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Chapter

Microbes as Artists of Life

Gayatri Sharma

Abstract

Scientists have been knocking the wood to ascertain the symbiotic relationships of tiny living creatures, that is, microorganisms with other beings such as plants, animals, insects, and humans. The concept of “symbiosis” got its existence in 1879, which means “living together.” Microorganisms show a great deal of diverse interactions such as commensalism (moochers), mutualism (both benefitted), and parasitism (one benefitted and other unharmed) with other living beings and mutualism being the most common of all, thus forming a range of antagonistic to cooperative symbiotic relationships. These tiny creatures interact with plants by forming lichens (fungi and algae), mycorrhizae (plants and roots of higher plants), root nodules (*Rhizobium*) and acting as keyworkers in plant’s rhizosphere promoting growth and development. Microbial community also extends itself to kingdom Animalia establishing relationships with phylum Mammalia including humans, animals, and the most abundant species of phylum Arthropoda, that is, insects such as termites, which have colonization of bacteria in gut to digest wood cellulose. Scientists have discovered that most studied organisms—mussels found in deep-sea hydrothermal vents too live in a mutualistic association whereby bacteria get protection and mussels get nutrition as bacteria use chemicals from hydrothermal fluid producing organic compounds.

Keywords: symbiosis, lichens, mycorrhizae, root nodulation, leghemoglobin, soil structure, PGPRs, siderophores, antibiosis, rhizosphere, insect vectors, mussels, deep-sea hydrothermal vents, nematodes, LAC bacteria, gut microbiota, bobtail squid, host-microbial interaction

1. Introduction

Since the birth of this universe, milky way, or be it an organism, nature had been always playing its role as a balancer to ensure the easy survival of every being. The law of nature “symbiosis” has got its existence since times gone and will continue as an eternal process in life. The greatest example in this context is the phenomenon of photosynthesis and respiration. Have you ever wondered how the living beings learnt the art to live in harmony? The answer lies in the fact that nature is the driving force behind this. Starting from microscopic bacteria to humans, all living beings are inter-linked through a chain of interaction—symbiosis, that is, the art of living of different organisms with cooperation. The term “symbiosis” was coined by **Anton de Bary**, who was a German botanist, microbiologist, founding father of plant pathology and modern mycology in 1879. It has its origin from ancient Greek words “syn” meaning together and “bios” meaning life. It has been used to describe mutualistic beneficial

relationship between different organisms and now can be broadly applied to different multitudes of relationships, that is, beneficial, harmful, or neutral.

Microbes are the most studied creatures; without them life would be nearly meaningless. The role they play in the ecosystem cannot be replaced by any other living organism. Fungi, bacteria, protozoa, and algae such as cyanobacteria have distinct structural organization, which displays a great deal of behavioral patterns serving various purposes. Nowadays, microbes are studied for their interactions in the environment and for utilizing it in research studies and also for the benefit of mankind.

“Life would not long remain possible in the absence of microbes”-Louis Pasteur [1].

This quote by Louis Pasteur (**Figure 1**) throws light on the microbial importance in our life. Thinking of an antimicrobial life is really a difficult task. From oceans to seas to land, microbes are ubiquitous. Prokaryotes account for nearly one-half of all global biomass. These cellular life forms such as *Prochlorococcus* and *Synechococcus*, residing in oceans, generate oxygen from photosynthesis. If such sources disappear from earth's surface, aerobic life would be in danger [1].

1.1 Let us take an example of N-cycle

Nitrobacter, *Nitrosomonas* are involved in nitrogen fixation; without them whole N-cycle would be disturbed. Rhizobium species such as *Rhizobium meliloti*, *Rhizobium trifolii*, *R. japonicum*, *Rhizobium leguminosarum* nodulate alfalfa, red clover, soyabean,

