2 Microbial Diversity in Soils

Bhoopander Giri[1], Pham Huong Giang[2], Rina Kumari[3], Ram Prasad[3], Ajit Varma[1]

1 Introduction

Soil microbiology emerged as a distinct branch of soil science in 1838 after the French agricultural chemist and farmer, Boussingault, showed that legumes could obtain nitrogen from air when grown in soil which was not heated. Fifty years later, a Dutch scientist, Beijerinck, isolated bacteria from nodules of legume roots. Since then, a number of investigations have been conducted in the area of soil microbiology. However, scientists are still investigating soil microbial diversity.

Soil is the outer covering of the earth, which consists of loosely arranged layers of materials composed of inorganic and organic compounds in different stages of organization (Tate 1995; Kapoor et al. 2002). It is a natural medium in which microbes live, multiply and die. Microbial diversity in the soil is a critical environmental topic that concerns people from all walks of life. Interest in microbial diversity has grown rapidly in the scientific community (Wilson 1988; Franklin 1993; Benizri et al. 2002). Increasing attention is being drawn to microorganisms because the fertility of soil depends not only on its chemical composition, but also on the qualitative and quantitative nature of microorganisms inhabiting it. Maintenance of viable, diverse populations and functioning microbial communities in the soil is essential for sustainable agriculture (Beare et al. 1995; Benizri et al. 2002). Soil contains a wide range of microorganisms descried as a 'black box' (Paul and Clark 1989).

Microorganisms are generally divided into five major taxonomic categories: algae, bacteria, fungi, protists and viruses (Prescott et al. 1996; Hurst 2002). In soil, they are closely associated with soil particles, mainly clay–organic matter complexes (Foster 1988). Often, microbes can be found as single cells or as microcolonies embedded in a matrix of polysaccha-

[1]School of Life Science, Jawaharlal Nehru University, New Delhi 110067, India and Amity Institute of Herbal and Microbial Studies, Sector 125, New Super Express Highway, Noida, Tel: 95120-2432400, Fax: 95120-2432200, e-mail: ajitvarma@aihmr.amity.edu
[2]International Centre for Genetic Engineering and Biotechnology (UNO, Triesta, Italy) New Delhi, India
[3]Ch. Charan Singh University, Meerut, Uttar Pradesh, India

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rides (Smiles 1988; Wood 1989). Their activity and interaction with other microbes and larger organisms and with soil particles depend largely on conditions at the microhabitat level that may differ among microhabitats even over very small distances (Wieland et al. 2001). The microhabitats for soil microorganisms include the interior as well as exterior surfaces of soil aggregates for varying sizes and compositions. Soil can therefore be regarded as highly heterogeneous with respect to the distribution of soil matter and organisms (Beare et al. 1995).

2 Origin of Microbial Diversity

The diversity of microorganisms has a much longer evolutionary history than plants or animals and thus has had more time to evolve into diverse forms. Microorganisms have been exposed to and have survived cataclysmic conditions unknown by higher animals and plants. Plants and animals are relative newcomers and have only had to prove their adaptive capacity for several hundred million years, a fairly short period in evolutionary time. During this time, conditions on the earth's surface were conducive to the survival of plants and animals. Certainly, there have been many examples of species extinction, however, by and large, the temperature has remained fairly stable, there have been few collisions with really large meteors, volcanic activity has been moderate, and the oceans have remained homogeneous and oxygenated.

Microorganisms have proved their ability to face challenges unimaginable to us today. Moreover, microorganisms did not simply occupy various niches offered by earth. Through their chemical activities, they transformed the earth and its atmosphere in a number of ways. Some of these changes actually contributed to making the earth habitable for the plants and animals that appeared much later.

The earth is about 4.5 billion years old. Scientists estimate that the first living creature appeared about 4 billion years ago, shortly after the earth's surface had cooled enough to allow liquid water to form (Fig. 1). These creatures were most similar to modern-day prokaryotes – bacteria and archaea. Because some microorganisms living on earth today are capable of growing in boiling water, life could clearly have begun while the earth's surface was still very hot. Moreover, the sun was only about two-thirds as bright as it is today, therefore, the earth's surface would have become habitable faster than if the sun had been brighter.

Life during the high-impact period would not have been easy. Some impacts were powerful enough to vaporize oceans, creating clouds of steam that would have sterilized the earth's surface. These events may not have

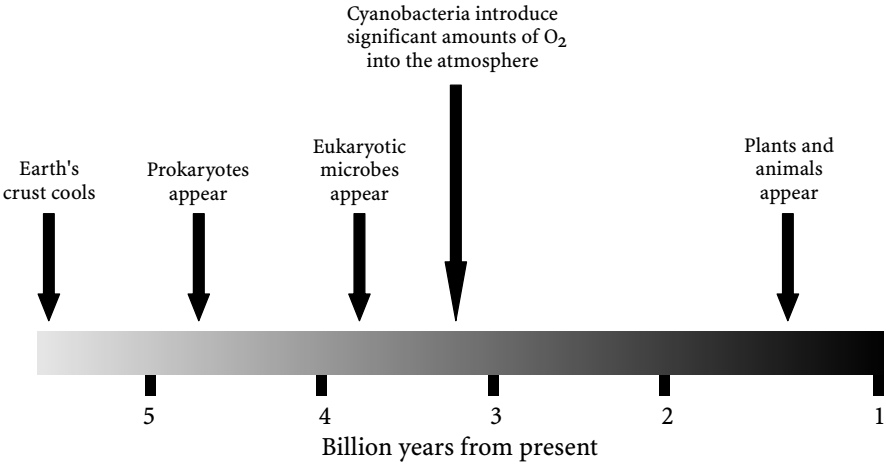

Fig. 1. Approximate timing of major events in the history of life on earth. (Salyers and Whitt 2001)

completely obliterated emerging life forms. Microorganisms could have survived this period deep underground. Some may have had the capacity of modern microorganisms to produce tough survival forms called spores. Although direct exposure to steam would have killed them, some spores could have survived under slightly cooler conditions that would still have been hot enough to kill an actively growing microorganism.

Some microorganisms may actually have been able to live on the earth's surface. One bacterium, *Deinococcus radiodurans*, can survive doses of radiation 3000 times greater than the lethal dose for humans. Most organisms, however, probably developed in the subsurface of landmasses or beneath the ocean surface where they were protected to some degree from UV radiation.

2.1 Oxygen Revolution

The revolutionary development occurred between 2.5 and 2 billion years ago, changing the earth and its atmosphere completely. Oxygen began to appear in significant amounts in the earth's atmosphere as a result of a microbial metabolic process called oxygenic photosynthesis. Although many compounds such as water contained bound oxygen, there had been no oxygen in the atmosphere. Oxygen photosynthesis differed from earlier forms of photosynthesis, in that it splits water and released oxygen. The bacteria responsive to this new type of photosynthesis are called cyanobacteria. The first appearance of oxygen left a tangible geological record: banded iron formations in rock. Iron in the earth's crust combined with oxygen

to form black iron oxides, producing dark bands. Cyanobacteria also left a fossil record. Some cyanobacteria accumulated to form large mounds called stromatolites. Geologists have found fossilized stromatolites dating back 3 billion years and microfossils of individual cyanobacteria cells that date to 3.5 billion years ago. Cyanobacteria brought the oxygen level of the earth's atmosphere up to about 10% of today's level, high enough to create conditions that favored the evolution of oxygen-utilizing organisms.

2.2 Origin of the First Eukaryotes

Because many eukaryotes are oxygen-dependent, scientists had theorized that protozoa first appeared about 2 billion years ago. However, there are modern protozoa that live in anoxic environments, so protozoa could have emerged before the appearance of oxygen in the atmosphere. It is estimated that the time of appearance of the first protozoa dates back to about 3 billion years ago. Algae presumably appeared after cyanobacteria because their chloroplasts were derived from cyanobacteria. They probably evolved within the last 2 billion years. The fungi appeared only comparatively recently, during the last several hundred million years. It is thought that terrestrial fungi might have co-evolved with plants because they are closely associated with them. Fungi are often thought to be exclusively terrestrial. However, they are also reported in marine and other locations far from land (Salyers and Whitt 2001).

