9 Biological Properties of Soils

A large number of organisms live in the soil. They perform a variety of functions for their growth and reproduction. For these functions of soil organisms, soils behave like a living entity. Soil components photosynthesize, respire, and reproduce. In addition, they produce organic matter, consume organic matter, and decompose them. Some of them burrow in the soil, make spaces for their accommodation and movement, and mix surface and subsoil materials together. Soil becomes a dynamic body for the activity of soil organisms. The changes that are caused by soil organisms have their impact on soil fertility and productivity. A sterile soil is not a soil in the real sense. Although soil biota, which includes living roots and soil organisms, occupies a very small fraction of the total soil volume (<0.5%), it has tremendous influences on soil properties and soil processes. However, soil organisms are usually the most active in the surface soil zone of 0–15 cm, because this zone has accumulation of organic residues and available nutrients. Soil depth, organic matter and nutrients, microclimate, and physical and chemical soil environment influence the structure and function of soil biota.

9.1 Plant Roots, Rhizoplane, and Rhizosphere Are Unique Ecological Niches

Roots are the adsorbing and anchoring device of the vascular plants. Roots have some other functions as well. For example, there are food-storage roots, water-storage roots, propagative roots, pneumatophores, aerial roots, buttress roots, parasitic roots, and mycorrhizas. Roots of some plant species are effective soil binders. Dead roots leave channels that bring water and oxygen down to the organisms living in the soil. Roots bring nutrients from deeper layers to the surface. A plant with an expansive root system has a greater ability to adsorb water, oxygen, and nutrients from the soil. A well-developed root system keeps the plants healthy. The depth and volume of soil occupied by roots depend on plant species and soil conditions. Roots of most arable crop plants are limited to about 0–15 cm of the soil depth. Tree roots may, however, penetrate to greater depths. Probably, the most important ecological function, the roots perform, is the modulation of biological activity in soils of their vicinity. Fine and small roots (<5 mm) and coarse roots (>5 mm) are two major components of belowground biomass. Roots respire, and they are the major sources of carbon dioxide within the soil.

A part of the carbon fixed in the leaves during photosynthesis is carried to the roots via phloem and is translocated to the soil as a mixture of soluble and insoluble substances, together with sloughed cells. This process is known as rhizodeposition. Rhizodeposition brings a huge quantity of carbon and nutrients (up to 10–25% of carbon fixed by photosynthesis and 30–40% of the photosynthates translocated to the roots). Rhizodeposition releases several substances in the root zone, including exudates of water-soluble, low molecular weight compounds leached from the roots without metabolic control by the plant; secretions of low molecular weight compounds released by metabolic processes; and mucilages secreted by Golgi organelles in the root cap, hydrolysates of the polysaccharides of the primary cell wall and sloughed root cap cells, mucilage secreted by epidermal cells and root hairs, and those produced by bacterial degradation of dead epidermal cells. Rhizodeposition also includes mucigel, a gelatinous material at the surface of roots. There are lysates and sloughed cells from the epidermis and cortex of roots (Lavelle and Spain 2003).

Plant roots have enormous effects on population and functions of the soil organisms. Activities of soil flora and fauna on the rhizoplane (surface of the root) and in the rhizosphere (around the root) are different from other zones of the soil. Clark (1949) proposed the term “rhizoplane” to refer to the immediate surface of plant roots together with any closely adhering particles of soil or debris. Many microorganisms colonize the rhizoplane for the utilization of metabolites secreted by the roots. Rhizoplane microorganisms can influence plant growth and development. There are some bacteria which inhabit the rhizoplane and promote growth of

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plants. They are called plant growth-promoting bacteria (PGPB). Plant growth-promoting activities have been reported for several bacterial species, including *Pseudomonas, Azospirillum, Azotobacter, Klebsiella, Enterobacter, Alcaligenes, Arthrobacter, Burkholderia, Bacillus*, and *Serratia* (Han and Lee 2005). Some fungi inhabit the root surface in a mycelial state. They belong to the genera *Mortierella, Cephalosporium, Trichoderma, Penicillium, Gliocladium, Gliomastix, Fusarium, Cylindrocarpon, Botrytis*, *Coniothyrium, Mucor, Phoma, Pythium*, and *Aspergillus*.

The German scientist Hiltner introduced the term "rhizosphere" in 1904 to denote that region of the soil which is influenced by plant roots. Rhizosphere is characterized by greater microbiological and faunal activity than the soil away from plant roots. The rhizosphere soil differs in physical and chemical properties from the bulk soil (Whalley et al. 2005). Not only the population of microorganism is higher in the rhizosphere, but also the kinds of organisms and their requirements of metabolites are different. The rates of metabolic activity of the rhizosphere microorganisms are higher than those of the non-rhizosphere soil. It is, however, difficult to make a sharp demarcation in field between rhizosphere and non-rhizosphere zones of soil. The rhizosphere zone may be some millimeters wide, but it has no distinct boundary. It is an area of intense biological and chemical activity influenced by compounds exuded by the root and by microorganisms feeding on these compounds.

Plant roots exude a great variety of biochemical compounds such as amino acids, other organic acids, carbohydrates, sugars, vitamins, mucilage (polysaccharides), proteins, flavones, enzymes, hydrocyanic acid, glycosides, auxins, and saponins (Gupta and Mukerji 2002). Some of these substances supply food for the microorganisms; some others have growth-promoting or growth-inhibiting activity. However, the microorganisms mineralize organic matter and bring about other transformations that enhance nutrient availability for the plants. Root exudates stimulate the growth of many bacteria, including free-living nitrogen fixers of the genera *Azotobacter, Azospirillum*, and *Azoarcus*, the symbiotic nitrogen fixers of the genus *Rhizobium*, and several other bacteria and fungi, including the mycorrhizal fungi. All these activities make the rhizosphere the most dynamic environment in the soil. According to several estimates, the population of bacteria, fungi, and actinomycetes in the rhizosphere is five to ten times higher than the non-rhizosphere soil. The population of algae may be higher in the non-rhizosphere zone.

Very complex chemical, physical, and biological interactions occur between roots and their surrounding environment of soil. These interactions include root–root, root–insect, and root–microbe interactions, and they may be positive or negative. Positive interactions include symbiotic associations with bacteria and mycorrhizal fungi and root colonization by plant growth-promoting bacteria (PGPB). Plant growth-promoting bacteria were isolated from roots of a number of plants such as barley, bean, cotton, corn, groundnut, rice, various vegetables, wheat, and wood species (Manoharachary and Mukerji 2006). Negative interactions include competition or parasitism among plants, pathogenesis by bacteria or fungi, and invertebrate herbivory (Bais et al. 2006). Chemical interaction for plant–plant interference or allelopathy is one mechanism of suppression of growth of one plant by another. In addition, a number of phytotoxic compounds in plant root exudates have been identified, including 7,8-benzoflavone, catechin, juglone, 8- hydroxyquinoline, sorgoleone, and 5,7,4'-trihydroxy-3',5'-dimethoxyflavone (Bais et al. 2006). Spores or other propagules of many pathogenic fungi such as *Rhizoctonia, Fusarium, Sclerotium, Aphanomyces, Pythium, Colletotrichum, Verticillium*, and *Phytophthora* are shown to germinate as a result of stimulation and/or food sources provided by root exudates of susceptible cultivars of host plants.

9.2 Mycorrhizas Are Fungal Roots That Extend Enormously the Adsorbing Surface

The term mycorrhiza (*fungus–root*) was first applied to fungus–tree associations in 1885 by the German forest pathologist A.B. Frank (Jhonson 2009). A mycorrhiza is a symbiotic association between a fungus and a root of a vascular plant. It is a mutualistic association which provides the fungus with carbohydrates such as glucose and sucrose synthesized by the plant, and the plant, in return, gets the benefits of the huge mycelial network that adsorbs water and nutrients from a larger volume of soil. Mycorrhizal mycelia are much finer in diameter than the smallest root and can explore a large volume of soil for absorption of water and nutrients. Mycorrhizas are especially beneficial for the plant partner in nutrient-poor soils.

