Chapter 15
Morphological and Physiological Aspects of Symbiotic Plant–Microbe Interactions and Their Significance

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15.1 Introduction

Symbiosis, i.e., “the permanent association between two or more specifically distinct organisms, at least during a part of the life cycle,” is an important aspect of life on earth. Evolutionarily, plants require positive associations with specialized microbes to sustain their normal growth and development in certain ecological niches. Plants form two such important interactions with microorganisms, viz., mycorrhiza, and with N_2-fixing *Rhizobium*. In the former, the roots of plants are infected by certain fungi that help them acquire phosphate from the soil (Smith and Read 1997; Smith et al. 2003). Fungus in return obtains organic nutrition in the form of carbohydrates and other growth substances from plants and also ideal ecological niche, essential for their growth and development. Two major types of mycorrhizal fungi that are important for plant growth and development are ectomycorrhiza (ECM) and endomycorrhiza (AMF). Through their roles in uptake of nutrients, arbuscular mycorrhizae (AM) fungi were perhaps important in the colonization of land by plants (Heckman et al. 2001). In AMF, arbuscules (branched, microscopic haustorial structures) are the major sites of nutrient exchange and contain mycorrhiza-specific plant phosphate transporters at their edge (Harrison et al. 2002; Manchanda and Garg 2007). In the latter, agricultural symbiosis, occurs between rhizobial bacteria and roots of legumes, such as soybeans and pea, where the plant provides its beneficial partner with carbohydrates, together with other nutrients, and in return receives valuable fixed nitrogen in the form of ammonia and amino acids from it (Udvardi and Day 1997). These associations can increase agricultural production and improve soil fertility and therefore have great prospective as a supplementary, renewable, and ecofriendly source of plant nutrients (Marx 2004). Both associations are extreme in terms of host specificity (Manchanda and Garg 2007). Nodulation almost exclusively

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occurs in legumes, whereas AMF show little host specificity, and more than 80% of terrestrial plants form symbiotic association with fungi of the phylum Glomeromycota (Schüßler et al. 2001; Garg et al. 2006). Both these associations, i.e., plant–fungus and legume–*Rhizobium*, act synergistically.

Mycorrhizal fungi improve nitrogen and phosphorus uptake; the higher levels of phosphorus in the plants facilitate the action of nitrogenase enzyme leading to fixation of more nitrogen, which further promotes the development of mycorrhizae in the plant. Certain strains of *Rhizobium* are able to tolerate abiotic stress such as low water content, salt stress, acid and alkaline pH, presence of fertilizers, and heavy metals and effectively fix nitrogen through symbiotic association (Zahran 1999). *Piriformospora indica* is a unique endophytic fungus which colonizes roots of many plants species and establishes symbiotic association with these. The fungus confers tolerance to biotic and abiotic stresses and promotes plant growth and development especially in nutrient-deficient soils (Johnson et al. 2014). In this chapter, an effort has been made to summarize and highlight morphological and structural features of these plant–microbe symbionts along with their ecological significance.

15.2 *Rhizobium*–Legume Symbiosis

Mutualism is a type of symbiotic relation between associating species for mutual benefit to both partners. One of the families in plants, Fabaceae, has an evolved symbiotic relation with a class of proteobacteria which are nitrogen-fixing soil bacteria capable of forming root or stem nodules in leguminous plants and exceptionally with a nonlegume, *Parasponia* (Akkermans et al. 1978; Trinick 1979; Jordan 1982). Most of species involved in symbiosis with legumes belong to class *Alphaproteobacteria*, which includes genera *Azorhizobium*, *Allorhizobium*, *Mesorhizobium*, *Rhizobium*, *Bradyrhizobium*, and *Sinorhizobium* (Dreyfus and Dommergues 1981; Dreyfus et al. 1988; Jordan 1982; Chen et al. 1988; Jarvis et al. 1997; De Lajudie et al. 1998), while some belong to class Betaproteobacteria as *Burkholderia* and *Cupriavidus* (Gyaneshwar et al. 2011).

After establishment of symbiosis, the bacteria fix atmospheric nitrogen and provide it to the host plant. This provides an advantage to the host plant which allows it to grow without the addition of nitrogen fertilizers. Thus, biological nitrogen fixation is a profitable proposition for plants as there is huge increase in agronomic yield since it alone contributes to 65% of the worldwide nitrogen invested in agriculture (Brelles-Marino and Ane 2008).

Bradyrhizobium sp. forms symbiotic association with *Parasponia andersonii* (Ulmaceae), which is the only non-legume plant having symbiotic nitrogen fixation along with root nodule formation (Akkermans et al. 1978; Trinick 1979; Jordan 1982). There are some non-legumes having endosymbiotic association with *Rhizobium*, but they do not form nodules in the host plant, for example, in rice, *Rhizobium oryzicola*, *R. pseudoryzae*, and *R. rhizoryzae*; *R. oryzae* (Peng et al. 2008; Zhang et al. 2011, 2015) and *R. populi* in *Populus euphratica* (Rozahon et al. 2014) have symbiotic association without nodulation.

The genus *Rhizobium* was described for the first time by Frank in 1889. The bacteria involved in legume symbiosis are categorized as diazotrophs because they catalyze conversion of atmospheric free nitrogen to ammonia, a form readily absorbed by plants (Lipsanen and Lindström 1988). It is a Gram-negative, free-living, saprotrophic soil bacterium which encodes an enzyme nitrogenase responsible for the nitrogen-fixing ability. Various steps are involved in invasion of leguminous roots. These include host bacterial recognition, infection process, nodule formation, colonization in nodules of the legumes, bacteroid formation, and nitrogen fixation (Sharifi 1983; Dreyfus et al. 1988).

15.2.1 Host Bacterial Specificity

There is high level of specificity in interaction between host plant and bacterial species, and only the compatible bacterial species are able to induce nodulation in plant. This specific interaction has been reported in various symbiont pairs, as in *Cicer arietinum*, only *Rhizobium ciceri*, and, in *Parasponia*, only *Bradyrhizobium japonicum* are able to form nodules in roots (Trinick 1979; Tillard and Drevon 1988).

Such symbiotic interaction is initiated as host plants roots secrete (iso)flavonoids (Redmond et al. 1986; Le Strange et al. 1990) and lectins (Bohlool and Schmidt 1974; Diaz et al. 1986, 1989) in the rhizosphere which are recognized by compatible bacterial species. Using immunoassays, it was found that there is a strong relation between infection by *Rhizobium leguminosarum* and presence of lectins on the surface of roots of *Pisum sativum*. Lectin was found concentrated more at tip of growing root hairs and on epidermal cells of young root hairs where it was present as dense small patches and is not distributed uniformly (Diaz et al. 1986).

On recognition of compatible species, there is induction of bacterial genes called nodulation factors (Nod factors) which lead to formation of nodules in host roots. Thus, there is an exchange of chemical signals for recognition of both mutualistic partners (Fig. 15.1). Also, in this symbiotic association, host plant provides carbon source to the bacteroids to meet its energy need for bacteroid differentiation and nitrogen fixation, which is malate in most species (Salminen and Streeter 1992), while glutamate (Bergersen and Turner 1988) and sucrose (Gordon et al. 1999) have also been reported. These bacteroids need an environment with low oxygen levels for optimal expression of enzymes of the nitrogenase complex and thus nitrogen fixation. The anaerobic conditions within the nodule are maintained by a plant-based oxygen-binding protein, the leghemoglobin (Downie and Oldroyd 2004; Ott et al. 2005).

Luteolin, a flavonoid isolated from *Medicago sativa*, dihydroxyflavone from *Trifolium repens*, and isoflavones from *Glycine max* (Kosslak et al. 1987) were the first few Nod factor inducers which were characterized (Redmond et al. 1986; Peters et al. 1986). Later other compounds such as jasmonates (Rosas et al. 1998), xanthones (Mabood et al. 2006), and lectins (Bohlool and Schmidt 1974) have also been shown to stimulate nod gene expression. Phenolics like vanillin from a nonlegume crop,

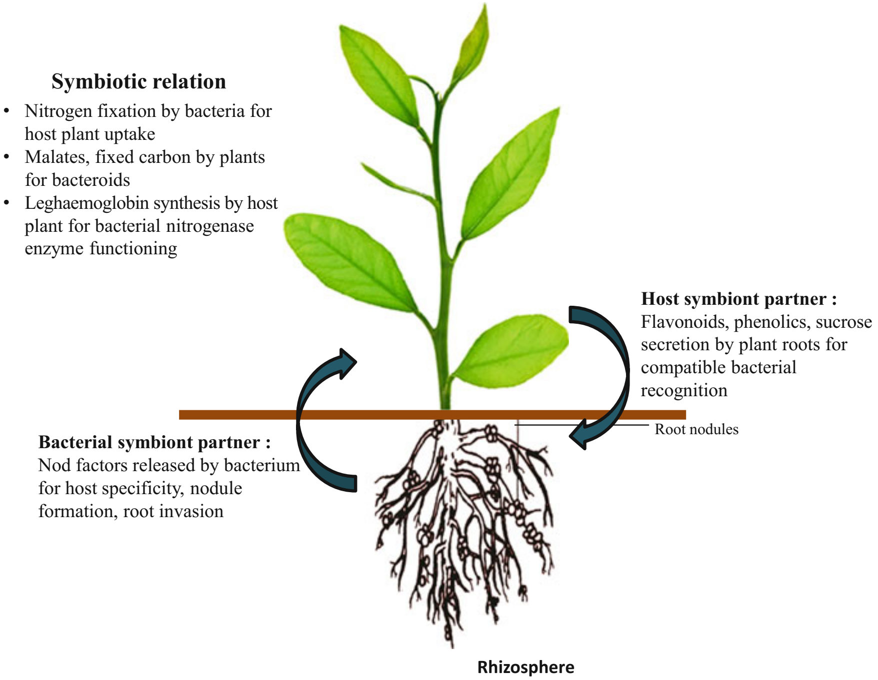

Fig 15.1 Bacterial host specificity in legume–*Rhizobium* interaction showing exchange of signals from both the partners. Flavonoids and lectins are released by plant roots in root exudate and bacteria release nod factors in the rhizosphere

wheat, were shown to induce transcription of nod genes in *Rhizobium* sp. (Le Strange et al. 1990). Promoter of nodA gene of *Rhizobium leguminosarum* has been found to be directly upregulated by flavonoids and flavones released by plants (Zaat et al. 1987). Aldonic acids, monosaccharides with a carboxyl group, were also observed to be inducers of nod genes in *Rhizobium lupini*, *Mesorhizobium loti*, and *Sinorhizobium meliloti* (Gagnon and Ibrahim 1998). Induction of bacterial gene expression by plant exudates provides an insight into plant–microbe interactions during establishment of symbiosis.

