Soil Environ. 38(2): 127-150, 2019
DOI:10.25252/SE/19/71659
Online ISSN: 2075-1141
Print ISSN: 2074-9546

Beneficial and pathogenic plant-microbe interactions: A review

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[Received:** September 17, 2018* ***Accepted:** December 04, 2018**]

Abstract

Just like animals and human beings, plants also accommodate a countless number of microorganisms as hosts. Microorganisms enjoy this hospitality by developing an interaction with the plants either in a synergistic way benefiting each other or in an antagonistic manner damaging their hosts. Such types of mutualistic and pathogenic interactions also take place among microbial community. Proteins, metabolites and certain molecular mechanisms determine whether the intruder is a symbiotic or pathogenic microorganism. Various bacteria and fungi interact symbiotically and play significant role in plant growth promotion. Certain species of fungi, oomycetes, bacteria and nematodes are also pathogenic in nature and cause impact on soil and plant. Soil serves as a big substrate for microbial community, which are important in a number of ways owing to their role in mineralization, nutrient availability and are sources of industrial products such as enzymes, hormones, antibiotics, vitamins etc. This review will improve our understanding about relationships between plants and their microbial friends and foes. The mechanisms adopted by soil microbes to contribute in the betterment of soil leading towards enhanced plant growth as well as pathogenicity caused by these microbes have also been discussed. Recent advances to recognize the molecular mechanisms involved in such interactions have also been discussed. Recent advances made in this field and the areas needing further research have also been mentioned.

Keywords: Microbes, interactions, disease, plant, soil, growth

Plant-microbe interactions

Rhizosphere is a zone surrounding the plant roots having maximum microbial activity. Many plant growths promoting microorganisms that are associated with the plant root system depend on root exudates for their survival (Whipps, 1990). Root exudates contain a variety of compounds including polysaccharides and proteins. Microorganisms residing in the soil environment play a major role in ecosystem functioning. Several fungal and bacterial species are present in the rhizosphere. These microbial species interact with each other and with plants. Such interactions may be friendly or hostile as described by a broad range of scientific studies (Saharan and Nehra, 2011; Nadeem *et al*., 2013; Schikora, 2018; Ding *et al*., 2019; Wille *et al*., 2019). The plant-microbe interactions take place above and below ground; however, plant-microbe interactions are more complex below the ground than above the soil surface (Bais *et al*., 2004). The manipulation of these interactions is not only important for understanding the ecological role of microbial population but also for sustainable agriculture.

The interactions among microbial community and plants are very complex. The microbial association with plants is not only useful for improving plant growth under normal condition, but also protects plants from adverse environment by promoting plant growth under stress conditions. Microbes such as mycorrhizal fungi and rhizobia, which associate with plant roots, provide mineral nutrients to plants in exchange of carbon required for their growth. A number of bacterial strains have been reported that cause significant effect on plant growth and development under stressed conditions including salinity, drought, heavy metal, temperature and pathogen (Belimov *et al.* 2005; Trivedi and Sa, 2008; Singh *et al*., 2010; Nadeem *et al*., 2016; Numan *et al*., 2018). Inoculation of BERA71 isolate of *Bacillus subtilis* increased photosynthetic activity and reduced the levels of reactive oxygen species (ROS) in chickpea plants grown in saline soil conditions (Abd_Allah *et al*., 2018). Plant growth promoting strains of *Pseudomonas spp*. were considered as drought tolerant owing to their withstanding a substrate metric potential of -1.0 MPa [30% polyethylene glycol 8000] (Chandra *et al*., 2018). Similarly, mycorrhizae fungi also play important role to facilitate plant growth under various kinds of stresses by mechanisms like enhancing antioxidant system and osmolytes production in addition to supply of nutrients to the host plant (Tang *et al*., 2009; Nadeem *et al*., 2014; Habibzadeh,2015; Quiroga *et al*., 2019).