3 Types of Soil Microorganisms

Microscope studies led to the recognition of a profoundly important dichotomy among the various groups of organisms with respect to their internal architecture of the cell; two radically different kinds of organisms co-exist in the contemporary living world. The more complex cells constitute eukaryotes (organisms with a true nucleus), which include algae, fungi and protists (Fig. 2). Evolutionary studies revealed a great diversity of eukaryotic organisms as compared to prokaryotic microorganisms (Fig. 3). The less complex cell constitutes prokaryotes, comprising two microbial groups: the eubacteria (including cyanobacteria, the group once known as blue-green algae) and the archaebacteria, a heterogeneous group of microorganisms with prokaryotic structure. These organisms show characteristic features and play some beneficial roles to mankind (Table 1). Considering the cell structure and function as criteria, there are three groups of cellular organisms: eukaryotes, eubacteria, and the archaebacte-

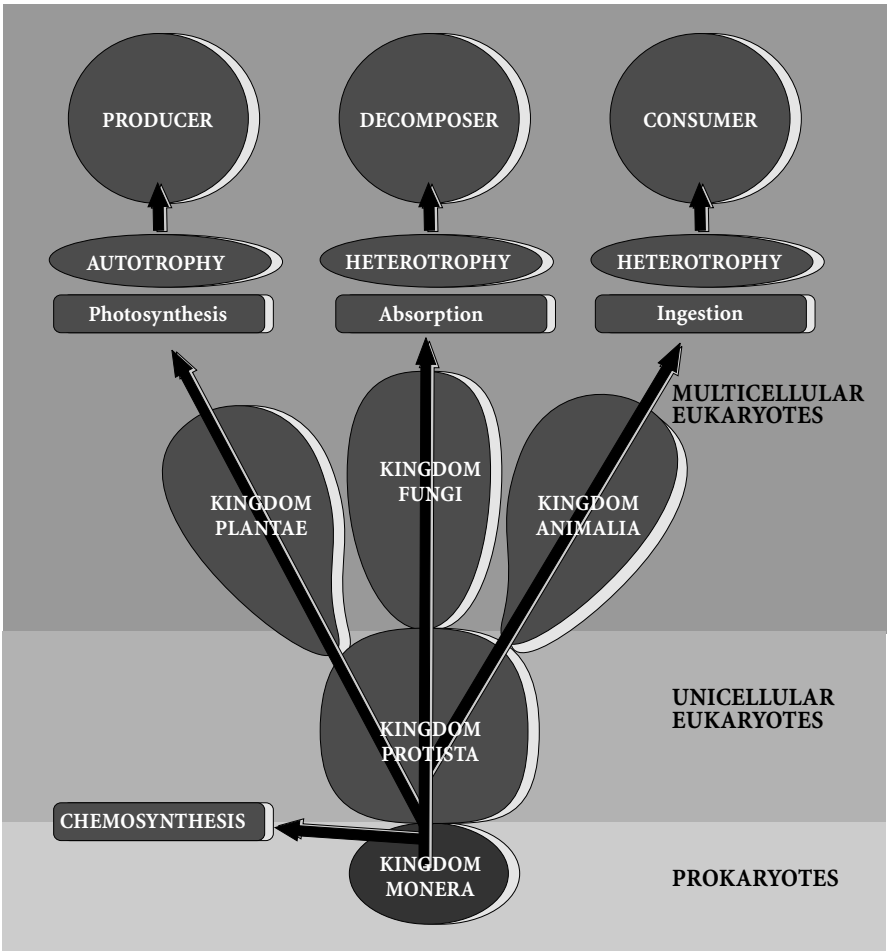

Fig. 2. The five-kingdom system showing diversity of organisms (http://www.npc.edu/Bio105/media_htm/M1_L7.01.htm)

ria. The eukaryotes can be subdivided into three further groups: the plants, animals and fungi. The eubacteria can be subdivided into purple, green, gram-positive and gram-negative eubacteria on the basis of the cell wall. On the basis of their nutritional requirements, prokaryotes have been categorized as Photoautotrophs, Photoheterotrophs, Chemolithoautotrophs, And Chemolithohetetrpophs (Table 2). Bacteria have also been classified as oxybionts and anoxybionts on the basis of their oxygen metabolism. Prokaryote diversity, however, is not only restricted to relationships to molecular oxygen or to their ability to utilize radiant energy to capture energy. Optimal diversity also depends on soil pH, temperatures (cold, ambient, hot), inorganic salts, etc. (Herman et al. 1993; Hurst 2002).

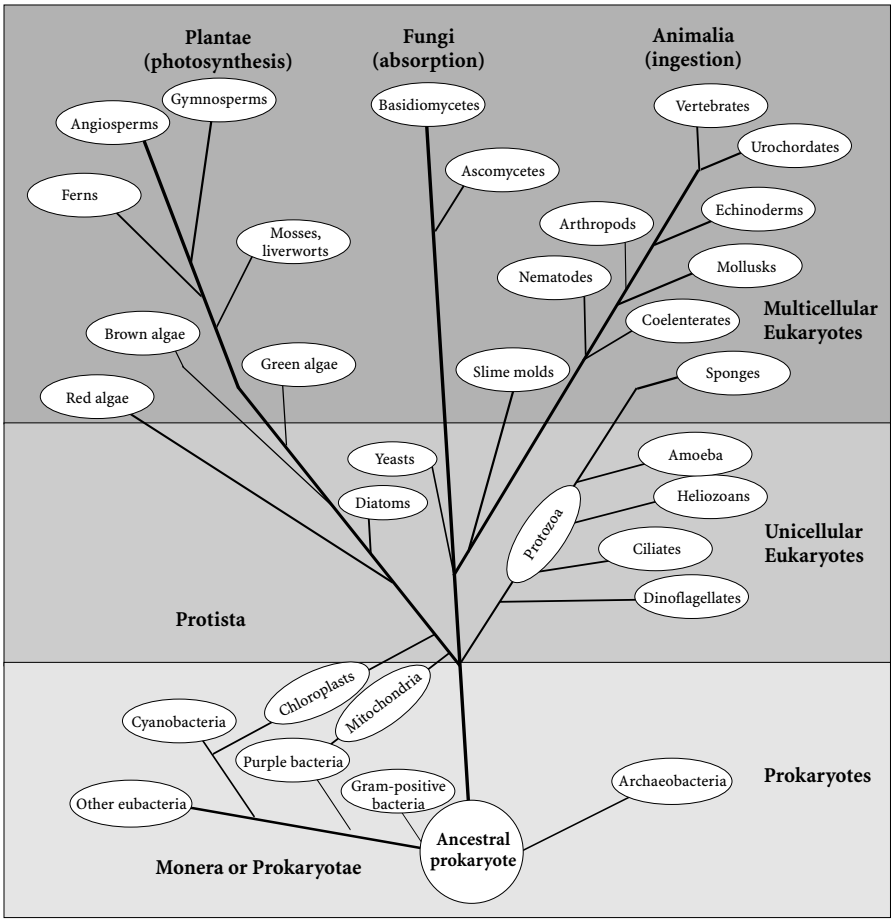

Fig. 3. A simplified diagram showing the diversity of organisms. (Modified after Prescott et al. 1996)

3.1 Eubacteria

Eubacteria are prokaryotic microorganisms. They are recognized as the most dominant group of microorganisms among the various kinds of soil (Table 3; Liesack and Stackebrandt 1992; Visscher et al. 1992; Borneman et al. 1996). They are present in all types of soil, but their population decreases as the depth of soil increases (Duineveld et al. 2001; Wieland et al. 2001). In general, horizon A (soil with organic matter) of a soil profile consists of more microorganisms than horizon B (silicate clay minerals plus organic

Table 1. Comparison of the main types of microorganisms

Microorganisms	Characteristics	Beneficial roles
Prokaryotes		
Bacteria	Rigid cell wall, divided by binary fission, some capable of photosynthesis	Recycle biomass, control atmospheric composition, component of phytoplankton and soil microbial populations
Archaea	Rigid cell wall, unusual membrane structure, photosynthetic membrane, lack chlorophyll	Produce and consume low molecular weight compounds, aid bacteria in recycling dead biomass, some are extremophiles
Eukaryotes		
Fungi	Rigid cell wall, single-cell form (yeast), reproducing by budding, multicellular form (hyphae, mycelium), no photosynthetic members	Recycling biomass, stimulate plant growth
Algae	Rigid cell wall, photosynthetic	Important component of phytoplankton

Table 2. Nutritional aspects of microbial diversity

Nutritional type	Energy source	Carbqon source	Examples
Photoautotroph	Light	Carbon dioxide (CO_2)	Photosynthetic bacteria (green sulfur and purple sulfur bacteria), cyanobacteria, extreme halophiles
Photoheterotroph	Light	Organic compounds	Purple non-sulfur and green non-sulfur bacteria
Chemolitho-autotroph	Inorganic compounds	Carbon dioxide (CO_2)	*Nitrosomonas*, *Nitrobacter*
Chemolitho-heterotroph	Organic compounds	Organic compounds	Most bacteria, fungi, and all animals

matter) and C (weathered parent material; Bruns and Slatar 1982; Subba Rao 1997).

Bacteria live in soil as cocci (sphere, 0.5 µm), bacilli (rod, 0.5–0.3 µm) or spiral (Fig. 4). The bacilli are common in soil, whereas spirilli are very rare in natural environments (Baudoin et al. 2001, 2002). Bacteria have been

Table 3. Microbial diversity of major groups in soils. (Modified after Hawksworth 1991a)

Major groups	Number of microbial species			Species in culture	
	Described species	Estimated species	Total species (%)	Number	Total estimated species (%)
Bacteria	3,000	30,000	10	2,300	7.0
Fungi	69,000	1,500,000	5	11,500	0.8
Algae	40,000	60,000	67	1,600	2.5

classified into two broad categories, the autochthonous and the zymogenous organisms. The autochthonous or indigenous populations are more uniform and constant in soil, since their nutrition is derived from native soil organic or mineral matter (*Arthrobacteria* and *Nocardia*; Herman et al. 1993). The zymogenous bacteria require the input of an external substrate, and their activity in soils is variable. They often produce resting propagules (*Pseudomonas* and *Bacillus*). When specific substrates are added to soil, the number of zymogenous bacteria increases and gradually declines when the added substrate is exhausted (cellulose decomposers, nitrogen utilizing bacteria, *Nitrosomonas*, *Nitrobacter*).

