such as P, K, Fe, Zn, Mn, and Cu. For this reason, the presence of these nutrients is relatively more in the bulk soil; however, the plant available fraction and the concentration in the rhizosphere soil solution may be insufficient to satisfy plant requirements (Rengel 2001). The important mechanisms suggested for low nutrient availability are capacity to take up nutrient in soil having low availability of that nutrient or in other words acquisition efficiency and capacity to produce more amount of organic matter per unit of nutrient taken up, i.e., utilization efficiency.

3.8 Water Dynamics

Soil biology could help to maintain in soil water dynamics such as infiltration and water holding capacity. With increase in organic matter in the soil, soil aggregation increases more, and the pore space and the porosity of the soil enhance. Earthworms also aid in this process by burrowing through the soil, creating tunnels for water and roots to travel. Due to increase in pore space, the amount of water that can effectively infiltrate into the soil profile generally increases. Soil biology helps to get the water in the ground and to minimize run off. Enhancing in available water holding capacity of a soil is also aided by soil biology. In general, biologically active soil is rich in organic matter which is very efficient at holding water. This process tends to be more effective on coarser soils. Clay substrate soils may have a lesser impact as the clay itself is the driver for its capacity to hold water.

3.9 Soil Health

Soil health is defined as "Capacity of a specific kind of a soil to function within natural or managed ecosystem boundaries to sustain plant and animal productivity, maintain and enhance soil and water quality and support human health and habitation" (Anonymous 1995). High-quality and good health soils should have good tilth, sufficient soil depth, required nutrient supply, small population of plant pathogens and insect pests, good soil drainage, large population of beneficial organisms, and low weed pressure and contain no chemical or toxins that may harm the crops. A healthy soil sustains productivity, maintains environmental quality, and enhances plant and animal health. The key to soil health is organic matter. This soil fraction is consisting of plant and animal residues, in various stages of decomposition. It actually contains organic carbon and nitrogen. Carbon is a source of energy, and nitrogen is a source of protein for microorganisms in the soil. Some of the microorganisms are pathogens which cause plant disease, but in a healthy soil, the vast majorities of these organisms are beneficial and help prevent any one type of organism such as a plant pathogen from being dominant. There are three distinct parts in soil organic matter; they are as follows: living organic matter (about 15%) consists mainly of bacteria, actinomycetes, fungi, protozoa, and algae, which are also called decomposers; besides this other living soil organic matter includes nematodes, insects, earthworms, plant roots, and small animals; dead organic matter (about 15%) serves as food for living organisms and include dead microbes, old plant roots, crop residues, and bodies of larger insects and animals; very dead organic matter (about 70%) are well-decomposed, dark-colored organic substances also called humus. Humus continues to decompose, but at a very slow rate. Organic matters improve many physical, chemical, and biological characteristics of the soil, including water holding capacity, cation exchange capacity, pH buffering capacity, and chelating of micronutrients. Furthermore, well-decomposed soil organic matter improves soil structure by increasing aggregation, enhancing biological activities in the soil, slowly releasing nutrients, and suppressing some diseases. A loss of soil organic matter can lead to soil erosion, loss of fertility, compaction, and general land degradation. For sustainability to farming systems and maintenance of soil health, the enhancement of organic matter level in the soil is crucial. The collection of organic matter within soil makes a balance between the return or addition of plant

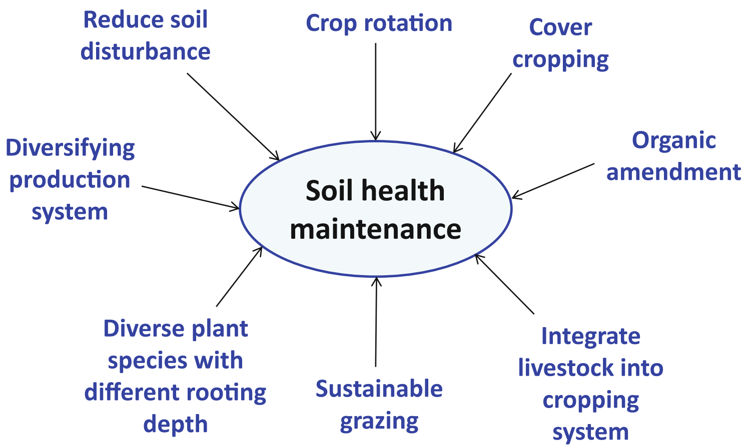

Fig. 3.1 Suggested strategies to maintain soil health

and animal residues and their subsequent loss due to the decay of these residues by microorganisms and mismanagement of soil. The best way to keep the organic matter level is to add about 4 tons per hectare of dry matter annually to the fields. It can also be maintained by using soil amendments such as manure and compost and/or on-time establishment of cover crops. The important game plan to maintain soil health is shown under Fig. 3.1. The most important is to reduce soil disturbance both under farmland and rangelands as intensive soil tillage always encourages soil degradation. Tillage is highly destructive as it destructs the habitat and the population of soil organisms that really helps in maintaining and improving the soil health. They also can cause rapid loss of organic matter from the soil which is not only the food of the microbes but also helps in the binding of soil aggregate. The organic matter is oxidized during tillage operation; therefore, conservation tillage is preferable for better soil health. There are many reduced tillage methods such as strip tillage or no tillage that can produce similar crop yields as the conventional plow-till method in arid and semi-arid farmlands (Darapuneni et al. 2019; Idowu et al. 2019). It is indicated by adopting to reduced tillage practices; crop producers can remain profitable in terms of yield and at the same time conserve and improve the soil health of their fields as well as fewer field passes for land preparation, leading to savings in fuel and tillage costs.

It is always better to go for crop rotation which can be of any length depending on the farmer preference. Legume-cereal rotation is always preferable; cover crops also can be included in the rotation cycle for better health management. The main factor in rotation is that a variety of crops belonging to different families are being grown in the same soil. The major advantage of crop rotation is to break the disease cycle in the given field. If crop families are different, the pathogen cycle becomes disrupted resulting in the huge reduction of pathogen population in the soil. Moreover, it helps to build up microbial population and diversity in the soil (Vukicevich et al. 2016). In general, more diversity of soil microorganisms results in better soil health. The land

Table 3.4 Identified measurements for soil health assessment under arid and semi-arid agroecosystems

Physical indicators	Chemical indicators	Biological indicators
Available water capacity	Soil pH	Carbon mineralization
Aggregate size distribution	Soil primary nutrients (N, P, K)	Permanganate oxidizable carbon
Soil compaction level	Soil micronutrients (Zn, Fe)	Microbial diversity index
Soil bulk density	Soil salinity	Soil organic matter
Soil texture	Soil sodicity	Nitrogen mineralization
Wet aggregate stability	Reactive carbon	Total microbial biomass
Soil crust	Soil nitrate	Soil enzyme activity

is also protected from erosion after growing cover crops which may add more root exudates and biomass for soil improvement. Although soil health improvement derived from cover crops may be undetectable, it is an important way to increase the soil organic matter especially in arid and semi-arid areas. Moreover, after using leguminous cover crops, the fixed nitrogen can be translocated into the plants and made available for the subsequent crop after residue decomposition. Instigate diversity in the production system helps to build a healthy soil. It may be use of mixed varieties, mixed cropping, integrating livestock into crop production, cover cropping, crop rotation, fallowing fields, hedgerows, and many other practices. Diversified farming also helps in nutrient cycling, soil water management, pest control, and habitats for pollinators. With the introduction of animal grazing into crop production system, a tremendous improvement of soil health was observed through increases in microbial community size, soil organic matter, and total nitrogen compared to conventional cropland (Ghimire et al. 2019). Diversifying crop production on a farm can also help to minimize losses since production risks are spread across different commodities that the farm produces. Addition of soil organic amendments improves soil conditions and stimulates soil biodiversity. The amendments may be manure, compost, biochar, etc. It has been observed that a regular addition of organic amendments can improve soil fertility, soil biological functions, as well as soil physical characteristics (Diacono and Montemurro 2011). It can also help to increase microbial activity that breaks down organic materials and releases nutrients. Organic amendments are excellent material to improve soil health, but we should know the properties of amendment before adding to soil. The minimum data set required for best set of measurements to estimating soil health (Rezaei et al. 2006) is presented in Table 3.4. This minimum data set can also be designated as soil quality indicators.

Integrating livestock into the cropping system can improve the efficiency of farm resource utilization and decrease the requirements of synthetic fertilizers and pesticides while improving soil health (Ghimire et al. 2019). System supported by livestock supports the growth of wide microbial communities resulting to accumulated organic matter and development of healthy soils. The decomposition of leftover plant residues speeds up by grazing which ultimately enhances the availability of nutrients like nitrogen, phosphorus, and sulfur. But negative impact is also observed due to over-grazing; therefore, a balance of crop-range-livestock is critical for maintaining or improving soil health under livestock integrated system. To obtain long-term sustainability, it is essential to introduce species with diverse rooting depth. In general, more diversity of species results in better soil health because of increase in soil carbon sequestration and soil diversity (Chen et al. 2018). Plant roots also help to aggregate soil particles after releasing various compounds that bind the particles or glue it. This process is also important for infiltration, water retention, and erosion control. To introduce plants of different rooting depth will also bring opportunity for plants with deeper roots to capture nutrients that may otherwise be lost to leaching. Grazing strategies are important under rangeland system as they can affect soil health positively or negatively. Due to overgrazing the plant communities being grazed are rapidly depleted or damaged, and they become a useless land for future grazing. The important factors to be considered to maintain soil health while grazing are the stocking species and density should be controlled, wet field should not be used for grazing, and the field must have enough vegetation cover. In a nutshell, long-term strategy is needed for soil health management. For example, the land managers should be well educated on soil health and its maintenance, they need to give careful thoughts and well verge of their farm situation, the planning should be full proof after identifying the health management strategies, they should share the information for rectification if any through discussion, and finally they should be prepared to invest either money or time.

3.10 Soil Amendments

Organisms in soil require some favorable soil conditions for their growth and functioning. Neutral pH soil is preferred by most of the organisms. For example, most bacteria and actinomycetes like neutral pH for better growth; however, fungi growth is optimum under slightly acidic soil conditions. It has also been found that the growth and activity of microorganisms are adversely affected under drought, soil sodicity, and acidity. Low dehydrogenase activity was also reported under sodic and saline soils of arid and semi-arid regions in comparison to the normal soil (Batra and Manna 1997). Use of lime in acidic soils raises the soil pH and permits better survival of inoculated and native microbes in soil. To sustainably manage the acid soils, combined use of manure, lime, and chemical fertilizers and/or manure and chemical fertilizer has been noticed more promising. On the other hand, gypsum and pyrite are the proper amendments for sodic soils to protect soil biota and plants from toxicity of sodium and alkalinity.

The population of soil organisms can be managed after providing the suitable management practices. Soil biology can also be managed by inoculating the soil with desirable species or reducing the activity of undesirable ones. For example, farmers can inoculate soil or seeds with nitrogen-fixing bacteria, or they can introduce bacteria, nematodes, and insects that are predators of pest of their crops, or they can add nitrification inhibitors to reduce the activity of specific bacteria that convert ammonium to nitrate. The effect of inoculants may be temporary if the organisms cannot compete with the native population and cannot adjust with the new environment. Moreover, it has been found that mix of organisms sometimes get more fruitful results than the application of a specific species. The soil biological properties can also be improved after continuous application of different bio-inoculants which then become the indigenous population. Continuous application of soil beneficial organisms such as nitrogen-fixing bacteria, phosphorus solubilizers or mobilizers, blue green algae, and mycorrhizae has exhibited to enhance the soil health, plant nutrient uptake, aggregation, soil structure and porosity, and heavy metal tolerance. Rhizobium inoculation in mung bean guides significant improvement in the population of total bacteria and actinomycetes as well as rhizobium population in the rhizosphere which may be due to the enormous plant growth due to inoculation (Singh and Tarafdar 2002).

3.11 Conclusions

Soil biology has tremendous role on soil health management for sustainable agricultural production. Healthy soil can resist the adverse fluctuations in growing conditions. To adopt soil health practices, it is possible to build and maintain healthy soils to improve soil productivity. In general, origin and nature of the soil as well as relative composition of its inorganic and organic constituents dictate the quality of the soil. Soil organic matter has good impact on the physical, chemical, and biological properties of the soil. Organic matter also helps to maintain good soil structure to authorize the soil to absorb water and retain nutrients that help the growth and life of soil biota by providing energy from carbon compounds. Nutrient generally released after decomposition of organic matter used by plant and microorganisms and the availability of these nutrients depend on the amount and type of organic matter. To manage soil biology and to maintain biological activity in the soil, timing tillage, proper choice of fertilizers and pesticides, choice of compost and manure, as well as managing habitats in the soil are very important. Ion is mopped up from the soil by root interception, mass flow, and diffusion out of which much flow is responsible for majority of nutrient uptake by plants. The fundamental process of nutrient cycles is mineralization, immobilization, sorption, precipitation, weathering, and losses. To meet the crop needs, nutrient present in available and exchangeable pools is most critical.

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Chapter 4

Pedosphere: A Hot Spot of the Largest and Most Complex Diversity of Microorganisms Among Terrestrial Ecosystems

Manisha Rani

Abstract The pedosphere is the outer layer of the earth and is a big habitat for different types of flora and fauna. The microbial biodiversity is not only complex in their physiological aspects, but their behaviour and efficiency to regulate all bio-geochemical cycles are also typical in a particular site. The interaction of all kind of microflora and microfauna with plant roots and other meso- and macroflora and meso- and macrofauna makes the pedosphere a hub for the most suitable habitat for all forms of biodiversity. This huge bioreserve of pedosphere is comprised by bacteria and *Archaea*, fungi, protists and many more eukaryotes, such as nematodes, oribatid, mites, centipedes and millipedes, enchytraeids, tardigrades, springtails, ants, ground beetles and earthworms. Soil biota, especially the microforms, is responsible to create life dynamics in pedosphere. Most of them are involved in beneficial plant growth-promoting activity and play important role to maintain the food web. As per the weight of microbial carbon per gram of the soil bacteria contributed with highest numbers of about 1 billion, actinomycetes are several hundred million, fungi are 10–20 million, algae are 10,000 to 3 million, protozoa cells are up to 1 million, and nematodes are 50 or more. The present chapter provides an insight about the microbial biodiversity of the pedosphere which makes it a lining and dynamic system to sustain life.

Keywords Pedosphere · Soil biota · Microflora · Microfauna · Microbial biodiversity

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B. Giri et al. (eds.), *Structure and Functions of Pedosphere*,
https://doi.org/10.1007/978-981-16-8770-9_4

4.1 Introduction

Pedosphere (from Greek words pedon, soil, and sphaira, ball) is the soil cover of the Earth, similar to other terrestrial envelopes, i.e. the geospheres, the lithosphere, the hydrosphere and the atmosphere (Dobrovolsky 2008). The Russian scientist Yarilov (1905) was the first, who used the term pedosphere in his book *Pedology as Independent Natural-Scientific Discipline About the Earth*. The pedosphere can also be considered as the skin or cover of the earth, i.e. geoderma, consisting of soil horizons and all other abiotic and biotic components which are diverse by their properties and composition. The diverse qualities of the soils are the result of century-old weathering effect of the solar heat, the climatic elements, and flora and fauna upon surface layers of the land and rocks. This concept was first developed in 1883 by a Russian scientist Vasilii V. Dokuchaev (1846–1903), in his well-known book *Russian Chernozem*. He is also considered as the "Father of Soil Science". He explained soils as "fully independent natural-historic bodies, which are a result of extremely complicated interaction between (of) local climate, vegetable and animal organisms, composition and structure of parent rocks, relief of terrain, and, at last, an age of the country" (Dokuchaev 1949). The term soil is often used interchangeably with pedosphere and can considered a habitat where lithosphere, atmosphere, hydrosphere and the biosphere interact (Brady and Weil 2002).

The earth's mantle, i.e. pedosphere, is a true representative of all regional specifications and reflecting influences of bio-climatic and litho-geomorphologic changes over time. Soil can perform seven different functions; the following are some especially relevant for ecological aspect:

- Acting as a unique habitat for biodiversity
- Acting as a nutrient bin and foot hold for plant
- Providing a platform for all bio-geo-chemical cycles to maintain fertility and detoxification of soil system

The soil constituents are categorized into four major components: minerals, water, air and organic matter. In general conditions, their percentage by volume is depicted in Fig. 4.1, but it varies tremendously in different sites. As water and air are found in pore space, the ratio of air-filled pore space to water-filled pore space varies with seasonal changes and cultural practices for the particular location. The mineral matter is identical for a location, but the organic matter depends on interaction of all bio-geo-chemical characteristics with other three components, i.e. water, air and mineral matter. The soil organic matter consists of dead and decaying residues and living macro- and microfauna and macro- and microflora (Fig. 4.2). All the pedospheric functions related to nutrient cycling and detoxification are actually a reflection of activity of soil life or soil biota. The soil food web represents the dynamics of soil system. Soil organisms inhabiting the soil and their size may vary from microscopic range to small mammals, which depend on other soil organisms for their life. Soil biota is the life force of soil. More living organisms occur in soil than in all other ecosystems combined.

Fig. 4.1 Components of soil by volume (%)

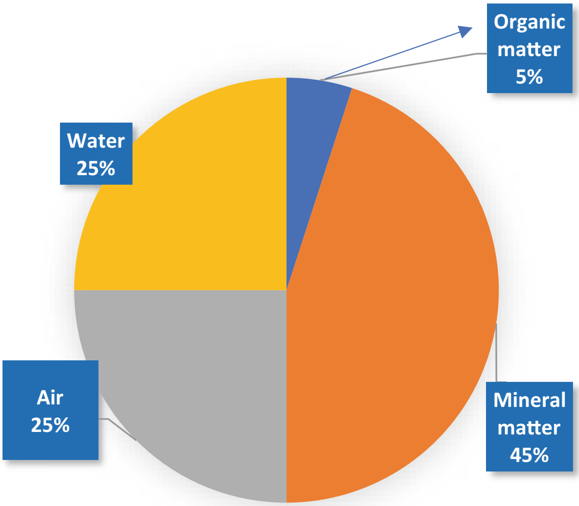
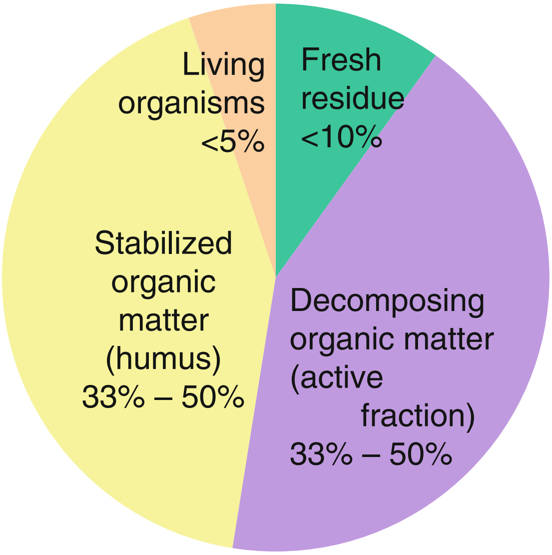


Fig. 4.2 Composition of soil organic matter



There may be over one million different types of organisms living in pedosphere. It is a main reservoir of biodiversity (Bardgett and Van der Putten 2014). This huge reservoir is comprised of bacteria and *Archaea*, fungi, protists and many more eukaryotes, such as nematodes, oribatid mites, centipedes and millipedes, enchytraeids, tardigrades, springtails, ants, ground beetles and earthworms (Coleman and Whitman 2005; Zheng et al. 2013; Fierer 2017). Soil is the reservoir of a huge diversity of living forms (Lavelle and Spain 2002; Bardgett 2005). Most of

Table 4.1 Soil biota involvement in different pedospheric processes

Processes under pedosphere	Examples of related soil biota
C cycling	Microbial biomass, methanogens
Decomposition of organic matter	Microarthropods, saprotrophic fungi
N cycling	Nitrifiers, denitrifiers
P cycling	Phosphatase, mycorrhiza
S cycling	S-reducing bacteria
Bio-aggregation of soil	Soil fungi, worms
Degradation/immobilization of pollutants	Fungi, worms
Bioturbation	Earthworms, ants

them are involved in beneficial plant growth-promoting activity and play an important role to maintain the food web.

As per the weight of microbial carbon per gram of the soil bacteria contributed with highest numbers of about 1 billion, actinomycetes are several hundred million, fungi are 10–20 million, algae are 10,000–3 million, protozoa cells are up to 1 million, and nematodes are 50 or more. Arthropods can number up to 100 per square foot, and earthworms from 5 to 30 per square foot. However, some species of bacteria, fungi, insects and nematode may cause diseases in plants and also feed on beneficial microbial population. Diverse populations of soil microorganisms maintain a system of checks and balances that maintain bio-chemical cycling and natural system of disease management in pedosphere.

All beneficial microorganisms (like fungus, *Trichoderma*, and bacterium, *Pseudomonas fluorescens*) colonize plant roots and protect them from disease-causing organisms. Some of these organisms are isolated nowadays from soil to sell commercially as biological control agents. In agriculture field several microbial communities are very specific about their function like nitrogen-fixing bacteria. Some examples of such specific functions are given in Table 4.1.

Activity of soil biota contributes to maintain soil quality and health, hence controlling and regulating several key processes. The number of colonies and their efficiency to play their typical role depend upon natural and anthropogenic disturbances (De Luca et al. 2002) and land use changes (Grunzweig et al. 2004), across multiple time scales. The supportive microclimatic habitat created by the interaction of physical and chemical properties of pedosphere helps to evolve complex bacterial populations (Ranjard and Richaume 2001).

4.2 Soil Biota

The microflora and microfauna are very smaller in size, i.e. <200 μm. Microflora are classified in the kingdom Protista, which lack the ability to form distinct tissue or organs for performing specific functions and include bacteria, actinomycetes, fungi and algae. Fauna are classified in the kingdom Animalia and include such diverse organisms as protozoa, nematodes, mites, collembola, arthropods, earthworms, beetles, ants and termites. Fauna can be further divided by size of body into microfauna, mesofauna, and macrofauna (Gilyarov 1949; Swift et al. 1998).

The major soil microflora and microfauna groups are classified as follows:

1. Soil flora—subdivided into:
    a. Microflora: size range 1–100 μm, e.g. bacteria, actinomycetes, fungi and algae
    b. Macroflora: size range 20 mm upwards, e.g. roots of higher plants
2. Soil fauna—subdivided into:
    a. Megafauna: size range 20 mm upwards, e.g. moles, rabbits, and rodents
    b. Macrofauna: (>10 mm length, >2 mm width), e.g. woodlice, earthworm, beetles, centipedes, slugs, snails and ants
    c. Mesofauna: (0.2–10 mm length, 0.1–2 mm width), e.g. tardigrades, mites and springtails
    d. Microfauna: (<0.2 mm length, <0.1 mm width), e.g. protozoa (Swift et al. 1998)

The soil biota belongs to the following kingdoms of taxonomy:

- Plantae—plants
- Animalia—rodents, worms, insects, nematodes and arthropods
- Fungi—moulds, mushrooms, mycorrhizae
- Protista—ciliates, protozoa, amoebae
- Monera—bacteria, actinomycetes

4.2.1 Bacteria

Bacteria are basically single-celled prokaryotic microbes that are so abundant that a pinch of soil contains millions of it. Bacteria vary widely in shape and size. The numbers, types and biomass are specific for place to place, and within the same soil profile, their distribution depends upon soil physical and chemical properties and seasonal variations. The pedospheric soil biota needs organic carbon to build their cells. The soil bacteria could be classified based on the energy and C sources that they use to complete their life cycle (Table 4.2).

Chemoheterotrophs obtain the organic carbon by converting carbon dioxide (CO_2) to organic compounds with either light energy (photoautotrophs) or chemical

Table 4.2 Grouping of organisms according to energy and C sources

	Carbon source	
Energy source	Autotrophs (fix CO_2)	Heterotrophs (utilize organic C)
Light (photo-)	Photoautotrophs	Photoheterotrophs
Chemical (chemo-)	Chemoautotrophs	Chemoheterotrophs

Table 4.3 Classification of bacteria based on shape

Shape of bacterial cell	Shape
1. Cocci	Unicellular, spherical, elliptical shape, oval cells
2. Bacilli	Rod-shaped or cylindrical cells
3. Vibrio	Curved and comma-shaped rods
4. Spirilla	Rigid spiral forms

energy (chemoautotrophs). Photoheterotrophs utilize organic carbon to conduct photosynthesis, so they are able to utilize organic and inorganic forms of C (e.g. green and purple bacteria). Chemoautotrophs utilize energy which is released through the oxidation of inorganic compounds. As per their ability to work in presence of oxygen (aerobes) or in absence of oxygen (anaerobes), bacteria can also be classified (Sachidanand et al. 2019). Obligate aerobes require oxygen to live (*Pseudomonas*), facultative anaerobes can grow in the absence of oxygen but can also use oxygen (*E. coli*, *Staphylococcus*), obligate anaerobes are unable to survive in the presence of oxygen (*Clostridium*), aerotolerant anaerobes tolerate presence of oxygen but cannot use oxygen (*Lactobacillus*), and microaerophiles require only low concentration of oxygen (*Campylobacter*).

Soil pH is also a key role player for bacterial growth (Shiba 1989; Yurkov and Beatty 1998). Acidophiles grow best at an acidic pH (*Thiobacillus thiooxidans*, *Thiobacillus ferrooxidans*, *Thermoplasma*, *Sulfolobus*), alkaliphiles grow best at an alkaline pH (*Vibrio cholerae*), and neutrophiles grow at neutral pH (*E. coli*). Bacteria can also be classified based on their tolerance for salt concentration. Halophiles survive in presence of moderate to large salt concentrations (*Archaebacteria*, *Halobacterium*, *Halococcus*), extreme or obligate halophiles require comparatively very high salt concentrations to survive (Bacteria in Dead Sea), and facultative halophiles can tolerate up to 2% salt concentration or more. Further bacterial cells are also divided based on the presence of flagella (atrichous, monotrichous, lophotrichous, amphitrichous, and peritrichous) and based on spore formation or non-spore formation characteristics (Trivedi et al. 2010).

Another classification of bacteria is based on their morphology and differential staining properties, i.e. (1) Gram positive and (2) Gram negative. classified them by shape (Table 4.3). (Soule, 1932)

Besides the above four major shapes, actinomycetes are branching filamentous bacteria, and mycoplasmas do not possess a stable morphology. Bacteria can be classified into the following major types based on their temperature response:

The area around the root which is inhabited by different microorganisms is named as rhizosphere. This term was first used by the German agronomist and plant physiologist Lorenz Hiltner (1904). All those beneficial bacteria which habitat the rhizosphere are named as plant growth -promoting rhizobacteria (PGPR). Somers et al. (2004) classified PGPR based on their functional activities as:

a. Biofertilizers—involve in nutrient cycling
b. Phyto-stimulators—release some chemicals which promote growth
c. Rhizoremediators—involve in detoxification of pollutants

Antoun and Prevost (2005) suggested one more group which acts as biopesticides, which control diseases by production of such antibiotic or antifungal metabolites. It has been proven by several studies that a single PGPR can perform multiple roles in rhizosphere (Kloepper 2003). Those PGPR may present in rhizosphere on the root surface (extracellular PGPR-ePGPR) and in the spaces between cells of the root cortex and intracellular (iPGPR), generally in nodular structures (Figueiredo et al. 2011). Some examples of ePGPR are Agrobacterium, Arthrobacter, *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Erwinia*, *Flavobacterium*, *Micrococcous*, *Pseudomonas* and *Serratia*. Similarly, some examples of the iPGPR are *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium* and *Rhizobium* of the family Rhizobiaceae (Bhattacharyya and Jha 2012). Moreover, numerous actinomycetes are also one of the major components of rhizosphere microbial communities displaying marvellous plant growth beneficial traits. It was observed that *Micromonospora* sp., *Streptomyces* sp., *Streptosporangium* sp. and *Thermobifida* sp. have potential to fight against different root fungal pathogens as biocontrol agents (Bhattacharyya and Jha 2012).

Bacteria primarily act as decomposing agents and usually break down complex organic material. By doing this, the bacteria release nutrients that other organisms could not access. This ability to convert non-available form of any nutrient to available form is an integral role for nutrient cycling.

Some of the ubiquitous and dominant phylotypes included *Alphaproteobacteria* (*Bradyrhizobium* sp., *Sphingomonas* sp., *Rhodoplanes* sp., *Devosia* sp., and *Kaistobacter* sp.), *Betaproteobacteria* (*Methylibium* sp. and *Ramlibacter*), *Actinobacteria* (*Streptomyces* sp., *Salinbacterium* sp. and *Mycobacterium* sp.), *Acidobacteria* (*Candidatus* sp., and *Salibacter*) and *Planctomycetes* (Paolo 2020).

Some common pedospheric bacteria are the species of *Pseudomonas*, *Arthrobacter*, *Achromobacter*, *Bacillus*, *Clostridium*, *Micrococcus*, *Flavobacterium*, *Azotobacter*, *Chromobacterium* and *Mycobacterium*. Chemosynthetic autotrophic bacteria present in the soil are the species of *Thiobacillus*, *Ferrobacillus*, *Nitrosomonas* and *Nitrobacter*. Major functional role of bacteria includes N fixers, nitrifiers, denitrifiers, decomposer and pathogen. *Azotobacter chroococcum*, *Azospirillum brasilense*, *Agrobacterium radiobacter*, *Gluconobacter diazotrophicus*, *Bacillus polymyxa*, *Flavobacterium* and *Herbaspirillum* are common groups which participate in nitrogen fixation.

4.2.2 Actinomycetes

Actinomycetes are the most widely distributed group of microorganisms in nature which primarily inhabit the soil (Oskay et al. 2004), and they have beneficial roles in soil nutrient cycling and agricultural productivity (Elliot and Lynch 1995). Actinomycetes are aerobic, spore-forming, Gram-positive organisms belonging to the order *Actinomycetales* characterized with substrate and aerial mycelium growth. They form thread-like filaments or hyphae in the soil. The delicate mycelia often grow in all directions from a central point and produce an appearance that has been compared with the rays of sun or of a star. Therefore, the *Actinomycetes* are also called 'ray fungi'. *Actinomycetes* are often considered as the evolutionary link between fungi and bacteria, but major characteristics of the *Actinomycetes* are more similar to bacteria than fungi (Sapkota et al. 2020). Activity of *Actinomycetes* is the main reason for characteristic smell of soil after rain or after ploughing. They have also been the source of a number of significant therapeutic medicines. They are responsible for decomposition of complex organic compounds and pollutants. Actinomycetes are among the group of organisms which lead to the bioremediation of soils (Imada 2005). *Actinomycetes* play a lead role for formation of stable humus and stabilization of compost piles and interact with other soil microorganisms to fasten the rate of breaking down the complex plant residues such as cellulose and animal residues to maintain the biotic equilibrium of soil (Bhatti et al. 2017). Species of *Streptomyces*, *Micromonospora* and *Nocardia* are common in the pedosphere.

4.2.3 Fungi

There are at least 100,000 different species of fungi have been identified, but it is estimated that there may be about 3.8 million species worldwide (Blackwell 2011; Hawksworth and Lücking 2017). There are four major groups of soil fungus: *Zygomycota*, *Ascomycota*, *Basidiomycota* and *Deuteromycota*. Zygomycota are less than 1000 species and are mostly common bread moulds. Ascomycetes have about 30,000 species and are mostly yeasts used in baking. Basidiomycetes include most mushrooms, toadstools and puffballs, while *Deuteromycota* include the lichens and the mycorrhizal fungus (Lavelle and Spain 2005).

Fungi can be microscopic, like yeasts, or they can form a very large fruiting body. For example, the record of biggest single organism was awarded to *Armillaria ostoyae* hyphae, which inhabited an area of 880 hectares in the state of Oregon in the USA (Zhang 2017). Fungi are heterotrophs as they receive carbon source originates from the decomposition of organic compounds or residues (Sylvia et al. 2005). Ascomycetes fungi are microscopic in size and dominate in agricultural soils and grassland, while the Basidiomycetes have large fruiting bodies or mushrooms that dominate in high residue and forested soil (Dick 2009). They are aerobic and widely distributed in pedosphere in almost every range of soil pH and temperature (Frąc et al. 2015). They prefer low pH for growth in an undisturbed soil (Lavelle and Spain 2002). Many species of pedospheric fungi have the ability to act as an effective biosorbent of toxic metals such as cadmium, copper, mercury, lead and zinc, by accumulating them in their fruiting bodies. Though these elements may inhibit their growth and affect their reproduction (Baldrian 2003).

Soil fungi can be classified into three functional groups based on their role in ecological balance including (1) biological controllers, (2) ecosystem regulators and (3) species participating in organic matter decomposition and compound transformations (Swift 2005; Gardi et al. 2013). The first group of fungi which act as biological controllers are pathogens or parasites and cause reduced production or death when they colonize roots and other organisms. Root pathogenic fungi, such as *Verticillium*, *Pythium* and *Rhizoctonia*, cause major economic losses in agriculture. Biological controllers can regulate diseases, pests and the growth of other organisms (Bagyaraj and Ashwin 2017), for example, *Glomus* sp. or *Trichoderma* sp. suppressing fungal pathogens (Dawidziuk et al. 2016). Species of *Trichoderma* (*T. asperellum*, *T. atroviride*, *T. harzianum*, *T. virens* and *T. viride*) are frequently used in biocontrol and are known as biostimulants for horticultural crops (López-Bucio et al. 2015). Nematode-trapping fungi that parasitize disease-causing nematodes and fungi that feed on insects may be useful as biocontrol agents. The major groups of soil-borne root pathogenic fungi and oomycetes constitute the genera *Fusarium* (Michielse and Rep 2009), *Verticillium* (Klosterman et al. 2009), *Rhizoctonia* (Gonzalez et al. 2011), *Pythium, Phytophthora* (Van West et al. 2003) and many others, of global and local importance.

The second group of fungi which act as the ecosystem regulators are responsible for creating more suitable habitat in pedosphere for all beneficial soil microbial population which are involved in regulating the dynamics of physiological processes in the soil environment. Fungi have a mutual relationship with plants, which is called a mycorrhizae network (Magdoff et al. 2000). They also help to improve soil physical characteristics, like soil structure development and soil porosity. The fungi can be thought of as the “threads” of the soil fabric. The fungal hyphae bound soil particles and roots to create a network which stabilizes aggregates and is also helpful to decompose complex compounds and then reabsorb (Žifčáková et al. 2016). The mutual and pathogenic relationship of fungal populations with the diverse flora and fauna community can influence nutrient availability and cycling (Wardle 2002; Wagg et al. 2014; Hannula and Van Veen 2016). Certain fungi can assist plants to extract phosphorus from the mineral pool like *Penicillium radicum* and *Penicillium bilaiae*, which can be inoculated to seeds.

The third major group of fungi which are involved in facilitating plants to acquire nutrients from soil and make them available in the pedosphere belong to Arbuscular mycorrhizal fungi (AMF). These organisms act as soil structure builders as the specific types of chemicals in the soil (Rillig and Mummey 2006) and establish symbiotic relationship with plant roots, thereby enhancing water retention and improving uptake of nutrients in soil system (Farzaneh et al. 2011). Inoculation with AMF respond to significant increase in the yield of crop plants as observed in numerous experiments (Bagyaraj et al. 2015; Bagyaraj and Ashwin 2017). Decomposers are also called saprophytic fungi which decompose cellulose and lignin in the soil. Sugar fungi called *Zygomycetes* decompose the simple sugars, but most fungi decompose the more complex or hard-to-decompose organic residues which are high in cellulose, hemicellulose, lignin, etc. Some of the by-products of this decomposition may turn to humus and remain in the soil for thousands of years (Lavelle and Spain 2005; Lowenfels and Lewis 2006; Ingham 2009).

Moreover, fungi participate in nitrogen fixation, uptake of nutrients, hormone production, biological control against root pathogens and protection against drought (Bagyaraj and Ashwin 2017). They also play an important role in the stabilization of soil organic matter and decomposition of residues (Treseder and Lennon 2015). The fungal diversity is among the key role player to support plant biodiversity, ecosystem variability and productivity (Van der Heijden et al. 2008; Wagg et al. 2014 Schulz-Bohm et al. 2017). Some important pedosphere-inhabiting microfungi are the species of *Aspergillus*, *Botrytis*, *Cephalosporium*, *Penicillium*, *Aspergillus niger*, *A. candidus*, *A. fumigatus*, *Pestalotiopsis disseminate*, *Cladosporium*, *Dematium*, *Monilia*, *Fusarium*, *Verticillium*, *Mucor*, *Rhizopus*, *Pythium*, *Cunninghamella*, *Chaetomium* and *Rhizoctonia*.

4.2.4 Protists

The term “Protista” is derived from the Greek word “protistos”, meaning *the very first*. Soils have higher protist diversity than aquatic ecosystems, but this diversity is still mostly unknown (Mahé et al. 2017). A protist is any single-celled eukaryotic organism but not an animal, plant or fungus. Soil protists include amoeba, ciliates and flagellates. Protists also include primary producers, decomposers, animal parasites and plant pathogens (Geisen et al. 2020). Based on their size, protists can be smaller than many bacteria (picoeukaryotic) (Staay et al. 2001; Caron et al. 2009; Not et al. 2009) or can form the largest single-celled organisms on the planet and several metres large multicellular brown algae (kelps). Protists also include flexible-bodied “naked amoeboid” or armoured forms (e.g. diatoms, testate amoebae). Many protists live as mutualistic or parasitic relationship with animals, plants, fungi and other protists or host ecto- and/or endosymbiotic prokaryotes (De Vargas et al. 2015). Their numbers can exceed hundreds of thousands of individuals in 1 gram of soil (Finlay 2002; Geisen et al. 2014).

As per the ecological versatility, protists can be grouped into four groups based on their feeding behaviour (Geisen et al. 2020):

a. Unicellular phagotrophs feeding on bacteria or on fungi, hence can control rate of growth of bacterial population in soil (Geisen et al. 2018).
b. Some protists live in symbiosis, parasitism, commensalism and mutualism, with fungi, other protists, plants and animals.
c. Some soil protists, such as oomycetes, can participate in organic matter degradation (saprotrophs).
d. Some soil protists contain chlorophyll (algae) and can be phototrophic or mixotrophic (Geisen et al. 2018). All functional groups of soil protists provide key roles for nutrient cycling in soils.

4.2.5 Algae

The term algae was first introduced by Linnaeus (1753), meaning the seaweeds (Latin). The algae are diverse in habitat, size, organization, physiology, biochemistry and reproduction. Basically, they are microscopic free-living or symbiotic autotrophs. Algae, more correctly named *photoautotrophic* protists, were divided into taxa based on their accessory photosynthetic pigments. Most photoautotrophic soil protists are found within the eukaryotic supergroups Stramenopiles (Diatoms, Eustigmatophyceae and Xanthophyceae (Zancan et al. 2006)) and Archaeplastidae (Chlorophyceae and Trebouxiophyceae (Zancan et al. 2006; Seppey et al. 2017). Therefore, algae, as a whole, are highly polyphyletic. Traditionally, soil algae have two major groups, one photoautotrophic prokaryotes (cyanobacteria, blue-green algae) and photoautotrophic protists (eukaryotic algae). There are about 170 genera, 1000 species of eukaryotic algae (Ettl and Gärtner 2014) and about 500 species of cyanobacteria (Pankratova 2006) found in the pedopshere. The soils of temperate zones may carry about 500 kg/ha algal biomass (Shtina and Gollerbach 1976). The algal flora of the pedosphere includes members of the Cyanochloronta, Chlorophycophyta, Euglenophycophyta, Chrysophycophyta and Rhodophycophyta. Microalgae constitute the basis of soil food webs, as they are photoautotrophs and play a key role in soil development (Zenova et al. 1995; Hu et al. 2003; Rahmonov and Piątek 2007; Langhans et al. 2009; Viles 2012).

The algae that grow on the surface of the soil are known as saprophytes. Many blue-greens, on the other hand, grow under the surface of the soil and are called cryptophytes. The algae growing in the desert soil may be typified as end edaphic (living in soil), epidaphic (living on the soil surface), hypolithic (growing on the lower surface of the stones on soil), chasmolithic (living in rock fissures) and endolithic algae (which are rock penetrating). Members of family Xanthophyceae, Eustigmatophyceae and diatoms play important role in the biogeochemical cycling of soil C (Yuan et al. 2012). Algae promote nutrient release and the weathering of silicates by creating a slightly acidic environment (Hoffmann 1998). They act an accelerator agent in biodegradation of soil organic matter (Gougoulias et al. 2018) and are responsible for weathering of soil formation, especially in deserts, alpine and polar regions (Hoffmann 1998; Borchhardt et al. 2017).

Most of the early recognized microscopic algae are also known from pedosphere, e.g. *Stichococcus* (Nägeli 1849), *Chlorella* (Beijerinck 1893), *Hormidium/Klebsormidium* (Kützing 1843), *Chlamydomonas* (Ehrenberg 1833), *Coccomyxa* (Schmidle 1901), *Scenedesmus* (Meyen 1829) or *Pleurastrum/Leptosira* (Borzì 1895). The common terrestrial members are *Oscillatoria sancta*, *Vaucheria geminate*, *Fritschiella* sp., *Chlorella lichina* and *Phormidium* sp. Species of *Chlorococcum*, *Protosiphon*, *Aphanocapsa*, *Anabaena*, *Chroococcus*, *Nostoc* and *Scytonema*.

4.2.6 Protozoa

Protozoans are single-celled organisms. Historically, protozoans were called "animal" protists as they are heterotrophic and showed animal-like behaviours. They are bigger in size than bacteria (generally 5–500 μm in diameter). The protozoans can be divided into four major groups: Amoeboid protozoans have pseudopodia (false feet) which help to change their shape and in capturing and engulfing food, e.g. Amoeba. Flagellated protozoans have flagella to move or to feed. They can be free-living as well as parasitic, e.g. Euglena. Ciliated protozoans have cilia all over their body which help in movement as well as nutrition, e.g. Paramecium. And Sporozoans have a spore-like stage in their life cycle. Sporozoa live as intracellular parasites in eukaryotes, and they are dormant in the absence of host cell. Sporozoa play a major role as parasites of soil invertebrates (Geisen et al. 2015; Mahé et al. 2017).

Most protozoa eat bacteria, but one group of amoebae, the vampyrellids, eat fungi, for example, flagellates (Ekelund et al. 2001; Flavin et al. 2000), ciliates (Petz et al. 1986; Foissner 1999) and a variety of amoebae (Chakraborty and Old 1982; Mrva 2010). Smirnov et al. (2007) and co-workers reported that *Paradermamoeba levis* can be cultivated on small vannellid amoebae. Mrva (2010) also observed that *Deuteramoeba algonquinensis* needed small amoebae or flagellates for growth and *Thecamoeba* spp. has been co-cultivated on other amoebae or ciliates (Page 1977).

Amoebozoa, and a great percentage of members of Rhizaria, are amoeboid (Smirnov et al. 2007; Smirnov et al. 2011). The amoeboid lifestyle is probably used as well by soil foraminiferans (Lejzerowicz et al. 2010; Geisen et al. 2015). Many soil Rhizaria have combined morphological variability as they can possess flagella and produce pseudopodia, both which make them well suitable for foraging between soil aggregates. This group within Rhizaria includes the Glissomonads and Cercomonads, which are among the most abundant protists in soils (Geisen et al. 2014, 2015). *Cryptodifflugia operculate* interact with a range of other soil organisms, most profoundly feeding and proliferating on a range of nematodes.

Certain shell-containing amoebae are encountered mostly in the litter soil horizon (Geisen et al. 2015). Basically, they belong to three eukaryotic supergroups, the Amoebozoa (Nikolaev et al. 2005), Rhizaria (Bhattacharyya and Jha 2012; Schulz-Böhm et al. 2017) and Stramenopiles. Protozoans are helpful in maintaining equilibrium of the microbial flora in the soil. Some important protozoans present in the soil are species of *Allantion*, *Biomyxa*, *Nuclearia*, *Trinema*, *Balantiophorus*, *Colpoda*, *Gastrostyla*, *Oxytricha*, *Pleurotricha* and *Vorticella*. Some are causing disease in plants e.g. *Spongospora subterranea* is an important soil-borne pathogen.

4.2.7 Fungus-Like Protists or Slime Moulds

Slime moulds are saprophytic; that is, they feed on microorganisms like fungi, bacteria and yeasts and decompose the dead organic matter (Alexopoulos et al.

1996). The most common slime moulds encountered in the landscape and garden belong to the genera *Physarum* sp. and *Fuligo* sp. Slime moulds are mainly classified as two types: (1) acellular also called as plasmodial slime moulds (Poinar and Waggoner 1992) and (2) cellular slime moulds. The slime moulds are creeping on debris, decaying on twigs or leaves, in pedosphere, on tree canopies and moist parts on the tree, on the forest floor and in cold and dark conditions (Conover 2001). They lack chlorophyll. A few of the slime moulds are parasitic and are found in the roots of plants of Brassicaceae family. A common slime mould which forms tiny brown tufts on rotting logs is *Stemonitis*. Another form which lives in rotting logs and is often used in research is *Physarum polycephalum*, *Dictyostelium discoideum*, *D. purpureum*, *P. violaceum*, *Mucilago*, *Didymium* and *Polysphondylium* (Bonner and Lamon 2005).

4.2.8 Viruses

Soil viruses are known for their ability to transfer genes from host to host, and they may influence the ecology of soil biological communities. They are potential cause of microbial mortality. Viruses are major players in global cycles, influencing the turnover and concentration of nutrients and gases (Johns 2015). Viruses are abundant in the rhizosphere (up to 10^{10} viruses per gram as reported by Williamson et al. 2017). Several workers reported their activities play a key role for dynamic soil biogeochemistry (Williamson et al. 2017; Pratama and Van Elsas 2018; Emerson et al. 2018; Trubl et al. 2018). The majority of viruses in soils are phages that infect bacteria, archaea, protists, fungi, nematodes, annelids, arthropods, plants and burrowing animals of pedospheric ecosystem (Williamson et al. 2012).

Soils probably harbour many novel viral species that, together, may represent a large reservoir of genetic diversity. Viruses act as consumers in the food web, and as they can infect all soil biota, they have the potential to impact prey across trophic scales (Schoelz and Stewart 2018; Emerson 2019). Much of the diversity was *Narnaviridae* that may parasitize fungi or *Leviviridae*, which may infect *Proteobacteria* (Starr et al. 2019). Viral genomes have been isolated for biocontrol purpose and for self-assembling nanomaterials (Glare et al. 2012; Wen and Steinmetz 2016). Several workers also reported their use as biocontrol agents for culling invasive organisms, including fire ants and moths (Harrison et al. 2014; Valles et al. 2018). Viruses are also being investigated as biocontrol agents for devastating plant pathogens, such as *Fusarium* sp., *Rosellinia necatrix* and *Botrytis cinerea* (Zhang et al. 2014; Martínez-Álvarez et al. 2014; Osaki et al. 2016; Wang et al. 2016; Mu et al. 2018). All such novel viruses which can be used as biocontrol agents are new hope for organic cultivators as well as serve as new biotechnology tools which can contribute to advances in environmental biotechnology.

4.3 Conclusion

Soil microorganisms act both roles of components and producers of soil organic matter. Abundant soil organic carbon improves soil quality and nutrient availability and sustains soil health. Soil microorganisms may also support the reactions to reduce atmospheric greenhouse gases and help to limit the impact of greenhouse gas-induced climate change. The balance in pedospheric conditions (available carbon sources, porosity, moisture, aeration, temperature, acidity/alkalinity and available inorganic nutrients) is based on the efficiency of all soil biota, specially the microbial biomass. The soil health depends on the diversified substantial quantities of microbial biomass. The microbial community of pedosphere produces polysaccharides, mucilage or other kinds of organic compounds which have gummy properties that help to cement soil aggregates, which ultimately create a greater number of micropores to make water and air balance of living pedospheric system.

Collectively, soil microorganisms which are living in the pedosphere play an essential role to regulate all bio-geochemical cycles, which include decomposing organic matter, cycling nutrients and detoxifying the soil. Without the cycling of nutrient elements, they could not be consumed by the other organisms including plants, and this activity is essential for the continuation of life on Earth. The interaction of soil microfauna and fauna with all other three components, i.e. water, air and mineral matter, of the pedosphere creates a living system to not only sustain the plant, animal and human life but also create health dynamics of the environment. As soil or pedosphere is a habitat where the integration of lithosphere, atmosphere, hydrosphere and the biosphere occur (Brady and Weil 2002), its diverse nature helps to maintain equilibrium of all living activities in nature.

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Chapter 5
Soil Acidity: Development, Impacts, and Management

Nguyen Hue

Abstract Soil acidity is a serious problem worldwide. Its causes can be both natural and anthropogenic. Natural processes involve (a) leaching losses of base cations such as calcium (Ca^{2+}), magnesium (Mg^{2+}), and potassium (K^+) and replacing with proton (H^+) and aluminum (Al^{3+}) on the surface of soil particles wherever rainfall is substantial; (b) weathering of rock and soil minerals; (c) hydrolysis of Al^{3+}; (d) differential uptake, i.e., more cations than anions are absorbed by plants; and (e) oxidation of soil organic matter and sulfide minerals. Human-induced processes include (a) the release of SO_2 and NO_x gases into the atmosphere by fossil fuel consumption that forms acid rain and (b) the excessive use of ammonium (NH_4^+)-containing fertilizers. Soil acidity reduces crop production, forest health, and aquatic lives. The main culprits are the toxicities of Al and/or manganese (Mn) and the deficiency of Ca and to a lesser extent of Mg, phosphorus (P), and molybdenum (Mo). Aluminum toxicity usually damages the root system first, whereas Mn toxicity adversely affects above-ground plant parts. Calcium deficiency impairs cell growth and integrity causing poor crop production and quality. To manage soil acidity, liming with OH^--producing materials (e.g., $CaCO_3$, $CaMg(CO_3)_2$, or $CaSiO_3$) is traditionally employed; alternatively, materials such as gypsum, animal and green manures, or biochar, if available, could be applied for "short-term" amelioration. Selecting and growing acidity-tolerant plants are also a viable strategy in dealing with acid soils that occupy nearly 30% of the ice-free land area of the world.

Keywords Soil acidity · Aluminum toxicity · Manganese toxicity · Calcium deficiency · Lime requirement · Acid-tolerant plants

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B. Giri et al. (eds.), *Structure and Functions of Pedosphere*,
https://doi.org/10.1007/978-981-16-8770-9_5

5.1 Introduction

Soil acidity is a term describing the unique properties of soils with a pH value (1:1 in water) below 7.0, the mid-point of the pH scale (0–14). By definition, pH is the negative logarithm of the hydrogen ion or proton (H^+) activity in the soil solution. The lower the pH, the more acidic the soil. In fact, acid soils are classified into many levels from extremely acid to neutral and slightly alkaline based on their pH values (Table 5.1). About 30% of the global ice-free land is acid (Fig. 5.1). And nearly 75% of the acid soils also overlay acid subsoils (Havlin et al. 2017). Most acid soils occur in the Americas (1780 million ha), Africa (880 million ha), and Asia (690 million ha) (Sumner and Noble 2003). Acid soils are a serious constraint to food production and have adverse ecological impacts from crop failure to forest decline (Bolan et al. 2005; Sanchez 2019). Figure 5.2 illustrates this point for a highly weathered acid soil in South Africa where no crop can grow if the soil (pH 3.84) was not amended (Fig. 5.2).

Table 5.1 Different levels of acidity of a soil (adapted from Havlin et al. 2017)

Descriptive acidity levels	pH range
Extremely acid	<4.5
Very strongly acid	4.5–5.0
Strongly acid	5.1–5.5
Moderately acid	5.6–6.0
Slightly acid	6.1–6.5
Neutral	6.6–7.3
Slightly alkaline	7.4–7.8

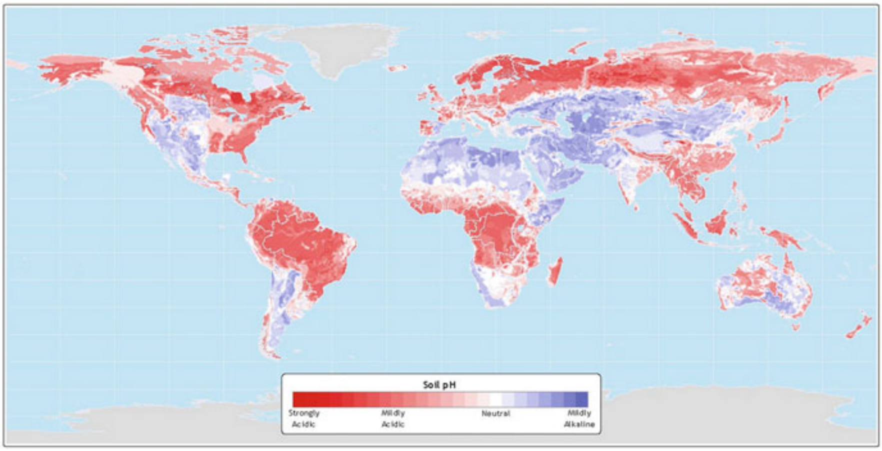


Fig. 5.1 Major acid soil regions in the world (accessed 9 March 2021). Source: https://nelson.wisc.edu/sage/data-and-models/atlas/maps/soilph/atl_soilph.jpg

Fig. 5.2 Crop response to lime on an acid soil in KwaZulu-Natal, South Africa. Source: https://commons.wikimedia.org/wiki/File:Crops_in_acid_soil_demo_2017_05_09_6748i.jpg (accessed 17 April 2021)

5.2 Development of Soil Acidity

Production of H^+ ions acidifies soils, and that process can occur naturally or anthropogenically. However, these two pathways are often interrelated and may not be clearly distinguishable (e.g., effects of SO_2 from volcano activity vs. from coal burning on the formation of acid rain).

5.2.1 *Naturally Occurring Acid Soils*

Acid soils are common in humid, tropical regions. Wherever rainfall is substantial (and often exceeds evapotranspiration), soil acidification takes place. That is because rain is naturally acidic (pH ~5.6) mainly because of atmospheric CO_2 dissolution as shown below:

$$\begin{aligned} CO_2(\text{gas}) + H_2O\ (\text{liquid}) &\rightarrow H_2CO_3(\text{aqueous}) \\ &\leftrightarrow HCO_3{}^- + H^+(\text{stands for reaction}) \end{aligned} \tag{5.1}$$

The H^+ ions (protons and sometimes written as H_3O^+ when in water) gradually displace other positively charged ions, which are held on the soil surface (called exchangeable cations) such as Ca^{2+}, Mg^{2+}, and K^+. These cations are termed base cations and are essential for plant growth. The H^+ ions become a part of the soil's solid, while an equivalent number of base cations is released into the soil solution and is subject to loss by leaching (Fig. 5.3). Proton-saturated soils are not stable and will be further weathered (transformed) to more stable minerals, eventually to oxides

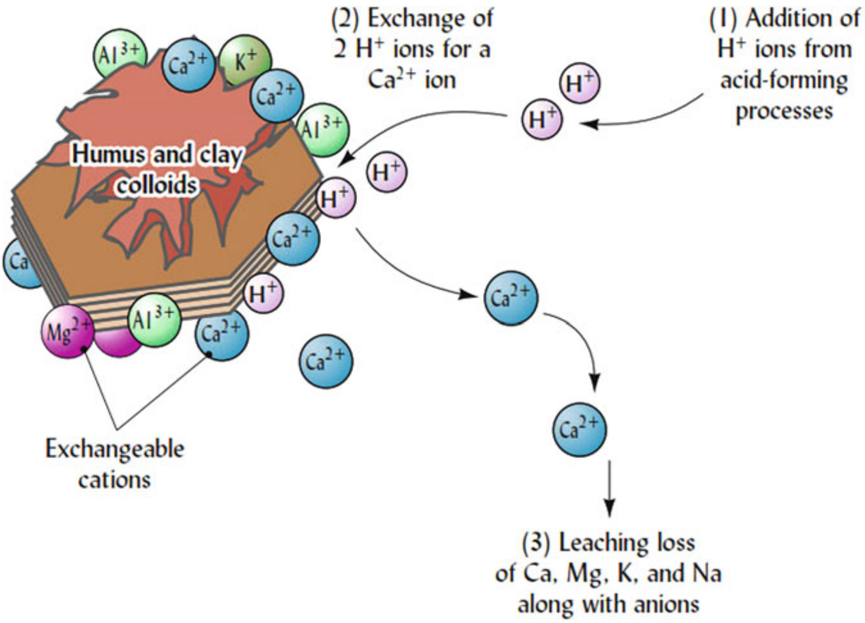


Fig. 5.3 Leaching of exchangeable cations (e.g., Ca^{2+} ion) by H^+ from acidity generating sources (adapted from Weil and Brady 2017)

and hydroxides of Al, iron (Fe), Mn, and titanium (Ti) (Robarge 2008; Strawn et al. 2020). As an example, the transformation of smectite to kaolinite and finally to gibbsite is chemically shown below (Sposito 1989).

$$\begin{aligned}&\underset{\text{(smectite)}}{Al_{0.3}[Si_{7.5}Al_{0.5}]Al_{3.6}Mg_{0.4}O_{20}(OH)_4} + 0.8H^+ + 8.2H_2O \\ &\quad\leftrightarrow 1.1\underset{\text{(kaolinite)}}{[Si_4Al_4O_{10}(OH)_8]} + 3.1Si(OH)_4 + 0.4Mg^{2+}\end{aligned} \tag{5.2}$$

$$\underset{\text{(kaolinite)}}{Si_4Al_4O_{10}(OH)_8} + 10H_2O \leftrightarrow \underset{\text{(gibbsite)}}{2Al_2(OH)_6} + 4Si(OH)_4 \tag{5.3}$$

In fact, under acidic conditions, minerals such as kaolinite or even gibbsite can be dissolved to produce soluble Al^{3+} (Robarge 2008; Hue 2008).

$$\underset{\text{(kaolinite)}}{Si_4Al_4O_{10}(OH)_8} + 12H^+ \leftrightarrow \underset{\text{(soluble Al)}}{4Al^{3+}} + 4Si(OH)_4 + 2H_2O \tag{5.4}$$

and

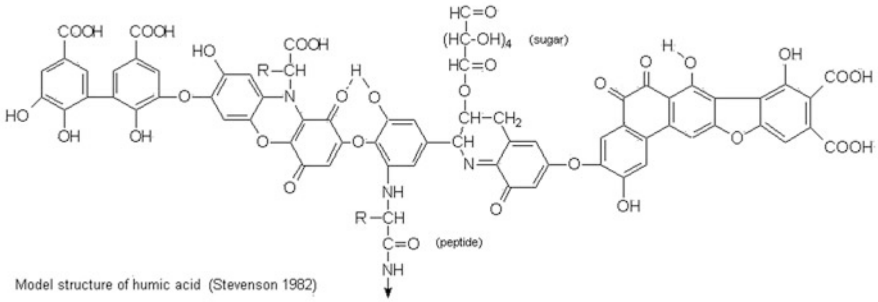


Fig. 5.4 A proposed chemical structure of humic acid (a component of SOM) (adapted from Stevenson 1982)

$$Al_2(OH)_6 + 6H^+ \leftrightarrow 2Al^{3+} + 6H_2O \tag{5.5}$$

Soluble Al^{3+}, having small crystal radius (0.5 A^0) and high charge (+3), forms a sixfold coordination (octahedral configuration) with six surrounding water molecules and undergoes further hydrolysis (splitting water molecules) as shown below for the first four reactions (McBride 1994; Robarge 2008).

$$Al(H_2O)_6{}^{3+} + H_2O \leftrightarrow Al(OH)(H_2O)_5{}^{2+} + H_3O^+ \quad K_1 = 10^{-4.97}$$
$$K \text{ is equilibrium constant)} \tag{5.6}$$

$$Al(OH)(H_2O)_5{}^{2+} + H_2O \leftrightarrow Al(OH)_2(H_2O)_4{}^{+} + H_3O^+ \quad K_2 = 10^{-4.93} \tag{5.7}$$

$$Al(OH)_2(H_2O)_4{}^{+} + H_2O \leftrightarrow Al(OH)_3(H_2O)_3{}^{0} + H_3O^+ \quad K_3 = 10^{-5.7} \tag{5.8}$$

$$Al(OH)3(H_2O)_3{}^{0} + H_2O \leftrightarrow Al(OH)_4(H_2O)_2{}^{-} + H_3O^+ \quad K_4 = 10^{-7.4} \tag{5.9}$$

Soil acidity, thus, intensifies by these hydrolytic Al species along with H_3O^+ (proton in water).

Another source of protons is the oxidation of soil organic matter (SOM). SOM is formed from microbial decomposition of forest litter and dead plant and animal tissues present in soils. Chemical structure of SOM is complex but contains many acid functional groups, such as carboxylic, phenolic, and ketonic (Stevenson 1982; see Fig. 5.4). Given the K values of these functional groups, particularly carboxylic group (R-COOH) range from 10^{-1} to 10^{-7}, SOM can deprotonate and release protons along with the corresponding conjugated organic anions which can complex metals, especially Al.

$$R\text{-}COOH \leftrightarrow R\text{-}COO^- + H^+ \quad K = 10^{-1} - 10^{-7} \tag{5.10}$$

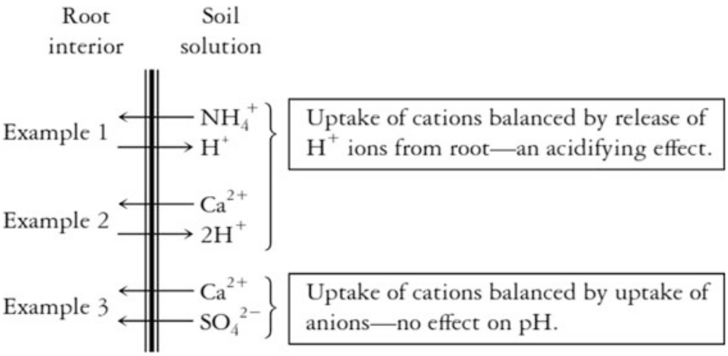


Fig. 5.5 Possible differential uptake of cations and anions by roots (adapted from Weil and Brady 2017)

Differential uptake of cations and anions by plant roots may also contribute to soil acidity. For each positive charge taken in as a cation, a root must maintain charge balance by absorbing an equivalent anion or by exuding a positive charge as a different cation (electrical neutrality must be maintained). In some plants, particularly legumes, more cations (e.g., K^+, NH_4^+, Ca^{2+}, and Mg^{2+}) are absorbed than anions (e.g., NO_3^-, SO_4^{2-}, $H_2PO_4^-$). Thus, such plants usually exude H^+ ions into the soil solution resulting in lower soil pH (Fig. 5.5).

Oxidation of elemental sulfur (S) and S-containing minerals forms sulfuric acid and releases large quantities of protons. Coastal wetland areas in Southeast Asia (e.g., Indonesia, Malaysia, Thailand, Vietnam), coastal Australia, Northern Europe (e.g., The Netherlands), West Africa, and the Southern United States (e.g., Florida, Georgia, Louisiana, the Carolinas) commonly contain soils formed from sediments having considerable quantities of sulfide minerals, such as pyrite (FeS_2) and monosulfides (Andriesse and van Mensvoort 2017). Sulfides begin to oxidize once they are exposed to an aerobic environment. Such oxidizing environment can occur by natural events (e.g., oceanic retreat or tectonic uplift) or by human activities, such as dredging or draining land for agriculture, forestry, or other developments. The principal reactions involved are (Weil and Brady 2017):

$$\begin{array}{ll} FeS_2 + 3\tfrac{1}{2}O_2 + H_2O \leftrightarrow & FeSO_4 + H_2SO_4 \\ \text{(pyrite)} & \text{(ferrous sulfate)} \end{array} \tag{5.11}$$

$$\begin{array}{ll} FeSO_4 + \tfrac{1}{2}O_2 + 1\tfrac{1}{2}H_2O \leftrightarrow & FeOOH + H_2SO_4 \\ & \text{(iron (ferric) oxyhydroxide or goethite mineral)} \end{array} \tag{5.12}$$

The resulting large quantities of H_2SO_4 lower soil pH values to below 3.5, sometimes even as low as 2.0. These S-oxidizing reactions can occur chemically, but will proceed much faster with the help of some microbes, such as *Thiobacillus ferrooxidans*.

5.2.2 Anthropogenic Sources of Acidity

Combustion of fossil fuels and the smelting of S-containing metal ores emit enormous quantities of nitrogen (N) and S-containing gases into the atmosphere (Fig. 5.6). More specifically, much of the world's coal used for energy contains approximately 2% S, half of which is FeS_2 and the remainder is organic (Blake 2005). Coal burning produces SO_2 as follows:

$$4FeS_2 + 11O_2 \leftrightarrow 2Fe_2O_3 + 8SO_2 \tag{5.13}$$

Nitric oxide (NO) and nitrogen dioxide (NO_2)—collectively called NO_x—enter the atmosphere mainly from the burning of fossil fuels in motor vehicles and stationary furnaces. The formation of NO from N_2 and O_2 occurs at high temperatures.

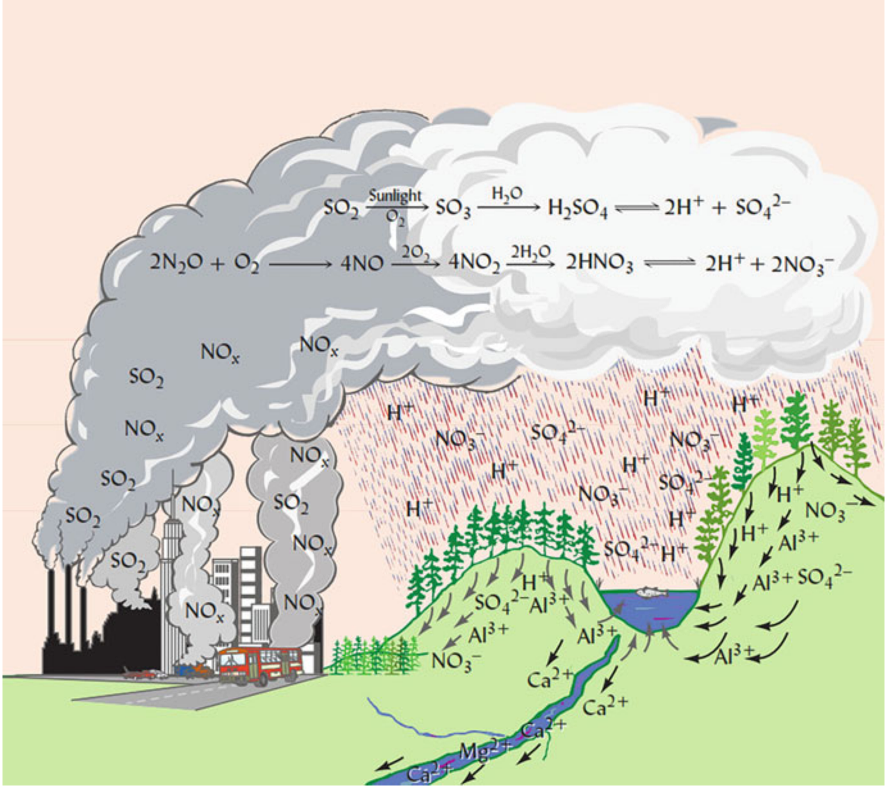


Fig. 5.6 Release of SO_2 and NO_x gases by fossil fuel burning activities (adapted from Weil and Brady 2017)

$$N_2 + O_2 \leftrightarrow 2NO, \text{and } NO + ½O_2 \leftrightarrow NO_2 \quad (5.14)$$

Once NO_x has been formed, rapid cooling of exhaust gases prevents further reaction and traps the oxides in the atmosphere (NO is also formed naturally in the atmosphere through reaction of O_2 and N_2 caused by lightning). In the presence of water vapor and O_2, NO_2 is oxidized to HNO_3 as follows:

$$2NO_2 + ½O_2 + H_2O \leftrightarrow 2HNO_3 \quad (5.15)$$

A combination of H_2SO_4 and HNO_3 in the atmosphere will form acid rain, a popular term which includes all forms of acidified precipitation: rain, snow, fog, and dry deposition. The pH of acid rain commonly is between 4.0 and 4.5 and may be as low as 2.0 (normal, clean rainwater has a pH ~5.6 due to dissolved CO_2). The serious impacts of acid rain fall on downwind areas from major industrial centers, weakly buffered lakes and streams, as well as forest (Blake 2005; Vance 2017).

Under intensive agronomic crop production, the use of ammoniacal fertilizers has considerably acidified the soils (Cao et al. 2019), even with anhydrous ammonia (NH_3). The principal reactions are:

$$NH_3 + H_2O \leftrightarrow NH_4^+ + OH^- \quad (5.16)$$

Reaction (5.16) will temporarily (2–4 weeks) raise the soil pH.

$$NH_4^+ + 2O_2 \leftrightarrow NO_3^- + H_2O + 2H^+ (\text{nitrification process}) \quad (5.17)$$

Net reaction ((5.16) + (5.17)) yields

$$NH_3 + 2O_2 \leftrightarrow NO_3^- + H_2O + H^+ \quad (5.18)$$

Thus, eventually one mole of N added as NH_3 will produce one mole of H^+ as shown in (5.18).

The application of the common urea fertilizer has also undergone similar reactions after being hydrolyzed with the help of urease enzyme produced by soil microbes.

$$\underset{\text{(urea)}}{NH_2\text{-}CO\text{-}NH_2} + H_2O \leftrightarrow 2NH_3 + CO_2 \quad (5.19)$$

Elemental S added either by man or by volcanic eruption (in 2008, the Kilauea volcano in Hawaii, USA, which had been erupting continuously since 1983, released over 1000 tons/day of SO_2 gas) is also oxidized to produce strong H_2SO_4 acid.

Table 5.2 Common N and S fertilizers, their chemical reactions, and their potential acidity production

Fertilizer source	Soil reaction	Mole H^+/mole N or S
Anhydrous ammonia	$NH_3 + 2O_2 \rightarrow NO_3^- + H_2O + H^+$	1
Urea	$(NH_2)_2CO + 4O_2 \rightarrow 2NO_3^- + H_2O + CO_2 + 2H^+$	1
Ammonium nitrate	$NH_4NO_3 + 2O_2 \rightarrow 2NO_3^- + H_2O + 2H^+$	1
Ammonium sulfate	$(NH_4)_2SO_4 + 4O_2 \rightarrow 2NO_3^- + H_2O + SO_4^{2-} + 4H^+$	2
Monoammonium phosphate	$NH_4H_2PO_4 + O_2 \rightarrow NO_3^- + H_2PO_4^- + H_2O + 2H^+$	2
Elemental S	$S + 1\,½\,O_2 + H_2O \rightarrow SO_4^{2-} + 2H^+$	2
Ammonium thiosulfate	$(NH_4)_2S_2O_3 + 6O_2 \rightarrow 2SO_4^{2-} + 2NO_3^- + H_2O + 6H^+$	1.5

$$S + O_2 \leftrightarrow SO_2; SO_2 + ½O_2 + H_2O \leftrightarrow 2H^+ + SO_4^{2-} \tag{5.20}$$

Table 5.2 shows the theoretical quantity of acidity produced per unit of N or S fertilizer applied (Havlin et al. 2017).

5.3 Impacts of Soil Acidity

5.3.1 Aluminum Toxicity

The most common and severely harmful effect of soil acidity is Al toxicity to plants, microbial community, and the environment (Weil and Brady 2017; Patra et al. 2021). In acid, weathered soils of the tropics, Al in soil solution is often controlled by the solubility of gibbsite mineral ($Al_2(OH)_6$ but often written as $Al(OH)_3$). Thus, Al activity (or effective concentration) as a function of pH can be predicted by the following dissolution reaction of gibbsite and its equilibrium constant (K).

$$\begin{array}{ll} Al(OH)_3 + 3H^+ \leftrightarrow Al^{3+} + 3H_2O & K = 10^{8.04} \\ \text{(gibbsite)} & \end{array} \tag{5.21}$$

or

$$\left(Al^{3+}\right) = 10^{8.04}\left(H^+\right)^3 \tag{5.22}$$

Reaction (5.22) predicts that for each unit pH drop, Al^{3+} activity would increase by 1000-fold. In other words, in order to keep (Al^{3+}) at sub-micromolar levels, soil pH must be maintained above 5.0. This is because trivalent Al^{3+} is the most toxic Al

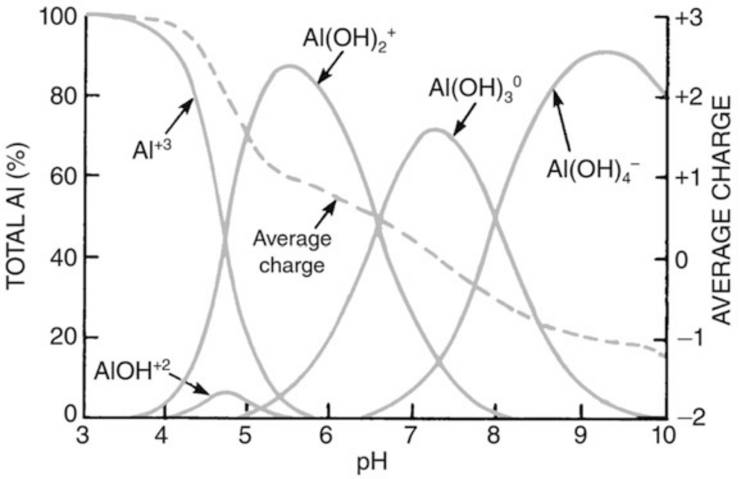


Fig. 5.7 Distribution of Aluminum (Al) hydrolytic species as a function of pH

form to plants and animals, and Al^{3+} activity as low as 1–10 μM in soil solution would damage many crops (Kamprath 1984; Kinraide et al. 2005; Parker 2005; Miyasaka et al. 2007; Hue 2011; Blamey et al. 2015).

Determination of Al^{3+} in soil solution is not an easy task because of its many hydrolytic species having variable degrees of toxicity as shown in Fig. 5.7 (and derived from Reactions (5.6)–(5.9)). Al^{3+} can also form complexes with other soil solution ions, such as fluoride (F^-), $SO_4{}^{2-}$, $H_2PO_4{}^-$, and organic anions (e.g., citrate, malate, oxalate; Hue et al. 1986). It is simpler to measure exchangeable Al (as extracted with a neutral salt such as 1M KCl) and Al saturation percentage (ratio of exchangeable Al to CEC $*$ 100). There is a strong positive correlation between soluble Al^{3+}, soil pH, and exchangeable Al (Kamprath and Smyth 2005; Smyth 2012; Sanchez 2019). Figure 5.8 from the work on an Oxisol in Puerto Rico as cited by Sanchez (2019) shows that an Al saturation percentage range of 40–60% would be toxic (yield drops by half) to most crops.

Aluminum toxicity usually damages the root system first, while the tops may look normal or may present drought stress and P or Ca deficiency. Aluminum-affected roots tend to be shortened and swollen, having a stubby appearance (Fig. 5.9). A high level of Al impairs root elongation and decreases nutrient uptake; it interferes with cell division at the root apex, increases the rigidity of the cell wall by crosslinking of pectins which usually carry negative charge, and reduces DNA replication because of increased rigidity of the double helix (Gupta et al. 2013; Eekhout et al. 2017; Bojorquez-Quintal et al. 2017).

Fig. 5.8 Crop yields as a function of soil Al saturation % (adapted from Sanchez 2019)

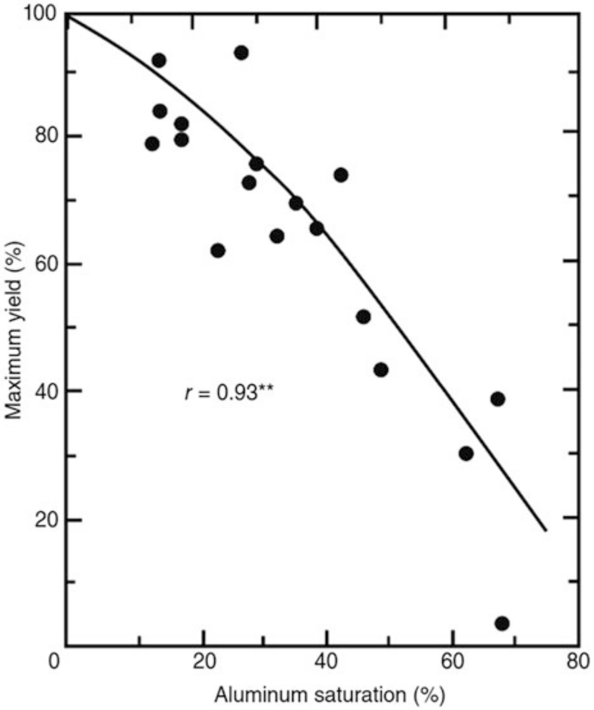
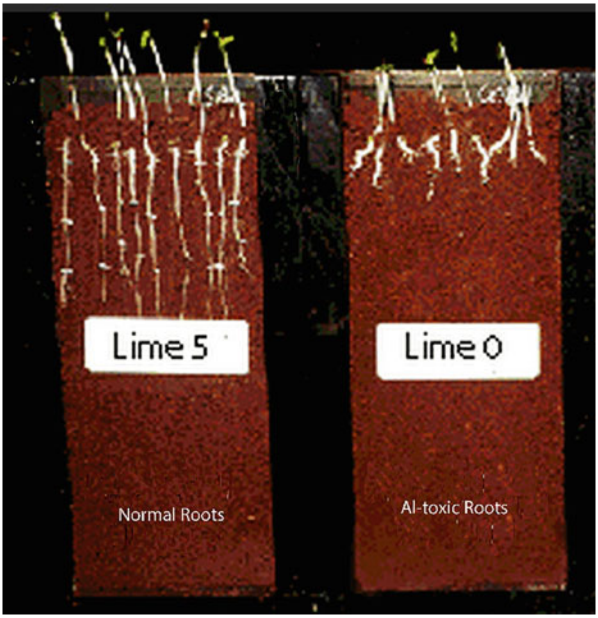


Fig. 5.9 Aluminum effect on roots. Sesbania seedlings grown in an Ultisol (non-amended pH 4.2, right; and limed pH 5.5, left) of Hawaii



5.3.2 Manganese Toxicity

Some soils in the tropics, particularly those of the Oxisol order, can contain high levels of Mn. For example, the Wahiawa series, Oxisol order, in Hawaii has 1.2–1.6% total Mn mostly as MnO_2 (Hue et al. 2001). For comparison, background levels of total Mn in world's soils average about 0.05% (500 mg/kg dry weight) (WHO 2004). Under acidic conditions and with the supply of electron (e^-) from SOM, MnO_2 will dissolve into soluble Mn^{2+} according to the reaction:

$$MnO_2 + 4H^+ + 2e^- \leftrightarrow Mn^{2+} + 2H_2O \tag{5.23}$$

Equilibrium constant of (5.23) can be expressed as:

$$K = \left(Mn^{2+}\right) / \left\{ \left(H^+\right)^4 * \left(e^-\right)^2 \right\} \tag{5.24}$$

If we assume that the system is poised, meaning log (H^+) + log(e^-) constant, which is often the case in soils (Lindsay 1979), then (5.24) becomes (Hue and Mai 2002)

$$\mathrm{Log}\left(Mn^{2+}\right) = \mathrm{constant} - 2\mathrm{pH} \tag{5.25}$$

Reaction (5.25) would predict that for every pH unit decrease, (Mn^{2+}) activity (and concentration) would increase by 100-fold. In reality, however, because soil solution may contain other inorganic and organic ions/molecules that can complex Mn^{2+} and keep more Mn^{2+} in solution regardless of pH, Mn^{2+} only increases about 10-fold for each pH unit drop as shown in Fig. 5.10.

Hue and Mai (2002) also reported that a Mn concentration of 36 µM (or 2 mg/L) in the saturated paste caused toxicity in watermelon (*Citrullus lanatus* cv. Crimson Sweet) grown on the Wahiawa Oxisol; and the corresponding soil pH was 5.7.

Unlike Al, Mn toxicity first shows up in plant tops. The symptoms vary among plant species, but often specific for a given species. For example, stunted, crinkled, and chlorotic leaves are the Mn toxicity symptoms in soybean (*Glycine max*) (Fig. 5.11a). In watermelon, Mn toxicity first appears as dark brown spots on leaves (Fig. 5.11b); then the leaf margins dry up (necrosis), and finally the entire leaf dies out and falls off just a few days after flowering (Hue et al. 1998). Also, unlike Al, the leaf tissue content of Mn usually correlates with Mn toxicity, which begins at around 200 mg/kg in sensitive plants to over 5000 mg/kg in tolerant ones. Figure 5.12 illustrates leaf Mn levels and yield of bean (*Phaseolus vulgaris*) and cabbage (*Brassica* sp.) as a function of soil pH (Weil and Brady 2017).