Nod factors which initiate the root invasion by bacteria are chemically lipochito-oligosaccharides (Truchet et al. 1991; Denarie et al. 1996). *Rhizobium meliloti* establishes its host specificity by a sulfated and acylated glucosamine oligosaccharide signal (Lerouge et al. 1990). Lipopolysaccharide (LPS) which is essentially present in Gram-negative bacteria may also additionally contribute at various stages of host–bacteria recognition (Noel et al. 1986; Carlson et al. 1987). Expression of Nod genes is an indispensable factor in nodulation of specific host plants (Kondorosi et al. 1984) as mutations in these genes alter the host specificity and thus alter the host range (Rhijn and Vanderleyden 1995).

15.2.2 Establishment of Endosymbiosis

Once nodulation factors (NFs) are recognized by host, there is induction of high levels of calcium as well as influx of calcium ions from extracellular environment (Ehrhardt et al. 1996; Cárdenas et al. 1999) and higher pH (elevated H^+ levels) in the cells of root hairs, which brings about changes in root hair cytoskeleton (Sieberer et al. 2005). Ca^{2+} spikes were observed in all legume–*Rhizobium* symbiosis, but in a non-nodulating legume, *Cercis*, no such Ca^{2+} spikes were observed in response to Nod factors of its symbiont partner, *Sinorhizobium fredii*. *Parasponia andersonii*, a nonlegume shows calcium oscillations in response to *S. fredii*, but its close relative, *Trema tomentosa*, a non-nodulating species does not have such spikes (Granqvist et al. 2015). Additionally, in most cases, there is change in pH of host cells which makes it slightly alkaline. In alfaalfa root cells, there is rapid change in pH by 0.2–0.3 units in response to *Rhizobium meliloti* nod factors (Felle et al. 1996). This is immediately followed by initiation of root hair curling that further traps rhizobia and initiates infection process (Downie et al. 1985). The bacteria enter root hair via infection threads which are inward growth of the root hair cell membrane. The hydrolytic enzymes encoded by *Rhizobium* seem to carry out penetration into the root hair by degradation of its cell wall (Newcomb 1979). Here the bacteria, being endosymbiotic, enter plant cells by endocytosis from the infection threads (Callaham and Torrey 1981; Dazzo et al. 1984). The bacteria which get differentiated into its nitrogen-fixing form within root nodule cells of host are termed as bacteroids (Bergersen 1974), and the host–bacteroid association together is known as symbiosome (Roth et al. 1988; Oke and Long 1999). Hydrogen peroxide seems to control the process of bacterial differentiation into nitrogen-fixing, symbiotic form (Puppo et al. 2013). Symbiosome has a plant-derived membrane around each bacteroid in the infection thread forming an organelle in cytosol (Roth et al. 1988). The membrane originates from three sources: the host infection-thread membrane, ER of plant cell, and de novo synthesis by Golgi and ER (Roth and Stacey 1989). Upon infection, a single bacteroid is enclosed in a single-membrane envelope; later more than one bacteroid found within many symbiosome compartments and the membrane which surrounds bacteria undergoing senescence begin disintegration and dissolution (Tu 1977).

Simultaneously, there are increased cell divisions in root cortex cells (Dudley et al. 1987; Oldroyd and Downie 2008) and establishment of a nodule primordium which undergo continuous mitotic activity to form specialized structures called root nodules which act as localized sites for symbiotic nitrogen fixation in most legumes (Libbenga and Harkes 1973). Each cell of nodule is filled with thousands of symbiosomes (Roth et al. 1988). During symbiosome formation, it has been observed in pea and soybean root nodules that host cells undergo numerous changes in ultrastructure like extensive arrangements of rough endoplasmic reticulum along with vacuole formation (Kijne and Pluvque 1979). The form of bacteroids varies considerably ranging from long-rod, short-rod, long-club, short-club, spherical, ellipsoid, pear-shaped, and L- and Y-shaped, which eventually assume pear or spherical shapes.

15.2.3 Root Morphogenesis for Nodule Formation

In most of the legumes, infection initiates from entry of infection thread which carries bacteria via extension of the root hair into the root cortex cells via breaks in root hair epidermis and root hair (Oldroyd and Downie 2008). The root cells susceptible to invasion are immediately beneath root tip where root hairs are still growing. In response to bacterial invasion, root hairs deform and curl which is mediated by changes in cytoskeleton in root cells (Cárdenas et al. 1998). This curling of root hair further traps bacterial cells in the rhizosphere (Callaham and Torrey 1981). The infection thread is thus an invagination of root cell's plasma membrane itself. As infection thread grows toward the pericycle and cortex, root cortical cells dedifferentiate and enter active cell division to establish nodule primordium (Oldroyd and Downie 2008). The important role of the presence of this specialized structure is because of the fact that nitrogenase enzyme is extremely sensitive to aerobic conditions and nodule maintains the compartment with low oxygen concentrations.

Nodules can be divided into two types, determinate and indeterminate (Fig. 15.2), depending on the transient and persistent nature of host cell proliferation (Oke and Long 1999). Determinate nodules have no meristem and contain homogenous population of symbiotic cells, for example, in *Phaseolus vulgaris* and *Lotus japonicus* roots, determinate nodules are formed, wherein the meristematic activity ceases early during nodule development, and the nodule assumes a spherical shape. On the other hand, active cell division is maintained in indeterminate nodules, for example, nodules of *Medicago sativa*, *M. truncatula*, *Pisum sativum*, and *Vicia sativa* (Sprent 1980; Ferguson 2013). A nodule meristem is present in the apical region which by constant production of new cells and continuous growth form elongated nodule. The type of nodule to be formed is specified by the host plant (Sprent 1980). Cells in outer cortex of root and not pericycle assume meristematic activity and subsequently form nodule-like structure (Newcomb 1979). Indeterminate nodules of *Pisum sativum*

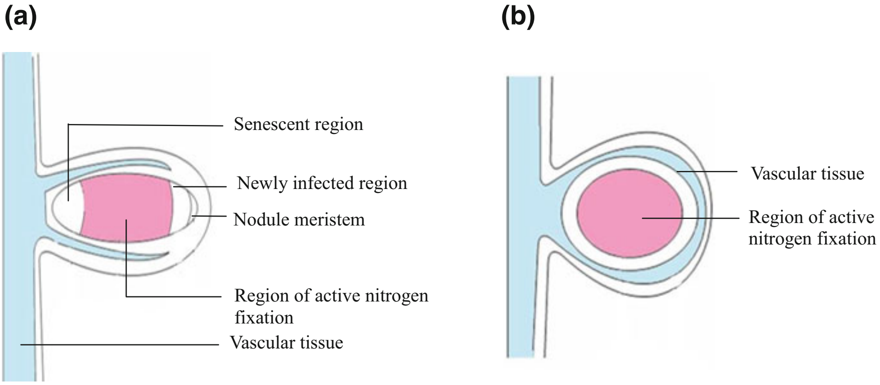

Fig 15.2 Indeterminate (**a**) and determinate (**b**) root nodules showing regions of active nitrogen fixation (marked in pink) with high expression of leghemoglobin protein

possess an active meristem that continues to divide and add new cells, few of which may be subsequently infected. Bacterial cells divide and grow in large numbers as infection thread progresses, and they lose their dividing ability as they colonize the inner cortex and get differentiated as bacteroids (Libbenga and Harkes 1973). Determinate nodule is differentiated into two zones: central infection zone, containing both infected and uninfected cells, surrounding layers of uninfected cells of outer cortex (Udvardi and Poole 2013). In the outer cortex cells, there is expansion of infection thread, while the cells of inner cortex carry out rapid cell division. Metabolites from plant body are transported to the nodule through the vascular tissue reaching the cortex (Rae et al. 1992).

15.2.4 Nitrogen Fixation in Nodules

Genes required for nodulation (Nod) and nitrogen fixation (Nif) are present in a large-sized plasmid (>100 Kb) called symbiosis (*Sym*) plasmid (Nuti et al. 1979; Prakash et al. 1981; Banfalvi et al. 1981; Rosenberg et al. 1981). Rhizobial enzyme nitrogenase, which converts atmospheric dinitrogen to ammonia, is a complex, made up of six protein subunits (two each of NifH, NifD, and NifK), and contains iron–sulfur clusters and two iron–molybdenum cofactors (Fe_7MoS_9N) called FeMo cofactors, which is the site of nitrogen reduction (Downie 2014). The iron–protein component is the smaller part of the enzyme, which gets reduced and transfers electrons to the molybdenum–iron part of the protein which is the larger component and is the catalytic site where dinitrogen binds and actually gets reduced (Dixon and Kahn 2004). These nitrogenase metallocenters are very sensitive to the presence of oxygen and must be active only in an environment with a low level of oxygen. Legume nodules resolve this requirement of low free O_2 levels by expressing high levels of leghemoglobins. These are oxygen-chelating proteins which maintain very low intracellular levels of O_2, while the bacteroids continue to carry out oxidative phosphorylation using a cytochrome oxidase (with a high affinity for O_2). Thus, net effect allows high levels of ATP synthesis required by bacteria for nitrogen fixation yet no oxidative damage to nitrogenase. Additionally, oxygen diffusion into the nodule is also regulated by an oxygen diffusion barrier at nodule periphery (Dixon and Kahn 2004).