Seven types of mycorrhizas (arbuscular, ecto-, ectendo-, arbutoid, monotropoid, ericoid, and orchidaceous mycorrhizas) are generally encountered. Among these types, the arbuscular and ectomycorrhizas are the most abundant and widespread (Siddiqui and Pichtel 2008). Except ectomycorrhizas, the others were earlier taken together as endomycorrhiza. The hyphae of ectomycorrhizal fungi do not penetrate individual cells within the root but constitute a hyphal sheath, or mantle, covering the root tip and a Hartig net of hyphae surrounding the plant cells within the root cortex. Outside the root, the fungal mycelium forms an extensive network. On the other hand, the hyphae of endomycorrhizal fungi penetrate the cell wall and invaginate the cell membrane. Ectomycorrhizas are found to form association between the roots of woody plants such as birch, dipterocarp, eucalyptus, oak, pine, and rose families and fungi belonging to the

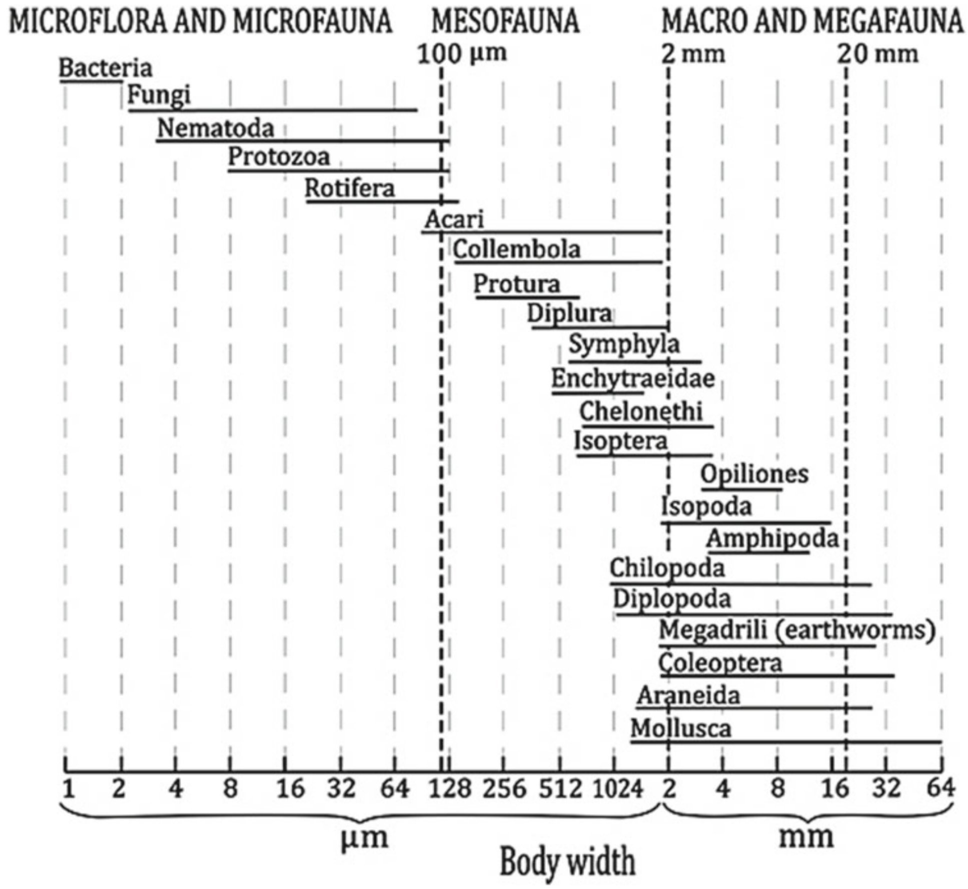

Fig. 9.1 Classification of soil fauna on the basis of body width

Basidiomycota, Ascomycota, and Zygomycota. Arbuscular mycorrhizas, or AM (formerly known as vesicular-arbuscular mycorrhizas, or VAM), are mycorrhizas whose hyphae enter the plant cells, producing either balloon-like structures (vesicles) or dichotomously branching invaginations (arbuscules). The fungal hyphae do not penetrate the protoplast, but invaginate the cell membrane. The structure of the arbuscules greatly increases the contact surface area between the hypha and the cell cytoplasm to facilitate the transfer of nutrients between them. Mycorrhizas have synergistic relations with some soil microorganisms (e.g., between *Glomus fasciculatum* and *Frankia*) and antagonistic relations with some others (such as between *G. fasciculatum* and *Pythium ultimum*).

9.3 Soil Organisms Include Macro- and Microflora and Fauna

Soil organisms are classified in many different ways. Conventionally, they are divided into flora and fauna. Besides plant roots, the other important component of soil flora is the microflora. Soil fauna is further divided into microfauna (body width <0.1 mm), mesofauna (body width 0.1–2.0 mm), and macrofauna (body width >2 mm) on the basis of their sizes. Examples of these categories are microflora—bacteria, algae, fungi; microfauna—protozoa and some nematodes; mesofauna—microarthropods and enchytraeids; and macrofauna—earthworms, termites, and millipedes.

9.3.1 Soil Fauna Are Diverse in Population and Function

Soil fauna include the major heterotrophs in soil systems; some of them are herbivores that feed on roots of living plants, but most live on dead plant matter, microbes, or both. Others are carnivores, parasites, or predators. They include life forms that live, for a part or whole of their life time, in the soil. Ladybird beetle is a transient species that hibernates in the soil but lives in the plant stratum; gnats live aboveground but they lay eggs in the soil and their larvae feed on decomposing organic residues. Cutworms are temporary soil residents; their larvae feed on plant seedlings. There are permanent soil residents such as collembolans. Swift et al. (1979) gave a classification scheme of soil fauna according to body width, which is shown in Fig. 9.1.

Body width of the fauna is related to their microhabitats. The microfauna (protozoa, small nematodes) inhabit water films. The mesofauna inhabit air-filled pore spaces; they cannot create spaces for themselves. The macrofauna make their own spaces through their burrowing activities, and like the megafauna, they can have large influences on gross soil structure (van Vliet and Hendrix 2003). Earthworms, termites, and ants alter the physical structure of the soil, influencing rates of nutrient and energy flow; they are "ecosystem engineers." Microarthropods fragment decomposing litter and improve its availability to microbes; they are litter transformers. Coleman et al. (2004) gave an account of soil fauna which is summarized below.

9.3.1.1 The Microfauna

Protozoa represent the microfauna of the soil and litter and belong to four ecological groups: flagellates, naked amoebae, testate amoebae, and ciliates (Lousier and Bamforth 1990). Protozoa are mainly distributed in the upper few centimeters of a soil profile:

1. Flagellates have one or more whiplike propulsive organs known as flagella. They are more numerous and active than other protozoa. They play a significant role in nutrient turnover by their feeding activities, with bacteria as their principal prey items.
2. Naked amoebae are very numerous and active in a wide range of agricultural, grassland, and forested soils. The principal feeding mode for the amoebae is phagotrophic (engulfing), with bacteria, fungi, algae, and other fine particulate organic matter. They inhabit very small pores in soil aggregates.
3. Testate amoebae are less numerous than naked amoebae, except in moist, forested systems where they thrive. They perform functions similar to naked amoebae.
4. Ciliates tend to be restricted to very moist or seasonally moist habitats. They are less numerous than others, with a general range of 10–500 g^{-1} of litter or soil. Like other protozoa, ciliates have resistant or encysted forms from which they can emerge when conditions become favorable for growth and reproduction.

Probably the most important ecological function the microfauna perform in soil is the regulation of microbial population and activity in the rhizosphere. Microfauna also play important roles in release of available nutrients, accretion and loss of soil organic carbon, and bioremediation of contaminated soils. Microfauna mineralize and immobilize N, P, and S and maintain nutrient balance in the rhizosphere. They suppress bacterial and fungal pathogens.

9.3.1.2 The Mesofauna

Rotifera

Rotifera are considered to be aquatic organisms and are found in water films and water-filled pores. Rotifers may also be found in tens of thousands per square meter in unsaturated soils. Rotifers have been found in leaf litter on forest floors.

Nematoda

Nematodes are also called roundworms. They are among the most numerous of the multicellular organisms in soil. They are also inhabitants of water films or water-filled pore spaces in soils. The body is cylindrical, tapering at the ends. Nematodes may be concentrated in the rhizosphere. Ingham et al. (1985) found up to 70% of the bacterial- and fungal-feeding nematodes in the rhizosphere. Nematodes seek areas of concentrated organic matter.

Tardigrada

These are micrometazoans and are called "water bears" because of their microursine appearance. Their slow movement resembles a tortoise. Tardigrades have four pairs of legs, equipped with claws on the distal end, of various sizes and forms. Tardigrades survive in extreme environmental stresses. Five types of latency (virtual cessation of metabolism) have been described: encystment, anoxybiosis, cryobiosis, osmobiosis, and anhydrobiosis. They feed on algal cells and debris and probably have a rather broad diet of various microbial-rich bits of soil organic matter. Tardigrades have also been observed to feed voraciously on nematodes.

Microarthropods

Microarthropods mainly include mites and collembolans and are found in most types of soils. Hundreds of thousands of individuals belonging to thousands of different species may be found within a square meter forest floor. Microarthropods have a significant impact on the decomposition processes of organic detritus. Many microarthropods feed on fungi and nematodes. Microarthropods in turn are prey for macroarthropods such as spiders, beetles, ants, and centipedes. Some smaller megafauna (toads, salamanders) may also feed upon microarthropods. Soil mites usually outnumber collembolans but may become more abundant in some situations. Among the mites, the oribatids usually dominate but the delicate Prostigmata may develop large populations in cultivated soils with a surface crust of algae.

Collembolans are also called "springtails" because many of the species are able to jump with a lever attached to the bottom of the abdomen. They also have a unique ventral tube (collophore), which may function in osmoregulation. They occur throughout the upper soil layer, where their major food is fungi associated with decaying vegetation. They are often the most numerous of the microarthropods in the rhizosphere.

The soil mites (Acari) are chelicerate arthropods related to the spiders and are the most abundant microarthropods in many types of soils. Four suborders of mites occur frequently in soils: the Oribatei, the Prostigmata, the Mesostigmata, and the Astigmata. Among them, the oribatids are the characteristic mites of the soil and are usually fungivores, detritivores, or both. Mesostigmatid mites are nearly all predators on other small fauna, although some few species are fungivores. Acarid mites are found associated with rich, decomposing nitrogen sources.