Manganese toxicity in plants is partially alleviated by high levels of tissue Ca, so the Mn/Ca ratio is often used to diagnose Mn toxicity in addition to the absolute Mn concentration in leaf (Hue et al. 1998; WHO 2004). High Mn, on the other hand,

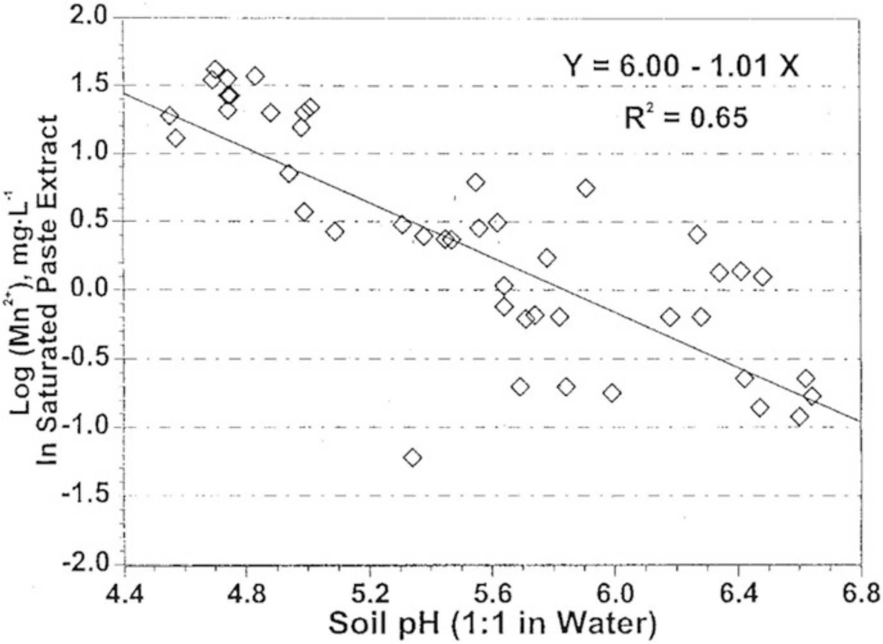


Fig. 5.10 Manganese (Mn^{2+}) concentration in the saturated paste extract of an Oxisol of Hawaii as a function of soil pH (adapted from Hue and Mai 2002)

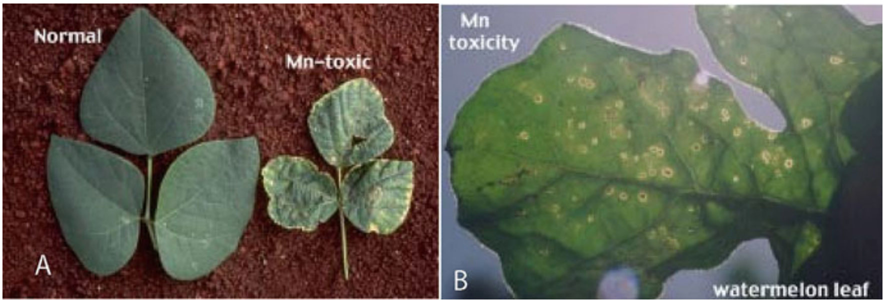


Fig. 5.11 Manganese toxicity symptoms in soybean (*Glycine max*) (**a**), and in watermelon (*Citrullus lanatus)* (**b**)

may reduce the uptake of iron (Fe); Mn toxicity is often accompanied by Fe deficiency symptoms (Mengle and Kirkby 1979; Silva et al. 2006; Eaton 2015).

At low levels, Mn is an essential nutrient because it is a co-factor of many enzymes. Decarboxylases and dehydrogenases of the tri-carboxylic cycle (TCA) are activated by Mn (Eaton 2015). At high levels, however, Mn can cause oxidative stress by over-production of reactive oxygen species and increased peroxidase activity (Horigushi and Fukumoto 1987; Martinez-Finley et al. 2013).

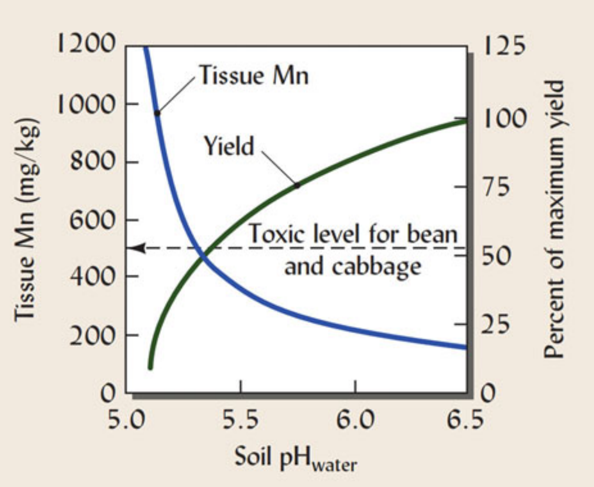


Fig. 5.12 Manganese concentration in plant tissue and relative crop yield as a function of soil pH (adapted from Weil and Brady 2017)

5.3.3 Hydrogen Ion (H^+) Toxicity

At pH levels below 4.0–4.5, H^+ ions themselves are of sufficient concentration to be toxic to some plants, mainly by damaging the root membranes (Adams 1984; Weil and Brady 2017). Such low pH, even in the absence of high Al or Mn, has been found to kill certain soil bacteria, such as *Rhizobium* bacteria which are more sensitive to low pH than their host in the nitrogen-fixation symbiosis. The nitrifying bacteria responsible for the conversion of NH_4^+ to NO_3^- perform best at soil pH >5.5 (Sanchez 2019).

Low pH (pH ~3–4) of acid rain can damage buildings, sculptures, and monuments that are constructed using weatherable materials like limestone, marble, bronze, and galvanized steel (National Science and Technology Council 2005). Agricultural soils are less impacted by acid rain (and H^+) because of their relatively higher buffering capacity than those of forests and aquatic environments (Vance 2017). In the United States, many important forest areas, such as the Adirondacks of New York and the Green Mountains of Vermont, have experienced sustained decreases in tree growth in the late 1900s (National Acid Precipitation Assessment Program 1992). Because of acid rain, base cations (e.g., Ca, Mg) in forest soils would be leached, and more Al becomes soluble. Along with NO_3^- and SO_4^{2-}, these cations end up in water bodies and adversely affect aquatic lives. In general, when water pH of streams and lakes drops below 5.0, many fish are affected and even die. Influx of H^+ and/or Al^{3+} into fish gills stimulates excessive efflux of Na^+ that can cause mortality (Bush 1997).

5.3.4 Calcium Deficiency

Although Al toxicity is often considered the central problem of soil acidity, Ca deficiency also occurs very often, especially in acid-weathered soils in the tropics (Sanchez 2019). For example, many acid soils in Hawaii are Oxisols characterized by high proportion of Fe and Al oxides and variable charges (Uehara and Gillman 1981; Fox et al. 1991). These soils have very low base cations, especially Ca. In fact, Ca deficiency is more common than Al toxicity in many acid soils of Hawaii (Hue 2008, 2011). As an example, the Kapaa series (Oxisol) on the Kauai island has only 0.7 cmol_c/kg Ca as extracted by 1M ammonium acetate pH 7.0. This value is far below the recommended exchangeable Ca level of 7.5 cmol_c/kg for optimal growth of most crops (Yost and Uchida 2000).

Since Ca is fairly immobile inside the plant, its deficiency symptoms appear first in meristematic tissues such as root tips, growing points of upper plant parts, and storage tissues (White and Broadley 2003; White 2015). In corn (*Zea mays*) and taro (*Colocasia esculenta*), Ca-deficient plants are stunted; young leaves are unable to fully unfurl, and then the leaf tips or margins soon die; in tomato (*Lycopersicon esculentum*), blossom end rot occurs in immature fruit when Ca is deficient (Fig. 5.13). In peanut (*Arachis hypogaea*), Ca deficiency adversely affect its below-ground fruit development and reduced pod yield (Adams 1984; Smyth

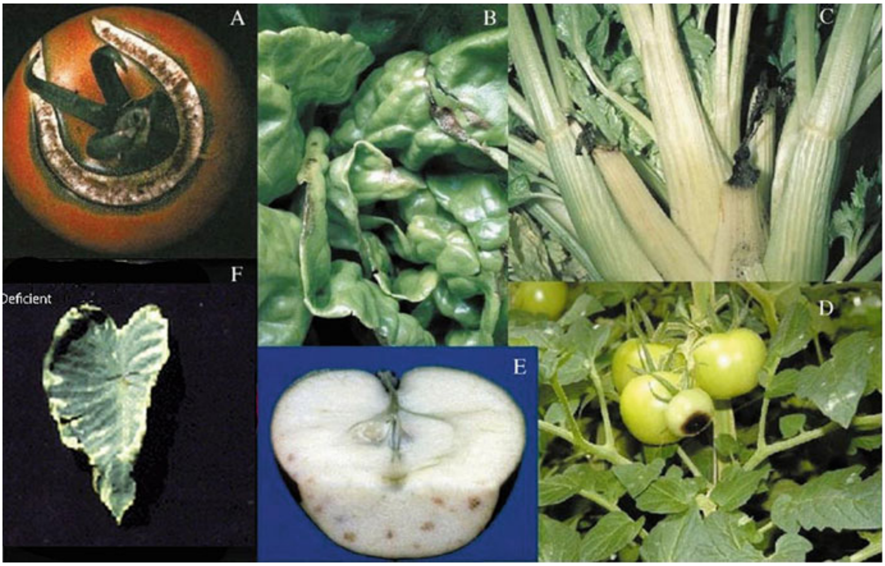


Fig. 5.13 Symptoms of Ca deficiency in some common crops: (**a**) cracking in tomato (*Lycopersicon esculentum*), (**b**) tipburn in lettuce (*Lactuca sativa*), (**c**) damaged tip in celery (*Apium graveolens*), (**d**) blossom end-rot in immature tomato fruit, (**e**) bitter pit in apples (*Malus* sp.), (**f**) necrotic leaf edge in taro (*Colocasia esculenta*). Images (**a**–**e**) are adapted from White and Broadley (2003); and (**f**) from Hue (2008)

2012). Abbas et al. (2018) reported that gypsum was required for one of the highest pod yields of peanut grown in a field in Berhampur, India, by Morita et al. (2011). They concluded that Ca was essential to the pegging and pod forming stages of peanut.

Calcium is required for cell elongation and cell division. Its deficiency impairs cell membrane permeability, causing leakage; leaf senescence and abscission are also affected by low Ca (Mengle and Kirkby 1979; White and Broadley 2003).

5.4 Management of Soil Acidity

Soil acidity can be managed by either amending the problem soils with materials that generate OH^- (liming materials) or growing plants that tolerate acidity. A combination of the two strategies would be desirable, wherever possible.

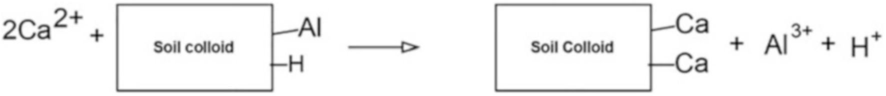
5.4.1 *Amending Acid Soils with Liming Materials*

To decrease soil acidity (and raise soil pH), the soil is usually amended with alkaline materials (lime) that provide conjugated bases of weak acids. These bases are anions, such as CO_3^{2-}, OH^-, and silicate (SiO_3^{2-}), that can react with H^+ and Al^{3+} ions to form water or precipitates in a series of steps as follows:

a. Lime is dissolved (slowly) by moisture in the soil to produce hydroxide ions (OH^-) and Ca^{2+}

$$CaCO_3 + H_2O\ (\text{moisture in soil}) \rightarrow Ca^{2+} + 2OH^- + CO_2(\text{gas}).$$

b. Newly produced Ca^{2+} will exchange with Al^{3+} and H^+ on the surface of acid soils.



c. Lime-produced OH^- will react with H^+ to form H_2O and with Al^{3+} to form solid $Al(OH)_3$:

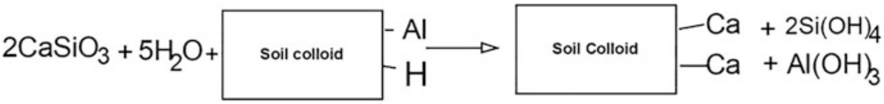
$$OH^- + H^+ \rightarrow H_2O$$

and

$$3OH^- + Al^{3+} \rightarrow Al(OH)_3(\text{solid})$$

Thus, liming eliminates toxic Al^{3+} and H^+ through the reactions with OH^-. Excess OH^- from the dissolved lime will raise the soil pH, which is the most recognizable effect of liming. Another benefit of liming is the supply of Ca^{2+} (if $CaCO_3$ is used) as well as Mg^{2+} (if dolomite [$CaMg(CO_3)_2$] is used) or even K^+ (if wood ash [K_2O, KOH, CaO, MgO] is used).

Silicates can be used as liming materials that do not contain carbon and therefore do not release CO_2 into the atmosphere when they react with acid soils. The most commonly used silicates are calcium silicate, a by-product of steel making. Calcium silicate reacts with an acid soil as follows:



Biochar is a solid material obtained from the thermochemical conversion (i.e., heating or pyrolysis) of biomass (e.g., discarded wood, crop residue, manure, biosolids, etc.) in an oxygen-limited environment (IBI 2012). Depending on the feedstock and the treatment process, most biochars have high surface area and contain many reactive surface functional acid groups, such as carboxylic and phenolic, that can complex Al, Mn, and Ca. The ash portion of biochar is composed mostly of K_2O, CaO, $CaCO_3$, and MgO, resulting in its alkaline pH (Hue 2020; Masud et al. 2020). Biochar application rates often are many tons (commonly 5–20 tons/ha) per hectare on average. Thus, biochar can be used as a liming material that effectively neutralizes all exchangeable Al in acid soils. An example of biochar use as a liming material on an acid Ultisol of Hawaii is shown in Fig. 5.14.

Commonly used liming materials and their relative neutralizing values are given in Table 5.3. The neutralizing value, or calcium carbonate equivalent (CCE), is defined as the amount of acid a given quantity of the lime will neutralize when it is totally dissolved. The relative neutralizing value is calculated as a percentage of the neutralizing power of pure $CaCO_3$, which is given a value of 100.

Because most liming materials dissolve slowly, they should be finely ground to increase their reactive surface for effective reactions with soil acidity components. Lime fineness is measured by using sieves with different mesh sizes. The standard mesh size numbers indicate the number of wires per inch. Thus, higher mesh size numbers signify smaller holes, which limit passage to finer particles. Note that 20–30 mesh lime is not as effective in raising soil pH as the finer lime (Fig. 5.15). Also, it seems that lime particles of 50–100 mesh size would be adequately effective in neutralizing soil acidity. Finer sizes (<100 mesh) would waste money (and harder

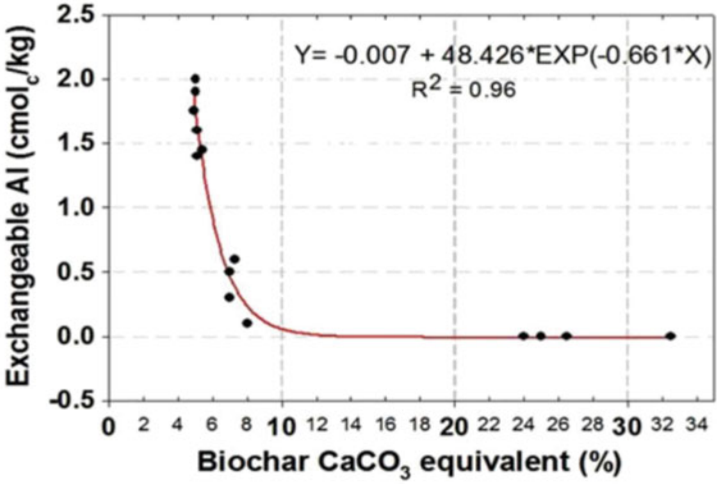


Fig. 5.14 Exchangeable Al of Hawaii's acid Ultisol as a function of biochar's acid neutralizing capacity (adapted from Berek and Hue 2016)

Table 5.3 Common liming materials, their chemical names and formulas, and relative neutralizing values (modified version of Weil and Brady 2017)

Liming material	Chemical name and formula	Relative neutralizing value
Calcitic limestone	Calcium carbonate, $CaCO_3$	100
Quick lime	Calcium oxide, CaO	150–175
Hydrated lime	Calcium hydroxide, $Ca(OH)_2$	120–135
Dolomitic lime	Calcium-magnesium carbonate, $CaMg(CO_3)_2$	95–108
Basic slag	Calcium silicate, $CaSiO_3$	70–90
Wood ashes	Mixture of oxides, CaO, MgO, K_2O, KOH	40–80
Biochar	Burned biomass, black carbon	5–30

to spread), whereas coarser grades may not react quickly enough. Furthermore, the full effect of liming might not be realized until several months after application.

In brief, the capacity to neutralize soil acidity depends on both the CCE and the particle size of the liming materials. Sometimes the two factors are combined and called the effective calcium carbonate equivalent (ECCE).

5.4.2 *Lime Requirements of Acid Soils*

5.4.2.1 Titration Curves with Commercially Available $CaCO_3$ Materials

The amount of lime required to raise soil pH from the initial value to a desired value can be accurately and specifically determined by this method as follows. Various

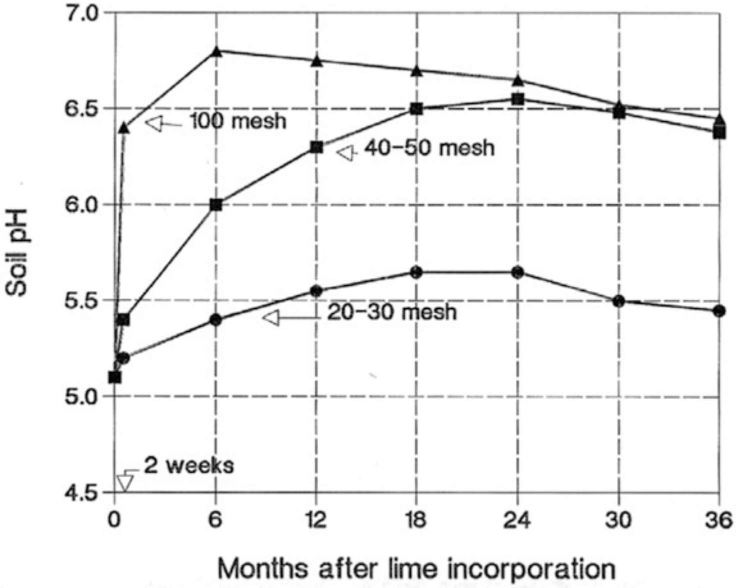


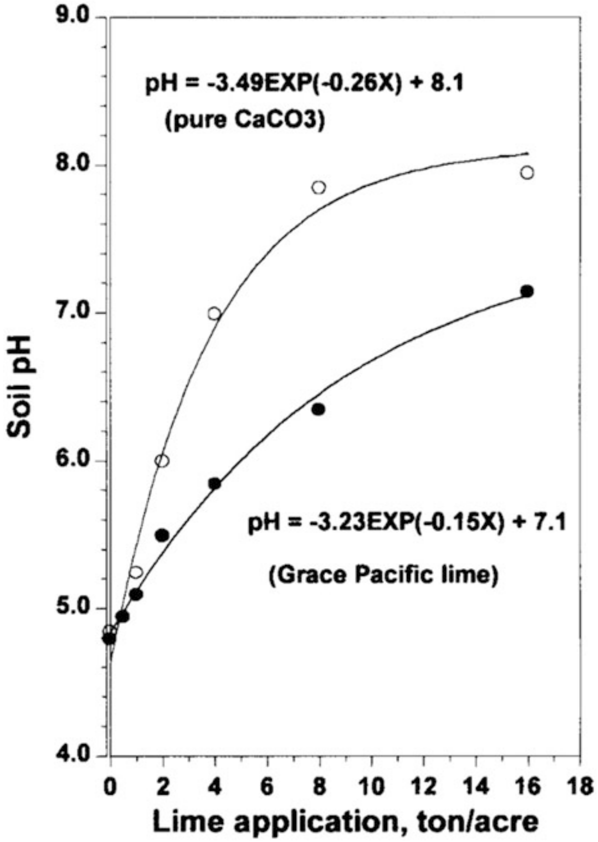
Fig. 5.15 Soil pH changes in time as affected by different particle sizes of a liming material

quantities of a commercially available lime source (e.g., 0, 0.25, 0.50, 1.0, 2.0, 4.0, and 8.0 g) are thoroughly mixed with 100 g acid soil. The mixture is then moistened to the field-water-holding capacity. Subsequently, the treated moist soil samples are air-dried gradually for a week or two, re-moistened, and dried again, so that the lime has had enough time to react with the soil acidity. At the end of the second incubation/equilibration period, soil pH (e.g., 20 g of the treated soil in 20 ml of water) is measured with a pH meter. An example of lime titration curves for an Oxisol from Hawaii using pure $CaCO_3$ and a local lime source is shown in Fig. 5.16.

5.4.2.2 Buffer pH Methods for Lime Requirement

A simpler and less time-consuming approach (often being used by soil testing laboratories) to estimating lime requirements is to equilibrate a soil sample with a multi-component solution that has a known initial pH value and is buffered against changes by acidity. This implies that the greater the acidity, the more the solution's buffering is overcome. Thus, the pH drops in the buffer solution equilibrated with a soil are proportional to the amount of base (i.e., lime) that would be needed to raise the pH of that soil. Empirical equations (derived from a database of several hundred soil samples) will estimate the quantity of lime required (in ton/ha) based on two factors: (1) buffer-solution pH drop and (2) desired final pH of the tested soil. For example, if pH of the buffer solution drops 0.20 unit, and the target soil pH is 6.5, then the regression equation (used by this buffer method) may recommend 3 tons of

Fig. 5.16 Lime titration curves of a Hawaiian Oxisol using pure $CaCO_3$ and a local lime source



lime per hectare. A popular buffer solution developed in Alabama in the 1960s (Adams and Evans 1962; Hue and Evans 1986) and its recent modified version (where the toxic p-nitrophenol was replaced with KH_2PO_4; Huluka 2005) for low CEC soils of the Southeast region of the United States could be well suited for acid weathered Oxisols and Ultisols of the tropics.

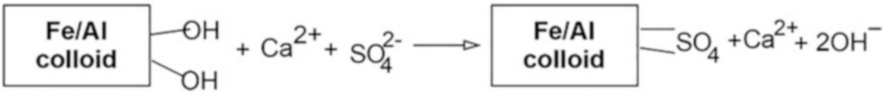
5.4.2.3 Lime Requirement Based on Exchangeable Al and Al Saturation Percentage

This method assumes that Al is the principal factor controlling soil acidity, so lime quantity must be provided to neutralize either all exchangeable Al or to decrease Al saturation percentage to a much lower and non-toxic level. However, precautions should be taken, because lime not only reacts with exchangeable acidity (exchangeable Al + exchangeable H) but also reacts with non-exchangeable acidity that includes Al bound to SOM and H^+ of carboxylic and phenolic functional groups of SOM and with OH of Fe and Al oxyhydroxides. Thus, lime requirements based on exchangeable Al should be increased by a factor of 1.5 to 3.0 in practice (Sanchez 2019).

5.4.2.4 Management of Acidity in Subsoil and in No-Till Condition

Where subsoil acidity is a problem or where either no lime is available or the plowing/tilling is not feasible, then approaches different from traditional liming practices should be explored.

Given the fact that gypsum ($CaSO_4.2H_2O$) is much more soluble than lime ($CaCO_3$), gypsum has been found to be effective in alleviating subsoil acidity without markedly changing soil pH (Sumner 1993). More specifically, by applying gypsum to the top soil, acid subsoil showed an increase in exchangeable Ca, a decrease in exchangeable Al, and, as a result, a marked increase in root growth (Sumner 1993). Contrary to lime whose OH^- ions are consumed by Al^{3+} and H^+ of the acid surface soil, preventing Ca^{2+} from moving downward, $SO_4{}^{2-}$ of the dissolved gypsum can accompany Ca^{2+} cations in leaching. Once the Ca^{2+} and $SO_4{}^{2-}$ ions move down to the subsoil, Ca^{2+} can replace Al^{3+} ions from the exchange site, and the released Al^{3+} can react with $SO_4{}^{2-}$ to form Al-SO_4 solids (e.g., basaluminite mineral) or soluble, but non-toxic $AlSO_4{}^+$ ion pair (Hue et al. 1985; Kinraide 1997). Furthermore, $SO_4{}^{2-}$ can replace terminal OH of Fe and Al oxyhydroxides, releasing some OH^- and raising soil pH and precipitating Al (Hue et al. 1985).



and

$$3Ca(OH)_2 + 2Al^{3+} \rightarrow 2Al(OH)_3 + 3Ca^{2+}$$

Figure 5.17 shows considerable reductions of exchangeable Al saturation in subsoil of an acid Ultisol by surface applications of gypsum or chicken manure (Hue and Licudine 1999).

In fact, application of organic materials (e.g., crop residues, animal wastes) not only can increase SOM but also ameliorates the detrimental effects of soil acidity as shown in Fig. 5.17 and Table 5.4. Such acidity ameliorating effects of organic materials are convincingly explained by Weil and Brady (2017) as quoted below:

1. High molecular weight organic matter can bind tightly with aluminum ions and prevent them from reaching toxic concentrations in the soil solution.
2. Low-molecular-weight organic acids produced by microbial decomposition or root exudation can form soluble complexes with aluminum ions that are nontoxic to plants and microbes.

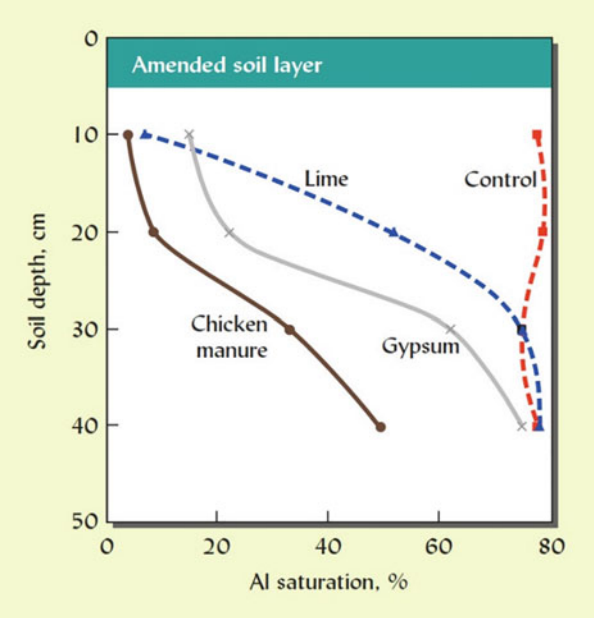


Fig. 5.17 Effect of Gypsum, lime, and chicken manure applied to the surface of an acid Ultisol of Hawaii on Al saturation percentage at different soil depths (Hue and Licudine 1999). Adapted from Weil and Brady (2017)

3. Many organic amendments contain substantial amounts of calcium held in organic complexes that can leach quite readily down the soil profile. Therefore, if such amendments as legume residues, animal manure, or sewage sludge are high in Ca, they can effectively combat aluminum toxicity and raise Ca and pH levels, not only in the surface soil where they are incorporated, but also quite deep into the subsoil.

5.4.3 Growing Acid-Tolerant Plants

When lime is not available because of high cost or poor transportation, it is better to solve soil acidity problems by growing acid-tolerant plant species than by trying to amend the soil. Due to their relatively high tolerance to Al and low requirement for Ca, some crops such as pineapple (*Ananas comosus*), sugarcane (*Saccharum officinarum*), and cassava (*Manihot esculenta*) can grow well in acid-weathered soils, whereas crops such as corn and soybean would perform poorly or even die. It is well known that the acidity tolerance varies among plant species, but such tolerance also varies widely among cultivars within a given species. Dr. Charles Foy of the USDA was one of the leading scientists who screened many wheat (*Triticum aestivum*) varieties for their tolerance to Al and to a lesser extent Mn (Foy and Brown 1964; Foy 1974; Johnson et al. 1997; Kamprath and Foy 1985). Some Al-tolerant genes, such as ALMT1 (a malate transporter) in wheat and Alt_{SB} (a citrate

Table 5.4 Effects of organic residues and lime on soil acidity, soil aluminum, soluble carbon and the growth of a legume forage plant, *Desmodium* intortum in acid tropical soils

Soil amendment type	Soil amendment amount	Soil pH	Exchangeable Al ($cmol_c$/kg soil)	Σ Inorganic Al ions in solution (μM)	Al^{3+} in solution (μM)	Oxidizable carbon in solution (mM)	Desmodium shoot dry weight (g/pot)	Desmodium relative yield (% of max.)
Control	None	4.55	2.49	18.25	4.18	0.12	2.86	32
Calcium hydroxide (slaked lime)	4 $cmol_c$ as $Ca(OH)_2$/kg soil	5.35	0.14	2.51	0.02	0.13	6.05	69
Cowpea leaves	10 g ground dry cowpea leaves/kg soil[a]	4.90	0.73	2.42	0.09	2.67	8.87	100
Cowpea ash	Ash from 10 g dry cowpea leaves/kg soil	4.95	1.55	8.85	0.62	0.17	5.97	72

Note that the organic material (cowpea leaves) raised the pH only 0.5 unit, but caused a dramatic reduction in the various forms of aluminum in the soil and soil solution, comparable to that caused by the slaked lime. The ash from cowpea leaves was less effective in reducing the aluminum. Only the cowpea leaves raised the amount of oxidizable carbon in solution, which in turn complexed the Al leaving much less in solution than otherwise expected at pH 4.9. The ash and lime each doubled the *Desmodium* yield, but the cowpea leaves tripled it. The data are means of two soils from Hawaii, USA, an Andisol and an Ultisol

Compiled from Hue (2011)

Adapted from Weil and Brady (2017)

[a] The 10 g dry cowpea leaves contained 0.91 $cmol_c$ as $Ca(OH)_2$. All pots were fertilized with an adequate supply of all nutrients except Ca

Fig. 5.18 Hydrangea (*Hydrangea macrophylla*) petals show red in low Al and blue in high Al conditions (adapted from Weil and Brady 2017)

transporter) in sorghum (*Sorghum bicolor*), have been identified as cited by Sanchez (2019). In corn (*Zea mays*), ZmAT6 gene has been shown to confer Al tolerance by scavenging reactive oxygen species (Du et al. 2020). Since plant breeding technologies have been grown rapidly in the past few decades, with breakthrough research in genetics and genomics, it is no doubt that many acidity-tolerant crops will soon be developed (Deka 2021).

Two main strategies have been suggested for Al tolerance in plants: (1) minimizing Al uptake by exclusion or avoidance and (2) detoxifying absorbed Al by chelation and vacuole containment. The chelation of Al, and to a lesser extent Mn, by reactive organic acids (mainly citric and malic and perhaps oxalic) either as root exudates or as cell metabolites is believed to be the main mechanism for acidity tolerance in many plant species (Kochian 2001; Liao et al. 2006; Gupta et al. 2013; Bojorquez-Quintal et al. 2017). In fact, some plant species such as tea (*Camellia sinensis*) and hydrangea (*Hydrangea macrophylla*) need high levels of Al for better growth and quality. Hydrangeas are known to change blossom (sepals) color from pink when grown in low-Al soils to bright blue (due to the biding of Al with the flower anthocyanin pigment called delphinidin-3-glucoside) in the presence of high Al (Fig. 5.18).

In the case of tea, Sun et al. (2020) reported that root growth was stimulated in the presence of Al: better growth in 200 and 1000 μM Al solutions than in the treatments of 100 μM Al or no Al solutions. Furthermore, the length of new roots in 1000 μM Al was twice that of new roots in the 200 μM Al treatment (Fig. 5.19). Tea shoots can contain as much as 3% Al, perhaps as Al-oxalate complexes (Morita et al. 2011).

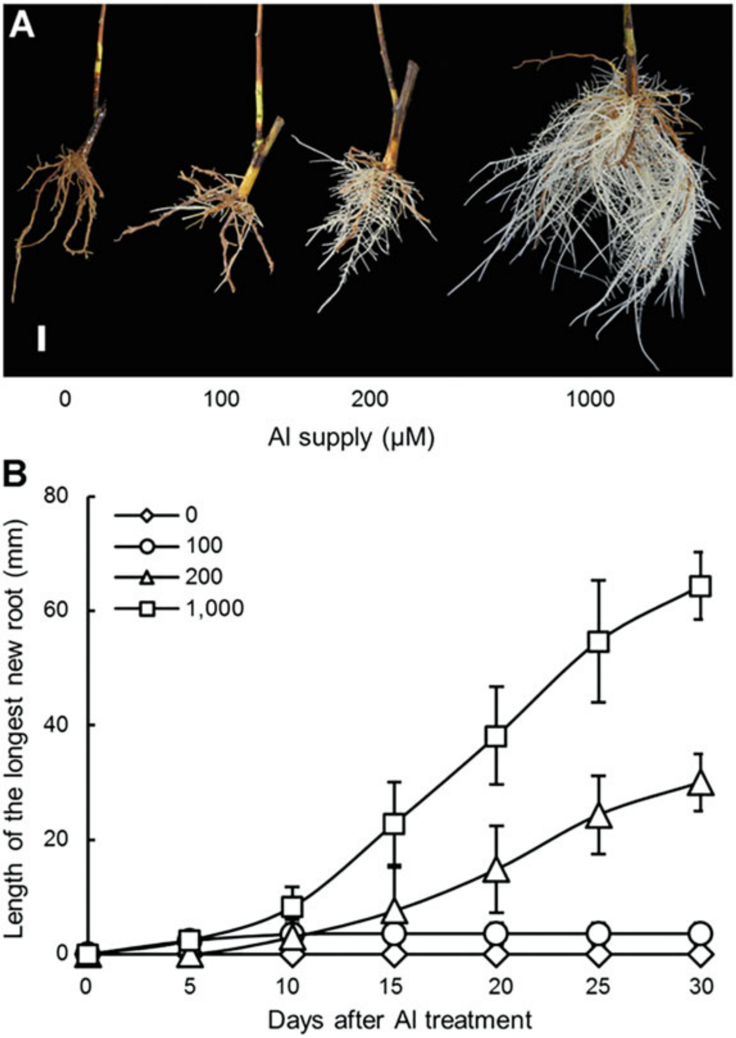


Fig. 5.19 Tea (*Camellia sinensis*) root responses to Al concentrations (**a**) and time after Al treatment (**b**) (adapted from Sun et al. 2020)

As with Al tolerance, there are differences in Mn tolerance among plant species and varieties within a species (Kamprath and Foy 1985; Foy et al. 1988). Macadamia (*Macadamia integrifolia*) leaves can contain as much as 1% Mn (dry weight basis) without any apparent toxicity symptoms (Warner and Fox 1972). Proteoid (cluster) roots apparently play a significant role in Mn accumulation in macadamia (Rengel 2000). Manganese tolerance seems to be controlled by many genes (Tang et al. 2021). In any case, in the tropics where most soils are acidic and highly weathered, there exist many tolerant species and cultivars that can provide a viable alternative to the management of soil acidity (Sanchez 2019).

5.5 Concluding Remarks

Acid soils occupy nearly 30% of ice-free area and over 50% arable land of the world. Soil acidity adversely affects crop production, forest growth, and aquatic lives. Soils become acidic through natural processes of weathering, especially in areas of high rainfall because base cations (e.g., Ca^{2+}, Mg^{2+}, K^+) are easily leached and are replaced with H^+ and Al^{3+}. Aluminum toxicity damages the root system first, while Mn toxicity appears predominantly in plant tops. Calcium deficiency places havoc on growing points such as root tips and meristems. Liming with common sources such as $CaCO_3$, $CaMg(CO_3)_2$ or $CaSiO_3$ can effectively raise soil pH and alleviate Al and/or Mn toxicities and Ca and/or Mg deficiencies. However, in some cases where lime is not available or is too costly, alternative management options need be sought, so do for subsoil acidity or no-till situations. Alternative strategies may include utilizing gypsum, organic manures (e.g., crop residue, animal waste), or a combination of those along with growing acidity-tolerant crops. With deep understanding and proper management in dealing with soil acidity, it is our hope that we can steadily increase food production to feed our ever-expanding population and to preserve/improve our environment for a better future in this planet.

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Chapter 6
Plant-Microbe Interactions in the Pedosphere Necessary for Plant to Overcome Various Stresses

Yachana Jha

Abstract The crop productivity is continuously constrained by biotic and abiotic stresses, which can be a great threat for global food security. The soil productivity is also continuously declining due to excessive use of chemical pesticides and inorganic fertilizer. So, the developments of sustainable and safer means for agriculture production means are needs of hours, and the use of ecologically safe biological agents is a best tool. Such biological agents include all soil microbes which have positive effect on both soil and associated plant. Any stress affects many physiological, biochemical, and molecular parameters of the plant and soil and directly influence the productivity. The soil microbes in the pedosphere have ability for plant growth promotion under normal condition as they regulate/produce plant hormones and siderophore and improve nutrition acquisition. While under abiotic stress it induces antioxidant system, to deal with biotic stress, it induce/acquire systemic resistance effectively. This plant-microbe interaction in the pedosphere of soil is vital for sustainable agriculture, as microbes play a vital role as an ecological engineer to solve environmental stress problems.

Keywords Soil microbes · Abiotic stress · Biotic stress · Phytohormones · Osmotic stress · Plant nutrients

6.1 Introduction

The outer most layer of the soil mantle is pedosphere, which is composed of soil and involved in soil formation processes. It is the site of dynamic interaction between the biotic, atmospheric, and hydrospheric components of the earth. So, pedosphere is very rich in terms of biodiversity and is the basis of terrestrial life on Earth. The soil formation, types, and its nutrient status are directly affected by the environmental conditions, and also soil biota types, association types, and habitat intensity directly depend on it. The hydrolytic activities of the soil microbes and weathering of rock

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B. Giri et al. (eds.), *Structure and Functions of Pedosphere*,
https://doi.org/10.1007/978-981-16-8770-9_6

determined the mineral constituents of soil and decide the nature of soil, like nutrients status, water holding capacity, aeration, and physical structure, in the pedosphere. The pedosphere is a hot spot for existence of highly diverse form of life starting from numerous microorganisms, plants, and animals, with different types of interaction among them (Hartman and Tringe 2019). Among all these interactions, the most important interaction for the existence of life on the earth is plant-microbe interaction. The association of microbial communities with plant root in the pedosphere is necessary for the proper growth of plant in normal as well as under stress conditions. The plant health, its biomass, and other physiological activities are directly or indirectly affected by types of plant-microbe interaction. In the pedosphere, the soil microbes play many critical roles for plants as in regulation of biogeochemical transformations as well as in nutrient cycling by mineralization, mobilization, and sequestration of soil mineral nutrients like phosphorus, potassium, iron, and zinc and disease prevention, infection, and transmission (Jha and Subramanian 2016). So, in the pedosphere the microorganism has antagonistic, mutualistic, or symbiotic association with the plant root which depends on nutrient availability in the form of root exudates. The root exudates are low-molecular-weight organic compound secreted by the plant root into the surrounding soil and are responsible for the complex interaction between the plant root, soil, and microbes. The root exudates consist of plant photosynthetic product such as different types of sugar as carbon source, proteins as nitrogen source, and various secondary metabolites as source of precursors for many metabolic pathways in microbes. The variation in amount of root exudates within the soil will determine the nutrient dynamics and hence affect the microbial population and diversity. The secretion mechanisms of these exudates are passive involving three separate pathways like vesicle transport, particle channels, and dissemination, whereas the synthesis and release are generally constitutive. Interactions in pedosphere basically depend on the chemical diversity of root exudates which is consist of many biologically active compounds responsible for specific association of plants and the microbial community (Canarini et al. 2019). Plants select a subset of microbes at different stages of their development for growth-specific functions, and such diversified microbial community with specific functions is directly influenced by the plant type, soil type, and environmental conditions. These microbial communities have a direct role in promoting plant growth and activation of plant defense mechanism against biotic stress and induced systemic tolerance toward different abiotic stress.

6.2 Effect of Plant-Microbe Interactions in the Pedosphere on Nutrient Status for Plant Growth Promotion

All terrestrial plants grow in the soil, but plant's association with microbes also plays a very important role both for the better survival of plant in that ecosystem and formation of soil. Formation of soil mainly takes place by weathering of rocks, but weathering process is directly influenced by plants, plant root, and root-associated microbes. The plant growth in such soil directly depends on the mineral constituent as well as concentration of important nutrient elements, and microbes in the pedosphere of the soil play an important role in the solubilization and mobilization of mineral nutrient for the growth of plant. Plant growth promotion can be achieved by the direct interaction between beneficial microbes and their host plant and also indirectly due to their antagonistic activity against plant pathogens. The nutrients are the environmental factor next to light and water, which is a major constraint for terrestrial plant growth. The plant growth promotion by microbes directly depends on the enhanced nutrient acquisition by the root and phytohormonal modulation (Jha 2019a). The pedosphere with efficient dynamic microbial ecologies and high concentration of organic matter positively influences plant growth without any chemical input. The specific plant-microbe interactions directly assist plant nutrition acquisition and have low requirement of chemical fertilizers by various mechanisms like increasing the surface area accessed by plant roots, nitrogen fixation, P and K solubilization, siderophore production, and Zn mobilization to fulfill the nutritional requirements of the plant in that soil. Such plant-microbe interactions also improve water and nutrient absorption of the plant, improve root development, modulate phytohormone, and regulate related plant enzymatic activity. Such associations are mostly symbiotic in which bacteria physically reside in plant tissue without doing substantive harm to the host plant (Jha 2019b). The root-associated bacteria have a gene for enzyme responsible for the production of ammonium/nitrate by utilizing dinitrogen gas as precursor in the host plant for biological nitrogen fixation. In this study, such beneficial plant-associated bacteria are isolated from the roots of *Suaeda nudiflora* wild mosque plant from the different sites of Gujarat, and serial dilution technique has been used for isolation of bacteria in semi-solid NFb medium with bromothymol blue as pH indicator. Isolation of pure culture and its maintenance have been done at 4 °C on the same medium. The identification of the isolates of interest is carried by morphological and cultural characteristics, biochemical tests, and molecular analysis. The molecular analysis of the isolates has been done by 16S rDNA gene amplification followed by sequencing using universal primer and BLAST analysis (Jha and Subramanian 2012). Both sequences have been used for phylogenetic profiling and submitted to gene bank having Gene Bank accession number FJ60287 which has been identified as *Stenotrophomonas* strain YJ3, HM756642 as *Lysinibacillus fusiformis* strain YJ4, and HM756643 as *Lysinibacillus sphaericus* strain YJ5. The ability of these isolated bacteria in plant growth and modulation of metabolites to protect plant under different stress has been analyzed in maize plant. The seed of selected maize variety Pioneer 30 V92 has been obtained from the main maize research station in Gujarat. The healthy seed has been properly surface sterilized and placed on tryptophan glucose yeast extract agar medium to check possible contamination. The seed completely free from contamination has been seeded in the pot containing sterilized soil mixed with isolated bacterial cultural suspension either alone or in mixture, and the seeded pots are placed in a growth chamber at 27 °C at 12 h light-dark cycle for a week. The effect of these isolated bacteria of pedosphere has been analyzed on nutrient status in maize leaves and its

Table 6.1 Effect of plant-microbe interactions in the pedosphere on plant growth promotion in maize plant under stress

Treatment	Germination (%)	Root length (cm)	Shoot length (cm)	Plant height (cm)	Dry weight (g plant^{-1})
Normal					
Control	71.3 ± 0.1	58.9 ± 1.2	98.2 ± 0.2	156 ± 1.3	68.2 ± 1.1
Control+ *L. fusiformis*	76.1 ± 1.1	61.7 ± 0.1	102.4 ± 1.4	162 ± 0.1	72.3 ± 0.1
Control+ *L. sphaericus*	74.4 ± 0.2	67.2 ± 1.3	111.8 ± 0.1	171 ± 0.2	71.7 ± 2.1
Control + *L. fusiformis* +*L. sphaericus*	82.6 ± 1.2	71.2 ± 0.1	121.5 ± 0.1	178 ± 1.1	76.2 ± 1.2
Stressed					
Control	38.1 ± 1.1	31.3 ± 0.1	54.4 ± 1.2	95.2 ± 1.1	43.1 ± 1.2
Control+ *L. fusiformis*	46.3 ± 0.1	35.1 ± 1.1	68.6 ± 1.3	102.4 ± 1.2	46.5 ± 0.1
Control+ *L. sphaericus*	49.2 ± 1.3	36.2 ± 1.3	71.1 ± 0.1	108.2 ± 0.1	47.9 ± 1.3
Control + *L. fusiformis* +*L. sphaericus*	51.7 ± 1.2	36.1 ± 0.1	76.2 ± 1.1	111.1 ± 0.1	49.1 ± 0.1

Values represents mean ± S.D. $n = 3$

growth promotion. The results of plant growth promotion by these root-associated bacteria showed a positive response on seed germination, plant height, and weight as shown in Table 6.1.

Nitrogen is one of the most limiting nutrients for the plant and has been assimilated in the form of nitrate, nitrite, and ammonia from the soil. Nitrogen is most abundant in the earth atmosphere, but only microbes have the ability for its conversion in usable form for the other living organisms. At the same time, nitrogen is not abundant in most soils, and input of chemical fertilizer is required for the proper growth of plant. Similarly, mineral nutrients like phosphorus, potassium, iron, and zinc are reactive, which remain strongly bounded to soil particles, and their availability is generally low for plant. So, the microbes having the ability for biological nitrogen fixation and solubilization of mineral nutrient in the pedosphere play a critical role for the growth of plant in its near vicinity (Jha and Yadav 2021). Such bacteria improve the soil fertility by decomposing organic residue from the soil, enhancing the soil humus formation, releasing mineral nutrient from insoluble inorganic forms, helping in biogeochemical cycling to maintain soil stability, etc. So, in this study, the root-associated bacteria are isolated on the NFB agar plate indicating that these isolates have ability for nitrogen fixation. In our study, the foliar contents of N, P, K, Fe, Zn, and Ca are estimated by using specific filter on digital flame photometry. The result of the study showed that the plants grown in pot containing sterilized soil mixed with isolated bacterial cultural suspension either alone or in mixture have higher concentration of nitrogen and all other mineral nutrients like P, K, Fe, Zn, and Ca (Table 6.2). Phosphorus is an indispensable

Table 6.2 Effect of plant-microbe interactions in the pedosphere on mineral nutrient concentration in maize under stress

Treatment	N (mg kg^{-1})	P (mg kg^{-1})	K (mg kg^{-1})	Fe (mg kg^{-1})	Zn (mg kg^{-1})	Ca (mg kg^{-1})
Normal						
Control	123.7 ± 0.01	176.1 ± 0.02	551.3 ± 0.01	158.2 ± 0.02	79.1 ± 0.01	121 ± 0.1
Control+ *L. fusiformis*	154.2 ± 0.12	195.6 ± 0.12	567.7 ± 0.02	165.1 ± 0.12	87.2 ± 0.04	132 ± 0.03
Control+ *L. sphaericus*	174.7 ± 0.23	187.7 ± 0.21	571.3 ± 1.02	171.3 ± 0.11	83.1 ± 0.02	129 ± 0.2
Control + *L. fusiformis* +*L. sphaericus*	171.7 ± 1.01	201.4 ± 0.13	587.7 ± 0.03	176.5 ± 0.21	88.6 ± 0.1	137 ± 0.12
Stressed						
Control	92.3 ± 0.01	145.4 ± 0.02	332.4 ± 0.01	117.3 ± 0.03	51.1 ± 0.02	63.3 ± 0.01
Control+ *L. fusiformis*	127.4 ± 0.21	157.1 ± 0.11	357.3 ± 0.02	121.2 ± 0.01	58.3 ± 0.01	66.3 ± 0.22
Control+ *L. sphaericus*	132.3 ± 0.03	163.3 ± 0.01	373.1 ± 1.02	129.7 ± 0.12	61.1 ± 0.21	69.3 ± 0.03
Control + *L. fusiformis* +*L. sphaericus*	134.9 ± 0.01	167.2 ± 0.03	381.3 ± 0.04	129.9 ± 0.03	62.7 ± 0.03	71.1 ± 0.2

Values are the means of replicates. Values with different letters are significantly different at $P < 0.05$ (Duncan's test)

nutrient for the growth and development of plants. It plays an important role in plant metabolism and reproduction and as a structural component, but usually present in lower concentration than the concentration of potassium, calcium, and nitrogen in all living *plant* cell. The shortage of phosphorus is instantly visualized as retarded plant growth as it has many critical roles in the transfer of genetic information from one generation to the next, *nutrient* movement, photosynthesis, energy transfer, and transformation of starch/sugars. Potassium is an osmotically active solute, which competes with sodium to protect the plant from adverse effect of salinity and help plant in water retention/absorption to maintain important metabolic activity (Jha 2017a). Iron is an important micronutrient for the plant and plays a critical role in photosynthesis/respiration. It serves as a prosthetic group of several important plant metabolic enzymes. But there is an indirect relationship between the demand of iron in the plant and solubility of iron in the soil. The biological activity of iron in the pedosphere is very limited as it forms highly insoluble ferric compounds at neutral pH of soil. It is a constituent of numerous enzymes and some pigments of the plant necessary for the specific metabolic activity. Similarly, zinc is another important micronutrient for plants and is an important component of many plant enzymes and proteins of metabolic pathway for internode elongation, hormone production, and growth (Jha 2019c). Ca^{2+} interactions have important effects on plant membrane properties and ion transport and lead to changes in cytoplasmic Ca^{2+} activity and therefore physiological properties such as plant growth, nutrition uptake, and water and ion transport under stress. The bacteria in the pedosphere can confer better nutrient availability, mobility, and acquisition as well as in the development of tolerance against adverse environmental condition to the surrounding plant. So, in this study, the effect of these isolated on the plant growth has been analyzed, and the result of the study showed that both the isolates have the ability for the plant growth promotion. Such bacteria in the pedosphere has antagonistic/synergistic association with other microorganisms which directly influences the plant growth rate by solubilizing nutrients for easy uptake, enhancing nutrient status, regulating phytohormone, and inducing resistance against plant pathogens (Bhat et al. 2020) so directly or indirectly helping in increasing crop yields and acting as an environmental friendly, sustainable tool for high-quality yield.

6.3 Effect of Plant-Microbe Interactions in the Pedosphere for Phytohormone Regulation

Plants by the help of phytohormone activate specific response against numerous external and internal stimuli for the proper growth of plant in its surrounding environment. Plant hormones directly/indirectly regulate several plant physiological functions and act remarkably in plant under stress. Some plant hormones like salicylic acid, jasmonates, cytokinins, ethylene, and abscisic acid are directly related with stress management. The pedosphere has numerous microbes which also influence the growth and survival of plant by producing and enhancing nutrient/water uptake by the root, by synthesizing/modulating growth-stimulating hormones, by activation defense enzymes, by inducing stress response gene, and by metabolizing growth inhibitory hormones (Monteiro et al. 2021). The hormones produced by microbes in the pedosphere also facilitate the plant-microbe interactions, which impose positive effect on plant under stress by modulating plant stress signal/phytohormone, by utilizing the stress biomolecule for its growth, by inducing more stress target protein to nullify the effect of stress effectors, by producing new sets of hormones, and by producing a variety of volatile substances having negative effect on other pathogenic microorganisms. Plant's fundamentally important processes have been regulated by the plant hormone (Jha 2020). Plant hormone has been produced in specific cell but act on wide target tissue to maintain plant physiology under normal as well as under stress. The hormones help in establishing relations, elicit resistance toward pathogens, induce antioxidant enzyme activity, and mediate gene expression. So, the plant-microbe interaction in the pedosphere affects the plant hormone systems either beneficially or detrimentally for plants depending on their growth environment. Auxin hormones produced by bacteria are mostly related directly to plant growth promotion and can also stimulate plant root growth to increase the root area for its interaction and improve mineral nutrition and water relations of the plant in the pedosphere (Jha 2017b). Changes in root growth and development are most important for adapting plants to either optimal or stressful environments. Bacterial hormone auxins accelerate root growth facilitating deeper access of the root for stored soil minerals and moisture, stimulating root branching, and optimizing root architecture. The isolated root-associated bacteria in this study has been analyzed for the production of phytohormones auxin, gibberellins, cytokinins, and abscisic acid, and results of the study indicate that both *L. fusiformis* and *L. sphaericus* have ability for production of these phytohormones in remarkable amount in presence of suitable media and condition (Table 6.3). Microbes in the pedosphere also produce gibberellins to facilitate enhanced shoot biomass and photosynthetic pigments in soybean under salt stress (Saeidi-Sar et al. 2013). Gibberellins naturally help plants to modify its physiological activity as per its changing environment for its better adaption toward fluctuating environmental conditions. Cytokinins (CK), an important group of plant hormones, are involved in maintaining cellular proliferation and differentiation and the prevention of senescence, therefore leading to the inhibition of premature leaf senescence. Similarly, the stress hormone abscisic acid acts as a signaling mediator for plants' adaptive response against stressed environment. It activates several metabolic activities like seed germination, bud dormancy, and stomatal closure normally, but under stress it imposes transcriptional and post-transcriptional regulation of genes associated with stress response. The root-associated bacteria produce all these phytohormones to help plant to withstand stress. The sugar product of photosynthesis acts as an important factor to modulate both root-associated bacteria and the plant growth regulators (Jha 2019d). The phytohormone like gibberellins, abscisic acid, and cytokinins acts as per the concentration of different sugars and its translocation to the specific sink. In plants, sugars and ABA act in a synchronized manner. ABA

Table 6.3 Effect of plant-microbe interactions in the pedosphere on phytohormone (auxin, gibberellins, cytokinins and abscisic acid) and osmoprotectent (proline, glycine-betaine and sugar) in maize under stress

Treatment	Auxin (μg ml^{-1})	Gibberelline (μg ml^{-1})	Cytokinin (μg ml^{-1})	Abscisic acid (μg ml^{-1})	Proline (mMol min^{-1} g^{-1})	Glycine-betaine (mMol min^{-1} g^{-1})	Sugar (% wt/wt)
Normal							
Control	1.21 ± 0.2	1.37 ± 0.1	1.32 ± 0.1	2.67 ± 0.2	1.7 ± 0.3	2.1 ± 1.3	21.2 ± 0.1
Control+ *L. fusiformis*	1.34 ± 1.1	1.67 ± 1.1	1.46 ± 1.2	2.72 ± 0.1	2.1 ± 1.2	2.7 ± 1.1	23.3 ± 0.3
Control+ *L. sphaericus*	1.45 ± 0.1	1.98 ± 0.2	1.54 ± 2.1	2.84 ± 0.3	2.8 ± 0.1	2.3 ± 0.1	24.7 ± 1.1
Control + *L. fusiformis* +*L. sphaericus*	1.49 ± 1.2	1.86 ± 2.1	1.62 ± 0.3	3.01 ± 1.1	2.9 ± 1.4	3.3 ± 1.3	27.2 ± 2.1
Stressed							
Control	0.87 ± 0.1	1.12 ± 1.2	1.13 ± 0.3	3.56 ± 1.3	1.3 ± 0.2	2.7 ± 1.1	13.1 ± 0.2
Control+ *L. fusiformis*	1.12 ± 1.2	1.32 ± 1.1	1.25 ± 1.1	2.79 ± 1.2	1.9 ± 1.3	3.1 ± 0.01	15.7 ± 0.1
Control+ *L. sphaericus*	1.23 ± 0.2	1.29 ± 0.2	1.43 ± 0.1	2.86 ± 0.1	2.5 ± 0.1	2.8 ± 0.02	16.3 ± 1.2
Control + *L. fusiformis* +*L. sphaericus*	132 ± 1.1	1.38 ± 0.3	1.54 ± 2.1	2.43 ± 1.1	2.7 ± 1.1	3.3 ± 0.1	17.3 ± 1.1

Values are the means of replicates. Values with different letters are significantly different at $P < 0.05$ (Duncan's Test)

plays a key role in conferring plant to provide protection against drought and several stress responses.

6.4 Effect of Plant-Microbe Interactions in the Pedosphere on Osmotic Stress Management

The plant growth and development are continuously limited by different types of abiotic stress, and abiotic stress like drought and salinity is directly related with pedosphere as well as plant root. In desire to achieve high yield, farmers use heavy irrigation with water having high mineral content in crop field, which is the major cause of salinity. Drought and salinity have common effect on plant physiology, and it is one of the most imperative environmental stresses, due to many reasons like high and low temperatures, high intensity of light, and low rainfall. It is a multidimensional stress and affects plant at all levels as morphological, biochemical, physiological, and molecular level (Jha 2018a). Under such stress accumulation of ions and salt takes place in the pedosphere and on the upper surface of soil, resulting in ion toxicity and inhibition of water absorption by the roots due to the osmotic effect in the plants. This osmotic stress not only affects the plant but also affects the biodiversity, structure, and activities of bacterial communities in the pedosphere. The electrical conductivity of the soil and sodium content of the soil are two important factors which decide the bacterial communities in the soil. These groups of bacteria have ability for the production and accumulation from the environment of organic solutes in its cytoplasm to counter the osmotic effect known as organic osmolytes (Kumar et al. 2020). These organic osmolytes can be amino acids, glucosyl glycerol, sugar alcohols, and sugars. So, plant interaction with such bacteria in the pedosphere is a symbiotic relation where bacteria association helps the plant to survive in adverse environmental condition; in place of it, it acquires nutrient and shelter from the plant. Plants also have natural ability for the production and accumulation of osmolyte to combat osmotic stress. Plant osmolytes also neutralizes the osmotic effect of the salinity for the proper functioning of plant biochemical and metabolic activity (Jha and Subramanian 2021). The plant osmolytes include glycine, proline, betaine, glutamate, sugar alcohols, and di- and oligo-saccharides. Among these osmolytes sugar is mainly a plant derivative having a special role as osmoprotectants as well as promotes the colonization of the bacteria inhabiting in/on the plants, and sugar alcohols act as osmoregulators and signaling molecules (Jha et al. 2021). The organic osmolytes as γ-aminobutyric acid, proline, and betaine are small amino acids are responsible for maintaining enzyme activity under osmotic stress. The main effect of osmotic stress is water constraints, which has adverse effect upon plant production and productivity (Fahad et al. 2017). Osmotic stress-mediated water constraint has serious effect on plant physiology like reduction in chlorophyll content, lowered photosynthesis, reduced gaseous exchange, and stomatal closure. Water being a universal solvent affects several metabolic and physiological activities of a plant. The effect of isolated bacteria *L. fusiformis* and *L. sphaericus* of pedosphere has been analyzed on organic osmolyte production and accumulation in maize leaves for its survival under osmotic stress. The result of the study shows that both the isolated bacteria alone and in mixture are able to accumulate osmoprotectants like in the maize leave. The accumulation of different types of sugars and in different concentration in the plant has been observed due to isolated bacteria (Table 6.3). Sugar is the main product of photosynthesis, which acts as reserve for the production of other important precursor for other metabolic activities in the cells and tissues normally, but under osmotic stress it acts as osmoprotectants to stabilize biomolecules in the stressed cell. The 30–50% of the osmotic adjustment in plant is carried out by the soluble sugars, which remarkably help in maintaining the growth and function of bio-molecule in plant tissues and osmotic adjustment and act as compatible osmolytes for osmoregulation (Nounjan et al. 2018). Similarly, the small amino acids glycine and proline have versatile functions in plants. They are building blocks of functional and structural protein, which has been associated with root/shoot apical meristems. In rapidly dividing cell, it has versatile functions as for embryo development and involved in floral transition. During plant development, it acts as dehydration protector of cellular structures. Glycine and proline alter the transporter proteins, like amino acid permeases, and modify selective compatible solute to maintain cell osmolarity. Such an osmoprotectant permits supplementary water to be taken up from the environment to counteract the effect of osmosis (Deole and Hoff 2020). Limiting the absorption of water from the soil causes increasing ionic stress in plant cells and the pedosphere bacteria appear to confer tolerance to osmotic stress, via modulating the transcription factors, which activate adaptive responses by inducing expression of genes encoding ion channels and transporters to eliminate the accumulation of toxic ions in the cytosol, genes involved in the synthesis of osmoprotectants and antioxidant defense mechanism (Bharti et al. 2016).

6.5 Effect of Plant-Microbe Interactions in the Pedosphere on Biotic Stress Management

The plant-microbe interaction is common in the pedosphere for proper growth of the plant, and plant roots are site for colonization of diversity of beneficial and deleterious microbes. The chemical signals in the form of root exudates attract specific group of microbes. The pathogenic interaction is responsible for the massive devastation of crop yield by altering hormonal regulation mechanism, nutrient imbalance, and physiological disorder, while beneficial interaction triggers specific signal for the better survival of the plant under normal as well as stress conditions (Velásquez et al. 2018). The beneficial interactions further secrete diverse elicitors to activate biochemical changes in plants to induce disease resistance in the plant. The beneficial pedospheric microbes encourage disease resistance by enhancing

Table 6.4 Ability of isolated bacteria of pedosphere for antibiotics, siderophores and HCN production

Treatment	Antibiotics potency (%)	Siderophores (% siderophore unit psu)	HCN (ppm)
L. fusiformis	76	84	34
L. sphaericus	82	71	47

accumulation of secondary metabolites, cell wall reinforcement, and cellular burst and activating PCD (Jha and Subramanian 2015). They also induce defense-related hormones like ethylene, salicylic acid, jasmonic acid, and reactive oxygen species and oxidative burst to trigger signal transduction activated defense mechanism. Defensive reaction mechanisms activated by root-associated bacteria microbes in the pedosphere involve two pathways, systemic acquired resistance and induce systematic resistance. The beneficial microbe interaction generally induced systematic resistance, which involves accumulation of PR proteins and SA, while ISR relies on pathways regulated by jasmonate and ethylene under biotic stress (Jha 2022). The pathogenic microbe interaction induces a systemic acquired resistance associated with the production of pathogenesis-related proteins, nitrogen oxygen species, and reactive oxygen species to create a complex network by modulating jasmonate, salicylic acid, and ethylene for efficient pathogenic interaction. In the infected plant, stress hormone ethylene coordinated with regulatory factors for the induction of expression of PR genes (Jha 2019f). The non-pathogenic microbes of the pedosphere upon interaction with the root produced allopathic compound, to reduce competition for nutrient and niche and release elicitor to induce resistance in plant as well as immunize plant against broad-spectrum pathogens (Pršić and Ongena 2020). The allopathic compounds such as antibiotics, siderophores, phenolic, and HCN have the ability to directly inhibit the progression of pathogenic microorganism. The effect of isolated bacteria *L. fusiformis* and *L. sphaericus* from the pedosphere has been analyzed for the production of antibiotics, siderophores, HCN, phenolic, and flavonoid and activation of PCD in maize leaves for its protection under biotic stress. The results of the study show that both the isolated bacteria have the ability for the antibiotic, siderophore, and HCN production and also for the production of phenolic and flavonoid and activation of PCD in maize leave in the presence of fungal pathogen (Table 6.4).

The growth of competitor microbes has been checked by production of antibiotics by the microbes in the pedosphere and also helps in plant disease management. Antibiotics are a low-molecular-weight compounds having major role in induced systemic resistance in plants. The siderophore-producing bacteria in the pedosphere limits the availability of iron for the growth of pathogenic microbes in the surrounding; at the same time, it will supply iron to the associated plant for its proper growth (Ahmed and Holmström 2014). The chlorosis and low crop productivity are iron deficiency-associated symptoms, as iron is necessary for the numerous metalloenzymes of important physiological activity like respiration and photosynthesis. The root-associated bacteria having ability for the production of phenolic compound also check growth of pathogenic microbes in the pedosphere, and group of bacteria got associated with the plant root directly depend on root exudates. The root exudates are the source of mainly organic acids, sugars, and amino acids for the growth of microbes, but root exudates also secrete complex secondary metabolites as phenolic compounds, flavonoids, and terpenes (Gargallo-Garriga et al. 2018). Microbial as well as plant phenolics act as signaling biomolecule to activate secondary responses in plants as to activate the phytoalexins and pathogenesis-related protein production to restrict/destruct the pathogen growth. Phenolics are responsible for the modification of cell walls or other physical barriers like papillae/appositions. Similarly, group of bacteria in the pedosphere has ability for production of chemical compounds like HCN for the destruction of pathogenic microbes as it is toxic for plant pathogens acting as biocontrol agent (Rijavec and Lapanje 2016). At the same time, the HCN promotes the mobilization of elements from rock-forming minerals and modify solubility of these elements for the plant growth under low nutrient condition. Thus, the sequence of events activated as defense response by the root-associated bacteria can induce host cell death for the protection of surrounding cell from infection and necrosis, accumulation of toxic phenols, modification of cell walls by phenolic substituents or physical barriers such as appositions or papillae, and, finally, the synthesis of specific antibiotics such as phytoalexins (Jha 2019e). So, the beneficial *microbes* in the pedosphere form an association with plant roots to improve *plant health* as well as activate induced systemic resistance for plant protection which can considered as an eco-friendly and cost-effective means for the control of diseases. Further growing cost of pesticides and their harmful effects on soil are highly noticeable, so use of such strategy can be an alternative and sustainable approach to replace pesticides and chemical fertilizers.

6.5.1 Effect of Plant-Microbe Interactions in the Pedosphere on Abiotic Stress Management

The water, light, minerals, carbon, and suitable climatic condition are necessary for the optimal plant growth reproduction; any change in climatic condition limits the plant productivity. Extreme conditions like salinity and drought, high or low temperature, etc. activate a complex mechanism in plant to develop tolerance. The effects of unfavorable conditions initially appear at the cellular levels, thereafter at physiological and metabolic level (Isah 2019). Among all abiotic stress, water stress most adversely affects the plant physiology including the photosynthetic capability. Prolonged water stress alters stomatal opening; reduces leaf water potential, seed number, seed viability, seed size, and leaf size; delays flowering; suppresses root growth; and delays fruiting. The growth and development of plants are adversely influenced by exposure to high/low light intensities, which drastically alter all physiological process (Jha 2018b). The production of reactive oxygen species takes place due to high-intensity light, which is highly reactive and reacts with all important enzymes and biomolecules and induces photooxidation. Plant initiates a rapid and efficient complex stress-specific signaling cascade response after sensing the stress stimuli, which include production of stress hormone, accumulation of low-molecular-weight osmolytes, production of hydrolytic secondary metabolites like flavonoids/phenolic, and induction of stress-specific genes to stimulate appropriate tolerance mechanism (Jha and Subramanian 2014). So, plant smartly sense, manage, maintain, and escape from changing environmental state by inducing complex phenomenon which involves dynamic and real-time changes at physiological, metabolic, cellular, transcriptome, and genetic levels. To contest such stressful condition, the beneficial microbes in the pedosphere colonize with the plant root to help stressed plant by applying different indirect/various direct mechanisms (Kumar and Verma 2018). Soil microbiota like *Azospirillum*, *Pseudomonas*, *Enterobacter*, *Burkholderia*, *Bacillus*, and *Lysinibacillus* has been well reported for development of tolerance to the associated plants. Such bacteria have ability for plant growth promotion by induction of production of antioxidants, phytohormone, and reactive oxygen species. Root architecture is thought to be more sensitive in sensing abiotic stress in the soils. The effect of isolated bacteria *L. fusiformis* and *L. sphaericus* of pedosphere has been analyzed on the induction of antioxidant enzyme activity like superoxide dismutases, peroxidase, and catalase in maize leaves for its survival under abiotic stress. The result of the study shows that both the isolated bacteria alone and in mixture able to induction of SOD, peroxidase, and catalase in the maize leave has been observed (Table 6.5). The antioxidant enzyme activity is responsible for neutralizing the generated hydrogen peroxides in the mitochondria and chloroplast. The antioxidant enzyme superoxide dismutases, peroxidase, and catalase can scavenge oxyintermediates and free radicals for the removal of hydrogen peroxides and also help in detoxification of ROS (Snezhkina et al. 2019). The superoxide dismutase enzyme catalyzes the conversion of superoxide radicals generated in the plant due to abiotic stress into hydrogen peroxide, and hydrogen peroxide is converted into water and molecular oxygen by peroxidase and catalase enzyme. The canalization reaction of superoxide dismutase enzyme causes accumulation of hydrogen peroxide which can generate highly reactive hydroxyl ions, which can react with all important macromolecule and hamper the molecular events of the plant cell. So, the superoxide dismutases, peroxidase, and catalase by coordinated action can be able to check the formation of reactive oxides under stress (Radi 2018). Such bacteria help plant root for improved exploitation of soil water and maintenance of root turgor and induce changes in soil structure and root morphology. The mechanisms for mitigating water stress by such root-associated bacteria are by changing symplastic/apoplastic water partitioning and enhancing root growth and density.

6.6 Conclusion

The nature of soil is continuously deteriorating due to continuous use of chemical in the crop field for increased crop production, but such excess use of chemical is polluting our soil recourses and creates great problem in crop productivity

Table 6.5 Effect of plant-microbe interactions in the pedosphere on phenolic, flavonoids and activate PCD and on the induction of SOD, peroxidase and catalase in maize under stress

Treatment	Flavonoids	Phenolics (mg g^{-1} of the gallic acid)	PCD (Evan blue conc mg/cell)	SOD (mmol min^{-1} g^{-1} FW)	Peroxidase (mmol min^{-1} g^{-1} FW)	Catalase (mmol min^{-1} g^{-1} FW)
Normal						
Control	78.2 ± 0.1	0.77 ± 0.2	24.7 ± 2.1	21.3 ± 0.1	14.2 ± 0.2	12.6 ± 1.1
Control+ *L. fusiformis*	82.4 ± 1.1	0.83 ± 0.1	21.2 ± 1.1	23.7 ± 2.1	16.8 ± 1.1	13.2 ± 0.2
Control+ *L. sphaericus*	87.3 ± 2.1	0.87 ± 2.1	20.9 ± 0.1	21.4 ± 0.2	17.1 ± 0.1	14.7 ± 1.3
Control + *L. fusiformis* +*L. sphaericus*	88.2 ± 1.2	0.85 ± 1.1	18.7 ± 0.3	29.1 ± 0.3	19.3 ± 0.2	15.1 ± 0.1
Stressed						
Control	117.2 ± 0.1	0.86 ± 1.1	35.2 ± 1.1	18.2 ± 1.1	18.7 ± 1.3	16.4 ± 0.1
Control+ *L. fusiformis*	121.6 ± 1.1	0.97 ± 1.7	32.8 ± 3.1	21.2 ± 0.1	17.3 ± 0.1	14.7 ± 0.3
Control+ *L. sphaericus*	127.2 ± 1.4	1.01 ± 0.1	31.3 ± 0.1	24.1 ± 1.3	17.8 ± 1.1	141 ± 0.1
Control + *L. fusiformis* +*L. sphaericus*	132.1 ± 2.1	1.12 ± 1.3	29.6 ± 1.1	27.1 ± 0.1	15.2 ± 1.1	12.9 ± 1.2

Values are the means of replicates. Values with different letters are significantly different at $P < 0.05$ (Duncan's test)

worldwide. The world population is continuously growing, and our land resources are proportionally decreasing due to environmental stress as well as human activity. So, for the protection of our land resources and the rejuvenation of soil resources, there should be reduced chemical input in the crop field without compromising the crop production. The maintenance of quality and quantity of agricultural production deserves an environmentally friendly technology, and use of root-associated bacteria in the pedosphere of soil can be a desired tool to overcome the adverse effects of chemical. Such bacteria has the ability for the soil rejuvenation as well as help the surrounding plant to achieve its full potential under normal condition and better sustain under stress.

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Chapter 7
Where Land Meets Sea: Biology of Coastal Soils

Gederts Ievinsh

Abstract The aim of the present review is to analyze functionally important plant-microbe interactions in soil leading to establishment of characteristic vegetation patterns in coastal habitats with a special emphasis on sea wrack-dependent vegetation. Effect of fluctuating salinity on microbial diversity and activity is analyzed, further focusing on specific features of nitrogen cycle in coastal habitats. Two types of plant symbioses—with mycorrhizal fungi and nitrogen-fixing bacteria—are emphasized as being of special functional importance for coastal plants. As importance of sea wrack deposits for stimulation of microbial processes in coastal habitats is almost a completely neglected aspect of biology of coastal soils, an attempt is made to provide overview of general aspects of establishment of drift line vegetation, followed by outline of possible functionally important microbiological activities. It is concluded that, in order to get better insight in ecological mechanisms underlying vegetation establishment and maintenance in coastal habitats affected by wrack deposition, assessment of microbiological processes is of critical importance both at the level of functional activity and taxonomical diversity.

Keywords Coastal plants · Drift line habitats · Microbial diversity · Mycorrhiza · Nitrogen cycling · Nitrogen-fixing bacteria · Salinity · Sea wrack

7.1 Introduction

Habitats along a sea coast can be characterized as extremely heterogeneous in respect to abiotic and biotic environmental factors, which have immense importance for physiological adaptations of coastal plants (Ievinsh 2006). Several general plant characteristics (as high phenotypic plasticity, ability of clonal propagation, seed dormancy) as well as plant interactions (microbial symbiosis) have been identified as determining characteristic vegetation structure and plant responses to prevailing

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B. Giri et al. (eds.), *Structure and Functions of Pedosphere*,
https://doi.org/10.1007/978-981-16-8770-9_7

factors. There is no doubt that soil both as a substrate for plant growth and place of acquisition of water and mineral nutrients represents a central location for essential processes in the establishment and maintenance of coastal plants. However, the role of soil-related processes besides water uptake and mineral nutrition for growth and physiology of coastal plants is a less studied aspect in plant biology.

Given the fact that plants can successfully grow and fully reproduce even without a soil, it is of no surprise that plant growth substrate in some coastal habitats does not resemble soil or there are no typical characteristics present, which are usually associated with soil. Moreover, vegetation establishment in places where there is no permanent plant cover, like different types of beaches, is rather sporadic and temporary. While general functional aspects of soil formation in linear systems similar to chronosequences in a sea coast ecosystem are relatively well established (Jones et al. 2008), including also direct effects on vegetation establishment, there is no information available on biological relationships forming the basis of seemingly stochastic plant establishment episodes prevailing in many coastal habitats.

However, within the present review, it is not intended to focus on soil classification or aspects of pedogenesis in coastal habitats. There are a number of excellent reviews on these topics available in the recent literature, as the one dealing with soil formation in tidal and subtidal environments, analyzing humus forms in hydric and subaqueous soils (Zanella et al. 2018). Instead, the emphasis will be given to analysis of functionally important plant-microbe interactions in soils of coastal habitats, in order to identify significant gaps in our knowledge of coastal soil biology. Therefore, the term “soil” in this review will be used in its generic sense, namely, as any natural substrate suitable for plant establishment. One of the most important assumptions used during the analysis will be that plants are both cause and result of soil establishment, with microbial processes and their interactions with other organisms being critical in this respect.

There is a reason to believe that heterogeneity is a general characteristic in coastal ecosystems, also in respect to microbiological processes. Thus, it is established that different coastal habitats are extremely variable in respect to both microbial diversity and biomass. In habitats with relatively low level of organic matter as in different types of beaches and sand dunes, also low microbial biomass is expected to be found, resulting in low overall activity of microbial processes (Jones et al. 2008). However, salt-affected coastal wetlands are hotspots of microbial activity with extremely high rate of accumulation of organic matter and mineralization (Bai et al. 2017).

In contrast to tide-affected wetland systems (coastal salt marshes), with pronounced zonality both in abiotic conditions and vegetation characteristics, non-tidal systems usually have no clear zonation and are more spatially heterogeneous. Tidal wetland systems are the only ones relatively well-characterized in respect to microbial diversity and different types of microorganism-dependent processes (Lv et al. 2016; Morrissey et al. 2014). In comparison to coastal wetland systems, other coastal habitat types such as sand beach, shingle beach, sand dunes, etc. have been more rarely studied in respect to microbial processes. Moreover, these processes are often characterized only by a particular result in a form of changes in soil chemical constituents, but not by particular activity performed by a certain group of microorganisms (Eriksson et al. 2003; Gerlach et al. 1994).

When biological aspects of coastal soils are considered, influencing environmental interactions assessed are usually limited to one or several of the better-known factors, including salinity, waterlogging, soil fertility, seasonality, and vegetation features. One relatively neglected aspect in coastal biology is related to drift line material-dependent (wrack-dependent) vegetation systems in coastal habitats. Nevertheless, importance of this type of influence on establishment of pioneer vegetation on coastal habitats has been well known for a relatively long time (Lemoine and Faucon 2005; Rodil et al. 2019), but there is a significant gap in knowledge on microbial aspects of vegetation establishment and maintenance in these habitats. Therefore, the aim of the present review is to analyze functionally important plant-microbe interactions in soil leading to establishment of characteristic vegetation patterns in coastal habitats with a special emphasis on sea wrack-dependent vegetation.

7.2 Microbial Diversity and Activity in Coastal Soils

7.2.1 Effect of Salinity

Salinity is one of the major factors affecting biological processes in soils of coastal habitats. Effects of salinity on structure of decomposing microorganisms and their functional processes have been analyzed relatively recently in an excellent review (Rath and Rousk 2015); therefore, in the present review, focus will be mainly on effects on microbiome with possible relation to plants. While it seems that in general salinity has more pronounced direct effect on vegetation, it is also possible that changes in nitrogen availability in wetland soil due to salinity-altered nitrogen cycle can have effects on biomass accumulation and plant physiological status. For example, it is relatively well documented that changes in salinity greatly affect nitrogen cycling in soils. One of the most noticeable phenomena in this respect is increased NH_4^+ availability in soils of fresh marshes occurring as a result to rise in salinity, possibly due to inhibition of nitrifying enzyme activities by chloride (Baldwin et al. 2006).

A major evidence for changes in microbial communities due to fluctuations in soil salinity levels mainly comes from studies in coastal wetland ecosystems only seldom affected by a seawater intrusion. For mostly freshwater-adapted wetlands, loss of organic carbon is a characteristic response to saltwater intrusion due to increased rates of microbial decomposition, as established both in field and laboratory experiments (Chambers et al. 2013; Neubauer et al. 2013). Inhibition of nitrogen cycle (Neubauer et al. 2019) and decrease in microbial diversity (Morrissey et al. 2014) are other consequences of wetland salinization. On the other hand, desalinization measures through freshwater restoration improve microbial diversity and denitrification rate in saltwater-affected wetlands (Huang et al. 2021). Some studies have compared diversity of bacterial communities along a salinity gradient in coastal wetlands, showing that salinity itself is the main driver of structural variation in these communities (Li et al. 2019). In contrast, seasonal changes in temperature had low effect on bacterial communities (Lv et al. 2016), but changes in vegetation coverage and composition with changes in salinity occurred in parallel to bacterial variation (Yu et al. 2012).

In a complex laboratory study, both denitrification rate and denitrification enzyme activity were measured following simulated freshwater intrusion or salinity episodes using soil and sediment samples collected from coastal salt marsh as well as fresh marsh (Marks et al. 2016). While fresh marsh soils and sediments had higher activity of denitrification enzymes, all samples reached high denitrification capacity when exposed to optimum conditions. Denitrification rates in fresh marsh soil were stimulated by pulses of intermediate salinity, while seawater salinity resulted in decrease of the rate. Surprisingly, pulses of freshwater in salt marsh soils almost completely blocked their denitrification capacity. Consequently, denitrifying microbial consortia in coastal soils are specifically adapted to saline conditions and are extremely sensitive to any shifts in salinity. This seems to be at least in part related to complex adaptation of microorganisms to a certain range of osmotic values, widely recognized as hypoosmotic (low salinity) or hyperosmotic (increased salinity) conditions. Evidently any type of osmotic stress as a result of a significant shift from adapted conditions can directly disrupt cellular homeostasis, usually leading to loss of functions and even cell lysis (Rath and Rousk 2015).

Consequently, results from studies on salinity effects on soil microbiological functions are difficult to generalize due to high variation in experimental conditions, timing, and measured parameters. From a point of a predictability level and, consequently, any practical use of the abovementioned results, a link needs to be established not only between salinity and different functional properties of microbiome but also with microbial tolerance to salt as based on sequence assessments (Rath and Rousk 2015).

7.2.2 Decomposition of Organic Matter

Decomposition of plant litter is a stepwise process, with heterotrophic microorganisms involved first in degradation of relatively labile low molecular weight compounds (as carbohydrates and proteins), resulting in increase of proportion of recalcitrant high molecular weight compounds (as lignin), requiring more energy for degradation (Steinmuller and Chambers 2019). It is believed that in general bacteria decompose relatively labile compounds, while fungi act on more complex forms of organic material (Garcia-Pausas and Paterson 2011). However, fungal biomass in any given situation is dominating, but relative functional contribution of the two groups is largely variable depending on particular interactions between soils, vegetation, and environmental factors (Strickland and Rousk 2010). Interestingly, in a sea-affected habitat, structure of microbial communities is changed by salinity, and, in general, increased salinity results in a shift from fungal-dominated to bacterial-dominated communities, both at the level of microbial activity and contribution to soil organic carbon pool (Chen et al. 2017, 2021).

In oxygen-deprived conditions of coastal wetlands, accumulation of organic carbon with time is a characteristic feature, being related to slower decomposition of organic matter due to lack of terminal electron acceptors (White et al. 2019). As a result, organic carbon is preserved in anoxic conditions of waterlogged or submerged coastal substrates in a form of recognizable organic remains or humic components (Zanella et al. 2018). However, under the influence of oxygenated seawater, minimally processed soil organic matter together with bioavailable N and P reserves can undergo rapid mineralization (Steinmuller and Chambers 2019).

7.3 Fungal Interactions

7.3.1 Fungi in Coastal Soils

There is no doubt that fungal communities in coastal soils are affected by the type and characteristics of dominant vegetation. One of the most general trends of fungal diversity is related to overall soil fertility. Thus, *Basidiomycota* is a dominant fungal group in environments with high fertility and, consequently, high plant biomass production, but *Ascomycota* is characteristic of ecosystems with low C and nutrient availability (Sterkenburg et al. 2015). However, fungal-related studies in coastal habitats are relatively rare in comparison to these aimed at bacterial-mediated processes.

One prominent model system aiming to establish fungal community relationships is related to tidal salt marshes. There, clear chronosequence of soil formation has been used to assess patterns in fungal community composition and taxonomic and eco-physiological diversity (Dini-Andreote et al. 2016). While early-successional salt march soil had 10- to 100-fold lower fungal abundance in comparison to more mature soils, their taxonomical richness was comparable. Moreover, highly dynamic nature of tidal regime in early-successional soils resulted in significant temporal variation in fungal β-diversity.

In the particular system, due to the presence of clear gradients of several environmental factors, it is difficult to discriminate between direct environmental or indirect plant-associated effects on microbial communities. Another possibility is to study the effect of plant invasions on microbial diversity and processes, possibly excluding direct environment-related differences. Habitat degradation as a result of long-term invasion of exotic plant species in coastal wetlands is supported by a characteristic trend in fungal community changes, namely, decrease in abundance of *Basidiomycota* and increase in *Ascomycota* (Yang et al. 2019).

7.3.2 *Mycorrhizal Symbiosis in Coastal Habitats*

It is often argued that plant species from several major dicotyledonous plant families like Brassicaceae, Caryophyllaceae, and Chenopodiaceae and all monocotyledonous families besides Poaceae are nonmycorrhizal (Bothe 2012). This seems to contradict to the fact that many halophyte species are representatives of these families, and it is generally accepted that mycorrhizal symbiosis is an important factor for establishment of vegetation in coastal habitats (Logan et al. 1989). Absence of arbuscules in mycorrhizal structures of plant roots is often used as an indication of nonfunctional relationship (Koske and Gemma 1990), but presence of intensively branched hyphal structures and arbuscules indicates active exchange between the symbionts, while vesicular structures point to resource storage (Brundrett 1991).