Ammonia that is produced by the bacteroid diffuses out to plant cytosol due to concentration gradient of ammonia (Udvardi and Day 1990). The fixed nitrogen is transported to other parts of plants in various forms as ureides, allantoin, allantoic acid, amides, and amino acids, specially glutamine and asparagine (Sprent 1980).

15.2.5 Molecular Interactions Involved During Endosymbiosis and Nodulation

There are specific interactions at root surface of host with *Rhizobium* species determined by the presence of polysaccharides (lipochitooligosaccharides) on surface of the bacteria and flavonoids in the exudates of plant roots (Truchet et al. 1991; van Brussel et al. 1992). Genetic loci of Nod genes on Sym plasmid have been cloned and well-characterized in *Rhizobium meliloti* (Debelle et al. 1986) and *R. phaseoli* (Downie et al. 1985). Nod genes are grouped in two categories, the common and host-specific nod genes (Kondorosi et al. 1984). The common nodABC genes containing operon are conserved across all *Rhizobium* sp. (Torok et al. 1984; Martinez et al. 1993), and these can be interchanged between different rhizobial species, while it is not possible for host-specific nod genes, which determine host specificity for the bacterial strain (Kondorosi et al. 1984).

Bacteria need essentially six genes, nodABCDEF (Marvel et al. 1987), that are arranged as three different operons, nodABC, nodD, and nodFE (Rossen et al. 1985; Debelle et al. 1986). These are not conserved in structure and function among rhizobia, but they are still necessary for the nodule formation (Kondorosi et al. 1984). Additionally, nodH and nodQ are required which are involved in determination of host range in *R. leguminosarum* bv. *viciae* and recognize plant-specific signals present in exudates (Faucher et al. 1989).

The NodD gene is regulatory nod gene as it codes for a protein which binds to conserved region upstream of the nod operons and activates their expression. Its product acts as a transcriptional activator of other nod genes in the presence of plant signals as flavonoids and lectins (Rossen et al. 1985; Rostas et al. 1986). NodD has regulatory function across all species of *Rhizobium*, *Bradyrhizobium*, and *Azorhizobium* strains. The number of nodD gene copies varies among different species (Rhijn et al. 1993). NodD protein product belongs to LysR family of transcriptional activators which has common features as they are activated by chemicals and carry a helix-turn-helix motif for specific DNA-binding ability. The protein acts as cytoplasmic membrane-localized receptor where it interacts with plant-released inducers and transduces the signal to nod operon ABC, thus transcriptionally activating the operon (Fisher et al. 1988). Subtractive hybridization studies have been carried out to identify genes upregulated during root nodule development (Gamas et al. 1996). NodABC operon controls curling of host root hair, rhizobial penetration, formation of infection thread, and nodule development, while nodFE unit regulates invasion of infection thread within root hair (Downie et al. 1985; Debelle et al. 1986).

Other nod genes involved were also later discovered. The protein coded by nodM was found to be involved in transcriptional regulation of operons nodA, B, C, I, J, F, and E (Spaink et al. 1987). This Nod factor further activates transcription of many downstream genes in host plant cell NSP1, NSP2, CYCLOPS/IPD3, ERN1, and NIN which are involved in organogenesis and meristem formation (Laloum et al. 2014). Thus, there is change in levels of phytohormones as cytokinins, ABA, gibberellins, and auxins within nodules during this phase (Phillips and Torrey 1970; Phillips 1971; Williams and Mallorca 1982; Badenoch-Jones et al. 1984; Dangar and Basu 1987). A study using *Rhizobium japonicum* cultures and pea epicotyl showed that that there are high levels of GA in nodule compared to the rest of root tissues which is produced by bacteroid itself and not by the host cell (Williams and Mallorca 1982). Similarly, cytokinin was isolated from a nodulating *Rhizobium japonicum* strain which induced cell divisions in a soybean callus tissue grown in cytokinin lacking medium (Phillips and Torrey 1970).

There is also upregulation of genes involved in production of leghemoglobin protein (Garg and Jain 2013). In *Lotus japonicus*, using cDNA arrays approximately 860 genes were found to be highly upregulated in nodules than in roots. One-third of these expressed genes were involved in metabolism and transport, and over 100 in signaling, or in transcriptional or posttranscriptional regulation of gene expression. Genes required for pathways such as glycolysis, CO_2 fixation, amino acid biosynthesis, and purine, haem, and redox metabolism were also found to be upregulated in nodules (Colebatch et al. 2004).

An induction of 18–20 nodule-specific proteins in host cells called nodulins was observed in root nodules of *Glycine max* in response to *Rhizobium japonicum* association. These nodulins constituted 7–11% of the total protein synthesized in cytoplasm of the host cell which was not present in the uninfected roots, bacteroids, and free-living *Rhizobium*. Thus, there is induction of specific nodulins which are essential for development of symbiosis in the legume root nodules (Legocki and Verma 1980). These genes are structurally and functionally conserved in *Rhizobium*, *Azorhizobium*, and *Bradyrhizobium* spp. (Dobert et al. 1994).

15.2.6 Autoregulation of Nodulation in Legumes

The host plant itself determines the number of nodules that are formed through active signaling pathway called autoregulation of nodulation (AON). It is a negative self-regulating mechanism to control number of nodules when not required. It involves transfer of a signal from older nodule primordia to cortical cells of newly forming nodule. The regulation of root nodules involves nitrate inhibition and is shoot controlled (Francisco and Akao 1993). In mutants lacking autoregulation, hypernodulation is observed wherein the roots form excess nodules.

There is differentiation of few regions in root cells into regulatory regions which involves root to shoot and shoot to root signaling (Reid et al. 2011). At molecular level, the regulation seems to be through short peptides (related to the nonsymbiotic CLAVATA3 peptide of *Arabidopsis*) which are synthesized in these regulatory cell clusters. Autoregulation of nodulation is systemic regulatory pathway, while nodulation initiation is local mechanism. Both pathways involve by a peptide CLAVATA/ESR-related (CLE) protein which represses excessive nodulation via negative feedback loops. These peptides are 12–13 amino acids long and have leucine-rich repeat (LRR) receptor kinase through which it acts (Hastwell et al. 2015).

The CLE peptides mediate nodule inhibition responses to control the number of nodules according to plant requirements (Reid et al. 2011).

15.3 Ecological Aspects of Stem and Root Nodulation

15.3.1 Stem Nodulation: Ecological Significance

Although roots are the sites for nodulation in most plants, there are reports of stem nodulation as in *Sesbania rostrata* (Dreyfus and Dommergues 1981). *Azorhizobium caulinodans* is the specific symbiont partner which infects these adventitious roots and has ability to form both stem and root nodules on *Sesbania*. The nodules develop from dormant root primordia abundantly present in stem which get activated in the presence of certain transcripts as H4-1Sr (Goormachtig et al. 1997). Using 16S rRNA sequence, it was found that stem-nodulating strains are phylogenetically very diverse compared to various root-nodulating *Rhizobium* sp., and they form a separate subbranch on the phylogenetic tree (Dreyfus et al. 1988). These N_2-fixing nodules are formed on subepidermal primordia of the adventive roots on the stems (Alazard 1985; Ladha et al. 1992). Twenty-one species of the genus *Aeschynomene* (Alazard 1985; Becker et al. 1988) and three species of the genus *Sesbania* (Dreyfus and Dommergues 1981) are some of the species reported to show stem nodulation. *Sesbania* shows stem nodulation in response to flooding and waterlogged conditions (Trinchant and Rigaud 1989). Stem nodulation, thus, seems to be an evolutionary adaptation to waterlogged conditions and has immense ecological significance. There are some unique features of plants having stem nodulation: rapid growth of plants, more number of sites from which infection can take place, photosynthetic nature of stem nodule, and thus ability to carry out dual functions, photosynthesis and nitrogen fixation (Ladha et al. 1992).

15.3.2 Ecological Significance of Root Nodulation

A few strains of *Rhizobium* have been shown to tolerate various stress conditions as salt and drought stress and carry out nitrogen fixation for host plant, thus improving productivity (Zahran 1999). An acid-tolerant *Rhizobium leguminosarum* biovar *trifolii* strain was shown to have less membrane permeability and high proton expulsion ability compared to acid-sensitive strain (Chen et al. 1993). Thus, there is an immense scope of its application in reclaiming degraded lands.

A study on biotic stress revealed that in *Phaseolus lunatus*, the nitrogen fixed during rhizobial symbiosis was being sanctioned for production of nitrogen-containing cyanogenic defense compounds against an insect herbivore, Mexican bean beetle (*Epilachna varivestis* Muls); thus symbiosis was involved in improving plant growth in dual ways, plant growth and better resistance to biotic stress (Thamer et al. 2011).

15.3.3 Evolutionary Significance of **Rhizobium**–*Plant Symbiosis: Coevolution of Symbionts*

The symbiotic relation between members of Fabaceae and group "rhizobia," which is a polyphyletic group (Jarvis et al. 1997), is an ideal model to understand the evolutionary basis of symbiosis (De Mita 2007). It is hypothesized that coevolution has taken place through mutual interaction of host plants and *Rhizobium* sp. in the soil making it one of the most efficient symbiotic associations even though both partners can survive in the absence of each other. Evolution of nod genes especially those involved in nodulation might be present in a single bacterial lineage, and there would have been horizontal gene transfer among the different rhizobial species (Hirsch et al. 1995).