There is a diverse group of other small arthropods among mesofauna. These microarthropods have relatively small biomasses and probably have comparatively less impact on soil ecology. They include small spiders and centipedes, occasionally small millipedes, insect larvae, and adult insects.

Protura: Proturans are small, wingless, primitive insects readily recognized by their lack of antennae. Proturans occur in a variety of soils worldwide, often associated with plant roots and litter.

Diplura: Diplurans are small, elongate, delicate, primitive insects. Most diplurans are euedaphic, but some are nocturnal cryptozoans, hiding under stones or under bark during the day. They occur in tropical and temperate soils in low densities. They are predators on mites and other small arthropods but also ingest fungal mycelia and detritus.

Pseudoscorpionida: Pseudoscorpions resemble the scorpions, except that they lack tails and stingers. They are found in almost all types of soil. Pseudoscorpions are small cryptozoans, hiding under rocks and bark of trees, but they are found occasionally in leaf litters in the forest floor.

Symphyla: Symphylids are small, white, eyeless, elongate, many legged invertebrates that resemble tiny centipedes. They differ from centipedes in several characteristics, but superficially symphylids have 12 body segments and 12 pairs of legs, whereas centipedes have at least 15 pairs of legs, the first pair modified as fangs. Some species are pests feeding on roots of seedlings.

Pauropoda: Pauropods are myriapods with 8–11 pairs of legs and a branched antenna. They are white to colorless and blind; these characteristics make them members of the true euedaphic fauna. Pauropods occur in soils worldwide.

Enchytraeidae

Enchytraeidae is an important family of terrestrial Oligochaeta. This group of small unpigmented worms is also known as "pot worms." It consists of about 600 species in 28 genera. Species from 19 of these genera are found in soil. Members of the family are typically 10–20 mm in length and they are anatomically similar to the earthworms, except for the miniaturization and rearrangement of features overall. They possess setae (except in one genus), and a clitellum in segments XII and XIII, which contains both male and female pores.

Mesofauna live in existing pore spaces within and between the aggregates in the soil. They are small and like macrofauna they cannot make their own spaces themselves. Most of them chew and fragment organic debris and aid in their decomposition. They turn over soil organic residues and participate in nutrient recycling.

9.3.1.3 The Macrofauna

Macroarthropods

Macroarthropods are a group of larger insects, spiders, myriapods, and others. Their typical body lengths range from 10 mm to 15 cm (Shelley 2002). Many macroarthropods are cryptozoans; they dwell beneath stones, logs, under bark, or in cracks and crevices. Macroarthropods have direct effects on soil structure, porosity, aeration, and water movement. Termites and ants are important movers and mixers of soil; they bring deeper soil to the surface and on top of the litter layer. Emerging nymphal stages of cicadas may disturb soil structure. Scarabaeid beetles' larvae sometimes churn the soil in grasslands. Many macroarthropods are temporary soil residents. Macroarthropods may have a major influence on the microarthropod community. For example, Collembola are important food items for spiders.

Isopoda

Soil isopods are crustaceans; they occur under rocks and in similar habitats. They are generally saprovores. They can also feed upon roots or foliage of seedlings. Isopods possess heavy, sclerotized mandibles and are capable of fragmentation of decaying plant residues. In the laboratory, terrestrial isopods feed upon fecal pellets dropped by themselves or by any other isopods.

Diplopoda

Diplopoda (millipedes) are widely distributed saprophages. They are major consumers of organic debris in temperate and tropical hardwood forests. Millipedes become abundant in moist calcium-rich areas. They have a calcareous exoskeleton, and because of their high densities, they can be a significant sink for calcium. They can be important in calcium cycling. Millipedes are selective feeders; they avoid leaf litter high in polyphenols and favor those with high calcium content.

Chilopoda

Chilopoda (centipedes) are common predators in soil and litter. They occur in biomes ranging from forest to desert. Lithobius are the common brown, flat centipedes of litter in hardwood forests. The elongate, slim geophilomorph centipedes are euedaphic in forest habitats, where they prey on earthworms, enchytraeids, and Diptera larvae. All centipedes are predators.

Scorpionida

The scorpions (arachnid) have long legs, segmented, stinger-bearing abdomen, and chelate palpi. They are common creatures. They are inhabitants of warm, dry, tropical, and temperate regions but they are the most abundant in deserts. Scorpions are typical cryptozoans that hide under rocks or logs, or in crevices, during the day and emerge at night to feed.

Araneae

Araneae (spiders) are another familiar group of carnivores. They are found in all terrestrial environments except polar regions. Many species are found in aboveground habitats, but some are cryptozoans in litter and on the soil surface. Some small spiders are euedaphic. Some of the small litter-inhabiting spiders could be considered microarthropods.

Opiliones

Opiliones are delicate, shy, and the largest arachnids in woodlands. Their bodies are small but their legs are unusually long which suggest that their habitat is litter surface or exposed areas. There are smaller shorter-legged forms that inhabit loose leaf litter or small spaces. Some species occur high in foliage, others in subcanopy, some on soil surface, and some in litter layers.

Uropygi

Uropygi contain large species, up to 10 cm in length. It has a distinctive, long, whiplike tail but no stinger. The arachnid emits acetic acid, when disturbed, from a gland at the base of the tail. Uropygids are nocturnal predators.

The Pterygote Insects

Many winged insects (Pterygota) are residents of soils. Some are permanent soil inhabitants spending whole of its life in or on soil. Immature stages of other species are true soil dwellers but their adults are flying insects. All major winged insect orders—the Coleoptera (beetles), Lepidoptera (butterflies and moths), Hymenoptera (bees, wasps and ants), and Diptera (flies)—include soil-dwelling species. Termites belong to Isoptera and they are saprophages. The Homoptera (aphids, cicadas), Orthoptera (grasshoppers and crickets), and minor orders such as the Dermaptera (earwigs) contain soil-dwelling species. Of 26 pterygote insect orders, all but seven contain at least some soil-dwelling species.

Coleoptera

Beetles are the largest order of insects. They have soil species that are predatory, phytophagous, or saprovores. Most of them are transient members. The ground beetles (Carabidae) are among the more familiar insects active on soil surface of agroecosystems.

Hymenoptera

One of the largest orders of insects is the Hymenoptera. They have two groups of great importance: the ants and the ground-dwelling wasps. The ants are the most significant family of soil insects for their large influence on soil structure. Some bees and wasps nest in soil and also have some impacts on soils. Ants are widely distributed, numerous, and diverse.

Diptera

Many of the true flies are soil dwellers in some stages of their life cycles. Many species that live in aboveground habitats pupate in the soil. Many species of fly larvae are important saprovores in soils. They are restricted to moist soils rich in organic matter. Fly larvae have a major impact on decomposition rates of carrion. Maggots of various types hasten the decomposition rate significantly.

Isoptera

The Isoptera (termites) are among the most important of soil fauna for their impact on soil structure and on decomposition of detritus. Some termites possess a gut flora of protozoans, which enable them to digest cellulose. Their normal food is wood that has come into contact with soil. Most species of termites construct spectacular mounds. Termitidae do not have protozoan symbionts, but possess an array of microbial symbionts (bacteria and fungi) that enable them to digest the humified organic matter in tropical soils. There are wood-feeding, plant-feeding, and humus-feeding termites.

Other Pterygota

The Orthoptera, grasshoppers and crickets, lay eggs in soils and some are active on the soil surface. The Psocoptera, psocids, are a small order of insects that occasionally become abundant in leaf litter. They feed on organic detritus, algae, lichens, and fungus. The order Homoptera, cicadas, aphids, and others, has members important as belowground herbivores and as soil movers.

Gastropoda

Soil gastropods (snails and slugs) are major herbivores and detritivores in agroecosystems. They favor moist conditions and the presence of significant amounts of calcium for their metabolic needs, but some gastropods exist successfully in low pH and low calcium environments.

Oligochaeta: Earthworms

The most familiar and often the most important of the soil fauna with respect to soil processes are the earthworms. They fragment plant residues, bury them in, and mix them well with the soil. More than 3,500 earthworm species have been identified so far. Earthworms are classified within the phylum Annelida, class Oligochaeta, and order Opisthopora. Ten of the 16 families consist of the terrestrial forms commonly known as earthworms. Species within the families Lumbricidae and Megascolecidae are ecologically important.

Earthworms are soft-bodied, segmented animals. In length they range from a few millimeters to more than a meter. They consist of a simple, tube-within-a-tube body plan, the outer tube constituting the body proper and the internal tube comprising the alimentary canal. Soil material is ingested and drawn through the mouth into a muscular buccal cavity and then through the pharynx into the esophagus. Many species have a muscular esophageal gizzard that grinds and mixes food material as it passes through. Earthworms are called ecosystem engineers because they have pronounced effects on soil structure, aeration, and water movement by their burrowing activities as well as their ingestion of soil and production of castings (van Vliet and Hendrix 2003). Casts are produced after earthworms ingest mineral soil and particulate organic matter, mix them together and enrich them with organic secretions in the gut, and then egest the material as a slurry or as discrete fecal pellets within or upon the soil. Turnover rates of soil through earthworm casting range from 40 to 70 t $ha^{-1}year^{-1}$ in temperate grasslands to 500–1,000 t $ha^{-1}year^{-1}$ in tropical savannas. Earthworm burrowing in soil creates macropores of various sizes, depths, lengths, and orientations, depending on their species and soil type. Continuous macropores resulting from earthworm burrowing may enhance water infiltration by functioning as bypass flow pathways through saturated soils.