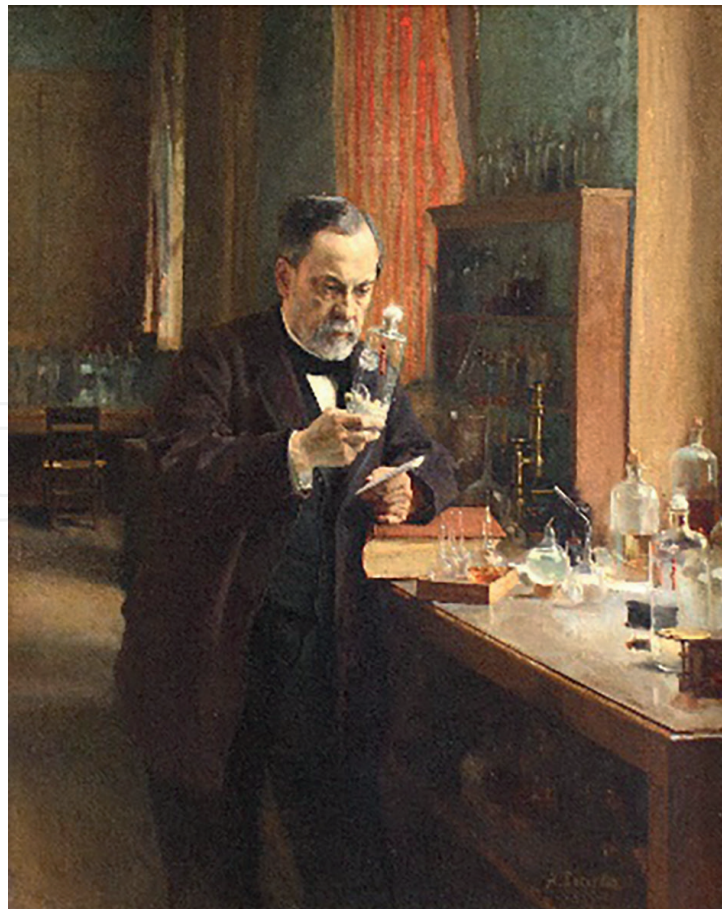


Figure 1. Louis Pasteur in his lab, painting by a. Edelfeldt in 1885 (modified as per reference number 1, taken from Wikipedia).

peas respectively. *Pseudomonas*, and *Bacillus* are involved in breakdown of proteins in the process called aminization. Apart from these, the roles played by denitrifiers such as *Pseudomonas*, *Bacillus denitrificans* (facultative anaerobes), and *Thiobacillus denitrificans* (autotrophs) are responsible for reduction of nitrates and nitrites into oxides of N and nitrogen gas. For a moment, if we imagine the absence of any one of these microbes, the **N-cycle** would not be able to complete and the natural equilibrium will be disrupted. Similarly, phosphorus-solubilizing bacteria such as *Bacillus megatherium* and *Pseudomonas striatus* increase P availability under ideal conditions. What would be the fate of other cycles if microbes involved in them are removed? Simply, the answer would be imbalance in nature that would threaten the existence of all life forms. Hence, microbes are an important part of ecosystem, their respective works can only be done by them, and there is no substitute for their roles in this ecosystem. Being talented with different arts, they add colors to the life of other living beings with their healthy and positive interactions but at the same time can even act the other way. One must remember that these tiny creatures with their artistic behavior could be promising at one end and ominous on the other.

2. Microbes and Symbiosis

2.1 History

Although seventeenth century marked the discovery of microorganisms, their existence had been since the beginning of life on the earth. They have been the part of various types of interactions that are important for survival. These interactions, which are beneficial in the ecosystem, are referred to as what we call “**symbiosis**.” Symbiosis has been law of nature as previously said. The discoveries and the research studies in its context have their origin since nineteenth century. The term “**symbiosis**” was used by **Albert Bernhard Frank** in 1877 to describe the mutualistic relationship in lichens. An integrative approach with a classification of “co-actions” was proposed by **Edward Haskell** in 1949 [2].

2.2 Microbial Symbiosis

Microorganisms have been always an important part of ecosystem. These microscopic entities perform the main role in soil and plant biology enhancing their properties and quality. Microbial symbiosis has been a topic of discussion among scientists with some putting their view forward that it should refer only to mutualism while others have a view point that it refers to all the biological interactions—mutualism, commensalism, and parasitism, but excluding predation (**Figure 2**). Mutualism is a type of interaction in which both organisms are mutually benefitted from each other and the survival of one would be nearly impossible without the other one. Commensalism is an interaction in which one organism is benefitted from the other and the other one is neither harmed nor benefitted. These can also be called as moochers. Parasitism involves interaction of a microbe as a parasite with the host. Hence, the microbes form important and useful symbiotic associations, and the phenomenon is called as **microbial symbiosis**.

Microbes have also been a major topic of phylogenetic studies, so evolutionarily, microbial symbiosis is an important survival mechanism, for example, some free-living bacterium that was descended by mitochondria found a symbiotic relationship

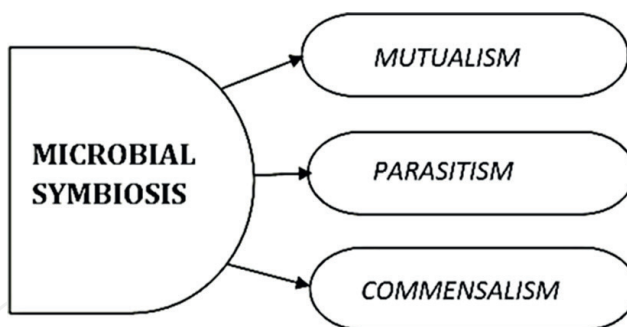


Figure 2.
Types of microbial symbiosis.

with a eukaryotic cell, and it proceeded toward permanency as this was mutually beneficial as a means of coexistence [3]. Microbial communities exist in various ways in nature; it can be complex, dynamic, or as simple as that of lichen. The most common example of this is of bacterial colonies present in the intestine of humans as well as animals participating in the process of digestion by breaking down complex food substances, synthesizing vital nutrients for the body such as riboflavin, vitamin B12, or other essential nutrients that are not synthesized by body itself.

These friendly microbial communities maintain natural balance and equilibrium in the body living inside the host. So, in this association, the host is benefitted by synthesis of important nutrients by these microflorae, and in the turn, bacteria are benefitted too since they get hospitable growth habitat to survive and food material to act on.