Plant-rhizobial association was originally necrotrophic, however evolutionary mechanisms seem to be in favour of biotrophy. Since there is establishment of interdependence between *Rhizobium* and legumes over evolutionary time scale, there has been modification of both leghaemoglobin of host and nitrogen fixing mechanisms of *Rhizobium* to enhance nitrogen fixation (Sharifi 1983).

According to one school of thought, rhizobia repress the host immune system for its entry and establishment inside plant cells as symbiont. For further successful establishment, the host has developed mechanisms of nutrient supply to the symbiotic partner. The secretion of various chemicals by plant cells further promotes invasion by bacteria. For selection of partner, signals produced by the symbiont are used by the host and vice versa (Noe and Hammerstein 1994). There are evidences that interaction with *Rhizobium* has a beneficial effect on legume growth (Kaschuk et al. 2010). In one such study, 15 plants from 12 genotypes of *Medicago truncatula* were grown with a mixture of three *Rhizobium* strains. Most *M. truncatula* plants developed a larger number of nodules with more beneficial *Rhizobium* strains and hence give evidence for partner choice. Also, there was increased frequency of beneficial *Rhizobium* strains in the rhizosphere suggesting how partner's selection also affects bacterial fitness in competitive environment (Heath and Tiffin 2009).

There are many mutant strains of *Rhizobium* which are noncompatible with host but still elicit nodule formation, although such nodules have been found to be ineffective in nitrogen fixation capability and are devoid of leghemoglobin. These nodules possess distinct structure compared to normal nodules and undergo all initial recognition processes as bacterial colonization around roots, root hair curling, and root cortex cell divisions. However, these lack infection thread formation and production of leghemoglobin and ureide (Vandenbosch et al. 1985).

Although host symbionts provide important services to bacterial partner, it seems to penalize rhizobia that fail to fix N_2 inside their root nodules. It was shown by series of experiments that noncooperation (analogous to cheating) leads to reduction in reproductive rate of bacteria by 50% and there was reduced supply of sanctions against these bacteria (Kiers et al. 2003). In this mutualistic interaction, there may be conflict of interest resources if certain bacterial individuals “cheat” by not fixing nitrogen while continuing to accept carbon source from host partner. There are many evidences that support the possibility of “defaulter” rhizobia strains which provide little or no evident benefit to host in the population. So, effective strains have to overcome competition over these strains which are selected by the host. This is done by host withholding resources from noneffective partners (unproductive symbionts) which is determined by host’s incentives, thus screening away nonprofitable members and selecting right mutualists (Archetti et al. 2011).

15.4 Mycorrhizal Associations

Mycorrhiza (pl. mycorrhizae, mycorrhizas; Gr. mykes, fungus; rhiza, roots) is a symbiotic, nonpathogenic, or weakly pathogenic association of a fungus and plant roots or underground organs. The association serves mutual benefits: carbohydrates synthesized by plants are used by the fungus and in return receive nutrients especially nitrogen and phosphorus from the fungi (Smith and Read 2008). Fungus uses these carbohydrates for its growth and in the synthesis of molecules like glomalin, the release of which in the soil environment improves the soil structure and increases organic matter content (Kaur et al. 2014). It has been estimated that about 80% of the N and P contents of plant have been acquired from mycorrhiza indicating their importance in plant nutrition (van der Heijden et al. 2008). Besides providing nutritional benefits to their hosts, mycorrhizal fungi also contribute toward ecological significance such as decreased susceptibility to biotic diseases, tolerance to heavy metals, drought tolerance, etc. (Luo et al. 2009; Beniwal et al. 2010). These dual organisms were first described in detail by Frank (1885) who observed it on the roots of several trees of temperate forests. In 1887, Frank divided these mycorrhizae into two types: (a) ectotrophic and (b) endotrophic. In the former, the fungus forms a sheath on the surface of the root and hyphae grow in the soil and between the outer cortical cells of the root. In the latter, the fungal hyphae enter the cortical cells of the root and colonize the roots of a host plant intracellularly enveloped by the plasmalemma of the host (Eshel and Beeckman 2013).

Mycorrhizae are extremely common in the context of phylogeny and ecology (Kistner and Parniske 2002; Bonfante and Genre 2010). These symbiotic relationships are estimated to occur in about 92% plant families and at least 80% of the vascular plants (Wang and Qui 2006). These include angiosperms, gymnosperms, pteridophytes, and some bryophytes (especially liverworts) (Read et al. 2000a, b). However, plants from the families Brassicaceae, Chenopodiaceae, and Proteaceae rarely, if ever, have mycorrhizal association (Vierheilig et al. 2003).

Based on fossil records and phylogenetic analyses, it has been suggested that more than 450 million years ago certain early Devonian period plants have established a close association with filamentous, i.e., mycorrhizal, fungi (Srivastava et al. 1996; Schüßler et al. 2009; Lee et al. 2012; Torres-Cortes et al. 2015). It is believed that translocation of plants from water to land has been possible because of this association only (Simon et al. 1993; Read et al. 2000a, b; Lum and Hirsch 2003; Bücking et al. 2012).

Mycorrhizal fungi have been classified on the basis of the extent of plant root penetration, production of external mantle or sheath, and inter- and intracellular structures formed by them inside the plant root (Morton and Benny 1990; Walker 1992; Smith and Read 1997; Manoharachary et al. 2000). Seven different types of mycorrhizal fungi have been recognized (Harley and Smith 1983), such as endomycorrhiza, ectomycorrhiza, ectendomycorrhiza, arbutoid mycorrhiza, monotropoid mycorrhiza, ericoid mycorrhiza, and orchid mycorrhiza (Table 15.1). Among them, two major types of mycorrhizal fungi that are important for plant growth and development are ectomycorrhiza (EM/ECM) and endomycorrhiza or arbuscular mycorrhiza (AM). These two types are different as the ectomycorrhizal fungi typically form a thick sheath, or mantle, of mycelium around roots, and some of the mycelium penetrates between cortical cells. The hyphae instead of penetrating individual cells within the root cortex get surrounded

Table 15.1 The major types of mycorrhizae and their ecological significance

Mycorrhizal plants	Typical host plant	Fungi involved	Major significance
Ectomycorrhizae	Forest trees, mainly in temperate and boreal regions	*Amanita*, *Boletus*, *Lactarius*, *Pisolithus*, and *Rhizopogon* (Agaricomycetes) and *Tuber* (Ascomycetes)	Nitrogen uptake from soil
Arbuscular mycorrhizae	Many crop plants	Glomeromycota	Phosphorus uptake from soil
Ectendomycorrhizae (Srivastava et al. 1996; Smith and Read 1997)	Mainly pines, spruce, and larch	*Wilcoxina* (Ascomycetes)	Mineral nutrient uptake from soil
Orchidaceous mycorrhizae (Singh and Varma 2000)	Orchids (Orchidaceae)	*Armillaria*, *Mycena*, *Rhizoctonia*, (Agaricomycetes), *Russula* (Russulales), *Thelephora* (Thelephorales)	Fungi supply the plant with sugars or in some orchids, plants obtain sugars from ectomycorrhizal fungi attached to trees
Ericoid Mycorrhizae (Read 1996; Selosse et al. 2007)	Heathland plants of family Ericaceae, e.g., *Calluna*, *Erica*, *Vaccinium*, etc.	*Hymenoscyphus* (Helotiales) and *Pseudogymnoascus*	Nitrogen and phosphorus uptake from soil
Monotropoid mycorrhizae (Manoharachary et al. 2002)	Non-photosynthetic plants of family Monotropaceae, e.g., *Monotropa*	*Boletus edulis* (Agaricomycetes)	Plants obtain carbohydrate from ectomycorrhizal fungi, itself attached to trees
Arbutoid mycorrhizae (Molina and Trappe 1982)	*Arbutus*, *Arctostaphylos*, *Pyrola*	Basidiomycota, similar to ectomycorrhizal fungi	Mineral nutrient uptake from soil

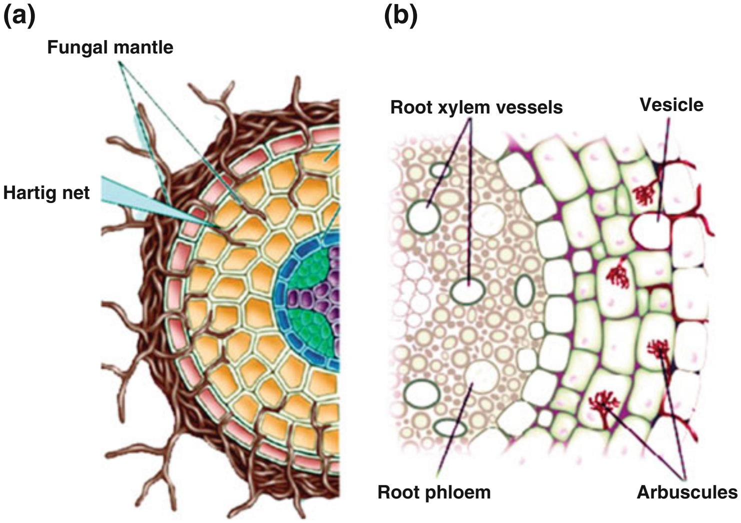

Fig 15.3 (**a**) Ectomycorrhiza (ECM) and (**b**) arbuscular mycorrhizal fungi (AMF); note that mycelium remains outside the root system and hyphae penetrate into root tissue through intracellular spaces; in AMF hyphae are intracellular and form vesicle and arbuscules

by a network of hyphae called the Hartig net for mutual exchange (Fig. 15.3a). The hyphae ensheath root tips forming a typical mantle characterized by differences in color, thickness, presence, and lengths of emanating hyphae (Sethi and Walia 2018). The hyphae of AM/endomycorrhizal fungi grow within the root itself and extend outward from the root into surrounding soil. The hyphae enter the root through either the epidermis or root hairs and invaginate the cell membrane after penetrating through cell wall. The hyphae grow between and into root cortical cells, where they form dichotomously branched treelike structure, arbuscules, and form oval structures, vesicles (Fig. 15.3b). AM fungi develop mainly small spores in the soil, whereas ectomycorrhizal fungi develop aboveground fruit bodies in the surrounding area of trees (Redecker and Schüßler 2014).