Earthworms may have some detrimental effects. These include removing and burying of surface residues that would otherwise protect soil surfaces from erosion; increasing erosion and surface sealing by free casts; creating nuisance by castings on the surface of lawns and golf greens; dispersing weed seeds in gardens and agricultural fields; transmitting plant or animal pathogens; increasing losses of soil nitrogen through leaching and denitrification; and increasing soil carbon loss through enhanced microbial respiration.

9.3.2 Soil Microflora Include Bacteria, Fungi, and Algae

9.3.2.1 Bacteria

Bacteria are unicellular prokaryotes; they do not have any distinct nuclear zone in the cytoplasm. Their sizes range from 0.3 to more than 3 µm. Bacteria may be classified on the basis of cell morphology (cocci, bacilli, spirilla), cell wall structure (Gram-positive and Gram-negative through specific staining), presence of endospores, mobility of cells, and shape and position of flagella, if any.

Bacteria live in soil as cocci (sphere, 0.5 µm), bacilli (rod, 0.5–0.3 µm), or spirilla, the bacilli being more common and spirilla being rare in soil (Baudoin et al. 2002). There are again autochthonous and zymogenous bacteria. The autochthonous bacteria get their nutrition from native soil organic or mineral matter (*Arthrobacteria* and *Nocardia*). On the other hand, the zymogenous bacteria require additional external substrate (*Pseudomonas* and *Bacillus*). The number of zymogenous bacteria increases when they get appropriate substrate and gradually declines when the added substrate is exhausted (cellulose decomposers, nitrogen transformers) (Giri et al. 2005).

On the basis of the energy source that they use (light or energy from redox reactions) and the nature of the electron donor (organic or mineral), bacteria are divided into four categories: (1) photolithotrophic bacteria using energy from light and inorganic reduced substance (essentially sulfides) as electron donors; (2) photoorganotrophic bacteria which are photosynthetic organisms using oxidizable organic substrates as electron donors; (3) chemolithotrophic bacteria using the energy produced by redox reactions and four kinds of mineral substrates as electron donors (reduced nitrogen, sulfur or iron compounds and hydrogen); (4) chemoorganotrophic bacteria are typical heterotrophic organisms taking their energy from redox reactions and using organic compounds as electron donors. There are also obligate chemoautotrophs such as *Nitrobacter* utilizing nitrite and *Nitrosomonas* utilizing ammonium, while *Thiobacillus* converts inorganic sulfur compounds to sulfate and *Ferrobacillus* converts ferrous ions to ferric ions (Baudoin et al. 2002).

Functional categories of bacteria are defined by the chemical transformations they perform. Some of the most common examples are cellulolytic, chitinolytic, nitrifiers, N-fixers, denitrifiers, etc. The most common soil bacteria belong to the genera *Pseudomonas, Arthrobacter, Clostridium, Achromobacter, Bacillus, Micrococcus, Flavobacterium, Corynebacterium, Sarcina, Azosprillium*, and *Mycobacteria*. Another group of bacteria common in soil is the myxobacteria belonging to the genera *Myxococcus, Chondrococcus, Archangium, Polyangium, Cytophaga*, and *Sporocytophaga*. The latter two genera are cellulolytic and, hence, are dominant in cellulose-rich environments. Bacteria can withstand extreme climates, although temperature and moisture influence their population. Some bacteria can thrive in arctic zones where the temperature is below freezing point and some others in arid desert soils where temperatures are very high. Based on the temperature tolerance, bacteria are grouped as psychrophilous (below 20°C), mesophyllous (15–45°C), and thermophilous (45–65°C). However, mesophyllous bacteria constitute the bulk of soil bacteria. Soil pH, farm practices, fertilizers and pesticide applications, and organic matter amendments affect population and activity of bacteria in soil.

The cyanobacteria are Gram-negative eubacteria characterized by their ability to perform oxygenic photosynthesis. They are true prokaryotic microorganisms. They have some characteristics common to algae for which they were earlier named "blue-green algae." Cyanobacteria contain a pigment known as phycocyanin, in addition to chlorophyll, which gives a special blue-green color to these organisms. The dominant cyanobacteria belong to the genera *Chroococcus, Aphanocapsa, Lyngbya, Oscillatoria, Phormidium, Microcoleus, Cylindrospermum, Anabaena, Nostoc, Scytonema*, and *Fischerella* (Benizri et al. 2002). Some cyanobacteria also possess heterocysts, which are involved in nitrogen fixation.

9.3.2.2 Actinobacteria

The Actinobacteria (formerly called Actinomycetes) are filamentous bacteria. They are mostly Gram-positive. They possess a ramified pseudomycelium whose diameter (0.5–1 μm) is much smaller than that of fungi. The Actinobacteria resemble bacteria in that they have a very simple cell structure and are about the same size in cross section. They resemble filamentous fungi in that they produce a branched filamentous network. The network compared to fungi, however, is usually less extensive. They are poorly tolerant of soil acidity and most are unable to grow in soils with acidity more than pH 5. The most conducive range of pH for Actinobacteria is between 6.5 and 8.0. Waterlogging of soil is unfavorable for the growth of Actinobacteria, whereas desert soils of arid and semiarid zones sustain sizeable populations, probably due to the resistance of spores to desiccation. The commonest genera of Actinobacteria are *Streptomyces*. In contrast, *Nocardia, Micromonospora, Actinomyces, Actinoplanes*, and *Streptosporangium* are only encountered occasionally. Although there is evidence that Actinobacteria are abundant in soils, it is generally concluded that they are not as important as bacteria and fungi as decomposers (Foth 1990).

9.3.2.3 Fungi

Fungi are heterotrophic organisms. A large number of fungi live on dead organic matter; they are saprophytes. Others live on living plant or animal tissue; they are parasites. Some fungi are deadly pathogens of plants and animals. Saprophytes depend on organic detritus for carbon and decompose them in course of their growth and nutrition. The quality and quantity of organic matter affect the population and activity of saprophytic fungi in soils. Fungi have filamentous mycelium composed of individual hyphae. The hyphae may be uni-, bi-, or multinucleate and septate or nonseptate (Hawksworth 1991).

In acid soils fungi dominate the microbial community because acidic soils are not favorable for most of bacteria and Actinobacteria. Fungi are also present in neutral or alkaline soils, and some can tolerate a pH over 9.0. Since fungi are strictly aerobic, they are generally abundant in arable soils. Their numbers decrease in waterlogged soils. However, moist organic detritus such as leaf litter or wood are ideal habitat for fungi. Some fungi dwell in deep layers of soils. They are not generally found in the surface soil. Probably, the type of organic substrate is behind this selectivity.

Fungi are classified into Phycomycetes, Ascomycetes, Basidiomycetes, and Fungi Imperfecti (Alexander 1977). Phycomycetes constitute an important class of parasitic or saprophytic fungi. The fungal body may be an undifferentiated mass of protoplasm to a well-developed and much-branched mycelium. Reproduction is mainly sexual, by the formation of conidia or sporangia. Ascomycetes include fungi which produce spores inside a sac called an ascus. Each ascus usually contains 4–8 spores depending on the species. The Basidiomycetes fungi constitute the most conspicuous group of fungi in the environment and include mushrooms, puffballs, and bracket fungi. Basidiomycetes produce a highly specialized sporangium, the basidia. Many fungi, commonly isolated from soils, come under the class Fungi Imperfecti because they produce abundant asexual spores but lack sexual stages (Lynch 1987). Many members of Asco- and Basidiomycetes can degrade very complex organic compounds such as cellulose or lignin. Many others live as mycorrhizas on roots of higher plants and obtain simple sugars from their plant partners.

The following genera of fungi are most commonly found in soils: *Acrostalagmus, Aspergillus, Botrytis, Cephalosporium, Gliocladium, Monilia, Penicillium, Scopulariopsis, Spicaria, Trichoderma, Trichothecium, Verticillium, Alternaria, Cladosporium, Pilularia, Cylindrocarpon* and *Fusarium, Absidia, Cunninghamella, Mortierella, Mucor, Rhizopus, Zygorhynchus, Pythium, Chaetomium*, and *Rhizoctonia* (Hawksworth 1991). Many yeasts belonging to true Ascomycetes such as *Saccharomyces* and those belonging to Fungi Imperfecti such as *Candida* have been isolated from soils. However, their number in soil is relatively low. Certain fungi like *Alternaria, Aspergillus, Cladosporium, Dematium, Gliocladium, Helminthosporium, Humicola*, and *Metarhizium* produce substances similar to humic substance in soil and, hence, may be important in the maintenance of soil organic matter (Hawksworth 1991).