Definitely, one would wonder how beautifully these wonderful tiny creatures live their life artistically! These fascinating creatures have great associations with plants, animals, and insects and have coevolved by creating specific niches closely associated with them by adapting the way of living in the course of symbiotic interaction.

3. Microbial symbiosis with plants and in soil

Microbes are known to form symbiotic associations with plants interacting with its rhizosphere and phyllosphere, and their interactions in the soil are advantageous in maintaining soil properties. These interactions of microbes with organisms of kingdom “**Plantae**” are depicted below (**Figure 3**):

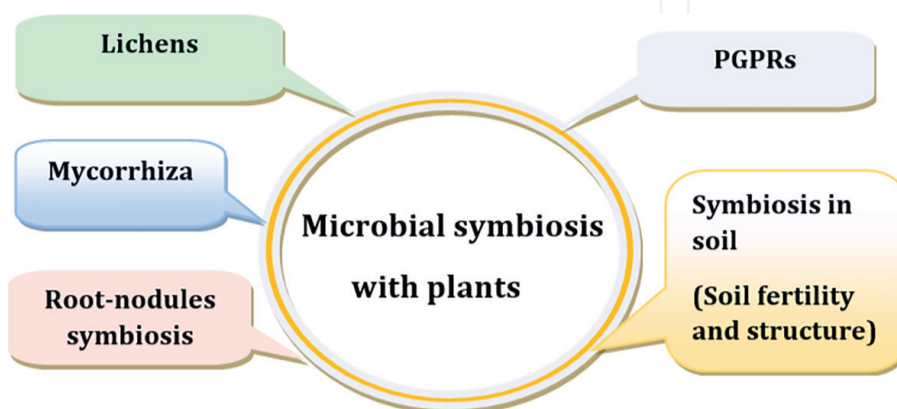


Figure 3.
Microbial symbiosis with plants.

3.1 Lichens

The simplest example of symbiosis is lichens. It is the mutualistic association of algae or cyanobacteria with fungus (ascomycetes/basidiomycetes) representing self-supporting symbiosis. In this, chlorophyll-containing partner. That is, algae provide simple carbohydrates and vitamins, which are absorbed by fungal component, and in turn fungi contribute by absorbing water from air and protecting algae as the upper thallus of fungi provides shade for underlying algae, some of which are photo-sensitive. Although appearing as a single plant-like organism, these lichens are made up of various cells of algae interwoven into matrix of fungal component. They cover 6–8% of earth surface, and approximately 20,000 different kinds of lichens have been reported till date having different structure and appearance—leaf-like, crust-like, powdery, filamentous, etc., growing on walls, trunks, in soil, etc. These organisms have the tendency to survive in a variety of conditions (extreme to mild) as they produce thallus of different forms, that is, **crustose, foliose, or fruticose (Figure 4)** that favors their growth in different climates; however, lichens have been economically important only as they produce various pigments that can be used as dyes. They are the best indicators of pollution due to their sensitive nature also they are widely used as food,

Uses of lichens:

- Most of the lichens such as *Bryoria fremontii* (horsehair lichen), *Umbilicaria spp.* and *Lasalia spp.*, and *Umbilicaria esculenta*, are used as staple food and delicacies [4].
- Another use of lichens is in lichenometry, which is a technique to determine the age of exposed rock on the basis of size of lichen thalli, and lichens used for this purpose are *Xanthoria*, *Rhizocarpon*, etc. [4].
- Lichens produce metabolites such as usnic acid, which are similar to antibiotics and act as bactericidal agent against bacteria such as *E. coli* [4].

3.2 Mycorrhizae

Mycorrhizal interactions are associations of fungus (belonging to alomeromycota) with plant's rhizosphere, its root system playing an important role in enhancing plant nutrition and growth. This interaction can be seen as an important innovation of terrestrial plants in which plants being photosynthetic provide food to fungi and fungi provides water and nutrition to plants and also offer protection from various types of biotic and abiotic stresses (Smith and Read, 2008) [5]. Fungus can colonize vascular



Figure 4. Types of lichens medicine, and in perfumes, for example, *Cetraria islandica*, used as appetite stimulating source, *Evernia prunastri* mostly used in perfume industry. The structures are undergoing fast evolution to serve different purposes.