While AM are formed with roots of the majority of higher plant species including grasses, herbs, and trees, EM have only been detected in woody species (Brundrett 2009). Most tree species of the boreal and temperate climatic zone have association with EM fungi, whereas AM associations are widespread in the tropical ecosystem. However, there are exceptions. On a global scale, more than 7500 different EM species have been identified, and estimates suggest that the total numbers will be in a range from 25,000 to 30,000 (Rinaldi et al. 2008). With the advent of new methods, knowledge on the composition and diversity of mycorrhizal species in the different ecosystems is currently rapidly increasing suggesting that EM diversity is similar in temperate, tropical, and boreal forests (Tedersoo and Nara 2010; Lang et al. 2011).

15.5 Ectomycorrhiza

Ectomycorrhizae (ECM) (also known as ectotrophic mycorrhizae or sheathing mycorrhizae) are found mainly on woody plants, including many species of coniferous and broad-leaved trees in temperate and boreal regions. They are estimated to form symbiotic association with about 6000 plant species (Brundrett 2009), viz., on trees such as *Pinus* (pines, Pinaceae), *Picea* (spruce, Pinaceae), *Quercus* (oak, Fagaceae), *Fagus* (beech, Fagaceae), *Betula* (birch, Betulaceae), and *Eucalyptus* (eucalyptus, Myrtaceae). The fungi involved in ectomycorrhizal associations are principally members of Agaricomycetes (e.g., *Amanita*, *Boletus*, *Russula*, *Hebeloma*, *Lactarius*, *Pisolithus*, etc.) and few Ascomycota, such as truffles (*Tuber*) (Boroujeni and Hemmatinezhad 2015).

In this association, the fungal hyphae form a sheath-like covering or mantle on the surface of root and enhance the surface area of the roots, with hyphae forming the branching network in the intercellular surface between the epidermis and cortex, known as Hartig net named after Robert Hartig, who is considered the father of forest biology (Blasius et al. 1986). The most apparent feature of ECM is that although the major part of the fungus is in close contact with the root cells, there is no penetration of the host cells (Dighton 2009). It means that the bulk of the fungal mass is located outside the plant roots, hence the name ectotrophic (outside-feeding) or ectomycorrhizae for these mycorrhizae. In this association, the fungus helps in the nutrient and water uptake for the host and, in return, obtains carbohydrate from the host plant. The fungal mycelium, outside the root, forms an extensive network within the soil and leaf litter. The fungal hyphae often grow into the root system of adjacent plant and create a new mycorrhizal association, thereby, linking the different plants through a common mycorrhizal network. This mycorrhizal network helps in the movement of nutrients between different plants and thereby promotes ecosystem succession (Wilson et al. 2006).

The hyphae grow outward from the mantle replacing the root hairs for the absorption of minerals from the soil. Because of the absence of root hairs and the entire root being enclosed by the sheath, there is no direct contact between younger roots and the soil. Thus, all mineral nutrients and water absorbed by the roots have to pass through the fungal sheath. This uptake is facilitated by the extensive network of individual hyphae or aggregated mycelial cords or rhizomorphs, which radiate from the surface of the root sheath into the soil and transport nutrients back to the mycorrhizal sheath.

The fungus colonizes the root in a series of complex events. In the first precontact phase or early phase, the fungus is attracted toward the root. On contact with the root hair, hyphae start growing along with it until they find the surface of the main root (Jacobs et al. 1989). On the main root, morphogenetic changes get initiated leading to the development of mantle. The mantle forms an interphase between the root and the soil. It is a sheath-like covering on the outer surface of the root, leading to root bifurcation and clustering. Sometimes, they are referred as pseudoparenchymatous, as they resemble the parenchymatous tissue of the plant (Dighton 2009). The active mycorrhizal zone appears several millimeters behind the root tip. In older roots it persists even after the association becomes inactive and functions as storage structure and propagule (Massicotte et al. 1987). Once the inner layer of mantle is fully established, the hyphae start penetrating the epidermal cells. Ectomycorrhizal fungi break down the wall polymers locally by secreting certain hydrolytic enzymes like cellulase and pectinase. Soon the fungus colonizes the root cell, and the symbiotic association between the two gets established. Some ectomycorrhizal fungi are also known to produce certain proteins, the ectomycorrhizins, which favor the development of fungal hyphae inside the plant cell. For the development of Hartig net, the hyphae from the inner layer of mantle penetrate mechanically and enter the middle lamella present between the epidermal and cortical cells. Sometime, the fungus releases certain hydrolytic enzymes which solubilize the middle lamella and activate the process.

Once colonization of a certain root part is accomplished and the mantle and Hartig net are well developed, the exchange of nutrients begins between both partners in the Hartig net, leading to the functional mycorrhiza, called late phase (Martin 2007). The tip of the hyphae, forming the Hartig net, accumulates in the mitochondria and endoplasmic reticulum in large number, suggesting that the transfer of nutrients is localized to this part. The hyphae arising from the mantle are long and grow several centimeters in the soil (Anderson and Cairney 2007). Besides providing nutritional benefits, the mantle layer may provide tolerance against heavy metals and high salt concentration and may exclude nematodes from the root. Once colonization is accomplished or equilibrium is established in terms of colonization, the fungus does not penetrate any further. The biotrophic (equilibrium) phase, where efficient nutrient exchange occurs, may be maintained for a certain period of time, depending on the species involved (Smith and Read 2008), until the mycorrhiza undergoes senescence (Felten et al. 2012). Outside the mantle, the mycelium may extend into the soil by a few centimeters or much farther if a particular fungus has the capacity to form mycelial cords or rhizomorphs. This extensive network of rhizomorph and mycelial cords ramifies through the soil from the mycorrhizal sheath. This network can link many different plants within a habitat—even plants of different species, because of the general lack of host specificity of these fungi (Arnebrant et al. 1993; He et al. 2006).

Through this networking, the ectomycorrhizal fungi play several important roles in ecosystem functioning, such as:

- Ectomycorrhizae may connect many of the plants in a community, i.e., the young tree seedlings can be linked to a “mother” tree by a common mycorrhizal network, so that the nutrients can be tapped by seedlings growing nearby in shade from the one growing in sun, thus allowing the seedling to survive under conditions where otherwise they might be superseded by mature plants (Monika et al. 2015).
- An estimated 70–90% of ectomycorrhizal rootlets die and are replaced each year. If these rootlets were not connected, they would decompose, and at least some of the nutrients would be leached from the soil. The mycelial connections could help

to retain mineral nutrients by withdrawing them from the degenerating mycorrhizae to others that are still healthy.

- As the mycelial cords and network of hyphae extend several meters beyond the root zone, it can exploit large volume of soil for nutrients and help in improving the water status of the soil. This role can be largely important in soils with poor water retention, such as former mining sites where trees are planted for land reclamation or under conditions of drought.
- Ectomycorrhizae are efficient in cycling of nutrients, i.e., capturing substances such as phosphates, nitrogen compounds, and cations that are released by exudation from the leaf canopy and leaf fall and returning them to the root system.
- Where phosphates and water are transported to the plant by the fungus, the fungus benefits from these associations by obtaining carbohydrates from the plant. Trees invest a considerable amount of photosynthate to support the fungal biomass—conservatively estimated at 10% or more of the annual photosynthetic production of a tree. Fruiting bodies of Basidiomycetes absorb these carbohydrates maximally. Some achlorophyllous plants may also fulfil their carbon needs by plugging their roots into this mycorrhizal network. This strategy also observed in orchid mycorrhizae is known as mycoheterotrophy.
- Ectomycorrhizal fungi have been found to be particularly prevalent in litter layer (humus) in comparison with lower soil horizons. In these layers nutrients vary widely due to leaf fall, precipitation, activities of animals, etc.; thus they may be particularly useful to the tree in such environments. Since these mycorrhizae can grow well in nutrient-poor or dry soils, it is possible that they have the capacity to produce hydrolytic enzymes and are capable of solubilizing phosphorus and nitrogen from complex sources.
- Many ectomycorrhizal fungi can grow on simple organic media in culture (France and Reid 1984), but they have poor or no ability to degrade cellulose and lignin, as seen in wood decomposer fungi of the Ascomycota and Basidiomycota. So, the ectomycorrhizal fungi seem to be ecologically adapted to grow as symbionts.

15.5.1 Benefits of Ectomycorrhizae

15.5.1.1 Plant Nutrition

Root proliferation in plants is relatively slow. ECM enhances the plant growth, through improvement in nutrients uptake. ECM absorb and stores plant nutrients like nitrogen, phosphorus, potassium and calcium etc. in their mantle thereby help in establishment of high yielding forests, land recuperation and establishment of exotic plant species. Influence of ECM on root exudates is important for the nutrient exchange and mineralization process in the soil (Moore et al. 2011). The mycorrhizal association increases the surface area of the plant roots, due to which its access to soil resources is increased. Extraradical mycelium also plays a direct role in nutrient mobilization by secreting enzymes, absorption, and transport of elite nutrients. They secrete significant quantities of chitinase, phosphatase, and protease, which help to dissolve hard-to-capture nutrients such as organic phosphorus, nitrogen, and iron. Most of the ECM secrete acid phosphatase in the mycosphere, which hydrolyze the organic phosphate into orthophosphate (Bolan 1991).