Ten orders are included in the class Schizomycetes. Of these, three orders, *Pseudomonas*, *Eubacteria* and *Actinomycetes*, contain the species of bacteria which are predominantly reported in the soil (Gaskins et al. 1984; Benson 1988; Paul and Clark 1989; Liesack and Stackebrandt 1992; Benizri et al. 2001). The most common bacteria belong to the genera *Pseudomonas*, *Arthrobacter*, *Clostridium*, *Achromobacter*, *Bacillus*, *Micrococcus*, *Flavobacterium*, *Corynebacterium*, *Sarcina*, *Azosprillium*, and *Mycobacteria* (Loper et al. 1985; Bruck 1987; Lynch 1987a, b). *Escherichia* is encountered rarely in soils except as a contaminant from sewage, whereas *Aerobacter* is frequently encountered and is probably a normal inhabitant of certain soils (Subba Rao 1997). 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 (Slater 1988; Benizri et al. 2001).

Bacteria can withstand extreme climates, although temperature and moisture influence their population (Woese 1987; Benizri et al. 2002). In Arctic zones where the temperature is below freezing point, bacteria can thrive as luxuriantly as they do in arid desert soils, where temperatures are very high (Moreno et al. 1986). Such bacteria form spores possessing a tough outer covering, facilitating the survival of bacteria in all adverse environments. Survival by spore formation under extreme conditions should

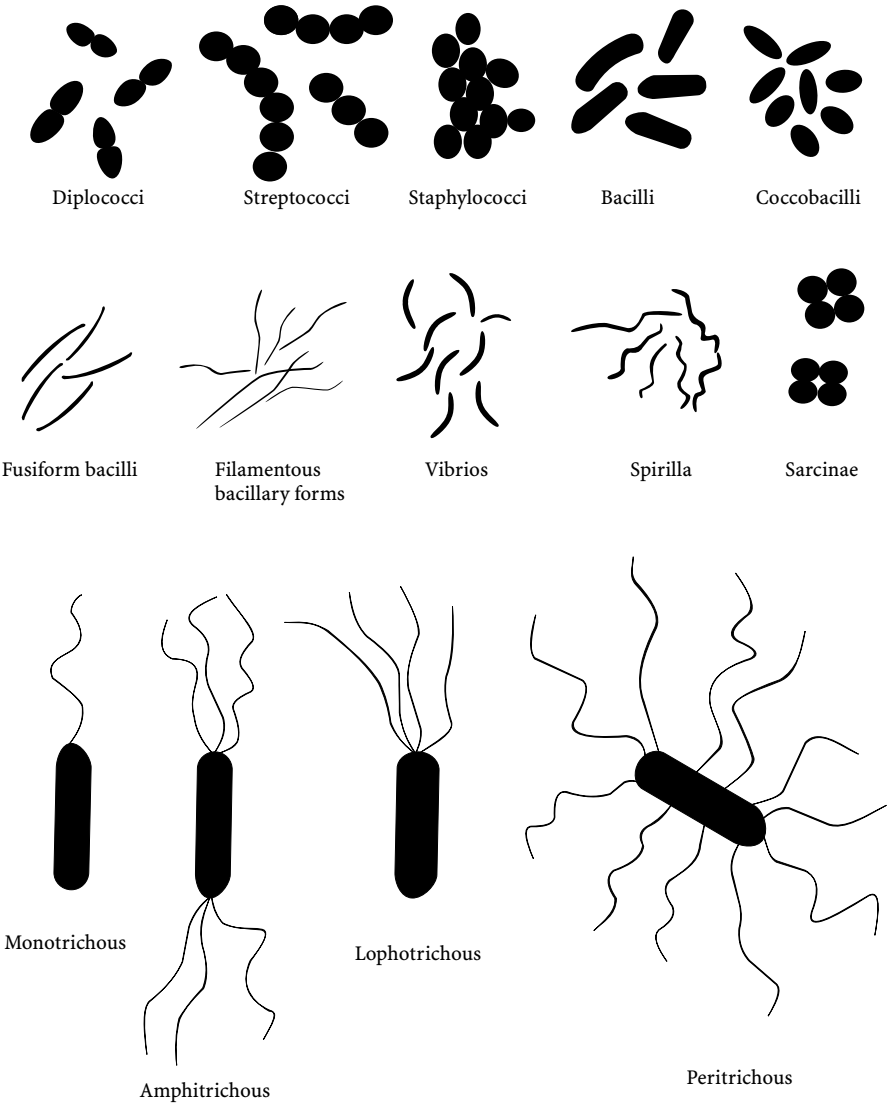

Fig. 4. Diversity of major forms of soil bacteria

be differentiated from tolerance to different temperature ranges, which is one of the factors determining the population of bacteria in soil (Burr and Caesar 1984).

Based on the temperature tolerance, bacteria are grouped as mesophyllous (15–45 °C), psychrophilous (below 20 °C) and thermophilous (45–65 °C; Subba Rao 1997). However, mesophyllous bacteria constitute the

bulk of soil bacteria (Barber and Lynch 1997). Other factors affecting bacterial population in soil are pH, farm practices, fertilizers and pesticide applications and organic matter amendments (Tate 1987).

Autotrophic and heterotrophic bacteria are present in a wide range of soils (Tate 1995). Autotrophic bacteria (purple and green bacteria) synthesize their own organic matter from CO_2 or inorganic carbon sources, whereas heterotrophic bacteria depend on pre-formed organic matter for their nutrition and energy support. Photoautotrophs derive their energy from sunlight that they catch and transform into chemical energy through the bacteriochlorophyll pigment. Chemoautotrophs oxidize inorganic materials to derive energy and at the same time, they gain carbon from CO_2 (Tate 1995). There is a group of bacteria known as obligate chemoautotrophs. Within this group, *Nitrobacter* utilizes nitrite and *Nitrosomonas* ammonium, while *Thiobacillus* converts inorganic sulfur compounds to sulfate and *Ferrobacillus* converts ferrous ions to ferric ions (Alexander and Clark 1965; Baudoin et al. 2002).

The cyanobacteria are a structurally diverse assembly of gram-negative eubacteria characterized by their ability to perform oxygenic photosynthesis. They are considered true prokaryotic microorganisms (Stanier et al. 1986). They have characteristics common to bacteria and algae and are therefore often 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 *Chrococcus*, *Aphanocapsa*, *Lyngbya*, *Oscillatoria*, *Phormidium*, *Microcoleus*, *Cylindrospermum*, *Anabaena*, *Nostoc*, *Scytonema*, and *Fischerella* (Subba Rao 1997; Benizri et al. 2002). Some cyanobacteria also possess heterocysts, which are implicated in nitrogen fixation. The rice fields are a good habitat for the development of certain cyanobacteria where they fix atmospheric nitrogen (Prescott et al. 1996).

Actinomycetes are soil microorganisms with sufficient distinctive features to delimit them into a distinct group within the prokaryotes. Actinomycetes are clubbed with further bacteria in the class of the Schizomycetes, but confined to the order Actinomycetales. They bear certain similarities to Fungi Imperfecti in the branching of the aerial mycelium, which profusely sporulates, and in the formation of distinct clumps or pellets in liquid cultures (Benson 1988).

The number of actinomycetes increases in the presence of decomposing organic matter. They are intolerant to acidity and their numbers decline below pH 5.0. The most conducive range of pH is between 6.5 and 8.0. Waterlogging of soil is unfavorable for the growth of actinomycetes, whereas desert soils of arid and semi-arid zones sustain sizeable populations, probably due to the resistance of spores to desiccation. The percentage of actinomycetes in the total microbial populations increases with the depth of

soil. Actinomycetes can be isolated in sufficient number even from the C horizon (weathered parent material) of soil profiles. The commonest genera of actinomycetes are *Streptomyces* (nearly 70%). In contrast, *Nocardia* and *Micromonspora* and in particular, *Actinomyces*, *Actinoplanes* and *Streptosporangium* are only encountered occasionally (Prescott et al. 1996; Subba Rao 1997). Temperatures between 25 and 30 °C are conducive for the growth of actinomycetes although thermophilic cultures growing at 55 and 65 °C are common in compost heaps where they are numerically extensive and belong mostly to the genera *Thermoactinomyces* and *Streptomyces*.