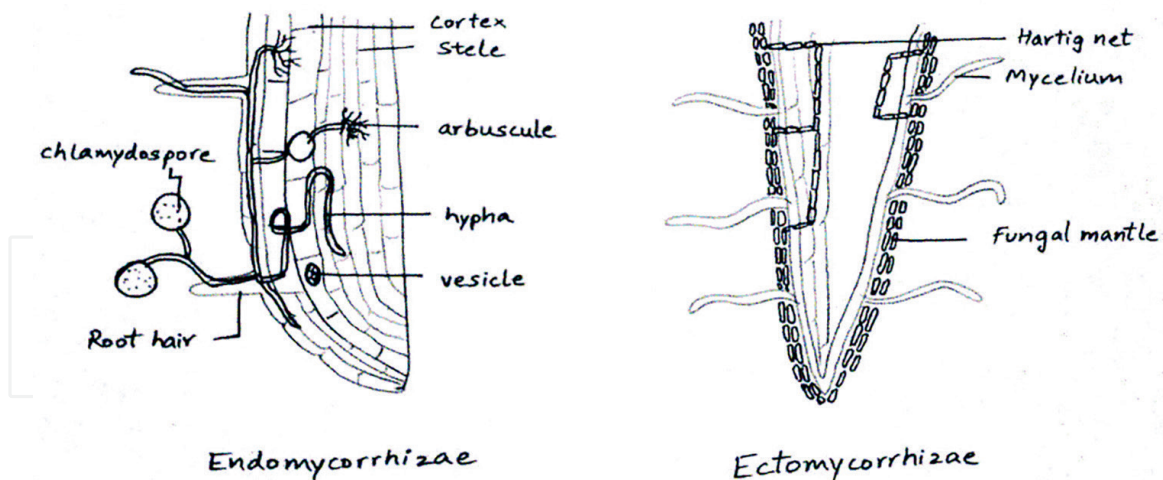


Figure 5.
Types of mycorrhizae – Endomycorrhizae and ectomycorrhizae.

plant's root system either intercellularly, for example, arbuscular mycorrhizal fungi or extracellularly. Hence, mycorrhizae are mainly divided into two groups (as shown in **Figure 5**)—endomycorrhizae (fungal hyphae penetrate cell wall and cell membrane) and ectomycorrhizae (fungal hyphae do not penetrate individual cells).

3.2.1 Endomycorrhizae

Endomycorrhizae are classified as arbuscular, ericoid, orchid, and monotropoid. **Arbuscular mycorrhizae** are the mycorrhizae in which hyphae penetrate plant cells producing vesicles or arbuscules as nutrient exchange medium as they increase the surface area for easy transfer of nutrients between them [5]. Fungi produce glomalin (glycoprotein) acting as a carbon store in soil. **Ericoid mycorrhizae** form dense coils of hyphae in the outermost epidermal layer of root cells and extend into the soil. They have saprotrophic nature enabling plants to receive nutrients. **Orchid mycorrhizae** are the mycorrhizal associations, which are myco-heterotrophic and form pelotons (coils) for nutrient exchange but do not have energy reserved [5]. **Monotropoid mycorrhizae** are mixotrophic and derive carbon from mycobiont component. This is not a mutualistic but a parasitic association [5].

3.2.2 Ectomycorrhizae

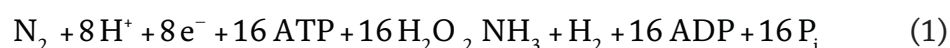
It refers to a mycorrhizal association in which fungal component forms sheath over the root surface or tip sending hyphae into intercellular spaces of cortex forming hartig-net. It includes **arbutoid** mycorrhizae. Arbutoids usually have fungal component belonging to basidiomycetes. They look similar to ericoid and monotropoid mycorrhizae and can be revealed only by anatomy tests. They proliferate mycelium into intercellular spaces forming dense hyphal complexes, hence are important type of ectomycorrhizal fungi. These often form extensive network in soil and leaf litter [5].

Another type of mycorrhizal association is ectendomycorrhizae in which hartig net is formed outside root tips but penetrates the cortical cells occasionally. These associations enhance nutrient and water uptake, increase crop quality and yield, increase seedling establishment, reduce fertilizer use, thereby increasing efficiency of the plant.

3.3 Root-nodules symbiosis

This is the very useful phenomenon in the leguminous plants. Legumes and N-fixing bacteria, that is, *Rhizobium* establishes root nodule symbiosis specifically in which bacterial species take part in interactions with root nodules of leguminous plants in rhizosphere. N-fixing bacteria (*Rhizobium* sp.) are stimulated by the flavonoids released by legumes in **low N condition**, and the bacteria respond by releasing nodulation factor, which initiates nodule formation, and the bacteria enter through deformed root hairs into the host plant root system forming infection thread and penetrate the cell wall. Infection initiates cell division in root cells and forms nodules (**Figure 6**). Functional nodules appear pinkish due to the presence of leghemoglobin. This type of symbiotic association helps in nitrogen fixation through reactions catalyzed by nitrogenase enzyme, thereby enhancing **N status** of soil as the bacteria convert atmospheric nitrogen to ammonium used up by the plant. For example, bacteria *Rhizobium leguminosarum*, *Bradyrhizobium*, and *Sinorhizobium* fix nitrogen in peas and soybean, respectively. Except this, *Lotus japonicus* has also been used as a key model for leguminosae family for studying the mechanism of symbiosis with *Rhizobium* sp. taking part in nodule formation [6]. In this association, *Rhizobium* is benefitted by getting shelter and organic carbon for its growth.