15.5.1.2 Resistance to Abiotic Stress

ECM association helps plants to overcome different kinds of stress such as soil salinity, alkalinity, acidity and drought conditions (Boroujeni and Hemmatinezhad 2015). The ECM plants exhibit better growth than the non-mycorrhizal ones especially in the arid and semiarid regions where low moisture and high temperature are very critical for survival and growth of the plants (Sandeep et al. 2015). Studies have shown that the ectomycorrhizal fungi provide resistant to drought stress in the seedlings of spruce plant. The ECM association enhances the absorbing area of root surface and improves the soil root contact. Besides, the fungal hyphae can penetrate the soil pore more easily than the root hair, thereby, increasing the access to deep water system. ECM symbiosis with poplar species has been found to improved salt tolerance in salt stress soils. The fungus, by changing the concentration of nutrients and phytohormones and ratios of fatty acids, alters the leaf physiology leading to prevent chlorosis and leaf shedding. ECM fungus *Scleroderma bermudense* was able to improve salt stress in *Coccoloba uvifera* (sea grape) seedlings (Bandou et al. 2006).

15.5.1.3 Phytoremediation

Phytoremediation, a process that includes all kinds of biological, physical, and chemical activities carried out by plants, is used for the remediation of soil contaminated with pollutants such as heavy metals, salts, organic compounds, etc. (Coninx et al. 2017). Fast-growing plants with deep root system and high transpiration rate are generally ideal for this purpose. They produce certain root exudates which enhance the growth of microbial community and create the favorable environment by altering pH and osmotic potential that stimulate the degradation of toxic compounds. Majority of such trees live in symbiotic association with ectomycorrhizal fungi. For example, *Populus* forms symbiotic association with more than 60 different ectomycorrhizal fungal species. Ectomycorrhizal symbiosis between *Populus* and *Paxillus involutus* has shown improved plant growth and increase in phytostabilization potential (Bojarczuk et al. 2015; Szuba et al. 2017). ECM increase the plant tolerance to heavy metals by forming a sheath-like covering that acts as a filter, thereby restricting their movement to root cortex.

Ectomycorrhizal fungi and their extraradical mycelium increase the surface area for the establishment of microbial communities. Their synergistic, competitive, and antagonistic effect shifts the soil microflora toward those communities capable of degrading the soil pollutants. Studies on gray poplar (*P.* × *canescens*), natural hybrid between *P. alba* (white poplar) and *P. tremula* (European aspen), showed that it accumulates high amounts of Cd and Zn when grown in metal-polluted soil (Durand et al. 2011; He et al. 2013) than stressed non-mycorrhizal roots. Inoculation of young poplar plants with mycorrhizal fungi may be used for bioremediation of soils contaminated with toxic metals (Bojarczuk et al. 2015). ECM symbionts can alter mechanism of heavy metal detoxification by influencing physiological and molecular processes of the poplar (Luo et al. 2014).

15.5.1.4 Resistance to Biotic Stress

Ectomycorrhizal fungi are known to inhibit the growth of numerous soilborne pathogens on root surface of host plants by producing certain compounds or antifungal and antibiotic substances (Moore et al. 2011). Compact arrangement of hyphae in fungal mantle protects the root against nematodes and soilborne pathogens and stimulates the plant growth by reducing the severity of diseases. Studies have shown that ECM fungi such as *Lactarius deliciosus* and *Boletus* sp. antagonize plant pathogen *Rhizoctonia solani*. *Lactarius camphoratus* and *Cortinarius* sp. have been found to produce antifungal antibiotics known as “chloromycorrhiza” and “mycorrhizin A” against the phytopathogens like *Rhizoctonia solani*, *Pythium debaryanum*, and *Fusarium oxysporum* (Sandeep et al. 2015).

15.5.1.5 Growth Hormones

Plants with mycorrhizal associations exhibit higher content of growth regulators like cytokinins and auxins as compared to the non-mycorrhizal ones. It indicates that benefits to the higher plants provided by the fungal symbiosis are not just limited to inorganic and organic nutrients from the soil. The fungal symbiont provides the host plant with growth hormones, auxin, cytokinins, and gibberellins, and also growth-regulating B vitamins, thereby producing above normal level of these potent substances, which in turn influence the growth and development of host plant (Sandeep et al. 2015).

15.6 Endomycorrhizal Fungi (AMF)

Before 1974 the term vesicular–arbuscular mycorrhizae was used commonly for the mycorrhizal associations where vesicles and arbuscules were observed in the roots. Later, it was recognized that some fungi form mycorrhizae with arbuscules only and lack the ability to form vesicles in roots of the plants (e.g., *Gigaspora* and *Scutellospora*). It was therefore proposed that the more general term, “arbuscular mycorrhizae (AM)” should be used. Arbuscular mycorrhiza (AM) represents a symbiosis between terrestrial plant roots and fungi of phylum Glomeromycota. The symbiosis derives its name from the Latin word arbusculum (little tree) for typical tuft-like structures formed by fine dichotomously branched fungal hyphae and the Greek word for fungus roots. These are the most common type of mycorrhizae with worldwide distribution. Up to around 80% of investigated species, mainly land plants, among them vascular plants, are known to form AM (Brundrett 2009; Bonfante and Genre 2010). The remainder either are non-mycorrhizal or form one of the other types of mycorrhiza, i.e., ectomycorrhiza, orchid mycorrhiza, or ericoid mycorrhiza. However, many gymnosperms, pteridophytes, and some bryophytes also form AM or AM-like associations. Thus, AM are found ubiquitously in soils wherever their hosts are available (Gerdeman 1968).

On the basis of the molecular studies, AMF have been assigned to a monophyletic group, the Glomeromycota, which is one of the smallest fungal groups. It presently includes 5 orders, 14 families, 29 genera, and approximately 230 described species (Morton and Redecker 2001; Spain et al. 2006; Palenzuela et al. 2008; Oehl et al. 2008, 2011a, b; Schüßler and Walker 2010). Almost all members of this group such as *Acaulospora*, *Archaeospora*, *Gigaspora*, *Entrophospora*, *Glomus*, *Paraglomus*, and *Scutellospora* form mycorrhizae with crop plants and have not been grown in axenic culture, away from their host plants (Rosendahl 2008). Therefore, they are considered to be wholly dependent on plants for their carbon and energy sources.

Roots containing AM fungi show no outward signs of infection. Instead, they look like normal roots, and the extent of colonization by fungal hyphae can only be judged by special techniques. One special method for this is to use differential interference contrast microscope. But the more common method is to treat roots with strong alkali, to destroy the plant protoplasm, and then to stain the roots with a fungal dye such as trypan blue. Fungal hyphae can be observed clearly in such preparations colonizing the roots extensively by growing among the root cortical cells, often producing large, swollen vesicles, and by penetrating individual root cortical cells to form treelike branching structures termed arbuscules (Vierheilig et al. 2005). The arbuscules are sites of nutrient exchange between the fungus and the host (Miyasaka et al. 2003). After germination, the germ tubes show limited growth in vitro, and extended growth can only be observed if the fungus is in association with living root tissues. Therefore, it can be inferred that such mycorrhizal fungi are obligate mutualistic symbionts. AM associations are very ancient, and structures resembling extant arbuscules have been discovered in the fossilized rhizome tissues of early vascular plants.

The AM fungi play an important role in overcoming biotic stresses faced by plants. These fungi increase growth of plant by enhancing uptake of soil nutrient, increasing plant tolerance to drought, and protecting plants against pathogens, nematodes, and insects (Whipps 2004; Pozo and Azcón-Aguilar 2007; Gianinazzi et al. 2010; Jung et al. 2012; Jeffries and Barea 2012).

15.6.1 Systematic Position of AMF

Considerable changes have taken place in the classification of AMF in the last few decades. Earlier in the 1990s, they were classified in Zygomycota exclusively on the basis of phenotypic characteristics like spore morphology and the structure and development of spore wall (Gerdemann and Trappe 1974; Walker 1992). Recent studies based on nuclear-encoded rRNA gene markers suggested that these fungal symbionts form a monophyletic group of true fungi, the phylum Glomeromycota. The phylum Glomeromycota was earlier divided into four orders, namely, Diversisporales, Archaesporales, Glomerales, and Paraglomerales (Schüßler et al. 2001). One of the most widely accepted classification system for AMF was provided by Oehl et al. (2011a, b), who proposed the establishment of a fifth order, namely, Gigasporales (Fig. 15.4). They based their classification on morphological and genetic features (Pagano et al. 2016). They have described four families, Diversisporaceae, Acaulosporaceae, Sacculosporaceae, and Pacisporaceae, within the order Diversisporales (Błaszkowski 2012; Medina et al. 2014), and five families, Scutellosporaceae, Gigasporaceae, Intraomatosporaceae, Dentiscutataceae, and Racocetraceae, within the order Gigasporales (Silva et al. 2012; Pontes et al. 2013; Marinho et al. 2014). Glomerales describes two families, the Enthrophosporaceae and Glomeraceae (Sieverding et al. 2014; Błaszkowski et al. 2015). The order