Detailed analysis of a problem related to mycorrhizal vs nonmycorrhizal nature of certain taxonomic plant groups is outside the scope of this review, but some examples need to be provided to understand methodological problems of functional evaluation of this type of plant-microorganism interactions in coastal habitats. *Triglochin maritima* is a typical halophytic species, often characterized as nonmycorrhizal (Hildebrandt et al. 2001). However, *T. maritima* showed morphological structures in roots characteristic for functionally active mycorrhizal symbiosis (arbuscules, linear hyphae, vesicles with storage lipid inclusions), but mycorrhizal intensity was below 5% (Fig. 7.1; Druva-Lusite and Ievinsh 2010). When seasonal trend of intensity and frequency of mycorrhizal symbiosis was analyzed, it appeared that *T. maritima* had extremely low level of mycorrhization at the beginning of the vegetation season, increasing up to 20% intensity in July with tendency to decrease further, but arbuscules appeared only in July further increasing up to 25% in September (Karlsons et al. 2017). Several additional plant species from coastal habitats often suggested as nonmycorrhizal were identified as having mycorrhizal structures in their roots, including *Bolboschoenus maritimus* and *Silene borysthenica* (hyphal coils and vesicles), *Phleum arenarium* and *Trifolium fragiferum* (vesicles), and *Alyssum gmelinii* (hyphal coils, vesicles, and arbuscules),

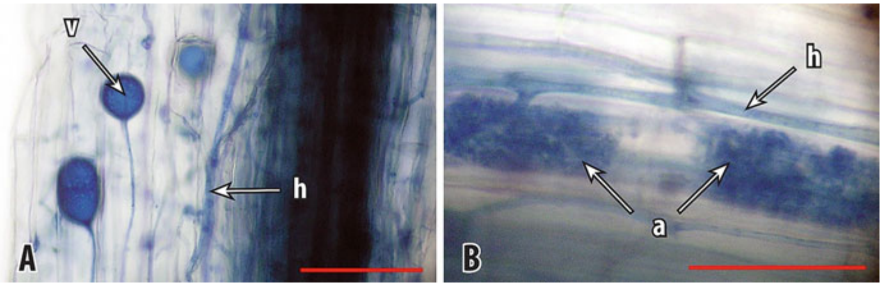

Fig. 7.1 Structures of arbuscular mycorrhiza in root fragments of a salt marsh plant *Triglochin maritima* showing vesicles and hyphal fragments (**a**) and arbuscules (**b**). *h* hyphae, *v* vesicles, *a* arbuscules. Bar indicates 100 μm. Reproduced with permission from Druva-Lusite and Ievinsh (2010)

suggesting functionally active symbiotic relationship (Druva-Lusite and Ievinsh 2010). Therefore, it can be suggested that low intensity of mycorrhization together with presence of typical morphological characteristics of functionally active symbiosis indicates effect of adverse environmental conditions on a fungal component.

In a series of studies aimed to establish functional diversity and importance of mycorrhizal symbiosis for rare and endangered coastal plant species of the Baltic Sea, it was established that differences in intensity of symbiosis and variability of anatomical structures found in roots were higher for plant species from wet coastal habitats in comparison to these growing in dry habitats (Andersone et al. 2011; Druva-Lusite and Ievinsh 2010; Druva-Lusite et al. 2008; Druva-Lūsīte et al. 2020; Karlsons et al. 2017; Samsone et al. 2009). Among the most important factors affecting functional aspects of mycorrhizal diversity were soil flooding and changes in soil salinity, but not availability of plant mineral nutrients. From these two factors, high salinity usually had more negative effect on mycorrhizal symbiosis in comparison to soil flooding, leading to significant decrease in intensity of colonization and changes in fungal diversity (Karlsons et al. 2017). However, for species with relatively high level of physiological adaptation to conditions of a coastal salt marsh, as *Hydrocotyle vulgaris*, mycorrhizal symbiosis was stimulated by moderately increasing soil salinity and suppressed by relatively high salinity (Druva-Lūsīte et al. 2020). When soil salinity as environmental factor was excluded, *H. vulgaris* plants from sites with higher intensity of photosynthetically active radiation had higher intensity of mycorrhizal colonization in roots.

Significant evidence has accumulated within recent years on a role of mycorrhizal symbiosis in plant adaptation to adverse environmental conditions in addition to its significant role in mineral nutrient and water acquisition. An excellent review aimed at summarizing role of arbuscular mycorrhiza in salinity tolerance of halophytic plants emphasized the complexity of ecological aspects of the symbiosis (Bothe 2012).

Mycorrhizal fungi-produced soil particle-binding glomalin is a significant factor contributing to soil aggregate stability, which is important for soil C sequestration (Blanco-Canqui and Lal 2004) and maintenance of sustainable soil structure (Six et al. 2006). Glomalin appears to be tightly bound in cell walls of hyphae and spores and is released in soil as a result of hyphal destruction but not through secretion (Driver et al. 2005). Importance of mycorrhiza-released glomalin in aggregate formation in coastal soils has been shown (Zhang et al. 2020a, b). In particular, concentration of glomalin-related soil protein positively correlated with intensity of mycorrhizal colonization. Being an insoluble molecule with glue-like properties, glomalin is very stable in soil conditions, but its concentration fluctuates seasonally (Zhang et al. 2020a, b).

7.4 Nitrogen Cycle in Coastal Habitats

7.4.1 Nitrogen Cycle: Nitrification and Denitrification

In general, coastal salt marshes, similar to other wetland systems, are hotspots of nitrogen cycling (Bai et al. 2017). Bacterial-dependent nitrification and denitrification form the basis of nitrogen cycling in coastal salt marsh habitats (Thompson et al. 1995). These processes are clearly spatially and temporally variable and dependent on dominant plant species (Cornwell et al. 1999; Eriksson et al. 2003). Denitrification is performed by facultative anaerobic soil microorganisms and leads to reduction of nitrate to gaseous nitrogen. Coastal wetlands as partially hypoxic systems significantly contribute to atmospheric N_2O formation through denitrification processes. Denitrification as heterotrophic activity depletes soil organic carbon pool, acting as electron donors for denitrification process. Nitrite and nitrate reduction (denitrification) in anaerobic coastal soils is associated with CH_4 oxidation, linking nitrogen and carbon cycles (Zheng et al. 2020).

Similar to other microbial processes, denitrification activity is highly vulnerable to increased soil salinity. It seems that in coastal wetlands, seawater flooding vs freshwater intrusion leads to significant fluctuations in denitrification activity as a result in changes of microbial community composition (Huang et al. 2021). Higher flooding frequency causes higher denitrification rates in salt marshes, and the process was further accelerated by high organic matter and NO_3-N content (Bai et al. 2017).

Vegetation strongly affects denitrification rate in coastal salt marshes. Change of plant species composition through invasion of exotic species can significantly alter composition of microbial community and, consequently, activity of soil biochemical processes. Thus, presence of invasive *Spartina alterniflora* as dominated vegetation increased total denitrification rate 5.5 times through significant increase in denitrifying bacteria richness and diversity (Zhang et al. 2020a, b). These plants accumulate extremely large biomass in comparison to native species and are characterized by presence of aerenchyma promoting rhizosphere oxygenation, and resulting increase in total soil organic carbon and available phosphorus seems to be positively related to increased denitrification. While total soil nitrogen significantly decreased with dominance of *S. alterniflora*, balance between particular forms of N changed, appearing as decrease in nitrate and increase in ammonium concentration.

In addition to denitrifying bacteria, also filamentous fungi can have important role in denitrification. It was shown that *Aspergillus* sp. greatly contributed to total denitrifying activity in *Spartina alterniflora*-dominated coastal wetland (Zhang et al. 2020a, b).

One important aspect of plant-dependent denitrification control and, more broadly, the rate of decomposition of organic matter is related to negative effect of plant litter with high concentration of phenolic substances (Bridgham and Richardson 2003; Dodla et al. 2008).

Wet saline coastal habitats (wet meadows and salt marshes) could differ significantly from dry coastal habitats in respect to features of nitrogen cycle. However, the latter have not been intensively studied in this respect, especially, at the level of microbial activity. Low capacity for mineralization and nitrification in sand dune soils is long proposed to be the processes leading to low concentration of plant-available nitrogen limiting plant growth (Kachi and Hirose 1983). It is interesting to note that existence of a clear gradient in soil nitrogen concentration and nitrogen mineralization intensity along a coastal dune succession has been used as a classical proof for increase of nutrient conservation ability during the course of succession (Gerlach et al. 1994).

Many of bacteria involved in mineralization of organic matter and N turnover could have additional potential effects on plant growth. In the view of applied agrobiotechnology, these microorganisms are known as plant growth-promoting rhizobacteria (PGPR). Use of PGPR could benefit plants through increase of availability of mineral elements in soil or production of biologically active substances, acting as growth promoters or elicitors of general defense responses (for a review, see Pii et al. 2015). However, in the context of the present review, free-living rhizosphere bacteria in coastal habitats could be essential constituents of biotic interactions between plants and microorganisms, being important for establishment of vegetation and maintenance of physiological adaptations to highly heterogeneous conditions (Otlewska et al. 2020).

7.4.2 Nitrogen Cycle: Biological Nitrogen Fixation

Nitrogen is one of the essential plant macronutrients, which has been shown to be a limiting factor in soils of many ecosystems, including dry coastal habitats. Plant species of legume family (Fabaceae) have developed biologically rather unique ability to form symbiosis with nitrogen-fixing bacteria. Important contribution of biological N fixation to nitrogen availability at early stages of vegetation establishment in coastal dunes has been proposed as based on N accumulation vs atmospheric deposition rates (Jones et al. 2008). While cover of symbiotic legume species in dune systems can reach up to 11% (Jones et al. 2002), the major relative contribution to biological N fixation in soil seems to be by cyanobacteria (Jones et al. 2008). Similar to inland desert systems (Russow et al. 2008), biological soil crusts on coastal dunes with high diversity of cyanobacteria and algae (Schulz et al. 2016) are major contributors to soil nitrogen pool in mostly N-limited conditions of sand dunes. However, it seems that in more dynamic conditions of sand overflow as in embryonic and primary sand dunes on active coasts, free-living rhizospheric microorganisms are of main importance.

Coastal legume species from different habitats seems to be specifically dependent on symbiosis with N-fixing bacteria. Perennial species of clover, *Trifolium fragiferum*, is found in Northern Europe exclusively in salt-affected wet coastal meadows. In controlled conditions, the species showed pronounced dependence on

Fig. 7.2 Effect of symbiotic N-fixing bacteria on morphology of *Trifolium fragiferum* plants after 25 days of cultivation. From left to right: asymbiotic plant, plant inoculated with bacteria from *Trifolium fragiferum*, plant inoculated with bacteria from *Trifolium repens*. Courtesy G. Ievinsh

Fig. 7.3 Effect of symbiotic N-fixing bacteria and sand accretion on morphology of *Anthyllis maritima* plants after 6 weeks of cultivation. –, asymbiotic plant; +, symbiotic plant; numbers indicate sand accretion intensity. Courtesy G. Ievinsh

bacterial symbiosis. When cultivated asymbiotically at identical level of plant-available mineral nutrients, *T. fragiferum* plants had decreased leaf chlorophyll concentration, lowered growth potential, and altered pattern of ion accumulation (Fig. 7.2). Another coastal legume species, *Anthyllis maritima* from primary sand dunes, was greatly affected by asymbiotic cultivation in controlled conditions, expressed as decreased leaf chlorophyll concentration, altered growth, and changes in responses to sand burial (Fig. 7.3).

A broader ecological significance of symbiotic N fixation by coastal legume species can be proposed, as a significant part of fixed nitrogen compounds is stored in nodule structures and can significantly improve soil N availability after release from decayed nodules in a N-limited coastal habitat. Non-legume species can have an advantage from growth in a direct presence of N-fixing legume species, as a significant part of symbiotically fixed N can be transferred through soil (Mahmud et al. 2020).

7.5 Drift Line Vegetation and Sea Wrack Deposits

Drift line vegetation on coasts of the Baltic Sea and other parts of the world is one of the least studied aspects in coastal biology. Studies at the plant community level have been made on a local scale in Latvia (Laime and Tjarve 2012), but no functional assessment has been performed so far. In a study comparing various beach and foredune habitats on the Atlantic (the Netherlands) and Mediterranean (Italy) coasts, it was found that annual vegetation of drift lines showed a high structural and certain floristic similarity between both sites (Feola et al. 2011). Spatial segregation and temporal instability of drift line communities in nature make them especially vulnerable and difficult to assess functionally. Historically, most closely but only partially related to drift line vegetation were studies on cycling on organic matter and minerals in a sea-shore meadow, aiming also to understand the role of various types of litter as related to plant biomass accumulation (Tyler 1971; Wallentinus 1973).

Beach drift line material or wrack (phytodetritus) is an important constituent of chemical element cycling in coastal ecosystems with a critical role as an environment for microorganisms and invertebrate animals (Lastra et al. 2015). Most importantly, in the context of the present review, it represents a crucial source of fertilization for establishment of beach vegetation, and it can also carry seeds of coastal plant species. Composition of wrack material itself is very variable and depends on many abiotic and biotic factors, but it is important to note that in general it can contain (1) detached aquatic macrovegetation from sea (both algae and aquatic vascular plants); (2) drifting macroalgae from sea; (3) plant litter from shore washed to sea during seasonal storms or other high wave events, containing also seeds of terrestrial plants; and (4) vegetative propagules of terrestrial plants. Deposited material can be washed back to sea repeatedly during high water events, especially, when its buoyancy has increased after drying on beach (Mews et al. 2008).

From a plant point, drift line material-associated species are usually considered as nitrophilous, because of relatively high growth rates, especially, in comparison to typical embryonic dune and foredune species, and growth stimulation by nitrogen compounds (Jefferies 1977; Moreau et al. 2013). From a microbiological point, nitrogen-rich organic drift line deposits at the beginning of the vegetation season contain mostly organic forms of nitrogen; therefore, plant growth will depend on microbiological activity of nitrogen mineralization and nitrification. It can be hypothesized that high microbiological activity early in the season, including ammonification and nitrification, is important for successful establishment of vegetation. However, these reactions can be greatly altered in anaerobic conditions as in the case of substrate inundation, especially, in a form of seawater, when reductive processes can prevail, leading to significant changes in plant availability of mineral elements (Schat 1984). In addition, both free-living and symbiotic nitrogen-fixing bacteria convert gaseous nitrogen into ammonia, but leguminous species with symbiotic rhizobacteria only seldom appear in drift line plant communities (only examples in temperate zone include *Anthyllis maritima*, *Medicago lupulina*, and *Vicia cracca*; Laime and Tjarve 2012). Consequently, mainly free-living nitrogen-fixing bacteria could have functional contribution to drift line nitrogen budget in addition to the wrack itself.

To further illustrate the complexity of reactions related to N turnover, it has been shown that bacteria release urea and amino acids (e.g., alanine) and their conjugates (e.g., glycine betaine, especially, in saline conditions) (Ventosa et al. 1998; Vranova et al. 2011). In this context, it is interesting that typical salt marsh species (e.g., *Salicornia europaea* and *Aster tripolium*) are capable for uptake of wide range of nitrogen compounds, including dissolved organic forms of nitrogen, as amino acid alanine (Quintã et al. 2014). In addition, plants have less characterized ability for uptake of quaternary ammonium compounds, including betaine (Warren 2013). This can have further consequences in respect to plant adaptations, as mineral nutrient availability in general and presence of different forms of nitrogen have been shown to affect plant salinity tolerance (Barhoumi et al. 2010).

In Europe, specific drift line vegetation is classified as “annual vegetation of drift lines” (EUH code 1210; Fig. 7.4). However, in a result of wider analysis, it becomes clear that not only this specific habitat type but also other coastal habitats can be significantly affected by drift material accumulation. Several types of drift material-affected coastal microhabitats can be distinguished in nature, the differences between them being due to coastal geomorphological processes, leading to formation of various types of plant associations (Fig. 7.5). An option featured in Fig. 7.5a represents classical case of drift line vegetation, formed on active coasts on sandy beach, consisting mostly of annual plants (*Atriplex* spp., *Cakile maritima*, *Chenopodium rubrum*), where stable conditions necessary for plant establishment and growth are rather temporary. These habitats are scattered along the beach and can be formed and destructed several times during a single vegetation season. A variation of this habitat can be found on less active sandy beach coasts, where seasonal fluctuation of sea level results in formation of relatively permanent puddles or small lagoons (Fig. 7.5b). Accumulation of drift material, followed by other organic sediments, results in formation of slightly more enduring vegetation complexes on wetter substrate, where there is an appearance of both annual and short-lived perennial plants. In addition to *Atriplex* spp., *Cakile maritima*, and *Chenopodium rubrum*, wider range of other annual and some perennial species appear, including *Agrostis stolonifera*, *Bidens tripartita*, *Chenopodium album*, *Polygonum lapathifolium*, *Potentilla anserina*, *Salsola kali*, etc. (Fig. 7.6). Typical macrophytic species appear in places where presence of water is more or less stable, including *Ranunculus sceleratus*, *Scirpus tabernaemontani*, and *Typha latifolia*, but evidently these are less affected by accumulation of drift material. On relatively passive rocky (Figs. 7.5c and 7.7) and sandy or shingle beaches (Fig. 7.5d), localization of typical drift line vegetation closer to a coastline is accompanied by

Fig. 7.4 European Union protected habitat "annual vegetation of drift lines" (EUH code 1210) with dominating *Atriplex* ssp. Coast of the Riga Gulf of the Baltic Sea, Jūrmala, near estuary of river Lielupe, Latvia. Courtesy G. Ievinsh

development of wet coastal meadow, somehow affecting also species composition on drift lines, leading to appearance of several typical coastal marsh species *Tripolium pannonicum* subsp. *tripolium* (syn. *Aster tripolium*), *Plantago maritima*, and *Triglochin maritima*, among others. On relatively passive coasts where geomorphological conditions lead to formation of depressions in a beach zone or close to it, instead of wet coastal meadow, development of salt marsh is evident (Fig. 7.5e). While this habitat mainly depends on secondary accumulation of organic matter, in zones of terrain changes, accumulation of primary drift material can occur, leading to

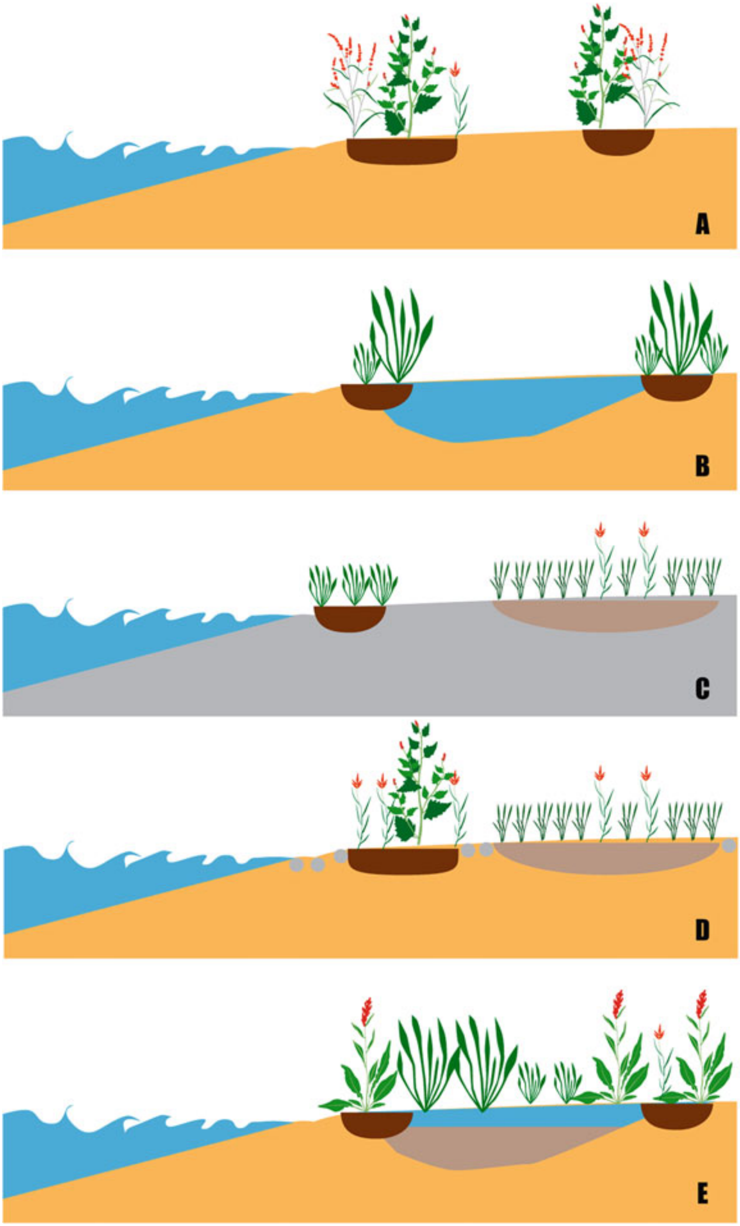

Fig. 7.5 Coastal habitats of the Baltic Sea with significant dependence on accumulation and dynamics of drift (wrack) material. (**a**) annual vegetation on drift lines in sand beach on relatively active coast, (**b**) annual and short- or medium-term perennial vegetation in poodles and lagoons on less active coasts, (**c**) short- or medium-term perennial vegetation on stable shingle or rocky beaches with development of stable perennial vegetation further from the coastline (coastal meadow), (**d**) annual and short- or medium-term perennial vegetation in poodles and lagoons on less active coasts, (**e**) medium- and long-term perennial vegetation in passive sand beaches with development of salt marsh. Brown areas indicate current accumulation of drift material; light brown areas indicate secondary accumulation of organic material

Fig. 7.6 Vegetation complex of annual and perennial plant species around and within a relatively permanent puddle. Coast of the Riga Gulf of the Baltic Sea, Ainaži, Latvia. Courtesy G. Ievinsh

Fig. 7.7 Wrack material-dependent vegetation on a rocky beach with dominating *Tripolium pannonicum* subsp. *tripolium* (syn. *Aster tripolium*). Coast of the Baltic Sea, Ohessaare, island of Saaremaa, Estonia. Courtesy G. Ievinsh

formation of more or less typical drift line vegetation. Another aspect with importance for ecology and biogeochemistry of coastal ecotone is that both amount and species composition of wrack material change with beach type, evidently being affected by substrate type (sand, gravel, pebbles) and intensity of wave exposure (Orr et al. 2005).

Several lines of evidence prove the relationship between beach wrack deposition and vegetation development. From a rather simple point of coastal habitat restoration management, it has been shown that preserving sea deposits on beach and refraining from mechanical raking lead to spontaneous restoration of embryonic and even primary white dunes as a result of initial development of sea deposit-dependent annual pioneer vegetation of halo-nitrophilic plants (Lemoine and Faucon 2005). The whole-island survey of relationship between seagrass wrack accumulation and structure and diversity of coastal dune vegetation has been performed in Sardinia, Italy (Del Vecchio et al. 2017). In general, beaches with high intensity of wrack accumulation showed significantly larger vegetation cover as well as higher plant species diversity. Importantly, this effect was more pronounced in nearshore zone, evidently diminishing inland. Results of chemical analysis of concentration of different forms of nitrogen (inorganic vs organic) in sand beaches in conjunction with quantification of sea wrack input indeed showed high correlation between the input and dissolved nitrogen content, further supporting the view that pioneer beach vegetation is largely dependent on transformation of organic matter from sea deposits (Dugan et al. 2011; Rodil et al. 2019).

Colonization of wrack material by invertebrates and microorganisms is an initial stage of wrack decomposition, further leading to release of plant-available mineral elements (Olabarria et al. 2007). It is evident that fragmentation of organic matter by feeding invertebrates leads to mixing with microorganisms and increase in surface area, benefiting decomposition processes (van Egmond et al. 2019). Arthropods (mainly dipterans and spiders) are also suggested as vectors transporting wrack material inland, leading to secondary stimulation of vegetation development (Mellbrand et al. 2011). Creation of favorable conditions (stabilization of humidity, temperature, etc.) is contributed by burial of wrack material by sand, and this appears to be a crucial factor for maintenance of plant growth (van Egmond et al. 2019).

Similar to terrestrial plant litter, also sea wrack material containing macroalgae and vascular plants is a rich source of phenolic compounds. Initial phenolic concentration depends on macrophyte species; during initial decomposition phase on beach, concentration of phenolic compounds in wrack material significantly decreases (Gómez et al. 2011). Differences in chemical composition of wrack material can explain frequently found species-specific decomposition rates of wrack samples (Mews et al. 2008).

There is no information available in the scientific literature on rhizosphere microbiological characteristics in drift line habitats. There are some studies on microbial community structure and functional characteristics in freshwater wetland and also in salt marsh habitats though. Thus, it was shown that wetland plant species are important determinants of microbiological communities in rhizosphere, further affected by differences in environmental factors (Clairmont et al. 2019). In typical

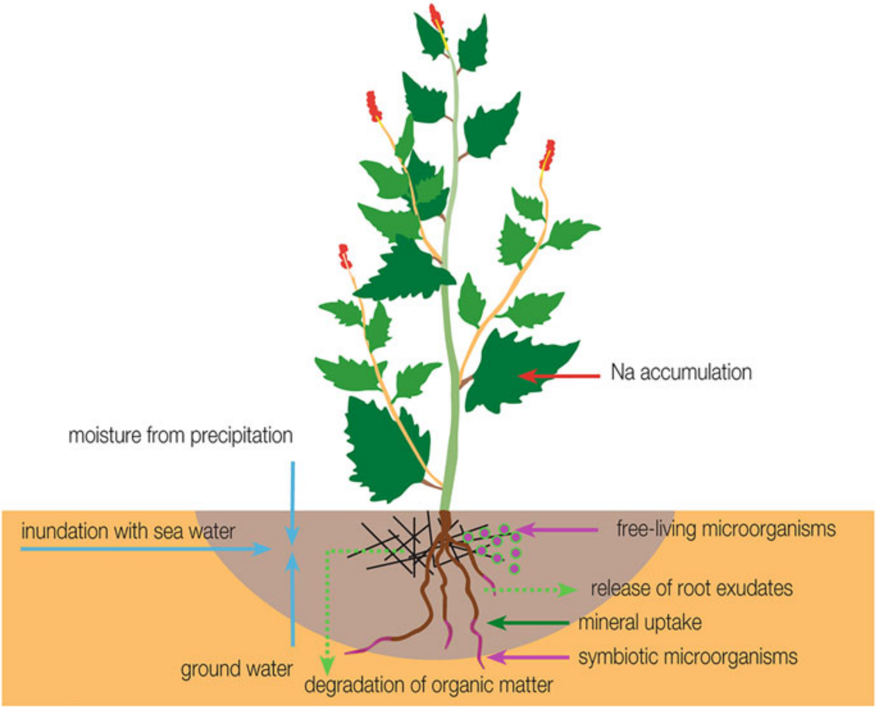

Fig. 7.8 Functionally important plant biotic and abiotic interactions for habitat sustainability in drift line material-affected vegetation

tide-affected coastal salt marshes, there are significant changes in composition and eco-functional characteristics of fungal community along the successional gradient, with soil structure and organic matter content being important determining factors (Dini-Andreote et al. 2016). Therefore, it is more likely that microbiological characteristics in drift line habitats will be significantly affected by plant species, seawater-related changes in soil salinity, as well as nature of deposited drift line material.

Overview of functionally important plant biotic and abiotic interactions in drift line material-affected coastal habitats ensuring their sustainability is shown in Fig. 7.8. Most importantly, microbial community structure in salt-affected coastal habitats is significantly affected by plant species (Cong et al. 2011), which can be at least partially explained by secretion of different root exudates in a species-specific manner (Jing et al. 2019). The aspects of propagule material availability and control of seed dormancy were not included in this scheme. However, it is interesting to note that limited experimental evidence suggests that the main source of propagules in these habitats is drift line material itself (Wolters et al. 2017). Moreover, seeds of many coastal species are characterized by innate dormancy and ability to germinate even during or after prolonged exposure to salinity in freshwater conditions

(Neubauer et al. 2019). These adaptations could be important also for reproduction of typical drift line material-dependent plant species. Many typical coastal plant species are distributed along a coast by sea currents in a form of floating seeds and can be redistributed by the means of drift line material (Wolters and Bakker 2002).

7.6 Conclusions and Perspectives

It can be proposed that microbiologically dependent processes of organic matter decomposition in drift line habitats leading to mineralization of essential plant elements need to be relatively fast in order to ensure plant development. It seems that nitrophilous plant species characteristic for such habitats could have specific physiological mechanisms of adaptation of mineral nutrition. Together with N-fixing bacteria, either symbiotic or free-living, mycorrhizal symbiosis can be viewed as an important aspect to consider in respect to plant adaptation to highly heterogeneous environmental conditions of the sea coast habitats. With a special importance for a drift line-associated vegetation is a fact that a mechanism of codispersal involving both plant and mycorrhizal propagules is established in beach habitats (Koske and Gemma 1990). In addition, mycorrhizal fungi in a form of hyphae and spores can survive for a prolonged period of time in plant debris containing only dead rhizome fragments, which can act as fungal inocula for establishment of functional mycorrhizal symbiosis (Biermann and Linderman 1983).

From a point of plant reproduction, it is evident that a specific complex of biological mechanisms is necessary for establishment of drift line vegetation, involving both seed maturation, induction of dormancy, and dormancy release, possibly via seed-coat degrading microorganisms. Continuous fluctuation of salinity and soil moisture could have an important regulative role during sequence of these events. To get better insight in ecological mechanisms underlying vegetation establishment and maintenance in coastal habitats affected by drift line material (wrack) deposition, assessment of microbiological processes is of critical importance both at the level of functional activity and taxonomical diversity.

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Chapter 8
Soil Enzymes and Their Role in Nutrient Cycling

Neemisha and Sandeep Sharma

Abstract Soil is a dynamic living non-renewable resource that acts as an interface between agriculture and environment. Soil enzymes play critical role in soil processes ranging from biochemical reactions in plants, animals, and microbes to decomposition of organic matter, soil structure stabilization and nutrients cycling. Different microbes and enzymes are involved in cycling of carbon (C), nitrogen (N), phosphorus (P), and sulfur (S) in an ecosystem. The nutrient cycles function as a result of biological and physico-chemical reactions in soil. The nutrients cycling in an ecosystem are primarily governed by soil microbes and enzyme activities. The biochemical reactions of these cycles are accomplished by enzymes such as amidases, arylsulphatase, cellulases, dehydrogenase, glucosidases, laccase, phosphatases, and urease. These enzymes serve as biological indicators that help to identify variations in soil physical, chemical, and biological properties. Enzymes respond faster to soil management practices long before other soil quality indicator changes are detectable and their method of detection is simple, easy, and quick. In this chapter, we will discuss about the major enzymes involved in the cycling of C, N, P, S, and their mechanisms of action, role in maintaining soil health and factors that affect their activities in soil.

Keywords Soil enzymes · biochemical reactions · organic matter · nutrients cycle

8.1 Introduction

Soil being an essential resource to biosphere and human beings, is also among the most complex and least understood systems. In soil several biological indicators (soil respiration, microbial biomass, soil fauna, soil organisms (abundance, diversity, structure, community, and food web) etc. are used to assess the quality of soil (Alkorta et al. 2003). Soil organisms respond quickly to agricultural management

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B. Giri et al. (eds.), *Structure and Functions of Pedosphere*,
https://doi.org/10.1007/978-981-16-8770-9_8

practices and climate change. Several useful soil and ecosystem functions are associated with soil organisms such as nutrients cycling, decomposition of organic matter, detoxification of toxicants, suppression of harmful and pathogenic organisms. Microbes and plants secrete certain enzymes into the soil that catalyze specific reactions to release nutrients and the plant growth depends positively on these nutrients (Kandeler et al. 2011). Majority of microbes exist in soil as communities, where they interact in close association with the soil environment. The extracellular enzyme secreted by these organisms play crucial role in transformations of C, N, P, and S at elementary level of nutrient cycling. As compared to physico-chemical parameters of soil, the enzyme activities have been considered as sensitive indicators for soil quality and health (Gelsomino et al. 2006). Plants provide suitable environmental conditions, microhabitats and food reserve for these microorganisms to grow in the rhizosphere (Prober et al. 2015) which in-turn forms various associations with plants like symbiosis, ecto-mycorhizza and endo-mycorhizza and improve the nutrient supply to the plants and ultimately increase their yield (Abbott et al. 2015). The plant–microbe interaction in the rhizosphere control the processes like mineralization, transformation of nutrients, organic matter decomposition and agrochemical degradation and improve the soil fertility (Glick 2010; Rajkumar et al. 2013; Song et al. 2019).

Biological indicators are the most informative agents that tell us about the processes and functions mediated by soil organisms. Bacteria, fungi, and plant roots, are primarily responsible for secreting enzyme and hence make possible the flux of C, N, and other essential elements in biogeochemical cycles. The first stage to characterize soil metabolic potential, its quality, fertility, and resilience (natural and anthropogenic factors) is through measuring enzymatic catalysis, understanding the factors that regulate enzyme expression and to determine rates of substrate turnover. A better understanding of the role of soil enzymes activity in the ecosystem will potentially provide a unique opportunity for developing an integrated biological assessment of soils. Moreover, soil biological activities are easy to measure, and produce a rapid response to changes in soil management practices (Caldwell 2005). A good ecological indicator must meet certain conditions (Dale and Beyeler 2001) as: easy measurements, low variability in response, sensitivity to managements and environmental changes, ability to produce consistent, reproducible, and predictable responses to the changes. Moreover, the procedures for enzyme assays are simple and quick. The extracellular enzymes produced by microbes brings about processing and recovery of key nutrients from detrital inputs and accumulated soil organic matter into assimilable subunits (sugars, amino acids, NH_4^+, PO_4^{-3}) (Caldwell 2005). Bacteria are the most abundant microorganisms present in the soil with population of 10^7–10^9 per gram soil and fungi has the highest biomass. They secrete various enzymes and are able to either mineralize or partially transform the toxic metabolite into non-toxic form in the soil, where it gets immobilized as humic acid (Murphy 2016). Soil contains free enzymes, immobilized extracellular enzymes and enzymes within microbial cells (intracellular enzymes). Soil enzymes increase decomposition rate of plant residues and help in the release plant-available nutrients.

They serve as catalysts that increases the rate of chemical reactions (Tabatabai 1994) however, they are influenced by several cultural management practices.

8.2 Enzymes Involved in Carbon Cycle

Carbon is critical element that contributes for proper functioning and productivity of an ecosystem. Carbon adds quality and life to soil ultimately prevailing healthy conditions in soil system. The availability or release of carbon is mainly dependent on soil management. In C-cycling soil microbes work in soil to decompose the organic matter (Plant/animal) and convert it into simpler forms. This conversion is brought about by several enzymes which work on different constituents of plants and animals. Some of these enzymes that specifically act on specific components of plant and animals are cellulase, hemicellulase, laccase, chitinases, and invertase.

8.2.1 Cellulase

Cellulose is a linear polymer made up of β-1,4 linked glucose molecules and cellulases are the enzymes that catalyze the degradation of cellulose. Cellulose is the most abundant biopolymer in plant cell walls (Lynd et al. 2005). Naturally, a combination of three enzymes causes hydrolysis of cellulose and these are endoglucanases, exoglucanases, and β-glucosidase (Yang et al. 2013). Among these, the most common, important, and widely used soil quality indicator is β-glucosidase (Bandick and Dick 1999) which is found in microbes (bacteria, yeasts, and fungi), plants, and animals. The last stage of cellulose degradation process is carried out by β-glucosidase where cellobiose residue is hydrolyzed (Gil-Sotres et al. 2005). The hydrolysis and biodegradation of various β-glucosides in plant debris is carried out by β-glucosidase and the final product is glucose which serves as the energy source for growth and activity of several microbes in the soil (Esen 1993; Merino et al. 2016). β-glucosidase, is considered as one of the most important enzyme for soil quality testing. Cellulase activity in soil is determined on the basis of degradation of substrates such as the cellulose polymer of cellophane, carboxy methyl cellulose, cellulose powder and filter paper assay, and its activity is measured by the DNS method (Pancholy and Rice 1973).

8.2.2 Amylase

Starch is a polymer of glucose linked by α (1 → 4) glycosidic bonds and it is hydrolyzed by enzyme amylase. Amylases are classified into two types: α- and β-amylase. α-Amylase is produced by microorganisms, plants, and, animals, whereas, β-amylase is produced only by plants. α-Amylase breaks α (1 → 4) glycosidic bond of starch molecule, resulting in the formation of dextrins (Thoma et al. 1971). β-Amylase breaks down starch resulting in the formation of maltose which is further hydrolyzed to glucose units by maltase. The activities of amylase are dependent on several factors including cultural practices, type of vegetation, environment, and soil types. Amylase activities of soil may be directly influenced by the enzyme and exudates secreted by the plants or indirectly by synthetic activities of microorganisms (Ross 1975; Makoi and Ndakidemi 2008).

8.2.3 Chitinase

Chitinases are glycosyl hydrolases that catalyze the hydrolytic cleavage of the β-1,4-glycoside bond present in bioplolymers of *N*-acetylglucosamine (Collinge et al. 1993). Chitin is the second most abundant polymer in nature after cellulose (Singh et al. 2016). Chitinases are widespread in nature however, their functions are confined to type of organism. They are present in as bacteria and fungi (nutritional needs), plants, and animals (defence against pathogen attacks) and viruses (Singh et al. 2016). Chitinases are classified as endochitinases and exochinases. Endochitinases cleave chitin randomly at internal sites, forming soluble low molecular massmultimers of β-1,4-linked *N*-acetylglucosamine and exochitinases are further classified into two types as chitobiosidases (release of diacetylchitobiose) and 1,4-β-*N*-acetylglucosaminidases (cleave endochitinases and chitobiosidases to β-1,4-linked *N*-acetylglucosamine (Sahai and Manocha 1993; Botha et al. 1998; Singh et al. 2016). Plant chitinases play major role by providing defence mechanism against pathogens either by secreting antifungal substances or by eliciting plant defensive responses (Suarez et al. 2001; Gomez et al. 2002). Chitinases helps to convert chitin-containing biomass into depolymerized products, control of insect and fungal pathogens of plants and serves as an indicator of the actively growing fungi in the soil.

8.2.4 Laccase

Laccase is a multi-copper oxidase that catalyzes the oxidation of one electron of wide range of phenolic compounds. They need molecular oxygen as co-substrate and release water, so they are considered as eco-friendly enzymes. Laccases are widely disturbed in higher plants, bacteria, fungi, lichens, and insects. It is very important enzyme of carbon cycle as it is involved in the degradation of several xeno-aromatics. Lignin like complex polymers are mainly degraded by laccase producing white-rot fungi along with other extracellular oxidases (Baldrian 2006; Thurston 1994; Claus and Filip 1988). Laccase has significant role in both lignification and delignification due to its ability to bring about polymerization and depolymerization of compounds (Hatakka 1994; Strong and Claus 2011).

8.2.5 Hemicellulase

Hemicellulase (endo-1,4-β-xylanase) enzymes are mainly responsible for decomposition of the polysaccharides of xylose. These are involved in decomposition of the hemicelluloses into short chain glycosides.

8.2.6 Invertase

Invertase catalyzes the hydrolysis of sucrose to glucose and fructose under either acidic or alkaline conditions. This enzyme is present in several organisms as bacteria, actinomycetes, fungi, plants, and animals.

8.3 Enzymes Involved in Nitrogen Cycle

Nitrogen is the most limiting nutrient that is required by the crops in huge quantity. The nitrogen cycle consists of four main steps: nitrogen fixation, ammonification, nitrification, and denitrification. Different microbes and their enzymes completes this cyclic process (Fig. 8.1)

8.3.1 Amidohydrolases

Amidohydrolases are involved in hydrolysis of C–N bond of amides native and added organic N to soils. These include amidase, L-glutaminase, L-asparaginase, and urease that release ammonium into the environment. L-asparaginase catalyzes the hydrolysis of L-asparagine to produce L-aspartic acid and NH_3 and it is mostly found in microorganisms. Whereas, L-glutaminase, catalyze the hydrolysis of L-glutamine to L-glutamic acid and NH_3 and it is widely distributed in plants, animals, and microorganisms (Bacteria, fungi, and yeasts). Estimation of L-asparaginase in soil is used to understand the impact of soil management on N cycling in agricultural ecosystems (Kandeler et al. 2011).

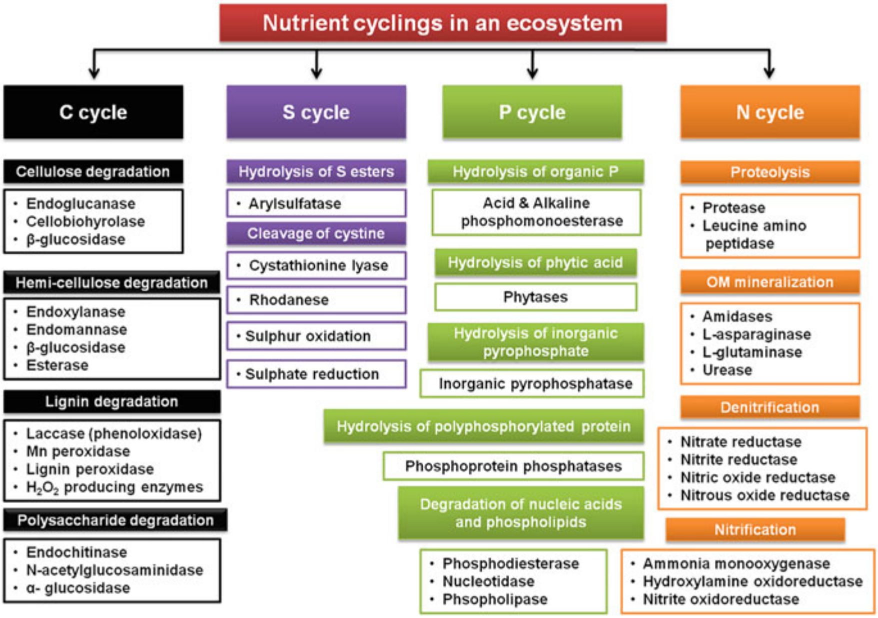

Fig. 8.1 Nutrient cycling of different elements and enzymes associated with these elements

8.3.2 *Amidase*

Amidase (acylamidase, amidohydrolase, acylase, and deaminase) catalyzes the hydrolysis of carbon–nitrogen bond of aliphatic amides producing ammonia and their corresponding carboxylic acids. The enzyme works well at optimum pH of 8.5 and inactivates at temperatures above 60 °C. The substrate of this enzyme is aliphatic amides (formamide, acetamide) from synthetic nitrogeneous fertilizers and aromatic amides. This is an inducible enzyme in presence of substrate increases in concentration. Amidases are classified on the basis of catalytic activity (seven types: D-aminopeptidase, aliphatic amidases, aromatic amidases, enantioslective amidases, α-amino amidase, arylalkylacyl amidases, wide spectrum amidases), amino acid sequence (two types: signature amidases and aliphatic amidases) and phylogenetic relationship (two types: aspartic proteinases and sulfhydryl enzymes) (Chebrou et al. 1996; Pace and Brenner 2001; Fournand and Arnaud 2001; Pertsovich et al. 2005). Amidases play very important role in soil because their distribution in soil profiles helps in reducing the rates of hydrolysis of N fertilizers applied. Ammonia and carboxylic acids are by products of amidase action that serves important role in soil nutrient cycling, metabolic processes and N mineralization. This enzyme controls N in ecosystems contributes toward assessing soil degradation or quality.

8.3.3 Urease

Urease enzyme hydrolyzes urea to ammonia and carbon dioxide. This reaction increases the pH of soil and causes instant loss of N through volatilization of NH_3 (Zhang et al. 2014). Urease is produced intra as well as extracellularly in soil microbes and plants. Several factors affect urease stability in soil such as their association with soil organo-mineral or humus-urease complexes is more stable and highly resistant to higher temperatures and proteolytic attack. In agricultural soils urease activity detect N mineralization when soil is amended with organic material. The urease activity is affected by soil properties that include soil nutrient supply, soil pH, S_{MBN}, S_N, N fertilizers, tillage, agrochemicals use and cropping systems (Moghimian et al. 2017). The hydrolysis of urea occurs in the presence of soil enzyme urease and thus NH_4^+ is made available to the plants (Wang et al. 2008).

8.3.4 Proteases

Protease is widely distributed in nature and produced by plants, animals, and microbes through their metabolic activities. This enzyme brings about initial hydrolysis of protein bound to organic nitrogen to polypeptides and oligo-peptides to simple amino acids. The hydrolysis of proteins is an important step in the nitrogen cycle where proteases hydrolyze both native and added proteins in soil (Dedeken and Voets 1965; Raju et al. 2017). The addition of organic inputs increases protease activity in soil whereas, the treatment of crops with agrochemicals often reduces protease activity in soil (Raju et al. 2017).

8.3.5 Nitrification Enzymes

Nitrification is biological process of oxidation of ammonia to nitrite and nitrate in a two-step procedure which is mediated by microbes and their enzymes. In first step ammonia is oxidized to hydroxylamine by ammonia-oxidizing bacteria through monooxygenase enzyme followed by its conversion to nitrite by hydroxylamine oxidoreductase. The nitrite is further oxidized to nitrate by the nitrite-oxidizing bacteria through ammonia monooxygenase enzyme and this is the rate-limiting step in nitrification process (Kandeler et al. 2011).

8.3.6 *Denitrification Enzymes*

Denitrification process is a four step reaction where nitrate is reduced to dinitrogen gas. The first step consists of reduction of nitrate to nitrite by nitrate reductase; second step reduction of nitrite (NO_2^-) to nitric oxide by nitrite reductases; third nitric oxide is converted to nitrous oxide by nitric oxide reductase and finally nitrous oxide is converted to nitrogen by nitrous oxide reductase. Majority of prokaryotes (bacteria) have capability to reduce nitrate. Nitrate reductase activity helps in understanding greenhouse gas fluxes from terrestrial ecosystems.

8.4 Enzymes Involved in Phosphorus Cycle

Phosphorus (P) is essential to living organisms and it is found in two forms, organic and inorganic. Organic P contributes to plant mineral nutrition only after its dephosphorylation to release inorganic phosphate, which is of particular importance in phosphate-deficient natural or cultivated ecosystems. The cycling of P in soil dependent on immobilization, mineralization, and redistribution of P. Phosphatases are a broad group of enzymes that catalyze the hydrolysis of esters and anhydrides of phosphoric acid and also serves as good indicators of soil fertility (Acosta-Martínez and Tabataba 2011). Judicious use of P helps in plant growth, development and enhance yield and soil health however, its deficiency causes stunted growth and excess causes environmental implications. The recycling of P forms in soil is mainly mediated by phosphatases (Fig. 8.1) and through addition of manures and fertilizers, into free phosphates (PO_4^{3-}) that can be taken up by plants and soil microorganisms.

8.4.1 *Phosphatases*

Phosphatases catalyze the hydrolysis of both esters and anhydrides of phosphoric acid (Schmidt and Laskowski 1961). On the basis of number of ester bonds, these enzymes are classified into three types as phosphomonoesterases, phosphodiesterases, and phosphotriesterases (Acosta-Martínez and Tabataba 2011). Phosphatases are responsible for at least 50% of soils total P transformations. Phosphates are of different types such as acid and alkaline phosphomonoesterase, phosphoprotein phosphatases, phytases, nucleotidases, phosphodiesterases, phospholipases, and inorganic pyrophosphatase (Nannipieri et al. 2011). According to Burns et al. (2013) these enzymes are associated with active microbial cells, either intracellular or attached to the outer cell surface, extracellular, present in cell debris or dead cells or bacterial spores or entrapped in humic matter (Nannipieri et al. 2011). In soils, phosphatases mainly originate from soil microorganisms, however, they are also present in the rhizosphere (area around the roots where highest microbial activity is found under the influence of root exudates) and detritosphere (this is the area around decomposed plant material in soil, where microbial community and organic carbon fractions are different than rhizosphere). Higher activities of both acid and alkaline phosphomonoesterase are found near the rhizoplane and it is depended on type of soil, age of plant, and plant species (Tarafdar and Jungk 1987; Tabatabai and Bremner 1969). Phosphatase activity increases with the increase in organic matter content however, it decreases with soil depth (Tabatabai and Dick 1979). The phosphatase activity in soil is affected by soil properties, temperature management practices, tillage, application of manures or sewage sludge and pollutants, addition of fresh litter, and seasonal variation in moisture.

8.5 Enzymes Involved in Sulfur Cycle

Sulfur (S) is an essential nutrient required by microbes and plants and its fate in the soil is mainly dependent on microbial activities. S is an important component of S-containing amino acids (methionine and cysteine), sulfated carbohydrates, vitamins (biotin and thiamine), alkaloids (alicin), and functional molecules (glutathione) (Tabatabai 1994; Dotaniya et al. 2019). In soil, sulfur is present in two forms organic and inorganic S. Organic sulfur account for 90–98% which exists as organic sulfate S and carbon-bonded S forms. In plant, sulfur is taken up as inorganic sulfate and its availability is dependent on either mineralization or mobilization from organic sulfur (Makoi and Ndakidemi 2008). These transformation reactions are mainly catalyzed by enzymes released into the soil environment by microorganisms, plant roots, and soil fauna (Klose et al. 2011). Some of the enzymes involved in S cycle are mentioned in Fig. 8.1.

8.5.1 Arylsulfatases

The soil enzymes which bring about the conversion of organic S to inorganic S into soil solution are known as sulfatases. These enzymes are responsible for the S ester hydrolysis in soil. The synthesis of sulfatases in soil is induced by bacterial population in S-limiting conditions (McGill and Colle 1981). The population of aryl sulfatase is affected by S concentration, crop growth stage and bacterial population in soil. The release of sulfate from soluble and insoluble sulfate esters in the soil is affected by different factors such as pH of soil, organic matter, concentration of sulfate esters, and heavy metal pollution.

8.6 Enzymes as Indicators of Overall Microbial Diversity

8.6.1 Dehydrogenase

Soil dehydrogenases belong to the class oxidoreductase enzymes (Gu et al. 2009). Dehydrogenase (DHA) is a sensitive indicator of overall microbial activity in the soil as it brings about oxidation- reduction reactions in living cells (Alef and Nannipieri 1995; Majchrzak et al. 2016). These enzymes transfer hydrogen from organic substrates to inorganic acceptors and causes biological oxidation of SOM (Zhang et al. 2010). DHA do not accumulate extracellular in the soil. The external factors either stimulate or inhibit dehydrogenase activity in the soil. The factors that stimulate dehydrogenase activity are soil temperature, moisture, pH, aeration, organic matter content and season of the year. The factors that inhibit dehydrogenase activity of the soil are soil profile depth, fertilization and pesticide amendments and, heavy metal presence (Wolińska and Stepniewska 2012).

8.6.2 Fluorescein Diacetate Hydrolysis

Hydrolysis of the fluorescein diacetate (3′,6′-diacetylfluorescein) is used to estimate microbial activity in soil. FDA hydrolysis measures microbial decomposer activity and microbial decomposition and contribute to 90% of the energy flow in soil system therefore; it provides a good estimate of total microbial activity. This enzymatic reaction produces fluorescein, that can be quantified by spectrophotometry. FDA has been used to determine amounts of active bacteria, fungi, and acetylesterases in living cells (Schnürer and Rosswall 1982). FDA is hydrolyzed by three enzymes i.e., esterases, proteases, and lipases, which are involved in the microbial decomposition of organic matter in soil. FDA hydrolysis can be used efficiently to estimate microbial activity in soil having different types of cultural practices, organic and inorganic inputs and microbial inoculants (Sánchez-Monedero et al. 2008). Moreover, this enzyme helps in determining potential of the soil to support biochemical processes, which are essential for maintaining soil fertility as well as soil health (Patle et al. 2018).

8.6.3 Catalase

Catalase brings about conversion of hydrogen peroxide to water and oxygen. This redox enzyme system is very important for synthesis of soil humus and for preventing toxicity of hydrogen peroxide to soil enzymes.

8.7 Soil Enzymes in Ecosystem Functioning

8.7.1 Soil Enzymes as Bioindicators

A bioindicator is defined a microorganism, its part, its product (enzyme), collection of organisms, or biological process used to obtain information on the quality of all or part of the environment (Killham 2002). Soil enzyme activities provides an early indication of changes in soil quality and health due to any factors. In addition, soil enzyme activities can be used as a measure of soil productivity and fertility, an indicative of biological equilibrium in an ecosystem, to better understand changes in ecological processes within the soil ecosystem and an active indicator of soil pollution (Antonious 2003; Gunjal et al. 2019). These soil enzyme activities are influenced by both enviromental changes as well as soil fertility level. Soil organic carbon (SOC) is the key constituent of soil organic matter (SOM) and is considered as a good indicator of soil health. Soils with high SOM content are known to enhance water availability, aggregate formation, adequate aeration, improve porosity, water infiltration, deliver adequate quantity of nutrients to plants, improve soil fertility and enhance food production (Shah et al. 2020).

8.7.2 Soil Enzymes in Functioning of Nutrient Cycling

Soil enzymes regulate ecosystem functioning and in particular play a key role in nutrient cycling (Makoi and Ndakidemi 2008). Soil enzymes play a pivotal role in nutrients cycling as they perform several biochemical reactions that are necessary for the life processes of soil microbes and also maintain the structure of soil, formation and decomposition of organic matter and nutrient transformations (Joshi et al. 2018). Majority of soil process such as decomposition and transformations of soil organic matter, release of inorganic nutrients for plant growth; N_2 fixation; nitrification; denitrification; and detoxification of xenobiotics, bioremediation are performed by soil enzymes (Sherene 2017). Soil enzymes play major role in cycling of carbon (β-glucosidase, endoglucanase, cellobiohyrolase, β-galactosidase, endoxylasnase, endomannase, β-glycosidase, esterase, laccase, Mn peroxidise, lignin peroxidise, endochitinase, N-acetylglucosaminidase, α-glucosidase), N (protease, peptidase, urease, N-acetylglucosaminidase), P (phosphomonoesterase, phosphodiesterase), and S (arylsulphatase) cycle (Kandeler et al. 2011; Baldrian 2009). In a study made by Ullah et al. (2019) an enhancement in enzyme activities involved in the C, N, and P cycling of was observed by the addition of N addition, showing that soil microbes produce more enzymes under high N conditions.

8.7.3 Factors Affecting Soil Enzyme Activities

Activity of enzymes in soil is dependent on several factors including soil properties (soil pH, OM, total nitrogen, phosphorus, sulfur, heavy metals), addition of inputs, climatic conditions, vegetation, cropping systems. Liu et al. (2021) studied soil enzyme activities in peatlands in permafrost regions and found that soil substrate, ammonical nitrogen, soil moisture content and nitrate nitrogen were the main factors affecting soil enzymes activities significantly. The addition of nitrogen in soil enhances activities of glycosidases (β-cellobiosidase, β-glucosidase, β-xylosidase, and α-glucosidase) and which help in the breakdown of cellulose, chitin, carbohydrates, and in N mineralization (Jian et al. 2016; Saiya-Cork et al. 2002). The addition of N resulted in increase in soil acidity and SOC which significantly affected C-cycling enzymes. Song et al. (2019) showed that total organic carbon, total nitrogen and dissolved organic carbon in soil are correlated with β-glucosidase, acid phosphatase, invertase, and urease activities. Roberto et al. (2009) determined the geometric mean enzyme activity to study the effect of organic and conventionally managed plots on enzyme activities and nematode population. Higher nematode population and enzyme activities were observed in organically managed plots. Urease activity was higher in soils under vegetation than vegetation free soils (Reddy et al. 1987; Gupta and Bhardwaj 1990). Similarly soil enzymes like invertase, soil phosphatase serves as an important indicator of stress in the soil (Liu et al. 2021). Using organic fertilizers like compost, straw mulch and sewage sludge increases and soil tillage decreases the activity of urease. In addition, application of wintery wastewater in four different vineyard soils increased soil urease activity more than municipal water. Elbl et al. (2019) applied organic amendments (compost and vermicompost) in the soil which resulted in higher microbial biomass, DHA, FDA, and phosphatase activities as compared to inorganic fertilizers. Vegetation degradation is a change in the structure of the vegetation community, plays an essential role in changes in soil nutrient and enzyme activities. Greatest variation in soil nutrients and enzyme activities were observed on surface and deeper layers of soil. Vegetation degradation also resulted in reduction in soil carbon storage and nutrient cycling capacity. Wang et al. (2020) studied the variations of soil organic carbon components and enzyme activities (catalase, sucrase, urease, and amylase) in four vegetation types and reported that sucrase and urease activities were significantly correlated with soil organic and particulate organic carbon content and microbial biomass carbon significantly affected catalase activity. Mangalassery et al. (2015) determined the potential of zero tillage in microbial community functioning as reflected by reduced respiration rates and greater enzyme activities. The soil under zero tillage management accumulated greater amounts of total and aromatic carbon. Baoyi et al. (2014) showed that straw returning and deep tillage increased soil microbial and enzyme activities (catalase, phosphatase, saccharase, urease). In this way, soil enzymes activities respond differently to different inputs, management practices and environmental conditions.

8.8 Conclusion

Soil enzymatic activity serves as a critical indicator of soil fertility, quality, and health because it play key biochemical functions in the overall process of organic matter decomposition, nutrients cycling, mineralization, detoxification of toxicants, and suppression of noxious and pathogenic organisms. Measuring enzymatic catalysis and understanding the factors that regulate enzyme expression significantly contributes to assess the effect of agricultural management practices in improving soil quality and fertility. Thus, determining a suite of enzyme activities in soil amalgamate both the intra and extracellular enzymatic transformations in the soil biological system and also serves as the main feature for soil quality assessment.

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Chapter 9
Role of Rhizobiome in Mitigating Plastic Pollution in Pedosphere

Hodiayala Vasanaika Girish and Maddur Puttaswamy Raghavendra

Abstract Pedosphere is an intersection of the atmosphere, biosphere, hydrosphere, and lithosphere. It is referred as the soil mantle of the earth and soil in turn as a natural media. The organic and inorganic constituents along with soil structure and texture define the fertility, which in turn defined as the ability of the soil to support the plant growth. Any alterations in these factors impact the plant growth and will have a greater economic loss in case of agricultural crops. Soil environment is also dynamic in terms of its associated living organisms; rhizobiome in particular is the eco-friendly companion of the plants. It is providing beneficial benefits befitting plants for abiotic stress management, diseases and uptake of inorganic nutrients. The list of abiotic stress whether it is natural or man-made is increasing day by day, and the recent addition is the pollution of pedosphere with plastic. Until now, directly, soil was treated as place to discard all kind of plastics via land filling (Garcia and Robertson, Science 358:870–872, 2017) and indirectly micro- and nanoplastics were added to soil through irrigation in agricultural land. Thus, the persistent materials are causing serious pollution issues even in pedosphere in general and rhizosphere in particular. Many studies/reviews were focused on specific regions and in specific ecosystem types, with pedosphere studies being the most limited. There is a huge knowledge gap, particularly in this field; hence, thorough research on pedosphere plastic pollution and its direct and indirect impact on plant growth are warranted. Current studies recounted biodegradation of polymers using different bacteria, bacterial consortia, biofilm-forming bacteria, and different fungi. Considering the extent of plastic pollution, it becomes inevitable in future to include these plastic degraders as plant growth promoters along with biopesticide and biofertilizer bioinoculants. Normally, biodegradation of plastic is influenced by numerous factors, from the type of microorganism to the type of polymers, their versatility and physicochemical properties, and the environmental conditions. This chapter covers

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B. Giri et al. (eds.), *Structure and Functions of Pedosphere*,
https://doi.org/10.1007/978-981-16-8770-9_9

microbial-induced fate of plastic in the environment and its biodegradation by microbes.

Keywords Plastic pollution · Plant growth · Rhizobiome · Biodegradation

9.1 Introduction

Microorganisms play vital role in the maintenance of numerous environmental processes, as they have evolved over millennia to mineralize and to transform diverse complex elements together with xenobiotics. They have become the front line in arresting the accumulation of numerous materials as they utilize these materials and recycle them into nontoxic compounds, which can be reutilized in the nature. Hence, microbial populations tackle numerous challenges in the environment by evolving their metabolic process through modification of genome to allow the incorporation of new compounds into their metabolic pathways and by extension into the biogeochemical cycles (Amobonye et al. 2020). Therefore, the capability of microbial community to acclimatize to the metabolism of dissimilar anthropogenic compounds has been well known based on the natural selection of mutants that possess the essential degrading enzymes and probably unique metabolic pathways with less specific substrate specificities.

Nevertheless, the undiscriminating overexploitation of nature and natural resources by human has resulted in unprecedented loss/threats in nature through the inception of xenobiotics at a quicker rate than the evolution and adaptation of the microbial community. Consequently, the self-cleaning capability of the environments is overwhelmed and the various pollutants' accumulation level is problematic. Topmost on the scale of these ever-accumulating, nondegradable pollutants is the synthetic plastics, which are man-made polymers derived from petroleum. Since from last sixty years, plastic materials have become necessary in all aspects of human endeavors, and it has replaced several naturally available resources.

Archaeologists and historians describe ages in history by the resources or technologies that affected humankind to the maximum extent such as the stone, bronze, or iron ages. Given the predominance of plastics in our society, it is not surprising that some ecologist/researchers have called our present day the "Plastic Age" (Costa et al. 2020). It is true considering the dependence on synthetic polymers in most aspects of human lives. Plastics are used on a large scale for a broad range of applications, due to their notable thermo-elastic and mechanical properties, stability and durability, high resistance, malleability, chemical inertness, light weight, low water permeability, and low cost (Raddadi and Fava 2019; Oliveira et al. 2020).

Nowadays, plastic is a vital part of everybody's life and ubiquity in an immeasurable number of objects, such as domestic utilities, packaging, soft drink bottles, garbage bags, and a multitude of objects. Plastics are also performing a significant role in the overall improvement of human wellness, as disposable medical tools and equipment are made with plastics (Correia et al. 2020). Production and usage of plastic in worldwide have massively enhanced in recent years in various activities

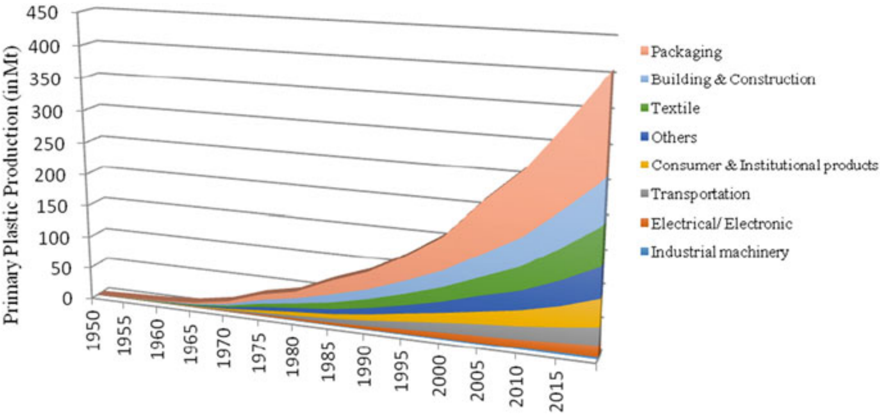


Fig. 9.1 Increase in worldwide production of plastics used in different sectors

and industrial sectors due to its physicochemical properties and versatile nature. Plastic has replaced metals, wood, glass, metal alloys, vegetable, paper, and animals' fibers with lots of advantages. As several of them are already scanty in nature, moreover production costs are much higher compared to plastic. Universally, demand for plastics is estimated to have annually increased since 1950s. In 2015, global plastic production reached 407 million tons per annum (Mtpa) (Fig. 9.1), making it more than the production of paper and aluminum. If production continues to grow at similar rates, plastic production will reach 1600 million tons per annum in 2050.

9.2 Global Production of Plastic and Management Systems

It is estimated that according to the recent statistics, the amount of global plastic waste between 1950 and 2015 was 7.8 billion tons (Oliveira et al. 2020; Ritchie and Roser 2018); in 2017 and 2018, it reached 350 and 381 million tons worldwide, respectively (Raddadi and Fava 2019). The improper plastic waste management has generated the accumulation of over 250 thousand tons of plastic waste floating in the ocean. Only 9% of this waste has been recycled, 12% is incinerated, and 79% still ends up in landfills or in the environment (Fig. 9.2) (Geyer et al. 2017; Oliveira et al. 2020). This indicates that 5 billion tons of plastic are either in landfills or in the natural environment. It is estimated that by 2050, the accumulating amount of plastics ever produced will reach 34 billion tons, with 12 billion tons of plastic waste either in landfills or in the environment as litter at current utilization levels (Mazhandu et al. 2020).

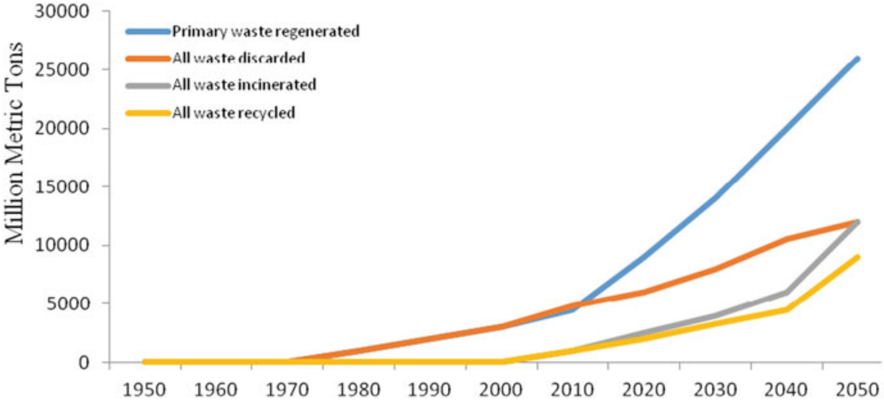


Fig. 9.2 Projection of increasing plastic waste generation and disposal in million metric tons

9.3 Adverse Impact of Plastic on Environment and Ecosystem

Despite the countless benefits accredited to plastic usage, unmanageable production, utilization, and unscientific disposal forms will elicit the depletion of natural resources, variation in climatic condition, environmental deprivation, and, in addition, negative impact on survival of plants and animals. In 2015, petroleum-based plastics emitted 1781 Mt of carbon dioxide equivalent during their life cycle (Fig. 9.3), and if this trend or scenario was maintained, the petroleum-based plastic emissions are set to increase to 6500 Mt CO_2 eq by 2050 (Zheng and Suh 2019; Mazhandu et al. 2020).

Based on plastic stability, versatile nature, and physicochemical properties, it can be categorized as a persistent pollutant. Their lifetime is determined by their chemical nature and the characteristics of the environment in which they are located.

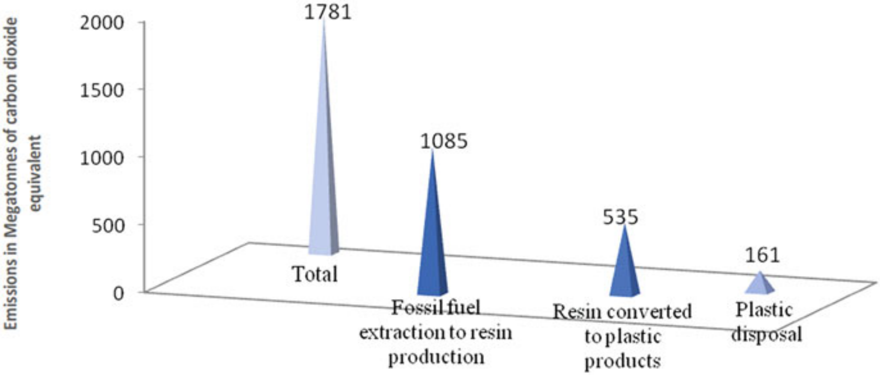


Fig. 9.3 Carbon dioxide emissions equivalent in 2015

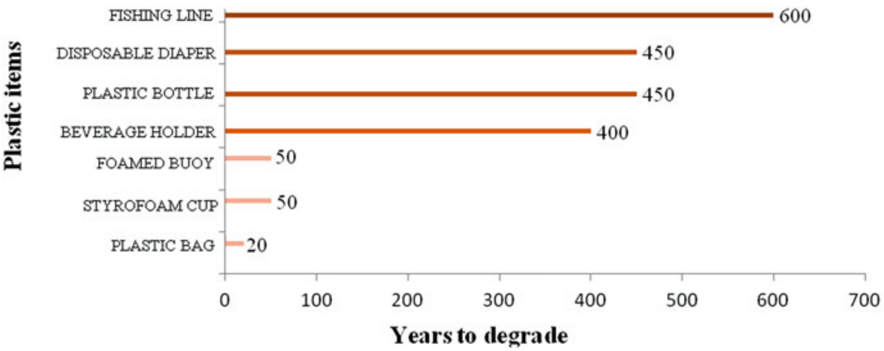


Fig. 9.4 Timeline of plastic degradation

Figure 9.4 shows the time line taken for several plastic items to deteriorate. Namely, plastic bottles takes 450 years to degrade (Mazhandu et al. 2020), and even then, they form microplastics, which are ingested by marine animals and have landed on our tables in the form of sea food as well as water and table salt (Mazhandu and Muzenda 2019). Roughly51 trillion microplastics are floating in the oceans basin, and this is 500 times more than the stars in our galaxy (Mazhandu et al. 2020). According to the United Nations Educational, Scientific, and Cultural Organization (UNESCO), over a million sea birds and more than 100,000 marine animals die yearly from plastic waste ingestion or entanglement (http://www.unesco.org/new/en/natural-sciences/iococeans/focus-areas/rio-20 ocean/blueprint-for-the-future-we-want/marine-pollution/facts-and-figures-onmarine-pollution/). The total global loss induced by plastic waste is about US$13 billion/year, which has also been recorded from tourism and fishing industries, together with losses from clean-up campaigns (UNEP 2021).

As there is unavailability of cheap replacements to plastics, it is difficult for industries and individuals to prohibit plastic in their day-to-day life. However, as plastics have low biodegradability rate in the environment, there are growing concerns about enormous accumulation in the ecosystem that can persist for many centuries and we are witnessing a great demand for solutions to mitigate this issue (Raddadi and Fava 2019). During the last few decades, an increasing amount of studies has recorded the occurrence and possible hazards of plastic particles in the marine environment. Whereas, limited information is available to understand plastic particles in the terrestrial environment and precisely quantity of plastic accumulates in the top soil, possible ecological impacts, possible sources, interaction of plastic particles with the soil environment.

9.4 Plasticulture

Previously, plastic pollution was considered as a major threat only to aquatic flora and fauna considering its wide spread distribution in ocean (Colton et al. 1974). Presently, problems of plastic pollution in the terrestrial ecosystem is also increasing with the same phase, the only difference is the data related to its distribution pattern, impact on terrestrial organisms, its role in altering soil texture and structure, rhizosphere microflora and direct impact on plants is yet to be completely unraveled through thorough scientific studies (Rillig 2012). Helen et al. (2017) and Ren et al. (2019) are of the opinion that plastic pollution in pedosphere or terrestrial ecosystem is a major concern, because agricultural soil is serving as a major reservoir of more microplastic mass compared to oceanic surface water.

As the world is awaiting the next green revolution, soil and ecological parameters are considered being important component of sustainable agriculture. Presently due to overemphasis on high yield, natural processes are compromised or ignored. One such recently introduced major cause of plastic pollution in agricultural land, especially pedosphere, is plasticulture. It is referred to as application of plastics in cultivation practices. Razor thin sheets of polyethylene film are usually applied across the farmland to avoid unnecessary competition between weeds and main crop for the natural resources, to moderate soil temperature through soil moisture content and to increase water use efficiency (Steinmetz et al. 2016). It was found successful in increasing the yield of cotton, maize, and wheat by 30%. Due to this successful achievement, presently it is estimated that 2500 square miles of agricultural land is under plasticulture practice. It is estimated that 4.4 million tons of plastic is used for this purpose, which is expected to double in future.

Along with plastic, mulch plastic is widely used in agriculture for micro-irrigation, pond liners, and greenhouses. Wide range of plastics viz. polyethylene, polyolefin, poly-methyl methacrylate, polycarbonate, polyvinyl chloride, ethylene-vinyl acetate copolymer, and polypropylenes is used for these purposes. Among these, polyethylene film can remain in the soil for several years not being biodegraded leading to serious problems associated with pedosphere pollution, which is generally referred to as white pollution (Liu et al. 2014; Steinmetz et al. 2016).

9.5 Potential Ecological Impacts of Plastic and Its Additives on Soil

Because of the predominance of plastic pollution, there is substantial research interest in understanding the possible impacts of plastic particles in the environment. Compared to studies on the aquatic ecosystem, still research on the potential impacts and effects of plastic particles on the soil ecosystem or inhabitants are incomplete and remain poorly understood. Plastic element accumulation in soil might have deleterious impacts on soil biotic agents. It also serves as a potential transport vector for toxic chemicals once they enter the soil environment. They contain chemical constituents like flame retardants, plasticizers (e.g., phthalates), UV stabilizers, and antioxidants that are supplementary during the production of plastic and can/may leach from plastic particles (Okoffo et al. 2021). Plastics have possibility to cause damage by leaching chemical additives, either combined during manufacturing process or adsorbed from the environment. These chemical constituents might be added to enhance the life of the plastic by providing resistance to oxidation, heat, or microbial degradation. Therefore, the degradation of plastic can be time-consuming and the additives may leach out and become hazards to biota (Ribeiro et al. 2019; Okoffo et al. 2021). Moreover, these chemical additives have potential to be freely ingested by soil biota, probably providing substantial means of transportation of these toxic chemicals, through both the food chain and environment, leading to undesirable health effects.

Many research studies have recorded the impact of plastics on soil organisms such as nematodes, oligochaetes, isopods, springtails, earthworms, and snails (Chae and An 2018; Judy et al. 2019). Toxicological study reports have demonstrated that the occurrence of plastic and its additives in the soil can inhibit the development of soil organisms, cause loss of weight, damage their gut and cause modifications in the microbial community, induce oxidative stress and show low immune responses, and cause reproductive problems and mortality (Rodriguez-Seijo et al. 2018; Ju et al. 2019; Judy et al. 2019; Okoffo et al. 2021).

Numerous studies have shown that the presence of plastic particles in the soil environment can cause significant alterations in soil physicochemical parameters such as bulk density, soil structure, nutritional contents, and capacity of water holding (de Souza Machado et al. 2019; Wan et al. 2019), which ultimately impact on growth of the plant, germination rate, root density, root growth, vegetative and reproductive growth, number of tillers and fruits, and relative chlorophyll content. However, such data are limited, likely because it is challenging to detect plastic elements in plant cells and tissues and the effect on food crops has not attracted adequate attention (Zhu et al. 2019).

Physical harm to the plant roots is reported due to adsorption of micro- and nanoplastics onto the roots (Jiang et al. 2019; Kalcikova et al. 2017). Change in rhizosphere communities also reported to play indirect role on the plants. Accumulation of the micro- and nanoplastics invites allochthonous microflora having the ability to use these plastics as substrate in rhizosphere creating unhealthy competition for the root exudates. Thorough research already revealed that the diversity of the rhizosphere microflora is decided by the composition of the root exudates, which serves as a nutrient for microflora supporting the plant in turn with available soil inorganic nutrients (Nazir et al. 2016; Ruger et al. 2021). Competition between autochthonous and plastic-dependent allochthonous microbes for space and root exudates in rhizosphere significantly impacts the plant growth-promoting rhizoflora. Even though there are several reports to prove the effect of the different plastics on rhizosphere microflora, reports on its direct impact on plants are scanty.

Table 9.1 Impact of microplastics on plant growth

Type of plastics	Plant	Effect	References
Nanoplastics of polystyrene with 100, 300, 500, and 700-nm particle size	*Cucumis sativus* L.	Exposure to 300-nm plastic significantly reduced the biomass, whereas 100-nm plastics significantly reduced chlorophyll, a and b, soluble sugar, proline, and carotenoid content. 700-nm plastic-treated plastic recorded significant increase in the expression of genes associated with peroxidase, and increase in content of malondialdehyde, proline, and hydrogen peroxide	Li et al. (2020)
1% biodegradable and polyethylene plastic particles	*Triticum aestivum* L.	Decrease in growth and fruit biomass	Qi et al. (2018)
Polylactic acid (PLA), polyethylene (PE), and cadmium (Cd)	*Triticum aestivum* L.	PLA recorded highly significant phytotoxicity, whereas PE without noticeable toxicity. Biomass and content of the chlorophyll are drastically reduced in leaves. Even alteration in soil pH was recorded. Operational taxonomic units and arbuscular mycorrhizal fungi community structure and diversity were varied significantly with different treatments	Wang et al. (2020)
Fragments of polyester terephthalate, polyethylene, polystyrene and polypropylene, polyester fibers, beads of polyamide beads	*Allium fistulosum* L.	Significant alterations in plant biomass, root characteristics, elemental composition of tissues, and even significant effect on soil microbial activities	Machado et al. (2019)
High-density polyethylene (HDPE), biodegradable polylactic acid (PLA), and microplastic clothing fibers	*Lolium perenne* L.	PLA treatment reduced the shoot height and affected seed germination. HDPE was shown to reduce the soil pH	Boots et al. (2019)

Among a few reports available, the tobacco cell culture-based study using fluorescent microplastic beads revealed that the microplastics can easily enter the plant cells by endocytosis (Bandmann et al. 2012). Another report published by Li et al. (2019) supports the uptake and accumulation of microplastics in whole plant culture of the edible plant. These directly provide scientific validation for bioaccumulation of microplastics in plant cells and its biomagnified impact on humans after consuming such edible plants. The available research data on direct impact of plastics on plant growth are compiled in Table 9.1.

9.6 Role of Microbiome in Soil Biodiversity

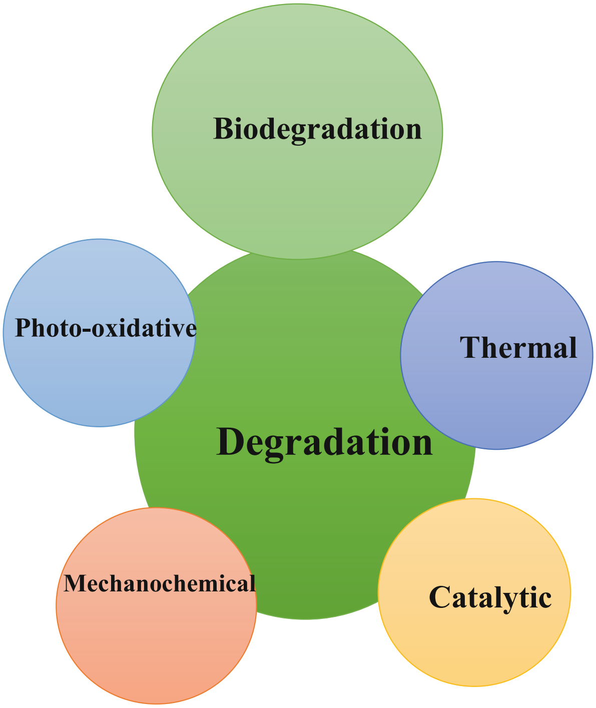
Soil has biodiversity belowground, from genes and species to the communities they form, as well as the ecological complexes to which they contribute and to which they belong, from soil micro-habitats to landscapes. Soil is one of the chief global reservoirs of biodiversity, and beyond 40% of living organisms in planet are associated during their life cycle directly with soils (Bardgett and van der Putten 2014). This reservoir includes from bacteria to human. It has been estimated that 1 g of soil contains up to 1 billion bacterial cells, comprising tens of thousands of taxa, up to 200 m of fungal hyphae, and a wide range of organisms including nematodes, earthworms, and arthropods (FAO 2020). Microorganisms in the soil are directly tied to nutrient recycling, especially carbon, nitrogen, sulfur, and phosphorus. Bacteria are a key class of microbes that preserve soil health and productivity.

9.7 Fate of Degradation of Plastic

After the usage of plastic, the most common method for disposing is the landfill, which acts as a principal source of plastic pollution in soil, and it is most significant ecological problem since they are not biodegradable under natural environmental conditions (Fesseha and Abebe 2019). According to Peng et al. (2018), developing countries are depending more on landfilling to dispose plastic wastes considering its operability and low cost involved. Hence, the accumulation of plastic wastes created a severe threat/loss to the biodiversity of the pedosphere. Unlike organic wastes discarded by humans, polyethylene (PE) and other petroleum-based plastics are extremely recalcitrant to natural degradation processes. Depending upon the nature of the plastic, degradation has been classified as thermal, catalytic, photo-oxidative, mechanochemical, and biodegradation (Fig. 9.5).

Generally, environmental degradation is termed as “aging,” which leads to accumulation of plastic. It comprises few chemical and mechanical mechanisms of treatment and depends on numerous factors. Mechanical degradation depends on solar light, temperature, and moisture and causes alterations in plastic bulk structure, like discoloration, cracking, changes in shape or optical characteristics, and flaking. Chemical effects refer to changes at the molecular level by chemically oxidizing or disrupting the long polymer chain into new molecules, usually with significantly shorter chain lengths (Atanasova et al. 2021). As environmental degradation is a slow process, mechanical or chemical man-made recycling is a main approach for plastic waste treatment (Ragaert et al. 2017). Since the process of mechanical recycling discharges inorganic and organic impurities in the waste and recycling using chemical process is accompanied by the use of toxic and expensive chemicals (Wei and Zimmermann 2017), biodegradation appears to be the most effective, alternative, and attractive process for disposal of plastic waste (Fesseha and Abebe 2019). It offers specificity in attacking plastics and being an inexpensive and

Fig. 9.5 Different types of plastic degradation



efficient process that does not yield any secondary pollutants (Atanasova et al. 2021).

9.8 Biodegradation of Plastic

Biodegradation is the process in which organic substances are broken down by living organisms. It is anticipated to be the main mechanism of loss for most toxic chemicals discharged into the environment (Devi et al. 2016). Biodegradation is the capability of various microorganisms to influence abiotic degradation through chemical, physical, or enzymatic action (Albertsson et al. 1987). Both synthetic and natural polymers are degraded and deteriorated by the involvement of various heterotrophic microorganisms (Gu et al. 2000). Generally, plastic degradation process is very slow; primarily, it is originated by abiotic environmental factors like temperature, moisture, UV, and pH. The method in which a microbial community established on a surface is known as "microfouling" or called as formation of biofilm. Biofilms, involving both microbial community and their extracellular polysaccharides, are extremely diverse and varying in both time and space. Various complex communities of microorganisms have developed exceptional approaches in order to use the plastic materials as a carbon and energy source. Several bacteria and fungi are engaged in the plastic degradation process. These microorganisms differ from one another and have their own optimum growth and environmental conditions. Generally, biodegradation is consisting of both enzyme-catalyzed hydrolysis and nonenzymatic hydrolysis (Devi et al. 2016).