3.2 Archaebacteria

Archaebacteria is a group of primitive prokaryotes, which were the earliest organisms to have appeared on the earth. Therefore, they are called the ancient bacteria. They even live in extreme hostile environments, like salt

Table 4. Diversity of archaebacteria

Archaebacteria	Characteristics
Methanogens *Methanococcus*, *Methanosprillum*	Generate methane when they oxide hydrogen gas as an energy source, using CO_2 as a terminal electron acceptor
Extreme halophiles *Halobacterium*, *Halorubrum*, *Natrinobacterium*, *Natronococcus*	Found near salt lakes, soda lakes, and brines. They produce pigments and can be seen as pink blooms in concentrated saltwater ponds
Methane-generating thermophiles *Methanothermus*	Found near hydrothermal vents; can grow at temperatures near 100 °C
Sulfur- and sulfate-reducing hyperthermophiles *Thermococcus*, *Archaeoglobus*, *Thermoproteus*, *Pyrodictium*, *Pyrolobus*	Obligate anaerobes that use sulfur or sulfate as a terminal electron acceptor, generating hydrogen sulfide. *Thermococcus*, and *Archaeoglobus* oxidize organic compounds as an energy source; *Thermoproteus*, *Pyrodictium*, and *Pyrolobus* oxidize H_2 as an energy source
Sulfer oxidizers *Sulfolobus*	Oxidize sulfur as a source of energy, using O_2 as a terminal electron acceptor to generate sulfuric acid
Thermophilic extreme acidophiles *Thermophilus*, *Picrophilus*	Grow only in extremely hot, acid environments

pans, salt marshes, hot sulfur springs, etc. Archaebacteria is a heterogeneous group that is phylogenetically very distant from the eubacteria and possesses very distinct characteristics (Table 4). They are characterized by the absence of peptidoglycan in their wall. Instead, their wall contains proteins and non-cellulosic polysaccharides. Their cell membrane contains branched chain lipids that enable them to bear extreme temperatures and pHs. Their rRNA nucleotides are quite different from those of other organisms (DeLong and Pace 2001; Huber et al. 2002).

Archaebacteria comprise two subgroups which are respectively obligate and facultative anoxybiont. Obligate anoxybionts live exclusively in the absence of oxygen and are killed in the presence of O_2. They comprise the methanogen and halophile species. Facultative anoxybionts are found in the presence of oxygen, but can live under anaerobic conditions. They are represented by thermoacidophiles (Tate 1995; Barns et al. 1996; Kyrpides and Olsen 1999).

3.2.1 Methanogens

Methanogens are strict anoxybionts occurring in marshy areas and characterized by their habit of producing CH_4 (methanogenesis) from CO_2 or fumaric acid. Methanogens are ubiquitous in highly reducing habitats. Some of them live as a symbiont in the rumen or first chamber of the stomach of ruminant animals. The most common species among methanogens are *Methanobacterium*, *Methanobrevibacter*, *Methanococcus*, *Methanospirillum*, and *Methanosarcina*. Methanogenesis is now attributed to more than 50 species of bacteria (Jones 1991). Their growth and survival depend directly on the activities of associated microflora, which enhance methanogenesis through the release of C substrates and the maintenance of reducing conditions (Tate 1995; Prescott et al. 1996).

3.2.2 Halophiles

Highly saline environments harbor large populations of a small and distinctive group of halophiles (*Halococcus* and *Halobacterium*). These archaebacteria live in extremely strong brine or salt solutions, salt beds and salt marshes. Some halophiles occur in deep sea volcanic vents at 100 °C, a temperature at which water remains liquid because of extreme hydrostatic pressures. In strong light, halophiles develop a purple pigmented membrane, which can absorb solar radiations. The absorbed light is utilized in the synthesis of ATP. These archaebacteria are unique because

they carry out their metabolic processes directly by the ATP produced by their pigmented membrane. They cannot convert CO_2 to sugar as in photosynthesis. Halophiles growing in salt beds give an offensive smell and undesirable pigmentation to the salt (Beare et al. 1995; Barns et al. 1996).

3.2.3 Thermoacidophiles

The thermoacidophiles occur in high temperature environments like hot sulfur springs, where temperature may be as high as 80 °C and pH as low as 2. These archaebacteria are chemoautotrophic and obtain energy and carbon by oxidizing sulfur under consumption of CO_2. Under aerobic conditions they oxidize sulfur to sulfuric acid. Some archaebacteria can also reduce sulfur to hydrogen sulfide in the absence of oxygen (Stanier et al. 1986; Tate 1995; Prescott et al. 1996).

3.3 Fungi

Fungi dominate all types of soils and represent the greatest diversity among soil microorganisms (Table 1). Fungi possess filamentous mycelium composed of individual hyphae. The hyphae may be uni-, bi- or multinucleate and nonseptate or septate (Hawksworth 1991b). All the environmental factors that influence the distribution of bacteria also apply in fungal flora of soils. However, the quality and quantity of organic matter have a direct bearing on fungal numbers in soils since fungi are heterotrophic organisms. Fungi are dominant in acid soils because an acidic environment is not conducive to the existence of either bacteria or actinomycetes, resulting in the monopoly of fungi for utilization of organic substrates (Bolton et al. 1993). They are also present in neutral or alkaline soils and some can tolerate a pH over 9.0. Arable soils contain abundant fungi since they are strictly aerobic and an excess of soil moisture decreases their numbers. Fungi exhibit a selective preference for various soil depths. Species common in lower depths are rarely found on the surface. This specific distribution is ruled by the availability of organic matter and by the ratio between oxygen and carbon dioxide in the soil atmosphere at various depths. Farm practices including crop rotation and fertilizer or pesticide applications influence the nature and dominance of fungal species (Hawksworth 1991a,b).

Fungi are classified into Phycomycetes, Ascomycetes, Basidiomycetes and Fungi imperfecti (Table 5; Alexander 1977). Many fungi, which are commonly isolated from soils, come under the class Fungi Imperfecti by virtue of the fact that they produce abundant asexual spores, but lack sex-

Table 5. Major groups of soil fungi

Group and representative members	Distinguishing characteristics	Asexual reproduction	Sexual reproduction
Zygomycetes *Rhizopus stolonifer* (black bread mold)	Multicellular, coenocytic mycelia	Asexual spores develop in sporangia on the tips of aerial hyphae	Sexual spores known as zygospores can remain dominant in adverse environment
Basidiomycetes *Agaricus campestris* (meadow mushroom), *Cryptococcus neoformans*	Multicellular, uninucleated mycelia. group includes mushrooms, smuts, rusts that affect the food supply	Commonly absent	Produce basidiospores that are born on club-shaped structures at the tips of the hyphae
Ascomycetes *Neurospora*, *Saccharomyces cerevisiae* (baker's yeast)	Unicellular and multicellular with septate hyphae	Common by budding, conidiophores	Involves the formation of an ascus on specialized hyphae
Deuteromycetes (Fungi Imperfecti) *Penicillium*, *Aspergillus*	A number of these are human pathogens	Budding	Absent or unknown

ual stages (Lynch 1987a, b). Members of this class are distinguished by their septate mycelium and a structure called conidiophore from which conidia or spores are continuously produced. The other three classes of fungi have both sexual and asexual means of reproduction. Phycomycetes members possess nonseptate and unicellular mycelia and produce an undefined number of specialized spore cells called sporangia. In Ascomycetes, the sporangium produces a species-specific number of meiotic spores (often four or eight) and different types of active or passive spore extrusion mechanisms are encountered. A higher specialization degree of the sporangium, the basidia, is reached in Basidiomycetes. Here, the number of produced meiotic spores (generally four) is constant. These result either from fragmentation of the basidia or from their budding in so-called ballistospores. The most important vegetative trait of soil fungi is their producing a mycelium capable of polarized growth toward adequate substrate sources. Fungi and especially members of the Asco- and Basidimycetes are able to degrade very complex organic compounds such as cellulose or lignin, but

many of them also live as root symbionts (mycorrhizas) and obtain simple sugars from their plant partners (Lynch and Hobbie 1988).

The following genera of fungi are most commonly encountered in soils (Fig. 4): *Acrostalagmus*, *Aspergillus*, *Botrytis*, *Cephalosporium*, *Gliocladium*, *Monilia*, *Penicillium*, *Scopulariopsis*, *Spicaria*, *Trichoderma*, *Trichothecium*, *Verticillium*, *Alternaria*, *Cladosporium*, *Pillularia*, *Cylindrocarpon* and *Fusarium*, *Absidia*, *Cunninghamella*, *Mortierella*, *Mucor*, *Rhizopus*, *Zygorynchus*, *Pythium*, *Chaetomium*, and *Rhizoctonia* (Newman 1985; Hawksworth 1991a; Subba Rao 1997). 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. Filamentous fungi in soil degrade organic matter and help in soil aggregation. 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 1991b).

3.4 Algae

Soil algae are ubiquitous in nature where moisture and sunlight are available. The algae, which are dominant in soils, are members of the class Chlorophyceae. Diatoms have also been found in soils. These microorganisms are visible to the unaided eye in the form of green scum on the surface of soils, whereas some algae are microscopic. In the soil, algae are not as plentiful as fungi (Table 3; Metting 1988). They may be unicellular (*Chlamydomonas*) or filamentous (*Spirogyra*, *Ulothrix*). Algae are photoautotrophic organisms by virtue of the presence of chlorophyll in their cells. They use CO_2 from the atmosphere and produce O_2. Algae have been found below the surface of the soil and beyond the reach of sunlight. However, their number here is low compared to that of algae inhabiting the surface of soil (Metting 1988; Subba Rao 1997). Some of the common green algae occurring in most soils belong to the genera *Chlorella*, *Chlamydomonas*, *Chlrococcum*, *Oedogonium*, *Chlorochytrium*, and *Protosiphone* (Metting 1988; Lynch 1990).