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It is also evident from literature that microbes interact negatively with plants and cause negative impacts on plant growth. Such negative impacts are due to their pathogenic nature that causes onset of various diseases or by the production of compounds that are harmful for the plants (Xiong and Fuhrmann, 1996; Pamp and Tolker-Nielsen, 2007; Vacheron *et al.*, 2013). The nature of interaction whether it will be friendly, or hostile is determined by the type of microbial specie as well as the mechanism of action adopted by the microbe. For example, cyanide production by some bacteria inhibits plant growth while phytohormones production by a variety of bacterial strains causes plant growth enhancement (Nadeem *et al.*, 2014).

The above discussion shows that plant-microbe interaction is very complex and better understanding of this aspect would be useful for promoting growth and development of plants on sustainable basis. The present review has been undertaken to insight the interactions among microbial community and to further update the knowledge about impact of this community on plant growth and development.

Fungi and oomycetes

Fungi and oomycetes have pathogenic and symbiotic relationship with plants. Plant pathogenic fungi are parasitic, and more than 10,000 species of fungi are pathogenic to plants (Agrios, 2005). Fungi occupy diverse environmental niches. Fungi have diverse lifestyle and having saprophytic, pathogenic and/or symbiotic interactions and boundaries of these interactions are not well defined (Grigoriev, 2013).

Plant pathogenic fungi

Most of the fungal strains also live as pathogen and cause certain diseases in plants. The study on the interactions of plants and phytopathogenic fungi is now becoming one of the most important and interesting subject of plant sciences. These pathogens may be biotrophic, necrotrophic or hemibiotrophic. Biotroph fungi obtain nutrients from living tissues through haustoria and necrotrophic fungi obtain their nutrients after killing the host tissues via enzymes and toxins. While, hemibiotrophic fungi follow the both phases i.e. a biotrophic phase followed by a necrotrophic stage (Pel and Pieterse, 2013; Lo Presti *et al.*, 2015). Owing to their diverse lifestyle they have the ability to colonize plant effectively. Pathogenic fungi cause detrimental effects on plant physiology. Plant fungal pathogens are economically important due to the threats they pose to the growth and production of most of the economically important crops. Agricultural crops, grasslands and forests are losing its economical values due to negative impact of pathogenic fungi in these areas. There is variability among fungal strains regarding severity of pathogenicity. Dean *et al.* (2012) reported the top ten plant pathogens in order of their severity. These include *Magnaporthe oryzae*, *Fusarium oxysporum*, *Puccinia* spp., *Fusarium graminearum*, *Blumeria graminis*, *Botrytis cinerea*, *Mycosphaerella graminicola*, *Colletotrichum* spp., *Ustilago maydis*, and *Melampsora lini.* Annual loss of about 15% has been estimated due to plant diseases caused by fungi (Lo Presti *et al.*, 2015). Some examples of pathogenic fungi along with their specific enzymes and host plant are highlighted in Table 1.

Table 1: Plant pathogenic fungi, enzymes and their host

Fungi	Enzymes	Hosts	References
Monilinia fructicola	Cutinase	Stone fruits	Lee *et al*. 2010
Fusarium solani	Cutinase	Potato	Morid *et al*., 2009
Botrytis cinerea	Cutinase, Lipase	Vegetables, Fruit plants	Choquer *et al*., 2007
Cryphonectria parasitica	Cutinase	Chestnut	Park and Kim, 2004
Didymella bryoniae	Polygalacturonases	Melon	Zhang *et al*., 2014
Colletotrichum gloeosporioides	Pectin lyase, Pectate lyase	Avocado	Miranda-Gomez *et al*., 2014
Aspergillus flavus	Pectinase	Cotton boll	Mellon, 2015
Botrytis cinerea	Endopolygalacturonase	Tomato	Nakajima and Akutsu, 2014
Fusarium compactum	Cellulolytic, Pectinolytic	Broom/rape	Babalola *et al*., 2010
Heterobasidion annosum	Arabinase	Conifer	Asiegbu, 2000
Botrytis cinerea	Xylanase	Trees, Fruit trees	Brito *et al*., 2006
Alternaria citri	Endopolygalacturonase	Citrus	Isshiki *et al*., 2001
Sclerotium rolfsii	Mannanase, Xylanase, Endoglucanase	Potao, Pumpkin, Corn	Sachslehner *et al*., 1998
Cochliobolus carbonum	Xylanase	Maize	Tonukari *et al*., 2000
Rhizopus stolonifer	Amylase	Wheat, Paddy, Bean	Saleem and Ebrahim, 2014
Aspergillus niger	Amylase	Wheat, Paddy, Bean	Saleem and Ebrahim, 2014