Reaction of N-fixation is as follows (Eq. (1)):



3.4 Symbiosis in soil: soil fertility and structure

Soil microbes enhance fertility and structure of soil by interacting in various ways. Microbial diversity in soil performs various functions in the rhizosphere of the plant such as organic matter decomposition, seed germination, recycling nutrients, N-fixation, manages soil stability by performing various biochemical processes, and

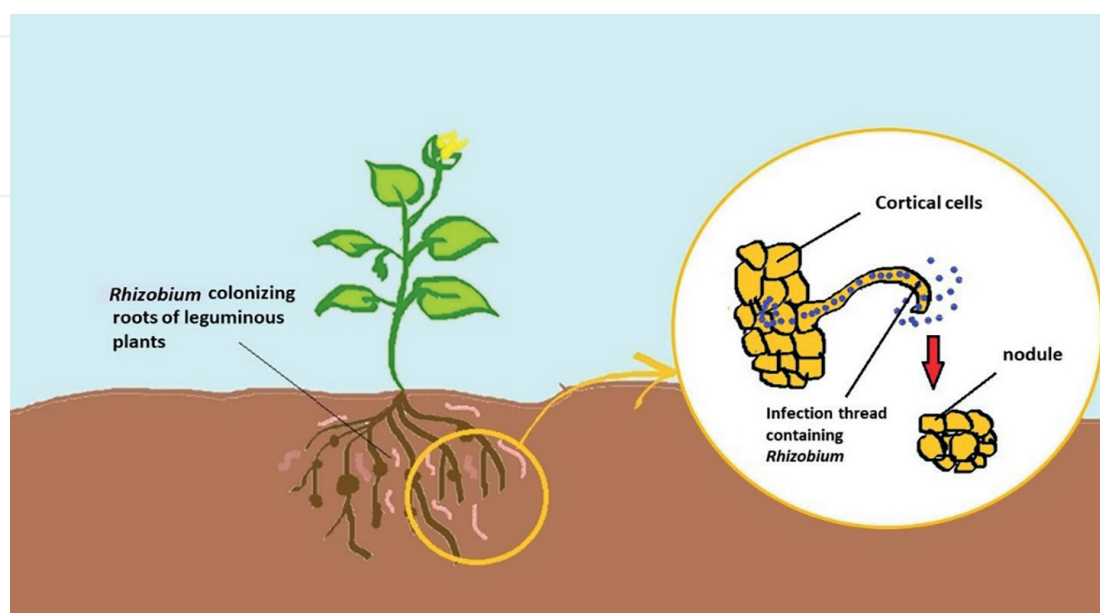


Figure 6.
Nitrogen fixation in leguminous plants by rhizobium.

themselves are benefitted with favorable growth conditions or shelter in soil. *Frankia* is associated with non-leguminous plants for N-fixation. *Azospirillum* is associated with plants as phosphate solubilizer.

3.5 Plant-growth-promoting rhizobacteria (PGPRs) and plant microbiome

PGPRs refer to plant-growth-promoting rhizobacteria, which are emerging as a leading topic of study since it is useful for sustainability of agriculture due to suppression of plant pathogens. These bacteria colonize roots of plants and thereby aim at improving the immune system of the plant against attack of disease-causing microbes. Basically, they offer biological control for the disease spread and are found in rhizosphere and rhizoplane (**Figure 7**).

Gray and Smith (2005) put forward the view that PGPRs range in their proximity to the root and association. They must colonize root, survive, and multiply in the rhizosphere or rhizoplane competing with other microflora so as to express plant growth promotion and protection activities. They act as rhizome mediators (degrade organic pollutants) phytostimulators, biofertilizers, and biopesticides [7]. For example, siderophores (low-molecular-weight iron chelators) produced by PGPRs to overcome iron deficiency allow solubilization of iron, *Pseudomonas fluorescens* produce siderophores pyoverdine that suppresses root rot disease, *Botrytis cinerea*, *Fusarium oxysporium*.

Various types of organic compounds such as ketones, pyrazine, and kanosamine are secreted by *Bacillus* sp. act as antagonists against pathogenic fungi. Actinomycetes, which are gram +ve spore-forming bacteria, too promote plant growth, act a biocontrol agent by inhibiting the proliferation of pathogens by degrading organic contaminants, breaking down dead plants. Beneficial effects of various rhizosphere microbes such as Firmicutes, *Pseudomonas*, and fungi belonging to *Trichoderma*, *Gliocladium*, etc., are recognized [8].

Siderophores are also involved in improvement of plant vigor as PGPRs (e.g., *Bacillus*, *Azotobacter*, *Azadirachta*, and *Burkholderia*) increase chlorophyll levels in