9.3.2.4 Algae

Algae need sunlight and moisture for proliferation. They are numerous in soils, particularly in the soil surface. Soil algae mainly belong to the class Chlorophyceae. There are also diatoms in soils. These microorganisms form green scum on the surface of soils and are visible to the naked eye, although most algae are microscopic. They are, however, less numerous than fungi in soil. Algae may be unicellular (*Chlamydomonas*) or filamentous (*Spirogyra, Ulothrix*). Algae contain chlorophyll and they are photoautotrophic organisms. They use CO_2 from the atmosphere and produce O_2. Some algae are found in deeper soil layers beyond the reach of sunlight. These forms obtain their energy largely from organic matter. Algae benefit the soil by contributing organic matter to the soil. Some of the common green algae occurring in most soils belong to the genera *Chlorella, Chlamydomonas, Chlorococcum, Oedogonium,*

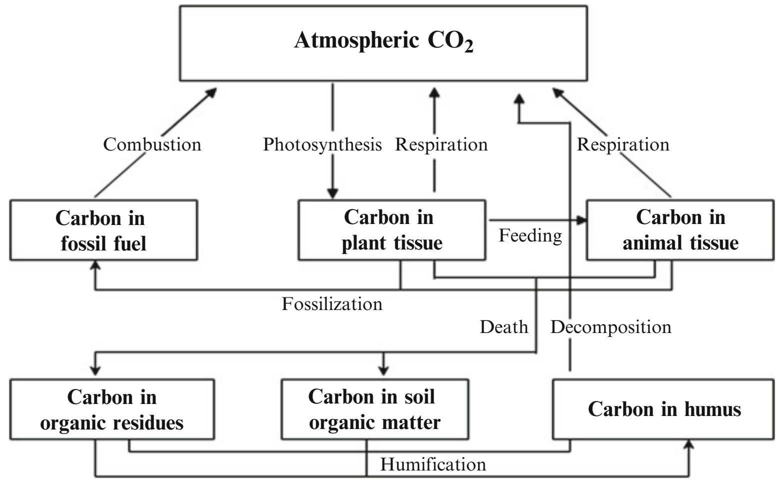

Fig. 9.2 The carbon cycle

Chlorochytrium, and *Protosiphon* (Lynch 1990). The earlier known blue-green algae are now cyanobacteria; they are included in bacteria.

9.4 Carbon, Nitrogen, Phosphorus, and Sulfur Cycles Are Biogeochemical Cycles

Soils are a sink of carbon, nitrogen, phosphorus, and sulfur. Carbon and nitrogen are added to soils from the atmosphere through physical and biological fixation mechanisms. Although sulfur may be found in the atmosphere as SO_2 and H_2S gases and particulates which fall to the ground as acid rain, phosphorus does not have an atmospheric component. In the terrestrial ecosystem, carbon and nitrogen are circulated through the atmosphere, pedosphere, and biosphere system. Huge quantities of C and N are fixed; huge quantities of C, N, P, and S are added to soils as organic residues. They are chemically and biologically transformed in soil, a large proportion are adsorbed by plants and again added to soils after their death and decay. A large proportion of these elements are exported with crop harvest and imported as fertilizers. In this way, these elements form ecological cycles. A considerable part of them is transferred to other ecosystems, such as lakes, streams, and oceans where they become a part of the greater global cycles.

9.4.1 Carbon Cycle Involves Release and Fixation of CO_2 to and from the Atmosphere

Biological energy transfer within the biosphere at landscape and ecosystem scales and within organisms goes hand in hand with the carbon cycle. Large carbon stores occur in the lithosphere, the biosphere, the atmosphere, and the hydrosphere. Mass transfers of carbon occur between the lithosphere, the biosphere, the seas and other water bodies, and the atmosphere as part of the global carbon cycle (Schlesinger 1997).

Carbon is stored as CO_2 in the atmosphere (2%), as biomass in land plants and soils (5%), as fossil fuels in a variety of geologic reservoirs (8%), and as a collection of ions in the ocean (85%). In the terrestrial ecosystem, the major carbon stores are the aboveground biomass, the litter layer, and the soil including plant roots. Within the soil, there are the living roots: the microbial biomass and the meso- and macrofauna. The soil organic matter component consists of dead residues of variable degrees of decomposition ranging from the recognizable plant and animal remains to the highly stable humic compounds. Carbon is distributed in different soil horizons through litterfall, root death and decomposition, leaching, and exudation. Carbon in soils occurs in a variety of compounds ranging in complexity from CO_2 and carbonates to large structured macromolecules.

Primary producers including plants and autotrophic microorganisms fix atmospheric CO_2 by the process of photosynthesis. Animals consume plants and other animals for their carbon. Huge carbon materials are added to soils with dead parts of organisms (Chap. 7), their excreta and exudates. These residues are deposited on the surface by litterfall and as crop residues and at variable depths by root death and exudation. Flora and fauna mix these materials with the soil. The dead organic matter is colonized by a variety of soil heterotrophic microorganisms, which derive energy for growth from the decomposition of complex organic molecules. During decomposition, essential elements are converted from organic combination to simple inorganic forms; this process is called mineralization. For example, organically combined N, P, and S appear as NH_4^+, $H_2PO_4^-$, and SO_4^{2-} ions, and a considerable amount of C is released as CO_2. The remainder of the substrate C used by the microorganisms is incorporated into microbial cell substance or microbial biomass, together with a variable proportion of other essential elements such as N, P, and S. This incorporation makes these elements unavailable for plant growth until the organisms die and decay; so the process is called immobilization. The carbon cycle is shown in Fig. 9.2.

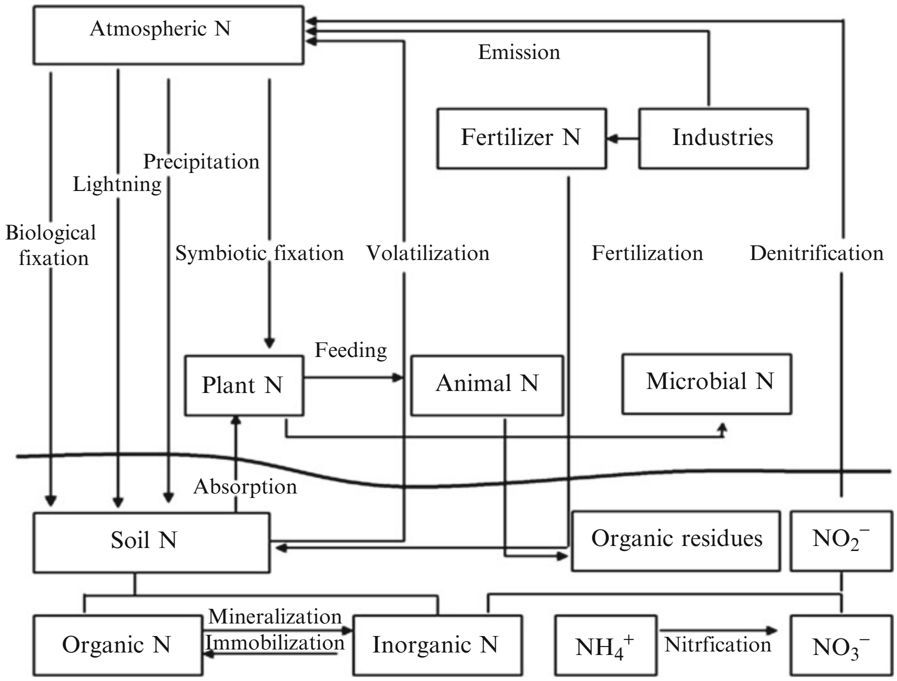

Fig. 9.3 The nitrogen cycle

During the course of decomposition of organic residues, recalcitrant substances accumulate and some new complex organic compounds are synthesized by microorganisms. Complexation of these substances with soil mineral matter produces humus. Thus, the important processes in the soil carbon cycle are immobilization, mineralization, and decomposition. In addition, humification is a concomitant process of decomposition and resynthesis by which stabilized humic materials are produced in soil.

9.4.2 Nitrogen Moves Through Soil–Organism–Atmosphere Pathway in a Cycle

The ultimate source of nitrogen is the atmosphere. It contains about 78% nitrogen in the mixture of gases called air. From atmosphere, some nitrogen is brought to the soil by atmospheric fixation and deposition with precipitation (Fig. 9.3).

A huge amount of nitrogen is chemically fixed in industries, a major part of which is used for manufacturing fertilizers. Large amount of nitrogen fertilizers is added to soils throughout the world for increased crop production. Added and native soil nitrogen is taken up by plants to make their body materials, namely, amino acids, proteins, nucleic acids, and nucleoproteins. Animals obtain their proteins from plants and other animals. Some microorganisms, with or without association with plants, utilize dinitrogen from the atmosphere. This is called biological nitrogen fixation. Plant and animal residues (excreta, anthropogenic wastes, fallen litter, crop residues, and dead organisms) return a significant proportion of nitrogen to the soil as organic nitrogen. Organic nitrogen is mineralized into inorganic nitrogen, NH_3, by soil microorganisms. Ammonia is converted into NO_3^- by the process of nitrification. Some ammonia is volatilized and some nitrate is denitrified and released again into the atmosphere. Thus, nitrogen moves in a cycle among the soil–organism–atmosphere components. This is known as the nitrogen cycle. The chief biological processes of this cycle are mineralization, immobilization, nitrification, nitrogen fixation, and denitrification.