Plant beneficial fungi

Plants and fungi have diverse relationship which range from pathogenic to symbiotic association. Mostly mutualism is based on the fact that fungi degrade organic material for availability of nutrients that are otherwise inaccessible to plants. In rhizosphere, plant and fungi communication at molecular level starts as plant secretes amino acids, sugars and organic acids, that activate the fungus to colonize the plant roots. The most well-known symbiotic relationship characterized by the unique morphological growth is called mycorrhizae (fungi roots). Mycorrhizae fungi living either in or on the plant roots are common in forest trees and are associated with more than 90% plant species (Bonfante and Genre, 2010; Delavaux *et al*., 2019). Mycorrhizae also develop in other crops like vegetables, fruits, ornamental plants, and cereals. Fungi benefit plants in terms of nutrients (nitrogen and phosphorus) and water uptake by increasing the root absorption surface area and protection from pathogens (Ziedan *et al*., 2011; van der Heijden *et al*., 2017). In case of endomycorrhizae, the roots are similar to normal plant roots in shape, size and color, whereas hyphae grow into feeder root's cortical cells and form arbuscules (a specialized feeding hyphae) and sometimes vesicles i.e. food storing hyphal swelling. In most of cases, endomycorrhizae having both arbuscules and vesicles, are called as VAM (Vesicular-arbuscular mycorrhizae). In returns, fungi take sugar (carbon) which plant synthesized via photosynthesis. Genes which activate plants' nitrogen transporters for uptake of nitrogen (both as organic and inorganic forms) are also identified in ecto- and endo-mycorrhizae during mycorrhization (Lucic *et al*., 2008; Cappellazzo *et al*., 2008; Guether *et al*., 2009). Plant carbohydrates (mannitol and trehalose) are metabolized by ectomycorrhizae, as most plants cannot metabolize these carbohydrates. Ectomycorrhizae also produce protease enzyme which cause protein degradation from leaf litter. Endomycorrhizal fungi absorb nutrients from soil with extra radicle hyphae and deliver to plant via branched arbuscule (Parniske, 2008). Ammonium transporters are active in cortical cells of plants having arbuscular sites (Kobae *et al*., 2010). The selected examples regarding positive impacts of mycorrhizae on plant growth have been presented in Table 2.