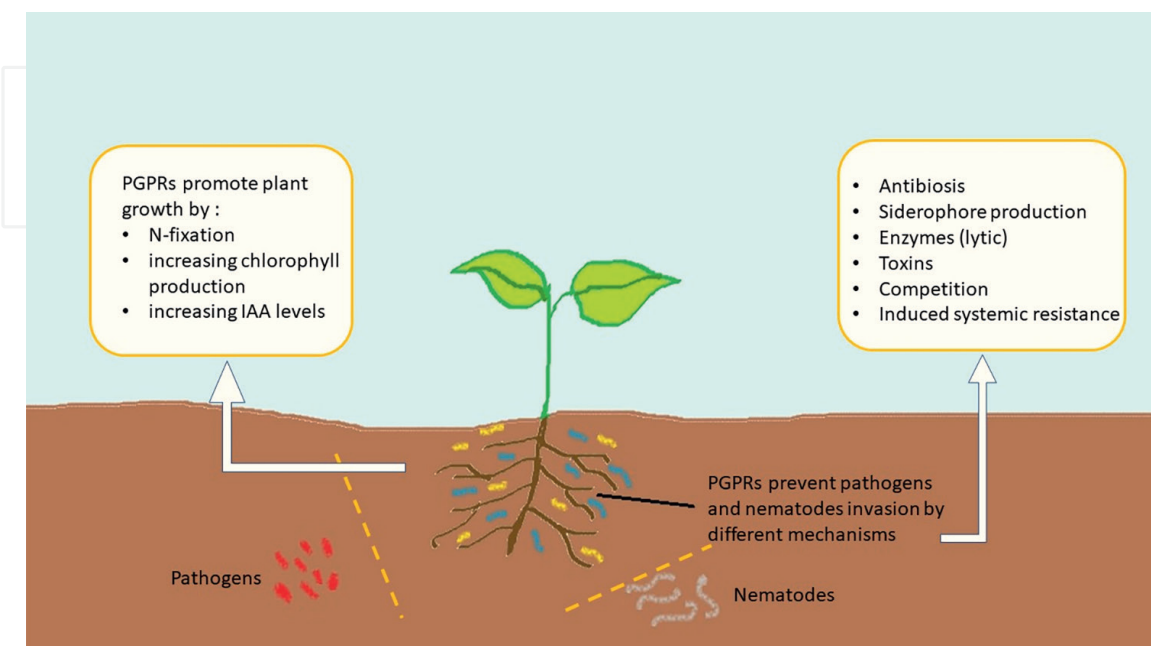


Figure 7.
Role of PGPRs in promoting plant growth.

plants. PGPRs such as *Pseudomonas*, *Bradyrhizobium*, *Enterobacter*, and *Agrobacterium* are responsible for production of IAA and promote root growth in plants. PGPRs also regulate salicylic acid pathway and jasmonate host plant stimulating resistance or defense response against various disease-causing microbes [8]. PGPRs have the potential to maintain growth of plant during stress conditions, for example, drought-tolerant type microbes in maize maintain water potential during stress.

Except this, PGPRs increase production of amino acids such as proline, production of sugars in plants, reduce antioxidant activity, and increase relative water content in maize. Soybean under drought stress has low content of chlorophyll, thereby photosynthesis decreases, but induction with *Pseudomonas putida* H-2-3 overcomes the stress by balancing chlorophyll content and development of biomass [8]. PGPRs also ameliorate affected soils by secreting phytohormone and thereby improving plant health. The rhizosphere microbiome surely intercommunicates in an artistic way and serves as the major light for research purposes or new discoveries.

4. Microbial symbiosis with animals

Microbes form different symbiotic relationships with animals too. Having diverse nature of their interactions, they interact with different organisms of kingdom “**Animalia**” such as insects and mammals (animals and humans) (**Figure 8**).

4.1 Symbiosis of microbes with insects

“**If insect is a plane, then microbes are its passengers.**” Insects and microbial symbiosis have proved a great synergy in the nature. With insect species accounting for about 80% of animal life on this wonderful planet, the earth, it is estimated that they have diverse population and represent the largest record of species with coleopterans as the highest of all known insect species. These species have undergone a great evolutionary history and adaptive success due to their potential for establishing symbiotic relationships with microbes—**endosymbionts**. Most common supportive example is the presence of microbiota in the insect gut (hindgut), which are acquired during their life and not inherited ones. Facultative and obligate anaerobic

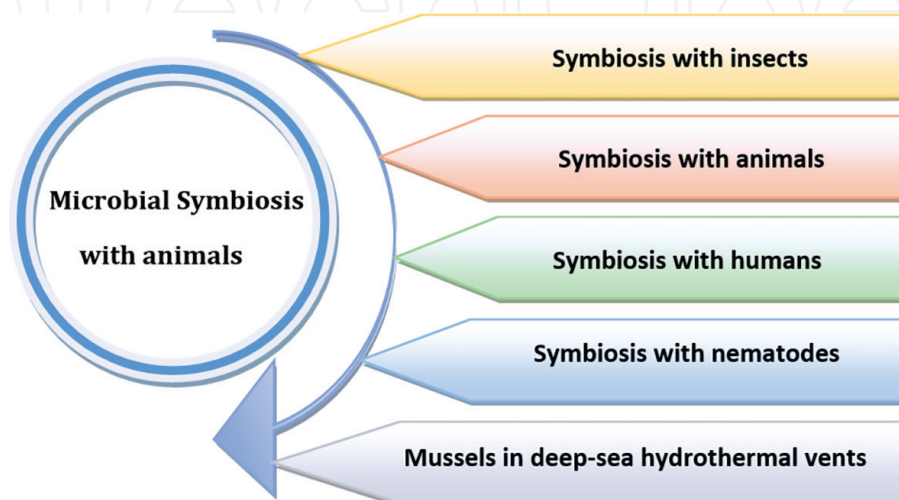


Figure 8.
Microbial symbiosis with animals.