9.4.2.1 Nitrogen Mineralization and Immobilization

During the course of decomposition of organic matter, organic nitrogenous compounds such as amino acids, peptides, proteins, and nucleoproteins that are present in soil organic matter are converted into inorganic nitrogen such as ammonium and nitrate (NH_4^+, NO_3^-). This process of conversion of organic nitrogen to inorganic nitrogen is called mineralization. It is carried out by a range of heterotrophic microorganisms, mainly fungi and bacteria. Through this process, organically bound unavailable nitrogen is made available to the plants. The rate of nitrogen mineralization is governed by the relative content of carbon and nitrogen in the organic residues. The higher the nitrogen contents of the organic matter, that is, the narrower the C/N ratio, the faster is the nitrogen mineralization. On the other hand, when low nitrogen residues are allowed to decompose, the decomposing microorganisms consume some available nitrogen (NH_4^+, NO_3^-) from the soil. In this process inorganic nitrogen is converted into organic nitrogen. The process is opposite to the mineralization and is called immobilization. Mineralization and immobilization can take place simultaneously. The dynamic nature of these competing processes causes either an increase in soil inorganic N or, conversely, a decrease when inorganic N is immobilized into organic forms.

$$\text{Organic nitrogen} \longrightarrow \text{inorganic nitrogen} \left[\text{mineralization}\right]$$

$$\text{Organic nitrogen} \longleftarrow \text{inorganic nitrogen} \left[\text{immobilization}\right]$$

Environmental factors affect the rate of N mineralization in the soil and thus the amount mineralized over time. Soil temperature and moisture content have a strong effect on N mineralization reactions. Microbial activity is limited at soil temperature near freezing and increases with rising soil temperature. Maximum N mineralization occurs when the soil temperature reaches 30–35°C. In dry soils, N mineralization is low because soil microorganism activity is limited by water availability. In saturated soils, lack of oxygen limits N mineralization because only soil microorganisms that can survive under anaerobic conditions are active. Soil management practices have a strong effect on the N mineralization potential of a soil. Intensive farming practices that rely heavily on tillage and synthetic fertilizers tend to decrease the soil's mineralizable N pool.

9.4.2.2 Nitrification

Nitrification is the biological oxidation of ammonium to nitrate. Nitrification occurs in two steps. In the first step, ammonia is oxidized to nitrite.

$$NH_3 + O_2 \rightarrow NO_2^- + 3H + +2e^-.$$

Nitrosomonas is the most frequently identified genus associated with this step, although other genera, including *Nitrosococcus* and *Nitrosospira*, may be involved. Some subgenera, *Nitrosolobus and Nitrosovibrio*, can also autotrophically oxidize ammonia. In the second step of the process, nitrite-oxidizing bacteria *Nitrobacter* oxidize nitrite to nitrate according to equation

$$NO_2^- + H_2O \rightarrow NO_3^- + 2H + +2e^-.$$

The nitrifying bacteria are Gram-negative chemoautotrophic organisms; they usually derive their energy for growth by oxidizing these inorganic nitrogen compounds. Nitrifying bacteria are most active at pH near neutrality and slightly alkaline conditions. Nitrification is low in acid soils. Acid-tolerant strains of nitrifying bacteria may carry out some nitrification in acid soils. Nitrifying bacteria are strict aerobes; they must have free oxygen to perform their work.

Nitrification is a biological process of tremendous environmental importance. Whatever nitrogen fertilizers are applied in soil, they are rapidly converted to nitrate by soil microorganisms. Adsorbed nitrate on soil colloids is quickly replaced by other anions, and very little nitrate can be retained in soil. Nitrate is transported with water and pollutes the groundwater. Excess nitrate in drinking water is involved in severe health hazards (Chap. 10).

9.4.2.3 Denitrification

Denitrification is the biological reduction of nitrate to nitrogen gas (N_2). It occurs in soils, particularly wet soils, and it causes loss of available nitrogen. Some bacteria known as denitrifying bacteria bring about this conversion. Denitrifying bacteria include representatives of *Pseudomonas, Achromobacter, Bacillus*, and *Micrococcus*. All denitrifying bacteria are aerobes, and they can use oxygen as electron acceptor for the oxidation of organic matter. When anaerobic conditions prevail (in soils with high moisture saturation, i.e., soils with low free O_2), they use the nitrates as electron acceptors and reduce them. Most denitrifiers produce nitrous oxide (N_2O) instead of dinitrogen (N_2) under aerobic conditions (Takaya et al. 2003). Denitrification involves a series of biological conversions.

$$NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2.$$

The net reaction may be written as

$$2\,NO_3^- + 10\,e^- + 12\,H^+ \rightarrow N_2 + 6\,H_2O.$$

9.4.2.4 Biological Nitrogen Fixation

Atmosphere contains thousands of tons of nitrogen over head, but even a single molecule of it cannot be used by plants and animals without the intervention of a group of microorganisms called diazotrophs. Diazotrophs fix atmospheric nitrogen either as free-living organisms or in association with a higher plant. The process can be represented by the following equation in which 2 mol of ammonia are produced from 1 mol of nitrogen gas:

$$N_2 + 8H^+ + 8e^- + 16ATP \rightarrow 2NH_3 + H_2 + 16ADP + 16Pi$$

Nitrogen fixers combine atmospheric nitrogen with other elements to form the organic compounds that make up the protoplasm of their cells. With the death of the nitrogen fixers, the nitrogen is liberated as ammonia and nitrates, forms available to plants.

9.4.2.5 Nonsymbiotic Nitrogen Fixation

There are many free-living bacteria capable of fixing atmospheric nitrogen in soil. They are all prokaryotes. However, there is a great diversity of metabolic types of free-living nitrogen-fixing bacteria. They may be obligate anaerobes,

Table 9.1 Important symbiotic nitrogen-fixing bacteria and their host plants

Species	Host plants
Rhizobium leguminosarum bv. *phaseoli*	Common bean
Rhizobium leguminosarum bv. *trifoli*	Clover
Rhizobium leguminosarum bv. *viceae*	Pea, vetch
Rhizobium tropici	Common bean
Rhizobium etli	Common bean
Mesorhizobium loti	*Lotus japonicus*
Azorhizobium caulinodans	Sesbania
Sinorhizobium meliloti	Alfalfa
Sinorhizobium fredii	Soybean
Bradyrhizobium japonicum	Soybean, cowpea, mung bean
Bradyrhizobium elkanii	Soybean, cowpea, mung bean

facultative aerobes, or aerobes. The dominant free-living nitrogen-fixing bacteria belong to the genera *Azotobacter, Azospirillum, Beijerinckia, Chromatium, Clostridium, Desulfovibrio, Klebsiella, Paenibacillus, Pseudomonas, Rhodopseudomonas, Rhodospirillum*, and *Thiobacillus* (Philippot and Germon 2005). Free-living nitrogen-fixing bacteria are widespread but the rates of nitrogen fixation by them are relatively low (<3 kg ha^{-1}year^{-1}). Free-living nitrogen fixers represent a range of bacteria including saprophytes living on plant residues, bacteria living in close association with the rhizosphere of plant roots, and bacteria which live entirely within plants (endophytes). There are both aerobes and anaerobes among nitrogen fixers. For example, *Azotobacter* and *Azospirillum* live in aerobic conditions, whereas others such as *Clostridium pasteurianum* live in oxygen-free (anaerobic) environment. The amount of nitrogen fixation by nonsymbiotic bacteria depends upon environmental conditions. These organisms are extremely sensitive to acidity. Nitrogen fixed by this means in soils with acidity more than pH 6 is negligible. Free-living nitrogen fixers need ample supply of calcium, potassium, phosphorus, and traces of iron, molybdenum, and manganese.

9.4.2.6 Symbiotic Nitrogen Fixation

Some plants, usually legumes, form symbiotic association with microorganisms, a group of bacteria known as *Rhizobium*. Most rhizobia form nodules in roots and stems of leguminous plants and can convert atmospheric nitrogen N_2 into NH_3 and then into amino acids in their tissue. This is known as symbiotic nitrogen fixation. Table 9.1 gives a list of rhizobia species and their hosts from an account by Stacey (2007).

Some Actinobacteria can also form symbiosis but on other plants than legumes. Some algae such as *Anabaena* can be associated symbiotically with the aquatic pteridophyte *Azolla*. These associations also have nitrogen-fixing capacity. But rhizobia are the most significant nitrogen fixers. However, rhizobia represent only a small fraction of the soil microflora with densities varying widely in a range of 10^2–10^4 bacteria g^{-1} soil. Rhizobia can live freely, although in small numbers, in soil, but they can fix nitrogen only when they are in nodules of plants.

Taxonomy of nodule bacteria has been subject to rapid changes. At present 12 genera and some 50 species of root- and stem-nodule bacteria are recognized. Graham (2008) gives a list of 11 genera with their host plants. These genera are *Allorhizobium, Azorhizobium, Blastobacter, Bradyrhizobium, Burkholderia, Devosia, Ensifer, Mesorhizobium, Ralstonia, Rhizobium*, and *Sinorhizobium*. Only a few of these organisms fix significant amounts of N_2 outside their host (Elliott et al. 2006).