4 Microbial Diversity and Biological Spheres

Factors such as resource availability, microclimatic conditions, soil solution chemistry and soil structure can significantly influence the size, composition and distribution of soil biotic communities (Wolters 1991; Baudoin

et al. 2001, 2002). Soils can be viewed as being composed of a number of biologically relevant spheres of influence that define much of their spatial and temporal heterogeneity. Examples of these spheres include the detritusphere, the drilosphere, the porosphere, the aggregatusphere and the rhizosphere. Although not mutually exclusive, each sphere has fairly distinct properties that regulate the interactions among organisms and the biogeochemical processes that they mediate (Beare et al. 1995).

4.1 The Detritusphere

The detritusphere corresponds to the zone of recognizable plant and animal detritus undergoing decay. Numerous studies have shown that the structure of decomposer communities is influenced by the chemical composition of plant detritus (Swift et al. 1979; Kjoller and Struwe 1982). In many cases, distinct communities of soil organisms, such as fungi (Wicklow et al. 1974) can be ascribed to ecosystems of similar vegetation cover. Diversity in microfungal communities often correlates well with the variance in the composition of the plant community (Christensen 1989), and can be related to the patchy distribution of resources. Disruptions to the soil ecosystem such as overgrazing, cultivation and fertilizer applications tend to reduce microhabitat heterogeneity and the diversity of corresponding microfungal communities (Gochenauer 1981; Boddy et al. 1988; Christensen 1989). Furthermore, microhabitat patches may create a mosaic of aerobic and anaerobic microsites that promote the activities of N_2-fixing and -denitrifying microorganisms in the detritusphere (Lynch and Harper 1985; Lynch 1990). Patterns of microbial colonization are influenced by nutrient fluxes in litter (Beare et al. 1992). Nutrient release from rapidly decaying litter fractions stimulates decomposition of adjacent recalcitrant litter (Seastedt 1984), while others suggest that inhibitory compounds such as phenolics and tannins may lower the decomposition of litter mixtures. Recent studies by Blair et al. (1990) provide support for these hypotheses, showing that interaction between litter types can alter decomposer communities and rates of nutrient release from single species litter.

4.2 The Drilosphere

The zone of earthworm influence, including maiden litter and soil volume descending along the burrow walls, is often referred to as the "drilosphere" (Hamilton and Dindal 1983; Lavelle et al. 1989). Drilosphere soils are enriched in N, P and humified organic matter in comparison to the surround-

ing soils. They are also estimated to contain a high percentage of the whole soil N_2-fixing and -denitrifying bacteria (Wolters 1991). However, the nature of these influences differs between the earthworm species, in accordance to their ecological classification. Shaw and Pawluk (1986) observed that deep burrowing anecic earthworms had effects on the soil fabric that were localized in the drilosphere. However, wherever endogeic species were also present, their activities tended to homogenize the surface soil horizons. Clearly, these interactions can greatly affect the heterogeneity of organisms and processes in soils.

4.3 The Porosphere

Soil structure can be defined as the arrangement of solids and voids in soils, covering a range of sizes from nanometers to centimeters (Oades 1993). The influence of soil biota spans the full range of sizes, affecting the pore size distribution through biopore development and the formation and disruption of soil aggregates. This milieu, termed the "porosphere" (Vannier 1987), is occupied by organisms the smallest of which range from bacteria, protozoa, nematodes to fungi. Larger soil biota such as plant roots, earthworms and other members of the macrofauna create smooth, cylindrically shaped macropores. These biopores extend considerable distances in the soil and change soil structure. Ants and termites form mounds and have patchy effects on soil structure (Lobry de Bruyn and Conacher 1990). However, mounds are also sites of nutrient enrichment due to subsoil nutrients brought to the surface and the storage of plant detritus in their galleries. In this zone several mycorrhizal fungi have been reported (Friese and Allen 1993). Evans and Miller (1988) demonstrated that macropores are the sites of concentrated mycorrhizal inocula. They found increasing rates of mycorrhizal infection and phosphorus availability related to increased plant growth.

4.4 The Aggregatusphere

Soil organisms have many wide-ranging effects on aggregation that can influence the physical, chemical and biological properties of soils (Lee and Foster 1991). Aggregates are comprised of a number of components, ranging from clay microstructures and fine particulate organic matter to microaggregates (50–250 µm), made up of these primary particles and macroaggregates (> 250 µm diameter), themselves composed of microaggregates (Oades and Waters 1991). The aggregatusphere encompasses all

these constituents, and defines a complex of constraints for the exchange of biota, solutes and gases, the properties of which depend on the scale at which it is viewed. The contribution of soil microorganisms to aggregation is most apparent in soils of lower clay content and low shrink–swell capacities, where the abiotic effects of wet–dry and freeze–thaw cycles are reduced (Oades 1993).

Microorganisms are the primary agents of aggregate stabilization. Both fungi and bacteria contribute to stabilization of soil aggregates through deposition of extracellular polysaccharides and formation of degraded, aromatic humic materials that form clay–polyvalent metal–organic matter complexes. Though not as persistent, fungi also contribute to aggregate stabilization through hyphal anchoring of particles. The influence of fungi and bacteria on aggregate stabilization varies widely among species and depends considerably on the nature of the available substrates (Aspiras et al. 1971) and on the products of rhizodepositions (Reid and Goss 1981). Furthermore, the type of land-use management can influence both the composition of microbial communities and their contribution to aggregate stabilization (Beare et al. 1994).

4.5 The Rhizosphere

The zone of primary root influence can be termed the "rhizosphere". It is a temporally and spatially variable environment where the products of rhizodeposition stimulate microbial activity and populations, thereby altering the balance between N mineralization and immobilization (Fig. 5; Clarholm 1985; Coleman et al. 1988). The biomass of soil microflora is usually greater in the rhizosphere than in root-free soil (Bowen and Rovira 1991). Some studies show that fungal species diversity is lower while the morphological diversity of bacteria and Actinomycetes is higher in the rhizoplane, the root surface, as compared to soil outside this zone (Bowen and Rovira 1991). The extent of these effects depends on the characteristics of root growth, including their production, turnover and architecture.

Root architecture influences and is influenced by the physical, chemical and biological properties of soils. Root system development responds strongly to soil fertility. The proportion of total plant production allocated below ground and the architecture of the root system (root length, branching frequency and mycorrhizal development) depend greatly on the distribution and availability of nutrients in soils (Fitter 1985). Increases in fine root proliferation, slower root turnover and greater allocation of plant C to mycorrhizal associates tend to occur when nutrients are low or patchily distributed. Depending on their source, root exudates can inhibit

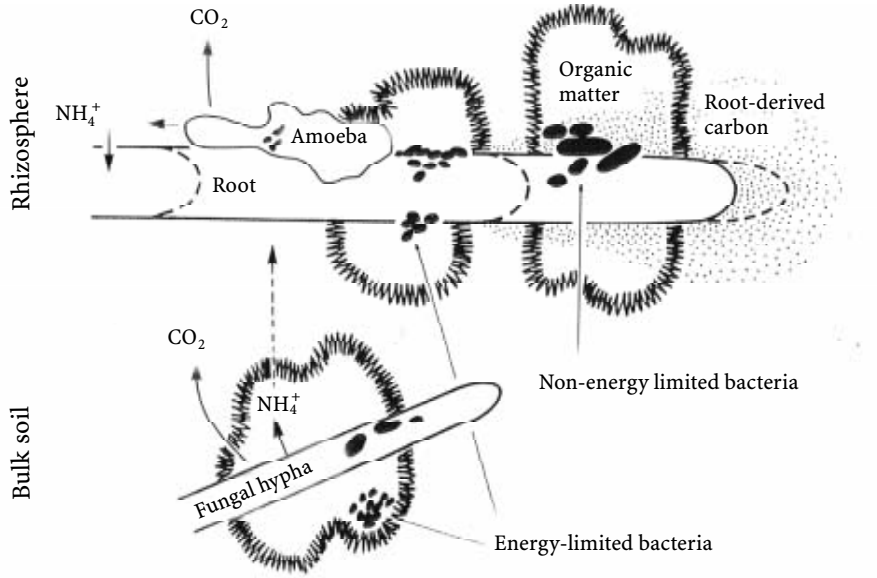

Fig. 5. Model of proposed interactions in the rhizosphere and in the bulk soil. Note the excessive production of root exudates towards the distal end of the root, intermingled with fungal hyphae

the growth of phytopathogenic microorganisms and alter the composition of the rhizosphere community. Though not well studied, mycorrhizal symbionts also influence characteristics of root exudates that shape the composition and activity of the rhizosphere community (Meyer and Linderman 1986).

5
Microbial Diversity and Chemical Transformation

The importance of microbial diversity for biogeochemical transformations can be viewed most directly through the specific chemical transformations that organisms perform. Their effects on biogeochemical transformations occur through both direct and indirect means. In this section, we review the direct effect of microorganisms (particularly bacteria, fungi) on biogeochemical transformations in soils (Beare et al. 1995).