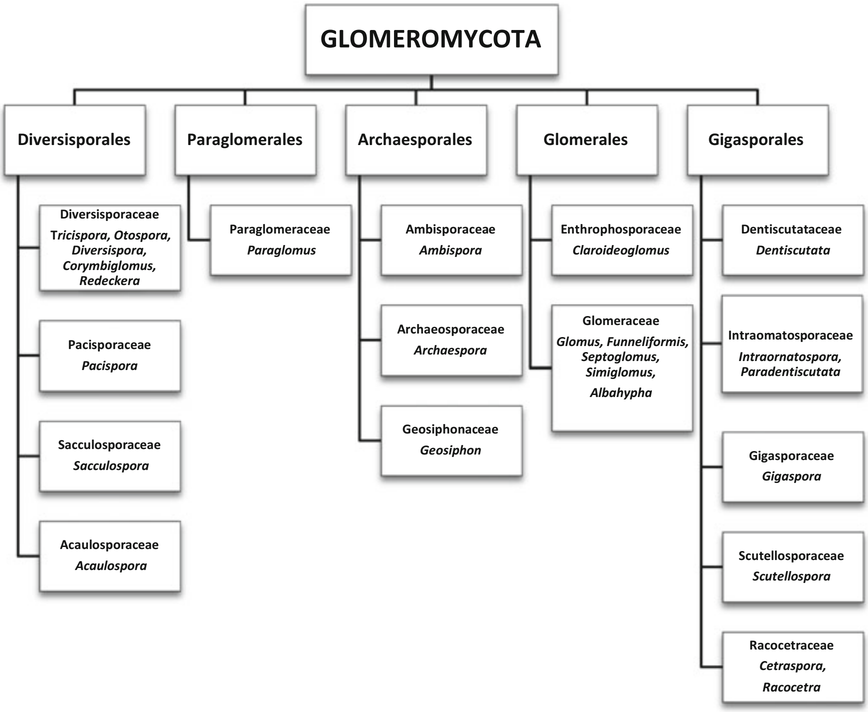

Fig 15.4 Classification of phylum Glomeromycota (Oehl et al. 2011a, b; Goto et al. 2012)

Archaeosporales describes three families, the Ambisporaceae, Geosiphonaceae, and Archaeosporaceae (Oehl et al. 2015). The fifth order Paraglomerales includes only one family, Paraglomeraceae.

15.6.2 Host Ranges and Communities of Arbuscular Mycorrhizae

The AM fungi have astonishingly wide host ranges, i.e., they are nonspecific in their host range and can colonize both herbaceous and woody plants. They are found everywhere where hosts to this symbiosis occur. Non-AM plants may have other kinds of mycorrhiza. Some families such as the Brassicaceae, Chenopodiaceae, and Cyperaceae although regarded as non-mycorrhizal have members that show colonization with these fungi (Smith and Read 2008). Different species of plants react differently to different mycorrhizal fungi. Plants in natural communities have been observed to be colonized by different strains of AM fungi. At least in artificial inoculations, an AM fungus obtained from one type of plant was found to colonize the roots of many unrelated plants. Moreover, the diversity of AM fungi can influence the plant biodiversity in natural ecosystems. With an increase in AM fungal diversity, there is an increase in plant biodiversity and productivity. Majority of fungi can grow at water potentials beyond the tolerance level of plants, so the arbuscular mycorrhizal fungi can be significant in semiarid environments, such as the deserts (Kamalvanshi et al. 2012).

15.6.3 Morphology and Reproduction

Because of their very peculiar evolutionary history, underground lifestyle, and genetic makeup, AM fungi are gifted with extraordinary biological characters (Bonfante and Genre 2008; Parniske 2008; Barea and Azcón-Aguilar 2012). The mycelium formed within the root tissues is coarse, aseptate, and coenocytic, contains hundreds of nuclei, and produces very large multinucleate spores with resistant thick walls containing chitin (Smith and Read 2008). Outside the root, the fungus produces large, distinctive spores which are easily visible to the naked eye. These can vary in diameter from 10 to 1000 μm, in color from hyaline to black and in surface texture from smooth to highly ornamented. These spores germinate and infect the roots from an appressorium-like infection structure on the root surface. Spore germination may be improved by plant-produced factors such as strigolactones. These compounds have been found to induce spore germination or hyphal branching near a potential host thereby increasing the chance of colonization (Akiyama et al. 2005; Besserer et al. 2006). From the initial entry points, the fungus grows extensively between the cells of the root cortex, often producing large, balloon-shaped, thick-walled vesicles, also known as intraradical vesicles, within the root. These vesicles are multinucleate and store large amount of lipids. Their primary function is believed to be storage; however, vesicles can also function as reproductive propagules for the fungus. In some plants, the fungal mycelium penetrates cortical cells of the root and forms extensive intracellular coils. More commonly, the hyphae penetrating host cells branch repeatedly to form dichotomous treelike structures, termed arbuscules. The individual arbuscules have a short active life only for less than 15 days and then degenerate, being replaced by new arbuscules, in other parts of the root. The fine tips of arbuscules are digested by the host cell so that only irregular clumps of fungal matrix remain. The plant and the fungal plasma membranes are separated by an apoplastic compartment known as periarbuscular space. The arbuscules thus can be considered a type of haustorium through which exchange of nutrient between the fungus and the root cells takes place (Bonfante-Fasolo and Grippiolo 1982). Consistent with this, the invaded cells remain alive because the plasmalemma invaginates to surround all the individual branches of the arbuscule and the membrane itself is never penetrated. From the infected root, thick-walled, coarse, mycelium comes out, which grows up to several centimeters into the surrounding soil and produces large (about 400 μm diameter), globose, thick-walled spores, sometimes known as chlamydospores. These spores contain lipid droplets, glycogen, proteins, and trehalose. They may be produced singly or in clusters and are often naked, but in some genera (e.g., *Glomus*) they may be covered by a weft of hyphae to form a sporocarp.

In the absence of any morphological proof for sexual reproduction in Glomeromycota, spores are assumed to be formed asexually (Redecker and Schüßler 2014). Although close examination of nuclear passage at the time of spore formation did not show sexual processes, combined studies including microscopic examination and molecular genetics have provided proof for genetic recombination (Sanders and Croll 2010) in the model AMF *Rhizopogon irregularis*. Being obligatorily biotrophic microbes (Schüßler and Walker 2011), AM fungi are unculturable and are not able to complete their life cycle without colonizing a host plant. This has hindered the study of the biology and the biotechnological applications of these fungi (Bago and Cano 2005; Rosendahl 2008).

15.6.4 Significance of Arbuscular Mycorrhizae

15.6.4.1 Absorption of Nutrients

Many studies have shown that the main role of AM fungi is to provide plants with water and mineral nutrients, especially phosphorus from the soil; in return the plant provides the fungus with sugars. Arbuscular mycorrhizal fungi exhibit higher metabolic rate and diffused distribution in the upper soil layers and play a significant role in the uptake and accumulation of minerals from soil and their translocation to the host plant (Bücking et al. 2012). In fact they serve as a very efficient extension of host root system. They absorb both macronutrients (P, N, K, and Ca) and micronutrients (Zn, Cu, and Mn) from soil and translocate them to the host. The mineral nutrients like P, Zn, and Cu, which do not readily diffuse through the soil due to their poor diffusion, become unavailable to host plant. The extraradical hyphae of AM fungi tend to proliferate several centimeters beyond the nutrient depletion zone, increasing the absorbing surface of host root. AM fungal hyphae extend into the soil penetrating the zone of nutrient depletion and enhance the effective uptake of immobile nutrients, therefore managing the deficiency of such elements in host plant. Phosphorus (P) is a vital soil nutrient for normal functioning of plant. The deficiency of P in soil may stop normal growth and development of plant. In terms of plant nutrition, phosphorus is second only to nitrogen as the major mineral nutrient that plants require, and yet phosphorus is a highly immobile element (Turk et al. 2006). When added to soil in the form of soluble phosphate fertilizers, the phosphate ion readily combines with calcium and other divalent cations, to form insoluble inorganic phosphates, or it combines with organic matter to produce insoluble organic phosphates. The natural rate of release of phosphate is thus extremely slow and is often a limiting factor for plant growth. The AM fungi produce extensive hyphal networks in soil, providing a large surface area for absorption of phosphorus. These fungi also release acid phosphatases to cleave phosphate from organic matter (Harrison and van Buuren 1995). They absorb phosphate in excess of requirements and store it in the form of polyphosphates, which can then be released to the plant when required. As a consequence of the enhanced nutrient uptake, the association also increases water uptake, reduces fertilizer input, reduces heavy metal and salt toxicity, etc.

15.6.4.2 Protection Against Pathogens

Plants colonized with AM fungi exhibit increased tolerance against certain root-borne diseases (Borowicz 2001). Several reports indicate positive effects of AM fungi on root-borne fungal diseases like wilt and root rot and stem- and leaf-borne diseases. The severity of nematode infection found to be reduced in the plants colonized with AM fungi (Veresoglou and Rillig 2012; Schouteden et al. 2015). The effects of mycorrhizal fungi on root pathogenic bacteria *Pseudomonas syringae* and tomato showed significant reduction in damage when plants are exposed to mycorrhizal colonization.

15.6.4.3 Salinity Stress

The significance of soil salinity for agricultural yield is huge. Due to the effects of high concentrations of salts on availability, uptake, transport, or physiological inactivation of a given nutrient, plants are deprived of essential mineral nutrients under saline conditions. This in turn causes the decrease in growth rate and net assimilation capacity (Hasanuzzaman et al. 2009, 2013) and also affects photosynthesis and other variables leading to huge losses in productivity (Mathur et al. 2007; Raziuddin et al. 2011). AM fungi alleviate adverse effects of salinity stress and improve salt tolerance of host plants by enhancing selective uptake of nutrients and prevention of nutritional disorder, accumulation of osmoregulators, and enhanced activities of antioxidant enzymes and molecules. AM hypha readily extends the fungal colony, and upon perception of signals from the nutrient ions, it produces branched absorbing structures or spores, which absorb and translocate these nutrients to the host (Hameed et al. 2014). Therefore, under saline conditions, mycorrhizal plants can potentially access nutrients from a larger area than the non-mycorrhizal controls, offering huge benefit to host plants by improving the uptake of essential nutrients.