Some shrub and tree species other than legumes form a symbiosis with a nitrogen-fixing Actinobacteria called *Frankia*. The genera that have been reported so far to fix nitrogen symbiotically are *Alnus, Ceanothus, Cerocarpus, Chamaebatia, Comptonia, Coraria, Cowania, Datisca, Dryas, Elaeagnus, Myrica, Purshia, Shepherdia, Colletia, Discaria, Kentrothamnus, Retanilla, Talguena, Trevoa, Hippophae, Allocasuarina, Casuarina, Ceuthostoma, Coriaria, and Gymnostoma* (Paul and Clark 1996). In addition, some lichenous fungi, liverworts, pteridophytes, gymnosperms, and angiosperms are able to establish symbioses with nitrogen-fixing cyanobacteria *Nostoc* and *Anabaena*. Symbiotic associations between rhizobia and leguminous plants may contribute from several tens to 350 kg N ha^{-1} year^{-1} depending on environmental conditions. BNF obtained with nonleguminous angiosperms producing symbiosis with *Frankia* is between 15 and 77 kg N ha^{-1} year^{-1} for *Casuarina equisetifolia* (Dommergues 1997), 29 and 117 kg N ha^{-1} year^{-1} for *Alnus nepalensis* (Shrama 1993), and 18 kg Nha^{-1} year^{-1} for *Myrica faya* (Vitousek and Walker 1989).

9.4.2.7 Nodulation

Roots of legumes release flavonoid compounds which trigger the production of nod factors by the bacteria. Due to this nod factor, a number of biochemical and morphological changes occur in roots; cell division is triggered to create the nodule. The bacteria attach to a point of the root and the root hair repeatedly winds around the bacteria until it fully encapsulates the bacteria. The bacteria encapsulated divide a number of times and form a microcolony. From this microcolony, the bacteria enter the developing nodule through a structure called an infection thread, which grows through the root hair into the basal part of the epidermis cell, and onward into the root cortex. They are then surrounded by a plant-derived membrane and differentiate into bacteroids that fix nitrogen.

9.4.2.8 Nitrogenase

An enzyme called nitrogenase produced by nitrogen-fixing organisms converts the gaseous nitrogen into the more available nitrogen form ammonia, which can later be assimilated

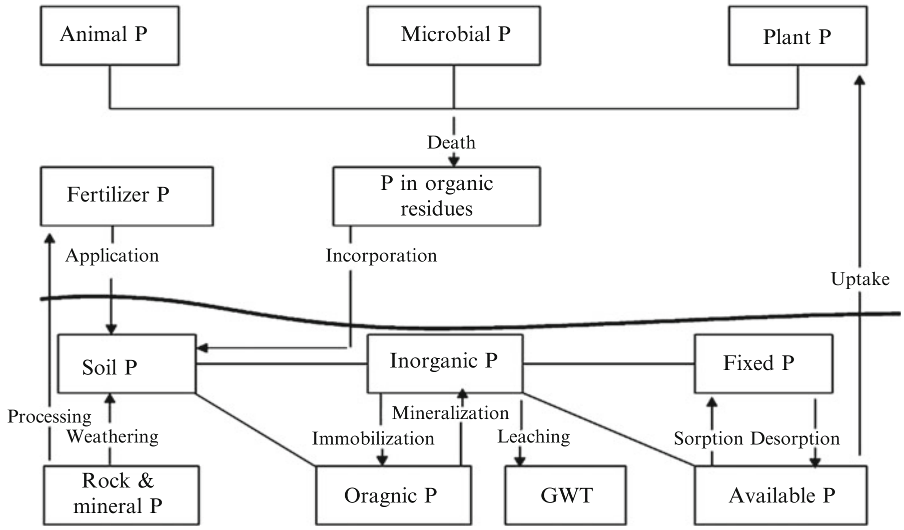

Fig. 9.4 The phosphorus cycle

into amino acids and proteins. A series of complex reactions are involved in nitrogen reduction. Nitrogenase activity requires large amounts of energy. Symbiotic nitrogen-fixing bacteria obtain required energy from the photosynthates of the host legume, but free-living bacteria must find their own source of energy, organic matter, within the soil. Nitrogenase requires the participation of about 20 genes for its synthesis and activity. Activities of these genes are suppressed at higher levels of available nitrogen (ammonium or nitrate) present in the environment. Nitrogenase is deactivated in the presence of oxygen, and all nitrogen-fixing bacteria (free-living and symbiotic) must therefore operate within oxygen-free (anaerobic) conditions. Free-living nitrogen fixers that exist only in aerobic conditions have evolved a specialized biochemical pathway to keep oxygen at very low levels within their cells.

9.4.3 Phosphorus Cycle Involves Transformations of Organic and Inorganic Phosphorus Substances

The phosphorus cycle in soil is shown in Fig. 9.4. During cycling in soil, phosphorus undergoes transformations involving interconversions of the three inorganic phosphate forms, available P, adsorbed P on organic as well as inorganic colloids, or precipitations with other ions or compounds, and primary mineral P. Also, organic P is mineralized to inorganic P and inorganic P is immobilized to organic P.

The primary source of phosphorus in soil is the mineral apatite ($Ca_5(PO_4)_3$(OH, F, Cl). Apatite is weathered, both chemically and biologically, into available phosphates. Available P is adsorbed from soil by plants and microorganisms for their physiological activity. In this way, soluble inorganic P is converted into organic phosphate compounds in the tissue of plants and microorganisms. This process is known as phosphorus immobilization. Animals get phosphorus through the food chain. After death of all these organisms, organic phosphate is added to soils in the form of their residues. Through decomposition of organic matter, P is released to the soil in the inorganic forms. This is called phosphorus mineralization. Mineralized P may again be adsorbed or precipitated, adsorbed by plants and microorganisms, or a part may be leached to groundwater. Therefore, the general transformation processes of the P cycle are weathering, precipitation, mineralization and immobilization, and adsorption and desorption. Weathering, mineralization, and desorption increase plant available P, while immobilization, precipitation, and adsorption decrease it. Among these processes, P solubilization, mineralization, and immobilization are biologically mediated.

9.4.3.1 Mineralization and Immobilization

Mineralization is the microbial conversion of organic P to inorganic P. By their action, fungi and bacteria make organically bound phosphorus into inorganic phosphate, usually $H_2PO_4^-$, a form available to plants. On the other hand, certain microorganisms especially bacteria assimilate soluble phosphate and use for cell synthesis; this process is known as immobilization. Mineralization of phosphate is generally rapid and more in virgin soils than cultivated land. Mineralization is favored by high temperatures and more in slightly acidic to neutral soils with high organic phosphorus content. The enzymes involved in mineralization of phosphate from organic phosphorus compound are collectively called phosphatases.

9.4.3.2 Solubilization

Many microorganisms can bring insoluble inorganic phosphate into solution. Plant roots and microorganisms solubilize phosphates through secretion of organic acids (e.g., lactic, acetic,

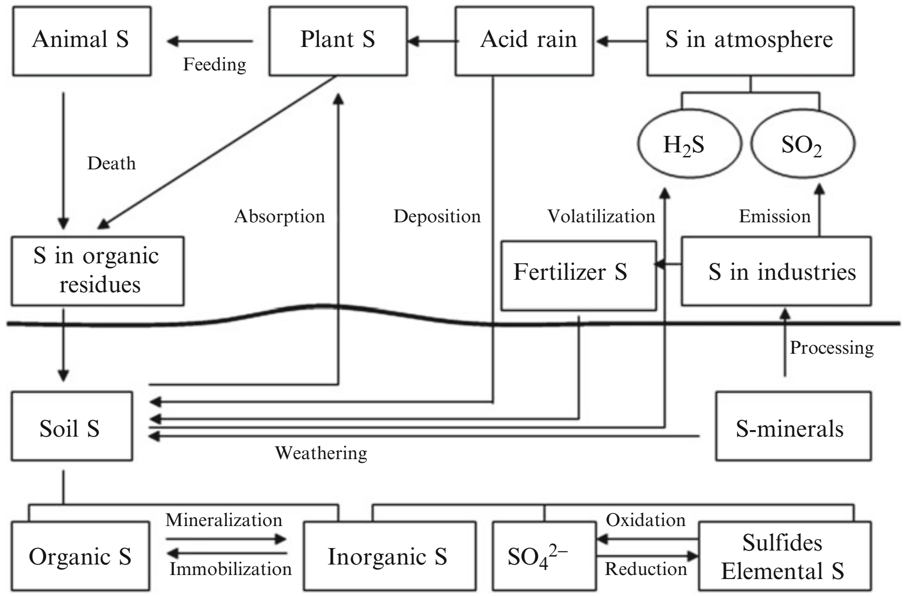

Fig. 9.5 The sulfur cycle

formic, fumaric, and succinic acids). Predominant phosphate dissolving/solubilizing microorganisms are bacteria of the genera *Pseudomonas, Bacillus, Micrococcus, Mycobacterium, Flavobacterium*, and fungi *Penicillium, Aspergillus, Fusarium*, etc. The commercially used species of phosphate solubilizing bacteria and fungi are *Bacillus polymyxa, Bacillus megaterium, Pseudomonas striata, Aspergillus* sp., and *Penicillium avamori*. Solubilization of phosphate by plant roots and soil microorganisms is substantially influenced by various soil factors, such as pH, moisture, and aeration. Phosphate solubilizing microorganisms are found concentrated in the rhizosphere. Their activity is reduced by acidity of soil. Considerable amounts of phosphate ions added in fertilizers may be transported to water reservoirs around agricultural lands. It causes eutrophication of water bodies (Chap. 10).