5.1 Nitrogen Transformation

Nitrogen availability is a key factor regulating the biological productivity of many ecosystems (Herbert 1999; Capone 2000). Soil microorganisms have long been recognized as important agents affecting N pools through various transformations. The assimilation into the organic form and subsequent release of inorganic N, as performed by a broad array of prokaryotic and eukaryotic organisms, comprise the inner core of the N cycle in nature (Alexander 1977; Paul and Clark 1989). However, it is the uniquely bacterial processes of N_2 fixation, nitrification, and denitrification that define the broader cycle and can affect directly the availability and form of N within particular ecosystems (Postgate 1987). In the nitrogen cycle, many bacteria (eubacteria and archaea) are involved in ammonification, but other N transformations are carried out by taxonomically narrow groups of microorganisms. Chemoautotrophic nitrification is accomplished by relatively few obligate aerobic soil bacteria (ammonium oxidizers and nitrite oxidizers) which oxidize NH_3 to NO_2 (*Nitrosomonas*, *Nitrococcus*) and NO_2 to NO_3 (*Nitrobacter*; Kaplan 1983). Heterotrophic nitrification is also known in several bacteria (*Arthrobacter*) and Actinomycetes, but probably accounts for relatively low levels of NO_3 production. Other steps in the N cycle, such as dissimilatory NO_3 and NO_2 reduction (*Mycobacterium*, *Clostridium*) and denitrification (*Pseudomonas*, *Bacillus*, *Thiobacillus*), are carried out by a few, widely distributed genera (Payne 1981). Asymbiotic N_2 fixation is carried out by aerobic (*Azotobacter*, *Beijerinckia*), microaerophilic (*Clostridium*) organotrophic bacteria as well as by free-living cyanobacteria that are sometimes abundant in soils. Symbiotic N_2 fixation is best known for bacterial (*Rhizobium*, *Bradyrhizobium*) associations with legumes, but also concerns some plant genera of nonleguminous angiosperms (*Alnus*, *Casuarina*, *Ceanothus*, *Myrica*) associated to specific Actinomycetes such as *Frankia*.

Fungi are major components of the soil biomass (Hawksworth 1991a,b) and are of considerable importance in regulating ecosystem processes (Dighton and Boddy 1989; Cromack and Cadwell 1992; Wainwright 1992). Though often grouped according to their specific enzymatic capabilities, most fungi have broad versatility in their chemoheterotrophic metabolisms. Despite this versatility and their prominent role in plant litter decomposition (Kjoller and Struwe 1982; Cromack and Cadwell 1992), many fungi maintain more specialized mechanisms for obtaining energy and nutrients (Wainwright 1992).

The important role of many fungi, including ectotrophic mycorrhizal species (Wainwright 1992; Lakhanpal 2000), in the ammonification of organic N is well established, but their contribution in other areas of the N

cycle has received little attention. Nitrification has long been known for *Aspergillus flavus*, but the broader range of fungal involvement has only recently been described (Killham 1987). Though autotrophic nitrification by bacteria is often assumed to dominate, the heterotrophic activities of fungi may account for a significant proportion of the nitrification in acid forest soils (Schimel et al. 1984). The extent of fungal nitrification in other soil systems remains poorly known. In contrast, several genera of fungi are known to play a role in nitrate reduction (*Fusarium*, *Acremonium* and *Aspergillus* spp.) though few studies have demonstrated significant levels of complete denitrification in fungi.

5.2 Phosphorus Transformation

Phosphorus is considered to be a major growth-limiting nutrient and unlike the case for nitrogen, there is no large atmospheric source that can be made biologically available (Ezawa et al. 2002). It is essential in both cellular energetics (ATP) and cellular structures (DNA, RNA, and phospholipids). Therefore, phosphate-dissolving soil microorganisms play a profound role (Schachtman et al. 1998). The role of bacteria in the P cycle appears somewhat less specialized. Although there is no microbially mediated gaseous flux of P, however, *Pseudomonas* and *Bacillus* are involved in the solubilization of inorganic phosphorus. Although bacteria have been used in the growth of plants, fungi seem to be better agents in the dissolution of phosphates (Barea 2000; Barea et al. 2002; Chalot et al. 2002). Phosphate-dissolving bacteria are known to reduce the pH of the substrate by secretion of a number of organic acids such as formic, acetic, propionic, lactic, glycolic, fumaric and succinic acids. As a group, soil bacteria are important to the short-term immobilization of P and the mineralization of organic phosphorus (Subba Rao 1997).

Somewhat more specialized groups of bacteria are involved in the transformation of metals in soils. Examples of these transformations include the reduction (*Bacillus*) and precipitation (Chladobacteriaceae) of iron as well as the chemolithotrophic oxidation of Fe^{2+} under acid conditions (*Thiobacillus ferroxidans*; Table 6). Some free-living fungi (*Aspergillus* and *Penicillium*) also excrete organic acids and Fe siderophores that solubilize insoluble forms of phosphate and contribute to the weathering of soil minerals (Mehta et al. 1979; Sollins et al. 1981).

Several enzymes are involved in the decomposition of the organic phosphorus compounds (Jennings 1995). Those enzymes that hydrolyze P-esters are commonly called phosphatases. The function of the phosphatase is to break down organic phosphates and polyphosphates, thus releasing or-

Table 6. Metabolism of chemolithoautrotrophs

Common name of organism	Source of energy	Oxidation reaction (energy yielding)	Important features of group	Common genera in group
Hydrogen bacteria	H_2 gas	$H_2 + ½\,O_2 \rightarrow H_2O$	Can also use simple organic compounds for energy	*Hydrogenomonas*
Sulfur bacteria	H_2S	$H_2S + ½\,O_2 \rightarrow H_2O + S$ $S + 1½\,O_2 + H_2O \rightarrow H_2SO_4$	Some organisms of this group can live at a pH of less than 1	*Thiobacillus*, *Beggiatoa*, *Thiothrix*
Iron bacteria (nonphoto-synthetic)	Reduced iron (Fe^{2+})	$2\,Fe^{2+} + ½\,O_2 + H_2O \rightarrow 2\,Fe^{3+} + 2\,OH^-$	Iron oxide present in the sheaths of these bacteria	*Sphaerotilus*, *Gallionella*
Nitrifying bacteria	NH_3	$NH_3 + 1½\,O_2 \rightarrow HNO_3 + H_2O$	Important in nitrogen cycle	*Nitrosomonas*
	HNO_2	$HNO_2 + 1½\,O_2 \rightarrow HNO_3$	Important in nitrogen cycle	*Nitrobacter*

thophosphate (Tabatabai 1982). In soils, there are two groups of phosphatases, the phosphoric monoester hydrolases and the phosphoric diester hydrolases. In the first group are enzymes such as phytase, nucleotidase and sugar phosphatases, while the second group contains the nuclease and phospholipases. More generally, these enzymes are divided into two groups named after their optimal pH activity. In soils, phosphatases generally exhibit three pH optima (5.0, 7.0, and 9.5), consequently representing acid, neutral and alkaline phosphatases, respectively. Apart from influencing the substrate, changes in the proton concentration and thus in the pH strongly influence the enzymes by altering their ionization state and solubility. Phosphatases are the most stable around their pH optimum and are irreversibly denatured at extreme pH values (Tabatabai 1982). Some fungi exhibit their highest acid phosphatase activity at acidic pH values. These fungi also display some activity at natural pH (Tarafdar and Rao 1996; Pant and Warmen 2000). Alkaline phosphatase from mycorrhizal fungi also showed some activity at natural pH (Bae and Borton 1989). Very little is known about the origin and production of natural phosphatases. Nannipieri et al. (1996) showed that part of the neutral phosphatase activity in soil could be correlated to the microbial biomass.

5.3 Sulfur Transformation

Sulfur is an important element from both a biochemical and geochemical point of view. It constitutes approximately 1% of the dry mass of organisms in which it has many structural and enzymatic functions. Sulfur also acts as a significant electron donor and acceptor in numerous bacterial metabolic pathways (Prescott et al. 1996; Hurst 2002). Sulfur can be found in a range of valence states from the highly reduced sulfide to the most oxidized form in sulfate. Microbial S transformations are closely linked with the carbon cycle in which S reduction coupled with organic matter utilization is a major mineralization pathway in anoxic habitats, while S oxidations can occur aerobically and anaerobically, whereby the concerned bacteria can be auto- and/or phototrophic (Jorgensen 1982, 1994).

Microorganisms of the S cycle are extremely diverse. They can be either oxybiont or anoxybiont. The anoxybiont sulfate-reducing bacteria (SRB), which are unique physiologically and genetically, are represented by several genera (Devereux and Stahl 1993). Sulfate-reducing bacteria are capable of utilizing iron and manganese as electron acceptors (Lovley and Phillips 1994). Oxygen-reduction has been demonstrated, but O_2-dependent growth has not been confirmed (van Niel and Gottschal 1998). Chemolithotrophic sulfur oxidation is mediated aerobically by colorless sulfur bacteria, some purple sulfur bacteria and SRB (Table 6). Anaerobically, nitrate respiring chemolithotrophs oxidize sulfide, and both oxygenic and anoxygenic phototrophic bacteria use sulfide as an electron donor for photosynthesis (Prescott et al. 1996). Sulfate-reducing bacteria may diminish the availability of sulfur for plant nutrition and thus influence agricultural production. *Desulfovibrio desulfuricans* is a species belonging to this class of bacteria (Hurst 2002). Bacteria capable of oxidizing inorganic sulfur compounds vary morphologically from nonfilamentous (*Thiobacillus*) to filamentous forms (*Beggiatoa*, *Thiothrix and Thioploca*). Among these bacteria, *Thiobacillus* deserves special mention as it produces sulfuric acid when elemental sulfur is added to soil with the result that the soil pH may fall as low as 2.0 after prolonged incubation with the bacterium. Several fungi and Actinomycetes have also been reported to be sulfur oxidizers (*Aspergillus*, *Penicillum*, *Microsporeum*). *Thiobacilli* can also be used in the manufacture of 'Biosuper', a form of organic fertilizer once favored in Australia. In Biosuper, a mixture of rock phosphate and gypsum is inoculated with *Thiobacillus thiooxidans*. Sulfuric acid produced in the mixture dissolves the phosphate, thus enhancing the phosphorus nutrition of plants (Widdel and Hansen 1991).