The biodegradation of polymeric materials is a complex process comprising numerous successive steps induced by the action of enzymes. The most significant type of enzymatic polymer cleavage reaction is hydrolysis. The bonds like ester, glycosidic, and peptide linkages are subjected to hydrolysis through nucleophilic attack on the carbonyl carbon atom (Schink et al. 1992). During degradation, extracellular enzyme from heterotrophic microorganisms break down complex polymers yielding short chains or smaller molecules, for example, oligomers, dimers, and monomers, which are smaller enough (water-soluble) to pass the semi-permeable outer bacterial membranes and then to be utilized as carbon and energy sources (Gu 2003; Devi et al. 2016). This preliminary process of polymer breaking down is called depolymerization. The pathways associated with polymer degradation are frequently determined by the condition of the environment. The decomposition of complete polymer yields organic acids, CO_2, CH_4, and H_2O (Devi et al. 2016; Atanasova et al. 2021). By this process, they increase to soil fertility, decrease the accumulation plastic in the surrounding environment, and decrease the cost of waste management. Furthermore, biodegradable plastics could be useful for the production of valuable metabolites (monomers and oligomers).

9.9 Factors Affecting Plastic Biodegradation

Biological degradation of polymers is affected by two key elements like internal factors such as polymer characteristic and polymer constituents, and external factors like polymer exposure conditions for biotic and abiotic conditions (Fig. 9.6). Factors affecting the degradability are governed on the origin of the polymer, polymer characteristics, chemical composition and its structure, processing characters, and the environmental degrading conditions. The polymer characteristics like molecular weight, crystallinity, mobility, type of functional groups, and substituent present in its structure, and plasticizers or additives added to the polymer all play an significant role in its degradation (Gu et al. 2000; Artham and Doble 2008). Abiotic environmental factors such as pH, temperature, UV radiation, and moisture can influence the rate of hydrolysis reaction during the degradation process. The increased moisture and temperature lead to enhance the microbial activity and hydrolysis reaction rates. Moreover, in the increased moisture conditions, fractionalization of polymer chains is induced which in turn leads to expansion of the accessible area for microorganisms, acclerating the rate of biodegradation (Ho et al. 1999). Among biotic factors, exoenzymes produced by diverse microorganisms may have active sites with altered shapes and hence more able to biodegrade certain polymers. For example, *Aspergillus flavus* and *A. niger* produce enzymes that more easily digest aliphatic

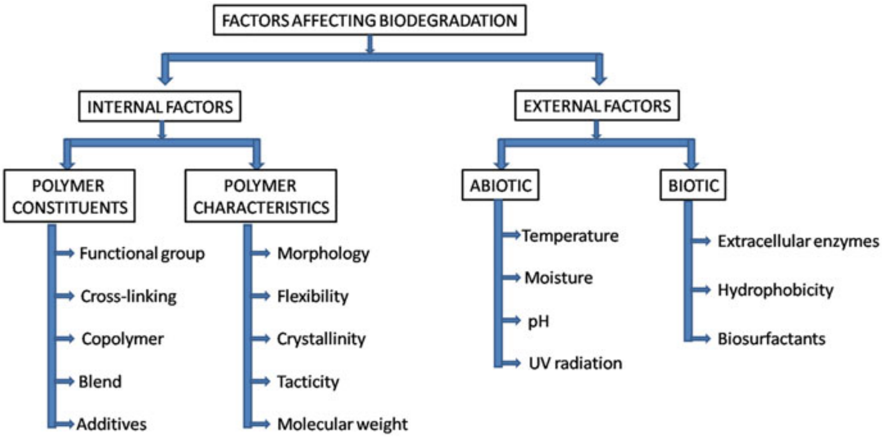


Fig. 9.6 Factors associated with plastic biodegradation

polyesters derived from 6-to 12-carbon di-acid monomers than those produced from other monomers (Devi et al. 2016).

9.10 Role of Microbial Community in Biodegradation Process

Microorganisms are renowned to be the engine of the earth's nutrient as they drive forefront for the transformation and cycling of nutrients in the surrounding environment. Their role in decomposition confirms that carbon and nutrients are released from diverse complex polymers of both synthetic and natural origins. They have been evaluated for their substantial roles in biodegradation and have been shown to degrade various materials such as metal compounds, antibiotics, petroleum, plastic, and other elements that have expanded prominence in this Anthropozoic era. Microbial community of all the classes are in the process of preventing the bioaccumulation of numerous organic and inorganic compounds in the surrounding environment. In this context, it is very essential to acknowledge their roles in the biodegradation of xenobiotic compounds, such as plastic polymers. The biotic factors of microbes on plastic degradation are chiefly attributed to the action of numerous microorganisms, which has been noticed as potential degraders based on their capability to acclimatize and use these biotic factors as their energy substrates and growth.

Microbes gaining energy by catalyzing energy-producing biochemical reactions include breaking of chemical bonds and transferring electrons away from the pollutants. This kind of biochemical reaction is known as oxidation–reduction reaction. Gained energy from these electron transfers is then "invested," along with few electrons and carbon from the pollutants, to yield more number of cells.

This method of destroying organic compounds with the presence of oxygen (O_2) is termed as aerobic respiration. In the process of aerobic respiration, microorganisms utilize oxygen to oxidize part of the carbon in the pollutants to carbon dioxide (CO_2), with the rest of the carbon used to produce new mass of cells. In the procedure, O_2 reduced to produce water. Therefore, the main by-products of aerobic respiration are CO_2, water, and an amplified community of microorganisms.

Numerous microbes can survive without the presence of oxygen by means of anaerobic respiration. In this process of respiration, sulfate (SO_4), nitrate (NO_3), and metals like iron (Fe_3) and manganese (Mn_4) can play the role of oxygen, as accepting electrons from the degrading pollutants. Hence, anaerobic respiration utilizes the inorganic chemicals as electron acceptors and the end products of this respiration might be hydrogen sulfide (H_2S), nitrogen gas (N_2), and methane (CH_4), and reduced forms of metals depend on the type of electron acceptor (Amobonye et al. 2020). The key mechanism for the degradation of plastics is oxidative method. These mechanisms reduce the molecular weight of the polymers. The intracellular and extracellular enzymes that are produced by the microorganisms transform the plastic into monomer, dimer, and oligomer. The end products formed during conversion penetrate into microbial cells where it can be used as source of energy. The dissimilar microbial community are responsible for the biodegradation of diverse categories of plastics.

Microbes are preferably suitable to the task of destruction of contaminant because they own enzymes that allow them to use contaminants as food in the surrounding environment. These complex groups of microbes use their several enzymatic systems to degrade the polymers into intermediates, which can be assimilated and metabolized subsequently for their energy needs (Amobonye et al. 2020). In this regard, different bacteria and fungi with the potential to biodegrade various plastic polymers have been investigated in recent times. Some of the microorganisms with plastic biodegradation potential are highlighted in Table 9.2.

9.11 Role of Enzymes in Plastic Biodegradation

Plastic-degrading enzymes involved in the biodegradation of polymers have been classified into two wide categories, namely intracellular and extracellular enzymes (Gu 2003). Relative percentage of the several enzymes produced by the microbes varies with species to species and even between strains of the same species. Every enzyme is very specific in their action on substrates. However, the best studied category among the two is the extracellular enzymes/exoenzymes, which own broad range of reactivity, from oxidative to hydrolytic functionality. These exoenzymes are chiefly involved in the depolymerization of the long carbon chains of the polymers to a mixture of dimers, oligomers and monomers. These diverse groups of enzymes have been found to act similarly to microbial laccases, lipases, peroxidases, cutinases, and esterases as have since been classified as such (Amobonye et al. 2020). Moreover, these exoenzymes are to be involved in heterogeneous reactions

Table 9.2 Biological degradation of plastic by microorganisms

Name of microorganism	Type of plastic	Reference
Achromobacter denitrificans	Polyethylene	Ambika et al. (2015)
Anoxybacillus rupiensis	Nylon	Mahdi et al. (2016)
Acinetobacter baumannii	Polyethylene	Pramila and Ramesh (2015)
Alcaligenes faecalis	Polymers	Ghosh et al. (2013)
Arthrobacter sp.	Polystyrene film	Lyklema et al. (1989)
Bacillus cereus	Polyethylene	Shahnawaz et al. (2016)
Bacillus subtilis	Polyethylene films of thickness 18 μm	Vimala and Mathew (2016)
Bacillus amyloliquefaciens	Polyethylene	Novotny et al. (2018)
Brevibacillus borstelensis	Polyethylene	Ghosh et al. (2013)
Bacillus gottheilii	Polyethylene terephthalate	Auta et al. (2017)
Desulfotomaculum nigrificans	Polyethylene bag	Begum et al. (2015)
Enterobacter sp.	Polyethylene	Ren et al. (2019)
Ideonella sakaiensis	Polyethylene terephthalate	Yoshida et al. (2016)
Lysinibacillus fusiformis	Polyethylene	Shahnawaz et al. (2016)
Micrococcus sp.	Polystyrene film	Lyklema et al. (1989)
Pseudomonas sp.	Polystyrene	Subramani and Sepperumal (2017)
Pseudomonas alcaligenes	Polyethylene bag	Begum et al. (2015)
Pseudomonas aestusnigri	Polyethylene terephthalate	Bollinger et al. (2020)
Pseudomonas stutzeri	Polymers	Ghosh et al. (2013)
Pseudomonas protegens	Polyurethane	Hung et al. (2016)
Rhodococcus ruber	Polyethylene	Hadad et al. (2005)
Stenotrophomonas pavanii	Polyethylene	Muhonja et al. (2018)
Streptomyces strains	Polyethylene bags	El-Shafei et al. (1998)
Sporosarcina globispora	Polypropylene	Helen et al. (2017)
Streptomyces sp. *Xanthomonas* sp., *Sphingobacterium* sp., and *Bacillus* sp.	Polymers Polystyrene	Caruso (2015) Eisaku and Linn (2003)
Clostridium thermocellum	Polyethylene terephthalate	Yan et al. (2021)
Exiguobacterium sp. YT2	Polystyrene	Yang et al. (2015)
Azotobacter beijerinckii HM121	Polystyrene	Nakamiya et al. (1997)
Rhodococcus ruber C208	Polyethylene film	Santo et al. (2013)
Aspergillus flavus	Polyvinyl chloride	Zhang et al. (2020)
A. fumigatus	Polyethylene	Muhonja et al. (2018)
Aspergillus nomius	Polyethylene	Abraham et al. (2017)
Aspergillus terreus	Polyethylene	Sangale et al. (2019)

(continued)

Table 9.2 (continued)

Name of microorganism	Type of plastic	Reference
Aspergillus sydowii	Polyethylene	Sangale et al. (2019)
Cephalosporium sp.	Polystyrene	Chaudhary and Vijayakumar (2019)
Cladosporium cladosporioides	Polyurethane	Alvarez-Barragan et al. (2016)
Cochliobolus sp.	Polyvinyl chloride	Sumathi et al. (2016)
Mucor sp.	Polystyrene	Chaudhary and Vijayakumar (2019)
Phanerochaete chrysosporium	Polypropylene	Jeyakumar et al. (2013)
Phanerochaete chrysosporium	Polyethylene	Iiyoshi et al. (1998)
Fusarium oxysporum, *F. falciforme*, and *Purpureocillium lilacinum*	Polyethylene film	Spina et al. (2021)

that take place at the liquid/solid interface, as they act on the macromolecules accessible at the surface of the solid plastic while present in the liquid phase (Chinaglia et al. 2018). Other groups of enzymes are involved in the surface functionalization of the hydrophobic plastic surfaces, degradation of the plastic metabolic intermediates into monomeric units, and the final mineralization of the final monomeric intermediates (Amobonye et al. 2020). A substantial percentage of intracellular enzymes are liable for the anaerobic and aerobic methods essential to transform the intermediates to compounds, and further assimilation takes place by the microorganisms. However, microbial enzymes induce the rate of biological degradation of plastics very effectively without causing any damage to the environment.

9.12 Key Suggestions

All components of the environment have a vital role to play in exploring opportunities for reducing conventional plastic usage and substituting it with alternate materials. There is a necessity for entrepreneurship and innovation, which can be stimulated by healthy competition. It is the responsibility of the individuals and the government, to promote the awareness about the effect of plastic materials on the environment and society and attempt to educate public about the possible substitute for plastic materials. There should be more finance on research and development of alternate materials, increase the awareness among consumers, certify that plastic products are appropriately stamp, and carefully evaluate potential answers to the existing crisis. Businesses man, governments, and individuals drive the major role in detaching the society by its dependency on a plastic material that remains to cause havoc in the ecosystem. Pedosphere is important component of biogeochemical cycle and harbors several microorganisms continuously thriving to balance the cycle need to be maintained in harmony. Even though research studies on the impact of plastic on pedosphere is scanty, its impact is really alarming.

9.13 Conclusion and Outlook

The advantages of plastic are unquestionable. The material is inexpensive, very easy to manufacture, and lightweight. These abilities have commanded to a boom in the manufacturing of plastic over the last 67 years. If this development continues worldwide, the production of plastic escalates over the next 5–15 years. If already produced plastic is not handled properly, it remains as a herculean task to free the world from plastic pollution. Unscientific production, utilization, and management of plastic will create enormous impact of ecosystem, if we fail; it remains as one of the prime environmental scourges of our time.

In the natural environment, diverse categories of microbes play a significant role in numerous steps involved in the biodegradation of polymers. The evaluation of synergism among those microorganisms will give an understanding for forthcoming efforts toward the biological degradation of these polymers. In case of polymers having high-molecular weight and hydrophobic surfaces, it is challenging for the microbes to form stable biofilms and degrading them into small molecular oligomers. Isolation and identification of microorganisms from different environmental condition can lead to novel unexplored strains, with superior performance. Numerous methodologies on plastic degradation are accessible, but the inexpensive, environment-friendly, and most acceptable method is degradation using microorganisms. The microbial community discharges the extracellular enzymes to degrading the plastic, but the exhaustive characterization of these extracellular enzymes is still needed to be carried out. The application of applied molecular techniques to identify and characterize the specific category of microbes involved in the biodegradation method will allow the enhanced understanding of the microorganisms involved in the attack of these plastic materials. Because of the inexhaustible capabilities of microbial communities and their constant adaptation to the altering environment, it is anticipated that supplementary in-depth evaluation in this particular area of investigation will rapidly result in viable biological degradation processes that can be established on a commercial scale. The isolated effective strains may remain as an important candidate to be bioaugmented to the pedosphere to clean up the already accumulated plastic. Bioformulations with potential plastic degraders with additional nitrogen fixing, phosphate, and potassium solubilizing ability will add up to further research in future.

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Chapter 10
Geochemical Characteristics of Mineral Elements: Arsenic, Fluorine, Lead, Nitrogen, and Carbon

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Abstract Arsenic, lead, fluorine, nitrogen, and carbon are common in the near-surface environment, but their concentrations in water, solids, and biota are highly variable. The distribution of As, Pb, F, N, and C in the environment is dependent on source, mineralogy, speciation, biological interactions, and geochemical controls. The As minerals interact with environment, and this renders either their dissolution or the formation of secondary minerals, or both. The distribution of the environmental arsenic is determined by the biogeochemical transformations with respect to the redox conditions, the pH, the availability of ions, the adsorption–desorption, dissolution, and the biological activity. The biological transformation and cycling of As can lead to oxidation or reduction of species that mobilize As. Besides, a significant proportion of As can also be remobilized from the soils through the process of anion exchange. Large variations can be observed on all spatial scales influenced by a variety of natural processes including nongeological influences such as climate and vegetation. Continental weathering of bedrocks contributes natural Pb to sediments, while mining and refining of Pb-bearing ores, which are subsequently used for industrial Pb applications, supply anthropogenic Pb to the environment. Lead geochemistry of rivers and costal environments plays a significant role in the biogeochemical cycling of Pb and pollutant delivery at the land–sea interface. Fluorine is ubiquitous in the environment with most deriving from natural sources, these being normal weathering processes resulting in F release from rocks and minerals, volcanic activity, and marine aerosol emission, together with biomass burning, being in part natural. However, there are several sources of anthropogenically derived F, which in some areas represent a threat to the biosphere. Together with carbon, oxygen, and hydrogen, nitrogen is one of the four most common elements in living cells and an essential constituent of proteins and nucleic acids, the two groups of substances that can be said to support life. The important nitrogen pools are soil organic matter, rocks (in fact the largest single pool), sediments, coal deposits, organic matter in ocean water, and nitrate in ocean water. The next most

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B. Giri et al. (eds.), *Structure and Functions of Pedosphere*,
https://doi.org/10.1007/978-981-16-8770-9_10

common gaseous form of nitrogen in the atmosphere after molecular nitrogen is dinitrogen oxide. The geochemistry of carbon is the transformations involving the element carbon within the systems of the earth. Carbon is important in the formation of organic mineral deposits, such as coal, petroleum, or natural gas. Most carbon is cycled through the atmosphere into living organisms and then respires back into the atmosphere. Carbon can form a huge variety of stable compound. It is an essential component of living matter. Carbon makes up only 0.08% of the combination of the lithosphere, hydrosphere, and atmosphere.

Keywords Mineral elements · Arsenic · Fluorine · Lead · Nitrogen · Carbon · Biogeochemical transformations · Environment

10.1 Introduction

Geochemistry emerged as a separate discipline in 1884 and began systematic surveys of the chemistry of rocks and minerals. Frank Worth Clarke indicated that the elements generally decrease in abundance as their atomic weights increase, which is summarized in their data of geochemistry (McSween and Huss 2010). In the early twentieth century, Max Hon Lane and William L. Bragg showed that X-ray scattering could be needed to determine the structures of crystals. In the 1920s and 1930s, Goldschmidt and his associates formulated a set of rules for how elements are grouped. The more common rock constituents are nearly all oxides; chlorides, sulfides, and fluorides are the only important exceptions to this, and their total amount in any rock is usually much less than 1%. By 1911, F W Clarke had calculated that a little more than 47% of the earth's crust consists of oxygen. It occurs principally in combination as oxides and various carbonates. These oxides combine in a haphazard way. Oxides react with other chemical entities to form apatite, limonite, olivine, enstatite, pyroxenes, amphiboles, biotite, and varieties of minerals.

Earth's crust is composed of 90% of silicate minerals, and their abundance in the earth is as follows: plagioclase feldspar (30%), alkali feldspar (12%), quartz (12%), pyroxene (11%), amphiboles (5%), micas (5%), and clay minerals (5%); the remaining silicate minerals make up another 3% of the earth's crust. Only 8% of the earth is composed of nonsilicate minerals such as carbonates, oxides, and sulfides. The chemical composition of the earth and other bodies is determined by two opposing processes: differentiation and mixing. In the earth's mantle, differentiation occurs at mid-ocean ridges through partial melting, with more refractory material remaining at the base of the lithosphere, while the remainder rises to form basalt. Trace metals readily form complexes with major ions in the ocean, including hydroxide, carbonate, and chloride and their chemical speciation changes depending on whether the environment is oxidized or reduced (Nameroff et al. 2002).

Arsenic is an important trace constituent in geothermal fluids, ranging in concentration from less than 0.1 to nearly 50 ppm. An evaluation of published fluid analyses from geothermal systems indicates that the As content of the reservoir fluids varies inversely with pH and directly with temperature. Aqueous as species occur in two oxidation states, As III and As V. As III predominates in the reservoir fluids, where H_3AsO_3 is inferred to be the dominant aqueous species. Both As III and As V occur in hot sparing fluids. The concentration of As in high-temperature reservoir fluids is regulated by reactions involving pyrite. Arsenopyrite and other As minerals are under saturated with respect to the high-temperature fluids found in most reservoir.

As has been used in medicine, agriculture, and industry. Although there is evidence that As is an essential element for animals, there is no consensus that it is essential for humans. Arsenic is one of the most prevalent toxic elements in the environment. The toxicity, mobility, and fate of arsenic in the environment are determined by a complex series of controls dependent on mineralogy, chemical speciation, and biological processes. The element was first described by Theophrastus in 300 BC and named arsenikon (Caley and Richards 1956). It was not until the thirteenth century that an alchemist, Albertus Magnus, was able to isolate the element from orpiment, an arsenic sulfide (As_2S_3). As a chemical element, arsenic is widely distributed in nature and can be concentrated in many different ways. In the earth's crust, arsenic is concentrated by magmatic and hydrothermal processes and has been used as a pathfinder for metallic ore deposits, particularly gold, tin, copper, and tungsten (Cohen and Bowell 2014).

While arsenic occurs in organic and inorganic forms, inorganic arsenic compounds are far more toxic than organic arsenic compounds (Brown and Ross 2002). Inorganic arsenic, most commonly found as arsenite (As^{3+}) or arsenate (As^{5+}), is mainly consumed by humans through drinking water (Maascheleyn et al. 1991; Welch et al. 2000; Kim et al. 2011), but can still be consumed if contaminated water is used for food preparation or irrigation (McCarty et al. 2011; World Health Organization 2016). Sources of inorganic arsenic include natural concentrations in certain minerals and anthropogenic sources from mining, industrial, and agricultural activities (Naujokas et al. 2013; Biswas et al. 2016). Excessive and chronic low-level arsenic exposure is associated with numerous negative health effects including but not limited to death, lung and skin cancer, black foot diseases, vascular and heart disease, skin problems, diabetes, and many more (Brown and Ross 2002; Tseng 2005; Kim et al. 2011; McCarty et al. 2011; Naujokas et al. 2013).

In recent decades, high concentrations of naturally occurring arsenic in groundwater have been observed globally, including locations in Southeast Asia, South America, and the western USA, which is of concern due to the potential health effects that people may experience in these places from high arsenic consumption (Nordstrom 2002; Smedley and Kinniburgh 2002; McCarty et al. 2011). In many areas of USA, drinking water is the primary route of human exposure to arsenic (Hopenhayn 2006). Bangladesh is widely recognized as the most problematic area because of the high concentrations of arsenic observed in the region and the large population that rely on and use the groundwater there (Nordstrom 2002; Smedley and Kinniburgh 2002). In Bangladesh, reducing conditions have led to the dissolution, desorption, and release of arsenic from metal oxide minerals into groundwater supplies. In addition, two main regimes of arsenic mobilization and arsenic concentrations in groundwater have been found to be higher in closed basins, regions with geothermal water, and in some mining districts where sulfides in tailings have been oxidized and leached arsenic into surface and groundwater (Biswas et al. 2016).

Fluoride is a part of the natural environment and is therefore constantly present in people's lives. However, concentration of fluoride can vary from one region to another. From a chemical point of view, it is the most electronegative and reactive of all the elements due to its small atomic radius. Since it is highly reactive, it is usually bound as inorganic fluoride and not found in its elementary state (Fawell et al. 2006). It ranks 13th in terrestrial abundance and represents 0.06–0.09% of weight of the earth's crust. Fluorine is present in the lithosphere, atmosphere, hydrosphere, and biosphere. A large amount of fluorine can be found in rocks of volcanic origin. It enters the environment through volcanic eruptions, rock dissolution, and numerous human activities (coal burning, ore processing, production and use of fertilizers, and industrial plants) (Fawell et al. 2006; Australian Government 2015). Fluoride is found in all natural waters. Seawater contains 1.2–1.5 ppm of fluoride. Freshwater concentrations are usually lower ranging from 0.01 to 0.3 ppm. Higher concentrations of fluoride in water can be present near hot springs of volcanic origin (Australian Government 2015). Normal accumulation of fluoride from the soil is low. Flora growing in acidic soil tends to accumulate more fluoride. There are some plants that can accumulate a few 100 ppm of fluoride; the best known is the tea plant (*Camellia sinensis*, syn. *Thea sinensis*) (Gao et al. 2014).

Fluoride (F) in water, like other naturally occurring chemical species, is beneficial to human health but can be toxic in excess (Ayoob and Gupta 2006). The drinking water standard recommended by the World Health Organization (WHO) for F is 1.5 mg/L (World Health Organization 2006). Elevated F concentrations in groundwater have been reported in India (Reddy et al. 2010), China (Currell et al. 2011), and eastern African countries (Gaciri and Davies 1993; Tekle-Haimanot et al. 2006). Even now, some villagers in China still drink high F groundwater without treatment because of the cost and inconvenience of alternative drinking water supplies. Groundwater F anomalies could be related to natural origins such as prolonged water–rock interactions and mineral weathering, or to anthropogenic contamination such as from fertilizer application. Potential sources of F in groundwater include various minerals such as fluorite, apatite, amphibole, and mica (Ayoob and Gupta 2006), which are commonly found in gneiss terrane (Latha et al. 1999; Young et al. 2011). The F concentration depends on the groundwater chemistry including pH and the concentrations of Na, Ca, and HCO_3 (Young et al. 2011). Naseem et al. (2010) found that high F groundwater originates from granitic rocks, typically from albite, biotite, hornblende, and pyroxene. Elevated groundwater F is documented in Shanxi and Inner Mongolia, about 500 km apart in China (Currell et al. 2011; Li et al. 2011; Wang et al. 1999).

Continental weathering of bedrocks contributes natural Pb to sediments, while mining and refining of Pb-bearing ores, which are subsequently used for industrial Pb applications, supply anthropogenic Pb to the environment. Lead compounds released into the atmosphere in the exhaust fumes of automobiles have produced abnormally high concentrations of lead in the blood of individuals continuously exposed to these fumes for long periods of time, but as yet there is no established instance of lead poisoning resulting directly from this source. Lead is one of the most dangerous inorganic contaminants owing to its high toxicity to living organisms (Nriagu and Pacyna 1988). The occurrence of high concentration of lead (Pb), one of the most hazard chemical elements in drinking water, has been recognized, over the past two or three decades, as a great public health concern in several parts of the world (Franco et al. 2009) Although surface water is still used as drinking water in some areas, groundwater from tubewells, which is considered relatively free of pathogens, is one of the main sources of drinking. Lead can enter the human body in several ways including through air, food, and water; of these, water is generally the most common medium of entry. The toxic metal lead, for instance, is commonly found in the sediments or rock and can be present in groundwater at concentrations that exceed safe levels for drinking water (Fergusson 1935). The biogeochemical cycle of lead has been greatly influenced by humans and such that up to 95% of Pb in the biosphere is estimated to be anthropogenic (Smith and Flegal 1995). Once emitted, Pb can persist and accumulate in the natural environment (Wright and Welbourn 2002). Effects of Pb exposure include a variety of detrimental health issues, most notably neurotoxicity (Tchounwou et al. 2012). Lead geochemistry of rivers and costal environments plays a significant role in the biogeochemical cycling of Pb and pollutant delivery at the land–sea interface. In aqueous environments, processes such as desorption, dissolution, resuspension, flocculation, deposition, and biotransformation allow Pb to be exchanged between bottom sediments, the water column, and the biota (Turner and Millward 2002). Previous studies demonstrate that aqueous Pb is largely scavenged by particles and removed to sediments (Marsan et al. 2014). Lead isotopic compositions of environmental samples reflect isotope signatures of their respective Pb sources. Thus, each Pb source possesses a unique isotopic composition or “fingerprint” by which it can be identified. Accordingly, Pb isotopes have been used to identify Pb sources and trace Pb pollution pathways in water systems.

From our earth-centric point of view, it is equally difficult to imagine life without carbon and nitrogen. These two elements, by virtue of their ability to form double bonds, allow the formation of a multitude of unsaturated and aromatic compounds that impart both structural strength and energetic versatility to earthly life. Nitrogen is abundant in the atmosphere, lithosphere, and hydrosphere of the earth. However, 99% of nitrogen is in the form of dinitrogen, which is inert and cannot be used by most living organisms. In order for living cells to use it for synthesis of vital bioorganic molecules like proteins, nucleic acids, and vitamins, molecular nitrogen has to be in its reduced or fixed form. Dinitrogen fixation, the process by which dinitrogen is reduced to ammonia, is therefore a very important process for the sustenance of life. Three processes are responsible for most of the dinitrogen fixation in the biosphere. Atmospheric fixation by lightning contributes approximately 5%–8% (5×109 kg N/year) of total fixed nitrogen (Myrold and Bottomley 2007). The enormous energy contained in lightning breaks dinitrogen molecules and enables their atoms to combine with oxygen in the air forming nitrogen oxides that dissolve in rain. These oxides of nitrogen then form nitrates that are carried to the earth in rainfall. Biological nitrogen fixation, a natural process by which certain prokaryotic microorganisms fix nitrogen by a highly specialized enzyme complex called nitrogenase, is an environmentally benign source of plant-usable fixed nitrogen. According to estimates, approximately 1 × 1011–1.4 × 1011 kg N (Myrold and Bottomley 2007) is fixed from the atmosphere every year.

The geochemistry of carbon is the study of the transformations involving the element carbon within the systems of the earth. Carbon is transformed by life and moves between the major phases of the earth, including the water bodies, atmosphere, and the rocky parts. Carbon is important in the formation of organic mineral deposits, such as coal, petroleum, or natural gas. Most carbon is cycled through the atmosphere into living organisms and then respires back into the atmosphere. However, an important part of the carbon cycle involves the trapping of living matter into sediments. The carbon then becomes part of a sedimentary rock. Human technology or natural processes such as weathering, or underground life or water can return the carbon from sedimentary rocks to the atmosphere. From that point, it can be transformed in the rock cycle into metamorphic rocks or melted into igneous rocks. Carbon can return to the surface of the earth by volcanoes or via uplift in tectonic processes. Carbon undergoes transformation in the mantle under pressure to diamond and other minerals and also exists in the earth's outer core in solution with iron and may also be present in the inner core. Carbon can form a huge variety stable compounds. It is an essential component of living matter. Living organisms can live in a limited range of conditions on the earth that are limited by temperature and the existence of liquid water. The potential habitability of other planets or moons can also be assessed by the existence of liquid water. Carbon makes up only 0.08% of the combination of the lithosphere, hydrosphere, and atmosphere. Yet, it is the twelfth most common element there. In the rock of the lithosphere, carbon commonly occurs as carbonate minerals containing calcium or magnesium. It is also found as fossil fuels in coal and petroleum and gas. Native forms of carbon are much rarer, requiring pressure to form. Pure carbon exists as graphite or diamond. On earth, C-12, ^{12}C, is by far the most common at 98.894%. C-13 is much rarer averaging 1.106%. This percentage can vary slightly, and its value is important in isotoprgeochemistry, whereby the origin of the carbon is suggested (Killops et al. 2005).

10.2 Arsenic

10.2.1 Background on Arsenic Occurrence

Arsenic is a naturally occurring trace element in rock, soil, plants, and the aquatic environment. Concentrations of arsenic in groundwater vary greatly owing to the uneven distribution of source materials and dynamic geochemical controls on aqueous arsenic mobility. Although arsenic can be introduced to the environment from anthropogenic sources, it commonly is present as a trace component in naturally occurring minerals, such as sulfides, hydrous metal oxides, coal, ironstones, clays, phosphates, silicates, and carbonates. Pyrite and iron oxides are important sources of elevated arsenic in groundwater because they are abundant in aquifers, leading to their dissemination throughout the aquifer matrix, joints, or bedding planes (Smedley and Kinniburgh 2002). Arsenic, present as arsenic minerals or as a trace component in other naturally occurring minerals in the soil and aquifers, can be released to or removed from the groundwater as a result of oxidation and reduction, dissolution and precipitation, and surface complexation reactions on mineral surfaces. Arsenian pyrite [$Fe(S,As)^2$], arsenopyrite (FeAsS), and (or) other unspecified sulfide minerals in bedrock and surficial sediments are common parent sources for naturally occurring arsenic in the environment (Foster et al. 2003). Substitution of arsenic for sulfur in sulfide minerals can increase their susceptibility to weathering and dissolution when exposed to oxidants. Arsenic released to solution by sulfide oxidation commonly has a valence state of V or III and forms the protonated oxyanion complexes, arsenate, or arsenite, respectively (Stollenwerk 2003). Arsenite is considered the more toxic of the two major oxyanion forms. Arsenate [As(V)] predominates in oxic groundwaters, whereas arsenite [As(III)] predominates in reducing sulfidic and methanic groundwaters (Stollenwerk 2003). The conversion of As(III) to As(V) in oxic waters may be relatively slow and can be measured in years (Eary and Schramke 1990) with pH, ferric iron, manganese, and bacteria strongly affecting the rate of oxidation. The reduction of As(V) to As(III) under anaerobic conditions is generally much faster than the oxidation of As(III) to As(V). Arsenic may be sourced from both naturally occurring solid materials (rocks, minerals, soils, sediments) and from anthropogenic (manufactured, synthesized) material (Table 10.1).

10.2.2 Arsenic in Rocks, Minerals, Soils, and Sediments

Arsenic is a relatively abundant trace element in the earth's upper crust with a mean concentration of around 5 ± 1 mg/kg (Rudnick and Gao 2003). Although not normally classified as a geochemically incompatible element, arsenic is comparatively readily solubilized by fluids and so is commonly enriched in magmatic–hydrothermal systems, particularly those associated with (plate tectonic) subduction zones and collision zones (Borisova et al. 2010)—modern/relatively modern (in a geological sense) examples of such regions include the Himalayas, the Rocky Mountains, and the Andes as well as geothermal areas of New Zealand, the Philippines, and Japan, while substantial granite-associated enrichments of arsenic in areas such as southwest England, central France, and Portugal reflect processes in similar environments over 300 million years ago. Accordingly, some of the highest arsenic concentrations recorded in crustal rocks are in granitoid-associated hydrothermal ore deposits (e.g., Panasqueira, Portugal—mean ore vein concentration ~ 8000 mg/kg (Polya 1989); mean hydrothermally altered meta-sediment concentration ~ 200 mg/kg (Polya 1988)). Arsenic is also enriched by fluvio-sedimentary processes and particularly in finer-grained, relatively high specific surface area sediments rich in

Table 10.1 Arsenic sources and concentrations in earth materials

Arsenic minerals	Chemical formula	Source	Reference
Native arsenic	As	Hydrothermal veins	Smedley and Kinniburgh (2002)
Niccolite	NiAs	Vein deposits and norites	Smedley and Kinniburgh (2002)
Realgar	AsS	Vein deposits, often associated with orpiment, clays, and limestones, also deposits from hot springs	Smedley and Kinniburgh (2002)
Orpiment	As_2S_3	Hydrothermal veins, hot springs, volcanic sublimation products	Smedley and Kinniburgh (2002)
Cobaltite	CoAsS	High-temperature deposits, metamorphic rocks	Smedley and Kinniburgh (2002)
Arsenopyrite	FeAsS	The most abundant As mineral, dominantly in mineral veins	Smedley and Kinniburgh (2002)
Tennantite	$(Cu,Fe)_{12}As_4S_{13}$	Hydrothermal veins	Smedley and Kinniburgh (2002)
Enargite	Cu_3AsS_4	Hydrothermal veins	Smedley and Kinniburgh (2002)
Arsenolite	As_2O_3	Secondary mineral formed by oxidation of arsenopyrite native arsenic and other As minerals	Smedley and Kinniburgh (2002)
Claudette	As_2O_3	Secondary mineral formed by oxidation of realgar arsenopyrite and other As minerals	Smedley and Kinniburgh (2002)
Scorodite	$FeAsO_4.2H_2O$	Secondary minerals	Smedley and Kinniburgh (2002)
Anabergite	$(Ni,Co)_3(AsO_4)_2.8H_2O$	Secondary minerals	Smedley and Kinniburgh (2002)

(continued)

Table 10.1 (continued)

Arsenic minerals	Chemical formula	Source	Reference
Hoernesite	$Mg_3(AsO_4)_2.8H_2O$	Secondary minerals, smelter wastes	Smedley and Kinniburgh (2002)
Hematolite	$(Mn,Mg)_4Al(AsO_4)(OH)_8$	Secondary minerals	Smedley and Kinniburgh (2002)
Conichalcite	$CaCu(AsO_4)(OH)$	Secondary minerals	Smedley and Kinniburgh (2002)
Pharmacosiderite	$Fe_3(AsO_4)_2(OH)_3.5H_2O$	Oxidation product of arsenopyrite and other As minerals	Smedley and Kinniburgh (2002)

Materials	Concentration As (mg/kg)	Process	
Igneous material		Cooling and solidification of magma or lava	Smith and Flegal 1995
Basalt	<1–113		Smith and Flegal 1995
Ultrabasics	<1–16		Smith and Flegal 1995
Granites	<1–15		Smith and Flegal 1995
Sedimentary material		Formed by the deposition of material (organic and/or minerals) at the earth's surface and within bodies of water	Smith and Flegal 1995
Shales and clays	<1–500		Smith and Flegal 1995
Sandstones	<1–120		Smith and Flegal 1995
Limestones	<1–20		Smith and Flegal 1995
Phosphorites	3–100		Smith and Flegal 1995

organic matter and/or ferric oxyhydroxides and phosphate mineral phases. Accordingly, rocks with some of the highest arsenic concentrations are coals (Finkelman et al. 1999), marine shales (Smedley and Kinniburgh 2002), ironstones (Appleton et al. 2012), glacial tills (Smedley and Kinniburgh 2002), and phosphorites (Lazareva and Pichler 2007). The most prominent high arsenic minerals are sulfides, loellingite ($FeAs_2$), realgar (As_4S_4), orpiment (As_2S_3), niccolite (NiAs), sulfosalts, enargite (Cu_3AsS_4) and oxides ($FeAsO_4 \cdot 2H_2O$), arsenolite (As_2O_3), and pharmacosiderite ($Fe_3(AsO_4)_2(OH)_3 \cdot 5H_2O$). Phosphate minerals, such as apatite and vivianite (Thinnappan et al. 2008), may locally be important hosts for arsenic, while many sulfide (Bostick and Fendorf 2003), carbonate, and clay minerals (Pascua et al. 2005) are known to be able to sorb arsenic in significant quantities. Several silicate minerals can incorporate 1000s mg/kg arsenic through the substitution of AsO_4 for SiO_4 (Charnock et al. 2007). Arsenic may also be sequestered by various sulfur-bearing moieties in organic matter.

10.2.3 Arsenic Mineralogy

Arsenic is mobilized in the environment through a combination of natural processes such as weathering reactions, biological activity, and volcanic emissions, as well as through a range of anthropogenic activities. It has only one stable isotope (75As) and is the 47th most abundant natural element. The average crustal abundance is 2.5 mg/kg (Hu and Gao 2008) and generally more abundant in marine shales and mudstones (Tourtelot 1964), with high concentrations associated with hydrothermal ore deposits, coal, and lignite deposits. High arsenic concentrations are also found in many oxide minerals and hydrous metal oxides, as sorbed and occluded species. Iron oxides are particularly well known to accumulate As up to concentrations of several weight percent. Arsenic (as As(III) or As(V)) can substitute for P(V), Si(IV), Al(III), Fe(III), and Ti(IV) in various mineral structures and is therefore present in many rock-forming minerals. The element is primarily concentrated in sulfide minerals where it can occur as an arsenide or sulfarsenide anion bound to transition metals (e.g., löllingite, $FeAs_2$; arsenopyrite, FeAsS) or in minerals where arsenic forms nominally a cation (e.g., realgar, AsS). The largest reservoir of arsenic in crustal rocks is probably pyrite, which contains trace to minor contents of this element. Besides being an important constituent of ore bodies, pyrite is also formed in low-temperature sedimentary environments under reducing conditions.

Authigenic pyrite is present in the sediments of many rivers, lakes, oceans, and aquifers and plays a very important role in the geochemical cycles of various elements. Through a series of intermediate phases, pyrite commonly forms in zones of intense reduction such as around buried and decomposing organic matter or in microenvironments where the sulfate-reducing bacteria generate appreciable amounts of sulfide. It is sometimes present in a characteristic form as framboidal pyrite. Pyrite is not stable in aerobic systems and oxidizes to hydrous iron oxides with the release of large amounts of sulfate, acidity, and associated trace

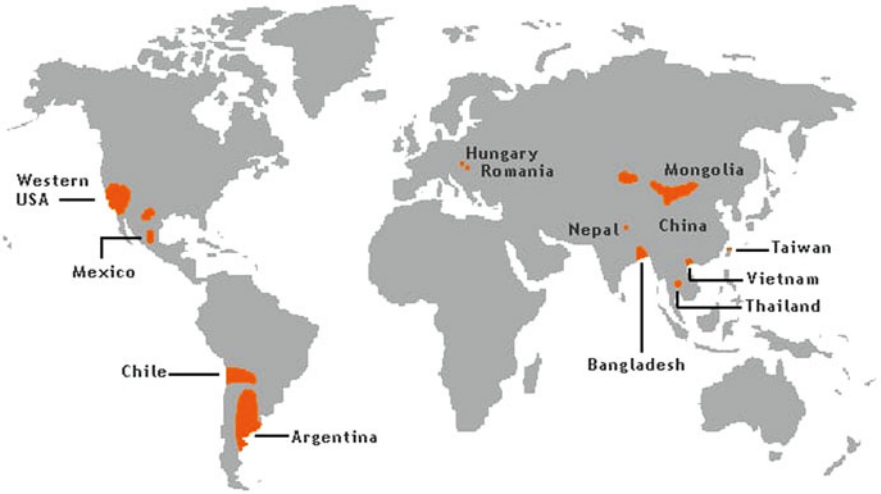

Fig. 10.1 Ground water arsenic contamination areas (Source: Arsenic.www.who.inf Retrieved 2020-11-28)

constituents, including As. The presence of pyrite as a minor constituent in sulfide-rich coals is ultimately responsible for the production of acid rain and coal mine-associated acid mine drainage and for the presence of As problems around coal mines and areas of intensive coal burning (Fig. 10.1).

10.2.4 Arsenic Geochemistry and Hydrogeochemistry

The geochemistry of arsenic has been reviewed by Thornton (1996). It is the main constituent of more than 200 mineral species, of which approximately 60% are arsenates, 20% sulfides and sulfosalts, and the remaining 20% include arsenides, arsenites, oxides, silicates, and elemental As (Onishi 1969). Arsenic is present in many mineral deposits and in particular those containing sulfide minerals. It is common in iron pyrite, galena, and chalcopyrite, and less common in sphalerite (Goldschmidt 1954). The most common arsenic mineral is arsenopyrite, FeAsS. Arsenic is used as an indicator for gold mineralization in geochemical surveys. The average concentration of As in igneous and sedimentary rocks is 2 mg/kg, and in most rocks, it ranges from 0.5 to 2.5 mg/kg (Kabata-Pendias and Pendias 1984), though higher concentrations are found in finer-grained argillaceous sediments and phosphorites. Arsenic is concentrated in some reducing marine sediments, which may contain up to 3000 mg/kg. Arsenic may be co-precipitated with iron hydroxides and sulfides in sedimentary rocks. Iron deposits, sedimentary iron ores, and manganese nodules are rich in arsenic. At moderate or high redox potentials, As can be stabilized as a series of pentavalent oxyanions, H_3As0_4, H_2As0_4, HAsO~, and AsO.

However, under most reducing conditions, the trivalent arsenite species (H_3As0_3) predominates. The retention of As in solution is linked by co-precipitation with elements such as Fe, Ba, Co, Ni, Pb, and Zn. In the Obuasi gold-mining area of Ghana, the highest concentrations of arsenic were found in a deeper part of the aquifer. Only a very minor fraction of the total arsenic in the oceans remains in solution in sea water, as the majority is sorbed on to suspended particulate material.

The geochemical processes that are involved in the oxidation, reduction, and bioavailability of chemical species of arsenic play a significant role in nature (Lièvremont et al. 2009). Arsenic has been associated with microorganisms as well, especially their metabolism (Lièvremont et al. 2009). Arsenic is partitioned between solid and dissolved phases, and this is associated with many biogeochemical processes. There are also several reactions that control the mobilization of arsenic in the natural environment. Most significant are the processes of dissolution–precipitation, adsorption, co-precipitation, and reduction–oxidation.

Oxidizing arsenic bacteria oxidize As(+3) enzymatically and produce arsenite oxidases. Oxygen and nitrate-reducing microorganisms utilize arsenite as an electron donor. Characteristic examples are the photoautotrophic, heterotrophic, and chemoautotrophic microorganisms. In these microorganisms, the adduced energy is used for the production of $CO_{2,}$ which is required for the generation of carbon and the growth of bacteria community (Lièvremont et al. 2009). The oxidation of the As(+3) species to the less bioavailable As(+5) compounds is crucial for the detoxification processes (Lièvremont et al. 2009). Such processes can be observed in extreme natural environments (Lièvremont et al. 2009). They are considered as primary energy resources for the chemolithotrophic metabolism of organisms in the era of the formation of the very first forms of life (Lièvremont et al. 2009). The microorganisms that can act as oxidizers of arsenite can also facilitate As(+3) oxidation in aerobic environments. They can also act as electron acceptors in anoxic conditions by using other ions in the order of $NO_3^- \rightarrow$ Mn oxides → Fe(III) oxides → sulfate. On the other hand, in the case of reducing bacteria, the process is the reduction of As (+5) to As(+3). The arsenate ions enter the cells via the phosphate transporters, due to structural homologies with phosphate ions. After reaching the cytoplasm, arsenate is reduced into arsenite. This is accomplished by the arsenate–reductase enzyme ArsC or the ArsAB complex. The reduction of arsenate to arsenite is implemented before it is excreted from the cell by the transmembrane protein ArsB. It is mentioned here that ArsB is also known as Acr3 in the context of some eukaryotic microorganisms. The transformation process followed by the excretion of arsenic is a common occurrence in the living world and is widespread in bacteria (Lièvremont et al. 2009). Metal oxides tend to be the primary sorbents of As in the environment, especially the oxides of iron (Fe) and aluminum (Al). In addition, Mn oxides can also sorb arsenic to some extent. According to different pH values, the OH groups can bind or release H^+ ions, and this results in the development of a surface charge. In this case, arsenic adsorbs this charge by the process of ligand exchange with OH and OH_2^+ surface functional groups.

Arsenic is absorbed by several clay minerals. The maximum adsorption of As(+5) is kaolinite, montmorillonite, illite, halloysite, and chlorite for pH values near 7. The adsorption is decreased with further increase in pH above 7. Adsorption of As(+3) by the same clay minerals is low at low pH values and is increased when pH increases. Arsenate is adsorbed to a greater extent than As(+3) on all clay minerals at $\mathrm{pH} < 7$. At higher pH values, adsorption of As(+5) and As(+3) is more comparable, and in some cases, As(+3) adsorption exceeds the one of As(+5). The OH groups that are associated with the Al ions exposed at the edges of clay particles are considered to be proton acceptors and are able to complex anionic species of As (Stollenwerk 2003).

Redox fluctuations, pH, and ions availability are responsible for the formation of insoluble sulfide precipitates such as arsenopyrite (FeAsS), realgar (AsS), and orpiment (As_2S_3) in reducing conditions (Matsunaga et al. 1996). Arsenic is also found in sedimentary environments, absorbed by Fe(+3) and Mn(+4) oxides—hydroxides after weathering of the sulfide minerals. In the case of the interaction of arsenopyrite with the ferric hydroxide, arsenic is adsorbed or co-precipitated with the ferrosoferric hydroxides (Ladeira and Ciminelli 2004). High levels of arsenic in natural waters due to the reductive dissolution of arsenic-rich iron oxyhydroxides (Li et al. 2007). In addition, oxidative dissolution of arsenic-rich pyrite or arsenopyrite is responsible for As existence in natural waters (Sullivan et al. 2003). In this case, the concentration of dissolved oxygen (DO) is the limiting factor for arsenopyrite dissolution in a variety of pH ranges (Saikia et al. 2011). Arsenic release rates seem to increase with increasing DO concentration and temperature and are similar at low (Chiou et al. 1995) pH.

The widespread arsenic contamination is thought to be related with As release from iron oxyhydroxides, probably due to the reaction of Fe-oxides/hydroxides with organic carbon (Smedley and Kinniburgh 2002). In such a case, the source of As is the adsorbed arsenic onto the surface of Fe oxide/hydroxide solid phases, and a parallel release of arsenic during the reductive dissolution of ferric oxides–hydroxides occurs (Kim et al. 2002). In addition, sorption of As(+3) onto Mn oxide/hydroxide phases has been reported by Panagopoulos and Panagiotaras (2011) in order to control geochemical processes in the groundwater pool of the Trifilia karst aquifer, in Western Greece. However, adsorbed arsenic species are weak acids and can affect the surface charge due to proton exchange reactions. Whether As adsorbs as a mononuclear or binuclear complex has implications for the level of protonation of the surface species, in the case of Fe oxide/hydroxide surfaces (Sverjensky and Fukushi 2006). Reductive dissolution of ferric oxides–hydroxides by organic matter contributes to the cycling of arsenic species into the environment (Nickson et al. 2000). Although there is sufficient knowledge on the geochemical processes that governs the arsenic occurrence and fate in nature, the extent to how microbes affecting arsenic fluxes in the environment must be further studied in order to better understand the overall biogeochemical cycling of arsenic in the natural environment. Biogeochemical processes potentially influence arsenic mobility in the natural environment and actually generate specific patterns of distribution and speciation during redox and complexation reactions so that arsenic undergoes a variety of ions and maximum adsorption capacities are observed in low to up near 7 pH values for chlorite, illite, halloysite, kaolinite, and montmorillonite clay minerals. However, adsorption capacity decreases as pH increases. An opposite behavior is apparent for

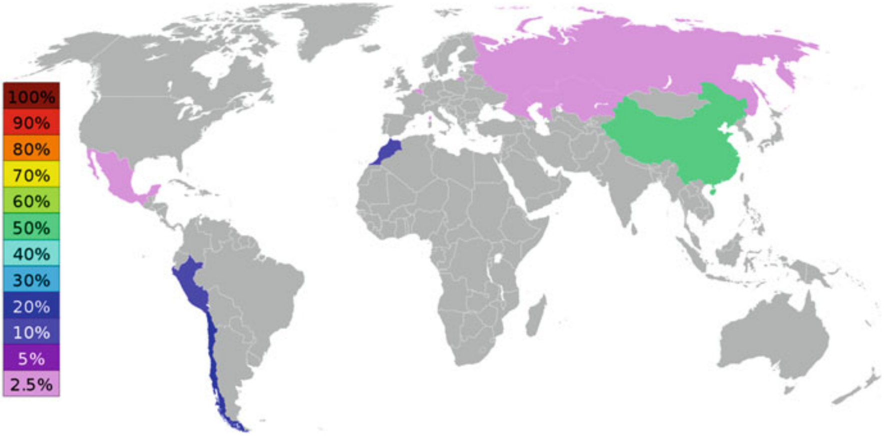

Fig. 10.2 Asenic output in 2006 (Courtesy: Wikipedia)

the As(+3) regarding the same clay minerals. In this case, adsorption of As(+3) increased with increasing pH, while adsorption was minimum at low pH values. Therefore, clay minerals can be applied for arsenic removal and remediation purposes and biogeochemical transformations.

In addition, the mobility and fate of arsenic in the environment are also related to co-precipitation and adsorption onto clay minerals, manganese oxides, and hydrous aluminum oxides. In the case of As(+5) ions, maximum adsorption capacities are observed in low to up near 7.0 pH values for chlorite, élite, halloysite, kaolinite, and montmorillonite clay minerals. However, adsorption capacity decreases as pH increases. An opposite behavior is apparent for the As(+3) regarding the same clay minerals. In this case, adsorption of As(+3) increased with increasing pH, while adsorption was minimum at low pH values. As a concluding remark is that at s, As (+5) ions adsorbed to a greater extent than As(+3) on all the abovementioned clay minerals, while at higher pH values, adsorption of As(+5) and As(+3) were more comparable, and in some cases, As(+3) adsorption exceeds that of As (Fig. 10.2).

10.2.5 Arsenic in the Environment

10.2.5.1 Arsenic in Minerals

Arsenic behavior is typical of many chalcophile elements in that it is released secondary As minerals including native arsenic, arsenates, and in rare cases arsenites (Drahota and Filippi 2009). The concentration by sulfide oxidation is modified by various biogeochemical processes and attenuated by adsorption and co-precipitation with Fe minerals, clays, and organic matter. It can form a large number of As in surface soils, which can be a useful indicator of sulfide mineral deposits (Boyle and

Jonasson 1973). In northwest-trending lobate pattern that mimics the distribution of the major gold deposits, As occurs in concentrations up to 54 mg/kg and reflects the concentration of As in pyrite that occurs within the gold-bearing zones (Thompson et al. 2002). The application of X-ray absorption near-edge spectra (XANES) of selected light-density minerals from the stream-sediment samples indicated As is associated with Al-bearing phases, such as gibbsite, amorphous Al oxyhydroxides, or aluminosilicate clay minerals as As(V) (Theodore et al. 2003).

10.2.5.2 Arsenic in Water

Arsenic occurs in the environment as the trivalent arsenite [As(III)] or pentavalent arsenate [As(V)]. Organic arsenic forms may be produced by biological activity, mostly in surface waters, but are rarely quantitatively important except in biological tissues where they may be dominant (Cullen and Reimer 1989). Arsenic is generally present as an oxysalt or oxyanion in oxic environments. In anaerobic soils, on the other hand, it is typically found combined with sulfur. Thus, in uncontaminated aerobic sediments and soils, arsenate is the predominant species, whereas in anaerobic sediments and soils, arsenite is the dominant species (Campbell and Nordstrom 2014). Over the natural range of Eh and pH in soils, both As(III) and As(V) can occur in a range of stable aqueous and solid forms. Thus, As dispersion in water can be extensive and concentrations can vary considerably in naturally occurring waters (Welch and Stollenwerk 2003).

Groundwater arsenic concentrations can vary significantly. Apart from volcanic and geothermal inputs and anthropogenic impacts including mining-influenced water (Webster and Nordstrom 2003), some large aquifers demonstrate natural concentrations above 50 μg/L. These aquifers have been reported from Bangladesh, West Bengal, Chile, Argentina, China, Mexico, Vietnam, and parts of Canada and USA (Chappells et al. 2014). The conditions controlling these elevated As levels are complex and relate to bedrock type, past and present hydrogeology, and geochemical environment. The most studied area of natural high As groundwater is in Bangladesh and West Bengal where high As in alluvial and deltaic aquifers has resulted in a significant human health impact (Smedley and Kinniburgh 2002).

The sediments were most likely derived from upland Himalayan catchments and West Bengal basement complex. The aquifers are capped by a layer of clay or silt that restricts the ingress of atmospheric oxygen and, together with organic matter in the sediments, has produced reducing conditions that favor the mobilization of As.

10.2.5.3 Arsenic in Biosphere

Arsenic is also present in the biosphere and can be transferred through the food chain. Although the element is not an essential nutrient, it can be taken up by pathways mimicking that of beneficial nutrients, for example, arsenate via the phosphate transporters and arsenite via the aquaglyceroporin channels

(Bhattacharjee et al. 2008). The total arsenic content of terrestrial plants is estimated to be 1.8 × 10^5 tons, approximately four orders of magnitude less than that in soil (Matschullat 2011). This difference reflects generally limited As bioaccumulation because of the low bioavailability of As in soil. There are exceptions, however, such as ferns that can accumulate more than 1000 mg/kg As and rice species that have been reported as being hyper-accumulators (Zhu et al. 2014).

In the tissue of living organisms, As occurs as As(III) or As(V) with As(III) predominant in reduced environments. Biological transformation can also lead to stabilization of As(III) in oxic environments as methylated As or arsenosugar compounds (Zhu et al. 2014). In marine organisms, As is commonly present as arsenobetaine (AB) and arsenosugars. Arsenic (III) is predominant in reduced environments, although it can occur in oxic environments as a result of biological transformation and redox disequilibrium (Zhu et al. 2014). In most living organisms, arsenite is predominant due to the prevailing low redox conditions. The activity of microbial methylation reactions is well understood. In the presence of microorganisms, methylation of the arsenic oxyanion may occur to form monomethylarsonic acid (MMAA), dimethylarsinic acid (DMAA), trimethylarsinic acid (TMAA), and dimethylarsine (DMA) (Zhu et al. 2014). The reduction of arsenate to arsenite may have been an important process in primeval biological cycles (Zhu et al. 2014).

In general, the thermodynamically most stable aqueous As species over the general groundwater pH range of 4 to 8 is H_2AsO_4-. Under reducing conditions, H_3AsO_3 will be the most stable aqueous arsenic species in the absence of complexing ions and methylating organisms. However, the rate of change in the oxidation state of As is not rapid unless microbially mediated, and microbial catalysis can change the distribution of redox species substantially from equilibrium (Zhu et al. 2014). Although some organisms can fully methylate As over a wide Eh-pH range, others are more specific in the As species with which they can react. These processes are also pH-dependent, and consequently, pH variations affect the distribution of organic and inorganic As species (Amend et al. 2014).

10.2.6 Fate of Arsenic in Nature

Since the primary source of arsenic in the natural environment is the arsenic minerals, the stability of these is a significant factor of controlling arsenic occurrence in nature. Table 10.2 presents the representative arsenic minerals and the Gibbs free energy of formation in their standard reference state. The interaction of the arsenic minerals with the environment results either to their dissolution or to the formation of secondary arsenic minerals, or even both. The most common valence states of arsenic in natural systems are the +3 and +5 states. However, arsenic can be found in the (−3) oxidation state (arsine), and an arsenic compound in this state is extremely

Table 10.2 Arsenic mineral, formula, crystal system, and free energy

Mineral	Formula	Crystal system	ΔfG^0 (kj/mol)
Arsenolite	As_2O_3	Cubic	−576.34
Claudetite	As_2O_3	Monoclinic	−576.53
AFA/pitticite	$FeX(AsO_4)y(SO_4)z.\ nH_2O$	Amorphous	−1268.72; −1267.1
Arseniosiderite	$Ca_2Fe_3O_2(AsO_4)_3.3(H_2O)$	Monoclinic	–
Kaatialaite	$Fe(H_2\ AsO_4)_3.5H_2O$	Monoclinic	–
Kankite	$Fe_3(AsO_4)0.3.5\ H_2O$	Monoclinic	–
Kolfanite	$Ca_2Fe_3O_2(AsO_4)_3.2(H_2O)$	Monoclinic	–
Parasymplesite	$Fe_3(AsO_4)0.8\ H_2O$	Monoclinic	–
Pharmacosiderite	$K[Fe_4(OH)_4(AsO_4)_3]0.6.5\ H_2O$	Cubic	–
Scorodite	$FeAsO_{4.}\ 2H_2O$	Orthorhombic	−1282.42; −1285.05; −1279.2; −1263.52
Symplesite	$Fe_3(AsO_4)_2.\ 8\ H_2O$	Triclinic	−3751.02; −3792.01
Yukonite	$Ca_7Fe_{12}(AsO_4)_{10}(OH)_{20}.15H_2O$	Amorphous	–
Beudantite	$PbFe_3(AsO_4)(SO_4)(OH)_6$	Hexagonal	−3055.6; −3081.12
Bukovskyite	$Fe_2(AsO_4)(SO_4)(OH).7H_2O$	Triclinic	−3480
Sarmientite	$Fe_2(AsO_4)(SO_4)(OH)0.5\ H_2O$	Monoclinic	–
Tooeleite	$Fe_6(AsO_3)_4\ (SO_4)(OH)_4.4\ H_2O$	Monoclinic	–
Zykaite	$Fe_4(AsO_4)_3(SO_4)(OH)0.15\ H_2O$	Orthorhombic	–
Haidingerite	$Ca(AsO_3OH).H_2O$	Orthorhombic	−1533
Hornesite	$Mg_3(AsO_4)_2.8H_2O$	Monoclinic	–
Pharmacolite	$Ca(HAsO_4).2H_2O$	Monoclinic	−1808.21
Picropharmacolite	$Ca_4Mg\ (AsO_4)_2(HAsO_3OH)_{2.}.11H_2O$	Triclinic	–
Weilite	$CaHAsO_4$	Triclinic	−1292.48
Adamite	$Zn_2(AsO_4)(OH)$		−1252.29
Annabergite	$Ni_3(AsO_4)_2.8H_2O$	Orthorhombic	−3488.57; −3482.34
Austinite	$CaZn(AsO_4)(OH)$	Orthorombic	−1651.13
Bayldonite	$PbCu_3(AsO_4)_2(OH)_2$	Triclinic	−1810.6
Clinoclase	$Cu_3(AsO_4)(OH)_3$	Monoclinic	−1209.48
Conichalcite	$CaCu(AsO_4)(OH)$	Orthorhombic	−1470.17
Cornubite	$Cu_5(AsO_4)_2(OH)_4$	Triclinic	–2057.9
Duftite	$PbCu(AsO_4)(OH)$	Orthorhombic	–959.92
Erythrite	$Co_3(AsO_4)_2.8H_2O$	Monoclinic	–
Euchroite	$Cu_2(AsO_4)(OH)0.3(H_2O)$	Orthorhombic	−1552.7
Fornacite	$Pb_2Cu(AsO_4)(CrO_4)(OH)$	Monoclinic	−1956.861
Kottigite	$Zn_3(AsO_4)_2.8H_2O$	Monoclinic	–4030.48
Legrandite	$Zn_2(AsO_4)(OH).H_2O$	Monoclinic	−1486.6
Mansfieldite	$AlAsO_4.2H_2O$	Orthorhombic	−1730.78; −1720.8
Mimetite	$Pb_5(AsO_4)_3Cl$	Hexagonal	–2675.5; –2616.8
Olivenite	$Cu_2(AsO_4)(OH)$	Monoclinic	–845.52
Schultenite	$Pb(AsO_3OH)$	Monoclinic	–805.66; –809.62

(continued)

Table 10.2 (continued)

Mineral	Formula	Crystal system	ΔfG^0 (kj/mol)
Sterlinghillite	$Mn_3(AsO_4)_2.4H_2O$	Monoclinic	−4045.17
Arsenopyrite	FeAsS	Monoclinic	−141.6
α,Realgar	AsS	Monoclinic	−31.3
ß,Realgar	AsS	Monoclinic	−30.9
α,Orpiment	As_2S_3		−84.9
Am,Orpiment	As_2S_3	Monoclinic	−76.8

toxic. This toxic oxidation state can be formed under very reducing conditions, and for this reason, its occurrence in nature is relatively rare. On the other hand, inorganic and organic species of As are present in the natural environment, with inorganic forms been typically more abundant in freshwater systems.

In aqueous systems, arsenic exhibits anionic behavior. In case of oxygenated waters, arsenic acid predominates only at extremely low pH values, namely for pH below 2. In the pH range of 2 to 11, it is in the form of H_2 AsO_4^- and $HAsO_4^{2-}$. In mildly reduced conditions and low pH values, arsenious acid is converted to H_2 AsO_3^- and this conversion is more frequent as pH increases. When the pH exceeds, 12 $HAsO_3^{2-}$ does appear. Arsenate [As(+5) and arsenite [As(+3) are the two most common inorganic forms of arsenic in freshwaters. As(+5) is thermodynamically stable under oxic conditions, while As(+3) is stable under more reducing conditions. However, As(+5) and As(+3) are often found in both oxic and anoxic waters and sediments. The oxidation of As(+3) by O_2 is slow, while bacterially mediated redox reactions can be much faster (Drahota and Filippi 2009). Arsenate is an anion at the pH of most natural waters (H_2 AsO_4^- and $HAsO_4^{2-}$), while arsenite is a neutral species.

In oxidative environments, the form H_2 AsO_4^- predominates with pH values below 6.9, whereas the $HAsO_4^{-2}$ ions predominate at higher pH levels. Arsenite (H_3 AsO_3) is the main arsenic chemical specie in natural waters with pH < 9 and in slightly reducing condition (Lièvremont et al. 2009). In aerobic waters, arsenic acid predominates only at extremely low pH (<2). At the pH range of 2 to 11, it is replaced by H_2 AsO_4^- and $HAsO_4^{2-}$ ions. Arsenious acid appears at low pH and under mildly reduced conditions, but it is replaced by H_2 $AsO_3{}^-$ as the pH increases. Only when the pH exceeds 12, the $HAsO_3^{2-}$ ion appears. The $HAsS_2$ arsenic chemical specie can form at low pH in the presence of sulfide ions. Arsine derivatives and arsenic metal can occur under extreme reducing conditions (Rakhunde et al. 2012). Arsenic changes its valence state and chemical form in the environment. In the pH range of 4 to 10, As(+5) species are negatively charged in water, and the predominant As(+3) species is neutral in charge.

10.2.7 Biogeochemical Cycling of Arsenic

Weathering of rocks, geothermal and volcanic activities, mining, and smelting release As from the lithosphere to the terrestrial and oceanic environments (Fig. 10.2). The biosphere reservoir appears to be fairly well characterized (Zhu et al. 2014). The concentrations of As in natural waters vary by more than four orders of magnitude depending on the source of As, the amount available and the local geochemical environment (Fig. 10.2). Under natural conditions, the greatest range and the highest concentrations of As are found in ground waters as a result of the strong influence of water–rock interactions and the greater tendency in aquifers for the physical and geochemical conditions to be favorable for As mobilization and accumulation. Concentrations are commonly higher when riverine inputs are affected by industrial or mining effluent or by geothermal water. In lake and river waters, As(V) is generally the predominant species, though significant seasonal variations in speciation and absolute concentration have been found (Gammons et al. 2007). Concentrations and relative proportions of As(V) and As(III) vary according to changes in input sources, redox conditions, and biological activity. The presence of As(III) may be maintained in oxic waters by biological reduction of As(V), particularly during summer months. Higher relative proportions of As(III) have been found in rivers close to inputs of As(III)-dominated industrial effluent and in waters with a component of geothermal water (Morin and Calas 2006).

Proportions of As(III) and As(V) are particularly variable in stratified lakes where redox gradients can be large and seasonally variable. As with estuarine waters, distinct changes in As speciation occur in lake profiles as a result of redox changes. Rapid oxidation of As(III) occurs during the early stages of lake turnover as a result of microbial activity (Oremland et al. 2000). This event precedes Fe(II) oxidation although the speciation of As in lakes does not always follow that expected from thermodynamic considerations. Welch et al. (1988) found that the Eh calculated from the As(V)-As(III) couple neither agreed with that from the Fe(II)-Fe(III) and other redox couples nor with the measured Eh.

Much of this redox disequilibrium has been attributed to the role of microorganisms in the cycling of As (Zhu et al. 2014). As a molecular analog of phosphate, arsenate uses a phosphate transport system to enter cells. Once inside, it inhibits the phosphorylation of ADP and thereby the synthesis of ATP, leading to its toxic legacy. Arsenate can also substitute for phosphate in various bio molecules, thus disrupting key pathways, including glycolysis. Arsenite is even more toxic than arsenate and enters the cell much like glycerol molecules. Arsenite binds with glutathione, a key enzyme in mammalian metabolism, inhibiting its function, and it binds to thiolates in cysteine residues, disrupting the function of many proteins (Mukhopadhyay et al. 2002).

Arsenic levels in edible plants are generally low, even in crops grown on contaminated land with lower levels in Fe-rich and clay-rich soils and higher levels in plants grown on sandy or organic-rich soils such as aridisols, alluvium, or peat (Abrahams and Thornton 1987). The degree of uptake is variable from species to species. Unlike marine and freshwater organisms grown in contact with sediments, the As level in plants remains below that of the associated soils. In plants, roots show higher As levels than stems, leaves, or fruit and lower plants and grasses have a greater uptake than higher-order plants. Arsenic uptake in plants can occur through aqueous transfer at the roots or from absorption of colloids or dissolved species through leaves. The cycling of As in the near-surface environment thus occurs not only through solution transfer but also through the decay of As-bearing vegetation and recycling of this material (Fig. 10.3).

10.3 Fluoride

10.3.1 Sources of Fluoride

Fluoride occurs in many minerals and in soil (WHO 2006), thus also in groundwater, and the average concentration in the USA is 0.26 mg/L (Centers for Disease Control and Prevention 1999; USDA 2005). Since the mid-1940s, fluoride has been added to many community water supplies with the aim of preventing tooth decay (Centers for Disease Control and Prevention 1999). In the USA, fluoridation is recommended at a concentration of 0.7 mg/L (U.S. Department of Health and Human Services 2015). Water fluoridation is applied in several other countries as well, such as Australia, Brazil, Canada, Chile, Ireland, New Zealand, and the UK. For adults in USA, fluoridated water and beverages contribute an average of about 80% of the daily total fluoride intake (estimated to average 2.91 mg) in fluoridated communities (U.S. Environmental protection Agency 2010). In addition to fluoridated water and other forms of caries prevention, tea is an important source of fluoride exposure, even if prepared with deionized water (Kakumanu and Rao 2013; Waugh et al. 2017). Additional sources of fluoride intake include certain foods, industrial emissions, supplements, pesticide residues, and certain pharmaceuticals that can release fluoride (National Research Council 2006). Few studies provide population-based data on fluoride exposure, although national data on plasma-fluoride concentrations are available from a recent NHANES study in the USA (Jain 2017) (Fig. 10.4).

10.3.2 Fluorine Geochemistry

10.3.2.1 Lithogeochemistry

Fluorine is the lightest of the halogen group and is the most electronegative element. As such, it is highly reactive, and it is widely stated in the literature that elemental fluorine does not exist naturally in the free state, but recently, Schmedt auf der Günne et al. (2012) have demonstrated the presence of F_2 in a radioactive variety of fluorite, antozonite, using NMR spectroscopy. However, F normally exists in nature

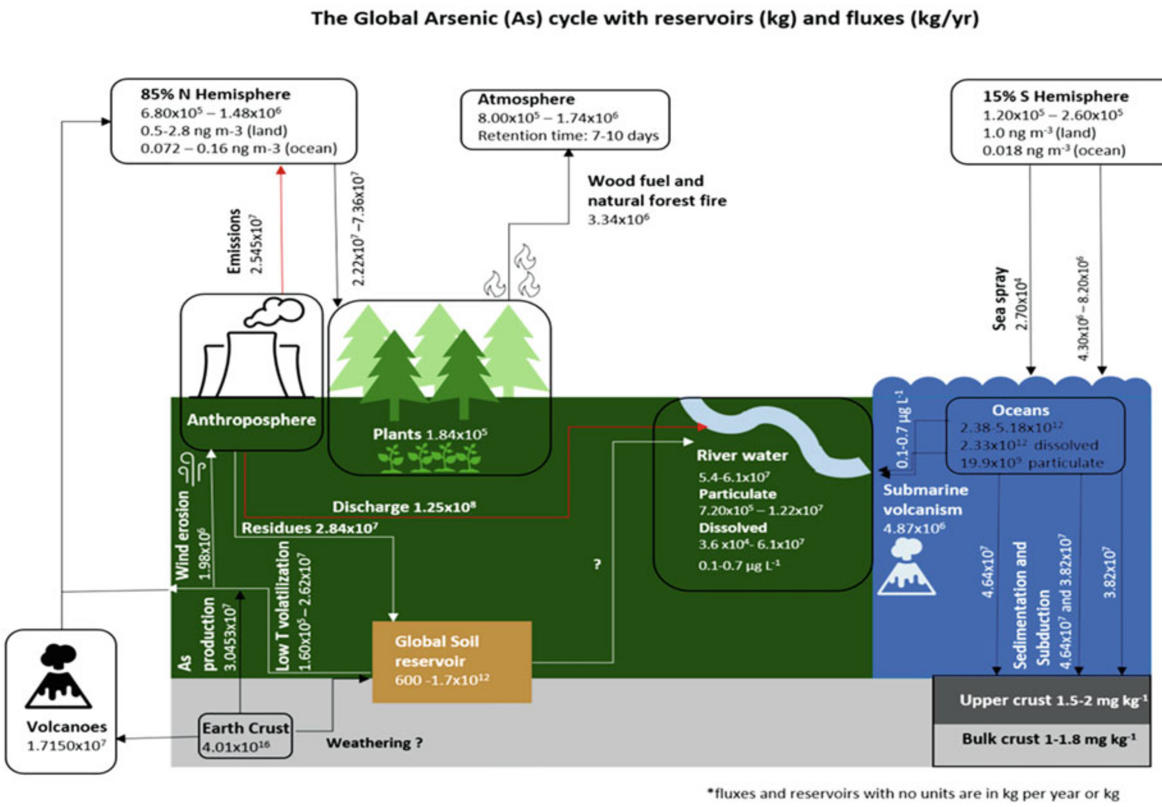

Fig. 10.3 Arsenic biogeochemical cycle (Courtesy: Wikipedia)

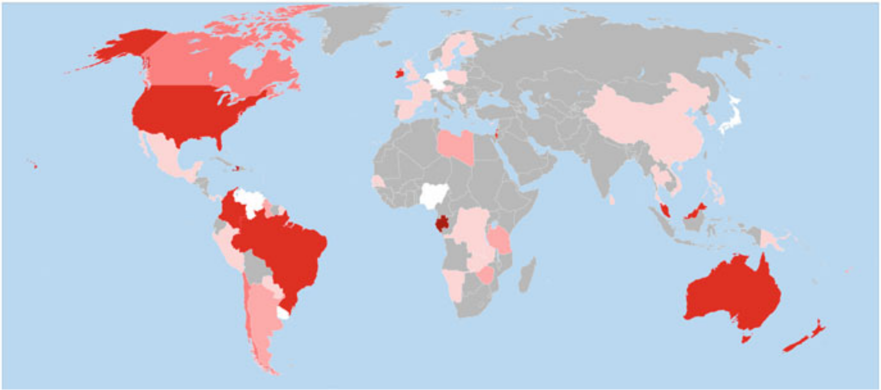

Fig. 10.4 Percentage of population receiving fluoridated water, including both artificial and natural fluoridation, as of 2012(Z). 80–100% 60–80% 40–60% 20–40% 1–20% < 1% unknown

as the F^- ion. Fluorine is a lithophile element being concentrated in the crust of the earth. Rudnick and Gao (2014) indicate that the bulk continental crust contains 553 mg/kg. Of the rock-forming minerals in which F is an essential constituent only fluorite (CaF_2) and, to a lesser extent, topaz ($Al_2SiO_4(F,OH)_2$) are relatively common, while cryolite (Na_3AlF_6) and bastnäsite ((Ce, La, Nd)CO_3F) can occur in some granitic pegmatites, and villamite (NaF) can occur in some per alkaline and nepheline-containing igneous rocks and has also been identified in evaporate minerals in Lake Magadi, Kenya. Several other minerals which contain F as an essential component have been identified in pegmatitic rocks and in metasomatically/hydrothermally altered rocks. In most rocks, these F-containing minerals account for a relatively small percentage of the total F content. It is, therefore, not surprising that hydroxyl-containing silicates and apatite are the major hosts of F in the lithosphere.

According to Koga and Rose-Koga (2018) in the rocks that make up the continental crust, F predominantly ranges up to 900 mg/kg, being fairly evenly distributed within the major rock types. However, within the different rock types, there are wide variations in F content. In general, the F content of igneous rocks increases with silica content being highest in felsic and lowest in ultramafic rocks. Thus, granitic pegmatites can contain concentrations of over 1 wt % F. Fluorine also becomes concentrated in the late stage hydrous fluids, which can lead to hydrothermal and metasomatic alteration of the granites resulting in extreme F enrichment. In addition, alkalic and silica under saturated igneous rocks are also generally F-rich, with some carbonatites containing up to 2.5 wt% F. Of the common sedimentary rocks, only shales are relatively enriched in F, ranging up to about 800 mg/kg, with sandstones and carbonates generally containing <300 mg/kg. However, sedimentary phosphorites are strongly enriched in F.

10.3.2.2 Soil Geochemistry

The fluorine content of most soils ranges between <10 and 1000 mg/kg; however, values in excess of 1 wt % have been recorded in uncontaminated soil. The F content of soils reflects that of the parent material, for example, high F soils occurring over F-rich granites. However, retention of F in a soil generally reflects its clay content as clay minerals strongly adsorb F^- with the greatest adsorption occurring in slightly acidic soils (Liu et al. 2014). As a result, clay-rich soils tend to be rich in F. In addition to the adsorption of F by clays in soil, according to Liu et al. (2014), F^- replaces OH− in the clay minerals. The strong ability of clay minerals to adsorb F^- causes it be retained in the subsurface horizons. Aluminum and Fe oxyhydroxides are also strong adsorbents of F^- in soil and aid in the immobilization of atmospherically deposited F. The ability of soils to retain F is well illustrated by the case of Mt. Etna volcano, Italy, where large quantities of F-rich gases are evolved continuously. The groundwaters in the aquifers occurring on the flanks of the volcano, which are important sources of potable water, have been protected due to the retention of F by the soils (D'Alessandro et al. 2012). The bioavailability of soil F is generally low, particularly in soils with a pH of 5.5–6.5, so that little soil F is incorporated in plants. In addition, soil-derived F is prevented from being incorporated into the aerial parts of plants through exclusion by the roots (Davison and Weinstein 2006) (Fig. 10.5).

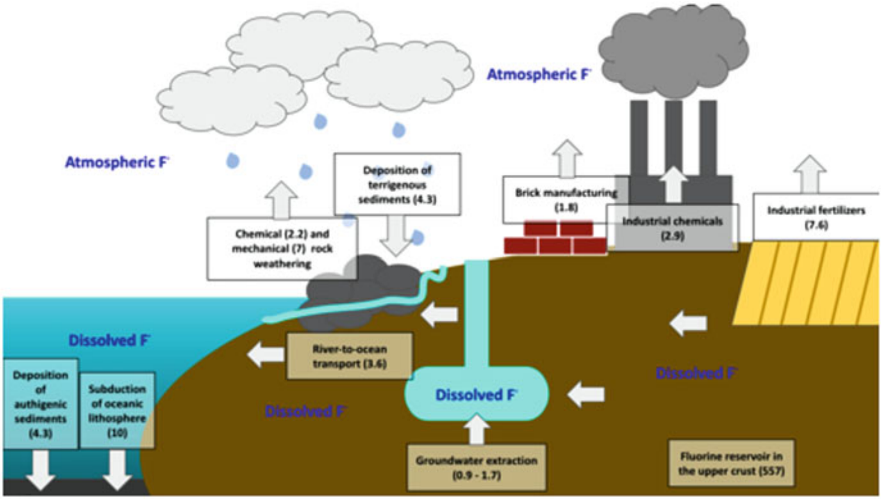

Fig. 10.5 Global biogeochemical cycle of Fluorine (Courtesy: Wikipedia)

10.3.3 Fluorine in the Environment

10.3.3.1 Vulcanicity

Fluorine is released from volcanoes predominantly as HF gas with minor amounts emitted in other gases such as Si-containing compounds (D'Alessandro 2006). Gaseous HF interacts with and is adsorbed onto the surface of volcanic ash, and during eruptions, the majority of F release is by way of ash. Francis et al. (1998) found that during quiescent degassing of Mount Etna, Sicily, Italy, 190 t of HF is released daily, which amounts to an annual release of almost 70,000 t, making it the largest point source of atmospheric F emissions on earth. While F-rich gases impact the whole environment in volcanic regions, the major concern regarding volcanogenic F is its impact on drinking waters and the deposition of F-containing ash on plants and soils in the vicinity of the eruption, the major pathway into the biosphere being via impacted waters and crops (D'Alessandro 2006). Fluorine in volcanic ash is solubilized in the digestive systems of grazing animals, and there are many examples of grazing animals developing chronic fluorosis as a result of ingestion of F-rich ash with both domestic and wild animals being affected (Ranjan and Ranjan 2015). Volcanic activity has resulted in F^- enrichment of surface and groundwaters in many countries. In Goma, Democratic Republic of the Congo, rainwater is a major source of potable water and, due to its interaction with a plume deriving from the Nyiragongo and Nyamuragira volcanoes, is enriched in F^-, which has resulted in dental fluorosis in the population (Balagizi et al. 2017). Volcanic emissions have been suggested to be the major source of F to the atmosphere. While F emissions from mid-ocean ridges and intraplate volcanoes are also likely to produce significant quantities of HF, it seems probable that global atmospheric emissions from volcanoes may not be as great as previously thought.

10.3.3.2 Marine-Derived Fluorine

It has been proposed that marine aerosols and spray make a very significant contribution to atmospheric F and to its geochemical cycle. Friend (1989) suggested that the annual marine flux of F, supposed to be 0.4 to 1 Mt., to the atmosphere is second only to the volcanic flux, while Tavener and Clark (2006) quote values of between 1 and 2 Mt. However, other authors suggest the lower value of 20,000 t for this flux. The mean F content of seawater is 1.3 mg/L, and it has been suggested that marine-derived F is an important component in the hydrogeochemical cycle of F^-. It has been suggested that F is emitted from seawater in gaseous and particulate forms, the gaseous component being HF. Relative to Cl, F is preferentially enriched in marine emanations to the atmosphere with the F/Cl ratio of precipitation being 10–1000 times that of seawater. It was also concluded that the major source of F^- in rainwater was anthropogenic.

10.3.3.3 Wind-Blown Dust

Weinstein (1977) suggested that wind-blown soil could make a significant contribution to atmospheric F content. On the basis that in the USA alone about 30 Mt. of soil are removed annually by wind action, this would add about 6000 t of F to the atmosphere. Analytical data on ice cores from Greenland and the French and Swiss Alps (Preunkert and Legrand 2001) suggest that wind-blown dust, deriving from soils, constitutes a significant source of F^{-} in precipitation. While the source of F^{-} through the 1930s to 1980 was predominantly anthropogenic, Preunkert and Legrand (2001) found that from 1980 to 2000 wind-blown dust accounted for $18 \pm 2\%$ of the $F-$ in ice cores from the Alps.

10.3.3.4 Biomass Burning

Biomass burning can result from natural processes and from human actions, with the latter being both intentional, as in the agricultural practice of stubble burning, and from accidental fires (Yadav and Devi 2018). While the great majority of biomass fires are anthropogenic ally sourced, natural fires tend to destroy larger areas of vegetation than human induced fires (Yadav and Devi 2018). Several authors have commented on the potential contribution of biomass burning to atmospheric releases of fluorine. Jayarathane et al. (2014) have attempted to determine the degree of F emission from biomass burning experimentally. On the basis of the results, Jayarathne et al. (2014) suggest that biomass burning releases significant amounts of fine particulates (PM2.5) containing F. The degree of F release varied with plant type and with geographic distribution. Jayarathane et al. (2014) estimate that 76,000 t of F are released annually from biomass burning.

10.3.4 Industrial Sources of Fluorine in the Environment

10.3.4.1 Coal Combustion

The world average for the F content of coal has been calculated to be 88 mg/kg (Ketris and Yudovich 2009), and a high percentage of this is released during combustion. Doley et al. (2004) state that emissions from coal-fired power stations represent the largest individual source of atmospheric F in Australia with impacts on plants being recorded. Studies in Europe have shown that fluorosis occurs in wild animals as a result of emissions from coal-fired power stations such as in the NW of the Czech Republic (Kierdorf et al. 2012).