Table 2: Impact of mycorrhizae on plant growth

Mycorrhizal fungi	Crop	Response	Reference
Glomus spp.	*Helianthus annuus*	Fungal inoculation enhanced the root growth and yield of sunflower	Adewole *et al*., 2010
Hymenoscyphus ericae	*Vaccinium corymbosum*, *Calluna vulgaris*	Improve the growth, Improve amino acid uptake	Eccher *et al*., 2009 Sokolovski *et al*., 2002
Acaulospora scrobiculata	*Pongamia pinnata*	Improve seedling growth	Jha *et al*., 2014
Scutellospora heterogama	*Passiflora alata*	Stimulate plant growth and inhibit nematode infection	Anjos *et al*., 2010
Scutellospora fulgida	*Asclepias syriaca*	Improve biomass, foliar P and trichome density	Vannette and Hunter, 2013
Glomus mosseae	*Solanum lycopersicum*	Improve growth and resistance against bacterial wilt	Tahat *et al*., 2012
Glomus clarum	*Cucumis sativus*	Improve yield, P and Zn uptake	Ortas, 2010
Glomus etunicatum	*Citrus aurantifolia*	Improve growth via increase in chlorophyll contents, photosynthesis rate	Shahsavar *et al*., 2016
Glomus intraradices	*Zea mays*	Improve maize seedlings tolerance to low temperature stress	Chen *et al*., 2014
Glomus fasciculatum	*Wedilia chinensis*	Improved total biomass and nutrition uptake	Nisha and Rajeshkumar, 2010
Scutellospora spp.	*Zea mays, Glycine max*	Improve the root and shoot growth	Jeong *et al*., 2006
Archaeosporatrappei	*Plantago lanceolata*	Tolerance to herbivory in the form of an increased growth rate	Bennett and Bever, 2007
Rhizophagus fasciculatus	*Solanum lycopersicum*, *Capsicum annuum*	Improve fruit yield, biomass, P accumulation in shoots	Padmavathi *et al*., 2015
Rhizophagus clarus	*Capsicum annuum*	Improve nitrogen and phosphorus uptake	Lee and Eom, 2015
Funneliformis mosseae	*Morus alba*	Improve growth via increase in chlorophyll contents, photosynthesis rate, stomatal conductance	Shi *et al*., 2016

Trichoderma fungi found as free living and produce antibiotics, compete with other pathogens and act as parasite of other pathogenic fungi (Harman *et al.*, 2004; Srinivas *et al.*, 2017). *Trichoderma* produces auxin related compounds and increases the aerial and root growth of *Arabidopsis* (Contreras-Cornejo *et al.*, 2009). *Trichoderma virens* during symbiotic relationship with maize plant increases the plant photosynthesis rate, produces elicitors that activate defense mechanism in maize leaves systemically (Vargas *et al.*, 2009). *Trichoderma* spp. release bioactive substances and enhances the plant's defense by inducing the local as well as systemic resistance after colonizing epidermis and cortical layer of roots (Harman *et al.*, 2006). This fungus also induces systemic resistance against pathogens (Viterbo *et al.*, 2007). *Trichoderma* spp. also affect the plant genes involved in ethylene biosynthesis, scavenging of reactive oxygen species (ROS), photorespiration, and modulates stomata opening, leaf transpiration via abscisic acid-dependent mechanism (Segarra *et al.*, 2007; Contreras-Cornejo *et al.*, 2015).

Mycorrhizal fungi also play role in the environmental science by forming symbiotic relationship with plants that reduces the nitrous oxide (N_2O) emission from soil and is helpful for environment as N_2O causes destruction of ozone layer. Therefore, this symbiotic relationship shows dual benefits in terms of plant as well as in reducing global warming (Bender *et al.*, 2014). Fungi having symbiotic association with plants also interfere with the insect’s behavior. Symbiotic relationship between fungi and plant brings changes in plant biochemistry which acts positively for plant and negatively for plant pests. Interaction studies proved that *Cucumis sativus* (Cucumber) have symbiotic relationship with fungus *Colletotrichum tropicale* that reduced the foliage damage significantly caused by *Atta colombica* (leaf cutting ant) (Estrada *et al.*, 2013).

Plant pathogenic oomycetes

Oomycetes are most important soil borne plant pathogens after fungi, cause mutilation to agricultural production and natural ecosystem. Oomycetes have unique molecular process for parasitizing their hosts that is different from true fungi but morphologically resembles due to filamentous growth habit. Oomycetes have nine genera, but two genera *Phytophthora* and *Pythium* are pathogenic with a number of species that parasitize a wide range of host plant; however, some saprophytes are beneficial to the environment. *Phytophthora* includes more than 60 species and most of these are pathogens to dicotyledonous as well as monocot plants. The most notable specie is *Phytophthora infestans* which was the main reason for the Irish potato famine. Other *important* diseases caused by *Phytophthora* include; soybean root rot, cocoa black pod and dieback and sudden oak death (Davidson, *et al.*, 2005).