9.4.4 Oxidation and Reduction Are the Main Processes of Sulfur Cycling

Soils contain several valence states of sulfur, ranging from −2 (as in sulfide and reduced organic sulfur) to +6 (as in sulfate). Some primary and secondary minerals such as pyrite (FeS_2) and gypsum ($CaSO_4{\cdot}2H_2O$) are the original sources of sulfur in soil. Mineral sulfate or sulfide is chemically and biologically transformed into ionic sulfate SO_4^{2-} in soil. This SO_4^{2-} ion is the available form for plants. Sulfate is also adsorbed by microorganisms to make their body material, the process being known as sulfur immobilization. These organisms reduce SO_4^{2-} to −SH groups through the assimilatory process. Microorganisms and plants produce some amino acids and proteins containing sulfur. With plant and animal residues and after death of microorganisms, organic sulfur is added to soils. Some microorganisms decompose and mineralize organic sulfur into H_2S, which in turn is biologically oxidized into sulfate. Some organisms also have the ability to oxidize the mineral pyrite producing sulfur oxides, sulfates, and sulfuric acid. Some microorganisms can reduce sulfate into elemental S, H_2S, and FeS_2. Some sulfur is liberated as sulfur oxides to the atmosphere from industries and vehicles through burning of fossil fuel. These oxides may react with water molecules to produce sulfuric acid which falls to the ground as acid rain. On the other hand, H_2S can volatilize from wetlands to the atmosphere. Thus, the important processes of the sulfur cycle are immobilization, mineralization, oxidation, and reduction (Fig. 9.5).

9.4.4.1 Biological Oxidation of Sulfur

Biological oxidation of sulfide to sulfate is one of the major reactions of the sulfur cycle. Prokaryotes exclusively bring about the oxidation of reduced inorganic sulfur compounds. There is a phylogenetically diverse group of sulfur-oxidizing prokaryotes. Aerobic sulfur oxidation is restricted to members of the order *Sulfolobales* in the domain *Archaea*. In the Domain *Bacteria* sulfur is oxidized by aerobic lithotrophs or by anaerobic phototrophs. The nonphototrophic obligate anaerobe *Wolinella succinogenes* oxidizes hydrogen sulfide to polysulfide during fumarate respiration (Friedrich et al. 2001).

Prokaryotes oxidize hydrogen sulfide, sulfur, sulfite, thiosulfate, and various polythionates in soil at varying soil reactions. Sulfur-oxidizing aerobic prokaryotes belong to genera like *Acidianus, Acidithiobacillus, Aquaspirillum, Aquifex,* *Bacillus, Beggiatoa, Methylobacterium, Paracoccus, Pseudomonas, Starkeya, Sulfolobus, Thermithiobacillus, Thiobacillus*, and *Xanthobacter* and are mainly mesophilic. Phototrophic anaerobic sulfur-oxidizing bacteria are mainly neutrophilic and mesophilic and belong to genera like *Allochromatium* (formerly *Chromatium*), *Chlorobium, Rhodobacter, Rhodopseudomonas, Rhodovulum*, and *Thiocapsa*. Lithoautotrophic growth in the dark has been described for *Thiocapsa roseopersicina, Allochromatium vinosum*, and other purple sulfur bacteria, as well as for purple nonsulfur bacteria like *Rhodovulum sulfidophilum* (formerly *Rhodobacter sulfidophilus*), *Rhodocyclus gelatinosus*, and *Rhodopseudomonas acidophila* (Friedrich et al. 2001).

9.4.4.2 Biological Reduction of Sulfur

Some bacteria and Archaea are capable of reducing sulfates to sulfides, especially to hydrogen sulfide. The sulfate-reducing bacteria, which reduce sulfate to obtain energy, are anaerobes and use sulfates as the terminal electron acceptors. Most sulfate-reducing bacteria can also reduce other oxidized inorganic sulfur compounds, such as sulfite, thiosulfate, or elemental sulfur. However, sulfur reduction involves the participation of very complex enzyme systems.

Sulfur-reducing organisms may be characterized by three groupings:

Group I. Sulfate reducers: They use lactate, pyruvate, many alcohols, and some fatty acids as electron donors when converting SO_4^{2-} to H_2S and produce acetate as an end product of metabolism.

Group II. Sulfate reducers: Use fatty acids (especially acetate) and oxidize substrate completely to CO_2 while converting SO_4^{2-} to H_2S; some may grow chemoautotrophically using H_2 as the electron donor (acetyl CoA pathway).

Group III. Dissimilatory sulfur reducers: Organisms that reduce elemental sulfur to sulfide, but cannot reduce sulfate to sulfide: $SO_4 \rightarrow S \rightarrow H_2S$; use acetate and ethanol as common electron donors.

Common sulfur-reducing bacteria belong to the genera *Desulfitobacterium, Desulfotomaculum, Desulfovibrio* (*Desulfovibrio africanus, Desulfovibrio desulfuricans, Desulfovibrio gigas, Desulfovibrio vulgaris*), and *Desulfuromonas*.

9.5 Management and Properties of Soils Affect Population and Function of Soil Microorganisms

Soil and crop management practices include plowing, sowing of seeds and transplanting of seedlings, application of manures, fertilizers, lime and pesticides, irrigation, etc. These practices affect the dynamics of soil organisms. Plowing and tillage operations facilitate aeration and expose the soil to light and heat. Fertilizers, manures, and lime provide nutrients. Cropping patterns have profound influences on soil organisms; some crops favor growth of certain groups of organisms by their excretion and exudation of sugars, enzymes, hormones, and vitamins. Liming of acid soils increases activity of bacteria and actinomycetes and lowers the population of fungi.

Pesticides (insecticides, fungicides, herbicides) often inhibit the growth and activity of nontarget organisms. Toxic pesticide residues may cause profound reduction in the normal microbial activity in the soil. Many soils have become contaminated with heavy metals and persistent organic pollutants by the use of sewage sludge as soil amendments and disposal or hazardous organic wastes on agricultural lands (Sect. 12.5). Šmejkalová et al. (2003) observed toxic effects of Cd, Pb, and Zn (although it is an essential element) on several parameters of microbial activity in soil. Cadmium and zinc exert toxic effects on nitrogen-fixing rhizobia (Leung and Chant 1990). Microorganisms are, however, sometimes employed to remediate soil pollution.

Soil texture, structure, and porosity affect the supply of moisture, oxygen, and warmth to organisms. Microbial population and activity proliferate best in the moisture range of 20–60%. Waterlogged conditions create anoxic situation (lack of oxygen) where anaerobic microflora become active and the aerobes get suppressed. Activities of soil microbes are often measured in terms of the amount of CO_2 evolved. The rate of CO_2 evolution is regulated by the oxygen supply in soil. Soil temperature influences all physical, chemical, and biological processes in soil. Extreme soil temperatures (hot and cold) are not conducive to good microbial activity. There are several groups of microorganisms based on their temperature requirement (Sect. 5.7.6). Most soil microorganisms like to grow within the temperature range of 20–45°C. Moisture and temperature in a geographic region depend also on the prevailing climate. There is seasonal variation within a climatic zone as well. For example, temperature remains below 5°C in winter in the temperate zone and the number and activity of microorganisms are reduced.

Among the chemical properties, mainly soil pH, organic matter, and nutrients influence the activity of soil organisms. Most of the soil bacteria, blue-green algae, diatoms, and protozoa prefer a neutral or slightly alkaline reaction between pH 6.5 and 7.5, and fungi grow in acidic reaction between pH 4.5 and 6.5, while actinomycetes prefer slightly alkaline soil reactions. Some organisms such as the nitrifying bacteria (*Nitrosomonas and Nitrobacter*) and the nitrogen-fixing *Azotobacter* cannot tolerate soil acidity, but nitrogen-fixing *Beijerinckia, Derxia*, and sulfur-oxidizing bacteria like *Thiobacillus thiooxidans* are active in acidic soils. Organic matter is the food of heterotrophic bacteria. So, when fresh organic residues are added to soils, their number and activity abruptly increase. As organic carbon is reduced due to decomposition, the number of heterotrophic organisms also decreases. Microbial population and activity are greatly influenced by the soil fertility in general and individual nutrient supply in particular. For example, activity and presence of nitrogen-fixing bacteria depend profoundly on the supply of available molybdenum and phosphorus.

Study Questions

1. How do you distinguish between rhizoplane and rhizosphere soils? What are the reasons of high biological activity and microbial diversity around roots?
2. What are the major groups of soil flora and fauna? Discuss the functions that micro- and macrofauna can perform in a soil.
3. Explain the significance of carbon cycling in nature. Discuss humification, mineralization, and immobilization.
4. Mention the types of interactions between roots and microorganisms. Narrate major biological transformations of the nitrogen cycle in soil. Discuss nitrification and denitrification processes and indicate their environmental impacts.
5. Explain important biological transformations that are performed by bacteria in soil. Discuss the factors that affect population and functions of bacteria in soil.

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