However, it is in China that the worst problems associated with F release from coal combustion have been manifested as it is a major producer of coal and consumes about half of the global total production (Finkelman and Tian 2018), it being the country's major energy resource (Yang et al. 2017). Dental fluorosis and skeletal fluorosis due to coal combustion have been reported in several Chinese provinces, with over 18 million people affected in 2000 (Li et al. 2003). It is likely that much of the exposure to F derives from the burning of coal in open stoves and utilization of the stoves to dry and preserve foodstuffs, such as corn and chillies with some also deriving from direct inhalation. While it has been suggested that the source of F is directly due to its release from coal (Liu et al. 2007), some authors have implicated the use of F-rich clay, used to bind the coal into briquettes, as a major source of F release during combustion (Dai et al. 2007).

10.3.4.2 Aluminum Smelting

Aluminum metal is produced from aluminum oxide by the Hall–Héroult process, whereby the Al_2O_3 is dissolved in molten cryolite (Na_3AlF_6), with some added AlF_3, and is subjected to electrolysis at 960 °C. During the electrolytic process, F is released into the atmosphere in both gaseous and particulate forms; the gaseous releases are almost entirely HF, but minor quantities of other F-containing gases such as CF_4 and C_2F_6 are also produced (Kvande 2014). The particulate species are Na and Al fluorides and cryolite. Environmental problems related to F release from Al smelters still occur. Rodriguez et al. (2012) determined the concentrations of F deposited on deciduous tree leaves around an Al smelter in Puerto Madryn, Patagonia. In all cases, there was pronounced distance decline in F contents of snow melt, and in the case of the Sayanogorsk and Krasnoyarsk smelters, values of 0.5–1 mg/kg were recorded at 29–30 km distance. In Victoria, Australia, in the vicinity of the Portland Al smelter, dental, and skeletal fluorosis has been identified in kangaroos (Kierdorf et al. 2016). The world production of primary Al in 2017 was 63 Mt. According to Tjahyono et al. (2011), most large Al smelters limit F emissions to 0.5–0.6 kg F/t Al.

10.3.4.3 Phosphoric Acid and Phosphate Fertilizer Manufacture

Phosphoric acid is manufactured from phosphate rock, which is essentially composed of apatite. In the wet manufacturing process, the phosphate rocks are reacted with acid, which can be hydrochloric, nitric, or sulfuric acid; however, for the manufacture of fertilizers, sulfuric acid is used. The thermal process involves conversion of the phosphate rock to elemental phosphorus, which is subsequently converted to phosphoric acid. The production of fertilizers utilizes 88% of the phosphate rock extracted globally, and the wet method of phosphoric acid production for fertilizer manufacture accounts for about 90% of global phosphoric acid production. Phosphate rock, which is extracted from several countries, contains appreciable quantities of F with those being utilized for fertilizer production generally containing from 2 to 4% F. During the wet process, much of the F is converted to HF and SiF_4 with 10–15% of these compounds being volatilized. Mirlean and Roisenberg (2007) in a study of F^- distribution around a phosphate fertilizer plant

Fig. 10.6 The gifblaar is one of the few organo-fluorine synthesizing organisms

in Rio Grande Brazil reported F^- values in rainwater of up to 3.04 mg/L within 2 km of the plant, the rainwater also having a pH of 4.1. Groundwater near the plant had a correspondingly low pH of 4.1 and elevated F^- content of 4.79 mg/L. The fine fractions of soils (<63 μm) in the vicinity of the plant were found to contain up to 2.37 wt % F^-. In addition to the release of F-containing compounds during the manufacture of phosphoric acid, it is apparent that significant quantities are also released from the waste phosphogypsum piles and from the associated water. It is apparent that F contamination can also occur as a result of extraction of phosphate rock (Fig. 10.6).

10.4 Lead

10.4.1 Migration of Lead in the Natural Environment

Natural concentrations of lead in lead ore deposits do not normally move appreciably in normal ground or surface water, because any lead dissolved from primary sulfide ore tends to combine with carbonate or sulfate ions to form insoluble lead carbonate or lead sulfate or else to be adsorbed by ferric hydroxide. Mechanical disintegration and transportation of these insoluble lead compounds can remove lead from the surface of lead ore bodies and disperse it to some extent. Lead can also be leached by acid waters, particularly those that are rich in organic material, and travel in solution as soluble lead organic complexes. In this form, it can be taken up by plants and enter the food chain, but examples are rare. In regions characterized by alkaline, neutral, or saline waters and soils, naturally occurring forms of lead do not enter either water or plants except in very minute traces. Lead minerals in a nonreactive host rock such as sandstone or quartzite have been known to dissolve in acid waters in amounts toxic to vegetation in a small area, but there are no known instances of lead poisoning in humans related to the natural occurrence of lead.

10.4.2 Lead in Rocks, Sediments, Fossil Fuels, and Minerals

The average abundance of lead in the earth's crust is approximately 15 ppm (parts per million), which is equivalent to half an ounce of lead per ton of rock. The lead contents of the common rock types that make up the crust of the earth range from about 30 ppm for granitic rocks, rhyolite, and black shale to about 1 ppm for evaporite sediments, basalt, and the ultramafic igneous rocks such as dunite, which are rich in iron and magnesium and poor in silica.

Although lead is a major constituent of more than 200 known minerals, most of these are very rare, and only three are commonly found in sufficient abundance to form minable lead deposits. These three are galena, the simple sulfide of lead; anglesite, the lead sulfate; and cerussite, the lead carbonate. Galena is a common primary constituent of sulfide ore deposits, anglesite and cerussite normally form by the oxidation of galena close to the surface.

Lead is also present in trace amounts in many of the common rock-forming minerals. The amount of lead in any one of these minerals varies widely, and the greater the normal lead content of such a mineral, the greater the observed variation is likely to be. For instance, potash feldspar generally contains the most lead of any of the common silicate minerals; whereas samples from one group of pegmatite dikes in Norway yielded 280 ppm lead, similar samples from another group of pegmatite dikes in the same region contained less than 10 ppm. The maximum amount of lead this mineral can contain is unknown, but 2800 ppm lead has been reported in a sample of a green variety of microcline called amazonite.

The common silicate minerals found in igneous rocks, in order of decreasing lead content, are (1) potash feldspar; (2) plagioclase feldspar and muscovite mica; (3) pyroxenes, amphiboles, and biotite mica; and (4) quartz. The common minerals of chemically precipitated sedimentary rocks (calcite, dolomite, gypsum, and halite) all normally contain less than 10 ppm lead. The lead content of the sedimentary clay minerals is extremely variable but is commonly on the order of 10–20 ppm.

10.4.3 Lead in Soil

Lead content of young residual soils is strongly influenced by that of the parent rock from which they are derived; however, this relationship is modified and may be obscured, by other factors in mature soils developed on deeply weathered parent material. These factors include oxidation and reduction reactions, linking of organic compounds by lead ions, base exchange reactions by clay, adsorption of lead by hydroxides of iron and manganese, local solution and transportation by organic acids, and cycling by vegetation. In general, lead is more mobile in acid soils than in alkaline soils, tending to be leached out of the former and to form residual concentrations in the latter. Relatively high total-lead concentrations in alkaline soil may reflect residual concentration of lead in an insoluble form, which is not available to plants.

10.4.4 Lead in Water

The concentration of lead in river water is low under natural conditions. Although small amounts of lead are widely distributed as a minor constituent in rock and soil minerals, lead is only slowly released by weathering processes. Even where the element is concentrated in ore deposits, the low solubility of lead in water that contains dissolved carbon dioxide species and has a pH near neutrality generally will maintain concentrations of lead in solution below a few tenths of a milligram per liter. The waterborne element tends to be complexed by relatively insoluble organic matter and may also be extracted from water by organisms. The median concentration of lead in river and lake water of the USA is about 2 pg/L. Concentrations of lead in seawater range from a few hundredths of a microgram per liter (a value of 0.03 pg/L is widely quoted) in the deeper parts of the ocean basins to 0.4 pg/L observed at several places both near shore and far offshore in surface waters of the Pacific Ocean. The higher near shore and near-surface concentrations, however, are ascribable to atmospheric fallout of lead particles or washing out of such particles by rainfall.

10.4.5 Lead in Vegetation

Lead occurs naturally in small amounts in all plants. The concentration of lead in vegetation varies not only with the individual species, but also as a complex function of climatic variations, parts of the plant, composition of the soil in which the plant grows and of the rock from which this soil is derived, and finally the effects of artificial contamination of both the water that nourishes the plant and the air that surrounds it. Anomalously high concentrations of lead in plants may reflect natural contamination from lead deposits or artificial contamination of the plant's environment by man. Extensive analyses of plants from primitive areas, unaffected by either of these sources of contamination, are required to establish normal background values for lead in natural vegetation.

Studies of seasonal variation in the lead content of trees suggest that lead concentration is highest in early spring at the beginning of the growing season, declines during the summer, and rises again in the fall. Lead also tends to concentrate in certain parts of a growing plant. In trees, the highest lead concentrations are usually found in the older twigs; somewhat less lead occurs in the young twigs, seeds, and trunk wood, still less in the leaves or needles, and least of all in the roots. On the other hand, lead content of the leaves of certain vegetables appears to be higher than that of their stems, and the lead in fruits and root vegetables is largely concentrated in the skin or peel. There appears to be a general tendency for lead to be more abundant in plant ash than in the soil, and more abundant in the soil than in the bedrock, but there are many exceptions.

The knowledge that certain plant species have the ability to absorb anomalous amounts of lead from lead-rich soils and their underlying parent materials has been used as a biogeochemical tool in prospecting for lead deposits for a quarter of a century. These accumulator plants include certain species of both evergreen and deciduous trees, as well as many shrubs and smaller plants. Contamination of food and forage crops by artificial lead compounds contained in insecticide sprays, automobile exhaust fumes, and industrial smoke is a matter of concern to public health workers. Anomalously high lead concentrations have been found in leafy vegetables and grasses grown in proximity to major highways, in crops grown on soil with a long history of treatment with lead-bearing insecticides, and in crops exposed to fallout from smelter smoke.

10.4.6 Lead in the Atmosphere

Lead enters the atmosphere largely in the exhaust fumes from internal combustion engines and, to a lesser extent, from the smoke produced by large-scale industrial burning of coal. Consequently, the lead content of the air is highest in urban industrial areas and lowest in rural areas. The average lead concentration in the air of large metropolitan areas is about 2.5 p.g/m^3. In rural areas, it is less than 0.5 p.g/m^3. The amount of lead present in the air at any particular place varies with traffic density, air temperature, and atmospheric conditions. The lead-bearing particles in the air are heavy and tend to collect in low areas with poor air circulation; lead concentrations greater than 40 p.g/m3 have been measured in the air of vehicular tunnels. In spite of this tendency of lead to accumulate close to the ground, traces of it enter the upper atmosphere and are carried widely around the earth to return to the surface in rain or snow (Fig. 10.7).

10.5 Nitrogen

10.5.1 Nitrogen in Planets

The carbon and nitrogen cycles involve similar conversions of various redox states (from completely oxidized to completely reduced). These transformations are catalyzed at the organismal level and lead to the movement of carbon and nitrogen among the biosphere, atmosphere, geosphere, and ocean; to this extent, the two cycles seem quite similar. Nitrogen resides primarily in the atmosphere as dinitrogen and trace amounts of N_2O (an important atmospheric biosignature) (Galloway 2004). With the exception of a few phyllosilicates that contain ammonia substituted

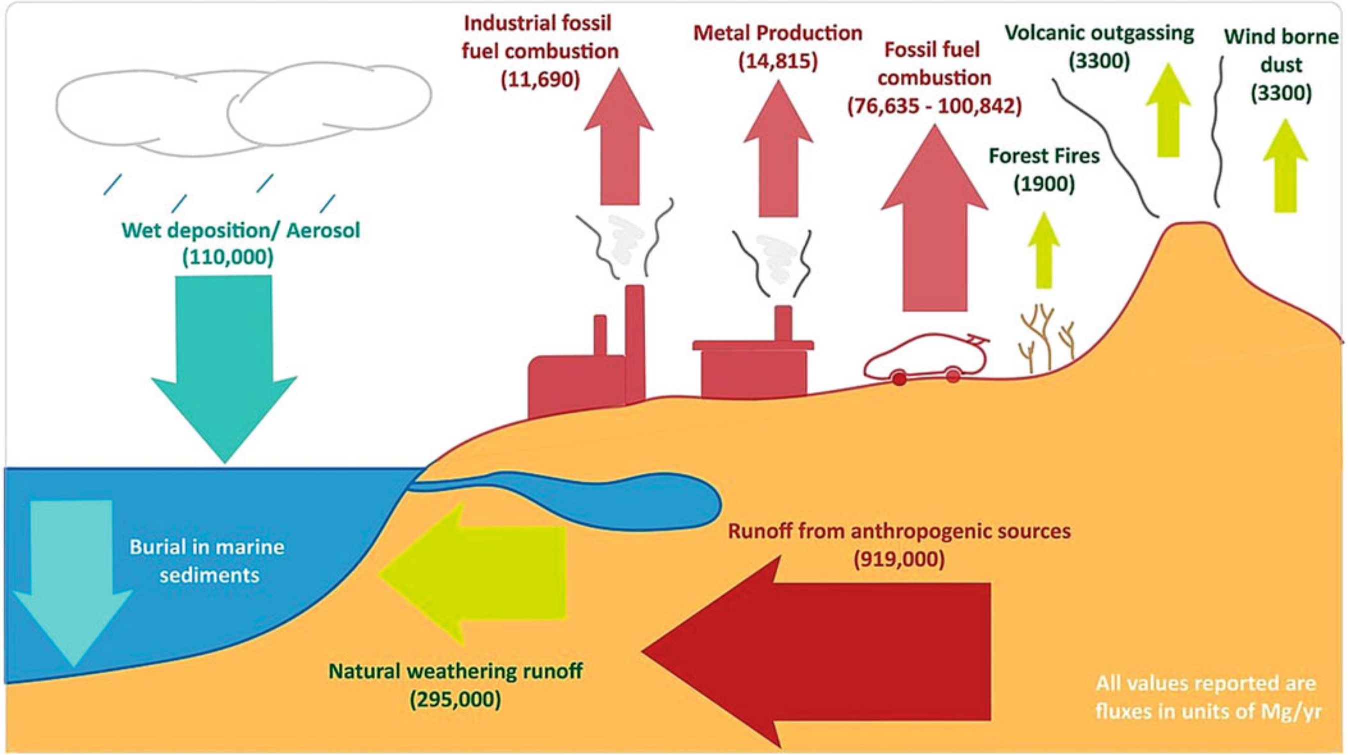

Fig. 10.7 The bio-geochemical cycle of lead

for potassium, nitrogen has no substantial geological reservoirs. Because of this unusual distribution, the amount of nitrogen found in the biosphere (in living species and deposited as shales) is actually a few percent of the total fixed nitrogen. Nitrogen is "fixed" from N_2 through both physical (such as nitrogen oxide formation by lightning) and biological processes. Minerals containing fixed nitrogen, such as nitrate and ammonium salts, tend to dissolve in the presence of even small amounts of liquid water. Thus, except for extremely dry sites such as the Atacama Desert, nitrogen moves from the continents to the oceans as soluble nitrates in water flow (Galloway 2004) and returns to the atmosphere as N_2 via denitrification, the return pathway that keeps the nitrogen cycle going. Nitrogen fixation—the transformation of N_2 to a reduced, biologically useful form is often touted as the great evolutionary invention that allowed life to prosper on earth (Smil 2001). Nitrates are not readily converted to N_2 by abiotic processes, so that in a biological oxidizing environment, any conversion of N_2 to soluble nitrates should result in the progressive loss of N_2 from the atmosphere and the accumulation of nitrates in the oceans. On a tectonically active planet such as earth, some nitrogen is returned on geological time scales via volcanic emissions, but given the absence of nitrogen-rich minerals, this effect will be relatively small (Kasting et al. 1993). Thus, if biological pathways such as denitrification (Van de Graaf et al. 1995) did not occur, the terrestrial nitrogen cycle could not be sustained. Even on earth, over the course of billions of years, abiotic processes such as lightning would substantially deplete the atmosphere of N_2, leaving an ocean of soluble nitrogen and a land mass substantially depleted in this element (Mancinelli and Banin 2003). Denitrification is the driving force for the return of nitrogen to the land and its equitable redistribution via nitrogen fixation.

On Mars, things are very different. N_2 constitutes only about 2.7% of a very thin atmosphere (Yung and DeMore 1999). Isotopic measurements of the Martian atmosphere suggest that the nitrogen has been lost from the planet over geological time (Yung and McElroy 1979), and to date, no ammonia has been identified. If nitrogen-containing life ever existed on Mars, then we would expect evidence of this to exist in the form of sedimentary deposits containing substantial amounts of nitrogen (Chicarelli et al. 1993). Given the lack of tectonic processing and the absence of continuing life that might recycle the evidence of the past, there might be relatively accessible and unaltered evidence for this life, perhaps visible even today in outflow channels. Alternatively, life may have never evolved, leaving perhaps only abiotic nitrate deposits, the understanding of which might reveal the workings of past planetary chemistry (Mancinelli and Banin 2003). It may well be that the form and amount of nitrogen could constitute a roadmap for understanding whether chemical or biological processes were involved in its deposition. At least on a body that has had a separation of continental and oceanic components, the existence of nitrogen on continents is not easy to explain without special life supplied chemistry. Saturn's moon Titan, already known to be replete with nitrogen, offers other problems and opportunities (9). Recent mass spectrometric analyses of the atmosphere of Enceladus, a moon of Saturn, revealed a peak at 28 mass units, which could be either N_2 or CO; no definitive assignment could be made (Kargel 2006). As noted above, there are some planetary bodies with adequate gravity and/or

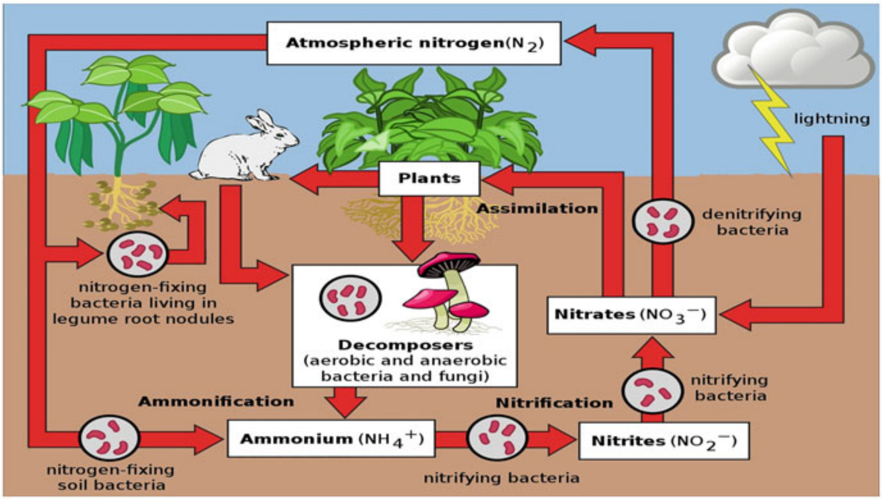

Fig. 10.8 Schematic representation of flow on Nitrogen in the Ecosystem

very low temperatures that might be expected to maintain their nitrogen gases without the help of the biota (Fig. 10.8).

10.5.2 The Nitrogen Cycle

Nitrogen accounts for 78% of air on a molar basis. Nitrogen is an essential component of the biosphere, and the atmosphere is an obvious source for this nitrogen. Conversion of the highly stable N_2 molecule to biologically available nitrogen, a process called fixation, is difficult. It is achieved in ecosystems by specialized symbiotic bacteria which can reduce atmospheric N_2 to ammonia (NH_3). The NH_3 is assimilated as organic nitrogen by the bacteria or by their host plants, which may in turn be consumed by animals. Eventually, these organisms excrete the nitrogen or die; the organic nitrogen is eaten by bacteria and mineralized to ammonium (NH_4^+), which may then be assimilated by other organism.

Bacteria may also use NH4+ as a source of energy by oxidizing it to nitrite (NO_2^-) and on to nitrate (NO_3^-). This process is called nitrification and requires the presence of oxygen. Nitrate is highly mobile in soil and is readily assimilated by plant and bacteria, providing another route for formation of organic nitrogen. Under conditions when O_2 is depleted in water or soil, bacteria may use NO_3^- as an alternate oxidant to convert organic carbon to CO_2. This process, called denitrification, converts NO_3^- to N_2 and thus returns nitrogen from the biosphere to the atmosphere.

An additional pathway for fixing atmospheric N_2 is by high-temperature oxidation of N_2 to NO in the atmosphere during combustion or lightning, followed by

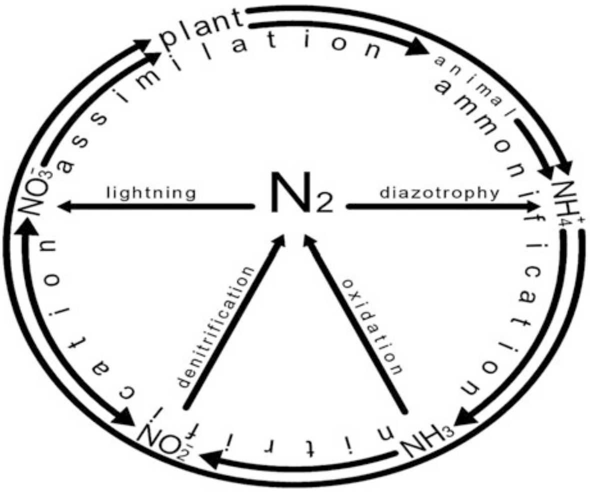

Fig. 10.9 Schematic representation of Classical Nitrogen Cycle

atmospheric oxidation of NO to HNO_3 which is water-soluble and scavenged by rain. In industrial regions of the world, the fixation of N_2 in combustion engines provides a source of nitrogen to the biosphere that is much larger than natural N_2 fixation, resulting in an unintentional fertilization effect.

Transfer of nitrogen to the lithosphere takes place by burial of dead organisms in the bottom of the ocean. These dead organisms are then incorporated into sedimentary rock. Eventually, the sedimentary rock is brought up to the surface of the continents and eroded, liberating the nitrogen and allowing its return to the biosphere. This process closes the nitrogen cycle in the surface reservoirs. An important observation is that human activity has greatly increased the rate of transfer of N_2 to the biosphere, resulting possibly in a global fertilization of the biosphere (Fig. 10.9).

10.6 Carbon

10.6.1 The Carbon Cycle

Carbon is the backbone of life on earth. We need carbon, but that need is also entwined with one of the most serious problems facing us today: global climate change. Most of earth's carbon about 65,500 billion metric tons is stored in rocks. The rest is in the ocean, atmosphere, plants, soil, and fossil fuels. Carbon flows between each reservoir in an exchange called the carbon cycle, which has slow and fast components. Any change in the cycle that shifts carbon out of one reservoir puts more carbon in the other reservoirs. Changes that put carbon gases into the atmosphere result in warmer temperatures on earth. Over the long term, the carbon cycle seems to maintain a balance that prevents all of earth's carbon from entering the

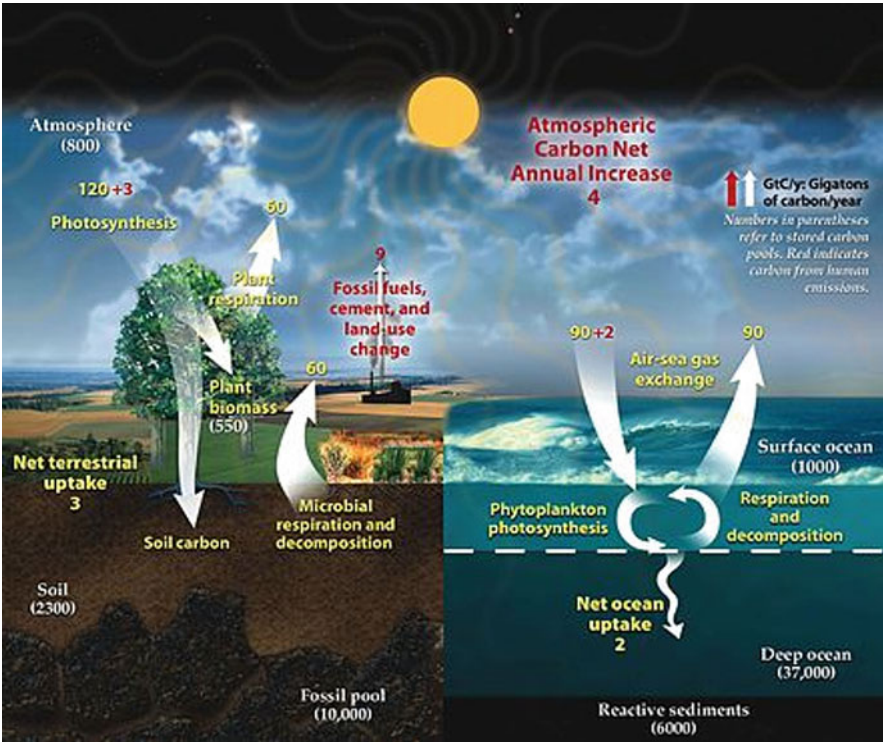

Fig. 10.10 The Fast and Slow global Carbon cycles (Diagram adapted from U.S.DOE, Biological and Environmental Research information system)

atmosphere. This balance helps keep earth's temperature relatively stable, like a thermostat. This thermostat works over a few hundred thousand years, as part of the slow carbon cycle. This means that for shorter time periods—tens to a hundred thousand years—the temperature of earth can vary. And, in fact, earth swings between ice ages and warmer interglacial periods on these time scales. Parts of the carbon cycle may even amplify these short-term temperature changes (Fig. 10.10).

On very long time scales (millions to tens of millions of years), the movement of tectonic plates and changes in the rate at which carbon seeps from the earth's interior may change the temperature on the thermostat. Earth has undergone such a change over the last 50 million years, from the extremely warm climates of the Cretaceous (roughly 145 to 65 million years ago) to the glacial climates of the Pleistocene (roughly 1.8 million to 11,500 years ago).

10.6.2 Effects of Changing the Carbon Cycle

The changes in the carbon cycle impact each reservoir. Excess carbon in the atmosphere warms the planet and helps plants on land grow more. Excess carbon in the ocean makes the water more acidic, putting marine life in danger.

10.6.2.1 Changes in the Atmosphere

It is significant that so much carbon dioxide stays in the atmosphere because CO_2 is the most important gas for controlling earth's temperature. Carbon dioxide, methane, and halocarbons are greenhouse gases that absorb a wide range of energy—including infrared energy emitted by the earth—and then re-emit it. The re-emitted energy travels out in all directions, but some returns to earth, where it heats the surface. Without greenhouse gases, earth would be a frozen -18 °C (0 °F). With too many greenhouse gases, earth would be like Venus, where the greenhouse atmosphere keeps temperatures around 400 °C (750 °F). Because, scientists know which wavelengths of energy each greenhouse gas absorbs, and the concentration of the gases in carbon dioxide causes about 20% of earth's greenhouse effect; water vapor accounts for about 50%; and clouds account for 25%. The rest is caused by small particles and minor greenhouse gases like methane.

Water vapor concentrations in the air are controlled by earth's temperature. Warmer temperatures evaporate more water from the oceans, expand air masses, and lead to higher humidity. Cooling causes water vapor to condense and fall out as rain, sleet, or snow. Carbon dioxide, on the other hand, remains a gas at a wider range of atmospheric temperatures than water. Carbon dioxide molecules provide the initial greenhouse heating needed to maintain water vapor concentrations. When carbon dioxide concentrations drop, earth cools, some water vapor falls out of the atmosphere, and the greenhouse warming caused by water vapor drops. Likewise, when carbon dioxide concentrations rise, air temperatures go up, and more water vapor evaporates into the atmosphere—which then amplifies greenhouse heating.

So, while carbon dioxide contributes less to the overall greenhouse effect than water vapor, scientists have found that carbon dioxide is the gas that sets the temperature. Carbon dioxide controls the amount of water vapor in the atmosphere and thus the size of the greenhouse effect.

10.6.2.2 Changes in the Ocean

This rise in temperature is not all the warming we will see based on current carbon dioxide concentrations. Greenhouse warming does not happen right away because the ocean soaks up heat. This means that earth's temperature will increase at least another 0.6 °C (1 °F) because of carbon dioxide already in the atmosphere. Ocean acidification affects marine organisms in two ways. First, carbonic acid reacts with carbonate ions in the water to form bicarbonate. However, those same carbonate ions are what shell-building animals like coral need to create calcium carbonate shells. With less carbonate available, the animals need to expend more energy to build their shells. As a result, the shells end up being thinner and more fragile.

Second, the more acidic water is, the better it dissolves calcium carbonate. In the long run, this reaction will allow the ocean to soak up excess carbon dioxide because more acidic water will dissolve more rock, release more carbonate ions, and increase the ocean's capacity to absorb carbon dioxide. In the meantime, though, more acidic water will dissolve the carbonate shells of marine organisms, making them pitted and weak. Warmer oceans, a product of the greenhouse effect, could also decrease the abundance of phytoplankton, which grow better in cool, nutrient-rich waters. This could limit the ocean's ability to take carbon from the atmosphere through the fast carbon cycle. On the other hand, carbon dioxide is essential for plant and phytoplankton growth. An increase in carbon dioxide could increase growth by fertilizing those few species of phytoplankton and ocean plants that take carbon dioxide directly from the water.

10.6.2.3 Land

Plants on land have taken up approximately 25% of the carbon dioxide that humans have put into the atmosphere. With more atmospheric carbon dioxide available to convert to plant matter in photosynthesis, plants were able to grow more. This increased growth is referred to as carbon fertilization. Models predict that plants might grow anywhere from 12 to 76% more if atmospheric carbon dioxide is doubled, as long as nothing else, like water shortages, limits their growth. Plants also need water, sunlight, and nutrients, especially nitrogen. If a plant does not have one of these things, it will not grow regardless of how abundant the other necessities are. There is a limit to how much carbon plants can take out of the atmosphere, and that limit varies from region to region. So far, it appears that carbon dioxide fertilization increases plant growth until the plant reaches a limit in the amount of water or nitrogen available.

Some of the changes in carbon absorption are the result of land use decisions. Agriculture has become much more intensive, so we can grow more food on less land. In high and mid-latitudes, abandoned farmland is reverting to forest, and these forests store much more carbon, both in wood and soil, than crops would. In many places, we prevent plant carbon from entering the atmosphere by extinguishing wildfires. This allows woody material to build up. All of these land use decisions are helping plants absorb human-released carbon in the Northern Hemisphere. In the tropics, however, forests are being removed, often through fire, and this releases carbon dioxide. As of 2008, deforestation accounted for about 12% of all human carbon dioxide emissions.

The biggest changes in the land carbon cycle are likely to come because of climate change. Carbon dioxide increases temperatures, extending the growing season and increasing humidity. Both factors have led to some additional plant growth. However, warmer temperatures also stress plants. With a longer, warmer growing season, plants need more water to survive. Scientists are already seeing evidence that plants in the Northern Hemisphere slow their growth in the summer because of warm temperatures and water shortages.

Dry, water-stressed plants are also more susceptible to fire and insects when growing seasons become longer. In the far north, where an increase in temperature has the greatest impact, the forests have already started to burn more, releasing carbon from the plants and the soil into the atmosphere. Tropical forests may also be extremely susceptible to drying. With less water, tropical trees slow their growth and take up less carbon, or die and release their stored carbon to the atmosphere.

The warming caused by rising greenhouse gases may also "bake" the soil, accelerating the rate at which carbon seeps out in some places. This is of particular concern in the far north, where frozen soil permafrost is thawing. Permafrost contains rich deposits of carbon from plant matter that has accumulated for thousands of years because the cold slows decay. When the soil warms, the organic matter decays and carbon in the form of methane and carbon dioxide seeps into the atmosphere. Current research estimates that permafrost in the Northern Hemisphere holds 1672 billion tons (petagrams) of organic carbon. If just 10% of this permafrost were to thaw, it could release enough extra carbon dioxide to the atmosphere to raise temperatures an additional 0.7 °C (1.3 °F) by 2100 (Fig. 10.10).

10.7 Summary and Conclusion

The distribution of As in the environment is dependent on source, mineralogy, speciation, biological interactions, and geochemical controls. Arsenic is common in the near-surface environment, but concentrations in water, solids, and biota are highly variable. Arsenic-rich environments are typically associated with chalcophile mineral deposits or geothermal activity. However, As-rich sediments and soils can also occur due to sedimentary and hydrogeological cycling of As-rich materials. The biological transformation and cycling of As can lead to oxidation or reduction of species that mobilize As. Methylation and demethylation may also occur and this may promote transfer of As in the food chain, affecting ecological toxicity. Predictive calculations of arsenic cycling are limited by the accuracy and precision of thermodynamic data for some minerals and aqueous species. Anthropogenic contamination is highly localized and provides notable hot spots. In understanding the dispersion of As in the environment, geological materials provide a basic framework for characterizing As concentrations in ecosystems. Large variations can be observed on all spatial scales influenced by a variety of natural processes including non-geological influences such as climate and vegetation.

A variety of factors controls the fate of arsenic in the environment. The major biogeochemical transformations of arsenic constituents depend on the primary arsenic source, the redox potential, pH, and microbial activity. However, the dissolution of arsenic minerals is the major source of the arsenic chemical species in the environment in specific physicochemical conditions. However, Fe oxide/hydroxide solid phases adsorbed As, and they can also release arsenic during their reductive dissolution. In aqueous systems, and in extremely low pH conditions pH < 2, arsenic acid occurs. In addition, between pH $= 2$ to pH $= 11$, it is in the form of $H_2\ AsO_4^-$ and $HAsO_4^{2-}$ chemical species. As the pH increases from low values, and in mildly reducing conditions, arsenious acid is converting to $H_2\ AsO_3\ ^-$. Under oxic conditions, Arsenate [As(+5)] is the thermodynamically stable phase of arsenic. In reducing conditions, arsenite [As (+3)] ions occurs. The As (+5) chemical species are adsorbed onto hydrous ferric oxides, and they also can be released during the microbial reduction of Fe(+3) solid phases.

In addition, the mobility and fate of arsenic in the environment are also related to co-precipitation and adsorption onto clay minerals, manganese oxides, and hydrous aluminum oxides. Although there is sufficient knowledge on the geochemical processes that governs the arsenic occurrence and fate in nature, the extent to how microbes affecting arsenic fluxes in the environment must be further studied in order to better understand the overall biogeochemical cycling of arsenic in the natural environment.

Natural concentrations of lead in lead ore deposits do not normally move appreciably in normal ground or surface water, because any lead dissolved from primary sulfide ore tends to combine with carbonate or sulfate ions to form insoluble lead carbonate or lead sulfate or else to be adsorbed by ferric hydroxide. Lead (Pb) is an environmental contaminant with proven human health effects. Bio-accessibility of Pb primarily depends on the solubility and, hence, the geochemical form of Pb, which in turn is a function of site-specific soil chemistry.

F is an essential constituent of some rock-forming minerals such as fluorite and apatite, its major occurrence in the lithosphere is within hydroxysilicate minerals where F^- occupies OH^- lattice sites. The majority of the F occurring in the secondary environment derives from natural weathering processes with some soils derived from F-rich parent rocks containing over 1 weight (wt) % F. Other natural sources of F are Vulcan city, wind-blown dust, and a minor marine-derived component, with biomass burning, being in part natural, also a source. Several anthropogenic sources of environmental F have also been identified. However, it is apparent that atmospheric F emissions are not transported globally and as such their effects are manifested only in the local environment. Emissions from industry sited close to urban centers can impact these environments together with domestic coal combustion and the release of F from high octane fuels in motor vehicles. A more recent source of F in the environment stems from the large number of fluorocarbon compounds in everyday use. Degradation of some of these fluorocarbon compounds together with pyrolysis of fluoropolymers and burning of household refuse has resulted in the deposition of organ fluorine compounds such trifluoroacetic acid.

Fluoride occurs naturally in our environment and is always present in our lives. Exposure can occur through dietary intake, respiration, and fluoride supplements. Fluoride can be toxic in extremely high concentrations. Its everyday use in concentrations present in beverages for dental hygiene is safe. Fluorine in the environment mainly derives from weathering of the lithosphere, its major reservoir in the lithosphere being OH^-containing minerals where F^- substitutes for OH^-. Of the other natural sources of environmental F, Vulcan city is the most important, but wind-blown dust and biomass burning make significant contributions. While it has been suggested that marine-derived F is a major source to the environment, it seems likely that its contribution has been over estimated and that it constitutes only a minor fraction of the total additions. While much of this is strongly held in soil, it is possible that some of the F will be mobilized into groundwater. Of the other anthropogenic sources, coal combustion has been widely held to be the major contributor. Therefore, it seems likely that while atmospheric F emissions represent a major threat to local environments, they are not transported globally. Within the urban environment, the occurrence of industrial sources of F emission in the peri-urban environment can have an impact, while domestic coal combustion and the release of F from high octane fuels in motor vehicles are also potential sources. Fluorine has a wide range of uses in modern society, it being incorporated into many compounds used in medicine and agriculture, and in the many fluoropolymers currently manufactured.

From our earth-centric point of view, it is equally difficult to imagine life without carbon and nitrogen. These two elements, by virtue of their ability to form double bonds, allow the formation of a multitude of unsaturated and aromatic compounds that impart both structural strength and energetic 99% of nitrogen is in the form of dinitrogen, which is inert and cannot be used by most living organisms. In order for living cells to use it for synthesis of vital bioorganic molecules like proteins, nucleic acids, and vitamins, molecular nitrogen has to be in its reduced or fixed form. Nitrogen is abundant in the atmosphere, lithosphere, and hydrosphere of the earth.

The geochemistry of carbon is the study of the transformations involving the element carbon within the systems of the earth. Carbon is transformed by life and moves between the major phases of the earth, including the water bodies, atmosphere, and the rocky parts. Carbon is important in the formation of organic mineral deposits, such as coal, petroleum, or natural gas. Most carbon is cycled through the atmosphere into living organisms and then respirated back into the atmosphere. Carbon makes up only 0.08% of the combination of the lithosphere, hydrosphere, and atmosphere.

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Chapter 11
Harnessing the Pedosphere Microbial Diversity in Sustainable Agriculture Production

Ravichandran Koshila Ravi, Loganathan Pavithra, and Thangavelu Muthukumar

Abstract There is a need to increase food productivity due to the ever-increasing human population worldwide. Modern agriculture practices including extensive application of synthetic chemicals for crop production and protection have led to decreased soil fertility and other hazards to the environment. However, the exploration of a wide range of microorganisms inhabiting the soil can improve crop growth and productivity. The plant–microbe interaction forms an important network in agriculture. The beneficial soil microorganisms including arbuscular mycorrhizal (AM) fungi, plant growth-promoting rhizobacteria (PGPR), nutrient-solubilizing bacteria, cyanobacteria, some groups of protozoa, and nematodes have a crucial role in plant's growth promotion, nutrient acquisition, imparting tolerance against different environmental stresses, and improving soil structure. Some of the important mechanisms involved in soil microbe-mediated processes are improved plant growth including phytohormone production, nutrient solubilization, and suppression of phytopathogens. The development of bioinoculants using efficient microbial consortiums can reduce the dependence on chemical fertilizers and could enhance crop productivity even under stressful conditions in an eco-friendly and cost-effective manner. In addition, soil health is strongly related to sustainable agriculture as the diversity and activity of soil microorganisms form a vital part of soil health. Therefore, in this chapter, we highlight the diversity of beneficial microbes in the pedosphere and their role in sustainable agriculture production.

Keywords Biofertilizers · Microbial indicator · Soil microorganism · Soil health · Sustainability

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B. Giri et al. (eds.), *Structure and Functions of Pedosphere*,
https://doi.org/10.1007/978-981-16-8770-9_11

11.1 Introduction

Soil is the most critical resource of the earth's crust that confers several benefits to humankind. Besides, offering 99% of food to humanity, soils also deliver a huge array of ecosystem services including carbon (C) storage, controlling the greenhouse gas, alleviation of the flood, offering support to the sprawling towns and cities, degradation and recycling of wastes, and monitoring the diseases and pests (Dominati et al. 2014). One of the prime challenges faced in the current scenario by world agriculture is the rising human population globally. The rapid increase in the growth of the human population is linked with enhanced consumption that subsequently leads to unusual pressure on soil via the development of agricultural production (Kopittke et al. 2019). Moreover, it is projected that the world population would approach ten billion by 2050. This ever-growing population would demand increased agricultural production and natural resources. Therefore, agriculture has attained a crossroad between a constantly growing population and conserving our environment. The agricultural practices also decrease along with the evolution and modernization of the current society. Therefore, it is the need of the hour to formulate the methods to increase agricultural productivity to feed the growing population. The agriculture management practices include greater application of synthetic fertilizers that are frequently assessed depending on their benefits for improving the economic status in production (Zhang et al. 2018). Nevertheless, the large-scale application of chemical fertilizers in agricultural production has resulted in soil degradation and affected several ecosystem processes (Alam 2014). To minimize the adverse effect of these chemical fertilizers, farmers should switch to organic sustainable agricultural practices. Integration of beneficial interactions between plant–microbe and microbe–microbe interactions could constitute an effective sustainable approach in increasing the production of agricultural products (Timmusk et al. 2017). Microbial-based nutrients/bioproducts are a crucial component of agriculture that enhances crop productivity in a sustainable manner (Bargaz et al. 2018).

Soil encompasses millions of microorganisms and insects belonging to various groups. The physicochemical characteristics of the soil are based on the pH, quality, and amount of soil organic matter and its redox potential. These crucially affect the structure and functions of the microscopic communities (Lombard et al. 2011). To understand the principles of sustainable agriculture, it is essential to know the chief role of the soil as a substrate for plant growth and microorganisms. Therefore, the soil is not only a module for crop production but also a living substrate that should be preserved for ever-lasting production and stability. Soil maintains the ecosystem processes and also renders support to the plant roots through providing crucial nutrients and minerals and prevents plants from soil erosion and other harmful chemicals, physical, or biological processes (Ghaley et al. 2014). Microorganisms play a pioneering role in the formation of soil and in soil ecology as they are known to be "natural soil engineers" and also monitor the nutrient flux in plants, promote dinitrogen (N_2) fixation, and eventually facilitate degradation of naturally occurring complex organic substances and xenobiotic pollutants in the soil (Kaviya et al. 2019). The distribution and diversity of microorganisms in the soil are highly heterogeneous. For example, microbial populations and communities are substantially different in the soil region influenced by plant roots (rhizosphere) and the surrounding bulk soil. The beneficial microbes residing in the rhizosphere stimulate plant growth through various biochemical processes such as regulating the plant hormone, enhancing the availability of soil nutrients, and defending against pathogenic microbes through various direct or indirect mechanisms (Jacoby et al. 2017; Liu et al. 2020). The present chapter focuses on the beneficial microbial diversity inhabiting the soil and its critical importance in sustainable agriculture.

11.2 Soil as a Sustainable Resource

Soil is a fundamental constituent of land resources, agricultural improvement, and ecological sustainability. Soil comprises organic components and minerals that unite as aggregates offering a three-dimensional fabric structure that holds moisture and plant nutrients and permits free circulation of air (Schoonover and Crim 2015). Soil sustainability is defined as "management of soil to meet the requirements of the present while simultaneously sustaining for future generations to obtain their own needs from the soil" (Abbott and Murphy 2007). Healthy and prolific soils are important to achieve the goals of sustainable development. Moreover, the preservation of soil health is a primary approach to agricultural sustainability. Soil serves as a medium for plant anchorage, provides essential minerals, nutrients, and water, and alleviates climate change via C sequestration and decreases the emission of greenhouse gases. Further, the soil is a storehouse for C and the repository of functional biodiversity, and decreases air and water pollution caused by various agrochemicals (White et al. 2014). Therefore, soil management is essential for improving crop production, sustainability of the environment, and human health.

The soil health and the directions of alterations with time are the core indicators of sustainable land management. Soil health is the capability of the soil to play a role as an important living system within land-use limitations and ecosystem to maintain the productivity of plants and animals, increase air and water quality, and enhance plant and animal health (Doran and Zeiss 2000). Sustainable use of soil could be achieved through (1) conservation of soil organic matter and availability of vital mineral and nutrients in the soil via recycling of organic matters in the agricultural field; (2) farming practices that decreases the organic C and nitrogen (N) loss from soils, prevent soil erosion, and sustain the agricultural production; (3) agronomic approaches to modify the soil chemistry for reducing the population of complex weeds, and (4) management of the toxic mineral accumulation in plants and soil (Doran 2002; Tahat et al. 2020). The microbial communities inhabiting the soil render an enormous strength to the soil health by affecting the physical, chemical, and biological conditions.

11.3 Beneficial Microbial Diversity in the Pedosphere

Microorganisms are the foundation of the ecosystem. Moreover, the significance of soil biota for the existence of all other life forms requires no special emphasis. As soil biota have pivotal roles in the soil processes, any kind of physiochemical/ biological modifications in soils would influence the soil microbial diversity. Soil microbes serve as fundamental driving mediators of various ecosystem processes including nutrient recycling, monitoring the dynamics of C sequestration and organic matter in the soil, greenhouse gas emission, and altering the soil structure. Besides, beneficial microbes provide resistance against various stresses in plants (Porter et al. 2020), fix N_2 (Koskey et al. 2017), protect plants against pests, and phytopathogens (De Corato 2020), enhance phosphorus (P) uptake (Kafle et al. 2019), degrade toxic heavy metals (Ahirwar et al. 2016), and improve soil fertility (Yilmaz and Sönmez 2017). Several studies have demonstrated that beneficial microorganisms such as arbuscular mycorrhizal (AM) fungi (Begum et al. 2019), rhizobacteria (Gowtham et al. 2018), some useful groups of nematodes (Ilieva-Makulec et al. 2014; Gebremikael et al. 2016), actinomycetes (Djebaili et al. 2020) and protozoa (Bonkowski 2004; Koller et al. 2013) aid in plant growth improvement, nutrient uptake, and improving soil health.

11.3.1 Protozoa

Protozoa are single-celled organisms that are larger than bacteria ranging between 5 and 500 μm in diameter. They are the most abundant soil organism next to bacteria and fungi and are larger than other soil microbes. They mostly feed on bacteria and consume soluble organic compounds and even fungi sometimes (Clarholm et al. 2007). Protozoa create the link between primary producers and the soil food web at the higher level that makes them primary consumers in the food web (Crotty et al. 2012). Soil protozoa have a key role in modulating the population of bacteria existing in the soil. Moreover, they have an essential role in nutrient mineralization through which nutrients could be made available to the plants and other microorganisms in the soil (Clarholm et al. 2007). Protozoa feeding on the bacteria are presumed to liberate N (nearly one-third) from bacterial biomass which later becomes accessible to plants for their growth (Griffiths 1994; Bonkowski 2004). In addition, protozoa preying promote the existence of useful microorganisms in soil by inhibiting the pathogens (Müller et al. 2013), enhance the plant growth hormone production (Krome et al. 2010), and also promote compound production related to pathogen inhibition, like antibiotics (Jousset and Bonkowski 2010). For example, Weidner et al. (2017) tested the effect of combined inoculation of soil protozoan, *Acanthamoeba castellanii* with nine different isolates of *Pseudomonas* in the wheat plants infected by root pathogen *Pythium ultimum*. The presence of bacterivorous *A. castellanii* reduced the effect of certain bacteria on the aggravation of the fungal disease severity in addition to improving plant growth. Therefore, dual inoculation of protozoa and useful bacterial isolates like *Pseudomonas* could be a potential method to enhance the beneficial activities of bacteria which in turn helps in plant growth promotion.

Bonkowski et al. (2000) carried out an experiment with ryegrass involving bacterivorous protozoa and nematode. In their experiment labeled ^{15}N and ^{13}C, plant litter poor in organic C was supplemented to the soil to form a hotspot for microbial processes. The results revealed that protozoan inoculation enhanced the biomass of ryegrass and N uptake in the plants by two folds, and the inclusion of ^{15}N from the labeled plant litter was enhanced by three folds. The contribution of soil protozoa in N mineralization involves processes like (1) grazing that facilitates the mineralization by microbes by maintaining the microbes in vigorously growing phase and by altering the bacterial community composition; (2) around 90% of the released N occur as nitrate and only 10% in the form of ammonium in the rhizosphere as a result of strong impact on functioning and diversity of microbes. As nitrate is extremely mobile in the soil, N uptake in presence of protozoa by plants might be reduced because of leaching losses only if nitrate mobilization does not match by a subsequent enhancement in the root uptake rates; and (3) as a result of the preceding point, root productions get significantly enhanced in the existence of protozoa, enabling plants to obtain benefits from the released N pool, and thus, grazing pressure steadily alters the nutrient competition in support of roots (Bonkowski et al. 2000). Therefore, protozoa help in the efficient nutrient uptake through expansion of the greater root surface by promoting lateral root production. For example, Bonkowski and Brandt (2002) proved that protozoa increased the number and length of secondary roots in *Lepidium sativum* plants. Furthermore, protozoa stimulated the presence of the auxin-synthesizing bacteria in the rhizosphere which in turn was attributed to increased growth of lateral roots. Hence, a greater root surface area could permit the absorption of nutrients and also enhance root exudations, thus promoting bacteria–protozoan interactions (Bonkowski 2004).

Koller et al. (2013) determined the effect of amoebae (*A. castellanii*) on mineralization of high and low (high C to N ratio) quality litter, plant growth, and nutrient uptake with *Plantago lanceolata* raised in a microcosm. The results of the study suggested that inoculation of amoebae increased the plant N uptake in low- and high-quality litter and also improved growth, photosynthesis, and C allocation in the plant as a result of high mobilization by amoebae. In addition, the effect of protozoa was more effective in treatments involving low-quality litter in which N supplement was limited to plants and microbes. The study also revealed that at low nutrient levels, amoebae enhanced the allocation of C to belowground interactions (Koller et al. 2013). In a recent study, Zheng et al. (2020) isolated around fifteen species of protozoa from the rhizosphere soil of *Beta vulgaris* during six different growth phases and suggested that the majority of the protozoan species had a crucial role in N supply during the early stage of *B. vulgaris* seedling development. In addition, protozoa assist in maintaining the soil's ecological balance. They are also used as a food source for other soil microbes and reduce the disease occurrence by competing/

feeding on pathogens. Hence, interactions between protozoa and plants are crucial during the competition for nutrients by both plants and microbes.

11.3.2 Nematodes

Nematodes belong to the roundworm phylum (Nematoda) has evolved around 500 million years ago (Sudhaus 2008). Nematodes are abundantly present in nearly all habitats including soil, marine, and freshwater. Soil forms the primary habitat for nematodes. The nematodes residing in the soil exist in the rhizosphere region where the activity of microorganisms is extremely high (Hailu and Hailu 2020). Nematodes existing in the agricultural soils are classified into five groups based on their feeding habits: plant parasites, omnivores, fungal feeders, bacterial feeders, and predators (Penfold and Collins 2012). Some nematodes are generally parasitic and even cause economic losses in crops. Agriculture management practices such as crop rotation, soil tillage, and utilization of organic amendments affect the biological and physicochemical traits of the soil that in turn affect the nematode population. Nevertheless, some groups of soil nematodes confer an essential role in improving crop production.

Nematodes are bestowed with several important functions in the soils. They increase the mineralization of nutrients, decompose the organic matter, and act as biocontrol agents (Mekonen et al. 2017). The bacterial and fungal feeding nematodes can maintain sufficient levels of available N in plants in agricultural systems that depend on organic sources of fertility. Nematodes directly take part in the conversion of nutrients to inorganic form from its organic form via their feeding interactions. For example, the bacterial-feeding nematode takes up N in the form of other N-containing elements or proteins in the bacterial cells and liberates additional N as ammonium that gets easily accessible to plants (Ilieva-Makulec et al. 2014). Nematodes indirectly promote decomposition and nutrient cycling by reviving the inactive fungal and bacterial colonies and via extending the bacteria and fungi to other accessible organic remains. Bacterivorous and fungivorous nematode are involved in soil microbial biomass turnover, thereby making nutrients accessible to the plants (Liu et al. 2006). Also, soil nematodes maintain soil fertility and control various pests and insects (Mekonen et al. 2017).

Soil nematodes create a link between above- and below-ground activities like plant production and decomposition of soil organic matter (Wardle et al. 2004). The plant-feeding nematodes enhance the discharge of root exudates rich in C into the soil, thereby promoting microbial growth which possibly results in increased breakdown of soil organic matter through the priming effect (Yeates et al. 1999; Kuzyakov 2002). The microbivorous nematode activity might be monitored by predatory nematodes and other soil organisms which modulate the nutrient availability (Neher 2001). Gebremikael et al. (2016) conducted an experiment involving the entire community of soil nematode mimicking nutrient-rich natural field conditions using a model plant (*Lolium perenne*) and a substrate amended with residues of fresh grass–clover to determine its role in nutrient mineralization and plant growth. The results revealed that the presence of nematodes enhanced the net N and P availability and plant biomass than in its absence, indicating that soil nematode communities associate above- and below-ground processes chiefly by promoting the availability of nutrients (Gebremikael et al. 2016). Therefore, beneficial soil nematodes also help in plant growth promotion and nutrient uptake.

11.3.3 Bacteria

Bacteria play a crucial role in crop production and biogeochemical cycles for many decades. The contribution of soil bacteria to sustainable agriculture production includes providing nutrients to crop plants, promotes plant growth via plant hormone production, suppresses phytopathogens, tolerates abiotic stresses in plants, and also improves soil fertility and structure (Sheirdil et al. 2019; Chandra et al. 2021). Moreover, the interaction between bacterial community and plant is the basis of plant and soil health. Besides, plant–bacteria interactions also have an important function in mobilization, solubilization of nutrients from inadequate nutrient reserves, and bioremediation of metals and polluted soil (Ghoreishi et al. 2017; Dinesh et al. 2018; Eshaghi et al. 2019). Some important groups of soil bacteria include plant growth-promoting rhizobacteria (PGPR), symbiotic and asymbiotic N_2-fixing bacteria, and associative N_2-fixers (Hayat et al. 2010). Among these, PGPR crucially contributes to plant growth promotion in a sustainable manner. Moreover, applications of different kinds of symbiotic (*Rhizobium*) and asymbiotic bacteria (*Azotobacter*, *Bacillus*, etc.) increase plant productivity (Ullah et al. 2017; Yousefi et al. 2017; Abdiev et al. 2019).

11.3.3.1 Plant Growth-Promoting Rhizobacteria

The PGPR that facilitates plant growth by associating with plant roots is commonly known as free-living bacteria which is useful for plant development. Some of the important PGPR includes the species of *Azospirillum*, *Bacillus*, *Enterobacter*, *Burkholderia*, *Rhizobium*, *Pseudomonas*, and *Variovorax* (Bhattacharyya and Jha 2012; Ahemad and Kibret 2014). The PGPR are characterized by certain important characteristics like the capability to colonize the root surface, proliferate and compete among other microorganisms, and enhance or increase plant growth and productivity (Kloepper 1994). The PGPR improves plant growth indirectly by reducing the suppressive effects of different pathogens as biocontrol agents on plant growth, or directly through increasing the essential nutrient and mineral acquisition or regulating the levels of plant hormones (Glick 2012). Therefore, PGPR is considered a capable agricultural input for sustainable production. Nutrient solubilization, siderophore and phytohormone production, and N_2-fixation are other mechanisms of PGPR involved in improving crop growth (Chauhan et al. 2017; Singh et al. 2020).

For instance, in a greenhouse study, Gowtham et al. (2018) observed that inoculation of PGPR isolate, *Bacillus amyloliquefaciens,* enhanced chili growth by inhibiting the anthracnose disease which was attributed to increased activity of defense enzymes by *B. amyloliquefaciens*. The microbial inoculants containing the isolates of four compatible PGPR strains (*Acinetobacter calcoaceticus, Advenella incenata, Serratia plymuthica*, and *Providencia rettgeri*) were reported to increase plant growth parameters and chlorophyll content of *Avena sativa*, *Cucumis sativus*, and *Medicago sativa* seedlings. In addition, all these PGPR strains enhanced the soil enzymes (urease, invertase, catalase, and alkaline phosphatase), organic C, and soil nutrients and in the rhizosphere of these three plants. Further, *A. incenata* and *P. rettgeri* strains were able to produce phytohormones like indole acetic acid (IAA), and *S. plymuthica* suppressed some of the pathogens such as *Fusarium oxysporum* and *Helminthosporium tritici-vulgaris* (Li et al. 2020a). Similarly, maize plants inoculated with two rhizobacterial strains (*Cupriavidus necator* and *Pseudomonas fluorescens*) enhanced the N and P use efficiency, thereby improving the maize growth under water stress conditions (Pereira et al. 2020). Therefore, the application of PGPR can be used as a bioinoculum to accomplish the sustainability of agriculture.

11.3.3.2 Actinomycetes

Actinomycetes are a copious group of prokaryotic soil microbes that persists in the soil as thread-like filaments and are characterized by aerial and substrate mycelium growth. It is spore-forming Gram-positive bacteria that live in both aerobic and anaerobic conditions at a minimum and maximum temperature ranging between 5 and 7 °C and 40 and 70 °C respectively. They have a crucial function in suppressing phytopathogens, recycling organic matter in the rhizosphere, and degrading complex polymers existing in the senescent plants, dead animals, and fungal material that consequently led to the production of numerous extracellular enzymes that helps in crop productivity (Bhatti et al. 2017). The distinctive actinomycetes in soil belong chiefly to the *Streptomyces* and *Micromonospora* groups. Actinomycetes aids in N_2-fixation by forming associations with some of the non-legume plants, which are later accessible to the host and to other neighboring plants. Generally, N cycling depends on N_2-fixing bacteria. For example, actinorhizal plants depend on *Frankia* species of actinobacteria to provide the fixed N. Around 15% of the fixed N is commonly obtained through symbiotic associations between different species of *Frankia* and their actinorhizal host plants. Further, actinomycetes are specialized decomposers as they degrade or break down cellulose, lignin, and chitin present in insects. The degradation of these components makes nutrients accessible to the plants. Also, thermophilic actinomycetes during composting processes decompose the organic substances at high temperatures (Mohan and Vijayakumar 2007).

As actinobacteria generally exist in the rhizosphere, they form an important division of the environment owing to their interactions with plants. Actinobacteria enhance nutrient availability, synthesize plant growth hormones, and also hinder growth of plant pathogens (Jose and Jha 2016). They help to regulate the biotic equilibrium of soil along with nutrient cycling. These aspects are directly linked with sustainable crop productivity. In addition, actinomycetes are potential biocontrol agents that prevent a wide array of bacterial and fungal pathogens. For example, *Streptomyces* species are commercially used as biofungicide (Minuto et al. 2006; Law et al. 2017). The plant growth-promoting potential of actinomycetes species was demonstrated under field conditions in some of the plants. For example, Gopalakrishnan et al. (2013) showed that five isolates of *Streptomyces* species (CAI-24, CAI-121, CAI-127, KAI-32, and KAI-90) significantly increased the stover and grain yield, and total dry biomass in rice plants under field conditions. The microbial C biomass, N and P contents, and organic C in soil were also enhanced in *Streptomyces* inoculated soil over control soil (Gopalakrishnan et al. 2013).

11.3.3.3 Cyanobacteria

Cyanobacteria, also known as blue-green algae are the group of photosynthetic prokaryotes which has evolved 3.5 billion years ago. They are known to be one of the oldest and abundant life forms in the earth’s atmosphere. These are unicellular, small oxygenic Gram-negative bacteria forming large colonies and are distributed in different ecological niches (Abed et al. 2009). They can withstand and survive in high pH and extreme salt concentrations (Lopez-Archilla et al. 2004). Cyanobacteria occur in different shapes and sizes and include a wide range of bacteria. They form an important source of fixed N and C (Pang et al. 2018). Cyanobacteria have a pivotal role in atmospheric N_2-fixation and photosynthesis, inhibit the growth of soil pathogens, degrade the toxic heavy metals, produce bioactive substances (metabolites, enzymes, and vitamins) contributing to plant growth, and provide resistance against various abiotic and biotic stresses (Kumar et al. 2018).

Cyanobacteria constitute an important emerging microbe in developing sustainable agricultural production. They are used in the development of biofertilizers, manage N deficiency in plants, and also improve the soil quality by enhancing the soil aeration and water-holding capacity. Some of the potential N_2-fixing cyanobacteria are *Anabaena variabilis*, *Aulosira fertilisima*, *Nostoc linckia*, and species of *Calothrix* and *Scytonema* (Poveda 2020). Moreover, it has been reported that around 20–30 kg N/ha is contributed as organic matter by cyanobacteria to the soil, which benefits the farmers who cannot afford costly synthetic fertilizers (Issa et al. 2014). In addition, plant growth hormones like auxin, gibberellin, cytokinin, and abscisic acid are produced by some species of cyanobacteria. For example, in a recent study, Zarezadeh et al. (2020) demonstrated that inoculation of cyanobacterial suspension (*Nostoc carneum*, *Nostoc punctiforme*, and *Wollea vaginicola*) in soil increased the growth as well as essential oil production in *Matricaria chamomilla* which was attributed to the production of growth-promoting auxins like IAA, indole 3-propionic acid (IPA), and indole 3-butyric acid (IBA). These plant growth-promoting traits of cyanobacteria enable them as a promising microorganism toward sustainable productivity.

11.3.4 Arbuscular Mycorrhizal Fungi

The AM fungal association found in around 71% of terrestrial plant roots is one of the familiar mutualistic relationships in the plant ecosystem and the fungi belongs to the phylum Glomeromycota (Cosme et al. 2018; Tedersoo et al. 2018). This symbiosis is the oldest association existing for more than 400 million years (Selosse et al. 2015). Arbuscular mycorrhizal fungi are obligate biotrophs and consist of fungal hyphae and spore-bearing numerous nuclei (Smith and Read 2008). To complete a life cycle, AM fungi rely on lipids and C supplied by the host plant (Jiang et al. 2017). These types of symbiosis are considered as a sequence of biological processes that impart various beneficial effects in both natural ecosystem and agroecosystem (Van der Heijden et al. 2015). The AM fungi develop various structure like intraradical hyphae, arbuscules, vesicles, and spores (in certain cases) which are formed within the plant roots, whereas spores and hyphae could be produced in the rhizosphere soil outside the root and form a greater surface area to create a contact between AM fungal structures and plant root cells and soil resources (Smith and Read 2008).

Arbuscules are the distinct structures of AM fungi formed in the root cortical cells that serve as a passage for transferring resources between the AM fungi and plant roots. These are highly branched structures and persist in the plant root for a short period depending upon the nutritional status of the host plant (Bonfante and Genre 2010). Apart from arbuscules, AM fungi produce round to oval-shaped lipid storage structures known as vesicles within the plant roots. These are mostly formed in the older plant roots. Vesicles are usually formed after the development of arbuscules. Both intraradical and extraradical hyphae form one of the important components in AM fungal symbiosis. The extraradical hyphae in the soil extend the surface area of roots and aids in accessing the nutrients subsequently enhancing the plant growth. The extraradical mycelium uptakes the soil nutrients and transfers them to the roots of the host plant, while the intraradical mycelium release nutrients to the apoplast in exchange for C from the host plant (Bowles et al. 2016).

A wide array of literature is available on the beneficial aspects of AM fungi on plant growth and development (Begum et al. 2019; Gao et al. 2020). In addition, AM fungi play a crucial role in mineral nutrient uptake, provide tolerance against biotic and abiotic stresses in plants, improve soil structure, detoxify heavy metals, defend against soil-borne and phytopathogens, and used in biofertilizer development (Cely et al. 2016; Zou et al. 2020). Moreover, AM fungi are considered natural growth promoters in the majority of the terrestrial plants, thereby formulating them as biofertilizers could be useful in sustainable agriculture. Different AM fungal species either individually or as the consortium has enhanced the growth of many crop plants such as maize (Mathur et al. 2018), sorghum (Nakmee et al. 2016), finger millet (Saharan et al. 2018; Kandhasamy et al. 2020), and wheat (Talaat and Shawky 2014) under normal and stressed conditions. The application of AM fungal biofertilizers could reduce the use of synthetic/chemical fertilizers up to 50% for efficient agriculture production depending upon the plant species and prevailing environmental conditions (Begum et al. 2019).

11.4 Plant–Microbe Interaction in Rhizosphere

The concept of plant–soil microbe interactions helps in understanding how plants respond to soil microorganisms in different soil environmental conditions. The soil microbial communities respond to the environmental changes rapidly leading to modifications in the outcome of plant–microbe and plant–plant interactions mediated by microorganisms (van der Putten et al. 2016; Fig. 11.1). Nevertheless, even without causing any modifications in the composition of the microbial communities, some changes in the environment can modify the effect of a single microbial community on plants (Hawkins and Crawford 2018). Different groups of microbes occupy the region surrounding the plant roots depending on the requirement of the nutrients. Rhizosphere possesses high microbial activities and is the crucial niche for the plant–microbe interactions. Most of the important functions such as nutrient

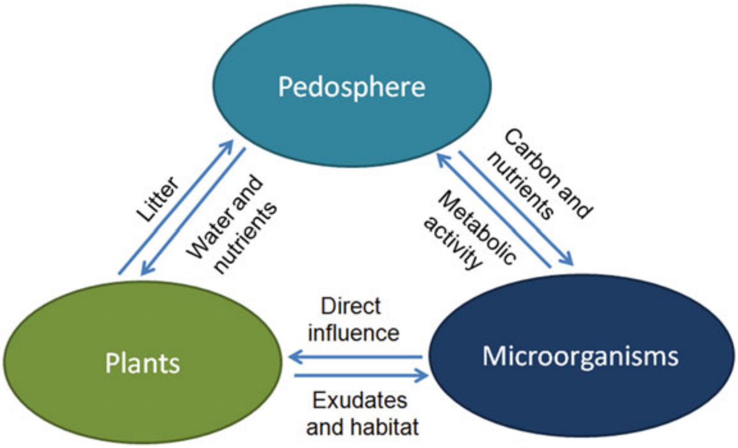

Fig. 11.1 Interactions between pedosphere, plants, and microorganisms. Both microorganisms and plants acquire their nutrients, and the former obtain carbon from the soil. Plants provide organic input into the soil in the form of litter, and microorganisms act on these litters through their metabolic activities and release inorganic nutrients. Plants provide habitat for endophytic microorganisms and carbon and other resources in the form of root exudates. Microorganisms directly affect plant growth through hormone production and protection against various biotic and abiotic stresses

uptake, the transformation of nutrients, exudations, and biogeochemical cycles occur in the rhizosphere. Plants are in perpetual contact with many of the soil microorganisms. The root exudates such as enzymes, amino acids, flavonoids, free oxygen and water, organic acids, sugars, and other metabolites help the growth of various microbes which may in turn aid in plant growth promotion, nutrient uptake, suppression of disease, and alleviate plant stress (Mommer et al. 2016; Canarini et al. 2019; Vives-Peris et al. 2020; Fig. 11.1). The plant root exudates owing to their high nutrient content also recruit pathogenic fungi like *Fusarium*, *Verticillium*, and *Rhizoctonia* in the rhizosphere of host plants that are vulnerable (Velmourougane et al. 2017).

11.4.1 Kinds of Plant–Soil Microbe Interaction

Plants exhibit various kinds of interactions with soil-inhabiting microbes that extend a broad range of environmental potentials like commensal, competitive, mutualistic, and neutral (Wu et al. 2009). The interaction between plants and microorganisms can either be beneficial or harmful ranging from mutualistic to pathogenic. The plants colonized by those microbes benefit the host plant or the residing microbes in any way and contribute to beneficial plant–microbe interactions (Velmourougane et al. 2017). The association of plants with endophytes, mycorrhizae, PGPR, and other N_2-fixing microbes results in various advantageous aspects for plants and for the microorganisms. On the other hand, some of the interactions of plants with soil microbes (soil pathogens) are detrimental which adversely impact the plant growth and other important processes concerning physiological processes (Schirawski and Perlin 2018).

11.4.1.1 Beneficial Interactions

One of the best examples of symbiotic association is the interaction between plants and AM fungi. As already mentioned, AM fungi impart several benefits to plants, especially in terms of nutrient uptake, and in turn obtain photosynthetically fixed C from the host plant (Smith and Read 2008). In addition, some of the AM fungal genera such as *Acaulospora*, *Glomus*, *Claroideoglomus*, and *Gigaspora* exhibit a synergetic relationship with other beneficial soil microbes such as N_2- fixers, PGPR, and phosphate solubilizers (Larimer et al. 2014; Cely et al. 2016; Hussain et al. 2021). For example, dual inoculation of AM fungi (*Glomus multisubtensum* and *Rhizophagus intraradices*) and phosphate-solubilizing bacteria (*Klebsiella variicola*) along with rock phosphate increased the growth of *Helianthus tuberosus* exhibiting synergism (Nacoon et al. 2020). The AM fungi and phosphate-solubilizing bacteria interact synergistically as phosphate-solubilizing bacteria solubilize the moderately available P compounds into orthophosphate which could be absorbed by AM fungi and transfered to the host plant.

Bacteria symbiotically associate with some of the plant roots that lead to the nodule formation and possess higher specificity to the host plants (Masson-Boivin et al. 2009). Plants colonized by these bacteria themselves benefit because of enhanced N supply. In addition, N_2-fixing bacteria residing in the plant rhizosphere can increase growth and N content in plants growing in N deficient soils (Mahmud et al. 2020). For instance, inoculation of *Azotobacter* and *Bacillus* species increased the plant growth and nutrient efficiency in several plants under both normal and stressed conditions (Masood et al. 2020; Aasfar et al. 2021). Therefore non-symbiotic N_2-fixing bacteria, in addition to symbiotic N_2-fixing bacteria that associate with the plants are also considered crucial. Therefore, the presence of these useful bacteria in soil could interact with plants, thereby improving plant growth and productivity.

The beneficial microorganisms also produce plant hormones that are crucial for plant growth which regulate the developmental processes in plants including abiotic stress tolerance (Wani et al. 2016). The closure of stomata and plant growth promotion mediated by abscisic acid alleviates osmotic and other stresses in plants (Waqas et al. 2012). The biosynthesis and signaling pathways regulated by abscisic acid get modified due to the beneficial microbes prevailing in the plant's endorhizosphere that could promote plant growth under stressed conditions (Khare et al. 2018). For instance, the endophytic fungus *Paecilomyces formosus* inoculated in rice plants raised under heat stress in controlled conditions improved the plant growth characteristics (shoot length, fresh and dry biomass, and chlorophyll content) which were evidenced by enhanced total protein concentration and low endogenous level of abscisic and jasmonic acid (Waqas et al. 2015).

Apart from soil microorganisms, the other plant root colonizing endophytes including dark septate endophytic (DSE) fungi also contribute to a sustainable agricultural system. They usually colonize the intercellular regions and cortical cells of the roots and form intracellular structures such as microsclerotia or moniliform hyphae (Sieber and Grünig 2013). The DSE fungi exhibit a wide array of interactions with their host plants. Like mycorrhizal fungi, DSE fungi are known to increase plant growth through the acquisition and transfer of nutrients to plants both under normal and stressed conditions. For instance, inoculation of DSE fungi, *Curvularia* species in *Populus tomentosa,* reduced the detrimental effects of salinity by enhancing the antibiotic and enzyme activity and chlorophyll and proline contents in the leaves (Pan et al. 2018). In addition, mineral solubilization and production of plant hormones by DSE fungi have also been reported (Priyadharsini and Muthukumar 2017).

Several inoculation experiments were conducted with numerous DSE fungal species to understand the interaction with their host plants. Zhu et al. (2018) reported the production of antioxidant enzymes (catalase, peroxidase, and superoxide dismutase) by the DSE fungal strain *Phialophora mustea* under heavy metal stress to avoid oxidative damage in tomato plants. In addition, DSE fungi also enhance nutrient uptake (C, N, and P) in plants, thereby increasing plant growth (Vergara et al. 2018). The DSE fungi are known to protect plants in situations where mycorrhizal symbiosis may be absent or non-functional. Therefore, DSE fungi are potentially known to increase tolerance of host plants against several abiotic stresses and enhance plant growth under low availability of water, saline conditions, and heavy metal-polluted soils (Yihui et al. 2017; Pan et al. 2018; Li et al. 2019). Moreover, numerous DSE fungi have been reported to tolerate various fungal diseases including cabbage wilt caused by *Verticillium longisporum* (Narisawa et al. 2004) and tomato wilt caused by *Verticillium dahliae* (Andrade-Linares et al. 2011). A recent study by Harsonowati et al. (2020) reported that the DSE fungus, *Cladophialophora chaetospira,* improved the plant growth of strawberry plants against strawberry Fusarium wilt caused by *Fusarium oxysporum formae*. Therefore, the DSE fungi could also be used as biocontrol agents against various plant diseases, thereby contributing to sustainable agriculture.

11.4.1.2 Detrimental Interactions

Soil consists of a considerable number of plant pathogens that adversely affect plant growth. Soil pathogens have an important role in modulating the association between plant productivity and diversity (Schnitzer et al. 2011). Mommer et al. (2018) suggested that the plant–pathogen interactions are based upon two assumptions among plant communities. First, species-specific pathogens get accumulated in the plants which are known as host specificity. These pathogens could decrease the functioning of their host and, however, do not have much influence on other plants. Negative density dependency is the second assumption which states the species-specific pathogen accumulation in plants and adverse effect on the functioning of the host plant decrease with reducing relative abundance of host plant species (Mommer et al. 2018). Therefore, pathogen pressure effectively constrains biomass productivity and reduces plant species richness and crop yield (Bever et al. 2015). Greater colonization of phytopathogens over useful microorganisms in the rhizosphere of vulnerable host plants will influence the survival of the plant and disrupt the diversity of indigenous soil biota in the rhizosphere. Therefore, alterations in community structure and population density in the indigenous microbial community may have a negative impact on the performance of the host plants and the microbes associated particularly in nutrient availability or metabolic activities linked with plants and microbes (Velmourougane et al. 2017). Of numerous phytopathogenic microbes, fungi cause an immense threat to the plant system. Some of the important soil-borne phytopathogens belong to the genera *Fusarium*, *Sclerotinia*, *Phytophthora*, *Pythium*, and *Verticillium* that cause yield loss up to 75% in most of the crop species (Mihajlović et al. 2017).

Besides these disease-causing soil microbes, plants release allelochemicals that either has a positive or negative impact on the neighboring plants and soil environment. The soil microbes can control the releasing rate of these harmful chemical compounds and thus influence seed germination (Xiao et al. 2020). Microorganisms influence these allelocompounds with negative and positive consequences (Lou et al. 2016). Microbes can deactivate the plant toxins that are soluble in water or degrade toxic compounds to decrease the allelopathic effects, thereby exhibiting a negative role in allelopathy (Jilan et al. 2008). Conversely, microbes can also liberate insoluble phytotoxins and convert the non-toxic compounds to phytotoxins, consequently indicating a synergism with allelochemicals (Lou et al. 2016). More studies concentrating on the aboveground chemical communication and physiological activities involving both positive and negative interactions with microbes are required to understand the complexity of plant–microbe interactions.

11.5 Functions of Soil Microbiota Toward Sustainable Agriculture

11.5.1 Biodegradation

Biodegradation is defined as any chemical or physical breakdown of any complex materials by the activity of biological organisms such as microbes for a sustainable ecological reclamation process (Fatimah Alshehrei 2017). Biodegradation plays an important role in the recycling of plant-based nutrients in the soil. A broad range of different microbial enzymes takes part in converting natural and artificial hydrocarbons into intermediate complexes that may be less harmful when compared to their parental compounds (Mohanan et al. 2020). Generally, the biodegradation processes involve two mechanisms such as aerobic and anaerobic biodegradation. Aerobic biodegradation is the breakdown of organic contaminants by microbes in the existence of oxygen. It is also known as aerobic respiration where microorganisms produce energy by utilizing oxygen as an electron acceptor. Contrarily, in anaerobic biodegradation, degradation of contaminants by microbes occurs in the absence of oxygen and the electron acceptor will be the compounds other than oxygen (Reineke 2001). Moreover, the biodegradation process is influenced by competition among microorganisms for C sources, adverse interactions among microbes or protozoa, and bacteriophages predation on microbes. Other factors such as soil type, temperature, nutrient, pH, moisture content, amount of contaminant and catalyst, oxygen levels, and oxidation–reduction potential also significantly affect the degradation activities (Mbachu et al. 2020).

Several microorganisms such as bacteria and fungi play an important role in biodegradation. Some of the effective bacterial and fungal genera involved in the degradation of soil pesticides include *Arthobacter*, *Pseudomonas*, *Bacillus*, *Penicillium*, *Trichoderma*, and *Aspergillus* (Doolotkeldieva et al. 2018; Yada et al. 2019). For example, Abd El-Ghany and Masmali (2016) reported two fungi (*Trichoderma harzianum* and *Metarhizium anisopliae*) with degradation capability of organophosphorous insecticides such as malathion, profenofos, and diazinon isolated from insecticide contaminated soils. Similarly, the bacterial strains isolated from three different dumpsites in Kyrgyzstan including *Micrococcus* sp., *P. fluorescens*, and *Bacillus polymyxa* exhibited higher rates of degradation activity on Aldrin pesticide (Doolotkeldieva et al. 2018). After the completion of pesticide biodegradation, water and carbon dioxide that are formed due to oxidation of parent compound render energy for metabolic activities to the microorganisms. The extracellular or intracellular enzymes produced by these microorganisms play a key role in the breakdown of chemical compounds (Parte et al. 2017). Therefore, the application of these microbial strains as inoculum could protect the environment from harmful organic insecticides/pesticides.

Moreover, other soil microbes such as AM fungi and PGPR can also degrade chemical compounds such as polycyclic aromatic hydrocarbons and polychlorinated biphenyl. Dong et al. (2014) revealed that co-inoculation of *R. intraradices* with *Serratia marcescens* in soil contaminated with petroleum hydrocarbon exhibited a higher rate of degradation (72.24%). In another greenhouse experiment, Ren et al. (2017) examined the efficiency of rhizobia (*Ensifer* sp.) and AM fungi (*Funneliformis mosseae*) symbiosis on the degradation of aromatic hydrocarbons using a legume plant, *Sesbania cannabina*, and found that tripartite interaction had 97% and 81–85% of maximum phenanthrene and pyrene dissipation respectively through promoting the activities of microbes and soil enzyme. Thus, this kind of triple mutual symbiosis aids in the improvement of the degradation efficiency of polycyclic aromatic hydrocarbons by legumes.

11.5.2 Bioremediation of Heavy Metals

Heavy metals are of economic importance among various industries and have become a crucial environmental threat affecting all the organisms in the ecosystem worldwide (Siddiquee et al. 2015; Okolo et al. 2016). Accumulation of heavy metals disturbs critical enzymatic activities, acts as redox catalysts during reactive oxygen species production, interrupts the regulation of ions, and also affects the DNA and protein formation (Gauthier et al. 2014). Some of the adverse effects caused by heavy metal accumulation in plants include chlorosis, reduction in biomass accumulation, hindrance in photosynthetic activity, water imbalance, altered nutrient absorption, and senescence which consequently leads to plant death (Singh et al. 2016). Heavy metals hamper the physiological process and create a nutritional imbalance in plants which could be carried to higher trophic level organisms with the probability of affecting human health. Moreover, heavy metals also change the physiological and biochemical characteristics of microbes. Nevertheless, most of the microorganisms of different groups have been reported to be potential and cost-effective substitutes for the elimination of heavy metals existing in the environment (Ahirwar et al. 2016; Verma and Kuila 2019).

One of the efficient techniques used in the removal of toxic heavy metals includes microbial bioremediation. The establishment of metal ions within the cells and then reducing the harmful metals into a harmless state and discharge of metal ions outside the cell are the processes involved in the removal of heavy metals by microorganisms. Soil is an important reserve for heavy metal contamination in the terrestrial ecosystem (Gadd 2010). Microorganisms in the soil have a vital role in the detoxification of heavy metals in contaminated soils. The use of rhizospheric microbes in the decontamination of heavy metals is known as rhizoremediation. Bacteria and fungi largely participate in heavy metal detoxification. In bacteria, species belonging to the genera *Bacillus*, *Arthrobacter,* and *Pseudomonas* are the most characterized bacteria found in heavy metal contaminated soil. Other bacterial populations like rhizobia, N_2-fixing microbes, and legume–rhizobia association can detoxify heavy metals and alleviate the soil conditions (Teng et al. 2015). The inoculation of *Pseudomonas aeruginosa* and *Burkholderia gladioli* improved the growth of tomato seedlings raised under cadmium stress. Further, shoots of tomato accumulated a low level of cadmium which was attributed to immobilization caused by these two microbes through a complex formation that consequently led to binding of metal to root, thereby averting the cadmium transition to shoots (Khanna et al. 2019).

The interaction between metal and soil microbes relies on physical and chemical properties of soil including soil type, pH, metal concentration, type of microorganisms, and metabolic activity. The plant growth-promoting microbes modify the bioavailability of metals in soil by several processes such as acidification, precipitation, chelation, and complexation (Mishra et al. 2017). Moreover, Merdy et al. (2009) suggested that acidic pH supports metal bioavailability and absorption. In such cases, organic acids secreted by growth-promoting microbes reduce the soil pH and segregate metal ions that are soluble (Turnau and Kottke 2005). For instance, gluconic acid produced by *Gluconacetobacter diazotrophicus* facilitated the solubilization of zinc (Saravanan et al. 2007). In addition, Seneviratne et al. (2017) proposed that organic acids such as acetic, maleic, and oxalic acids secreted by soil microbes act as natural chelating agents of heavy metals. During bioremediation, some of the filamentous fungi such as *Aspergillus terreus* or *Aspergillus niger* act as biosorbents as they can absorb metal ions such as copper, zinc, magnesium, and cobalt (Price et al. 2001; Cerino-córdova et al. 2012). The mycorrhizal fungi immobilize and decontaminate heavy metals by secreting oxalate crystals. The AM hyphae invade deeply into the soil aggregates and thus assimilate or chelate the heavy metal (Gadd et al. 2014). Experimental evidence has demonstrated that the application of bioinoculum containing heavy metal tolerant microbes is effective in detoxification of heavy metals in contaminated areas (Seneviratne et al. 2015; Migahed et al. 2017). Therefore, remediation of heavy metals by soil microbes could increase crop growth and productivity.