5.4 Iron Transformation

Certain bacteria oxidize ferrous iron to the ferric state, which precipitates as ferric hydroxide around cells (Table 6; Quastel 1995). These bacteria, commonly known as iron bacteria, are usually nonfilamentous and spherical or rod-shaped (*Gallionella*, *Siderophacus*, *Siderocapsa*, *Siderophaera*, *Ferribacterium*, *Naumanniela*, *Ochrobium*, *Sideromanas*, *Sideronema*, *Ferrobacillus*, *Siderobacter*, and *Siderococcus*). Filamentous forms resembling algae are also encountered (*Leptothrix*, *Sphaerotilus*, *Toxothrix*, *Crenothrix*, and *Colnothrix*). In addition to these bacteria, certain algae belonging to Cyanophyceae, also transform ferrous salts to the ferric state and deposit the precipitation around their filaments. The ferric hydroxide deposits give a brown or rust-red color to these organisms.

The iron bacteria can be grouped into: (1) obligate chemoautotrophs, capable of utilizing energy released in the process of ferric hydroxide formation (*Gallionella ferruginea*, *Thiobacillus ferroxidans*, and *Ferrobacillus ferroxidans*), (2) facultative chemoautotrophs, utilizing energy derived in the process of ferric hydroxide formation or alternatively from organic matter (*Leptothrix ochraceae*) and (3) heterotrophs represented by most other iron bacteria which do not derive energy from iron oxidation, but depend upon organic matter for their nutrition.

6 Microbial Diversity and Biotic Interactions

Due to their vast diversity, large populations and long evolutionary history, microorganisms have contributed greatly to the rich and complex interactions among soil organisms (Barea 2000; Barea et al. 2002). These interactions range from highly specific symbioses to diffused mutualisms.

Mycorrhizal symbioses are among the best-known examples of plant–microbe interactions and play a key role in regulating plant productivity and nutrient cycling (Barea et al. 1998, 2002; Berreck and Haselwandter 2001). Mycorrhizal fungi are found in 75–80% of all vascular plant species. Although these associations are often assumed to have weak specificity, it has been shown that many are highly specific, emphasizing the importance of diversity to ecosystem functioning. The root–microbe interactions are the key to understanding ecosystem function, and places mycorrhizas in perspective with the many other complex interactions taking place in the rhizosphere.

Mycorrhizal fungi interact with a wide range of other microorganisms in the rhizosphere (Bowen and Rovira 1999). These interactions may be

stimulatory or inhibitory; some may be competitive, while others may be mutualistic. Mycorrhizal fungi are found in the endorhizosphere, in the rhizosphere and in the bulk soil. In all these zones, they interact with the soil microbiota. The internal mycelium interacts mainly with the host root and other microorganisms inhabiting the area. The external mycelium interacts with many organisms, including bacteria, fungi, protozoa, nematodes, arthropods and large animals. Some interactions may be mutualistic while others may be difficult to define. Some bacteria such as fluorescent pseudomonas may proliferate in the hyposphere of mycorrhizal fungi (Lynch 1990). Competitive interactions between the mycorrhizal fungus and bacteria and other fungi have been observed, and there may be allelochemical interactions similar to antibiosis which can, however, be either stimulatory or suppressive (Srivastava et al. 1996; Bansal et al. 2000).

Formation of arbuscular mycorrhiza (AM) fungi changes plant physiology and certain nutritional and physical properties of the rhizosphere soil (Giri et al. 2001). This, in turn, affects colonization patterns of this region by soil microorganisms by the so-called mycorrhizosphere effect (for details, see Chap. 11). AM fungi thus interact with natural and introduced microorganisms in the mycorrhizosphere, hence affecting soil properties and quality (Gryndler 2000). The interactions of plant growth-promoting rhizobacteria (PGPR) and AM fungi have great importance in plant health and soil fertility (Azcon-Aguilar and Barea 1996). Conversely, soil organisms are known to affect AM formation and functioning (Barea et al. 2002). The microbial population in the rhizosphere can either interfere with or benefit the establishment of AM fungi (Vosatka and Gryndler 1999). Deleterious rhizosphere bacteria (Nehl et al. 1996) and mycoparasitic relationships (Jeffries 1997) have been found to interfere with AM development, while many microorganisms can stimulate AM formation and/or functioning (Gryndler 2000; Barea et al. 2002).

The microbial interactions in the mycorrhizosphere may involve a variety of bacteria and fungi with specific functional capabilities that may influence plant growth. This may include microbes such as strict or facultative anaerobes, extracellular chitinase producers, phosphate solubilizers, siderophores, antibiotic, hormone producers, and plant growth promoters (Linderman 1988; Barea 1997; Mukerji et al. 1997).

Recently, Varma and his colleagues have discovered a new root endophyte designated *Piriformospora indica*, belonging to the Hymenomycetes (Basidiomycota; Fig. 6; Verma et al. 1998; Varma et al. 1999; Koch et al. 2004; Pham et al. 2004a). *P. indica* hyphae colonize the root and show inter- and intracellular structures (vesicles and hyphal coils). The fungus grows on a wide range of synthetic simple and complex media (Pham et al. 2004b). The temperature range of the fungal growth is 20–35 °C; the optimum temperature and pH being 30 °C and 5.8, respectively. This new

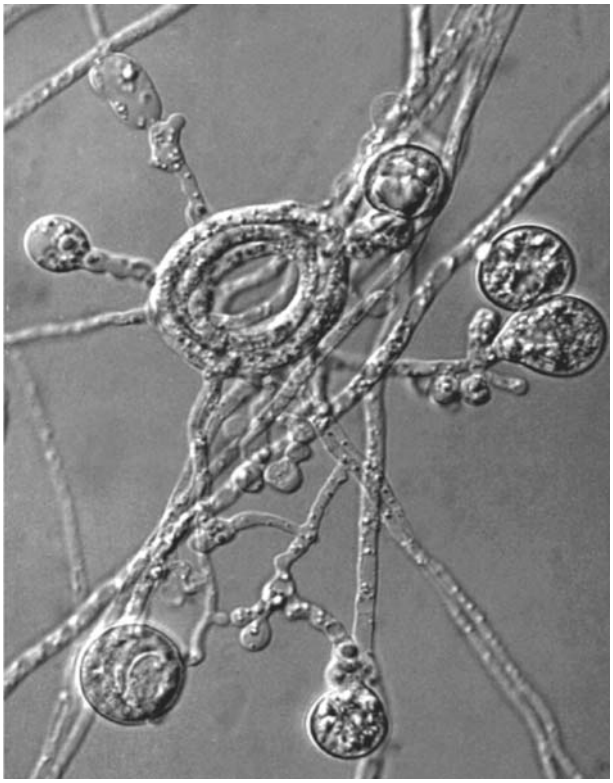

Fig. 6. *Piriformospora indica*: typical growth and differentiation on solidified nutrient medium. Note the pear-shaped spores and hypha coils. (Courtesy G Kost, Marburg, Germany)

fungus shows interactions with a wide range of soil microbiota. *P. indica* interacts with rhizobacteria, including *Pseudomonas florescence*, *Azotobacter chrococcum*, *Pseudomonas putrida*, *Bacillus subtilis*, *Azospirillum*, and *Bradyrhizobium* (Pham et al. 2004a,b).

On MMN media, a green alga *Chlamydomonas rienhardtii* and the *P. indica* showed a positive interaction. Both microorganisms grew well in perfect harmony. On the Kaefer medium, *P. indica* and a symbiotic fungus *Sebacina vermifera* grew normally without inhibiting each other. The most interesting part was after 7 days at the intersection of two colonies, when hyphae turned highly intertwined, thickened and produced a large number of chlamydospores (Singh et al. 2003).

Several commonly occurring soil fungi were tested for the interaction with *P. indica*. The results were highly diverse (Varma et al. 2001; Pham et al. 2004a). The growth of *Aspergillus sydowi*, *Rhizopus stolonifer*, and

Aspergillus niger was completely blocked by *P. indica*. *Cunninghemella echinulata* was partially blocked by *P. indica*, whereas *Rhizopus oryzae*, *Aspergillus flavus*, and *Aspergillus* sp. had completely blocked the growth of *P. indica*. Results indicate that *P. indica* interacts with a diverse group of soil fungi and its interaction varied from the negative to positive association (Kumari et al. 2003; Pham et al. 2004a).

P. indica showed a profound effect on disease control when challenged with a virulent root and seed pathogen *Gaeumannomyces graminis*. *P. indica* completely blocked growth of this pathogen. It indicates that *P. indica* acted as a potential agent for biological control of root diseases, however, the chemical nature of the inhibitory factor is still unknown.