15.6.4.4 Drought Stress

Arbuscular mycorrhizal fungi have the ability to improve plant biomass and nutrient uptake under drought conditions (Al-Karaki and Zak 2004; Gholamhoseini et al. 2013; Kapoor et al. 2013, Augé et al. 2015). The improved drought tolerance in mycorrhizal plants may be due to enhanced P nutrition, changes in root hydraulic conductance, soil–water relations and increased soil aggregate stability, greater soil available water, improved stomatal conductance and plant–water potential components (Auge 2001). Mycorrhiza-mediated changes in plant–water relations under drought stress conditions may involve complex interactions among multiple mechanisms (Wu and Xia 2003, 2004). However, the primary impact of this symbiosis changes in stomatal conductance and transpiration. Under drought stress, mycorrhizal and non-mycorrhizal plants differentially regulate the expression of several stress-related genes such as aquaporin in root tissue. Aquaporins are membrane intrinsic proteins which facilitate water uptake in plant root, following an osmotic gradient.

15.6.4.5 Heavy Metal

Heavy metals have been found naturally in a variety of habitats including agroecosystems, where these elements constitute a potential hazard for soil and plants. However, some of the heavy metals are serving as essential plant micronutrients such as copper, zinc, iron, and manganese which are required for normal functioning and improved plant growth (Karimi et al. 2011). On the other hand, some of the heavy metals such as mercury, lead, and cadmium have no biological functions but have been reported in plant tissues (Khodaverdiloo and Samadi 2011). Excessive levels of these elements in soil generally affect normal functioning and growth of plant, which, therefore, has been considered a serious matter of concern (Pandolfini et al. 1997; Keller et al. 2002; Voegelin et al. 2003; Kabata-Pendias and Mukherjee 2007). High concentrations of heavy metals in plant tissues influence the structures of enzymes, consequently affecting the structure of proteins and cell membrane, and also the permeability and functions of plants membranes (Giller et al. 1998). Besides, higher accumulation of heavy metals induces oxidative stress, which on the other hand affects plant growth and development.

15.7 Plant Growth-Promoting Root Endophyte: *Piriformospora indica*

The plant–mycorrhiza symbiosis is an integral and essential part of plant growth and development. These symbionts improve the growth of crops in nutrient-deficient soils with lower inputs of chemical fertilizers (Gianinazzi et al. 1995; Varma et al. 1999). In case where native mycorrhizal fungal inoculum is low, inoculation of fungi is the best method. Since AMF are obligate symbionts, they do not grow like any other fungi apart from their hosts. Because of the absence of a reliable pure culture, commercial production is the greatest hindrance in use and application of mycorrhizal biotechnology (Sudha et al. 1999). An adaptable and cultivable plant growth-promoting endophytic fungus, *Piriformospora*, was discovered from the rhizosphere of the woody shrubs *Prosopis juliflora* and *Ziziphus nummularia* in the sandy desert soil of Rajasthan, India (Verma et al. 1998). The fungus lacks host specificity and has been found to colonize monocot as well as dicot roots. It colonizes with a wide range of hosts including bryophytes, pteridophytes, and gymnosperms (Varma et al. 2001; Fakhro et al. 2009; Oelmüller et al. 2009; Qiang et al. 2011). The fungus promotes uptake of nutrients and enhances the tolerance of host plants against biotic (pathogens) and abiotic stresses (salinity, drought, etc.). Inoculation of plants with the fungus improves plant growth and yield (Varma et al. 2012). The fungus, named for its characteristic spore morphology, provides a model organism for the study of plant–microbe interactions and a new means for improving plant production. Molecular phylogenetics have shown that the fungus belongs to Basidiomycota (order Sebacinales, class Agaricomycetes) (Weiβ et al. 2004).

P. indica forms both inter- and intracellular hyphae in the root cortex. Within the cortical cells, the fungus often forms thick hyphal coils or branched structures and spore or vesicle-like structures within or between the cortical cells. Hyphae multiply within the host cortical tissues like AMF and never cross through the endodermis. Fungal spores are multinucleated, and hyphae are dimorphic and have dolipore septum with a continuous and straight parenthesome on either side (Sudha et al. 1999). It improves the overall growth of different grasses, trees, and herbaceous species, and the biggest advantage is that it can be cultivated on a number of complex and synthetic media.

P. indica produces pear-shaped, autofluorescent chlamydospores at the apex of hyphae; these are mostly flat, submerged into the substratum, and white and almost hyaline. The hyphae are thin walled, diameters ranging from 0.7 to 3.5 μm. The mycelia are often twisted and overlap each other, and connections are often observed. The cytoplasm of the chlamydospores is heavily packed with granular materials and usually contains 8–25 nuclei (Varma et al. 2012). Interestingly, the host range of

P. indica is very much similar to that of AMF. *P. indica* colonizes the roots of plants as diverse as *Oryza sativa*, *Zea mays* (Poaceae), *Solanum melongena*, *Nicotiana tabacum* (Solanaceae), *Glycine max*, *Cicer arietinum* (Fabaceae), *Petroselinum crispum* (Apiaceae), *Artemisia annua* (Asteraceae) and *Bacopa monnieri* (Plantaginaceae). Like arbuscular mycorrhizal fungi, *P. indica* has a great potential application in the pursuit of physiological and agronomical useful characters for crop improvement. In contrast to AMF, *P. indica* can be cultivated axenically on synthetic medium. It is therefore often used as biofertilizer and bioprotector in many crop species (Ansari et al. 2014). Its use in agriculture to improve water absorption, mineral uptake, photosynthesis, plant growth and development, and crop fitness has been well studied. The fungus colonizes the orchids resulting in better growth and increased rate of survival of seeds (Singh et al. 2000). The influence of *P. indica* on the growth of *Arabidopsis thaliana* plants under normal and salt stress conditions has been investigated, and it was found that *P. indica* colonization promotes plant growth and development by increasing biomass, lateral root density, and chlorophyll content under both conditions (Abdelaziz et al. 2017).

15.7.1 *Significance of Piriformospora indica*

15.7.1.1 Abiotic and Biotic Stress Tolerance

Piriformospora indica has been shown to enhance plant tolerance to a number of abiotic stresses like salinity, heavy metal toxicity, and low temperature (Baltruschat et al. 2008; Sun et al. 2010; Unnikumar et al. 2013; Ansari et al. 2013). *P. indica* colonization-mediated high-salinity tolerance was reported in *Triticum aestivum* (Zarea et al. 2012), that of drought stress tolerance in *Arabidopsis* seedlings (Sherameti et al. 2008), *Hordeum vulgare* (Waller et al. 2005), and strawberry (Husaini et al. 2012).

Interaction of *P. indica* with a diverse group of microorganisms such as *Pseudomonas fluorescens* (rhizobacteria), *Chlamydomonas reinhardtii*, *Aspergillus niger*, and *Rhizopus stolonifer* has been reported to improve plants against environmental stresses (Pham et al. 2004; Porras-Alfaro and Bayman 2011). Roots of *Hordeum vulgare* (barley) invaded with *P. indica* were found to be resistant against *Fusarium culmorum* infections and in shoots against *Blumeria graminis* (Waller et al. 2005; Deshmukh and Kogel 2007) and reduce the severity of disease caused by *V. dahliae* (Fakhro et al. 2010). The growth of pathogenic fungi such as *A. sydowii* and *R. stolonifer* has been reported to be entirely hindered by *P. indica*.

15.7.1.2 Acquisition of Phosphorous in Plants

Being one of the most essential mineral nutrients, phosphorus plays diverse regulatory, structural, and energy transfer roles (Balemi and Negisho 2012). Plants cannot directly utilize P present in the soil as it is mostly in the form of scarcely soluble complexes affecting therefore crop production (Balemi and Negisho 2012). Plants acquire P from the soil either directly by its own transporters or indirectly through mycorrhizal associations (Yadav et al. 2010). *P. indica* produces considerable amounts of acid phosphatases which facilitate the host plant to get sufficient amount of insoluble or complex forms of phosphate stored in the soil (Singh et al. 2000).

15.7.1.3 Improve Crop Plant Yield

In addition to plant growth and tolerance to biotic and abiotic stresses, the fungus stimulates the excess biomass production, early flowering, and seed production imparting biological hardening to tissue culture-raised plants (Yadav et al. 2010; Das et al. 2012). It improves crop yield by increasing the vegetative tissue yield, number of flowers (Rai et al. 2001; Dolatabadi et al. 2011), or seed weight (Peskan-Berghofer et al. 2004; Barazani et al. 2005). An increase in yield of barley due to a higher number of ears (Waller et al. 2005) and that of number of pods per plant and number of seeds per pod in green gram was found to be higher (Ray and Valsalakumar 2010).

15.8 Conclusion and Future Perspective

Symbiotic relations hold a lot of promise to agricultural industry as there is huge difference in terms of crop yield as the plant growth is proportional to levels of nitrogen and nutrients availability. Symbiosis or mutualism is a good strategy employed by plants for better adaptation and survival in competitive environment. Thus, in this chapter we attempted to highlight the importance of mutualistic plant–microbe interaction, viz., *Rhizobium*, mycorrhizae, and an endophyte *Piriformospora indica*. These endosymbionts are natural biofertilizers that are economical and safer source of plant nutrition compared to chemical fertilizers. The plants show improved growth and development and become resistant to biotic and abiotic stresses. These microbes increase agriculture production and improve soil fertility. Symbiotic association between species provides useful clue to understand evolutionary significance of these species. The evolutionary significance of cheating *Rhizobium* strains and induction of nonproductive nodules yet seem to be a mystery, which needs to be unraveled. Future researches need to be directed to understand various models on this symbiotic interaction and its long-term maintenance during the course of evolution. Thus, use of biotechnological advancements especially in areas of transcriptomics and proteomics can unravel the gene expression patterns in both partners during symbiotic interaction and thus would provide a better insight into the mechanism.

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