11.5.3 Nutrient Recycling

Soil microbes have a vital role in the biogeochemical cycling of nutrients present in the soil. This assures nutrient turnover and supplement of nutrients that are crucial for crop growth, by inter-conversion of various forms of nutrients such as sulfur, N, and P that are linked with the C cycle. Nutrient cycling is the movement of nutrients in a cyclic way from the ecosystem to different living organisms in the available form and consequently recycled back to the environment. The recycling of elements such as C, oxygen, hydrogen, sulfur, N, and P are important for the survival of organisms and to support plant development and productivity. All the microbial activities occurring in the soil contribute to nutrient cycling and other ecosystem services. Microbes participate in mineral recycling and organic matter decomposition that regulates the liberation of nutrients. These mineralized nutrients are taken up by plants along with water and constitute new organic matter and also help to sustain soil quality and structure for sustainable plant production (Prasad et al. 2021). Fungi are predominantly accountable for the recycling of nutrients via organic matter decomposition and nutrient acquisition (uptake and transfer) in plants by mycorrhizal fungi. Also, fungi act as an alternative source of nutrients that are essential for plant growth. Most of the fungi degrade hard soil organic matter and lignin (Knežević et al. 2013). Further, they decompose organic residues to let other soil microbes also participate in the breakdown process and convert these organic residues into usable ones. The majority of the plants is associated with AM fungi and obtains nutrients through AM fungal hyphae. The hyphae interlink with roots and the soil particles producing a hyphal network that stimulates the scavenging of the soil nutrients. These hyphae also liberate enzymes into soil and decompose intricate molecules that are again taken up by these filaments (Hodge et al. 2001). Hence, fungi serve as natural recycler due to their capacity to reabsorb and redistribute nutrients to plant roots from the soil.

The application of N fertilizer and soil management practices promotes several microbial processes (nitrification, denitrification, and mineralization) that have a pivotal role in greenhouse gas emissions (Pathak et al. 2003). The application of N synthetic fertilizers comprising ammonium and the conversion of organic N into ammonium facilitate nitrification with nitrifying bacteria and archaea which converts ammonium into nitrate (Fortuna et al. 2012). The soil C differs in nutrient concentration and chemical composition. Carbon recycling, decomposition, and microbial activities often result in enhanced organic matter. Soil organic C is an important source of energy for most soil microorganisms. The breakdown of organic matter and crop residues by microbes supplies C and other vital nutrients necessary for living organisms. Besides, nematodes and protozoa feed upon other soil microbes and liberate N as ammonium. These ammonium and nitrates are converted to and fro in the soil from which plants take up ammonium and soil nitrates through the mycorrhizal fungal network (Hoorman 2011).

11.5.4 Plant Stress Tolerance

The plant stress including various abiotic and biotic stresses is increasing with agricultural intensification, climate change, and shift in land use (Neumann et al. 2017; Porter et al. 2020). These stresses impact the plants differentially such as drought causes reduction in the development of shoot and root, decreases leaf area, alters stomatal movements, and decreases plant yield (Kumawat and Sharma 2018).

Likewise, salinity also negatively impacts the growth and development of plant through excessive ion uptake (Na^+ and Cl^-), creates a nutrient imbalance, induces stomatal closure, and inhibits shoot development, reduces metabolic activity, and causes premature senescence (Isayenkov and Maathuis 2019). Overall, the physiological process in the plants gets affected due to various kinds of stresses. Soil microorganisms especially bacteria and fungi including endophytes that reside in the plant tissues regulate the plants to overcome these various stresses (Porter et al. 2020). Several studies have demonstrated the efficiency of many microbes to ameliorate the adverse effects of stresses in plant growth. As already mentioned earlier in this chapter, PGPR promotes crop growth and yield under stressed environmental conditions through both direct and indirect mechanisms. The PGPR improves resistance against many phytopathogens in plants that causes various diseases (Xia et al. 2020). These rhizobacteria secrete some metabolites that target pathogens modifying the permeability of cell membrane resulting in cell death and produce siderophores which could limit the availability of iron, thereby inhibiting the growth of pathogens (Złoch et al. 2016). For instance, inoculation of two PGPR species, *Pseudomonas putida* and *Rothia* sp., in tomato plants infected by *Spodoptera litura* increased the plant biomass and fruit yield that was mediated by PGPR through enhanced production of proline and antioxidant enzymes, and also promoted protease and polyphenol oxidases activities and enhanced the phenolic and chlorophyll contents in tomato (Bano and Muqarab 2016). Similarly, improvement in plant growth under saline and water-stressed conditions by the application of rhizobacteria in several species such as wheat, oats, rice, and maize has also been reported (Gou et al. 2015; Sapre et al. 2018; Zafar-ul-Hye et al. 2019; Joshi et al. 2020).

The AM fungi also contribute to the amelioration of different kinds of stresses. The AM fungi provide resistance against drought or salinity by reducing the concentration of Na^+ and Cl^- ions through modification of hydraulic characteristics of soil, increased plant biomass accumulation and nutrient uptake, osmoregulation, alterations in root architecture, enhanced photosynthetic activities, modulation of plant hormones, and stomatal conductance (Evelin et al. 2019). In a study, wheat plants grown under the saline conditions when inoculated with AM inoculum containing spores of *Rhizophagus irregularis* and *F. mosseae* reduced the adverse effects of saline stress on wheat growth. In addition, AM-treated plants exhibited more shoot and root biomass, had increased shoot N content and N acquisition, and also displayed higher plasma membrane than non-AM-treated plants (Fileccia et al. 2017). Likewise, some of the AM fungal species such as *R. irregularis*, *F. mosseae,* and *R. intraradices* have been proved to be efficient against drought stress (He et al. 2017; Zhang et al. 2019). Moreover, many experiments have been conducted to test the efficiency of the combined effect of several beneficial soil microorganisms in combating the negative impact of stresses on plant growth and development (Table 11.1). Therefore, the application of a microbial consortium consisting of beneficial soil microorganisms can improve crop growth under stressed conditions.

Table 11.1 Effect of combined inoculation of beneficial soil microorganisms in plant stress alleviation

Plant species	[a]Microbial group	Plant growth-promoting microbes	Beneficial aspects	Reference
Casuarina obesa Miq.	AMF +PGPR	*Rhizophagus fasciculatus*, *Rhizophagus aggregatus*, *Pantoea agglomerans*, and *Bacillus* sp.	Improved salinity tolerance	Diagne et al. (2020)
Cucumis sativus L.	AMF +PGPF	*Funneliformis mosseae* and *Fusarium equiseti*	Increased plant growth and suppression of anthracnose and damping-off disease	Saldajeno and Hyakumachi (2011)
Glycine max L.	AMF +PGPR	*Rhizophagus clarus*, *Gigaspora gigantea*, *F. mosseae*, *Claroideoglomus etunicatum*, *Rhizobium* sp., and *Rhizobium cellulosilyticum*	Increased plant yield and fatty acid content under drought	Igiehon et al. (2021)
G. max	NFB +PGPR	*Pseudomonas putida* and *Bradyrhizobium japonicum*	Improved plant growth, nitrogen (N) and phosphorous (P) concentrations, and soluble leaf protein contents under salinity	Egamberdieva et al. (2017)
Helianthus annuus L.	AMF +PGPR	*Claroideoglomus claroideum* and *Pseudomonas libanensis*	Improved plant growth and phytoremediation of nickel metal-polluted saline soils	Ma et al. (2019)
Kosteletzkya virginica (L.) C. Presl ex A. Gray	AMF+PSB	*R. aggregatus*, *F. mosseae*, and *Mortierella* sp.	Increased plant growth parameters, soil enzyme activity, and AMF colonization under salinity	Zhang et al. (2011)
Lallemantia iberica (M. Bieb.) Fisch. & C.A.Mey.	AMF+SOB	*F. mosseae* and *Thiobacillus* sp.	Improved antioxidant enzymes activity, osmolytes, and nutrient concentration under salinity	Heydari and Pirzad (2020)
Solanum lycopersicum L.	AMF +PGPR	*F. mosseae*, *Enterobacter* sp., and *Enterobacter ludwigii*	Improved plant growth and tolerance to cadmium in contaminated soil	Li et al. (2020b)
S. lycopersicum	AMF+ saprophytic fungal consortium	*Rhizophagus irregularis*, *Bjerkandera adusta*, and *Mortierella* sp.	Reduced oxidative stress in in heavy metal contaminated soil by improving	Fuentes et al. (2016)

(continued)

Table 11.1 (continued)

Plant species	[a]Microbial group	Plant growth-promoting microbes	Beneficial aspects	Reference
			defense mechanisms and homeostasis	
Oryza sativa L.	AMF+NFB	*Rhizophagus intraradices* and *Azospirillum brasilense*	Increased plant growth, physiological characteristics under well-watered and drought conditions	Ruíz-Sánchez et al. (2011)
Prunus maritima Marshall	AMF+PSF	*F. mosseae* and *Apophysomyces spartima*	Increased plant growth, nutrient uptake, photosynthetic efficiency, and concentration of photosynthetic pigments under salinity	Zai et al. (2021)
Trifolium repens L.	AMF +PGPR	*R. intraradices*, *Bacillus megaterium*, and *P. putida*	Improved plant nutrient, decreased stomatal conductance, and activities of stress enzymes under drought	Ortiz et al. (2015)
Vigna unguiculata (L.) Walp.	NFB +PGPR	*Bradyrhizobium* sp., *Actinomadura* sp., *Paenibacillus graminis*, *Bacillus* sp., and *Streptomyces* sp.	Improved dinitrogen (N_2) fixation under salinity	Santos et al. (2018)
Zea mays L.	AMF +PGPB	*C. etunicatum* and *Methylobacterium oryzae*	Enhanced plant growth, AMF colonization, and nutrient accumulation under salinity	Lee et al. (2015)
Z. mays	AMF+PSB	*F. mosseae* and *Pseudomonas fluorescens*	Enhanced vegetative and reproductive characters of maize, root colonization, grain yield, P and N content in plant tissue under water deficit and normal conditions	Ghorchiani et al. (2018)

[a] *AMF* arbuscular mycorrhizal fungi, *NFB* nitrogen-fixing bacteria, *PGPR* plant growth-promoting rhizobacteria, *PGPB* plant growth-promoting bacteria, *PSB* phosphate-solubilizing bacteria, *PSF* phosphate-solubilizing fungi, *PGPF* plant growth-promoting fungi, *SOB* sulfur-oxidizing bacteria

11.5.5 Bioinoculants

The use of chemical fertilizers causes degradation of environmental ecology as well as human health. These chemical fertilizers destroy the indigenous microbial population that prevails in the vicinity (Mahanty et al. 2017). Alternative methods are greatly concerned to cope up with the food demand in a sustainable and an eco-friendly manner. Hence, the agricultural practices currently available must be altered by eliminating chemical fertilizers, pesticides, herbicides, fungicides, and insecticides instead incorporating the effective organic approach which is an ideal way for sustainable agricultural practices (Pretty and Bharucha 2015). The use of beneficial microbes as bioinoculants is arising as a promising alternative to those chemical fertilizers to uplift food safety and crop production (Mahanty et al. 2017). Bioinoculants are a promising approach that helps in increasing the plant biomass, yield, and chlorophyll content (Verma et al. 2019); leaf surface area, photosynthetic rate, water uptake capacity, and stomatal conductance (Enebe and Babalola 2018); expression of antioxidant enzymes under stress conditions (Harkousse et al. 2021); and production of phenolic compounds, anthocyanins, and carotenoid content in the plants (Arora et al. 2018). Hence, it is an alternate for chemical fertilizers in the establishment of sustainable agriculture.

Bioinoculants are organic substances that contain desired suitable living microorganisms which are capable of multiplying within the plant parts or in the rhizosphere of the plants to help in the proper supply of nutrients to the inoculated plants resulting in the increased plant growth (Malusa and Vassilev 2014). These microbes could be applied to seeds, plants, or soil that fixes the atmospheric N_2 and promotes the growth of the plants by solubilizing the insoluble nutrients such as iron, magnesium, N, P, and potassium (K); helps in the decomposition of the organic matter; and produces plant growth-promoting substances in the soil leading to increase in the soil fertility (Mazid and Khan 2014). Bioinoculants produced from effective microbes pave the way to regain soil fertility in eco-friendly and cost-effective manner (Singh et al. 2011). They are produced by incorporating the living cells or latent of efficient potential microbial strains that effectively help the plants in nutrient uptake by associating in the plant parts and rhizosphere of the soil (Kour et al. 2020). It has been reported that nearly 10–40% of crop yields are enhanced by the bioinoculant application. Further, bioinoculation also increases the protein content, essential amino acids, vitamins, and N_2-fixation in plants (Bhardwaj et al. 2014). Moreover, Kour et al. (2020) classified bioinoculants based on the affinity toward nutrients as N_2-fixing microbes that include symbiotic, free-living, and associative symbiotic N_2-fixing biofertilizers, and P- and K-solubilizing biofertilizers.

Symbiotic N_2-fixing biofertilizers mostly include the microbial group belonging to the genera *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Sinorhizobium*, and *Rhizobium* (Kour et al. 2020). In this process, the atmospheric N_2 is reduced to ammonia which assists the plants to produce various nitrogenous compounds, vitamins, and proteins. These phenomena take place in the presence of enzyme dinitrogenase reductase with iron as its cofactor and dinitrogenase with molybdenum and iron as its cofactor (Mahanty et al. 2017). As legume plants are associated with symbiotic microbes, the non-legume plants associate with *Azotobacter* which is a free-living bacterium that fixes the atmospheric N_2 without any symbiotic association in plants such as cotton, rice, and vegetables (Chen et al. 2018). Species of *Azotobacter beijerinckii*, *Azotobacter insignis*, *Azotobacter macrocytogenes*, and *Azotobacter vinelandii* (Latt et al. 2018) and cyanobacterial species such as *Anabaena*, *Nostoc*, *Calothrix, Aulosira*, and *Tolypothrix* sp. are used as bioinoculants. Romero-Perdomo et al. (2017) proved *Azotobacter chroococcum* as an efficient bacterial bioinoculant for cotton growth as evidenced by increased plant growth and other plant growth-promoting characteristics such as nutrient solubilization, phytohormone production, and nutrient uptake and decreased the dependency on N fertilization up to 50%. Some species of microbes such as *Azospirillum* are effective in increasing plant growth and helping the plants to resist various biotic and abiotic stresses (Curá et al. 2017; Steiner et al. 2020). It also helps in producing growth-promoting hormones such as IAA, cytokinin, and gibberellins (Vurukonda et al. 2016).

Some of the phosphate-solubilizing microbes that could be potentially used as biofertilizers inoculants include *Burkholderia, Corynebacterium*, *Serratia phosphatase* and species of *Xanthomonas*, *Cephalosporium*, *Alternaria*, *Rhizoctonia*, and *Mycobacterium* (Kalayu 2019). Likewise, K-solubilizing microbes include *Bacillus mucilaginosus*, *Bacillus cereus*, *A. terreus*, and *Streptomyces rochei* (Sun et al. 2020; Sukmadewi et al. 2020). The co-inoculation of phosphate-solubilizing fungi (*A. niger*) and bacteria (*Bacillus* sp.) indicated the positive synergetic effect by improving the plant biomass, leaf chlorophyll content, and yield of chickpea plants (Saxena et al. 2015). Similarly, in a pot experiment, Wang et al. (2019) demonstrated that seedlings of *Cyclocarya paliurus* co-inoculated with a consortium of phosphate-solubilizing (*Bacillus megaterium* and *P. fluorescens*) and N_2-fixing bacteria (*A. chroococcum* and *Azospirillum brasilense*) increased the nutrient uptake (P and N), biomass, plant growth, and bioactive compounds and also enhanced the soil nutrients, thereby proving their efficiency in plant growth promotion, and these microbial inoculants could be developed as bioinoculants for crop improvement.

The AM fungi are considered a natural bioinoculant in agricultural production owing to their several beneficial effects on plant health. Cely et al. (2016) examined the effect of *Rhizophagus clarus* inoculation along with and without different quantities of fertilizer application on plant growth and its efficiency to substitute chemical fertilizers in soybean and cotton cultivation under natural field conditions. The study indicated that AM fungal inoculation enhanced plant growth, nutrient uptake, and yield and increased the plant root colonization by 20% in both crop species. Thus, *R. clarus* inoculum could be used as a promising alternative bioinoculant and can minimize the use of fertilizers in soybean and cotton cultivation (Cely et al. 2016). In addition, several studies have revealed that the application of indigenous or exotic AM fungi increased plant growth by suppressing phytopathogens (Olowe et al. 2018; da Silva Campos 2020). Likewise, co-inoculation of AM fungi with other plant growth-promoting microorganisms also helps in crop improvement under stressed conditions (Mohamed et al. 2019; El-Sawah et al. 2021).

11.5.6 Soil Fertility

Soil fertility is the capability of the soil substrate to provide the nutrient and water essential for higher crop production. Soil fertility depends on various soil factors including pH, bulk density, electrical conductivity, available water capacity, and other various mineral nutrients (de Paul and Lal 2016). The organic C present in the soil is responsible for soil biological activity and crop productivity, and soil P is required for the phosphorylation process, cell signaling, and bioenergetics (Reeves 1997). Iron and manganese are used during photosynthesis for the absorption of light by chlorophyll pigments (Sirsat et al. 2018), and zinc is used up for the production of proteins, carbohydrates, and plant growth hormones and also for root development (Arunachalam et al. 2013). Soil fertility is always intertwined with plant nutrition or crop production, where the available nutrients are absorbed by the roots from the soil. Among various nutrients taken up by the plants, only 1% is reported to be prevalent in the available forms and the rest are either precipitated or present as complex compounds (Foth and Ellis 2018). Soil organic C: N: P is available in the ratio 186:13:1 according to the reports of Cleveland and Liptzin (2007).

The fertility of soil could be altered by the availability of nutrients in the soil and is measured either directly by soil parameters such as soil pH, organic matter, macronutrients, and soil enzyme activities (Ma et al. 2017) or indirectly by the plant growth and productivity measurements (Zheng et al. 2018). Soil fertility and crop yields are the two parallel factors that increase with the increase of the other, while the decline in one factor causes food insecurity (Awazi and Tchamba 2019). Soil fertility could be affected by various biotic and abiotic factors which include deforestation, soil erosion, heavy metal pollution, overgrazing, expanding population, and intensified agricultural practices (Rusinowski et al. 2019). It has been suggested that continuous cultivation throughout the year and tillage alters the physicochemical properties of the soil surface (Kiboi et al. 2019) and also causes a rapid decline in soil fertility by acidification of soil, soil compaction, and soil organic matter degradation. Soil fertility can be improved by crop rotation, crop residue management, and sustainable fertilizer applications (Agegnehu and Amede 2017). Fertilizer applications must be associated with organic resources, and the fertilizer must ensure the proper nutrient supply, enhanced soil aggregation, soil microbial activity, soil water penetration and withholding, confrontation to erosion, and nutrient transformation (Nalivata et al. 2017).

Microorganisms prevailing in the soil substantially contribute to the biological fertility of the soil. Soil microbes help in releasing nutrients from organic matter. They utilize C and the nutrients present in the organic substance during the decomposition process for their growth and liberate additional nutrients to the soil which can be absorbed by the plants. The N_2-fixing microorganisms are an essential source of N in agriculture and improve the fertility of the soil by fixing the atmospheric N. Also, the legume plants associate with other helpful microbes and help in increasing the nutrient content in the soil, thereby enhancing the crop growth and fertility of the soil. The saprophytic fungi decompose dead organic matter and convert it into carbon dioxide and other small compounds and have a key role in the C cycle and soil mineralization (Crowther et al. 2012). One of the important plant–root symbioses formed by AM fungi enhances the P uptake in the plants by extending their hyphal network from plant roots into the soil to access P that cannot be reached by plant roots (Smith and Read 2008). In addition, the phosphate- and K-solubilizing microbes existing in the soil improve the nutrient availability by enhancing the dissolution and release of K and P to the soil (Meena et al. 2014). Most soil protozoa feed on bacteria to obtain their nutrition and hence help in maintaining the soil equilibrium (Bonkowski 2004). Like protozoa, nematodes also play an important role in improving soil fertility through nutrient mineralization (Mekonen et al. 2017).

11.5.7 Soil Aggregation

Soil organic matter stabilizes soil structure, enhances nutrient recycling, and improves the physical characteristics of soil (Martens 2000). Soil aggregates refer to the arrangement or binding of numerous soil particles more strongly when compared to the adjacent soil particles and are the primary soil structural unit that regulates most of the soil physiochemical activities. Soil aggregates change the nature of plant roots and soil microorganisms in several ways; therefore, soil structure offers the primitive setting for mycorrhizal associations. Moreover, soil aggregation is vital for the growth of roots and ecosystem processes including C storage and preventing soil erosion (Six et al. 2006). It is modulated by various abiotic factors and regulated by plants and soil microbial diversity and their interactions (Rillig et al. 2015). The structure of soil can be indicated often through aggregate stability as they are important to enhance the fertility and sustainability of soil (Xie et al. 2015; Zheng et al. 2016). Soil microorganisms assist in the formation of aggregates and soil stabilization. Bacteria present in the soil stabilize soil aggregates through precipitating extracellular polysaccharides and forming hemic materials which form complex organic matter (Hashim et al. 2020). Predation by protozoa on bacterial communities promotes the bacterial inhabitants in soil decomposition process and also improves soil aggregation. Glomalin is a distinct soil protein produced by AM fungi that is discharged through fungal hyphae into the soil (Rillig 2004). This glycosylated protein plays a vital role in enhancing soil aggregations. The glomalin-related soil protein acts as a binding agent which unites the soil particles and enhances the development of water-stable aggregates (Zhu et al. 2019).

11.6 Soil Microbes as an Indicator of Soil Health

In terms of sustainable agriculture, soil health is significant for crop growth and productivity through various processes like biogeochemical cycles, phosphate solubilization, N_2-fixation, degradation of pollutants, inhibition of phytopathogens, and improving soil structure (Lehmann et al. 2020). Soil health is influenced by physical, chemical, and biological processes occurring in the soil (Arias et al. 2005). Soil harbors microorganisms of different kinds that perform various functions that influence plant health and play an important role in maintaining soil health. The major indicators of sustainable soil management could be known through the evaluation of soil health and its changes with time (Doran et al. 2002). As microbes have a crucial role in soil functioning, there must be a microbial measurement of soil health. Therefore, microbial data could be a promising approach to examine soil health. Moreover, soil microbes in particular bacteria, fungi, protozoa, and nematodes indicate the quality of the soil (Cardoso et al. 2013). The potential nutrient cycling in the environment can be indicated through fungal: bacterial ratios (De Vries and Bardgett 2012). Similarly, another valuable indicator of soil health includes the different types of bacterial communities (Maron et al. 2018). Soil consisting of a higher population of phytopathogenic fungi and bacteria is regarded as less healthy in comparison with soil consisting of fewer pathogens. Nevertheless, Lievens et al. (2006) proposed that possibility of increased plant disease does not essentially relate with the minor existence of soil pathogens.

Microbial indicators are more vulnerable to alterations caused in the environment when compared to physical and chemical indicators (Masto et al. 2009). Therefore, soil microbes could detect any disturbances in the environment in its initial stage. The soil microbial biomass is the main constituent of soil organic matter created by a diverse group of microbes and serves as an essential nutrient source that provides nutrients to plants owing to its continuous cycling (Sicardi et al. 2004). This is regarded as one of the major biological indicators of soil health. Nevertheless, Dalal (1998) claimed that measurement of microbial biomass may not exactly provide an assessment of soil health as various biotic and abiotic factors could bring alterations in soil microbial biomass either directly or indirectly. A higher population of mycorrhizal/ PGPR in soil indicates healthier soil that benefits plants through increased growth and nutrients. However, the presence of higher nitrifiers such as ammonia-oxidizing bacteria in soil exhibits higher nitrification rates which indicate more loss of soil N due to nitrification and leaching of nitrate (Fierer et al. 2021).

Besides fungi and bacteria, nematodes are also involved in the assessment of soil health as their type and number present in soil indicate alterations in the microorganisms as they ingest and affect the physiochemical nature of soils. The abundance of predatory and omnivorous nematodes reveals if the soil is influenced by any kind of disturbances or pollutants and indicates if the soil can inhibit pathogens. Owing to the permeable cuticle, nematodes respond with different reactions to pollutants and relate with the restoration capacity of the soil environment (Wasilewska 1989). Likewise, a few nematodes possess resistant phases like cryptobiosis or cysts which enable them to persist in inactive state during unfavorable environmental conditions for their growth. The manifestation of heat shock proteins that is highly conserved in nematodes gets increased when subjected to organic toxins or heat stress (Kammenga et al. 1998). One of the free-living nematodes, *Caenorhabditis elegans,* is commonly preferred to indicate the soil health in the agricultural system because of its short lifespan, cost-effective cultivation, the existence of complete genome sequence, and rapid response to the changes in the environment (Bouyanfif et al. 2019). Like nematodes, soil protozoa also respond to environmental changes rapidly due to their rapid growth and fragile exterior membrane. Any alterations in protozoan communities possibly affect soil fertility and soil formation. Protozoa persist in the soil in which higher organisms are absent because of its severe environmental conditions (Foissner 1999). The assessment of soil health through a wide range of soil microorganisms could help in sustainable agriculture and land management.

11.7 Conclusion

Soil is a sustainable resource that supports the survival of various organisms. The beneficial microorganisms inhabiting the pedosphere exhibit a wide array of important functions essential for sustainable crop production. These microbes can improve plant growth and productivity through various mechanisms. The production of phytohormones, increased nutrient uptake, phosphate and K solubilization, tolerance against environmental stresses, and plant disease are the major mechanisms through which soil microbes contribute to improving plant performance and crop yield. Further, owing to their plant growth-promoting traits, useful microbial strains such as AM fungi, PGPR, and other growth-promoting microbes can be developed as bioinoculants which could reduce the dependence on chemical fertilizers for agriculture sustainable land management and plant productivity. In addition to the maintenance of soil fertility and soil structure, soil microorganisms are used as an indicator to assess soil health. Therefore, soil microbes in the pedosphere have a critical role in various processes that can aid toward sustainable agriculture production.

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Chapter 12
Rhizospheric Metaproteomics: Current Status and Future Directions

Amit Singh Rana, Ashok Kumar Verma, and Ashutosh Dubey

Abstract Rhizosphere harbors unique and unidentified bacteria and protein. The quest to unearth all protein repertoires of this unexplored domain of microbial life has seen unprecedented growth over the last two decades. The beneficiary of this expedition is not only limited to existing ensemble of utilitarian biomolecules but also the whole interdisciplinary science and ultimately humankind in ways unimagined. Rhizosphere in its essence is vaguely defined as an area under direct influence of roots. This article discusses challenges in defining this extraordinary spatial interaction of microbes namely archaea, bacteria, fungi, viruses, and root. Rhizosphere brings forth a nutritional base to these microbes and is integral to plant growth, crop production, and ecosystem health. The exact mechanisms and working of this interaction are not yet clear but the use of advanced molecular methods, has given excess to understand these phenomena. This improves our ability to monitor terrestrial ecosystem and harness desirable resources, such as bioenergy production, crop yield maximization, and soil-based carbon sequestration. Multi-omics promises addition in the knowledge of current rhizospheric science. There is a need to understand proteomic techniques and technologies; methods and protocols are usually followed including challenges that need consideration moving forward.

Keywords Rhizosphere · Soil biodiversity · Microbial diversity · Plant growth-promoting rhizobacteria (PGPR) · Multi-omics · Metaproteomics

12.1 Introduction

A microbiological gradient zone in soil, in which maximum changes in the population of microflora are evident adjacent to the root and decline with distance away from it, loosely represents a rhizosphere. The term “Rhizosphere” was coined by

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B. Giri et al. (eds.), *Structure and Functions of Pedosphere*,
https://doi.org/10.1007/978-981-16-8770-9_12

Hiltner and defined it as an area of microbial activity around roots (Hiltner 1904). Others explained it as the volume of soil under direct influence of plant root tissue exudates and inhabited by rhizobacteria (Pinton et al. 2007). The microbial diversity in rhizosphere is far from elucidation, owing to the conventional technique of cultivating microbial population in laboratory, followed by identification. With the need to improve our understanding of microbial community and its interaction with root system and catch up with the challenge of setting up robust techniques to assess and modify soil health for better food production, disease-free plant, sustainable agroforests, and quality product, the role of rhizospheric microbes becomes vital (Atkinson and Watson 2000).

Integrated multi-omics collects dataset and information from multiple omes (various disciplines in biology whose name end in suffix omics, such as genomics and proteomics). Data from all protein contained are called proteome and analyzed with a variety of instruments. Metaproteomic analysis deals with the analysis of entire protein content of a given habitat (Wilmes et al. 2008). Metaproteome represents a distinct picture of whether genes are functionally active at the given time of sampling or not, courtesy of complex regulation of gene expression at transcriptional and/or translational level. Currently, there are a few integrated multi-omics results in rhizosphere science, but reports are increasing day by day to elucidate structural and functional aspects of the rhizosphere (White et al. 2017). For example, NGS 16S rRNA PCR amplicons (i.e., ribosomal RNA polymerase chain reaction amplification-based sequencing), which measures organism diversity, has revealed the microbial community structure, including the core members, in rhizosphere of white lupins (Marschner et al. 2002), *Arabidopsis thaliana* (Bulgarelli et al. 2012), maize (Peiffer et al. 2013), soybeans (Mendes et al. 2014), common annual grass (i.e., *Avena fatua*) (Shi et al. 2015), and coffee (Caldwell et al. 2015). In addition, excellent metagenomic studies have revealed functional metabolic potential of the rhizosphere (Knief et al. 2012).

12.2 Rhizosphere

The interaction between plant, soil, and microorganisms in soil is of very unique and dynamic manner and constitutes the rhizosphere of the plant, the region of soil directly under root's influence. Rhizosphere is a continuously changing microenvironment where any change either physical, chemical, or biochemical in near or distant vicinity can lead to amendments in various processes liable for several stages of nutrient availability. Calculated to be supporting an estimated 10^{11} microbial cells per gram root (Egamberdieva et al. 2008), with 10^{10} functional genes per gram soil, makes it arguably the most complex terrestrial microbial habitat on Earth (Prosser 2015). Three different zones of the rhizosphere are classified as the endorhizosphere (the endodermis and cortical layers inside the root), the rhizoplane (the root surface with mucilaginous polysaccharide layer), and the ectorhizosphere (soil particles past the root surface that are impacted by root exudates) (Lynch and Whipps 1991)

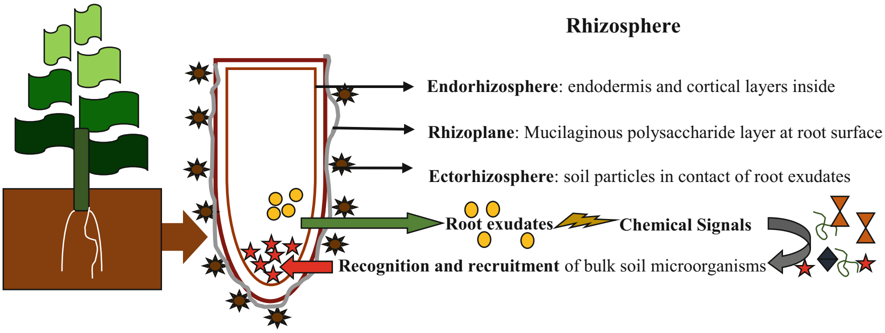

Fig. 12.1 Diagrammatic representation of rhizosphere components

(Fig. 12.1). The "endorhizosphere" is commonly referred to as "internal root colonization" as it is a physical location inside the plant rather than a "sphere" outside of the root. Endorhizosphere is abundant in various nutrients because of an aggregation of root exudates, compared to bulk soil (Dakora and Phillips 2002), including amino acids, sugars, organic acids, vitamins, and enzymes (Gray and Smith 2005). Root exudates release constitutes of ions, oxygen, and water, but most importantly include carbon-containing compounds (Uren 2000). Some root exudates repel pathogens, while others attract and cumulate beneficial microbes, solely based on the physiological status, species of plants, and microorganisms (Kang et al. 2010; Ahemad and Kibret 2014).

The rhizosphere is important for microorganism-driven carbon sequestration; ecosystem functioning; and nutrient cycling in terrestrial ecosystems (Berg and Smalla 2009). The importance of these various interactions and interplay of biotic and abiotic factors can be understood by the fact that rhizosphere management is bestowed with one of the most important scientific frontiers of this decade (McNear Jr 2013). Positive, negative, or neutral rhizobacterial interactions with plant roots can be witnessed in rhizosphere (Morgan et al. 2005). Rhizosphere's role is pivotal for plant growth promotion, nutrition, and crop quality, and attributes to carbon sequestration, nutrient cycling, and ecosystem functioning in rhizosphere (Singh et al. 2004; Berg and Smalla 2009).

12.3 Rhizosphere Microbiota

The presence of microorganisms is virtual in every habitat on earth and also accountable for diverse functions. Their natural habitat is mixed communities, where they cohabit and maintain intricate specific microenvironment known as the microbiota. Loosely, microbiota represents sum total of all microbial population and communities in a particular environment that directly or indirectly relates to function of that environment. Microorganisms are actively involved in biogeochemistry, which ensures recycling of elements such as carbon and nitrogen (Madsen 2011). Moreover, microorganisms intimately degrade anthropogenic complexes, prior to releasing wastes into the environment (Hussain et al. 2010). Suggestions to relate "omics" approaches to understand the big picture are not new and require undeniable attention (El Amrani et al. 2015).

Different "omics" approach to rhizospheric microbiota enlists the presence of diverse microbiome (microbiota's genome) that was immensely underestimated. The role of total microbiota has not been taken holistically to understand the rhizosphere yet and is greatly ignored. A minority of the microbial community, i.e., only up to 5%, has been known/cultured, and the remaining majority microbiome still remains to be explored. As expected, the microbial richness over shines in the rhizosphere as compared to the bulk soil. Rhizospheric zone is an area of intensive interaction among plant roots, microorganisms, and soil. The phenomenon of "rhizosphere effect" describes that, in comparison with bulk soil, the biomass and activity of microorganisms in the rhizosphere are enriched as a result of exudation of various chemical compounds by the root (Raaijmakers et al. 2009). This accounts for a greater microbiota in rhizosphere. Rhizosphere and bulk soil metagenomic studies using pyrosequencing technique have concluded a number of microbial hubs in rhizosphere as compared to bulk soils (Alzubaidy et al. 2016). As hypothesized, the activity of enzymes and functional potential of microbial community in the rhizosphere are much higher than bulk soil (Asmar et al. 1995). For instance, in the studies with maize, a total of 5777 genes (93.2% of total 6201 genes) were detected in the rhizosphere, while only 1983 genes (32.0%) were detected in the bulk soils, confirming expected results. In the rhizosphere part, the magnitude of genes from bacteria, archaea, and fungi were 5390, 103, and 246 genes, respectively, whereas in bulk soil a mere 1849, 38, and 84 genes for the same were reported. Also, to note was the fact that 53 gene families (out of 248) were detected only in the rhizosphere. This highlights the greater richness of species and their functions in the maize rhizosphere soil, than bulk soil (Li et al. 2014). No doubt that soil is a much more complex area that has numerous biodiversity and biotic/abiotic factors, which plays a great part in microbiota composition. The rhizospheric microflora diverges according to the plant host species itself; additionally, the presence of neighboring plants strongly influences microbiota below ground (De Deyn et al. 2011). Plants often control their rhizosphere microbiome composition as different plant species try to promote a different set of their own microbes (Turner et al. 2013; Ofek-Lalzar et al. 2014). A variance of approximately 5.7% in the rhizosphere microbiome composition is recorded in accordance with genotype of host plant (Bulgarelli et al. 2015).

The influence of root exudates on the microbial structure and function is evident, and it is reported for maize that the amendment mucilage leads to higher production of N_2O than non-amended soil (Pérez-Jaramillo et al. 2016). Moreover, the addition of artificial root exudate promotes nitrate reduction and denitrification. These features of plants direct the recruitment of beneficial rhizosphere microbiome often called plant growth-promoting rhizobacteria (PGPR) and may lead to rhizodegrdation/rhizoremediation of xenobiotics through rhizofilteration and phytostabilization (Tyagi and Dubey 2015). *Agrobacterium*, *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia, Caulobacter, Chromobacterium, Erwinia, Flavobacterium, Micrococcous, Pseudomonas, Serratia,* and *Cellulomonas Flavigena* represent the PGPR genera present in rhizosphere (Gray and Smith 2005; Hossain et al. 2015; Duy et al. 2016; Disi et al. 2019; Hassan et al. 2019). Nitrogen-fixing endophytic rhizobacterial genera (*Allorhizobium, Azorhizobium, Bradyrhizobium, Mesorhizobium*, and *Rhizobium*, family *Rhizobiaceae*) colonize legume plants roots to form nodules and increase plant growth directly or indirectly (Wang and Martinez-Romero 2000; Kumawat et al. 2019 and Harman and Uphoff 2019). *Pantoea, Methylobacterium, Exiguobacterium, Paenibacillus*, and *Azoarcus* also colonize roots and are advantageous to plants (Chauhan et al. 2015). Another group of rhizobacteria that promote plant growth and suppress plant pathogens through root colonization is *Actinomycetes*. Some strains like *Streptomyces, Streptosporangium, Thermobifida*, and *Micromonospora* inhibit root fungal pathogens (Franco-Correa et al. 2010). PGPR is attracted by root-derived nutrients for root colonization and repels plant pathogens to avoid root damage. On the other hand, plant receives various nutrients through PGPR root colonization and division inside and outside of plant roots (Fig. 12.2).

PGPR root colonization is a prerequisite for plant growth promotion. Root colonization refers to the process of active root-growing region and multiplication in rhizosphere induced by rhizobacteria inoculums such as seed treatments (Parke 1991). Both active and passive movements of bacteria aid the dispersal of rhizobacteria from the inoculation site to the growing region of roots (Benizri et al. 2001). Passive transport on the root tip leads to root colonization by *Pseudomonas fluorescens* strain (Howie et al. 1987). O antigen of the bacterial lipopolysaccharides (LPS) plays important roles in root colonization, with some PGPR strain-dependent (Dekkers et al. 1998a, b). Reports have also shown that synthesis of B1 vitamin and nicotinamide adenine dinucleotide hydrate (NADH) dehydrogenase secretion contribute to root colonization by PGPR (Simons et al. 1996). Various studies reported type IV pili of bacteria (Steenhoudt and Vanderleyden 2000), secretion of a site-specific recombinase gene (Dekkers et al. 1998a, b), and teichoic acid (WTA) (Xu et al. 2019) all play roles in root colonization. PGPR significantly enhances plant nutrient uptake. This is mostly accomplished by solubilization of unavailable forms of nutrients (phosphate and nitrogen) and production of siderophores, which chelate and release iron for the plant in iron-limited conditions (Vessey 2003; Prasad et al. 2019; Bhat et al. 2019). It is well established that PGPR synthesizes and metabolizes phytohormones to either stimulate or inhibit hormone synthesis of host plant. Since hormones tend to have multiple functions in the plant, any deviations in quantity or/and localization may cause several effects on plant growth (Tsukanova et al. 2017), as reported for *B. subtilis* strain FB17 strain that had expressed multiple genes including auxin-regulated genes involved in metabolism, stress response, and plant defense in *Arabidopsis thaliana* roots during root colonization process (Lakshmanan et al. 2013). Thus, these PGPR and other plant-associated microbes potentially modify phytohormone concentrations and metabolism in plant tissue, to improve the cellular activities to prevent harmful outer environmental stresses, such as drought, salinity, nutrient deficiency, or heavy

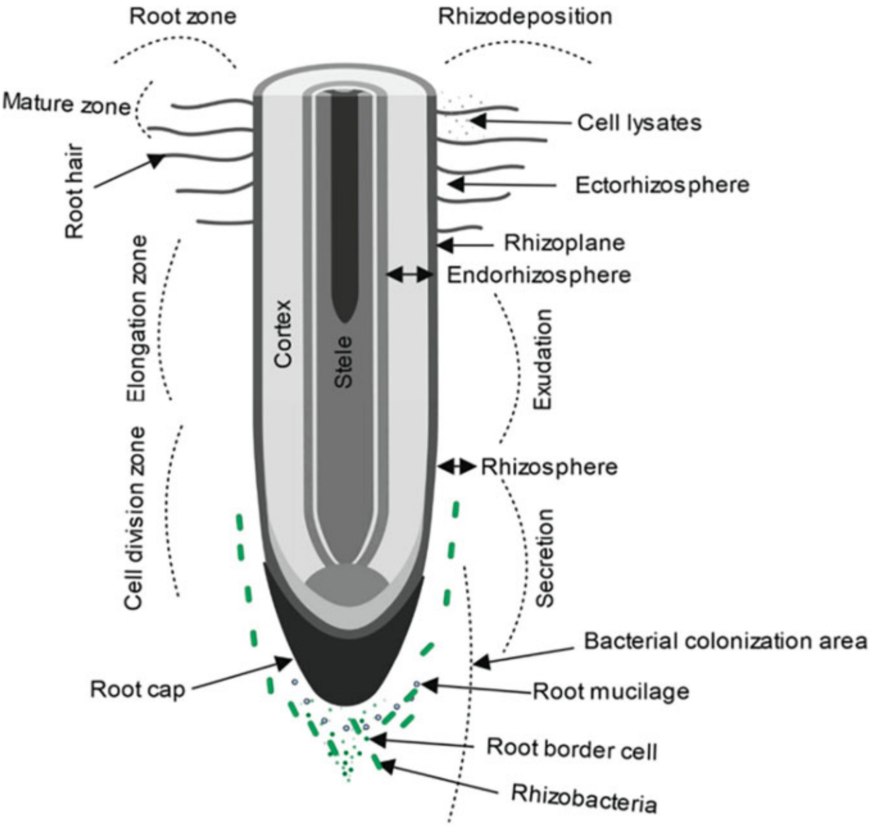

Fig. 12.2 Root zone types in the rhizosphere where rhizodeposition, root exudates, and root border cells provide nutrients for PGPR growth and root colonization (Hassan et al. 2019)

metal contamination (Egamberdieva et al. 2017). Rhizospheric microbes also play a significant role in the development of stress tolerance in the plants by phytohormonal modulations, ion homeostasis, and antioxidant enzyme-mediated defense (Dubey and Verma 2019).

12.4 Metaproteomics

Large-scale protein analysis constitutes proteomics, which to a great extent add to perceptive knowledge of gene function in present post-genomic era. There are three distinguished areas identified in proteomics viz. micro-characterization of protein for identification and post-translational modifications; comparison of protein expression levels with potential application in different fields; and studies of protein–protein interactions (Pandey and Mann 2000). While entire analysis of protein content in a given habitat constitutes metaproteomic analysis (Wilmes and Bond 2006), proteomic analysis has collectively been used to study the variation in protein expression profile involved in the physiological changes in microorganisms exposed to natural environment (Kim et al. 2004; Wilmes and Bond 2006; Keller and Hettich 2009). Two-dimensional polyacrylamide gel electrophoresis (2-DE) and mass spectrometry (MS) combined with bioinformatics are highly effective methods of proteomic analysis (Singh and Nagaraj 2006). Metaproteomic studies utilize two-dimensional electrophoresis (2-DE), mass spectroscopy (MS) with available database of protein sequence, and structural databases to mimic protein distribution and to analyze hydrocarbon-degrading microbial community, as well as catabolic enzymes that are associated with the biodegradation pathways (Kim et al. 2006). Metaproteomics can be broadly explained as systematic identification and investigation of all proteins found in a specific ecosystem to understand the functioning of that particular ecosystem at community level. It aids to investigate proteins that might be present at the core of any geochemical process and establish interlink between physical, chemical, and biochemical processes.

There are two approaches namely bottom-up or top-down pipelines for metaproteomic investigations. In bottom-up approach, the sample protein is digested in-gel or gel-free conditions and then subjected to LC-MS analysis, and then, acquired data familiarize the peptide and ultimately the proteins. However, in top-down approach the process of protein digestion is detoured and the separated protein samples are detected as such through LC-MS. The targeted approach is hybrid approach, which includes designating a particular peptide for selective reactive monitoring (SRM) fusing the two approaches to make a more hybrid approach (Picotti and Aebersold 2012). The most widely accepted, appreciated, and used is the bottom-up approach, i.e., more commonly called shot-gun proteomics. For targeted approach, sample proteins are digested with chemical or enzymatic method into peptides and then introduced for mass spectrometric scrutiny. Mostly trypsin is used for enzymatic digestion and digested products (tryptic peptides) are analyzed by online liquid chromatography mass spectrometry (LC–MS) with electrospray ionization (ESI) or matrix-assisted laser desorption/ionization (MALDI) (Fig. 12.3).

The bottom-up approach is more sensitive, is technically feasible, and has wider applicability to a complex environment than bottom-down approach (Bastida et al. 2009). Due to the low molecular weight of peptides than proteins, peptides are more soluble, easily ionized, separated, and identified with high resolution and mass accuracy, which assist the bioinformatic platforms (Amunugama et al. 2013).

The drawback with this approach is peptide or even several peptides not being specific to an individual protein or protein form, leading to protein interference problems. On the other hand, top-down approach is more powerful technique due to the powerful separation devices and high-throughput mass spectrometers. In this approach, no prior digestion before subjecting to MS is required instead intact protein is ionized and protein's molecular mass along with fragment ions is detected and identified. Increased protein coverage, which provides complete description of

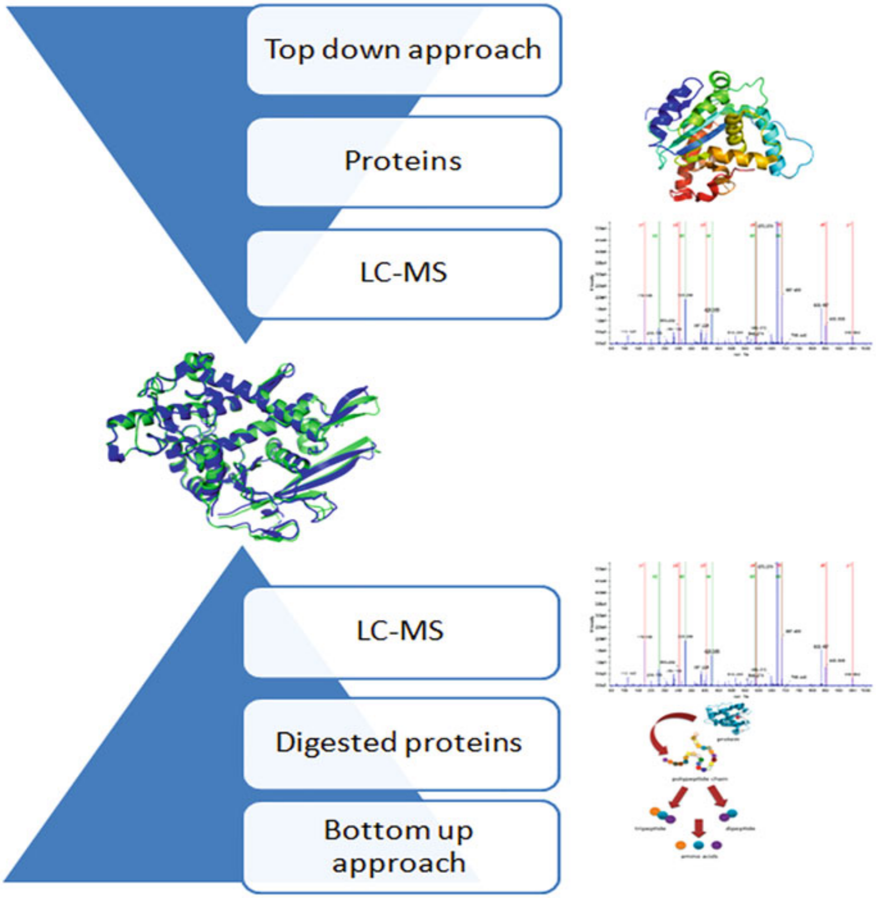

Fig. 12.3 Outline of two common metaproteomic approach

primary structure, alternative splicing, and posttranslational modification, is generally tapped beneficial with top-down approach (Kelleher 2004). This approach is more effectively used for single protein analysis or simple mixture of significant biological interest. Soil, which is a comparatively very complex matrix, has not seen the light of this approach. As there are always probabilities of random fragmentation of high molecular weight native proteins, peak intensities exhibit reduced sensitivity in bottom-up metaproteomic approach. Additionally, in traditional gel-based approach, poor protein recovery from eluted gel hinders the traditional approach. Moreover, ESI is not compatible with the use of ionic detergents, such as SDS in SDS-based approaches. Ionization of big molecule is also difficult as compared to small ones (Catherman et al. 2014).

There are attempts on the use of electrospray ionization (ESI) or matrix-assisted laser desorption/ionization (MALDI) and even more advanced ionization methods by use of electron capture dissociation and electron transfer dissociation, but findings just prompt to overcome hurdles in respect to sensitivity, separation, and ionization to develop a more robust errand for analyzing intricate soil samples (Zhang et al. 2011). Techniques, such as the terminal restriction fragment length polymorphism (T-RFLP), the denaturing gradient gel electrophoresis (DGGE), the single-strand conformation polymorphism (SSCP), and the reverse transcription polymerase chain reaction (RT-PCR), are indispensible to investigate the diversity of soil microbes at the genomic and transcriptomic levels. These techniques have been valuable to add on our knowledge on the microbial diversity in rhizospheric soil (Ge et al. 2002). Nonetheless, the function of microbial diversity still remains to be elucidated, since the mRNA abundance does not correlate with protein abundance, and the post-translational modifications cannot be predicted by mRNA and DNA as well for now. Similarly, biological process is not driven by microbes alone, but also fauna and plants. A large-scale study to identify soil proteins would significantly help to explore the soil ecological processes and understand the environmental factors and the search seems inevitable.

12.5 Characterization of Rhizospheric Proteins/Enzymes

12.5.1 Sample Collection and Storage

For better understanding of rhizospheric proteins collected, sample should synopsize the original nature of the sample. Collection depth should be adjudicated considering the system, as community functioning at different depths can provide differential analyses. Sieving for a more homogenized sample and plant-free matter is preferred, particularly studies focusing on bacterial and fungal lineage. A very pressing and crucial part for ceasing protease and rendering them inactive is to store the sample at −80 °C (Abiraami et al. 2020). Unprejudiced proteome extraction is needed for the appropriate and accurate output of the metaproteome. Extraction processes is hindered by major contaminants and constraints. Soil proteome extraction is demanding owing to its compound ambiguous matrix, which in turn is due to its heterogeneity and hydrophobic nature of colloids. The high microbial diversity to protein abundance hampers protein extraction. Humic substances, phenolic compounds (e.g., lignin), complex carbohydrates, and lipids in compound matrix add further complications. The intracellular nitrogen in cell is only 4% of total organic nitrogen, and in extracellular enzymes/amino acids, this number rises to 30–45% organic nitrogen. These extracellular enzymes get entrapped/adsorbed on the inorganic matrix such as clay or organic humus complex stabilizing them, thus preventing their extraction. All these factors viz. amino acid composition, isoelectric point, polarity, cation exchange capacity (CEC) (Giagnoni et al. 2011), and pH of protein and the charge on clay mineral and soil environmental parameters such as temperature (Keiblinger et al. 2012a, b) play an important role in sorption/desorption of proteins. The organic carbon (OC) and clay contents are also significant factors that strongly influence the extraction and analysis of proteins.

Epidermal keratin contamination is a major concern in protein recovery. However, in low concentration it does not pose any significant problem when compared to protein of interest, but when keratin concentration outweighs that of target proteins, in data-dependent MS analysis technique, the analysis capacity of the LC-MS system is overpowered and skews the peptides of interest estimations, and mostly underestimates it (Giagnoni et al. 2011, 2013).

The usual pipelines for protein extraction processes have four tenets:

(a) Cell lysis to release the proteins and other molecules present within cell.
(b) Protein extraction by mechanical, chemical, or enzymatic methods.
(c) Protein precipitation.
(d) Protein purification and concentration.

Protein extraction can be carried out from soil samples by cell lysis completed through two methods namely boiling and freeze–thaw methods (Ogunseitan 1993). In boiling method, sample is boiled in Tris-HCl (pH 6.8), dithiothreitol, SDS, glycerol, and bromophenol blue, centrifuged, and protein is recovered. While in freeze–thaw method, sample is first incubated for 1 h at 0 °C in a solution containing Tris-HCl (pH 7.6), EDTA, sucrose, dithiothreitol, lysozyme, and polyoxyethylene cetyl ether (Fig. 12.4). The sizes of proteins ranged from less than 14 kDa to greater than 97 kDa as extracted by both methods (Ogunseitan 1993).

Many updates and adjustments have been made to both boiling and freeze–thaw methods. It has been reported for metal-contaminated soil samples, the protein extraction can be carried out either through cell lysis by snap freezing in liquid nitrogen subsequently thawing to 25 °C or by bead beating followed by acetone precipitation to remove any present impurity. It was found that snap freeze–thaw method yielded 5% more protein than the bead beating method. For circumventing the use of protease inhibitor, most of the researchers prefer the protein extraction process at 4 °C, which inactivates the protease enzymes (Singleton et al. 2003).

Method of sequential extraction of soil metaproteome used citrate and SDS buffers, followed by pooling and phenol extraction. The method can detect glomalin-related soil proteins using 1D and 2D protein profiles; however, this approach had low resolution of 2DE separation and protein identification. It was not considered credible for deep proteome studies (Chen et al. 2009). 122 proteins were identified by a modified method of MALDI-TOF/TOF–MS, from a set of 1000 spots on a 2D gel of rice soil samples. A different comparative study has been reported that assesses the suitability of these protocols (Wang et al. 2011). The use of SDS followed by phenol purification resulted in a high number of proteins (454) than SDS without phenol (226 proteins) and NaOH-phenol (293 proteins) purification (Keiblinger et al. 2012a; b). Soils can be grouped into three classes on the basis of organic carbon content and other physical parameters, viz. (1) soil with relatively high OC content (i.e., 3.8%), (2) soil with low OC content (only up to 0.39%), and (3) soil with low OC content yet with high electrical conductivity and salinity. The report concluded that the salinity increased the cell extraction, protein separation,

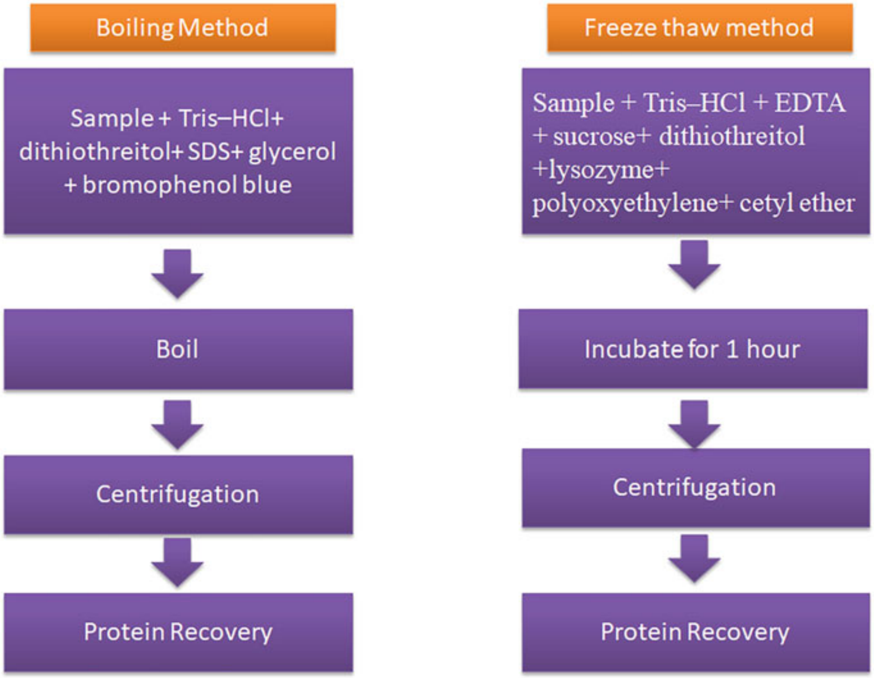

Fig. 12.4 Flowchart of two commonly used protein extraction methods

and identification, whereas the OC content negatively influenced it (Bastida et al. 2012). For the simultaneous extraction of metabolites, proteomes, and lipids from the soil sample, solvent-based protocol called MPLEx is applied. Chloroform, methanol, and water solvent were utilized to separate the sample constituents into simultaneous distinct fractions. Hydrophilic metabolites are in top aqueous phase followed by proteins in the interphase between the organic and aqueous phases and lipids in the bottom chloroform phase. The MPLEx protocol tested in nearly 3376 peptides, 105 lipids, and 102 polar metabolites (Nicora et al. 2018).

12.5.2 Protein Quantification

UV absorbance of aromatic amino acids, ninhydrin method quantifying a-NH_2–N by chromatographic methods (Stevenson and Cheng 1970), Kjeldahl procedure, and colorimetric methods such as the Lowry, Bradford, bicinchoninic acid, and Biuret (Schulten and Schnitzer 1997) assays are several methods used to determine protein concentration. However, these methods do not result in accurate protein concentration in soil due to its heterogeneous matrix and also interference from phenols or humic complexes (Roberts and Jones 2008). Humic substances, due to their aromatic rings structure, can increase UV absorbance, as it binds with CBB dye, leading to false-positive results, and current methods are not capable in distinguishing protein and humus complex (Abiraami et al. 2020).

A more accurate way is by converting proteins to amino acid residues by acid hydrolysis and estimating the concentration of amino acids by gas chromatography (GC) (Bastida et al. 2015). There are drawbacks, however, like time consumption, cost ineffectiveness, and detection of some non-proteinaceous materials like peptidoglycan. Hence, to date, colorimetric method is widely used for metaproteome quantification largely because it is rapid, simple, and inexpensive. Bradford assay is the most popular to quantify proteins due to its speed of reaction, the linearity of standard, and high sensitivity. Although commercial kits are available to quantify proteins, reportedly none of the commercial assay kits provide a reliable indicator of soil solution protein content as most methods detect proteins after conjugation with either chromophores or fluorophores. Hence, there is still much room to develop robust methods for protein quantification in the soil (Roberts and Jones 2008; Bastida et al. 2015).

12.5.3 Protein Purification

In order to obtain good proteome coverage, there is a need to remove humic substances from the soil; humic substance needs to be brought into solution; and desorption of the proteins from humic substances follows for their subsequent removal (Murase et al. 2003). In this respect, the pH of the extraction buffer plays an important role in co-extraction of humic complexes. Extracted extracellular protein is from greenhouse soil using phosphate buffer (pH 6.0), while buffer with higher pH extracted a large amount of non-proteinaceous organic matter along with protein. NaOH and sodium pyrophosphate are reported to extract humic compounds from soil (Simonart et al. 1967; Benndorf et al. 2007; Bastida et al. 2018). They also lyse bacteria and efficient for extraction of proteins. Ultrafiltration with 10 kDa spin filter for the purpose with formic acid for humus removal (Qian and Hettich 2017). Humus solubility is reduced by formic acid; the high molecular weight of humus is not filtered through 10 kDa membrane, while digested peptides can (Hultman et al. 2015).

Commercial kits for the extraction of microbial protein from soils without humic substances are available. However, these kits are expensive and not open to small adjustments required for specific soil types. Phenol is the most effective agent to remove interfering substances (e.g., humic acids), and up to now, the treatment with liquid phenol to soil extracts has been the gold standard. Phenol and water-phase separation extract protein, the organic phase, and humic acid in the water phase (Benndorf et al. 2007; Bastida et al. 2009). Trivalent aluminum ions (Al^{3+}) for coagulation of humic substance can also be followed (Mandalakis et al. 2018; Jin et al. 2018). Before extraction of proteins from soil samples, the addition of PVPP (polyvinylpyrrolidone) reverses the protein–humus complex formation, further to minimize proteolysis liquid nitrogen can be used to grind soil. Simple centrifugation can remove PVPP–humus complex, after the protein extraction (Keiblinger et al. 2012a, b).

12.5.4 Mass Spectrometry of Isolated Protein Samples

Mass spectrometry (MS) is an indispensable technique in chemistry that measures exact molecular weight and identifies certain structural units by reading fragments within the molecule. MS was restricted to determine m/z of macromolecules in the 1980s, since the hard ionization methods caused them to undergo rapid decomposition. However, the development of soft ionization method viz. electrospray ionization, matrix-assisted laser desorption/ionization time-of-flight (MALDI-TOF), and fast atom bombardment has transformed biochemistry.

The characterization of all available proteins at given growth condition is considered as metaproteomics (Pandey and Mann 2000), and for these metaproteomic studies, various analytical techniques are applied. Due to significant advancement in the mass spectrometry (MS) technologies, it primarily applied technique for metaproteomic explorations (White 3rd et al. 2017). Proteins are intricate biomolecules; hence, for accurate structural depiction mass analysis is combined with chromatography and reverse-phase liquid chromatography (LC) is applied with MS-based metaproteomic studies (Aebersold and Goodlett 2001), where electrospray ionization (ESI) is typically most common ionization method for liquid chromatography mass spectrometry (LC-MS). For high-throughput proteomic and metabolomic analysis, the emergence of the high-power mass spectrometry coupled accurately to LC systems has becomes an essential technique to explore the vast identification and characterization of the unique set of proteins expressed by microbial community.

12.5.5 Bioinformatic Analysis of MS-Based Proteome Data

Protein identification is done by the reference-based approach, which involves the fragmentation spectra obtained compared to spectra obtained theoretically after in silico digestion of a protein sequence present in the database (Fig. 12.5). The database search is generally preferred over de novo-based approach as it reduces time, requires lower computation expense, and exhibits higher compatibility with low mass accuracy spectra. MS/MS spectra can be searched against 2 different databases: RefSeq publicly available database and a second-translated metagenomic data plus RefSeq (Delmotte et al. 2009). The public databases widely used for metaproteomic work are UniProt, NCBI RefSeq, Ensemble, and Swissport. UniRef derived from UniProt database is a reference cluster that encompasses non-redundant protein sequence collection increasing the protein detection accuracy

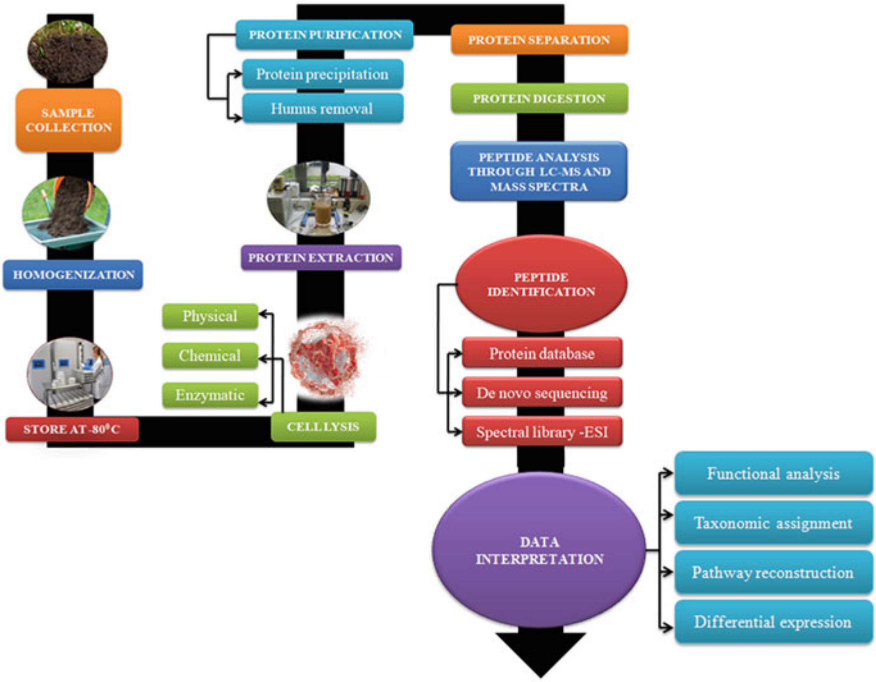

Fig. 12.5 General workflow for metaproteomic analysis from sample collection to data interpretation

(Lü et al. 2014). Software/search engines that use query as the databases available are SEQUEST (Diament and Noble 2011), Mascot (Perkins et al. 1999), Omssa (Geer et al. 2004), X!Tandem (Craig and Beavis 2004), and Andromeda (Cox et al. 2011).

These softwares come in packages combining multiple database search engines, such as Peptide shaker (Vaudel et al. 2015), SearchGUI (Vaudel et al. 2015), iProphet (Shteynberg et al. 2011), and MSblender (Kwon et al. 2011). The result obtained is informative as they combine and display data from individual search engines and also enlist a comparison of the results of individual search engine. MetaGOmics, a free web server, is an algorithm that uses peptide-centric approach with the input of FASTA sequence database and peptide sequence traces single peptide sequence to protein, which, in turn, can be found in many proteins originating from different microbial species. This problem of protein interference is then rectified using direct taxonomic and functional annotation at the peptide level, rather than accessing the protein. The metaproteome data find valuable role in optimizing energy recovery from lignocellulosic biomass, nutrient cycling monitoring, plant–microbe interaction, soil restoration, and bioremediation (Riffle et al. 2018).

12.6 Challenges and Future

With increasing world population, additional food demand is unavoidable. There is an immense challenge for agricultural soil to meet the expectations. In the last decades, the application of high amount of fertilizers and agrochemicals resulted in significant agricultural production, but there is an urgent need to shift toward more sustainable agricultural system, which accounts for exploitation of the endogenous sources of nutrients in soil from both an economic and environmental point of view. The availability of nutrients is a result of chemical, physical, and biological interlinks occurring in the rhizosphere, and the knowledge of these interactions can be accomplished by multi-omic studies specifically metaproteomics, which shall play a crucial role to predict the nutrient cycling in agroecosystems and to set up agronomic strategies, practices, and actions. This comes with the added challenge considering the fact that almost a third of the planet's earth is severely degraded with a serious consequence for the availability of arable fertile soils. In this context, an active rhizosphere management and engineering can achieve manipulating the rhizosphere to regulate and enhance taking up nutrients (or limit the acquisition of toxic elements) by higher plants. Furthermore, the control of the rhizosphere processes might represent an efficient tool to increase both the crop yield and quality in a sustainable agricultural production system. High time to encourage research to consider field conditions as most studies are carried out in controlled small laboratory scale parameters, and these results may not always extend equally to the field.

Multi-omic approach is expected to lead to a greater understanding of rhizosphere organisms and their roles in plant growth, crop production, and ecosystem health. However, novel omic techniques are initially developed for other research fields but can be modified for use in the rhizosphere. Considering the vastness of plant species on Earth, the road to build a more holistic view of the numerous and highly plant-specific rhizospheric communities is an enormous endeavor (Hultman et al. 2015). Techniques and technology undertaken to uncover the rhizospheric protein makeup are vital, as well to assist in answering the most pressing scientific questions. Inadequate knowledge and minimum planning of available technology at disposal more often than not create big problems in hindsight (White et al. 2017).

Metaproteomics has been undisputed in scientific community in recent years, with a promise of tireless identification of the function of each protein in the community and their regulation in expression under diverse environmental stress/conditions. This, however, is still in its pioneer stage as no complete picture of the proteome emerges from present studies. The high cost of metaproteomic analysis is a major constraint for researchers for being able to analyze more than one replicate and take up a comprehensive investigation. This leads to failed outputs, especially as soil exhibits high spatial and temporal variance. Moreover, the amount of soil sample used for extraction is generally very less (1–5 g), which renders researches unaware of a broader picture. More replicates and large samplings need to be followed in the future, assuming when the cost per sample drops for MS analysis as the technology becomes cheaper with more economical extraction kits becoming available. Another challenge is poor protein extraction efficiency, low protein purity due to humic interference, and environmental protein contamination, and results in poor protein yield. The bioinformatic aspect needs to be more user-friendly, easy, assessable, and shareable, and incomplete databases currently available can lead to ambiguous results in protein identification. Nevertheless, metaproteome analysis, along with the validation by complementary approaches such as protein-SIP, shall provide a deeper insight into ecosystem monitoring and functioning. Soil rhizosphere metaproteomics has pioneered a new field in microbial ecology, in which both microbial succession and the activity of specific phylogenetic groups can be studied on the basis of their proteome and contemplate any existing or new challenge with strategy (Abiraami et al. 2020).

Robust reference libraries and spectral databases with a high coverage of rhizosphere-specific compounds and peptides remain one immediate challenge. Without such libraries, our ability to perform and comprehend metaproteomic and metametabolomic studies of the rhizosphere is severely lacking.

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Chapter 13
Impact of Anthropogenic Activities on Soil Patterns and Diversity

Gaurav Kumar, Pooja Baweja, and Pinkey B. Gandhi

Abstract The impact of anthropogenic activities on soil characteristic properties is a great concern worldwide. The human impact is putting pressure on land use due to increasing population and growing food demands. Removal of top fertile layer due to human interventions creates a major threat on soil fertility, crop productivity, green forest cover, environment balance, etc. There is tremendous damage to soil resources in recent years due to change in land use and land cover methods. Due to urbanization and industrialization, there is extensive land covering for making buildings, industrial setups, and construction of roads. The subsequent changes in soil–landscape pattern are altering soil structure and properties. The rate of soil weathering and formation has altered. There is increase in rate of podzolization, laterization, and acidity of soil. In this chapter, an attempt has been made to study the impact of anthropogenic activities on soil ecosystem integrity including global soil pattern, soil profile, and physicochemical and biological parameters.

Keywords Anthropogenic activities · Soil diversity · Soil properties · Soil characterization

13.1 Introduction

Soil is a very valuable natural resource, since it provides food for human beings, feeds for livestock, fuel, and fibers, and also serves as an integral part of biogeochemical cycles (Yaalon 2000). Since the human civilization, soil has given birth

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B. Giri et al. (eds.), *Structure and Functions of Pedosphere*,
https://doi.org/10.1007/978-981-16-8770-9_13

and nourished a range of civilizations, cultures, and livelihoods of many. Soil is closely connected with the civilizations and culture of the ethnic groups and with their health, philosophy, livelihood, and religions (Minami 2009). Soils play a key role to ecosystems and human societies, and their significant importance requires a better understanding of how they evolve over a period of time (Cavicchioli et al. 2019; Zhou et al. 2020). Pedology (soil science) has conventionally been studied as the process of soil development and classification. Soil forms the uppermost/topmost layer of the earth's crust and is studied under diverse research areas covered under environmental sciences, geology, geomorphology, and physical geography.

It is a dynamic system and is considered healthy when there is no degradation of soil, and it can sustain itself, can endure biological productivity, and can maintain its environment (Baweja et al. 2020). Soil is considered healthy on three parameters such as biological parameters, which include microbes and respiration, physical parameters such as water-holding capacity, soil moisture, and soil texture. The chemical parameters include soil pH, salinity, and organic matter (Baweja et al. 2020). Loss of soil is a major environmental concern that results in ecosystem instability, land degradation, and productivity loss, and overall, it affects sustainability and healthy development of human society (Lal 1998; Borrelli et al. 2017). Soil loss has been studied globally, in terms of landforms and landscapes, with a special attention on the causes and influencing factors for the soil loss (Pimentel and Kounang 1998; Jetten et al. 1999; Boix-Fayos et al. 2006; Zhao et al. 2016).

The impact of human interference on different components of the soil ecosystem such as soil profile and microbial diversity is a great concern worldwide. The most substantial process, which influences local, regional, national, and global environment, is urbanization (Schaldach and Alcamo 2007; Napton et al. 2010). The problems related to environment degradation are associated with urbanization and are enormously distinct in metro cities or large cities experiencing intense anthropogenic activities (Radeloff et al. 2005). In recent past, anthropogenic activities in the rural settlement expansion have aggressively intensified. The rural expansion also poses a great threat to the natural ecosystems and resources, and leads to multiple environmental problems (Su et al. 2011). This natural resource is under tremendous pressure due to anthropogenic activities. The loss of soil resources due to human settlement and expansion under urbanization is one of the most prominent issues. The topsoil is being destroyed as land is being utilized for construction activities like housing, roads, or other constructions related to infrastructure developments (Scalenghe and Marsan 2009; Xiao et al. 2016).

13.2 Formation of Soil

Pedogenesis or the process of soil formation takes place through weathering or horizonization. Weathering involves both physical and chemical processes, whereas physical processes include change in temperature and expansion of ice in rock crevices. The chemical processes include oxidation, hydrolysis, carbonation, and soluviation. Some biological processes also contribute toward the soil formation process such as plant root development and excretion of organic acids from the roots (Howard 2017). Horizonization is a hallmark in the formation of soil. There is addition of different horizons or layers in the soil. The horizonization occurs in soils due to addition, losses, translocation, and transformation of different soil constituents. The soil profile consists of different horizons or layers of soil. These horizons have their own characteristic properties and composition. The different horizons are stacked one above the other. The different layers of a soil profile from top to bottom are O, A, E, C, B, and R (Singh et al. 2015). O Horizon is the uppermost layer and is mainly composed of decomposed organic material. Various contributors for organic material are dried and dead leaves, various grasses, twigs, surface organisms, fallen trees, etc. This horizon is generally black brown or dark brown in color as organic content is present in this layer. A horizon/humus layer—It is soft and porous and rich in organic material. Microorganisms such as earthworms, fungi, and bacteria are also present in this layer. This layer can hold enough air and water due to its porous nature. In this layer, seed germination and rooting take place. E horizon has low clay content and is most common in forest and chiefly composed of nutrients leached from O and A horizons. B horizon/subsoil is present above the bedrocks and below topsoil. It is harder and compact in comparison with topsoil. Humus content is less. It is chiefly composed of soluble minerals and organic matter. This layer can hold enough water in comparison with topsoil. It is light brown in color as clay soil is present. C horizon/saprolite is deprived of organic matter and made up of broken bedrock. Cemented geological materials are present. R horizon, the lowermost layer, is a compacted and cemented layer at the base of the soil profile.

Although weathering and horizonization occur naturally, various factors such as climate, geology, landscape, organisms, and time impact them majorly. Some anthropogenic factors also affect soil formation processes. Humans have always interacted with soil, and changes occurring in soil are relatively shorter on a time scale in comparison with destruction occurring due to natural factors, once destroyed soil cannot be renewed on human time scale. It is imperative to understand the disturbances occurring in soil due to agricultural practices, urbanization, industrialization, etc. (Sandor et al. 2005). Although the impact of human activities is increasing on ecosystem, many soils are still retaining their basic structure (Sandor et al. 2005).

13.3 Types of Soil Around the World

The Food and Agriculture Organization (FAO) of the world published "soil map of the world" (SMW) in the year 1974 (FAO 2001). This SMW contained information about soil around the world and consisted of 26 soil groups (first level) and a second-level classification of 106 "soil units" (FAO 2001). In 1990, the classification was revised and the third level of hierarchy was introduced as "Soil Subunits." In 1998, the International Union of Soil Sciences (IUSS) prepared a World Reference Base

(WRB) for Soil Resources (World Reference Base (WRB) 1998). The IUSS classification system was influenced by the classification proposed by FAO-UNESCO. WRB proposed 30 “Soil Reference Groups” in which more than 200 (second-level) soil units have been accommodated. The 30 Reference Soil Groups are aggregated in 10 “sets” (Table 13.1) (World Reference Base 1998).

13.4 Major Classification of Indian Soils

The Indian Council of Agriculture Research (ICAR) has divided Indian soil into 8 major groups (Balasubramanian 2017). The different groups are alluvial soil [43%], red soil [18.5%], black/regur soil [15%], arid/desert soil, laterite soil, saline soil, and peaty/marshy soil (Singh et al. 2015). The details of the soil characteristics are listed in Table 13.2.

13.5 Human Impacts on Soil Characteristics

The two most important processes, weathering and horizonization during soil formation, are impacted by human activities. The human impacts can be both beneficial and detrimental for soil (Bidwell and Hole 1965). There are five soil-forming factors such as parent material, topography, organisms, time, and climate. All these factors are being influenced by humans and are leading to altered soil properties. Soils are getting enriched with excess chemicals being added through agricultural processes, acid rains, surface run-offs, animal manures, etc. Soil erosion has increased due to various construction activities such as highway formation, buildings, mining, industrialization, and land reforms. Water management practices have severely impacted the soil-forming processes. Leaching and weathering of parent material have been accelerated by the use of sprinkler systems in agriculture (Howard 2017). Human activities such as agriculture, construction, excavation, and urbanization have exposed parent material for weathering, adding artifacts, altered soil chemical composition, and organic material. Humans have also modified soil-forming factors through climate change. There is an increase in mean global temperature and altered pattern of rainfall. Parent material is also affected by artificial addition of bone, shells, ash, etc. (Howard 2017). The various changes that occur in soil due to human impacts are as follows.

13.5.1 Accelerated Acidification

Acidification of soils is a natural process, and this process is spread worldwide. It is now accelerated by anthropogenic activities, which are a matter of serious concern.

Table 13.1 Classification of soil as proposed by World Reference Base (Source: World Reference Base (WRB) 1998)

S. no.	Type of soil	Nature	Soil characteristics	Distribution
SET I				
1	Histosols	Composed of primarily organic materials	Organic-rich soils, low bulk density, poorly drained	Amur Oblast, Borneo, Canada, Florida, New Guinea, Khabarovsk Krai, Scandinavia, Sumatra, West Siberian Plain, and some parts of Europe
SET II				
2	Anthrosols	Human activities have resulted in intense alteration of soil's properties	Highly modified soils These types of soils can be formed from any parent soil	Anthrosol types of soils can be found worldwide
SET III				
1	Andosols	Young fertile soils, formed by volcanic deposits Fertile soils, except in areas where soils are rich in phosphorus Contain high amount of allophane, ferrihydrite, and imogolite	Mineral soils, formation was conditioned by parent material	Chile, Colombia, East Africa, Ecuador, Hawaii, Italy, Iceland. Java, Japan, Mexico, Pacific Northwest USA, New Zealand, Rift
2	Arenosols	Sandy, very weak, or no development with coarse texture		Large areas of Africa, Australia (central and western), Middle East, and central China
3.	Vertisols	Dark-colored soil Rich in cracking and swelling clays		Australia, Ethiopia, India, Sudan, Latin America, and USA
SET-IV				
1	Fluvisols	Young soils Present in alluvial deposits Found in river plains, valleys, and tidal marshes	Topography/physiography of the terrain condition of these mineral soils	Amazon Basin, Argentina, Bolivia, Brazil, Central Africa, Ganges Plain of India, Paraguay, etc.
2	Gleysols	Near the surface, such soils have permanent or temporary wetness		Northern Russia, Siberia, Canada, Alaska, China, and Bangladesh
3	Leptosols	Very shallow soils. Present over hard rocks, gravel, or stony material		Particularly widespread in mountain areas, of Asia, northern Canada, Alaska, and South America. Also present in

(continued)

Table 13.1 (continued)

S. no.	Type of soil	Nature	Soil characteristics	Distribution
		Water-holding capacity is very low		Saharan and Arabian deserts
4	Regosols	Soils development is very limited		Mid-western USA, Northern Africa, Australia
SET V				
1	Cambisols	Poorly to moderately developed soils present in agricultural land	Mineral soils. Formation is conditioned by limited age	Found mainly in hilly areas and hilly marginal zones in the world
SET VI				
1	Acrisols	In such soils in subsurface, accumulation of clay is there	Mineral soils. Formation is conditioned by climate Favored in many places as its use for silviculture Has high cation exchange capacity The base saturation capacity is low	It is associated with humid, tropical climates Present in Africa (east and west part), Amazon Basin, Southeast Asia, USA Also found in subtropical and Mediterranean regions: China, Japan, and USA Also present in some part of France, Greece, and Italy
2	Alisols	Rich in exchangeable aluminum Clay content is high		
3	Ferralsols	Strongly weathered soils Physically stable Chemically poor		
4	Lixisols	Low activity clay Base saturation is high in subsoil		
5	Nitisols	Dark red, brown, or yellow-colored clay soils		
6	Plinthosols	Wet soils, irreversible in subsoil hardening mixture of clay, iron, and quartz present		
SET VII				
1	Calcisols	Soils secondary calcium carbonates	Mineral soils, formation is supported by arid and semi-arid climatic regions These soils develop in base-rich weathering material Mostly formed in alluvial, aeolian and, colluvial deposits	Present in plains to hilly land in arid and semi-arid regions
2	Durisols	Soils with cemented secondary silica		
3	Gypsisols	Soils with secondary gypsum		
4	Solonchaks	Strongly saline soils		
5	Solonetz	Soils with subsurface clay accumulation, rich in sodium		

(continued)

Table 13.1 (continued)

S. no.	Type of soil	Nature	Soil characteristics	Distribution
SET VIII				
1	Chernozems	Organic soils Rich in organic matter Dark-colored topsoil Subsoil is calcareous	Mineral soils, formation conditioned by climate It is very fertile and can produce high agricultural yields Present in steppes and steppic regions	Soils are found in the middle latitudes of both hemispheres, in zones commonly termed prairies in North America, pampas in Argentina, and steppes in Asia or in eastern Europe
2	Kastanozems	Dark brown topsoil High in organic matter content Subsoil is calcareous or gypsum-rich		
3	Phaeozems	Organic soil with thick, dark topsoil. Evidence of removal of carbonates present		
SET IX				
1	Albeluvisols	High clay content Irregular upper surface	Mineral soils whose formation is favored by subhumid temperate regions	Majorly in cold continental regions of Northeast Europe, Northwest Asia, and Southwest Canada
2	Luvisols	Soils with high base saturation level High activity clay present in subsoils		
3	Planosols	Topsoil water saturated (temporarily), bleached Subsoil slowly permeable		
4	Podzols	Acidic soils Iron–aluminum–organic compounds present		
5	Umbrisols	Soils having dark topsoil with organic matter		
SET X				
1	Cryosols	Mineral soils formed in permafrost regions	Its frozen soil and water logging present during periods of thaw	Principally found in the wilds of Alaska, Canada, China, Russia, and Arctic and Antarctica regions

Various activities such as fossil fuel burning, agronomic activities, and release of oxides of sulfur and nitrogen (SOx and Nox) are increasing acidification in soils (Pavlů et al. 2021). Soils with low buffering capacity such as soils with less organic matter and coarse texture have low pH. Agronomic activities such as extensive use of ammonium-based fertilizers release acids in soils. Leguminous plants also acidify soils (rhizosphere) through nitrogen fixation. In Australia, it has been observed that

Table 13.2 Major soil types of India

S. no.	Type of soil	Soil characteristics	Distribution
1	Alluvial soil	Formed by the deposition of the river loads It is easily tillable as it is light and porous It is the most fertile soil as it is rich in minerals, especially potash and lime It is suitable for cultivation of large varieties of rabi and kharif crops Alluvials in the drier areas are more alkaline	Northern Indian plains and river valleys
2	Red soil	Highly weathered soil Rich in kaolinite type (clay) Deficient in nitrogen, phosphorus, humus, lime, and free carbonates	Low rainfall area
3	Black/ regur soil	Best soil for cotton cultivation Mature soil with high water-retaining capacity It is rich in calcium, iron, aluminum, potassium, lime, and magnesium Swells and becomes sticky while wet Shrinks when dried	Most of the Deccan Plateau
4	Arid/ desert soil	Deposited chiefly by wind High salt content, less moisture, and humus High content of impure calcium carbonate (kankar). It restricts the infiltration of water	Arid and semi-arid regions
5	Laterite soil	Soft when wet and hard when dried Formed due to high leaching Lime and silica get leached away generally	Present in areas with high temperature and rainfall
6	Saline soil	Excess neutral soluble salts present Soluble salts make the clay fraction to flocculates, thus making the soils structure stable It may contain a considerable amount of sparingly soluble calcium compounds like gypsum	In coastal states of India
7	Peaty/ marshy soil	Vegetation growth less Organic matter/humus abundantly present which makes the soil alkaline and black in color	Parts of India with heavy rainfall and high humidity
8	Mountain soil	The soils are heterogeneous, immature in nature Low humus content, acidic, deficient in lime, potash, and phosphorus	Mountain regions of India

the increase in legume-based pastures and excessive use of nitrogenous fertilizers have increased the soil acidity (Lockwood et al. 2003).