prokaryotes such as **methanogens** and **protozoa** (in termites that help in digestion of wood cellulose) live in insects. Besides this, insects act as vectors for pathogenic microbes such as:

- *Trypanosoma* causing sleeping sickness transmitted by *Tsetse* flies
- *Plasmodium* causing malaria transmitted by female *Anopheles* mosquito
- *Leishmania* causing kala azar transmitted by Sand fly

Previous research studies conducted have shown the molecular basis of association between insect and microbes such as reactive oxygen species (immune effector) produced in the gut of *Drosophila melanogaster* and mosquito by dual-oxidases (DUOX) enzymes control microbiota in *Aedes* mosquito, but the population of microbes increases many folds if DUOX activity reduces. DUOX produces ROS, which is responsible for maintaining gut homeostasis in insect [9]. Even honey bees harbor gut bacteria to keep their hives healthy.

Pea aphids (*Acyrtosiphon pisum*) have an obligate symbiont *Buchnera aphidicola* that provides dietary nutrients lacking in insect host [10]. Gut microflora present in insect provides immunity, compensates nutrient deficiencies, and aids digestion. *Wolbachia* reflects a mutualistic relationship with many insects since it imparts resistance to its host against viruses. Molds of **Aspergillus**, **Cordyceps**, **Isaria**, etc., fungal species have also been associated with insect pests. Yeasts or yeast-like symbionts residing in the digestive tract of insects play a major role in metabolism and metamorphosis. Most popular is the interaction of insects and viruses, which also provides protective functions sometimes, for example, Pea aphid harboring *H.defensa* with *A. pisum* phage has great defensive power against parasitoid wasp attack as the phage infects bacteria, which further defends aphid against natural enemies [11]. **Hence, insects are key players in mutualistic symbiosis.**

4.2 Microbial symbiosis with animals

The most of the microbiota resides in the gut or gastrointestinal tract of animals, which are categorized as “luminal”—associated with lumen and others “mucosal,” that is, associated with mucus lining the intestinal epithelium. Residing in the gut of animals, microbes function by metabolizing dietary food components ingested by the host organism producing short chain fatty acids and vitamins that fulfill the energy needs. Apart from this, they act as shield from attack of pathogens performing their roles in physiology and act as filters by detoxifying various compounds. Many microbes, for example, *Bacteroides* genera, alter expression of enzymes such as carbohydrate-degrading enzymes.

Many recent research studies have shown microbes as the key players in the physiological functions including even neural functions in animals. In case of bobtail squid, a light organ contains luminescent bacteria (*Photobacterium mandapamensis*). This bacterium is important for development of light organ, and in cardinal fish, it is responsible for neural and anatomical functions [12].

Some latest research studies have also shown that microbes provide anti-predator defense by helping in camouflage and sponge-microbe symbiosis is emerging as model for putting light on animal-associated microbiota. Hence, associations of microbes with animals have unfolded and continue to unfold as a part of evolution.

4.3 Microbial symbiosis with humans

Human microbiome has always shown a remarkable range of art of living of microbes beginning from symbiosis to pathogenesis with human body being hub for multitude of various types of microbes—bacteria, fungi, viruses, etc. One of the hypotheses suggested that LAC bacteria and other bacteria colonizing in vagina are responsible for facilitating protective response and maintaining homeostasis. These symbiotic microbes such as *Lactobacillus salivarius* UCC118 release a toxin, that is, bacteriocin-ABP118, which is effective against food-borne pathogens including *Bacillus*, *Enterococcus*, and *Staphylococcus* species [13].

Another interesting interaction is represented by symbiotic microbes residing in skin that play a major role in priming T cells to respond to pathogens. *Staphylococcus epidermidis* and *Staphylococcus aureus*, which are coagulase negative staphylococci, belonging to Actinobacteria such as *Corynebacterium*, are the primary colonizers of human skin [14]. The best example of microbial symbiosis with humans is the presence of gut and gastrointestinal microbiome influencing host metabolism and health (**Figure 9**). For example, *Faecalibacterium prausnitzii* modulates eight urinary metabolites.

Humans are being considered as “**Superorganisms**” due to their diverse nature of interaction with microbial community [15]. So, gut bacteria have various metabolic proteins or agents that help in development of immunity and producing energy compounds from food left undigested by body, hence benefiting human health, and in turn, human gut provides conditions conducive to these microbes for their growth and development. Hence, trillions of microbes living in the human gut are known to play an important role in regulating metabolic functions, and this coexistence is considered to be the law of nature by various scientists.