Geosiphon pyriforme, a coenocytic soil fungus, lives in endocytobiotic association with a cyanobacterium, *Nostoc punctiforme* (Schüßler 2002). The symbiotic nature of the system was first recognized by von Wettstein (1915), who described it as a symbiosis between a heterotrophic siphonal chlorophycean alga and *Nostoc*. The fungus lives together with the cyanobacterium on the surface and in the upper layer of wet soils poor in inorganic nutrients, particularly in phosphate (Schüßler and Kluge 2001; Kluge et al. 2002). When a fungal hypha comes into contact with free-living *Nostoc* cells, the latter are incorporated by the fungus at the hyphal tip, which thereafter swells and forms a unicellular "bladder", about 1–2 mm in size and appearing on the soil surface (Fig. 7). Inside this bladder, the cyanobacteria are physiologically active and dividing. Due to the physiological activities of the endosymbiont, the consortium is capable of C- and N-autotrophic life. *Geosiphon* can be considered as a primitive endocytobiotic system, because the photobiont can be experimentally separated and cultured without the fungal partner, which is obligate symbiont. It has been suggested that *Geosiphon* could provide an important model system for another symbiosis, the arbuscular mycorrhiza. It bears a great potential for the study of many fundamental mechanisms and evolutionary questions concerning arbuscular mycorrhizas (Kluge et al. 1997)

Geosiphon pyriforme representing a symbiotic association between a glomalean fungus and a photoautotrophic prokaryotic alga could reflect an ancestral partnership. Thus, it is very plausible to assume that in the beginning of terrestrial plant life, other associations between glomalean fungi and photoautotrophic organisms also existed (Redecker et al. 2000).

Mollenhauer et al. (1996) studied the development of the symbiotic association *Geosiphon pyriforme*. Initially, the cells of the cyanobacterium *Nostoc punctiforme* live freely together with the future fungal partner in and on the soil. There, the partners come into contact, but a successful interaction of the fungus with *Nostoc* to form the symbiosis depends on the appropriate developmental stage of the cyanobacterium (Schüßler and Kluge 2001).

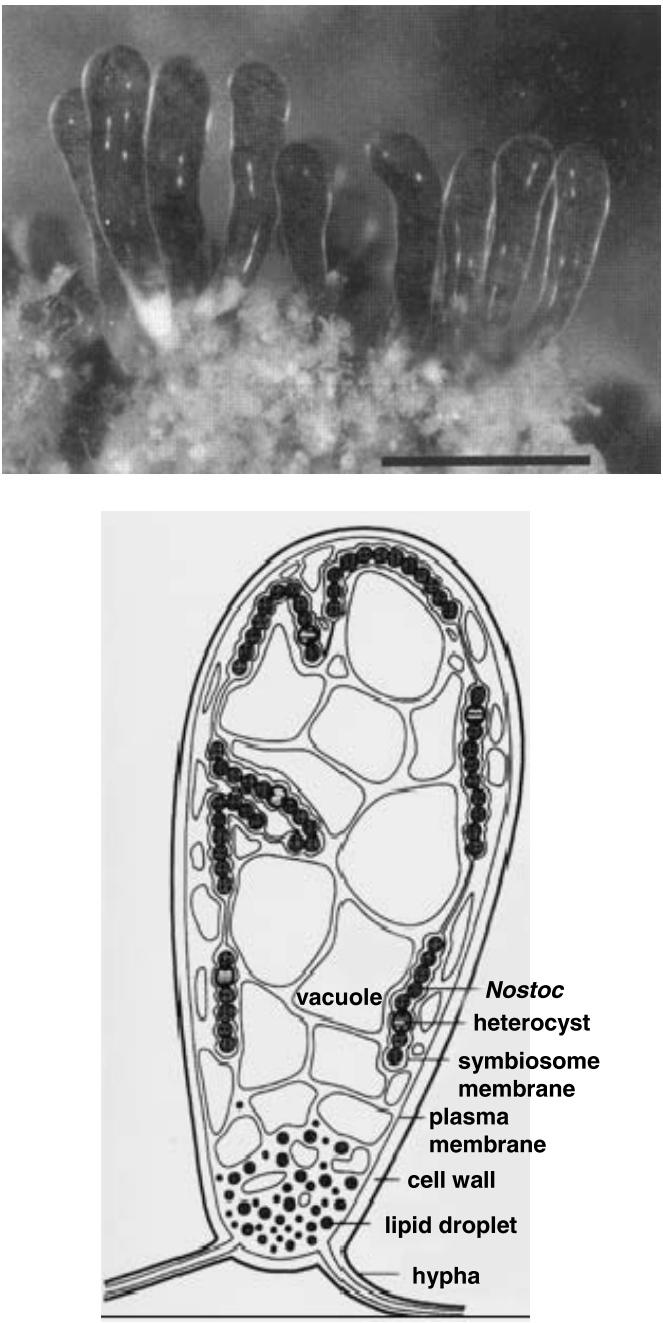

Fig. 7. *Above* Bladder of *Geosiphon pyriformae* on a natural substrate (Schüßler et al. 2001). *Below* Overview showing schematic drawing of bladder compartmentation. (Schüßler and Kluge 2001)

7
Conclusion

Microbiology is the study of microorganisms which exist in natural or artificial environments. The origin of scientific research in this field rests in the observation of Antony van Leeuwenhoek that was published in 1677 as "animalcula" or the "little animals", which lived and replicated in water. During the intervening centuries, the expansion of our knowledge has been based on increasingly detailed observations and experimentation, in which we have been aided by advancements in microscopy and the development of biochemical and mathematical tools. We have discovered that microorganisms cover our planet, living even in the fumaroles of surface volcanoes and in the sedimentary rocks within dry valleys. Microbes can be found as deep down as several kilometers, both in glacial ice sheets and in bedrock. At deep-ocean thermal vents, where the temperature of the water can reach several hundred degrees above its normal boiling point, the extremely high barometric pressure keeps water in its liquid state and microbial life bounds. The microorganisms chemically interact with their physical environment, and their most notable effect has been the creation of an oxidizing atmosphere on this planet. By way of these chemical interactions, microbes remain crucial to the biogeochemical cycling which supports the continuance of life on our planet, producing the elements that represent the basic ingredients of life such as carbon, hydrogen, nitrogen, oxygen, phosphorus and sulfur.

During the last few decades, we have begun learning how to harness microbial biosynthetic and degradative activities. This harnessing, including the intentional manipulation of microbial activities, constitutes the basis of microbial biotechnology, whereby we direct the activity of microorganisms within both natural and artificial environments for a variety of purposes. As one example, we utilize microorganisms as tools to help us achieve goals such as the production of materials which are beneficial to our existence, including numerous antibiotics, vitamins, and fuels such as biogas and ethanol. Microorganisms also are used as tools to help us intentionally degrade both natural and anthropogenic materials in wastewater digesters, compost, landfills, natural terrestrial environments, and natural or artificial aquatic environments. Sometimes we use microorganisms as tools to achieve agricultural goals such as protecting plants from insect damage. Furthermore, microbial processes, such as using microorganisms to leach metals from ores and to enhance the recovery of petroleum from wells, have been used as a means of minimizing the application of hazardous chemicals in geochemical recovery operations. Just as we sometimes use our knowledge of beneficial microbial processes to optimize their usefulness, at other times we try to prevent natural microbial activities such as

those which contribute to corrosion and decay of objects exposed to the environment.

Presently, we still use a microbial classification scheme which is very traditional and divides the microorganisms into five major taxonomic groups. Four of these are considered to be cellular, meaning that they possess cell membranes. These four are the algae, bacteria, fungi, and protozoans. The fifth group, the viruses, is acellular. Biochemically based phylogeny studies constantly provide us with suggestions for revising such groupings. The most recent suggestions divide the older "bacteria" group into two domains, the *Bacteria* and *Archaea*, while assigning the algae, fungi, and protozoa to be part of the domain *Eucarya* (Pennisi 1999). The viruses and some of their biological relatives, which previously were never included within any kingdom, could fit into the proposed domain *Akamara* (Hurst 2002). The most important aspect is our understanding that within ecosystems these groups of microorganisms naturally organize among themselves as they go about their interactions both with one another and with the macroorganisms on this planet. These interactions occur and can be studied on many levels: spatially, biochemically, and even genetically.

A rough estimate indicates that 10, 5 and 67% of soil bacteria, fungi and algae, respectively, have been described. Out of this, only 7, 0.8 and 2.5% of bacteria, fungi and algae, respectively, have been axenically cultured. This makes it difficult to ascribe their phylogenetic taxonomic position and biotechnological recognition. The number of species that compose the functional groups or the transformation power of one group is more important to earth. We do not know the importance of one species inside dynamic biological systems, what one species represents within the biological dynamic and especially, what importance can one species have in nutrient cycling? These questions could lead us to conclude that we need to review our vision of the soil microcosm, extend our understanding of the biological processes and interactions that occur in the soil–plant system. Functional aspects are more important than biodiversity in natural ecosystems. Functional groups which take part are: carbon, phosphorus, nitrogen and sulfur biogeochemical cycles.

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Part II
Microorganisms and Soil Genesis