In Europe, fossil fuel emissions have lowered down in comparison with the past, but in Asia, acidifiers have increased due to rapid industrialization (Kopáček and Veselý 2005; Smith et al. 2011). There is also an increase in the release of gases such as oxides of sulfur and nitrogen (SOx and Nox) into the atmosphere, which comes down through acid rain and acidifies the soils (Pavlů et al. 2021). In acidic soils, leaching exceeds the evapotranspiration and bases are lost from soil. Due to acidification, nutrient elements such as calcium and magnesium are lost and accumulation of toxic elements takes place in soil (Pavlů et al. 2021). The acceleration of acidity is more harmful in areas where the soils are already marginalized and any increase in acidity further degrades the soil quality.

13.5.2 Lateritization

The tropical soils are rich in laterite at many places. Laterite is a highly weathered extensive sheet rich in secondary oxides of iron and aluminum. Laterite formation occurs naturally during weathering, but this formation is accelerated due to various human activities. Laterite is getting hardened due to over-exposure to air resulting in its desiccation. Once hard, laterite does not support and favors plant growth, otherwise in normal conditions such soils produce good crops. In India, laterite soils in lower elevated areas are used to grow paddy. At high altitudes, laterites are used to grow tea, coffee, cinchona, and rubber (Singh et al. 2015). Due to human activities such as agricultural practices and cutting of tropical forests, the laterite sheets are being exposed at a greater rate and hardening is there extensively (Goudie 1973; Richter and Babbar 1991).

13.5.3 Salinity

Salinity in soils is measured by the presence of a high amount of soluble salts and is rich in sodium ions ($Na+$) in the soil solution (Qadir et al. 2008). The increase in soil salinity due to anthropogenic activities is going to affect soil structure and composition worldwide. Around 1.5 billion hectares of cultivated land, approximately 77 million hectares of cultivable land, is affected by excess salt concentration (Evelin et al. 2009; Moradi et al. 2011). Areas where evapotranspiration increases the precipitation are rich in saline soils such as arid and semi-arid areas of the world. In these areas, leaching does not take place, and thus, soluble salts remain there in soils, making them more saline. This is a major environmental issue. Salt accumulation takes place naturally by dust storms, rainstorms, weathering of rocks, and solution of bedrocks. Soil salinization is also caused by increased salinity in water resources and irrigation by marine waters in coastal agriculture. Human activities such as irrigation, vegetation clearance, and seawater rise increase secondary salinity (Goudie and Viles 1997; Rena et al. 2021). Soil salinity changes the fertile land into unfertile land and affects the growth and development of the plants and ultimately results in the loss of economy (Grieve et al. 2012). The hydrological and geological environment of an area also affects the soil salinity. Soil salinity when mixed with other minerals such as boron hampers the growth and development of plants (Ibekwe et al. 2010). Saline soils have high content of calcites and calcium salts. Sodic and saline-sodic soils have been reported from approximately 75 countries of the world, which are being used for agricultural practices (Qadir and Schubert 2002; Qadir et al. 2007).

13.5.4 Altered Soil Structure and Texture

Soil structure is defined as the spatial arrangement of individual particles of soil. The biological, chemical, and physical properties of soil depend upon the soil texture and structure. Soil structure is very crucial in determining soil fertility as nutrient availability to roots depends upon the soil structure. Soils rich in clay are more porous with fine-textured particles. Such soils are an important reservoir of plant nutrients, but root penetration is difficult. On the other hand, soils rich in aggregates are well-aerated, and roots can easily penetrate. Such soils have high water-holding capacity and are good for agriculture purposes. The presence of organic matter also modifies the pore size (Wheaton et al. 2008). Anthropogenic activities have already altered the soil characteristics and properties of soil. Urban soils are contaminated with high pH, and compacted soil sealing has occurred. Depositions (man-made and redeposited natural material), either removal or mixing of technogenic and natural substrates, and low aeration are also there in urban soils (Nehls and Wessolek 2011; Matziris et al. 2016; Penižek and Rohošková 2006). The soil profile is also newly created or changed making these soils as unique (Penižek and Rohošková 2006; Matziris et al. 2016). In rural areas, agricultural practices alter the soil structure. The use of heavy machinery, plowing, grazing, and uncontrolled irrigation damages the soil. Such practices compact the soils, changing chemical structure (Horn et al. 2000; Grieve et al. 2001). Soil compaction increases the soil resistance and makes it difficult for roots to penetrate, seedling germination, and exchange of gases (Chancellor 1977). The moisture content also changes, and the surface run-off and soil erosion get accelerated (Chancellor 1977).

13.5.5 Soil Carbon

Agricultural practices such as extensive cropping, deforestation, wetland drainage, biomass burning, climate change, accelerated soil erosion, and carbon leaching change carbon content of soil (Lal 2002). The changed land use and land cover strategies are altering soil carbon content due to decrease in organic matter. The land-use changes and management practices change the fluxes between soil and atmosphere (Bolin and Sukumar 2000). It plays a vital role in carbon dynamics. Land-use changes such as converting a forest land into an agricultural land always lead to loss of soil carbon (Noordwijk et al. 1997; Lal 2001, 2003, 2004). Since 1850, the soil carbon released globally into air amounts to be 156 pg (Houghton 2003; Sharma et al. 2019). When a farmland is converted into a cultivated land, there is 20–0% loss of soil organic carbon (Sombroek et al. 1993; Sharma et al. 2019).

Also, when grassland is converted to cropland, forest is converted to cropland or a plantation land, and grassland is converted to plantation land; there is loss of 59%, 42%, 13%, and 10% soil carbon (Guo and Gifford 2002). Reduction in soil carbon makes soil quality poor and decreases plant productivity (Sharma et al. 2019).

13.5.6 Impact on Soil Microbial Community

Soil microbes are amazingly most abundant and diverse group on land (Locey and Lennon 2016; Cavicchioli et al. 2019; Zhou et al. 2020). Approximately 1 trillion (10^{12}) microbial species are present on the earth (Locey and Lennon 2016; Zhou et al. 2020). It has been estimated that 1 g soil contains roughly one billion (10^9) bacterial cells (Wagg et al. 2014; Zhou et al. 2020). Soil microflora is an integral biological component of the soil ecosystem. These microorganisms play an important role in the maintenance of ecosystem by making soil fertile through decomposition of organic matter and nutrient cycling (Egbe et al. 2021; Yang et al. 2012). The microbial community present in soil is an important factor, which influences plant health. Plant disease resistance relies on the microbes present in rhizosphere (Wu et al. 2020). Absorption of nutrients by plants from soil depends upon the microflora of the soil. Any decrease or increase in this microflora may impact the soil and affects the nutrient absorption by plants (Giller et al. 1998). The irregular and arbitrary use of various inorganic fertilizers and chemical pesticides, and improper disposal of solid waste lead to destruction of physicochemical processes of soil, and also, it degrades the microbial ecosystems. Due to agricultural practices, microbial community structure gets altered, thereby decreasing the soil fertility. Such destructive impact of anthropogenic activities on soil profile and microbial diversity is a great concern worldwide (Cavicchioli et al. 2019; Zhou et al. 2020) (Fig. 13.1).

Pesticides such as insects (insecticides), weeds (herbicides), fungi (fungicides), rodents (rodenticides), and microbes (bactericides) are designed to kill or control pests (Meena et al. 2016). Wide varieties of pesticides, insecticides, and herbicides are being used globally in agricultural fields (Figs. 13.1 and 13.2) in tropical countries where crop loss is brutal due to humidity and high temperature. A report prepared by the World Health Organization (WHO) states that developing countries generally used more pesticides as compared to developed nations. FAO (2021) showed the uses of pesticides, insecticides, and herbicides worldwide and continent-wise over a period of 30 years (Fig. 13.2).

Broad range of pesticides is applied to increase the crop production. Majorly pesticides are used in tropical countries where crop loss is severe as pests multiply rapidly due to environmental conditions such as high temperature and humidity (Jayaraj et al. 2016; Kannan et al. 1993; Lakshmi 1993). A report prepared by the World Health Organization (WHO) states that developing countries generally use 80% of all pesticides production (Veil 1990). Many pesticides have been found to be harmful not only to soil environment but also to human health (Arcury and Quandt 2006; Lecours et al. 2012).

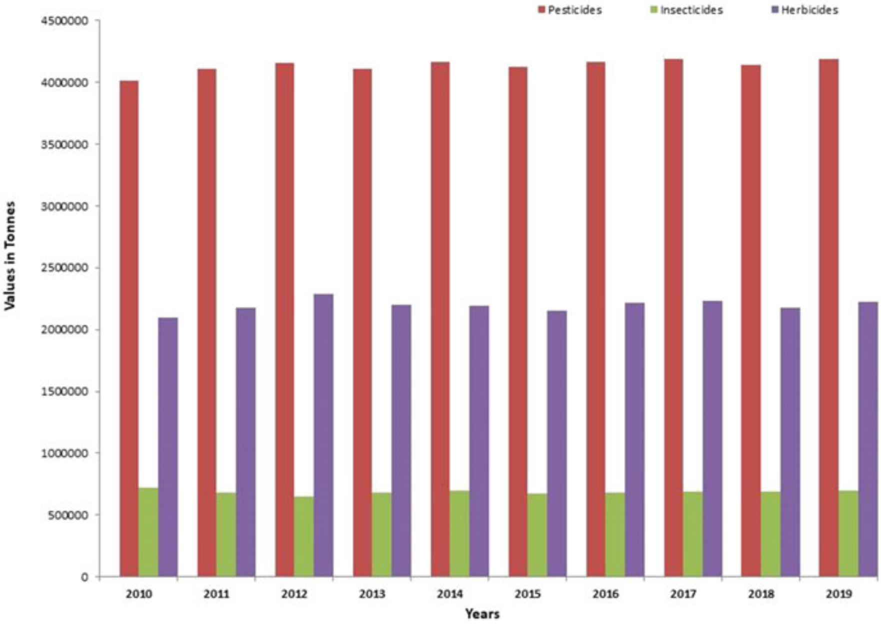

Fig. 13.1 Worldwide use of different types of pesticides over a period of 10 years (Data Source: FAO 2021)

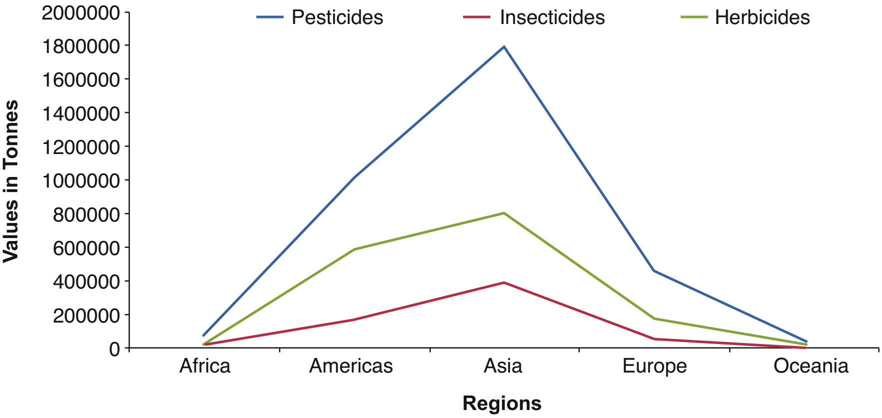

Fig. 13.2 Pesticides, insecticides, and herbicides used in different regions of world over a period of 30 years (Data Source: FAO 2021)

After World War II, DDT gained the popularity to be used as a pesticide. Earlier, nicotine (found in tobacco) was being used as pest control agent in agriculture fields (Wells 2018). DDT was identified as a pest control agent during World War II, and before being used as a pesticide in agriculture fields, it was used as a chemical to kill malaria mosquitos. Gradually, it was used as a pest control agent in agriculture for killing insects, rodents, and weeds (Meena et al. 2020). Later, it was identified that the random and irrational use of pesticides not only kills pests but also degrades soil microbial flora. It has been observed that more than 98% of insecticides and 95% of herbicides sprayed in agricultural fields reach nontarget soil microflora and destroy them (Miller 2004; Wang et al. 2006). Soil microorganisms are tremendously significant for the maintenance of soil structure, fertility, and functions (Bano and Iqbal 2016; Meena et al. 2020).

Semi-synthetic pesticides (organochlorines, OC) are also widely used in agricultural fields (Gupta 2004; FAO 2005; Jayaraj et al. 2016). The organochlorines are volatile in nature and belong to the class of persistent organic pollutants (POPs). The organochlorines are highly persistent in the environment (Jayaraj et al. 2016). The long-term application of persistent organochlorines pesticides (OCPs) is the main cause of soil pollution (Shahid et al. 2021). Singh and Singh (2019) reported that the increasing concentration of OCPs like lindane decreases soil beneficiary microbe *Microbacterium* sp. by decreasing the growth-related substances in soil. It has also been observed that other organophosphate pesticides such as acephate, glyphosate, monocrotophos, and phorate have severe impact on soil microbes by affecting their growth, physiology, and siderophore production ability (Kumar et al. 2019). Egbe et al. (2021) studied that in organochlorine pesticide-impacted soils, approximately 61,005 (bacteria) and 33,397 (fungi) species were missing, but these species were present in virgin soils. They thus concluded that those species can act as bio-indicators for ecotoxicity of OCPs in agricultural soils.

The application of herbicides to the soil is toxic for the microbial community, which in turn resulted in reduced microbial biomass (Rose et al. 2016). In field conditions, herbicides like sodium chlorate ($NaClO_3$) and sodium arsenate (Na_3AsO_3) also greatly influence soil microbial populations indirectly by their effects on vegetation, which provide habitat and food for many of them. Herbicides are not considered eco-friendly even if they can decay in a period of few months as they affect soil environment (Jayaraj et al. 2016). In comparison with manual weeding, it has been observed that spraying herbicides can cause more pathogenic attacks and diseases in plants. The major reason behind the adverse impact of herbicides is the process of their manufacturing. The uncontrolled and irregular use of chemicals leads to the destruction of the soil microbial ecosystem (Rose et al. 2016; Jayaraj et al. 2016).

Inorganic nitrogen fertilizers also lead to acidification of soil and contaminate them. This agrochemical pollution results in decline of soil organic matter (Sun et al. 2015; Wang et al. 2020). The soil contamination majorly impacts soil health and soil ecosystem, and finally, the primary productivity also gets decreased. Constant use of chemical fertilizer can alter the pH of soil and increase pests, acidification, and soil crust, which result in decreasing organic content and microbial community (Sun et al. 2015; Pahalvi et al. 2021). Application of chemical-based fertilizers decreases the soil microbial biomass at $pH < 5$ (Geisseler and Scow 2014). Using 16S rRNA gene amplicon sequencing and predictive metagenomics, the negative effect of application of inorganic fertilizers on rhizobacterial diversity has been well documented (Reid et al. 2021).

The industrial waste effluents have long-term effect on soil pollution, and they decrease the activity and diversity of soil bacteria (McGrath et al. 2001; Lasat 2002; Pečiulytė and Dirginčiutė-Volodkienė 2009; Subrahmanyam et al. 2016). Inorganic residues in industrial waste can cause serious problems related to their disposal (Wang et al. 2007). The improper chemical waste disposal from various industries causes soil contamination. As industrial effluents are rich in chemical substances, mostly acids or are toxic in nature, they directly affect the microbial ecosystem present in soil. The disposal of industrial waste, toxic chemicals, other effluents, oil, and fuel without any treatment before the release from industries leads to soil pollution (Subrahmanyam et al. 2016). Lack of awareness and management practices toward proper industrial waste disposal and regular unplanned constructions are causing excessive damage. These industrial effluents are posing threat to microbial ecosystems (Wang et al. 2007; Subrahmanyam et al. 2016).

Solid wastes such as disposal of cans, heavy metals, paper, and plastics are soil pollutants. Once mixed with soil, they change the composition of soil microbial communities (Xie et al. 2016). Improper disposal of electrical goods such as mobiles, televisions, air conditioners, and batteries disrupts soil health. These electronic gadgets contain harmful chemical substances like lead, lithium, and acids present in batteries. The presence of metals and heavy metals has adverse effect on microbial community resulting in decreased rate of organic matter decomposition, reduced soil respiration as the structure of soil also gets altered, and altered enzymatic activities (Tyler 1974; Xie et al. 2016). Heavy metals change the growth pattern and metabolic rate and also affect the morphology of soil microorganisms. Due to functional disturbance, the proteins in cell membrane get denatured, and thus, the integrity of membranes is lost (Leita et al. 1995). Leaking sewerage effluents also affect soil quality and characteristics. The sewage effluents cause soil pollution, change the chemical composition, and destroy beneficial soil microorganisms.

13.6 Conclusions and Future Recommendations

Soil is a valuable natural resource, which is an integral part of biogeochemical cycle and is under tremendous pressure. Agricultural practices, overuse of chemical fertilizers and pesticides, and changed land-use and land cover practices have resulted in the depletion of soil health and environment. Thus, there is a need to conserve soil resources. Some of the management practices, which can be adopted to assure soil conservation, are reforestation, crop management or crop rotation, prevention of erosion, and preservation of soil moisture. Reduction in the use of fertilizers and pesticides and promotion of organic fertilizers are also important measures, which need to be followed. Farmers must be trained with advanced and eco-friendly techniques to be used in agricultural practices. Since soil is a nonrenewable source at human time scale, there is a need to have sustainable approach for the maintenance of ecosystem.

Acknowledgments The authors are thankful to Principal, PGDAV College and Maitreyi College, University of Delhi, to provide all the necessary facilities to compile this manuscript.

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Chapter 14
Role of Soil Microbes to Assess Soil Health

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Abstract Maintaining healthy soils are necessary for developing healthy ecosystems and sustainable agricultural production. It is widely accepted that soil health is a very important management tool to correct unproductive and illness of soil. There is still a lack of clarity about how to measure soil health or what indicators should be taking care of for a satisfying conclusion, considering soil health is not wholly output of soil physical and chemical properties but includes soil biological characteristics. Biological activities mostly occurred in topsoil range up to 30–45 cm soil depth, where most of the soil microbes are living, comprising a tiny portion of about 0.5% of total soil volume and nearly 10% of total soil organic matter. Despite their small population, microbes play a vital role in organic matter decomposition and nitrogen-phosphorus-sulfur cycling. This way soil microbes transformed organic residues into readily available nutrients to plants. They also lead to the degradation/decomposition process of waste materials and some synthetic compounds. Soil microbes produce polysaccharides, which act as soil cementing agent and help in maintaining soil structure, improving aeration and water holding capacity, reducing soil crusting and compaction. Soil microbe shows the capability to assess the integrated measure of soil health, which cannot be achieved through chemical or physical assessment. They respond very quickly to surrounding environmental changes as well as

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B. Giri et al. (eds.), *Structure and Functions of Pedosphere*,
https://doi.org/10.1007/978-981-16-8770-9_14

environmental stress conditions. Thus, soil microbes can be an outstanding indicator of soil health. Therefore, there is a need to study on identification, dynamics, and efficiency of soil microbes capable to indicate soil nutrient status or stress conditions, for early signs of soil health improvement or alert to soil degradation. This chapter extensively focuses on the role of soil microbes to indicate soil health status.

Keywords Soil microbe · Soil health · Microbial activity · Microbial indicator · Organic matter · Nitrogen cycling

14.1 Introduction

Strengthening agriculture is one of the major goals for mankind, as agriculture comprises much more land use than any other sector. Improper management of agriculture results in reduction of biodiversity, loss of nutrients into water bodies, accumulation of harmful chemicals, and heavy metals in groundwater and leads to volatilization of nitrogen. These hazardous impacts are accelerated by industrial development, growing infrastructure, and waste dumping. Maintaining soil health is necessary for the development of global land ecosystems to stay sustained or to get well from natural or man-made disturbances, such as flood, drought, pollution, and other human exploitations including conventional agriculture (Keesstra et al. 2016; Kumawat et al. 2017, 2019). Therefore, soil protection should be under concern and proper studying of ecosystem processes is a vital issue to confirm that our soil is healthy. Biodiversity is described as the variations present among the organisms that include intra and interspecies diversity within an ecosystem. An ecosystem can be defined as a lively complex system of flora and fauna including microbial population and their surrounding environment acts as a functional agent. The requirement of an organized move toward soil protection is mandatory for the development of a healthy ecosystem in any part of the globe. To intent our soil healthy, special importance should be given to the improvement of soil biological characteristics along with chemical or physical properties (Abbott and Murphy 2003; Kumar et al. 2021). Soil living microbes indicate ecological impacts in soil. A range of programs related to the protection of nature are adopted in many countries, such as the soil health scheme in India launched in 2015 found to be effective among farming communities (Reddy 2018). Soil monitoring is largely neglected but since soil influences all lives in the terrestrial ecosystems. Thus with no soil monitoring, terrestrial monitoring cannot be complete.

14.2 Soil Health

It must be broad enough to define soil health, as it encompasses the many functions of soil, such as natural filter, plant growth material, and water movement (Brevik 2010). Air or water quality can be found defined well since a long time ago, but the definition of soil health was unclear in those times (Rahangdale et al. 2021; Sojka and Upchurch 1999). Air or water quality is mainly based on the permissible concentration of unsafe materials to human health. To define soil health based on this would cover only a little portion of the several roles played by soil. The healthiness of soil is the final output of continuous protection and deprivation processes, highly based on the soil biological components and influences on flora health, ecological health, and food safety (Howard 2020). Soil quality defined the condition of soil as associated with agricultural productivity (Kumawat et al. 2014; Bongiorno et al. 2019). Earlier, it was suggested that soil quality was not only restricted to soil productivity but also extended to cover relations with the adjoining ecosystem, along with human and animal health. In the first half of 1990s, the terms "soil health" and "soil quality" were first used in a program to assess and monitor soil conditions in Canada to explain the capability of the soil to bear crop growth without becoming degrading or harming the surrounding environment (Acton and Gregorich 1995). When we talk about soil health, it should also focus on the soil ecological characteristics, beyond its ability to just produce crops (Bonfante et al. 2020; Lehmann et al. 2020). These characteristics are primarily related to ecosystems and food chain. So it is the continuous capacity of soil to act as a crucial live ecosystem, to maintain biological activities, improve air and water qualities, and sustain the health of all organisms including human. Therefore, soil health is the continuous capability of a soil to maintain the growth of plants and retain its functions despite any certain changes.

14.3 Components of Soil

Our soil is mostly comprised of solid stage that bears particles of various sizes covered by water and gas molecules. The quantity and contents of these particles, water, and air in soil significantly vary with time and location. Normally water is discontinuous in nature, except during the saturated phase. Those soil pores that remained unfilled by water are filled by air (Stotzky 1997). In the soil system, there is frequent exchange of molecules among solid, liquid, and gas states those are occurred by several chemical, physical, and biological processes. These processes show an exceptional equilibrium among physical, chemical as well as biological factors (Rathfelder et al. 2000). Sustaining this equilibrium is of immense importance to soil health.

14.4 Role of Microbes in the Soil

Soil biological activities are mainly preformed in the top portion of the soil, up to a depth of 25–30 cm. In this top portion, biological fraction comprises a small part (<1%) of the total volume of soil, which is lesser than 1/tenth of the total soil organic matter (Kumar et al. 2013a, b, 2017; Gunina et al. 2017). This biological fraction mainly comprises soil living organisms primarily microbes. Regardless of their tiny population presence in total soil volume, microbes play a key role in nitrogen, phosphorus, and sulfur cycling as well as organic matter decomposition. These way microbes affect largely global nutrient and carbon cycling. The energy input required for flora is resulting from the microbial decomposition of organic matter. This way, organic matters are transformed into biomass, mineral nutrients, and atmospheric CO_2, H_2O (Powlson et al. 2011). Immobilizations of mineral nutrients in biomass are afterward released when microbes are preyed by protozoa, nematodes, or other microbes. Microbes are also related to the conversion and deprivation of organic wastes as well as artificial organic residues (Kumawat et al. 2018; Soobhany 2019). Apart from these activities, microbes also influence the physical breakdown of soil. Microbial population forms lots of polysaccharides, which act like cementing agents and help to maintain soil structure by stabilizing soil aggregates. Microbes affect water infiltration, water retention capability, soil compactability, crusting, and erodibility.

14.5 Microbes as Soil Health Parameters

Microbes can provide an integrated estimation of soil health, which cannot be achieved through physicochemical estimation. Microbes react very fast to environmental changes and they quickly adjust to new surroundings. The best-suited microbes will be the ones that thrive well and are dominant in a new environment. This adaptability brings microbial analyses to be perceptive in soil health evaluation and their changes and actions may take as an outstanding sign of change in soil health (Schloter et al. 2018; Fierer et al. 2021). They also react rapidly to environmental stress than higher organisms, due to their high surface area to volume in soil. The change in microbial population or actions can lead to measurable changes in soil characteristics, thereby provides an indicators of soil improvement or a sign of soil degradation (Fierer et al. 2021). The conversion period of the microbial biomass is quite less than the conversion period of total soil organic matter. Most of the microbial indicators have perceptive power relation to various soil conditions (Bhanwariya et al. 2013; Azarbad et al. 2013). It was reported that microbial biomass present in the soil is directly related to soil respiration (Rinku et al. 2014; Zhang et al. 2020). Biodegradation of toxic chemicals, heavy metals, and pesticides is under concern, which is directly linked with soil health. Effects of these toxic chemicals on soil health are greatly influenced by microbial actions. Though the heavy metal presence in the soil will not decrease over a short duration, but their biodegradation may. Biodegradation of polyhydrocarbons may be influenced by seasons because of more microbial activities that occur in some seasons (Isobe et al. 2018). So, the total amount of toxic chemicals in soil is definitely cannot be the proper indicator of its biodegradation as well as soil health. As a replacement for this, biodegradation has to be estimated in relation to precise microbial processes. In addition to this, microbes also react to integrate the effect of different chemical components mixture (Kumar et al. 2014; Tian et al. 2017), which cannot get by analyzing the chemical mixtures themselves.

Microbial indicator can be described as a parameter that indicates characteristics of the environmental factors or impacts, which may be out of the information obtained by experiential parameters (Schloter et al. 2018). Soil health indicators have been defined as assessable estimators for environmental processes those together suggested that whether the soil is performing normally. Microbial indicators can cover the estimation of various soil microbial processes (Moghimian et al. 2017) and other associated parameters.

14.6 Microbial Parameters of Soil Health

Microbial populations have multifunctional characteristics in the soil system; therefore, microbial indicators of soil health cover a range of microbial estimations. In this chapter, among the various microbes, the emphasis has been given on bacteria, fungi, and protozoa indicators. They can be categorized based on several soil health parameters, which may include biodiversity, carbon and nutrients cycling, biomass regulation, microbial actions, species of importance, and biodegradation. The indicators associated with the environmental processes, variations, and their population act together to obtain the endpoint. Some of these microbial indicators are ready to use for soil health determination. Only a few microbial indicators will be applied in a soil health analysis and choosing the right indicator is essential. In this chapter, each indicator is discussed relative to soil health and fitness for estimation. Microbial indicators for soil health are shown in Fig. 14.1.

14.6.1 Biodiversity Parameters

Knowledge regarding the microbial population structure and variety can be significant for studying the correlation among soil ecological parameters. Therefore, diversity of microbe's estimation has been suggested in soil health determination (Arias et al. 2005). The variety of a population is described as the richness of species and the role of each species making the total organism's population present in that soil system. Earlier, the diversity of a microbe's population was defined by Shannon-Weaver index. Traditionally, the species number has been recorded by taxonomic classifications, currently, molecular and biochemical methods are used as taxonomic classifications are inefficient. The advantage of a rich genetic diversity is a matter of discussion, as it is not all times associated with microbial functional diversity. In addition, the relationship between soil health and microbial diversity is not yet fully defined, even though it is considered that a rich microbial diversity is normally to point to a status of good soil health (Chaparro et al. 2012).

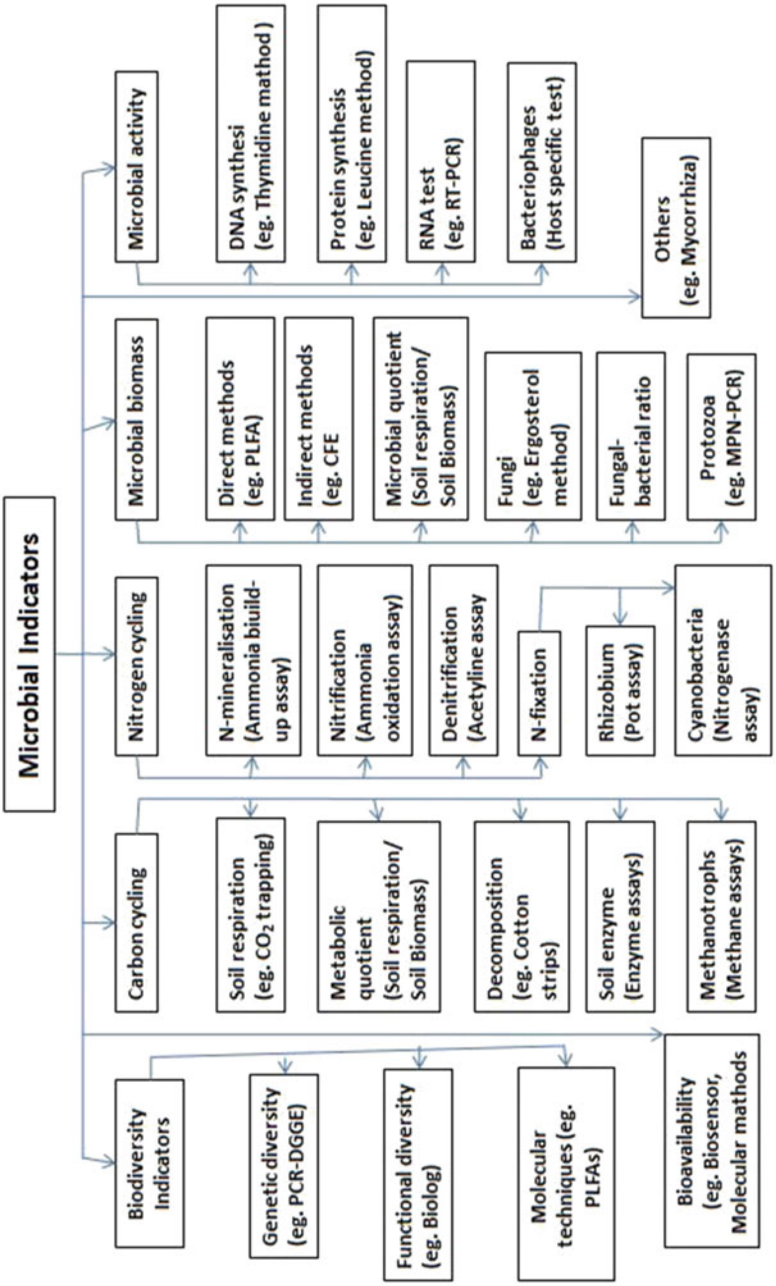

Fig. 14.1 Microbial indicators for soil health

14.6.1.1 Microbial Genetic Diversity

Environment is full of genetic resources, which can be the foundation of all genuine and possible functions related to soil health. The genetic variety of soil microbes is a sign of the availability of genetic resources. Estimation of microbial genetic diversity consists of various molecular techniques; out of those only a few so far were introduced into soil health evolution.

14.6.1.1.1 Bacterial Diversity

Bacterial genetic diversity is normally determined by variety of the 16S rDNA genes. These genes are present in all bacteria and show differences in principle compositions between the species. Therefore, these genes are widely used in phylogenetic affiliation of bacteria and huge databases are present related to rDNA (e.g., www.ncbi.nlm.nih.gov). It comprises of variables and offers the primer's design in the specific regions for attempting most of the distinct population of bacteria. In general, there are two techniques that have been used to inspect the variety of rDNA and its sequences in total DNA obtained from the microbial population, named as (a) PCR-DGGE (Denaturing gradient gel electrophoresis) and (b) T-RFLP (Terminal restriction fragment-length polymorphism). Both are mainly dependent on the difference in principal composition and the rDNA molecules structure. By using PCR with primers mainly focusing on all eucaryotes subgroups, a rDNA fragment structure of known dimension can be enlarged. Afterward, the compositions are separated through gel electrophoresis techniques. Through PCR-DGGE, the gel itself consists of a denaturing gradient which makes the rDNA structure denature and follows the gradient based on their principle composition. Through this PCR-DGGE technique, a heat gradient is formed across the gel, which causes a similar type of denaturation. The location and number of fragments structure indicate the lead bacteria in the population. PCR-DGGE and T-RFLP, both the techniques have low observability (resolution) of gel electrophoresis in case of a rich variety of bacterial populations can be a trouble. Soil microbial communities have hundreds of different bacterial strains, though it is difficult for resolution of larger than 50 bands on a gel (Johnsen et al. 2001). Depending on various practical conditions, are solution able bands on the gel, a specific bacterial species could have to comprise less than 1% of the total population (Casamayor et al. 2000). Identifying and sequencing the resolution able bands on the gel through both PCR-DGGE and T-RFLP techniques might be improved. T-RFLP is another process for exploring variety of rDNA microbe's populations. This method also depends on PCR magnification of 16S rDNA with particular primers. The specific primers are tagged at the terminus, which gives labeled PCR-based products. These PCR products are slice with various control enzymes at different times, this form labeled fragment structures that can be removed based on their size on gels. Control enzyme fragments structure having both of the terminus endpoints of the PCR-based product will be detected, if the PCR-based products are labeled at the terminal ends. The digested output of PCR-based products is loaded in a sequencing system that contains fragment structure size and amount. T-T-RLFP technique is used to study soil bacterial population in agricultural land (Buckley and Schmidt 2001). This method offers to compare among the various soils tested in different laboratories, though it needs advanced and costly equipments along with purified DNA.

14.6.1.1.2 Fungal Diversity

The traditional technique for determining the fungal variety in soil has mainly been based on number and fungus morphology. Most of the funguses in soil are living either found as dormant spores or mycelium. These spores, as well as mycelium, can be able to isolate from the soil, but without the fruiting stage, it is hard to identify the fungus. Moreover, the isolation and identification methods may be specific for selective fungal communities. Some molecular techniques principally based on 18S rDNA offer apparatus which can beat these issues. However, one of the key limitations is the restricted availability of fungal nucleic acid sequences in databases (Bridge and Spooner 2001). Fungal genetic diversity estimation among the soil fungal population could also be determined through PCR-DGGE as well as PCR-TGGE. Both techniques discussed briefly described above relative to bacteria.

14.6.1.1.3 Protozoan Diversity

Protozoans are known as lone cell eucaryotic organisms and representative of higher organisms over prokaryotes (Cavalier-Smith 2002). They mainly consist of exposed amoebae, cilia, and flagella. These groups of soil organisms have rich availability in soil and present in various environments. Protozoa are significant for soil health and fertility studies, as they respond fast to surrounding ecological changes and slow to move in the soil environment. They are considered as a vital fraction of any soil ecological system and regarded as an important alarming indicator (Johns 2017). In heavy metal contaminated soil, amended with sewage and sludge, protozoan bioassays are used as an indicator (Gilron and Lynn 2018). Normally, estimation of the variety of protozoa is done by taxonomic association to species or communities that depend on morphological characteristics. This process is very much labor and time-consuming, also needs experts. On the other hand, the protozoan variety can be estimated by several molecular methods. The variety of protozoa can be studied by PCR-DGGE focusing an 18S rDNA fragment structure. The PCR-DGGE technique is discussed above in relation to the genetic diversity of bacterial A technique of PCR-DGGE developed for Kinetoplastida protozoa was detected comparatively rich diversity of these organisms in sediments of freshwater bodies (Kostygov et al. 2021).

14.6.1.2 Microbial Functional Diversity

The microbial community often shows functional diversity within its population, which is important to regulate several functions of soil. Microbial functional diversity has been reported to be very sensitive to soil ecological changes (Zhou et al. 2020). However, the techniques used largely point to the potentiality of in vitro function. Microbial functional variety in soil ecosystem may be evaluated by enzyme expressions or nucleic acids diversity within the cells. Nucleic acids diversity (rRNA, mRNA, etc.) also suggests the particular enzymatic activity occurring in the cells. Microbial functional diversity indicators also indicate the microbial actions; therefore, this incorporates diversity and function.

14.6.1.2.1 Carbon Utilization Patterns

The utilization of carbon patterns can be estimated by Biolog assay (Khalil and Alsanius 2009; Rutgers et al. 2016). In Biolog assay, a soil sample extract is kept under incubation in a microplate with a system having hundreds of carbon sources and a redox-dye is present to point out microbial actions. Particular sets of carbon sources are used exclusively for the study of a particular soil microbial population. The outcome of the Biolog assay is a qualitative as well as a physiological result of the functions inside the microbial population. Diversity in the result can be determined by various statistical analyses. This assay is based on cell growth under the particular situation in the microplate and therefore reflecting only potential functional variation. Though, the method has been used largely, mainly because of the ease of handling and the capability to create inclusive data sets. The row data are processed by various statistical tools and understanding with data analysis is still undergoing (Khalil and Alsanius 2009). This assay is more responsive to microbial biomass as well as CO_2 emission estimations with respect to soil management measures (Nair and Ngouajio 2012). Biolog assay is suggested for soil analysis in some European countries including Netherland (Rutgers et al. 2016). Necessary precaution should be taken while using any assay, as it may be unavailable in the market or content may change in the future.

14.6.1.2.2 Enzyme Pattern

The microbial population mainly regulates enzymatic activities in soil, which may be produced by microbial cell or associated with free enzymes. Several enzymatic activities are going on soil system, but only actions of ectoenzymes and free enzymes are mainly taken under consideration for enzyme patterns diversity in the soil sample. Differences between cell-associated and free enzyme activities can be collected through filtration to extract microbial cells from the soil sample. The activities of enzymes are measured by incubation studies of the soil sample with either commercially used enzyme products or colorimetric products (Kumar et al. 2013a, b) for a specific purpose. Raw data obtained from the analysis are usually processed by various statistical procedures. In short incubation periods, the growth of cells and new enzyme formations are prohibited. It is suggested that various sets of enzyme activities are estimated, as limited dominating microbes reflecting high enzyme activities may result an unfair output. Biolog assay analysis may result in similar diversity patterns during testing of different types of soil, as this assay is related to in situ functions, though a lesser number of functions are generally estimated.

14.6.1.2.3 Diversity of mRNA

Cells are used mRNA molecules, which are copies of genes to release particular proteins. The nucleotide sequences present in mRNA act as a sign of the type of enzyme produced. Protein synthesis rate is correlated with mRNA concentration and is heavily influenced by microbial activities. So, the amount and variation of mRNA will result in a very precise idea of the actions of the microbial population. Identification and amount estimation of a particular mRNA can get by reverse transcription PCR (RT-PCR). Though, the technique of mRNA quantity measurement is still studies for improvement.

14.6.1.3 Structural Diversity

Phospholipid fatty acids (PLFAs) are stable polar components in cell walls found in particular subgroups of microbes, such as gram-positive or gram-negative bacteria, fungi, and actinomycetes (Quideau et al. 2016). So, specific PLFAs can be linked to particular microbial population. This technique helps compare the microbial communities present in the soil. PLFAs are extracted from soil and then determined by gas chromatography analysis (Thornton et al. 2011). Particular PLFAs are then recognized and its amount estimated followed by assessment of output by statistical analysis. This estimation also offers reproducible information profiles of soil for categorizing the dominant soil microbes without growing them in the laboratory. PLFAs analysis determines both microbial population composition as well as their biomass quantity, though the process is sensitive, time-taking, and needs skilled labor (Li et al. 2020). This analysis has been used commonly in soil pollution studies (Yao et al. 2015) and shows more accuracy than Biolog estimation for categorizing soil microbial populations.

14.6.1.3.1 Oligotrophic and Copiotrophic Bacteria

Oligotrophic bacteria are those that have less nutrient requirement and copiotrophic bacteria have a higher nutrient requirement. The ratio of these two types of bacteria showed the nutrient stress tolerance of the microbial species resides in soil. A higher ratio or oligotrophs domination may reflect a stable ecological environment with low substrate available. On the other hand, low ratio or copiotroph domination may point out that a soil system often receiving adequate organic matter. The ratio of oligotrophs to copiotrophs can be estimated through colony development on agar media (Lankiewicz et al. 2016). Developed colonies on agar media may be estimated by simply counting colony formation at particular time periods. These counts are supplemented by mean lag-stages and total numbers of bacterial subcommunities. Early development of colonies reflects the domination of copiotrophic bacteria, whereas late appearance signifies the presence of oligotrophic bacteria. The rRNA gene expression can be studied during the growth period in bacterial microcolonies by taking the dimension of the 16S rRNA rate by in situ hybridization. If the rRNA expression is lower during the growth period, this may signify oligotrophic bacterial dominance. The counting technique is very simple, easy to operate, and inexpensive.

14.6.2 Carbon Cycling Indicators

One of the main activities of the soil microbial population is to decompose the organic matter. Most of the soil microbes are heterotrophic in nature and depend on carbon sources outside from their population. Organic residue present in the soil is mainly coming from higher plants, which contain cellulose, hemicellulose, and lignin. Carbon cycling indicators suggest estimations at the ecosystem level.

14.6.2.1 Soil Respiration

The biological oxidation process of conversion of organic residues to CO_2 in soil by the activities of aerobic microbes is known as soil respiration, which plays a vital role in global carbon (C) cycle. This process releases photosynthetically fixed C in soil into the atmosphere. The metabolic activities of the microbial population living in soil can be determined by studying CO_2 production status of that soil. Although, it is an old method, but still regarded as most often used method for the determination of microorganism activities in soil and has always a positive correlation with organic matter as well as microbial biomass content in soil (Chen et al. 2019). Therefore, the majority of soil monitoring programs have soil respiration estimation. The respiration status of soil can be estimated by checking either CO_2 release or O_2 consumption status. Estimation of CO_2 concentration is more effective, as the atmospheric CO_2 concentration (0.033%) is very low compared to atmospheric O_2 concentration (20.9%). Estimation of CO_2 release from soil can be done by alkaline trapping method using simple tools. In this method, trapped CO_2 in NaOH solution is titrated against base solution or checks electrical conductivity by an electrical conductivity meter. The rate of respiration is greatly influenced by soil temperature, moisture, and nutrients status (Li et al. 2017). To make the estimation more precise and minimize errors, soil samples and chemical solutions must be standardized. Soil respiration measurements in field conditions are generally avoided due to high chances of environmental influence. Soil respiration also indicates heavy metal and pesticide toxicity (Xu et al. 2018).

14.6.2.2 Metabolic Quotient

The metabolic quotient (qCO_2) is calculated as the ratio of microbial respiration rate and total microbial biomass content in soil (Fernandes et al. 2005). Determination of microbial biomass is generally done by fumigating the soil sample followed by carbon extraction and estimation, while respiration rate is determined by trapping CO_2 in alkali solution (as mentioned in 2.1 soil respiration). The qCO_2 is an excellent indicator for soil health determination. Generally, qCO_2 has been found to decrease over time, as the organic matter gets utilized by microbes and is reduced over time. Metabolic quotient has been also largely used in the study of environmental factors including atmospheric temperature, soil pH, moisture, nutrient availability, and heavy metal status (Li et al. 2017). Normally, the maximum qCO_2 in the soil is obtained when the ecosystem stress level is very high. Interpretation of qCO_2 should be done carefully, as a high value may be due to heavy stress, a young ecosystem or a presence of respirable substrate in soil.

14.6.2.3 Decomposition

A change in microbial activities will ultimately change the decomposition rate of OM and therefore changes the availability and cycling of the vital organic matter bound plant nutrients N, S, and P. Understanding the decomposition status of OM is thus required to know the availability and recycling of plant nutrients. In situ incubation studies of various types of plant residues (litter bags) or more precise ways such as cotton strips or wood sticks are often used techniques to estimate OM decomposition status.

14.6.2.3.1 Litter Bags

The rate of litter decomposition can be determined by keeping the litter bags in the soil. The material used to manufacture litter bags is nylon and having mesh size provides free movements of gas, water, substances, and microorganisms. Specific mesh size gives an idea about the types of soil living organisms responsible for the decomposition inside the litterbag. The rate of decomposition is estimated by weight loss per unit time (Tuomi et al. 2009). The positive side of using this method for the determination of decomposition rate is that it is directly correlated with the natural decomposition process. On the other hand, the main drawback of this method is to get uniform plant litter in every season or year.

14.6.2.3.2 Cotton Strips and Wood Sticks

Another easy and effective method to determine decomposition rate is to use cotton strips (Tiegs et al. 2007) and wood sticks (Abril et al. 2015) in soil. The method of determination is similar to that of "litter bags" as discussed previously. Cotton strips gets decomposed and reduces lengths with periods, thus the weight of strips also gets loss which is measured with intervals loss (Tiegs et al. 2007). This method is more standardized over "litter bags" and also gives more precise results. Although, the result of these methods are varied, mainly due to the use of different materials having different decomposition rates. Since these methods are depending on the natural process and surrounding environmental factors, the rate of decomposition rate varies periodically. Cotton strips contain cellulose and wooden strips consist of lignin, so the former decomposed quicker than the latter one.

14.6.2.4 Soil Enzymes

Enzymes are known to act as important mediators for biological catabolic processes occurring in soil (Das and Varma 2010; Burns et al. 2013). Therefore, these catalysts offer important evaluation of reaction rates for vital soil processes. Soil enzymes greatly influence organic matter content, soil structure, microbial actions, etc. (Burns et al. 2013) and it changes quickly over other soil parameters, thus offering early indicators of soil health status through providing indications of microbial activity and soil fertility (Chae et al. 2017). Any interruption or disturbance in soil microbial community may result in changes in metabolic enzymes, which serve as an indication of ecosystem disturbance. This positive relationship has been found in the case of heavy metal pollution in soil. There are a large number of analyses available for soil enzyme activities (Nannipieri et al. 2018) including urease, dehydrogenase, phosphatases, and cellulases. Productions of these enzymes are widely affected by their sources, i.e., microbes or plant roots. Enzyme actions can be determined as in situ composition transformation rates. Determination of soil enzyme reaction is generally done by adding soluble substrate at an adequate concentration. Longer incubation periods must need to keep away from new microbial growth. Enzyme actions are often estimated by the addition of indicator reagents followed by a colorimetric reading measurement.

14.6.2.5 Methane Oxidation

Methane (CH_4) is available widely in the atmosphere as well as soil and is regarded as an important greenhouse gas responsible for global warming. Methane is produced by methanogenic bacteria and uptake by methane-oxidizing bacteria also known as methanotrophs (Whitman et al. 2006). An organic material-rich wetland is an ideal place for methane oxidation. Urban landfills comprising a high quantity of organic wastes act as a habitat of various methanotrophs. Oxidation is determined by incubating a soil sample in a closed jar and the release of methane is then measured by gas chromatography. The population of methanotrophs is a pointer of potential methane gas consumption that can be measured in soil by the in-situ method (Singh et al. 2018) or growth-dependent counting method. Estimation of the methanotrophic population can be also done by PCR-DGGE using16S rDNA primers.

14.6.3 Nitrogen Cycling Indicators

The conversion (mineralization) of nitrate (NO_3^-) to gaseous N_2 by soil microbes is a vital process of N cycling. N cycle comprises mineralization, nitrification, denitrification, and atmospheric N fixation. A group of soil microbes are responsible for mineralization of organic N to ammonium (NH_4^+). The rate of this process signifies the availability of organic matter and N pools to plants. NH_4^+ is immobilized by microbes or oxidized to NO_2^- and further NO_3^- by the actions of aerobic nitrifying bacteria (Romero et al. 2015). N leaching to the groundwater occurs because of the formation of easily leachable NO_3^-. Though, anaerobic denitrification reduced NO_3^- to gaseous N_2 via N_2O. A group of soil-living bacteria are responsible for this denitrification process. Both nitrification and denitrification collectively enhance losses of biologically available N as N_2O and N_2 may release to the environment. While gaseous N_2 can be again fixed into the soil by N_2 fixation by another group of N-fixing microbes.

14.6.3.1 N Mineralization

The rate of ammonification process gives an idea about the net N mineralization, as immobilization of NH_4^+ by soil microbes in soil occurs at the same time with the mineralization. Thus, its estimation reflects the possible rate of N mineralization in soil and is determined by the build-up of NH_4^+ in wet soil under anaerobic conditions for few weeks. Though, anaerobic incubation is ideal as there is low immobilization occurred and nitrification is reduced (Wichern et al. 2020). Estimation of potential N mineralization is integrated into soil monitoring programs (Griffiths et al. 2018). Mineralization of N is comparatively not sensitive over other estimations of N cycling as a large variety of microbes are involved in the process.

14.6.3.2 Nitrification

Nitrification is regarded as a more effective indicator over N mineralization, as a tiny portion of nitrifying bacteria is responsible for the process. Determination of nitrification measurements gives an idea about the number of nitrifying bacteria since NH_4^+ is essential to them. Moreover, nitrification and denitrification estimations may point out to status of NH_4^+ on low N soils (Deroo et al. 2021). Nitrification is estimated by the NH_4^+ oxidizing method, in which soil slurry is prepared to incubate with adequate NH_4^+ and chlorate, chlorate leads the oxidation process of NO_2^- to NO_3^-, which is further estimated by gas chromatography.

14.6.3.3 Denitrification

The ability of denitrification is a common characteristic among soil bacteria; hence it can reflect microbial biomass content (Stenberg et al. 1998). Since it is an anaerobic process, the rate of denitrification process in soil is largely influenced by abiotic factors such as precipitation and soil compaction. Therefore, soil management practices directly influence the rate of denitrification occurred in agricultural lands. The estimation of denitrification is done by the acetylene inhibition method as defined by Smith and Tiedje (1979). In this assessment, the reduction of N_2O to N_2 is inhibited by acetylene and released N_2O is determined by gas chromatography. Denitrification enzymes are produced only under anaerobic environments and not active under aerobic situations, though these enzyme-producing microbes are present in that soil. Thus, denitrification assessment may reveal historical anaerobic status and not essentially the amount of the active denitrifying microbial population.

14.6.3.4 N Fixation

Gaseous N_2 is released by anaerobic denitrification of nitrate NO_3^-. Atmospheric N_2 is stored in soil by different groups of N_2-fixing microbes including rhizobium or cyanobacteria by releasing nitrogenase enzyme.

14.6.3.4.1 Rhizobium

Rhizobium bacteria are widely known for their symbiotic associations with legume root systems and are abundantly found in soil. The bacteria live in root nodules and fix atmospheric N_2 for plant growth. On the other hand, the legume plant offers food for bacteria for their growth and multiplication. This symbiosis is highly host-specific (Kimeklis et al. 2019). Earlier, the size of the rhizobium population has taken as an indicator of soil health status (Andrade et al. 2002). Rhizobium has been also integrated as a biological indicator of heavy metal contamination studies in urban or agricultural soils (Ahmad et al. 2012) and as a microbial indicator in pesticide effectiveness studies in soil. The occurrence and variety of rhizobium present in soil can be known by an easy pot test by sowing a range of legume seeds and further determined nodules developed after a specific time, though the bacteria can be determined by isolation from soil using specific growth media. Currently, to check rhizobium diversity, a range of molecular techniques have been used, including PCR (Menna et al. 2009; Simbine et al. 2021) and bacterial colony hybridization. Estimation of rhizobium by simply cultivating legumes in the soil and analyzing nodule development is a quite easy method over the molecular methods, which are more technical. To determine the various subgroups of rhizobium, the bacterial colony hybridization method is regarded as the most excellent. An integration of quantitative and variety determination will give a better idea about the potentiality of soil to fix N.

14.6.3.4.2 Cyanobacteria

The cyanobacteria are photoautotrophic and nonsymbiotic in nature, also known as blue-green algae. The formation of microbiotic crusts in close association with topsoil helps to reduce erosion (Young et al. 2019). Cyanobacteria have generally been used to indicate the heavy metal presence in soil, thus used as an early indicator of soil pollution (Selim and Haffner 2020). There has been found a negative correlation between the cyanobacteria population and the amount of heavy metals in soil. It is reported as a too sensitive indicator of heavy metal contamination especially in sewage/sludge conditions (Jusoh and Chai 2020). Therefore, in laboratory conditions, it is regarded as an excellent biological method to determine heavy metals in test soil. Cyanobacteria size in the soil is positively correlated with nitrogenase activity, thus nitrogenase activity can be used to determine the number of cyanobacteria. Nitrogenase activity is estimated by the acetylene reduction assessment and produced ethylene measured by gas chromatography.

14.6.4 Microbial Biomass

The fraction of microbial biomass in the soil is directly responsible for energy transmission and nutrient regulation (Araújo et al. 2010). Several findings have suggested a positive relationship between the soil microbial biomass and the rate of organic matter decomposition (Horwath 2017; Barel et al. 2019). This fraction is also reported positively correlated with crop yield. The role of soil microbial biomass in the development of soil structure is widely accepted. It has also been suggested as an active indicator of organic carbon in the soil. The methods used for the determination of soil microbial biomass can be classified into direct methods and indirect methods.

14.6.4.1 Direct Methods

Direct methods of microbial biomass determination include microscopy and phospholipid fatty acid analysis. Though the phospholipid fatty acid analysis is time-taking, but offers very good results as it represents natural soil (Lewe et al. 2021). Determination of microbial biomass can be done by counting colonies or by taking measures of volume using conversion factors. The microscopy method is faster with automated image processor, colony counter, and sizes estimator of microbial biomass and tests many soil samples at a time. The quantity of phospholipid fatty acid in the soil can be determined by gas chromatography (Steinmetz et al. 2019). In this method, various subgroups of microbes can also be determined. Thus, this method has the potentiality to describe microbial biomass diversity in soil.

14.6.4.2 Indirect Methods

Indirect methods are usually considered cheaper, quicker, and easier to handle than direct methods. Data resulted from indirect methods were reported to be very similar to the direct methods. Among the indirect methods, chloroform fumigation is very common. This method is measured the total soil microbial biomass, including dead and alive (Oren et al. 2018). There are two types of chloroform fumigation methods: (1) incubation method and (2) extraction method. Chloroform kills the microbes present in the soil, followed by the size determination of the killed biomass by quantifying released CO_2 on a specific incubation period (incubation method) or by direct extraction of extractable carbon from the test soil right after the fumigation (extraction method). The CO_2 produced after fumigation is due to germination microbial spores using the carbon sources from killed microbes.

14.6.4.3 Microbial Quotient

Microbial quotient is the ratio of microbial biomass carbon and total carbon (Sun et al. 2020). Since microbial biomass carbon has close relation with total carbon, this ratio indicates organic matter dynamics in soil and is also used as a parameter of carbon build-up or loss. Microbial quotient overcomes the troubles of comparing different carbon trends in soils with various organic matter contents.

14.6.4.4 Fungal Biomass

The living fraction of fungal biomass can be determined by measuring the amount of specific fungal membrane molecules, e.g., ergosterol (Sun et al. 2020) or specific phospholipid fatty acids. The technique for quantification of ergosterol in the soil is easier than the estimation of phosphor lipid fatty acids. But main constraint of ergosterol estimation method is that oomycetous group of fungi and several yeasts are unable to produce ergosterol. Hyphal length measurement is recommended for accurate determinations of living fungal biomass (Gui et al. 2018), but it is a very time-taking and laborious method.

14.6.4.5 Ratio of Fungal-Bacterial Biomass

The ratio of fungal and bacterial biomass can easily be determined from estimations of fungal-specific and bacterial-specific phospholipid fatty acids (Zhou et al. 2019). This indicator has been used in soil health management research as a microbial parameter. A higher ratio is generally found in unfertilized or organically cultivated soil over chemically fertilized soil (Poeplau et al. 2019).

14.6.4.6 Protozoan Biomass

Biomass of microbial population under protozoan groups is estimated by extracting a soil sample followed by direct counting using a high-resolution microscope and calculated using conversion factor (Li et al. 2021). This method has been used for the determination of the active protozoan population, but the majority greater parts of protozoa are inactive (cysted) in nature. Therefore, protozoa extraction from soil followed by growing it in a suitable medium and then MPN counting can be more accurate, as this technique includes cysted biomass, though this method is time-consuming and laborious. Moreover, extraction of certain protozoa from soil and growing several protozoa under laboratory conditions are difficult. To overcome these constraints, a molecular method MPN-PCR has been developed to measure the amount of a specific group of protozoa living in the soil system, and has advantages over earlier methods.

14.6.5 Parameters of Microbial Activities

Estimation of microbial activities in the soil directly represents progress regarding organic matter decomposition and nutrient cycling through bacterial DNA and protein synthesis, or bacteriophage activity analysis is a measurement at the population level. DNA synthesis indicates the status of bacterial cell division and bacterial growth. Bacterial DNA synthesis can be done by integration of 14C thymidine or 3H into bacterial DNA. In this technique, soil sample extract has to go through short incubation with micro labeled thymidine followed by filtration to quantify micro labeled thymidine in the cells. The growth rate of bacteria is estimated by using a conversion factor (Kirchman and Ducklow 2018). Similar to DNA synthesis, protein synthesis has a close correlation to bacterial activities and can be analyzed by integration of 14C leucine into bacterial proteins. The method of leucine integration (Kirchman and Ducklow 2018) is similar to DNA synthesis (as mentioned above) and both analyses can be done in a single assay with different micro labels (Kirchman 2018). Estimation of protein synthesis is found to be more precise than DNA synthesis due to comparatively higher protein present in cells. Bacteriophage is a type of virus that infects replicates in host bacteria. Their replication depends on the activities of its host bacteria (Lourenço et al. 2018). Monitoring of the occurrence and host specificity of the free bacteriophages in the soil system indicates the activity of a particular bacterium or a group of bacteria. This is in contrast to the other microbial activity indicators, which measure the activity of whole microbial communities. Estimation of soil living bacteriophages can be done by a standard procedure of extraction and plaque assay with host bacteria.

14.6.6 Mycorrhiza

Important soil microbial species play vital functions in the soil system. Some of these species have been used in a soil health monitoring program. Mycorrhiza is one of them (Mahdi et al. 2017). Most of the higher plants have developed a natural symbiosis with mycorrhiza. Mycorrhiza fungi are broadly divided into two categories ectomycorrhiza fungi and endomycorrhiza fungi (Allen et al. 1995). They developed on plant roots and increase surface area (extraradical mycelium), thus supply plant nutrients. Mycorrhizal associations have been found to have a positive role on plant diversity (Mao et al. 2019), disease tolerance (Jacott et al. 2017), stress tolerance (Tiwari et al. 2021), and soil structure (Al-Maliki and Al-Masoudi 2018), thus improve soil health (Ranganathswamy et al. 2019). Vascular arbuscular mycorrhiza is highly influenced by host plants and soil cultural practices. They are very sensitive to heavy metal contamination and organic pollution. Therefore, it is used as a heavy metal contamination indicator in soil (Eijsackers et al. 2019). The presence and diversity of these fungi are estimated by extraction of their spores from test soil followed by counting in the microscope. Direct recognition and quantification of mycorrhiza in soil or in roots have better results over spore counting, as the number of spores are always not correlated with the biomass of mycorrhiza colonies. Molecular methods, such as rDNA PCR (Suzuki et al. 2020) and mycorrhiza-specific phospholipid fatty acid analysis (Drijber and Jeske 2019) have advantages over traditional methods.

14.6.7 Bioavailability Parameters

Chemical compounds are generally adsorbed by soil particles and become unavailable to organisms. The concentrations of bioavailable or biologically available concentrations are generally lower than the chemically extractable concentrations. Therefore, from an agricultural viewpoint, the bioavailable portion of a chemical may be more significant than its chemically extractable portion. Biosensor bacteria are developed to react quickly to specific environmental stress conditions by using reporter genes (Bilal and Iqbal 2019; Aynalem and Muleta 2021). Specific bacteria related to stress conditions are selected and genetically transformed by entering reporter genes having the ability to give a particular signal to a specific response. Biosensor bacteria actively react to chromium (Hilali et al. 2020), mercury, and cadmium (Kang et al. 2018) or salinity (Gaffney et al. 2021) in soil. Bacteria containing plasmid have been found more in heavy metal polluted soils (Malik et al. 2002). Therefore, quantification of plasmid containing bacterial population in the soil can be taken as an important parameter of environmental pollution. Plasmids are simply extracted from bacteria grown on agar media followed by a visualization of the plasmids by microscope using agarose gels. Monitoring of antibiotic-resistant bacteria in soil ecosystem will offer to determine the potential threat of these bacteria to human health or can be used as well as a parameter for urban or agricultural pollution. Quantification and diversity of antibiotic-resistant bacteria can be determined either by growing on suitable media or using molecular methods.

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Chapter 15
Ectomycorrhizal Networks and Silviculture in Mediterranean Forests

José Alfonso Domínguez-Núñez

Abstract In the current context in which mycological resources have acquired a strong socio-economic interest, forest mycological management is necessary, with objectives of ecological sustainability in their use and conservation. The key implication of soil fungi in forest biogeochemical processes and the new knowledge on ectomycorrhizal networks and edaphic microbial ecology, make it necessary to rethink traditional silviculture and to study its effects on forest fungal communities. In the Mediterranean region, the current prospects of climate change seem to increase the stress on forest soils and forest life, already affected by poor management and commercial overexploitation of mushrooms, among other causes. We review in this chapter the literature on silvicultural practices that have positively or negatively affected soil fungal diversity and yield, focusing especially on experiences in the Mediterranean forest. We briefly analyze the potential of mycorrhizal applications and the knowledge of ectomycorrhizal networks for their application in forest management. The application of retention silviculture practices, retaining trees, tree patches or understory during forest harvesting can help to preserve ectomycorrhizal networks, buffering the disturbances generated by silvicultural treatments.

Keywords Mushrooms · Management · Soil · Fungi · Thinnings · Clear-cutting · Mycelium · Microbiota · Drought · Diversity · Yield

15.1 Introduction

Nowadays, mushroom collecting in the wild, usually for food, has become a highly demanded activity. The concern for the conservation and promotion of edible wild mushrooms (especially ectomycorrhizal fungi-ECM) initiated the development of an original silviculture aimed at forests producing this resource (Martínez-Peña 2003).

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B. Giri et al. (eds.), *Structure and Functions of Pedosphere*,
https://doi.org/10.1007/978-981-16-8770-9_15

This silviculture, initially called mycological silviculture (Oria-de-Rueda 1988), comprises the set of techniques aimed at conserving and promoting the production of edible wild mushrooms in forests. The inclusion of the mycological resource in the management guidelines of forests has meant a greater attention to the multifunctionality of forest systems (Oria-de-Rueda et al. 2008a). In the 1980s, the first studies on the effects of silvicultural practices on the production of edible mushrooms are already present (e.g., Kardell and Eriksson 1987; Ohenoja 1988). In the Mediterranean area, the first experiences of forest management aimed at improving mushroom production were especially directed at black truffles in Italy (Mannozzi 1986; Pacioni 1987) and Spain (Reyna 1999).

Nowadays, in the face of challenges such as climate change and sustainability in the exploitation of natural resources, ECM fungi also acquire vital importance for their role in the functioning of forest ecosystems, in soil biogeochemical cycles, as well as for their contribution of different ecosystem services, including edible mushrooms. The discovery and study of mycorrhizal networks (MN) that interconnect different individuals of a plant community (Simard et al. 1997), intervening in the flow of carbon (C) and nutrients between individuals, as well as in their protection through a still not well known biochemical communication (Johnson and Gilbert 2015), highlight the need to better understand the effects of anthropogenic disturbances (such as silviculture) on the forest ecosystem, especially on the forest soil.

Mediterranean forests have historically hosted a great diversity of fungal species, many of great socioeconomic interest. The climatic characteristics of this region, with marked summer drought and periodic fires, have traditionally marked the soils and a specific type of forest management. The current prospects of climate change will increase the stress conditions on soils and soil life. In addition, currently the main causes of the progressive decline of fungal diversity in Mediterranean forests are logging and timber harvesting, resulting in habitat reduction (e.g., old-growth forests) (Dahlberg et al. 2010). The main cause of the lack of coarse dead wood in forests is related to silvicultural management. Removal of considerable amounts of wood from the understory affects fungal growth, the establishment of mycorrhizal associations with seedlings, and the maintenance of mycorrhizal fungal associations in seasonally dry forests (Huhndorf et al. 2004). Overexploitation of edible mycorrhizal species such as the genera *Amanita* Pers., *Cantharellus* Adans. ex Fr., *Boletus* L., and *Tuber* ex F.H. Wigg is also a major threat in Mediterranean forests (Venturella et al. 2016).

We review in this chapter those aspects of silviculture that may affect ECM fungal populations in the Mediterranean forest, important both for their role in the functioning of the forest ecosystem and for their economic-social value at present.

15.2 Forest Soils and Fungi

Forest soils are the natural resource that sustains forest ecosystems. They are soils that have been developed under forest cover and currently support it, or had other uses in the past (agriculture, grazing) and have been converted to forest. The most significant aspect of forest soil is its closed nutrient cycle with the forest. In addition, they tend to have long periods of time between harvests, low erosion rates, low fertilization rates under intensive management, and the potential to use very deep soil horizons for their livelihood (Comerford and Fox 2017). The concept of "solum," which includes the A, E, and B horizons and is considered to be the zone of pedogenic processes driven by biological activity does not always apply in forest soils, where tree roots may extend through the C horizon and into the R horizons.

Biota—the assemblage of living organisms—is an important factor in soil formation, creating organic matter, breaking down rock and modifying its composition, and transforming it into soil. Microbial communities are the most complex and diverse group of soil organisms, ranging in size from 0.5 to 5.0 μm and consisting predominantly of bacteria, fungi, actinomycetes, and lichens (Tate 1995; Brady and Weil 2002). These microorganisms coexist and interact with each other and with other soil organisms. The soil microbial community presents a complex and variable association between different levels of biological organization, which encompasses genetic variability and relative richness and regularity in the communities. Currently, there is a growing interest in the relationships between ecosystem diversity, structure, and function (Islam and Wright 2017).

Soil fungi are a highly diverse group of microscopic eukaryotic organisms belonging to the Kingdom Fungi (Mycota). Although some are unicellular fungi (e.g., yeasts), most are multicellular with a mycelial morphology comprising a network of tubular filaments (hyphae). The mycelial growth form is well adapted to the heterogeneous soil environment, where nutrient resources are spatially separated over large distances at the microbial scale. Fungi are heterotrophic and obtain carbon, nutrients, and energy through extracellular degradation and uptake of organic matter from their external environment. They generally require oxygen for growth. Fungi are an integral part of the soil biotic community, contributing significantly to the decomposition of organic matter, the release and turnover of nutrients, the formation and maintenance of soil structure, the extension of plant root systems through the formation of mycorrhizal networks, and the promotion and suppression of plant diseases (Deacon 1997). Soil fungi can be grouped into three functional groups: pathogenic, saprophytic, and mycorrhizal. While plant pathogenic fungi cause significant losses in agricultural crops each year, most soil fungi are beneficial and perform a number of critically important ecological functions. One of the main functions of fungi in any soil is the decomposition of plant residues. Saprophytic fungi produce a set of extracellular enzymes capable of depolymerizing plant cellular components such as cellulose, hemicellulose, and lignin. During the decomposition process, fungi simultaneously immobilize (i.e., retain in their biomass in organic form) and mineralize (i.e., release to the environment in inorganic form) nutrients, with the balance between these two processes determining the availability to plants of nutrients such as nitrogen, phosphorus, potassium, and sulfur. In addition to nutrient immobilization, it is known that fungi can accumulate toxic substances within the mycelium, including radionuclides and heavy metals (Killham 1994). The branching of fungal hyphae around soil particles, combined with the production of extracellular polysaccharides that serve as binding agents, promotes the formation of stable aggregates in the soil (Cannon 1997). This fungal-mediated process modifies air and water relations by altering soil permeability and may be an important mechanism for the physical protection of soil organic matter (Beare et al. 1997). Many saprophytic and mycorrhizal fungi promote plant disease suppression by either producing antibiotic inhibitors of disease-causing organisms or by outcompeting pathogens for available resources (Paul and Clark 1996).

Mutualistic associations involving fungi include lichens, endophytes, and mycorrhizal fungi. In all cases, a fungus establishes a mutually beneficial relationship with an autotrophic organism. Mycorrhizal fungi, which form an intimate association with plant roots, enhance the uptake and transfer of mineral nutrients to the plant host in exchange for carbon. In fact, mycorrhizae, not roots, are the main organs of nutrient uptake by terrestrial plants (Smith and Read 1997). Many species of mycorrhizal fungi are involved in water and nutrient uptake and may also provide protection against root pathogens (Paul and Clark 1996). Mycorrhizal fungi are currently grouped into several types (Smith and Read 1997). Arbuscular mycorrhizal (AM) fungi are the most common group and are of the order Glomales (Zygomycetes), which are associated with the roots of a wide range of plants (Smith and Read 1997).

Although less common than arbuscular mycorrhizal fungi, ECM fungi are especially important in forest ecosystems. Predominantly ECM plant families include the *Pinaceae, Fagaceae, Myrtaceae, Dipterocarpaceae, Salicaceae, Betulaceae*, and the legume subfamily *Caesalpinioideae*, among others (Smith and Read 1997). Although these species account for only about 3% of plant diversity, they include the dominant species of most temperate and boreal forests and some tropical forests. ECM fungi are mainly *Basidiomycetes*, as well as some *Ascomycetes* and some species of the *Zygomycete* genus *Endogone*. Many ECM fungi produce conspicuous carpophores, some of which are edible fungi of great socioeconomic importance (e.g., *amanita caesarea*, chanterelles, truffles, boletus, matsutake, etc.) (Dickie 2017).

15.3 The Mediterranean Forest: Soil Microbiota

Mediterranean soils are characterized by variability of soil properties, reduced water retention capacity, shallow soil horizons, large amounts of stony materials on the soil surface, different soil processes such as loss of carbonates, and high risk of erosion (Rodeghiero et al. 2011). Historically, fire has also been a major problem in the Mediterranean region. As of 2010, more than 5 Mha (approximately 6×10^5 ha yr^{-1};

FAO 2010) had been burned; 50% of the total number of forest fires and area burned occurred in Portugal and Spain (FAO 2010).

The depletion of organic matter content has been one of the main causes underlying the decrease in agronomic productivity in soils of the Mediterranean region (Khresat et al. 2008). In Spain, soil organic carbon is mainly dependent on climatic conditions (Rodríguez Martín et al. 2016). Regarding nitrogen, maximum losses can occur in early spring and autumn and minimum losses in summer, due to low soil water content (Samal et al. 2017).

Mediterranean ecosystems are characterized by stress factors, such as long periods of drought (IPCC 2007; Mooney 1989), which can compromise their fragile balances (Sardans and Peñuelas 2007). These events can strongly affect microbial activity involved in nutrient mineralization, with possible changes in soil degradation dynamics (Bastida et al. 2006), with progressive nutrient depletion due to soil erosion and drought (Sardans and Peñuelas 2005).

Mediterranean forests covered an area of more than 85 million hectares in 2010 (FAO 2010). Trees significantly affect the soil environment in several ways, through litterfall, labile C input, rhizodeposition, root turnover and effects on soil microclimate (Eviner and Chapin 2003). Especially, the quality of litter associated with different tree species influences microbial communities and their functionality (Thoms et al. 2010; Aponte et al. 2014). Some specialization of different microbial communities has also been observed in soil under different tree species (Schweitzer et al. 2011).

Recent research has shown that edaphic and climatic parameters are the main drivers of the composition, diversity, and metabolic potential of microbial communities in various environments, including forest soils (Wang et al. 2015); at different scales of study (Lladó et al. 2018) specific root traits, root exudates (Colin et al. 2017), forest species (Urbanová et al. 2015), soil pH (Tedersoo et al. 2014), soil temperature (von Rein et al. 2016), or edaphic moisture (Hartmann et al. 2017) may influence. In Mediterranean forests, there are hardly any studies in this regard, and focused mainly on the effect of soil moisture (Bastida et al. 2017) as the main limiting factor of microbial communities.

Mediterranean forest ecosystems are among the richest in fungi (Angelini et al. 2016) and constitute a unique natural heritage in terms of biological diversity (Scarascia-Mugnozza et al. 2000). It is estimated that about 50% of forest fungi are wood decomposers (Senn-Irlet et al. 2007). The existence of these organisms is therefore dependent on a continuous supply of dead wood due to their close involvement in the recycling of organic matter. In Mediterranean forests, many fungi specialize in colonizing plant twigs and small diameter pieces of wood (Junninen et al. 2006). More than 49 species of macromycetes from 23 families are target species (i.e., keystone or indicator species) of Mediterranean forests and Mediterranean maquis (Polemis et al. 2013).

Mediterranean ECM fungal species are very abundant (Rinaldi et al. 2008). One of the main limiting factors of plant growth in the Mediterranean environment is summer drought, so relative research on the ecophysiological (and especially hydric) effects of ECMs on Mediterranean hosts has been important, but remains still scarce;

in fact, most international studies have focused on dry temperate forests (British Columbia and Spain) and Mediterranean forests (Spain and California) (Schoonmaker et al. 2007; Querejeta et al. 2007; Dominguez-Núñez et al. 2006; Morte et al. 2010). Both water availability and fire (Taudière et al. 2017; Vasquez-Gassibe et al. 2014; Martín-Pinto et al. 2006) remain key factors in the interaction of Mediterranean ECM fungi with their hosts and habitats.

15.4 Mycorrizal Networks

Individual mycorrhizal fungi can infect the roots of different plants, potentially linking these plants into a common mycelial network or mycorrhizal network (MN); mycelial networks can represent as much as 40% of the soil surface in certain forest ecosystems, creating a unique environment that alters soil biogeochemistry and harbors distinct microbial communities compared to habitats without mycelial networks (Kluber et al. 2011). Mycorrhizal networks are considered ubiquitous in natural ecosystems and have been documented in boreal and temperate forests and woodlands (Beiler et al. 2010), tropical forests and woodlands (Onguene and Kuyper 2002), Mediterranean and sclerophyllous forests and chaparral (Richard et al. 2005), wooded savannas (Dickie et al. 2004), grasslands (Gai et al. 2009), and Arctic tundra (Deslippe and Simard 2011). It has been suggested that this may allow nutrients and C fixed by one plant to flow through mycelial links to other plants (Simard et al. 2002). Some achlorophyllous plants apparently obtain all their C from such mycelial links (Smith and Read 1997).

Recent work has shown that these mycorrhizal networks can also transport signals produced by plants in response to herbivore and pathogen infestation to neighboring plants before they themselves are attacked. The rate of transfer to uninfested plants is such that the mechanism is likely to have measurable benefits for plant protection. At present, little is known about the nature of the signals and the degree of control exerted by plants and fungi over their transmission (Johnson and Gilbert 2015). Communication between plants with signals through mycorrhizal fungi means that we must rethink our understanding of multitrophic interactions in nature.

Although arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) fungi are capable of forming these networks, our chapter will focus primarily on ECM networks and their interactions with silviculture in Mediterranean forests.

15.5 Some Aspects of the Silviculture and Management of Mediterranean Forests

Mediterranean silviculture has traditionally been multipurpose, because several products are managed simultaneously. The mixture of species, typical of Mediterranean forestry systems, contributes to increasing diversity and maintaining a high rate of biological functionality. The Mediterranean landscape has been characterized by the mixture of tree species, shrubs, and other typical elements of these systems, the grasslands. Under markedly Mediterranean climatic conditions, competition between species derives primarily from lack of water rather than lack of light. This is traditionally the main practical and conceptual difference between Mediterranean and Central European silviculture. A particular case of silviculture, or rather agroforestry, has been the Spanish "Dehesa", one of the most attractive and efficient systems, both conceptually and physically, with which to take advantage of the varied, though limited and seasonally fluctuating, resources of the poor soils of Mediterranean ecosystems.

Mediterranean areas are characterized by high annual climatic variability, with hot, dry summers, and irregular rainfall. Climate change scenarios point to increasing temperatures and changes in the precipitation regime in this region (Lindner and Calama 2013). In addition, the forests of the Mediterranean area have a long history of human exploitation. These key characteristics, together with the frequent occurrence of disturbances such as fires or pests, have influenced the composition, structure, and functioning of these ecosystems. Therefore, to maintain the level of ecosystem services in this region, forest management is necessary, especially in light of reports that climate change is resulting in a reduction in the carbon sink capacity of unmanaged Spanish Mediterranean forests due to reduced water availability (Vayreda et al. 2012).

Currently, silviculture is in transition toward ecosystem-based management, and new silvicultural approaches are emerging worldwide. However, the adoption of an alternative silvicultural approach is difficult in practice (Bravo-Oviedo et al. 2020).

Natural regeneration has long been a major concern in forest management of Mediterranean species. Natural regeneration is not usually successful in Mediterranean species for different reasons. Some of these reasons are directly related to forest management (the use of silvicultural systems leading to low densities; long rotations inducing poor seed yields during the regeneration period; excessive grazing; uncontrolled tillage activities; intensive pruning to provide firewood; etc.) (Calama et al. 2017).

It has been reported for Mediterranean environments, higher carbon stocks in uneven-aged (irregular) forest structures with respect to even-aged (regular) structures. This uneven aged structure implies greater soil protection along with other advantages of particular relevance in Mediterranean systems (Ruiz-Peinado et al. 2017).

In Europe, the traditional coppice system was widely used until the middle of the last century due to the demand for firewood and charcoal; however, the importance of this system started to decrease during the second half of the century. By the early twenty-first century, most coppice stands were no longer managed (Buckley and Mills 2015). Today, coppice stands are again gaining prominence due to their potential role in bioenergy production (Ruiz-Peinado et al. 2017). In the European Mediterranean area, coppice stands cover more than 15–10^6 ha (Bravo-Fernández et al. 2008), with more than 3.5–10^6 ha in Italy and more than 2.2–10^6 ha in Spain (Bravo-Fernández et al. 2008). Strategies that should be considered to recover these coppice forests include conversion to coppice, conversion to coppice with standards, or maintenance of the current coppice system (Bravo-Fernández et al. 2008). Therefore, in the Mediterranean area, coppice management for biomass production, using medium rotation periods, could also provide an important source of raw material for bioenergy purposes (Cañellas et al. 2004).

Reducing tree density through thinning treatments is one of the most important decisions in silviculture; it has proven to be a critical factor for seedling establishment in the forest understory (Paquette et al. 2006), and has long been a research topic of interest in forest science (Zeide 2001). Thinning increases light availability in the understory, but also affects the water balance in a more complex way (Aussenac 2000); thinning can affect seedling survival in water-limited areas, such as the Mediterranean area. Forest managers need information on appropriate management methods to improve the diversity and resilience of Mediterranean forests (Gavinet et al. 2015).

On the other hand, brush and shrub clearing (especially strip clearing) can be applied in Mediterranean areas to provide space for tree regeneration, either natural or human-induced (Pérez-Devesa et al. 2008). This operation also serves to reduce the risk of forest fires or to improve pastures for livestock, although a certain level of shrub cover can be maintained, which can be beneficial to improve pasture productivity (López-Díaz et al. 2015). The shrub cover in the Mediterranean area is also very important in terms of soil conservation which, in turn, is also vital for carbon sequestration and nutrient cycling, thus improving the sink capacity of the system (Ruiz-Peinado et al. 2017).

In southern Europe, agroforestry systems offer great potential for sequestering carbon, given the large area covered by these systems in the Iberian Peninsula, covering more than 5.5–10^6 ha (Marañón 1988). Restoration and management of tree and shrub strata in these systems will also have a substantial effect on soils (Ruiz-Peinado et al. 2017).

In the Mediterranean region, forest fires are the most important disturbance agents and fire risk must be taken into account in forest management (Costa et al. 2011). In this region, many species show adaptation strategies to the fire regime to increase their resilience to this disturbance: resprouting, serotiny, fire-stimulated germination, increased flammability, thick bark, etc. (e.g., Keeley et al. 2011). Loss of mineral soil carbon could be severe in the postfire period due to soil erosion, as the tree layer and forest floor could be greatly reduced. Prescribed fires could be used to reduce the risk of wildfires by reducing the fuel load.

On the other hand, Mediterranean soil afforestation can improve carbon sequestration and soil fertility (Jandl et al. 2007), as it generates increases in litterfall and rhizodeposition inputs, improved soil protection due to soil cover, increased nutrient availability, and increased soil water holding capacity (Fernández-Ondoño et al. 2010).

Mediterranean forests provide wood and many nontimbers forest products (NTFPs) such as firewood, game, cork, resin, mushrooms, wild fruits, recreational services, soil protection, biodiversity, landscape, CO_2 fixation, water regulation, etc. Some of these products are present in competitive markets (e.g., hunting, cork, and resin), while others remain outside the market as self-collected products for self-consumption, e.g., recreational services, mushroom picking, and threatened biodiversity services (Campos et al. 2017). Forest owners can self-consume all these products. This self-consumption is relevant in Mediterranean forest systems. Currently, to support multifunctionality in forest management, it is necessary to identify the effect of different silvicultural treatments on the provision of these ecosystem services (Del Rio et al. 2017), including edible mushrooms.