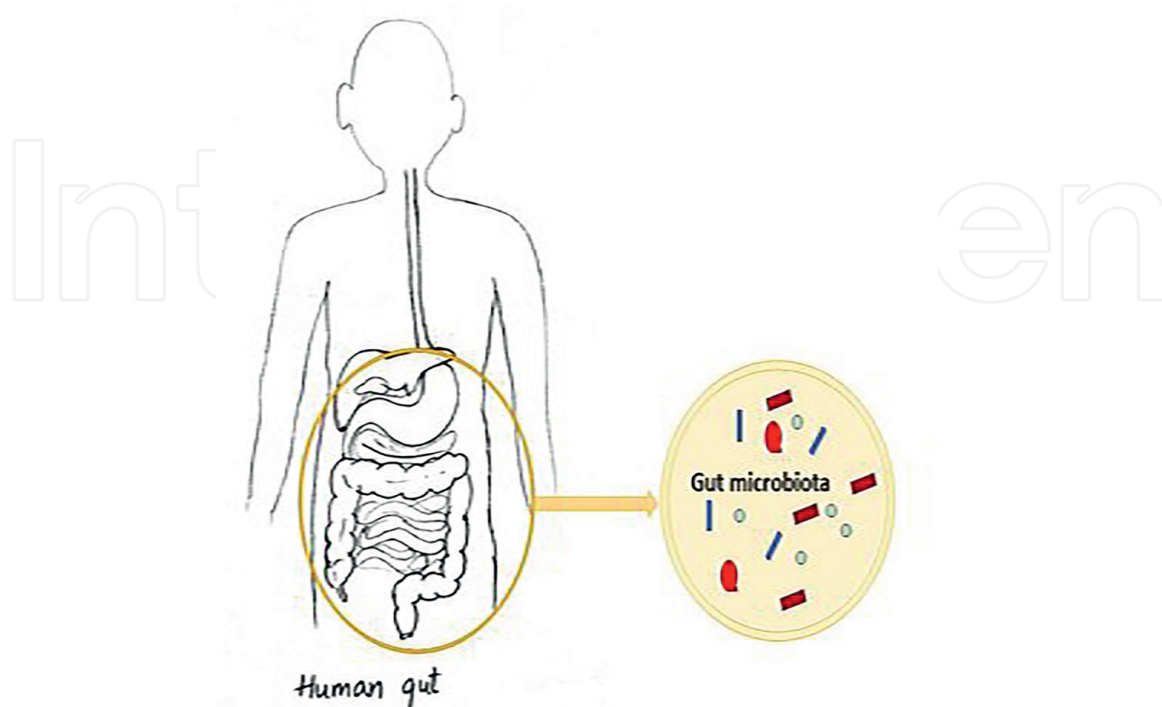


Figure 9. Microbial symbiosis with humans (gut microbiota).

4.4 Microbial symbiosis with nematodes

Obligatory relationship is present between a bacterium (*Xenorhabdus nematophilus*) and a nematode (*Steinernema carpocapse*). Bacteria live inside the nematode producing toxins that nematode uses to kill the insects infected by it. Both the organisms are dependent on each other for efficient survival [3].

4.5 Mussels in deep-sea hydrothermal vents

Mussels are the most widely studied organisms as they are found in hydrothermal vents and are capable of forming a mutualistic association with bacteria. Bacteria act as a source of nutrition because bacteria use chemicals from hydrothermal fluid producing organic compounds that serve nutritional purposes, and in turn mussels provide bacteria with optimum conditions for growth by providing protection and other useful materials [16]. They too are perfect example of give-and-take relationship in this ecosystem.

5. Conclusion

Microbes have always been an integral part of ecosystem. Life would not be possible without these creatures, which perform important roles in even unnoticed reactions or phenomenon starting from different cycles to deep-sea hydrothermal vents. Blessed with distinct behaviors, they live in diverse habitats and climatic conditions performing functions that could not be taken over by any other organism. Since the present era is focusing on the role of microbes, everyday a new discovery of their role in biosphere leaves everyone awestruck and astonished at same time. Scientists and researchers have regarded microbes as helping hands that can maintain the balance of nature. Though they have small size, the role they play is commendable. The scope of microbial study is ever-increasing with increase in involvement and use of microbes, healthy and positive interactions among themselves surely lead to growth and development of microbiology sector. Studying the positive art of living among microbes, that is, symbiosis, one can exploit it for applications in plant and soil biome enhancing their efficiency and also maintain equilibrium in nature that is very essential for proper functioning and creation of healthy environment. Hence, this area of research has wide scope, which is applicable not only in department of microbiology but also in soils, botany, plant pathology, biochemistry, biology, environmental studies making it a subject of huge importance. They function as diverse beings by showing various types of interactions such as lichens, mycorrhizae, root nodulation, and plant-growth-promoting rhizobacteria with plants and various others with insects, animals, humans (gut microbiota), etc., playing different roles and functions. They serve as hub for research studies due to their amazing yet mysterious art of living. **Hence, symbiosis sustains life and microbes acting as beacon of artistic life in nature.**

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Acronyms and abbreviations

LAC	lactic acid bacteria
PGPR	plant-growth-promoting rhizobacteria
VAM	vesicular arbuscular mycorrhiza
+ve	positive
ATP	adenosine triphosphate
ADP	adenosine diphosphate
DUOX	dual-oxidase enzyme
ROS	reactive oxygen species

Appendices and nomenclature

N	nitrogen element
N ₂	nitrogen gas
H	hydrogen
e ⁻	electrons
H ₂ O	water
NH ₃	ammonia
H ₂	hydrogen
P	phosphorus
P _i	inorganic phosphate

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