15.6 Effect of Silvicultural Practices in ECM Fungi

Silvicultural practices, such as various timber harvesting methods, and land preparation activities, can modify a number of physical and chemical properties of the soil, consequently affecting soil pore space, organic matter composition and quantity, forest floor and mineral temperatures, and soil moisture. Alteration of these properties, in turn, can negatively affect the density and diversity of soil microbiota (Hill et al. 1975; Marshall 1993), as well as alter their living space and food supply (Shaw et al. 1991).

Silvicultural practices are the most studied anthropogenic disturbances related to mycological resources. In Spain, studies on mycosilviculture have been slowly incorporated over the last two decades. Most of these studies have addressed the effect of thinning and its different degrees or intensities of application on the fungal communities (Bonet et al. 2012; Collado et al. 2018, 2020; Castaño et al. 2018b; Herrero et al. 2019; Bastida et al. 2019), although the effects of clear-cutting with or without retention trees (Goicoechea et al. 2009; Closa and Goicoechea 2010; Parladé et al. 2017, 2019), or scrub management (Hernández-Rodríguez et al. 2015; Mediavilla et al. 2017) have also been studied. However, some of these studies have been unspecific with respect to the types of treatments applied (Abrego et al. 2014). There is currently a great interest in the study of the effects of forest management on the overall biodiversity of the ecosystem, and specifically on the richness and diversity of fungal taxa; not only the study of edible or marketable fungi is of interest, but also the study of different functional groups, both ECM, wood-inhabiting fungi, and other saprotrophic fungi (Laiho and Prescott 2004; Lonsdale et al. 2008; Behnke-Borowczyk et al. 2021; Kouki and Salo 2020), as they are decisive in OM decomposition processes and soil biogeochemical cycles.

In any case, in this chapter we focus exclusively on ECM fungi.

15.6.1 Importance of Mycorrhizal Networks in Silviculture

In a forest that has undergone some kind of disturbance to its vegetation cover (e.g., any silvicultural treatment), the establishment of new forest seedlings (by natural regeneration or planting) is affected by the formation of ECM mycorrhizae that grow from existing plants, creating a mycorrhizal network between the new seedling and these other plants. These ECM networks appear to increase survival (Teste and Simard 2008), or growth (Booth 2004) of seedlings in most cases examined (van der Heijden and Horton 2009). Large, old trees have been shown to act as hubs in MNs, providing links to seedlings and thus playing key roles in facilitating regeneration through access to deep water and nutrient redistribution, as well as mycorrhizal colonization (Pickles and Simard 2017). Mycorrhizal networks allow for improved water distribution among connected plants (Bingham and Simard 2011) and may allow part of the fungal carbon needs to be met by the larger host (Wu et al. 2002), thus allowing newly arrived young seedlings to access a large nutrient acquisition network without a concomitant allocation of photosynthates. As stands age, individual mycelia of some ECM fungi increase in size, allowing mycorrhizal networks to become more extensive.

15.6.2 Regeneration Methods

In silviculture, regeneration methods have the main objective of ensuring the natural regeneration of the forest stand, and have traditionally been clear-cutting and shelterwood methods.

Clear-cutting consists of the total opening of the forest vegetation in units or blocks of more or less large surface. Clear-cutting results in a significant change in the physicochemical and biological properties of the soil as well as in the environmental filters that influence the ECM fungal community assemblage (Parke et al. 1983; Dickie et al. 2009). Immediately after logging, ECM fungi associated with dying roots of logged trees can effectively colonize young seedlings that may be incorporated by natural regeneration or selective planting (Hagerman and Durall 2004), but the availability of this source decreases with time since logging. With the loss of active ECM fungal mycelium associated with living roots (Lazaruk et al. 2005), sources of inoculum in large areas from logging are restricted to spore banks, sclerotia, and newly dispersed spores (Fleming 1984), the so-called “resistant propagules” (Baar et al. 1999). In Spanish forests, clear-cutting methods have traditionally been applied with moderation, given their Mediterranean climate, with marked summer drought. At least in the short-term, it seems that clear-cutting methods negatively affect the performance of fungi (Kardell and Eriksson 1987; Durall et al. 2006), mainly ECM fungi.

Currently, in so-called “retention” silviculture, some scattered or patchy mature trees are retained within the stand (Simard et al. 2021), as “mother” trees (Simard

2017), where the negative effect of clear-cutting on fungal performance can be reduced (Peter et al. 2013; Ágreda et al. 2014). Compared to clear-cutting, retaining a portion of legacy trees during clear-cutting can mitigate losses of fungal inoculum, structural and host plant diversity, C reserves and, in doing so, promote seedling regeneration and forest recovery (Simard et al. 2021).

From the point of view of fungal diversity and ecosystem functionality, retention silviculture can also be more positive compared to clear-cutting (Luoma et al. 2004), whether scattered tree retention (Churchland et al. 2021) or so-called retention patch (Simard et al. 2021) is applied, as microenvironmental changes occur at the site level, with localized effects (Varenius et al. 2016).

In addition to trees of the same species remaining after logging, other ECM host plants, trees or shrubs (alder, birch, trembling aspen, willow, poplar; *Betula* spp.; *Arctostaphylos* spp.; ericoid shrubs) may remain in a cutting block and act as reservoirs of ECM-active fungi (Massicotte et al. 1999; Grelet et al. 2010).

Considering fungal communities by functional groups (saprotrophs, wood-associated, ECM, parasites, etc.), the responses of the different groups to different forest disturbances are poorly known (Kouki and Salo 2020). In Spain, Parladé et al. (2019) observed in the short-term (5 years) that, after clear-cutting in *Pinus sylvestris* stands, the soil fungal composition changed, decreasing ECM fungal species and increasing saprotrophs, although these changes did not significantly affect fungal diversity.

On the other hand, to date, much of the studies on stand age class composition and its effects on fungal performance and diversity have been conducted in even-aged stands; however, there is a significant lack of knowledge on fungal performance in uneven aged stands, as well as on fungal performance in mature or old-growth forests (Tomao et al. 2017), especially in Mediterranean ecosystems. Apparently, silviculture of uneven aged stand by selective logging could have less impact on fungal diversity than silviculture of even aged stands, and even maintain fungal diversity similar to that of unmanaged forests (Purahong et al. 2014), although this is still unclear (Schall et al. 2020; Savilaakso et al. 2021). Most of these biodiversity studies have been initiated in boreal forests (Savilaakso et al. 2021), whereas, in Mediterranean forests, studies on the effect of forest management type on overall biodiversity and in particular, fungal biodiversity will need to be increased (Tomao et al. 2020).

15.6.3 Thinnings

In silviculture, thinnings are treatments to maintain and improve stand quality by reducing stand density.

Being one of the most studied silvicultural practices (Fig. 15.1), however, the effect of thinning on fungal performance is not clear, and may be different for different fungal species and different ecosystems. A review of the literature shows that forest thinning generates different responses in mycorrhizal ecosystems,

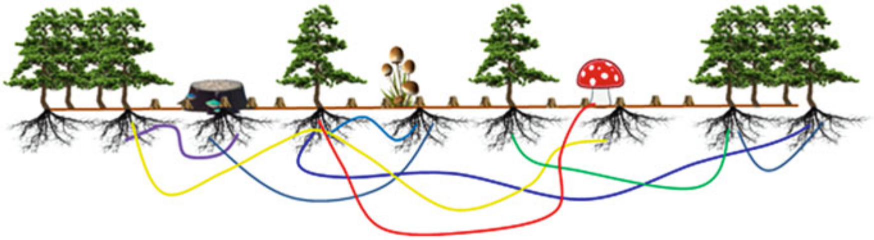

Fig. 15.1 Ectomycorrhizal networks after a forest thinning

modifying fungal succession patterns, influencing carpophore yields, and providing favorable conditions for certain fungal species, to the detriment of others (Tomao et al. 2020).

Several authors have found that forest thinning, especially in conifer stands, has a positive effect on carpophore yields of important marketable species (*Lactarius* spp., *Boletus* spp.), if medium-low density stands are created (Bonet et al. 2012; Tahvanainen et al. 2016). For example, Salerni and Perini (2004) observed in *Abies alba* forests that most *B. edulis* carpophores were recorded in medium thinning stations. Ayer et al. (2006) obtained similar results, finding higher fungal production in forests with medium densities. Others, such as Kranabetter and Kroeger (2001) reported only that thinning had no negative effect on ECM fungi.

A 20-year inventory of mushroom yields in mixed forests in Switzerland revealed a temporal relationship between thinning, tree growth reaction, and associated mushroom community reaction (Egli et al. 2010). Thinning favored strong-growing trees that produced more ECM carpophores than poor-growing trees. Many of the edible fungal species appeared exclusively after thinning: *Amanita rubescens*, *Boletus edulis*, *Craterellus cornucopioides*, *Hypholoma capnoides*, some *Russula* species, and *Xerocomus badius*. In addition, carpophore yields of saprotrophic species also increased after thinning. In contrast, negative effects of thinning have been reported for genera such as *Cantharellus* spp. although the yield recovered in the following 6 years (Pilz et al. 2006). However, high or low intensity thinning has also been reported to lead to reduced carpophore yield (Luoma et al. 2004). Ultimately, the response of fungal yield to thinning could depend on the intensity of forest thinning, the time period after disturbance, the fungal species, and possible soil disturbance (De Miguel 2018).

With respect to fungal biodiversity, there is the “intermediate disturbance hypothesis” (Osman 2015), which suggests that maximum levels of global biodiversity are observed under some frequency of intermediate disturbance, because few species are able to tolerate very intense disturbance regimes, and few species are able to compete successfully in habitats experiencing minimal disturbance regimes (Connell 1978; Muscolo et al. 2021). According to this hypothesis, and from the point of view of fungal biodiversity, the most suitable thinning would be those of medium intensity. ECM fungal diversity seems to be negatively affected by the effect of thinning, at least in the short- to medium-term (Bastida et al. 2019); there may be a decrease in species richness and/or changes in the composition of the ECM fungal community (Baral et al. 2015; Bastida et al. 2019); however, other Spanish authors such as Castaño et al. (2018b) did not observe immediate changes in soil fungal community composition, richness, and diversity, regardless of thinning intensity, as long as retention trees are left; anyway fungal species composition changed progressively over the years, both at species and functional guild level. Thinning can produce some immediate positive effects in favor of some fungal species of early successional stages, especially saprotrophic fungi of interest, such as *Morchella* sp. (Buée et al. 2005; Parisi et al. 2018).

In any case, it seems important to consider the time frame since the thinning was conducted, and the changes of the different fungal functional groups over time (Castaño et al. 2018a, b; Parladé et al. 2019).

Recently, Collado et al. (2020) propose that ECM fungi may respond to disturbances by increasing reproduction (carpophores) rather than colonizing the surrounding soil. In any case, the consequences of long-term silvicultural practices on the soil fungal community need to be better understood (Varenius et al. 2016; Tomao et al. 2020).

15.6.4 Other Practices and Disturbances

Current forest management guidelines recommend retaining and actively creating dead wood in forest harvesting operations (Anonymous 2019). The impact of removing woody debris from the forest, on yield, and ECM fungal diversity is unclear. Decaying wood provides habitat not only for saprotrophic fungi, but also for mycorrhizal fungi that engage in a symbiotic exchange of nutrients with the roots of their host tree (Tedersoo et al. 2003; Rajala et al. 2011). Some studies have reported negative effects of woody debris removal on the performance of important marketable ECM fungal species, such as *Boletus edulis* (Salerni and Perini 2004); however, other authors have reported the opposite trend for mycorrhizal species (Baar and Ter Braak 1996). Although downed dead wood may not be necessary to support the initial colonization of very young seedlings, in the long-term it is expected to increase the genetic and species diversity of ECM fungi in a stand.

Brush or understory removal is another silvicultural practice whose effect on fungal performance and diversity is also unclear. In principle, this practice releases more water and nutrients into the soil for trees and fungi (Nocentini et al. 2004). However, it must be considered whether the understory species to be cleared or removed can form mycorrhizal associations with fungi of interest at the site. Since host diversity increases the diversity of ECM fungi in a stand (DeBellis et al. 2006), clearing should be minimized as much as possible. Azul et al. (2009) revealed that current practices used to control shrub density, e.g., to prevent forest fires, lead to a decrease in the overall fruiting of superior fungi. On the other hand, the management of some shrubland species can be interesting from a mycological point of view. In

Spain, *Boletus edulis*, a very valuable species associated with mature stands of 50–70 years (Martínez-Peña et al. 2012), has also been reported associated with young forest systems dominated by *Cistus ladanifer* thickets, so some management methods have also been proposed (Martín-Pinto et al. 2006; Hernández-Rodríguez et al. 2017).

Forest logging, in the short-term, seems to negatively affect the presence of ECM fungi (Kouki and Salo 2020; Danielson et al. 2020), especially if logging procedures are frequently repeated at the same site. To minimize the impact of these forestry operations on soil fungal communities, low-impact logging methods are needed, along with careful monitoring.

To prevent fuel accumulation in fire-prone forest types, especially those in Mediterranean or semiarid climates, a variety of mechanisms are used. These include mechanical mastication, thinning, and prescribed burning, often in combination. Prescribed burning is also used to encourage natural pine regeneration in some ecosystems (Hancock et al. 2009). Prescribed burning can reduce yield and fungal diversity even more than clear-cutting (Hernández-Rodríguez et al. 2015), especially in the short-term, and depending on fire intensity and fuel volume. Exceptions may be opportunistic pyrophytic species, such as some species of *Morchella* spp. (Pilz et al. 2004). In northwestern Spain, plots of Mediterranean forest dominated by *Pinus pinaster* and *Cistus ladanifer* scrub were burned in a controlled manner (Martín-Pinto et al. 2006), and there was a decrease in the total dry weight of fungi, mycorrhizal species richness and diversity, and edible mushroom production. In contrast, Fernández de Ana (2000) observed an increase in the production of *Tricholoma equestre, T. portentosum*, *Lactarius deliciosus* or *Cantharellus cibarius*, after prescribed burning. Anyway, for ECM fungi, the effect of fire seems to be much more variable (Salo and Kouki 2018) and more studies are needed in this respect in different forest ecosystems.

Human mushrooms harvesting does not seem to have a direct impact on fungal yield, richness, or fungal biomass in the soil (Egli et al. 2006; Parladé et al. 2017), unless the soil is excessively trampled by mushroom pickers; this may cause soil compaction and a consequent decrease in carpophore yield. Sometimes, in these disturbed or compacted areas, some *Morchella* species may benefit (Pilz et al. 2006). A better understanding of the effects of trampling in areas visited by large numbers of mushroom pickers is needed to ensure the long-term provision of mushroom-based ecosystem services, and to conduct proper management planning (de Frutos et al. 2019).

15.6.5 Ectomycorrhizal Applications

In mycosilviculture, controlled mycorrhization could be, in hypothesis, a useful technique to incorporate inoculum of fungi of interest to the forest soil, especially after logging, and try to improve the production of carpophores and fungal biomass of the soil.

Considering ECM fungi as the mycological group of greatest interest in the temperate forest environment, it would be possible to incorporate mycorrhizal inoculum directly into the root niche of mature trees, or to incorporate the inoculum into the forest soil by planting mycorrhizal seedlings (Dominguez-Núñez et al. 2006); the latter is the most effective method to ensure root mycorrhization with a given ECM fungal species (Hall and Zambonelli 2012).

To date, most of the experiences of "domestication" of ECM fungi have been successfully carried out on a few species and in cultivation or plantation regimes: *Tuber melanosporum* (Mannozzi 1986; Pacioni 1987) especially, but also other species such as *Lactarius deliciosus* (Poitou et al. 1984), *Boletus edulis* (Oria-de-Rueda et al. 2008a, b), *Tricholoma matsutake* (Wang and Chen 2014; Yamanaka et al. 2020), or *Terfezia Claveryi* (Morte et al. 2008).

The use of mycorrhizal seedlings could help ensure inoculum availability for subsequently established plant species (Piñeiro et al. 2013). Inoculation will be especially necessary to afforest or reforest sites with degraded soils, harsh climatic conditions or low ECM fungal inoculum potential (Querejeta et al. 1998; Sebastiana et al. 2013) or when exotic tree species are planted in non-native soils (Dell et al. 2002; Chen et al. 2006).

In Spain, studies on the incorporation of mycorrhizal seedlings "in situ" with the aim of enriching the soil inoculum of edible fungi in natural forests have been scarcely carried out, these studies being mainly oriented to plantations of *Lactarius* spp. (Parladé et al. 2007) and Black truffle (Suz et al. 2008). For example, Reyna (1999) proposed the reinoculation of mature *Quercus* spp. trees potentially producing black truffle, as well as the reconnection of roots of mature *Quercus* spp. producing black truffle trees, by opening canopies, and the subsequent planting of truffle-mycorrhizated seedlings, although the results were not clear in the short-term (Garcia-Barreda and Reyna 2012). Although many positive results have been reported in greenhouse or plantation experiments, so far it is not clear that transplanting mycorrhizal plants in natural forests improves carpophore yield or soil fungal biomass (Tomao et al. 2020), although early molecular studies are promising (Hortal et al. 2008; Suz et al. 2008).

It would be necessary to take into account the successional dynamics of ECM fungal communities in order to help choose the most appropriate mycological management strategies in relation to mycorrhizal applications. "Niche theory" (e.g., host specificity and environmental selection) has been shown to play a vital role in mycorrhizal fungal community structuring in temperate and boreal mixed forests (Twieg et al. 2007; Uroz et al. 2016). Host specificity may promote niche differentiation (Dickie et al. 2002) allowing the survival of particular groups of mycorrhizal fungi. In contrast, the "neutral theory," proposes that stochastic processes (e.g., fungal dispersal limitation) would affect fungal spore dispersal and then alter fungal community composition (Peay and Bruns 2014).

In any case, these "in situ" mycorrhizal applications have been scarce and with unclear results, being necessary more long-term studies.

15.7 Conclusions and Future Considerations

As we learn more about the biology, biogeochemical dynamics and functionality of the forest soil, as well as new knowledge about the connection and communication of trees through mycorrhizal mycelial (Beiler et al. 2010), it is reasonable to rethink traditional concepts of silviculture and forest management.

Traditional silvicultural treatments should be reviewed from the approach of the interconnectedness of a plant community through these mycorrhizal networks, especially ECM fungi; comparative studies between ECM and AM network-forming trees in the same and different environments are needed (Pickles and Simard 2017). More knowledge is needed on the generation of these interconnections between tree stands of the same or different species or age, and how natural or anthropogenic disturbances (such as silviculture) affect these mycelial networks over time (Van Dorp et al. 2020).

So far, mycosilviculture has focused primarily on the study of those ECM fungal species that are edible and/or of commercial interest, but it would be appropriate to address other ECM species that, at a functional level, build and contribute to the complex web of mycorrhizal networks that interconnect tree stands and the understory. Rhizomorph-forming ECM fungi and medium- and long-range mycelial networks (Kaur and Reddy 2019) may be of great interest to study, as well as more ubiquitous mycorrhizal species that are capable of forming symbiotic associations with a wide variety of hosts. Field stable isotope probing experiments or other means of labeling nutrient or dissolved compound transfer (e.g., dyes) can be effective in assessing the potential for fungal species interconnectedness. These types of studies can help identify whether a broader range of network-forming fungi exists, as most network studies have focused on a small number of fungal species and hosts, typically *Suillus* and *Rhizopogon* associated with conifers (Pickles and Simard 2017).

The existence of mature trees (or “Mother trees”) that can generate the greatest number of mycorrhizal network connections or “nodes” between different individuals in the stand (Beiler et al. 2010) can be a conditioning factor and a scientific basis for the selection of the most appropriate silvicultural methods of regeneration, trying to identify and maintain in reserve these key trees for mycorrhizal networks; in this way, the disturbances generated by silvicultural treatments would not completely damage these mycorrhizal networks, and a certain capacity for their regeneration could remain. In environments such as the Mediterranean forest, mature trees and deep-rooted shrubs should be retained during logging operations, in order to maintain water relations by connecting with the water table for the supply of deep water to surface soils through hydraulic lift (Pickles and Simard 2017). A diversity of tree and shrub species, including genotypes migrated from warmer or drier climates (Pickles et al. 2015), should be managed for the resilience they confer to the ecosystem (Aitken and Bemmels 2016). Trying to minimize soil compaction around retained trees during forest harvesting can also help preserve MNs. In the Mediterranean forest, where drought intensity is expected to increase, it is also likely to be important to consider replanting in several years after harvesting to try to maximize the chances of successful regeneration (Pickles and Simard 2017).

In addition, selective planting of mycorrhizal seedlings with ECM species of interest could enrich the mycorrhizal inoculum of the forest soil, and improve and recover disturbed networks. It would be useful to develop a better knowledge of those ECM fungal species that, from a functional point of view, are facultative saprophytes; this dual ectomycorrhizal/saprophytic functionality could help in their responsiveness, resilience, viability, and recovery capacity in the face of a silvicultural disturbance; in the face of an interruption of its food source (host tree), the fungus could remain alive and dormant in saprotrophic conditions.

In general, silvicultural practices must be mitigated to protect fungal diversity and the loss of suitable habitats for threatened fungal species. In particular, trade in edible fungi needs to be regulated; laws to prevent overexploitation should be introduced in all European Mediterranean countries; and action plans for the conservation and management of selected species in Mediterranean forests are urgently needed (FAO and Plan Bleu 2018).

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Chapter 16

Mineralization of Soil Carbon, Nitrogen, and Phosphorus and Role of Nanofertilizers in Soil Fertility and Plant Growth

Rajni Gupta

Abstract Soil functions as a vital living ecosystem that sustains plants, animals, and humans. Soil is not an inert medium, but it contains living organisms such as bacteria, fungi, and other microbes that are foundation of an elegant symbiotic ecosystem. The majority of plants live in close association with the diversity of soil microorganisms. They play an essential role in establishing symbiotic associations and thereby contributing to the growth of plant and indeed help in maintaining soil health. In the rhizosphere, a myriad of plant–microbe interactions occurs; therefore, the microorganisms that inhabit the rhizosphere are of great significance. Among a variety of soil microorganisms, the microbes such as rhizobacteria and arbuscular mycorrhizal fungi play very significant role in facilitating nutrient supply to their host plants and improve soil fertility. The use of plant materials in soil works as a conditioner and influences the carbon, phosphorus, and nitrogen cycles in soil–plant system. The process of mineralization in the soil contributes to the circulation of these nutrients, which is actually achieved by the action of saprophytic and pathogenic microorganisms. Shrinking cultivable land coupled with increasing population has created an increasing and immediate demand for new technologies. In recent era, nanofertilizers are a booming field. Nanotechnology acts as driver for modern-day smart and efficient practice. They are also helping in the maintenance of soil nutrients, stimulate plant growth, and provide resistance to disease. In the present review, a holistic view of the interaction of soil, plant, and microbes, sequestration of minerals, and role of nanotechnology in maintaining the soil health have been discussed.

Keywords Microbes · AM fungi · Carbon · Nitrogen · Phosphorus · Nanofertilizers

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B. Giri et al. (eds.), *Structure and Functions of Pedosphere*,
https://doi.org/10.1007/978-981-16-8770-9_16

16.1 Introduction

The development of plants depends on the interaction of external factors such as light, gravity, and internal factors. In the soil, the growth of root system is affected by a wide range of soil properties; interestingly, the properties of soil are modified by the plant roots by way of secreting certain chemical substances. There are a plethora of dynamic reactions occurring at the root surface whose consequences are felt at a range of temporal and spatial scales. Young and Crawford (2004) have drawn attention to the important microbial and physical processes in soil. Concerns for terrestrial biotic diversity are also giving rise to the need for greater understanding of soil–plant interactions, leading to an integrated bio-geodiversity perspective in efforts to preserve land role of microbes in the dynamic generation of soil structure. Plant roots release certain compounds known as root exudates such as sugars, amino acids, fatty acids, nucleotides, secondary metabolites, and other important compounds, which are helpful in the establishment of rhizosphere microbial population. Microbes and plants receive and send multiple signals for recognition of microbes, mycorrhization, and quorum sensing (Oberai and Khanna 2018).

Soil organic matter mineralization is an important process in which carbon and other nutrients are converted to CO_2 and available form of nitrogen, phosphorus, and sulfur. Carbon mineralization is coupled with the release of mineral, i.e., N, P, and S, which can be driven by microbial requirement for C and nutrients for their growth, maintenance, and the production of enzymes (Vitousek et al. 2010). There is a positive ecological interaction of microbes with plants that helps in the promotion of plant growth. During the nineteenth century, the role of mycorrhiza and nodulating bacteria was well recognized (Morton 1981). However, some researchers (Valentine et al. 2012) reported that elongation of root is related to physical properties of soil rather than chemical properties. Later, it was revealed that *Pseudomonas* and *Azospirillum* also help in promotion of plant growth (Lin et al. 1983). There was a shift from an individual microbial strain to abundance and diversity of root microbiome through metagenomics. Outcome of these sequence studies is that rhizospheric niche is a hotspot of ecological richness, and enormous number of microbial taxa is there (Bulgarelli et al. 2013).

Recently, nanotechnology is proved to be a boon of this era, as it is widely used in various fields of science and technology. It is a most versatile technology, finding an application in material and living world. In various agricultural practices, nanotechnology has been utilized for the controlled arrival of agrochemicals and target-specific delivery of biomolecules (nucleotides, proteins, and activators) (Chhipa 2017). Soil is a natural matrix and rich in natural nanoparticles both as a primary particle and as agglomerates. Some nanoparticles influence crop improvements, plant advancement, yield, and huge number of them are aggregated in various plant tissues (Tripathi et al. 2017).

In the present review, emphasis is given to gain an understanding of how soil microbes boost plant growth and pedosphere in relation to root and soil microbe tailored to carry out specific functions and about the role of nanofertilizers in maintaining the soil health and enriching soil nutrients.

16.2 Pedosphere: A Center for Plant–Microbe Interactions

Soil works as a framework with the environment and use of land, plant, and living system efficiently. Solid soil keeps the network of relationships with plant roots, reuses fundamental supplements, and improves soil structure and soil water-holding capacity. The word pedosphere is derived from the Greek word “Pedon”—soil and “Spharia”—sphere. It is the outermost layer of earth, which is composed of soil and acts as a skin of earth develops due to interaction of biotic and abiotic interaction. Soil formation takes place with the physical and chemical breakdown of minerals due to which upper layer is formed. Plant roots and soil microbes play a great role in maintaining the equilibrium of gases in the atmosphere, as plant roots and microbes release CO_2 into the soil that escapes from the pedosphere to the atmosphere. By the process of sedimentation, rainfall, and gas diffusion, gases are added into the soil. Soil contains various types of microorganisms such as bacteria, actinomycetes, molds, algae, and protozoa. Each organism produces particular type of chemicals and influences the development of other organisms. These activities in soil are essential for the growth of plants. Microbes, insects, and worms bring about changes in soil and maintain the soil fertility. Animals present in soil are important in the development of soil profile. The conversion of raw organic matter to humus is facilitated by worms present in soil. Ants transport sandy and gravelly soil materials and incorporate the fragments of their vegetation in their mounds, better than earthworms. At place where water table is near the surface crabs and crawfish are active, they move and mix large amount of earth, and this activity influences soil aeration and water movement. Soil has definite layers of horizons physically, chemically, and biologically derived from the earth’s mantle. Each horizon has its own particular morphological, physiological, and constitutional features. These features are determined by their parent material, climate, biosphere, and topography. Every well-developed soil has its own characteristics, which is a mineral–biological complex of organic and inorganic substances. Soil microorganisms live chiefly in colloidal complex of organic and inorganic materials, supported by soil particles and saturated with water. Microorganisms present in the soil are influenced by moisture, temperature, pH, food supply, biotic factors, aeration, and radiant energy. Particular organism has its own requirements. Oxygen and hydrogen are available abundantly, but nitrogen is present in limited amount in air. Nitrogen-fixing bacteria and algae can use atmospheric nitrogen. Soil organic matter in the usual sense is more or less humidified material, which is a complex mass resulting from microbial action on dead organism. Partially humidified material is unstable and difficult to maintain. The circulation of nutritional elements in nature takes place by decomposition of plant and animal remains. Carbon is returned to circulation as carbon dioxide, and nitrogen is made available as ammonia and nitrate. Stabilized organic matter build-up in cultivated soils is always limited by moisture, temperature, and aeration and controls the C/N ratio in soil. The development of heterotrophs is influenced by the energy materials, and there is a competition between heterotrophs and microorganisms carrying on the decomposition. If nitrogen content is 1% or less, it is consumed by microorganisms and they compete with higher plants for more nitrogen. It can lead to nitrogen starvation and can be corrected by addition of inorganic nitrogen fertilizers. Final stage of decomposition is humification, characterized by the formation and gradual continual decomposition. The soil microorganisms are active in these zones of decomposition.

16.2.1 Root–Soil Interface

The interface between the soil and the root is complex and ill-defined boundary. Products are released from roots into the soil, which changes its physical and chemical properties, and stimulates the growth of microorganisms. In turn, the root tissues are associated with root products also provide physical shelter for many microorganisms. This complex environment, where root and soil meet, is known as rhizosphere. First time, this term was coined by Hiltner (1904), and it was employed in the specific context of the interaction between various bacteria and legume roots, in studies that he undertook on the value of green manures. Roots and soil particles are frequently in intimate contact, with root hairs, mucilage, and microbes forming a zone of multiple interactions between the plant and soil. Mucilage of both bacterial and plant origin is able to bind soil particles on drying and to retain the particles on subsequent rewetting; root soil and organisms interact to determine the rhizosphere environment. The fungus has its highest population near the root zone of the infected stubbles after the plant dies. The population of the fungi increase saprophytically manyfold in the infested plots. The dynamic capacity of soil–plant system and interface depends upon the release of nutrients, changing from a solid state to the soluble state, translocation to plant from the soil, and assimilation by plant. All these factors determine the relationship between the supply of nutrients and its uptake by plants (Comerford 2005). Biotic factors such as biomass and microbiome and edaphic factors such as moisture, pH, water-holding capacity, and cation exchange potential regulate the concentration of nutrients in soil.

Plant growth and development are controlled by the soil environment in the root region where microbial activity constitutes a major influencing force. Availability of nutrients in the rhizosphere is controlled by the combined effects of soil properties, plant characteristics, and the interaction of plant roots with microorganisms and the surrounding soil (Bowen and Rovira 1999). Roots play an integral role in root–soil interface in providing nutrients, water, and minerals with the help of ecto- and endomycorrhiza (Chugh et al. 2021). The loss of carbon compounds from intact root into soil is a widespread process. Root exudates are metabolites leaked and released passively across the membrane from intact cells along a concentration gradient. The uptake and transfer of nutrients from the soil to plants facilitate by the process of diffusion or bulk flow. Soil microorganisms are responsible for driving organic matter and nutrient cycling, maintaining soil fertility and plant health, and modulating primary productivity of ecosystem. Root exudates differ in secretion, lysates, gases, and mucilage. The release of low molecular weight root exudates is of particular importance for its nutrient dynamics in the rhizosphere. Different types of microorganisms are present around the root. They are of various types in their behavioral pattern with roots and can be symbiotic and parasitic. The composition and quantity of root exudate are changed when root is associated with pathogen such as *Pseudomonas putida* (Prinkyl and Vancura 1980) and free-living and symbiotic nitrogen fixers.

Arbuscular mycorrhizae (AM) are soil-borne fungi, and they can significantly improve plant nutrient uptake and resistance to several abiotic factors. They are obligate biotrophs and ingest the photosynthetic products and lipids to accomplish their life cycle (Jiang et al. 2017). AM fungi are symbiotic in their association, facilitate the host plants to grow vigorously under stress conditions by mediating a series of complex communication events between the plant roots and the fungus leading to increased photosynthetic rate and other gas-related traits (Birhane et al. 2012). AM fungi improve the quality of soil by influencing structure and texture of soil and plant health under the normal and stressed conditions. As AM fungi are natural growth regulators, improve the tolerance of plants and bring about changes in morphophysiological features. AM fungi have been suggested to be used as biofertilizer by several researchers, which is naturally present in soil and improve soil fertility and health. It can be a replacement of inorganic fertilizers. The external hyphae of AM fungi provide a physical or nutritional substrate for bacteria. Studies done by Bagyaraj and Menge (1978) reported that more number of bacteria and actinomycete were present in the mycorrhizosphere of AM-inoculated plants. Bansal and Mukerji (1994) reported decrease and alterations in the total number of fungal colonies in the rhizosphere of AM-inoculated plants. Increase in flow of phosphorus in mycorrhizal roots is about 3–4 times greater than in nonmycorrhizal roots. This is due to increased/efficient uptake and the existence and continued growth of extra-matrical mycelium into soil. Mycorrhizal roots can exploit the sources of P; therefore, plants colonized by mycorrhizal fungi are more effective in extracting P from soil.

16.2.2 Microorganism–Soil Interface

Microorganisms present in soil play a peculiar role in managing soil fertility. Soil fertility can be classified as active and potential. In case of active fertility, the nutrients are easily available to the plants, while in potential fertility nutrients get available by microbial and chemical action on organic matter; therefore, soil microorganisms play a vital role in providing the nutrients to plants. Nitrogen present in the atmosphere in gaseous form represents a vast store of potential fertility; however, plants cannot use this nitrogen at their own (Bollen 1959). Nitrogen-fixing bacteria absorb this gas from nitrogen and convert it to cell protein and make it available to plant.

Indeed, soil contains a huge number of microorganisms such as molds, algae, bacteria, fungi, actinomycetes, and protozoa, which produce chemicals and thereby affect the development of several organisms. These microorganisms are essential for the development of higher and lower plants and fertility of soil. Well-developed soil has its own distinctive profile characteristics. It is a mineral–biological complex of organic and inorganic substances. Soil fertility has three components: chemical, physical, and biological fertility. Biological interaction in relation to microbes and soil is a very complex and dynamic process; the organisms, which are present in the soil, interact with other components and play a vital role in nutrient cycling (Christopher 2017). Various microorganisms present in the soil play very important role as:

1. Acts like a cementing agent as they bind to soil particles, so that they reduce and prevent soil erosion.
2. Adds organic matter in soil.
3. Plays a major role in maintaining the soil fertility.
4. In barren area or soil, checks the loss of nitrates.
5. For longer period, can retain the water and increase the water-holding capacity.
6. When the microorganisms die, they increase the amount of organic carbon in soil.

16.2.3 Mineralization of Nitrogen

Biogeochemical cycling of nitrogen is changed by anthropogenic activities (Elser et al. 2007). Excess deposition of nitrogen has adverse effects on the soil health by way of acidification, nutrient imbalance, nitrate leaching, loss of biodiversity, and decline of forest (Bobbink et al. 2010). Temperate forests are usually nitrogen-limited, while the tropical forests are phosphorus-limited under natural conditions, and soil is acidic in nature and low in base cation (Hall and Matsoon 2003). Soil microorganisms are deriving force of decomposition process, but soil nutrient availability influences soil microbial activity and plant growth (Gilliam et al. 2011).

Endomycorrhizal fungi are also involved in nitrogen transfer from legumes to grasses (Haystead et al. 1988) as their extraradical hyphae have the ability to extract and transport nitrogen from the soil to plant. They contain some enzymes, which influence nitrogen fixation rates by reducing stress imposed on plants. Nitrogen exists in free form, nitrate, nitrite, ammonium ions, and organic nitrogen. Ammonium is less mobile in soil, and hyphae of endomycorrhizal fungi help in transport of such immobile ammonium to plant roots and showed increased nitrate reductase activity. Mycorrhiza can affect N-cycling, as it has capacity to extract N and transport it from soil to host plant. Its absorption and accumulation involve reduction mediated by nitrate reductase. Mycorrhizal interactions with the synthesis of nitrate reductase may be related to the improved availability of P to mycorrhizal plants (Ramarao et al. 1999). Termite nests represent large pools of nitrogen in many ecosystems, and the ability of plants to extract nitrogen via mycorrhizal hyphae could be an important pathway for nitrogen incorporation into actively cycling fractions (Salick et al. 1983). The extraradical mycelium can improve uptake of nutrients, so improves the development and plant growth. Nitrogen is a main source of fertilizer, as it is main source of soil nutrition. Smith et al. (2011) reported the role of AMF in uptake of soil nutrient, especially N and P, which promotes the growth of plants. It has been also reported that AMF has the ability to take substantial amount of nitrogen from dead and decayed material; later on, it increases their fitness and stays alive. AMF renders them the main stakeholder of global N pool, which is equivalent to fine roots. Several studies have shown that about 20–75% of the total N uptake of AM plants can be transferred by the AMF to their hosts.

Ramirez et al. (2012) reported that the addition of nitrogen to soil lessens microbial activity by changing soil bacterial communities, which are less capable of decomposing soil carbon pools. Strickland et al. (2009) found no relationship between microbial community structure and carbon mineralization process in soil. From these studies, it is clear that carbon cycling is changing in response to nitrogen addition, driven by complex interactions among microbial composition, enzymatic capability, and soil carbon chemistry. Liu et al. (2013) observed that microbial biomass plays a significant role in nutrient cycling of ecosystem as it represents the important labile pool of nutrients in soil. The abundant nitrogen in soil could increase fungal abundance and decrease carbon compounds (Fig. 16.1).

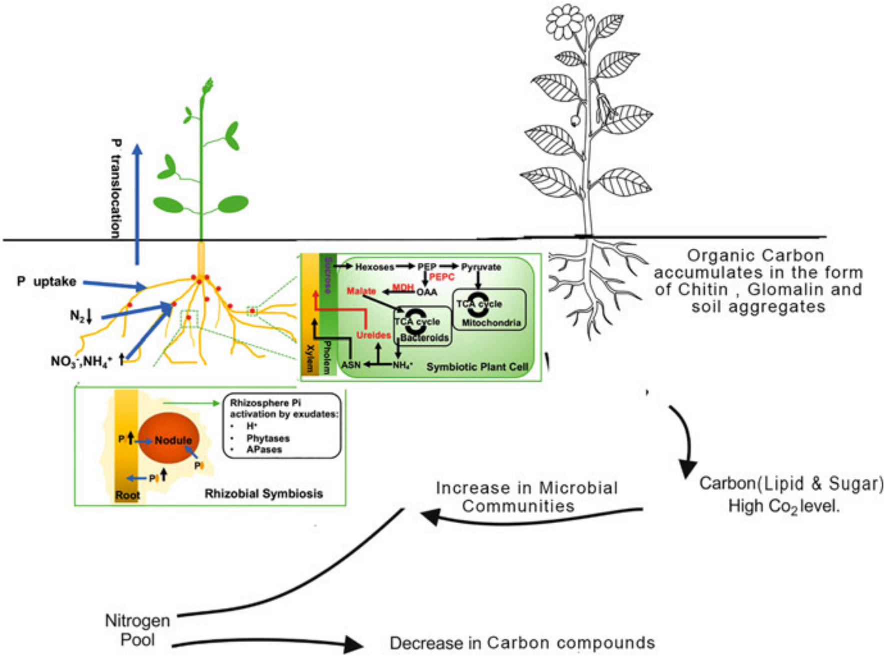


Fig. 16.1 Network of Mycorrhizal hyphae, *Rhizobium,* roots of plants present under the soil and communication of biochemical signalling and nutrient to maintain soil and plant health

16.2.4 Mineralization of Phosphorus

Soil is a major source of plant nutrients and is actually a complex ecosystem hosting bacteria, fungi, protists, and animals (Bonkowski et al. 2009; Muller et al. 2016). Various studies have been focused on alleviating pathogenic effects such as herbivory and infection (Strange and Scott 2005), or attenuating abiotic stress conditions (Yaish et al. 2016; Meena et al. 2017). However, there has also been longstanding interest in characterizing the positive ecological interactions that promote plant growth. Arbuscular mycorrhizal (AM) fungi have symbiotic relation with more than 90% of terrestrial plants (Gupta and Mukerji 2002). AM fungi are well known for its N, P, K, Ca, Zn, and S uptake and provide nutritional support to plants (Balliu et al. 2015). Phosphorus is transported predominately as polyphosphate down concentration gradient between hyphal tips and sink, so they can significantly boost the phosphorus concentration in root and shoot system both (Al-Hmoud et al. 2017). The nonsoluble phosphorus is trapped from beyond the depression zone and other microbes helps in circulation, following its entry into mycorrhizal hyphae and then translocated into the space of the symbiotic interface, is the unusual step in the transport process. AM fungi increased the rate of phosphorus movement between the soil and plant. AMF inoculation is directly linked to the uptake of N, P, and carbon, which move toward roots and promote the developments of tubers. AMF helps in uptake of P and N and helps in the development of plant under different irrigation conditions (Liu et al. 2018). Evelin et al. (2012) reported that AMF improves the uptake of all essential nutrients but decreases the uptake of Na and Cl, leading to growth stimulation. AMF inoculation improves C and N accumulation and N assimilation under ambient and elevated CO2 concentrations (Zhang et al. 2020).

There is a mechanism of mycorrhizal activities, which increases concentration of mobile soil phosphorus and its transport to host plant root.

1. Interaction between phosphate solubilizing bacteria and AM fungi.
2. Production of organic acids by AM fungi, solubilizing immobile phosphate.
3. Production of enzymes like phosphatase by AM fungi.

Azcon Aguliar et al. (1986) reported about AM fungal hyphae stimulate phosphate ions, transport them to plants, and increased the growth of plants. When plants were inoculated with AM fungi, acid phosphatase activity was found to be increased. The microbial phosphorus limitations can be a common problem in highly weathered soils, where phosphorus binds to the iron or aluminum sesquioxides (Jiang et al. 2017). Addition of phosphorus changes microbial community structure by increasing the abundance of AM fungi, which obtain carbon from their host plants in return of microbial nutrients (Smith and Read 2008). When phosphorus and nitrogen are limiting factor for plant growth, plants provide more carbon to the AM fungi in exchange of nutrients (Tresender 2004). Phosphate fertilizer can suppress the indigenous AM endophyte population more than selected endophyte added as an inoculant. Mycorrhizal fungi are more efficient absorbers for nutrients from the soil than the plant roots (Allen 1991); therefore, the adequate availability of AM fungi in the soil has often been found to boost plant growth. Soil pH can also be changed after additions of phosphorus that results in the increased AM biomass in soil (Rousk et al. 2010). AM fungal association with plant root appears to allow plants to acquire resource under the time of acute stress. These fungi can also increase the uptake of mineralized phosphorus by occupying the microsites of active decomposition. Bacteria like *Bacillus*, *Escherichia coli*, *Pseudomonas*, *Streptomyce*s, *Penicillium*, and *Curvularia*, and fungi like *Trichoderma* are commonly associated with dissolving phosphatic components such as rock phosphate and bone meal (Verma and Hock 1995).

16.2.5 Mineralization of Carbon

The health of soil, plants, animals, environment, and the individuals is one and indivisible. Strategy regarding the restoring soil has various benefits; for example, sequestration of carbon dioxide in soil as organic and inorganic carbon is known as carbon farming enables soil carbon stock to be traded as a farm commodity. For achieving global food and national security, it is essential to increase soil carbon stock. Carbon sequestration through conservation also helps to filter pollutants, renew freshwater supplies, increase water supplies and plant available water capacity, moderate soil temperature, and improve soil resilience against agronomic drought. These strategies can be helpful in reducing carbon footprints and can be cost-effective.

Prominent role of AMF as symbiotic association is to transfer soil mineral nutrients to their partner plants. AM fungi play a fundamental role in the global carbon cycle as these fungi can utilize 20% of plant photo-assimilates under ambient CO_2 conditions and store organic compounds such as chitin, glomalin, and other organic compounds that protect plants and promote soil aggregate formation (Jakobsen and Rosendahl 1990; Chang et al. 2012). High CO_2 level stimulates the use of photo-assimilates by the AM fungi and supports the growth of plant. This suggests that in terms of soil, higher level of sequestration may be achieved through mycorrhizal symbiosis (Alberton and Gorissen 2005). AM fungi play an important role in nutrient cycling.

Nutrient limitation is a key to predicting how the carbon cycle responds to environmental change to resolve this problem, which is a complex process (Townsend et al. 2011). These fungi capture the nutrients released by dying plants and translocate these to living plants. These fungi are important factor in decay-related nutrient transfer (Newman 1988). AM fungi play a critical role in nutrient cycling in ecosystem and also modify plant root systems. In recent years, great progress has been going on in relation to C: N: P stoichiometry in terrestrial ecosystem that focuses on microorganisms, plant leaves, and litter (Anzoni et al. 2010). So, C: N: P stoichiometry can be used as powerful tool to understand nutrient cycling and processes in soil (Cleveland and Liptzin 2017). Tian et al. (2010)

reported that soil C: N: P stoichiometry could be potential indicator for assessing soil nutrient status during soil development. Soil nutrient stoichiometry is more complex than in plants in the response to nutrient availability. Nutrient mobility in soil is influenced by both fertilization and plant uptake. Qaswar et al. (2019) studied the C: N: P stoichiometry that influences the soil nutrient in paddy soil. The SEM studies showed that soil C: N: P stoichiometry indirectly affected the P uptake by controlling P transformation and mobility in paddy soil. Comparison was made in no fertilization and chemical fertilization soil, i.e., CK and NPK treatments. The NPKM treatment significantly increases the phosphatase activities in both soils. The soil C: N and C:P ratios were highest in CK treatment, and no significant difference was observed between NPK and NPKM treatments in both soils.

16.3 Nanofertilizers: The Next-Generation Fertilizers

Nanotechnology engineering is the latest technology that explains unique targeted features with elevated strength. Term “Nanotechnology” was coined by “Noris Taniguichi” in 1974. Nanoparticles can be beneficial in the development of sustainable agriculture. The advancement in the fabrication of nanomaterials of different shapes and sizes may be helpful in the field of medicine, environmental science, and agriculture. Agriculture is facing various challenges such as nutrient deficiency, environmental pollution, and biotic and abiotic stress. With the emergence of nanotechnology, there is an enhancement in bioavailability, bioactivity, and adherence effects of nanoparticles (Gutierrez et al. 2011). Nanofertilizers are synthesized by protecting nutrients alone or in combination on the adsorbents with nanodimension. Nanofertilizers deliver nutrients in three ways;

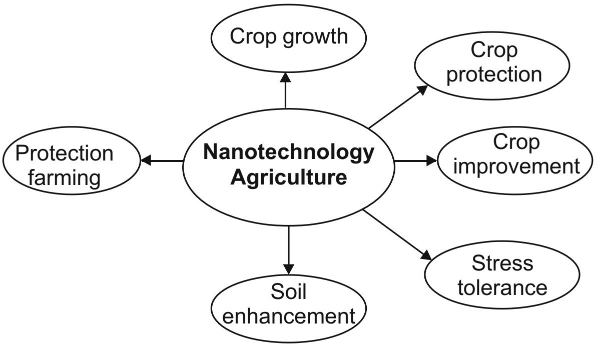
1. by coating nanotubes with a thin protective polymer film,
2. delivered as particles,
3. by emulsions of nanoscale dimensions (Nagula and Usha 2016).

Iranian researchers produced first nano-organic iron-chelated fertilizers. Nanomembrane-coated particles facilitate slow and steady release of nutrients, and this process helps to reduce loss of nutrients and fertilizer use and therefore improve the efficiency of crops (Subramanian and Tarafdar 2009).

16.4 Nanofertilizers in Soil: New Window for Sustainable Agriculture

To obtain higher agricultural productivity and to meet higher global population demand, plant mineral nutrition is an important factor. Nanotechnology can provide sustainable solutions by replacing traditional bulk fertilizers with their

Fig. 16.2 Application of nanotechnology



nanoparticulate counterparts having superior properties to overcome the current challenges of bioavailability, uptake of minerals increasing crop yield, reducing wastage of fertilizers, and protecting the environment.

Nanofertilizers can be formed by using microbial enzyme for breakdown of particular salts into nanoform. Nanofertilizers are eco-friendly and improve soil aggregation, moisture retention, and build-up of carbon. It is suitable for all varieties of crops including vegetables, food grains, and horticulture. Efficiency of elements can be increased by the use of nanofertilizers even toxicity of soil can be reduced (Naderi et al. 2011). Iron nanofertilizers are made up of organic and mineral material and are compatible with the environment and agricultural farms and organic material.

Iron and silicate nanoparticles originate from natural weathering of bedrocks, and iron oxides (2–5 nm length) nanoparticles are associated with organic matter in river-borne material (Allard et al. 2004). Plants can easily and rapidly absorb these compounds. Zeolite is an another nanoporous fertilizer, and release of the fertilizer to plant is slow, so that plants can absorb entire amount of nutrients from the fertilizer supplied (Naderi and Danesh-Shahraki 2013).

Recent advancements in tissue-engineered nanoparticle-based targeted delivery of CRISPR/CAS, m-RNA, and Sg RNA for the genetic modification of crops are a noteworthy scientific achievement (Ran et al. 2017). Nanotechnology provides superb solutions for environmental challenges such as the development of nanosensors has extensive prospects against environmental stress and increasing the combating potentials of plants against disease (Worrrall et al. 2018) (Fig. 16.2).

In our conventional method, agrochemicals are generally applied by the spraying method so that very low amount of fertilizer is available at a particular site rest to the crop, which is required in a very less amount for the plant growth. Loss of nutrients can be in the form of leaching, hydrolysis, photolysis degradation, and by microbial degradation (Nair et al. 2010). With the advancement in nanotechnology-based synthesis of slow or controlled release fertilizers, herbicides and pesticides have received an extra attention in agricultural farming (Panpatte et al. 2016).

Nanoparticles have some advantages:

1. Effective delivery of agrochemicals due to their large surface area.
2. Easy attachment.
3. Improve stability of agrochemicals.
4. Protect them from degradation.
5. Increase effectiveness of nutrient supply.
6. Reduce rate of loss of fertilizer nutrients into soil by leaching and leaking.

16.5 Plant Growth and Nanofertilizers

Nanotechnology is revolutionizing modern agriculture. The use of nanoparticles (NPs) is becoming popular in plant sciences, as vehicles of biomolecules (Parisi et al. 2015). Nanoparticles interact with plants and attribute to many morphological and physiological changes, depending upon the efficiency of nanoparticles. NP efficacy is dependent upon their size of chemical composition, reactivity, surface covering, and the amount of dose, which is effective. The NP encapsulate nutrients in a nanothin protective film or nano-emulsions, which ensures a stronghold of nutrients on the plant surface due to the higher surface tension of the nanocoating (Iavicoli et al. 2017), thus improves crop efficiency (Sanzari et al. 2018). Nanoclays and nanozeolites are used for efficient release and retention of water and nutrients in the soil (Mandal et al. 2019). Zeolite NPs have well-defined pore networks, which facilitate the slow release of agrochemicals. Nanofibers and nanowires help in the development of nanosensors and diagnostic devices for the detection of pesticides and fertilizers (Reguera 2018; Kundu et al. 2019). Prasad et al. (2012) investigated the effect of $ZnSO_4$ and nanoscale ZnO particles on the peanut seeds; however, results were not very promising. It was reported that plant growth in terms of plant height was significantly increased by 400 and 1000 ppm nanoscale ZnO, compared to control and bulk $ZnSO_4$ concentration.

Carbon nanotubes (CNTs) are allotropes of carbon that can be utilized as a vehicle to deliver desired molecules either nutrient or biocides into the seeds during germination. Nanoscience is also involved in the development of approaches to a range of in expensive nanotech applications for enhanced seed germination, plant growth, and development. Germination of seeds is a sensitive phase in the life cycle of plant as it is affected by different parameters, i.e., genetic trait environmental factor, moisture, and soil fertility. Liang et al. (2013) reported that treatment of seeds with different concentrations of carbon nanoparticles increased leaf area at the maturity age. Raliya et al. (2014) reported that nano-MgO (15 ppm) application in cluster bean significantly increases in the root length and root area and chlorophyll content was there. Rhizospheric microbial population was also increased by the application of ZnO nanoparticles (Raliya and Tarfdar 2013).

16.6 Green Nanoparticles

Nanotechnology offers effective application that varies from traditional chemical techniques to medicinal and environmental technologies. Nanoparticles can be organic, inorganic, or hybrid ranges from 1 to 100 nm. They exist in the natural form by the process of volcanic eruptions, photochemical reactions, erosion, plants, animals, or microorganisms (Dahoumane et al. 2017). Green method has triggered synthesis of AgNPs using different sources like plants, bacteria, fungi, and algae, so that with less contamination large amount of production can be achieved. It is an eco-friendly and biocompatible process, generally using the plant and microbe extract. A large number of microorganisms have been in use for the synthesis of nanoparticles, i.e., *Verticillium, Fusarium, Aspergillus, Phanerochaete chrysosporium*, diatoms, *Clostridium,* and *Klebsiella aerogenes,* which are silicon-, zinc-, silver-, and gold-based (Kitching et al. 2015).

16.7 Conclusions and Future Perspective

Microorganisms that frequently experience environmental changes have been found to be more resistant to various disturbances. The populations of microbial groups involved in C, N, and P cycling are mainly governed by soil C: N: P stoichiometry. Functionally specialized groups of microbes carry out ecosystem functions and are of pivotal importance for carbon and nutrient cycling in terrestrial ecosystem. Therefore, functional microbes that carry out integral biogeochemical processes are necessary for proper ecosystem functions. Nanoparticles recently have attracted research interest due to their surface area and other properties like absorption, sites for all involved molecules in a small space, which lead to faster transport of nutrients. The unique properties of materials at nanoscale open an excellent possibility for nanotechnology to be used in crop and soil management. Nanomaterials are used to regulate the controlled release of nutrients, fertilizers, and pesticides. Recent studies have shown that nanoparticles of essential minerals and nonessential elements affect plant growth, physiology, and development. Hence, the development of new technology for the production of nanoparticles, with their application, has special significance with reference to sustainable agriculture and environmental system.

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Chapter 17
Soil Proteomics: Diversity and Functions

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and Latha Muringatheri Ramaiyer

Abstract Soil is a finite natural resource enriched with various natural antimicrobial compounds including proteins and peptides that originated from different sources such as plants, animals, and microbes. Anthropogenic activities positively modified metabolic activities and soil microbial population. Proteomics is a field of study that gives an insight into the composition, functions, and interaction between soil proteins. The composition of total and functional proteins varies under stress conditions, which can be studied by proteomics. Further, when the situation changes, alteration in the expression of functional proteins occurs. The microbial community in soil serves as an indicator of soil quality. Characterization and classification of soil protein help to study the association of soil microbes in soil health enhancement, pollutant detoxification, and biogeochemical dynamics. The identification envisages which process of degradation influences protein and microorganisms.

Keywords Soil protein · Proteomics · Microbes · Soil health

17.1 Introduction

Soil is a natural environment inhabiting the greatest microbiota in terms of biomass and diversity in which soil microbes perform an essential task in the decomposition and transformation of soil materials and are involved in carbon, nitrogen, and phosphorus cycle system. Within this system, microorganisms perform an essential task in the decomposition and transformation of soil materials and are involved in

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B. Giri et al. (eds.), *Structure and Functions of Pedosphere*,
https://doi.org/10.1007/978-981-16-8770-9_17

carbon, nitrogen, and phosphorus cycles. However, the relationship between microbial community and the surrounding gained much more attention in recent years (Bastida et al. 2009). Monomeric amino acids linked by peptide bonds produce organic compounds called proteins. They are involved in various life processes such as extracellular substrate generation and metabolism (enzymes), transport of substrates, products, and catalysts across cell walls and within cellular compartment cell–cell communication. A glycoprotein viz. glomalin synthesized by the extraradical hyphae of arbuscular mycorrhizal fungi (AMF) was identified in 1996 (Wright et al. 1996). It represents the major portion of immobilized carbon in soil because of the resistance offered to microbial hydrolysis. Glomalin plays a crucial role in restraining global warming by acting as a carbon sink. Soil microorganisms play a vital role in transforming the nutrients into various forms through biochemical reactions. All these biochemical processes are catalyzed by enzymes, which are proteinaceous with catalytic properties. The energy required for the activation of reactions catalyzed by enzymes is relatively low as compared to non-enzyme-catalyzed reactions (Browman and Tabatabai 1978). Reaction rates of soil enzymes are markedly dependent on pH, ionic strength, temperature, and the presence or absence of inhibitors (Tabatabai 1982). Plant residue addition to the soil helps in augmenting soil enzymes. The activity of enzymes is higher in the rhizosphere than in bulk soil due to the presence of specific organisms (Skujins 1967). Hydrolases (they catalyze the hydrolytic cleavage of chemical bonds), oxidoreductases (they catalyze oxidation–reduction reactions), transferases (they catalyze the transfer of molecular substances among molecules), and lyases (they catalyze the removal of groups from substrate molecules without hydrolysis) are few important enzymes detected in soils (Dick and Tabatabai 1993). Enzymes are continuously synthesized, accumulated, and/or decomposed and hence play a key role in the transformation of plant nutrients in the soil ecosystem (Dick 1997; Tabatabai 1994). The process of mineralization of nutrients in the soil is catalyzed by the soil enzymes (Tate 1987). Plant–microbe interactions are influenced to a greater extent by the substances exuded by roots and rhizosphere microbial load. Plant type, physiological mechanism, biotic and abiotic stresses are the major driver that alters the amount of substances released by roots (Vives-Peris et al. 2020). Carbohydrates, amino acids, proteins, phenolic compounds, and some secondary metabolites are the substances released by the plant roots. The organic acids such as citric and malic acids are also liberated, which attract the microbes. The symbiotic association and plant growth-promoting rhizobacteria (PGPR) with plants are favored by root exudates. Herbivory, parasitism, competition, and allelopathy are some of the harmful interactions subdued by the exudates of roots as well (Olanrewaju et al. 2019). Plant and soil have intricate communication among them which remains less explored. Metaproteomic analyses provide a direct measure of rhizosphere microbial biomass, their multitude functions, and metabolic dynamics in the rhizosphere soil (Li et al. 2019; Zampieri et al. 2016). Proteomic studies on a large scale encompass their structure and physiological role. Proteins are fundamental units of biomolecules of living organisms. Sources of proteins and their interaction with other soil materials are shown in Fig. 17.1.

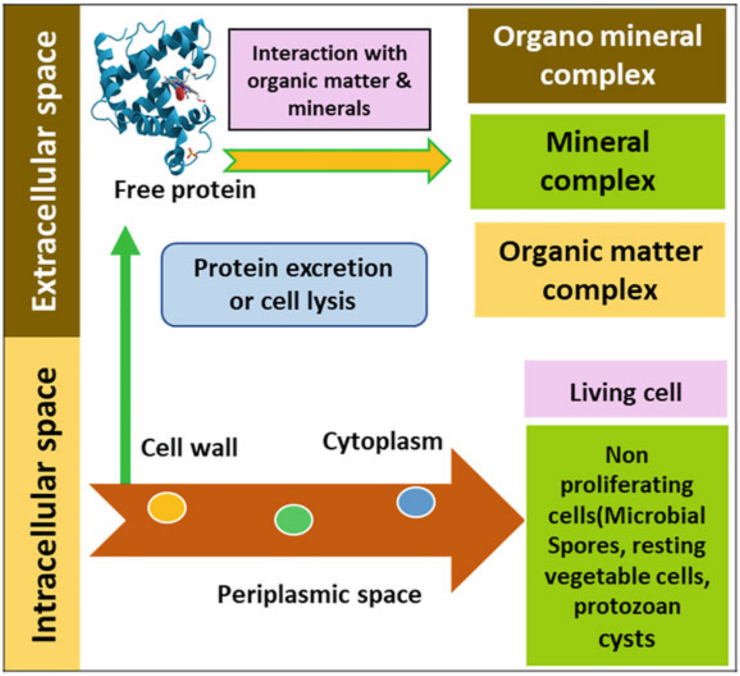

Fig. 17.1 Different sources of soil protein and interaction with organic matter and minerals

17.2 Metaproteomics Vs. Proteomics

Proteins liberated by a living organism are called proteome, which sounds like a word genome. The field of study, which includes a group of proteins released by microbes at a particular point of time in an ecosystem, is termed metaproteomics. To identify and characterize the activity of microbes and their metabolic pathways in different environments, metaproteomic study can be used (Benndorf et al. 2007; Maron et al. 2007; Zampieri et al. 2016). Protein distribution in the soil matrix is location-specific. Soil proteins are of two types viz. intracellular and extracellular proteins (Fig. 17.1). Cytoplasmic ectoenzymes and periplasmic enzymes present in gram-negative bacteria are grouped under intracellular proteins. Whereas proteins in soil solution or adsorbed to SOM or minerals in the soil are extracellular proteins (Nannipieri and Smalla 2006). In the field of metaproteomics, low abundance, less yield of extracted protein, and interference of SOM are a great challenge since soil proteins could not be amplified as that of DNA (Graves and Haystead 2002; Criquet et al. 2002). Soil harbors diverse microbiota abundant on earth, which makes it a complex and dynamic ecosystem. Soil microbiomes participate in the decomposition and transformation of soil materials, contaminant remediation, rhizospheric soils, and biogeochemical cycling of carbon and nitrogen (Bastida et al. 2010). The assessment of soil proteins qualitatively and quantitatively might provide valid information of microbial interaction with soil environment. Proteomics deals with the total protein investigation from one species, whereas metaproteomics is the study of total proteins from multiple soil microbes (Wilmes and Bond 2006; Rodriguez-Valera 2004). Metaproteomics or community proteogenomics, a subfield of proteomics, acts as a tool for the characterization of soil microbes at a functional level; in addition, the composition, abundance, and metabolism of individual members can also be assessed. The associated information favoring host–microbe interaction proteins in a host–microbe system might be studied (Kleiner 2019). Metaproteomics has advanced to a greater extent of understanding microorganisms and their geochemical environment (Schneider and Riedel 2010). The intrinsic metabolic function of proteins provides information in relating specific microbial activities in a multispecies community, unlike DNA and RNA. The information on the diversity of microbes in biogeochemical processes for specific habitats together with the phylogenetic origin and temporal distribution is essential for sustainable soil fertility management. Thus, the identification of the microbial proteins with their phylogenic origin and temporal distribution in a given habitat together with the analysis of their phylogenetic origin and their temporal distribution offers information on the role of microbial diversity in biogeochemical processes. The microbial functions in soils are well correlated with the proteome characterization in varied microbial communities (Wang et al. 2011) lake and groundwater (Benndorf et al. 2009), and leaf phyllosphere (Delmotte et al. 2009). Phosphorus and nitrogen metabolism in the rhizosphere is mainly facilitated by the microbial proteins liberated by the microbes belonging to the genera *Bacillus, Streptomyces,* and *Pseudomonas* in the grape vineyard subjected to integrated pest management (Bona et al. 2019). Protein stable isotope fingerprinting (protein SIF) and protein stable isotope probing (protein SIP) are the recent advanced techniques used to characterize carbon sources consumed by microbes and effect of differential incorporation of ^{15}N-labeled dietary proteins in the mouse microbiota, respectively (Smyth et al. 2020). The transformation of nutrients including carbon in the soil ecosystem is facilitated by the soil microbiota (Becher et al. 2013). The environmental factors and nutrients present in the leaf litter affect the structure and function of microbes during the decomposition process, which could be revealed by the quantitative metaproteomics (Schneider et al. 2012). The majority of the extracellular hydrolytic enzymes are of fungal origin involved in leaf litter decomposition, whereas no hydrolases originated from bacteria are detected in the decomposition process. The kind of decomposer community, activity, nutrient content, and stoichiometry affect microbial succession. The microbial activity is enhanced by the synthesis of extracellular enzymes and the high nutrient content of leaf litter.

17.2.1 Microbial Proteins

Fungi, bacteria, actinomycetes, and other microbes inhabiting and multiplying in soil accounting for various physicochemical reactions in soil result in enzyme

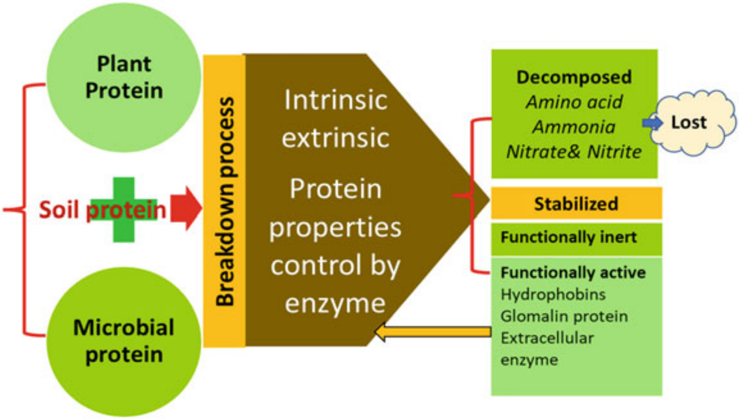

Fig. 17.2 Soil protein cycle

production, protein synthesis, and mineralization of soil nutrients. The protein in soil is grouped into (a) fungal proteins and (b) soil enzyme. Protein dynamics in the soil are depicted in Fig. 17.2.

17.2.2 *Fungal Proteins*

Sara Wright and coworkers in the early 1990s coined the term “Glomalin” to describe fungal proteins (Wright and Upadhyaya 1996). The nutrient composition of glomalin is 28–45%, 0.9–7.3%, and 0.03–0.1% of carbon, nitrogen, and phosphorus, respectively (Wang et al. 2014), and the concentration of metal ions varies with the soil type (Wu et al. 2014). Glomalin liberated by microorganisms in soil on biotic and abiotic stress is termed heat shock proteins. Glomalin-related soil protein (GRSP) is a hydrophobic glycoprotein released by the hyphae of AMF, which is abundant in soil. The concentration of GRSP is 2–5 g kg^{-1}, accounting for about 2% of soil organic carbon and about 15% of soil nitrogen. GRSP is mycorrhizal and non-mycorrhizal heat-resistant soil proteins, and their molecular weights range from 55 to 64 kDa (Rillig Matthias 2004; Gillespie et al. 2011). The role of GRSP in maintaining soil fertility and regulating SOC is vital. The accumulation and transmission of SOC in the soil are aided by GRSP. The adhesive effects of microbes on soil particles promote soil aggregation in the soil ecosystem (Wu et al. 2016). Stable soil aggregates improve the soil structure by protecting the organic materials of soil against microbial degradation and in turn promote good soil structure (Bronick and Lal 2005). The formation of a hydrophobic layer on the surface of soil aggregates restricts the loss of water within soil aggregates under drought stress (Nichols 2008). GRSP adsorbs and stabilizes pollutant metals (Cu, Cd, and Pb), which reduce their availability and toxic impact on other microbes and plants in soil (Rillig Matthias

2004; Wu et al. 2014). The unfavorable soil environment is mitigated by preventing water loss from soil by GRSP (Zou et al. 2014).

17.3 Functions of Fungal Proteins

Carbon provided by the host plants serves as a growth-promoting substance for the development of AMF. Photosynthetically fixed carbon approximately about 20% is provided by the host plant (Chen et al. 2015). The fixation and transformation of carbon in the soil are taken forward by GRSP, which enters the soil as carbon (Singh et al. 2017). The contribution of C (4–5%) to the SOC pool is significantly higher compared to microbial biomass carbon (MBC) (Kumar et al. 2018; Wu et al. 2014b). Thus, the contribution of GRSP in regulating SOC and soil fertility maintenance is crucial (Preger et al. 2007). The significant role of GRSP in promoting SOC accumulation is well correlated with its higher ratio of aliphatic and aromatic C chemical composition (Zhang et al. 2017). The stabilized structure of organic C in the soil is promoted by the sticky nature of GRSP and has a long turnover period in the soil (Zhang et al. 2017). Organic compounds like fructose, glycoproteins, peptides, and lipochitooligosaccharides are exuded by the hyphae of AMF into their surrounding bulk soil. GRSP detoxifies soil pollutants such as copper, lead, zinc, cadmium, aluminum, and manganese, which are having seriously adverse effects on various life forms in soils, including plants through adsorption by glomalin (Vodnik et al. 2008). Soil moisture is maintained by decreased water loss and improved soil wettability by GRSP (Feeney et al. 2004). It acts as a reservoir of nutrient elements such as C and N, and it affects the activity of soil microbes and helps in stabilizing the soil nutrient pools. Synergistic interaction of AMF with PGPR increases the levels of GRSP, which is responsible for the alleviation of plant stress (Hammer and Rillig 2011). GRSP binds 27.5% of copper in soil (Cornejo et al. 2008).

17.4 Soil Enzymes/Proteins

The enzymes in soil are originated from microbes, and they are either intracellular or free enzymes. The balanced interaction of various soil components is of greater importance in maintaining soil health. Soil health is evaluated by the physical, chemical, and biological components serving as soil health indicators. Soil with good health maintains the integrity of ecosystems to recover from biotic and abiotic stresses (Ellert et al. 1997). Mismanaged and contaminated soil causes deterioration of soil quality, which adversely affects all forms of life in the ecosystem (Singer and Ewing 2000). The quick response to changes in soil management and ease of measurement of the enzyme activity help in maintaining soil health. The soil enzyme activity and its role in soil health maintenance remain underexplored. Various chemical reactions in living systems are catalyzed by proteinaceous enzymes (Karigar and Rao 2011). The enzymes participate in the biogeocycles and transform various substrates into products. It is also worth mentioning the contribution of enzymes in organic residue decomposition, synthesis of humic substance, nitrification, oxidation, xenobiotic degradation, and nitrogen fixation processes (Kumar and Varma 2011). In terrestrial and aquatic ecosystems, soil enzymes contribute significantly to the biochemical processes. The activities of enzymes in soil serve as functional indicators providing information on reaction rates of various soil processes (Srinivasrao et al. 2017). Soil management changes are well indicated by the activity of enzymes present in the soil. The diversity enzymes depend to a greater extent upon the availability of resources, structure, and function of the soil microbial community. Extracellular enzymes produced by microbes decompose organic material (e.g., dead plants) and release nutrient elements into the soil for the uptake of plants. The concentration of N and P at a higher level promotes the synthesis of enzymes, which helps in increased nutrient recycling through the decomposition of plant material at a faster rate. The addition of accessible carbon (e.g., glucose) to microbes growing on new plant litter suppresses the synthesis of enzymes and degradation of litter (Srinivasrao et al. 2017). One of the important functions of soil microbes is the recovery of nutrients through biochemical reactions from detrital inputs for accumulation in SOM. The complex organic compounds are assimilated to subunits (sugars, amino acids, NH_4^+, and PO_4^{3-}) by the extracellular enzymes in soil. Soil enzymes such as amylase, catalase, urease, and sucrase are involved in the carbon cycle and serve as an important indicator of soil fertility. Soil carbohydrates are converted into glucose and sucrose by amylase and sucrase, which are essential for plants and microbes (Ge et al. 2011; Xie et al. 2017). Carbon–nitrogen bonds in organic matter are broken by urease and produce carbon dioxide and water by hydrolyzing ammonia or amino salts, and the redox ability of soil depends upon the activity of catalase (Baddam et al. 2016; Nowak et al. 2004).

Activity of catalse enzyme have a marked influence on the carbon cycle in soil. Endocellulases, cellobiohydrolases, and β-glucosidases are required for cellulolytic activities (Sinsabaugh et al. 1992), whereas polyphenol oxidases and peroxidases ligninolytic in nature (Kirk and Ferrell 1987). The activity of soil enzymes is affected by nutrient ratios, particularly between C and N. The response of the microbial community to nutrient sources largely depends upon the importance and the changes in nutrient sources. The content and composition of SOM, the activity of organisms, and the extent of biological processes in soil control the activity of soil enzymes. The catalytic action of enzymes and the availability of energy sources for microorganisms promote various biochemical reactions in soil (Kiss et al. 1978). The enzymes released in soil, plants, and microorganisms include amylase, arylsulfatases, β-glucosidase, cellulase, chitinase, dehydrogenase, phosphatase, protease, and urease (Miwa et al. 1937; James et al. 1991; Ganeshamurthy et al. 1995). The conservation of the ecosystem is also brought out by the soil enzymes through biomass production and bioremediation of polluted soils. The direct role of urease, hydrolase, transferase, oxidoreductase, and lyase in the transformation of nutrients, especially C, N, P, and S, is observed in soils. The cellular lysis of plants and

Table 17.1 Important soil enzymes and their essential functions

Soil proteins/ enzymes	Functions/enzyme reaction	Reference
Urease	Soil N transformation and urea hydrolysis	Kong et al. (2008)
Dehydrogenase	Regulates soil microbial activity/respiration, C cycling Electron transport system	Bastida et al. (2006)
β glucosidase	Release of carbohydrates in soil	Vinhal-Freitas et al. (2017)
Cellobiohydrolase (CBH)	Regulate the decomposition of organic matter	Ljungdahl and Eriksson (1985)
β-1,4-xylosidase (βX)	Regulate the decomposition of organic matter	Ljungdahl and Eriksson (1985)
α-Glucosidase	Cellobiose Hydrolysis	Shukla and Varma (2011)
Cellulase	Cellulose hydrolysis	
Phenol oxidase	Lignin hydrolysis	
Amidase	N-mineralization	
Protease	Mineralization	
Phosphatase	Release of PO_4	
Arylsulfatase	Release of SO_4	
Other soil enzymes	Hydrolysis	

microbes releases enzymes into the soil. Clay and organic molecules adsorb the proteins to immobilize and stabilize them through microencapsulation, formation of copolymers, and covalent bond (Dick and Tabatabai 1992). The short life cycle and enhanced metabolic activity of microorganisms result in the highest production of extracellular enzymes (Aşkın and Kızılkaya 2006). The application of organic matter to the soil helps in the synthesis of enzymes. The catabolic process of solid components of soil driven by enzymes and the reaction rates of important soil processes are assessed by their catalytic action. The changes in various aspects of soil health can be assessed by the activities of soil enzymes. Soil enzyme activity is an indicator of microbial activity, soil productivity, and the effects of soil pollutants (Tate 1995). Soil enzyme activity is determined by using well-defined assays (Dick et al. 1996; Tabatabai 1994a, b). The important soil enzymes and their functions are depicted in Table 17.1.

There are two types of soil enzymes: (1) constitutive (present in a constant amount in a cell), e.g., pyrophosphatase, and (2) inducible (present in traces but concentration increases when their substrate is available), e.g., amidase.

17.4.1 Arylsulfatase

Arylsulfatases are abundantly present in soil (Ganeshamurthy et al. 1995). Under a limited supply of S, these enzymes are liberated by bacteria and they are involved in the hydrolysis of sulfate esters (R–O–SO_3) to phenols (R–OH) and sulfate (McGill and Colle 1981; Kertesz and Mirleau 2004; Tabatabai 1994). Microbial biomass and rate of S immobilization are well correlated with the activity of arylsulfatase (Vong et al. 2003).

17.4.2 β-Glucosidase

It is a predominant enzyme present in soils (Eivazi and Tabatabai 1988; Tabatabai 1994). Based on the type of bond it hydrolyzes, they are named and play an important role in catalyzing the biodegradation of various β-glucosidase present in plant debris (Martinez and Tabatabai 1997). Glucose is the end product of hydrolysis, an important C energy source to microbes in the soil (Esen 1993).

17.4.3 Cellulase

Degradation of cellulose and polysaccharides is catalyzed by a group of enzymes called cellulases (Deng and Tabatabai 1994). Cellulases in soil are derived mainly from plant debris incorporated into the soil and soil microbes such as fungi and bacteria (Richmond 1991). The cellulolytic materials are degraded by these enzymes for microbial use and to improve soil health.

17.4.4 Chitinase

It is a key enzyme accountable for chitin (polyb-1-4-(2-acetamido-2-deoxy)-D-glucoside) degradation and hydrolysis. Chitin is the important cell wall component in fungi, and they use hyperparasitism mechanisms against pests and diseases (Chet and Henis 1975; Chet 1987).

17.4.5 Dehydrogenase

The activity of microorganisms in soil is indicated by the presence of dehydrogenase enzyme activity (Burns 1978). It occurs as an integral part of cells and does not accumulate as an extracellular enzyme in soil. Oxidation of SOM is catalyzed by these enzymes. These reactions are the part of respiration pathways of soil microorganisms and are influenced by the type of soil and soil air and water (Kandeler 1996).

17.4.6 Phosphatase

The role of phosphatases in the transformation of P in soil is crucial (Speir and Ross 1978). As evidenced from various studies, the secretion of acid phosphatases by plant roots in the P deficient soil enhances the solubilization and remobilization of phosphate to cope with P-stressed conditions by plants (Karthikeyan et al. 2002).

17.4.7 Proteases

Nitrogen transformation in the soil is affected by the enzyme proteases in the soil (Ladd and Jackson 1982), which is an important process regulating the amount of available N to plant. The protease enzyme is associated with the soil colloids (Nannipieri et al. 1996). This extracellular enzyme is an indicator of soil biological capacity and is essential for microbial build-up. It also affects the natural balance of microbes in different ecosystems (Burns 1982). The factors and properties affecting the activity of protease need to be studied to understand the functions of this enzyme in the maintenance of soil health and fertility.

17.4.8 Urease

Transformation of urea to ammonia and CO_2 is catalyzed by this enzyme, which results in a rise in soil pH and NH_3 volatilization (Andrews et al. 1989; Simpson and Freney 1988). Plants and microorganisms liberate urease enzyme, which occurs both as intra- and extracellular enzymes (Polacco 1977; Mobley and Hausinger 1989). The activity of this enzyme increases with an increase in temperature.

17.5 Factors Influencing Soil Microbial Proteins

Soil microbial protein activity is influenced by pH, temperature, presence of inhibitors, and reaction sites. Soil microbial biomass and activity are affected by the quality and quantity of SOM and nutrient inputs. Application of Farm Yard Manure, vermicompost, and leguminous cover crops increase the labile organic matter through increased microbial biomass in soil (Fierer et al. 2009; Kallenbach and Stuart Grandy 2011). The total enzymatic activity associated with active microorganisms and stabilized pool of clay humus complexes of the soil serves as an indicator for the decomposition and mineralization potential of nutrients in the soil (Burns et al. 2013; Schimel Joshua and Bennett 2004). The application of organic carbon-conserving management technologies increases soil enzyme activity

(Moeskops et al. 2010), but activities of specific enzymes are altered based on the composition of the organic inputs, availability of nutrients, soil type, texture, and pH (Acosta-Martínez et al. 2007). Enzymatic activity has enhanced the availability of limiting nutrients at constrained C:N:P ratio of microbial biomass to meet the metabolic demands of soil microbes (Allison et al. 2011). Rhizoexudates and substrates in the rhizosphere region of plants stimulate enzymatic activity. Certain chemical compounds of enzymatic reactions inhibit the activity of enzymes, e.g., in phosphorus-stressed soil phosphatase activity increases, but vice versa under high available phosphorous in the soil. Also, urease activity is suppressed by the release of more ammonium in soil due to the application of ammoniacal fertilizer. Soil compaction affects the mineralization of nutrients through the reduction in oxygen concentration in the soil, whereas anoxic condition favors water saturation and increased the rate of enzymatic reaction related to denitrification. The application of heavy metal-containing materials reduces the activity of amidase enzyme activity due to the toxic effect on soil organisms and roots (Dick 1994; Bandick and Dick 1999). The breakdown of organic matter is catalyzed by hydrolase and glucosidase; amidase, urease, phosphatase, and sulfatases are involved in the mineralization of nutrients. There is less evidence of other enzymes contributing to nutrient availability except for the activity of phosphatase. The co-application of organics and optimum fertilizers enhances soil microbiome including microbial necromass and the activity of enzymes (Srinivasarao et al. 2013). Tillage and residue treatments had a negligible effect on dehydrogenase, urease, and phosphatase activities (Cochran et al. 1989). Higher enzymatic activity is noticed in the summer season than in the winter season (Tiwari et al. 1989). An increase in soil salinity (EC) decreases enzyme activity. Changes in osmotic potential, specific ion toxicities, and the salting-out effect of soluble salts in salt-affected soils cause a decline in the activity of amylase, catalase, urease, and phosphatase (Iftikhar and Khan 1988). Kim and Hong (1988) reported that herbicides inhibited the enzyme activities in the early stage of treatment but increased the activities of urease and protease later. The application of compost and cattle manure also increased urease and alkaline phosphatase (Guan 1989).

17.6 Functions of Soil Enzymes/Proteins

Urease, a ubiquitous enzyme in natural soil, is produced by plants, fungi, and bacteria that liberate this enzyme, and it catalyzes the hydrolysis of urea into ammonium (NH_4^+). Urease is involved in biocementation, erosion control, and bioremediation of heavy metal-contaminated soils. Higher bacterial exudation contributes to the synthesis of extracellular polymeric substances (EPS) by SOM built-up. Environmental pollutants are detoxified by the peroxidase enzyme (Bansal and Kanwar 2013).

17.7 Conclusion

Soil proteins are considered as building blocks of soil health; the properties of soil are continuously renewed by proteins. It is imperative to explore the essentiality of proteins in sustaining soil health and its microbial-mediated soil nutrient dynamics in different ecosystems. Soil protein often occurs as microbial protein, enzyme, and extracellular polymeric substances, which may have a beneficial effect on the microbiome, environmental management, growth of the crop, and nutrient utilization of plants grown in a different ecosystem. Several advanced assay techniques were employed to identify the soil proteins and the results indicated that diverse proteins are distributed in soil under different ecosystems. The microbiome variations across the ecosystem represent multiple soil proteins. Studies focusing on new protein and diverse enzymes from microbes could be the beneficial intervention influencing their activities in improving plant growth to render eco-friendly environments to sustain soil and human health for feature endeavors.

17.8 Future Prospects of Soil Proteomics

This chapter allows a critical assessment of environmental proteomic successes and focuses on soil and the environment. Researchers use proteomics to identify limitations and requirements in biochemical pathways functioning in complex ecological matrices using foreseeable future. The number of unique proteins and variability in their expression levels in various ecosystems overwhelms the capabilities of electrophoresis-assisted proteomics. The importance of sophisticated off-gel proteomics and bioinformatics is of prime importance. Soil “microbiomics,” the assimilation of metagenomics, comprising proteomics, transcriptomics, and metabolomics, is used in creating datasets from various soils, and will speed up progress in soil and environmental proteomics, allowing for comprehensive cross-laboratory data validation among the growing number of environmental biologists who will take on the challenge in the coming decades.

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