Pythium includes >100 important pathogenic species and some of these are *Pythium aphanidermatum, P. ultimum*, *P. phragmitis, P. litorale, P. dissotocum* and many more near about 125. These are occurring in soil, water, sand and peat as well. Some of these are harmful plant pathogens and cause a number of diseases including rots of seedlings and roots, damping off and decaying of fruits and vegetables (Hayden *et al.*, 2013; Bouwmeester *et al.*, 2018).

Plant beneficial oomycetes

Fighting of beneficial microorganisms with root pathogens and modulating the plant immunity in pathogenic agricultural ecosystem is referred to as positive symbiosis. Some oomycetes like *Pythium oligandrum* reduces the infections caused by pathogenic microbes (Yacoub *et al.*, 2018). *Pythium* protect the plant from pathogen attack directly, through mycoparasitism and antagonism or indirectly by induction of defense responses. *P. oligandrum* uses specific mechanisms to attack its prey. Through the production of microbe-associated molecular patterns, it activates the jasmonic acid and ethylene-dependent signaling pathways. It reduces systemic resistance of the plant against pathogen (Benhamou *et al.*, 2012).

Mycoparasitism that is the ability of a parasite to attack a pathogen is a key component of *P. oligandrum* antagonistic process. *P. oligandrum* interactions with fungal/oomycetes pathogens occur after extracellular sensing mechanism that precedes with attachment and penetration in the host hyphae (Benhamou, *et al.*, 1999). It is observed that *P. oligandrum* transcripts the production of encoding proteases, glucanases, cellulases, protease inhibitors, putative effectors and elicitors which is the first step of mycoparasitism (Horner, *et al.*, 2012). After recognition, the binding of antagonist to the host takes place. The activity of hydrolytic enzymes enhances the degradation of host cell walls that facilitates the entry into cell and provides carbon sources required for active growth and development. On penetration, multiplication of antagonistic cells occurs and *P. oligandrum* forms several papilla-like structures at penetration sites. Owing to this interaction, pathogen's hyphae appear as empty shells with highly altered cell walls and *P. oligandrum* cells can be observed in dead host hyphae. Similarly, *Phytophthora parasitica* interaction with *P. oligandrum* represents the *Phytophthora parasitica* hyphae, exhibiting altered cell walls after mycoparasitm, which proves that *P. oligandrum* synthesize the cellulose in response of pathogen signal. The mechanism of action used by *P. oligandrum* for enhancing plant defense has been presented in Figure 1.

P. oligandrum is considered as a rhizosphere competent that have the capability to extend into root tissues without destroying them. This type of association is useful for the plants as it provides localized and systemic induced resistance to various biotic responses. On invasion by pathogen, sudden degradation of invading hyphae and pathogen's cells gradually degenerates and converted in to empty walled structures. Plant defense reactions are mainly characterized by the formation of discrete wall appositions after establishment of *P. oligandrum* with plant roots. The induction of phenylpropanoid and terpenoid pathways take place that lead to the accumulation of rishitin, a well-known phytoalexin (Le-Floch *et al.*, 2005). After accumulation of phenolics, *P. oligandrum* starts to alter its hyphae and shows positive response as plant defense reactions. The mode of action of *P. oligandrum* shows resemblance with *Trichoderma* which have been considered as an opportunistic symbiotic fungus (Trillas and Segarra, 2009). The concomitantly degeneration of *P. oligandrum* hyphae with the accumulation of plant defense reactions indicates that like the other mutualistic agents those work through the production of effectors-like molecules, *P. oligandrum* is not able to short circuit plant defense responses (Plett, *et al.*, 2011; Zamioudis and Piesterse, 2012).

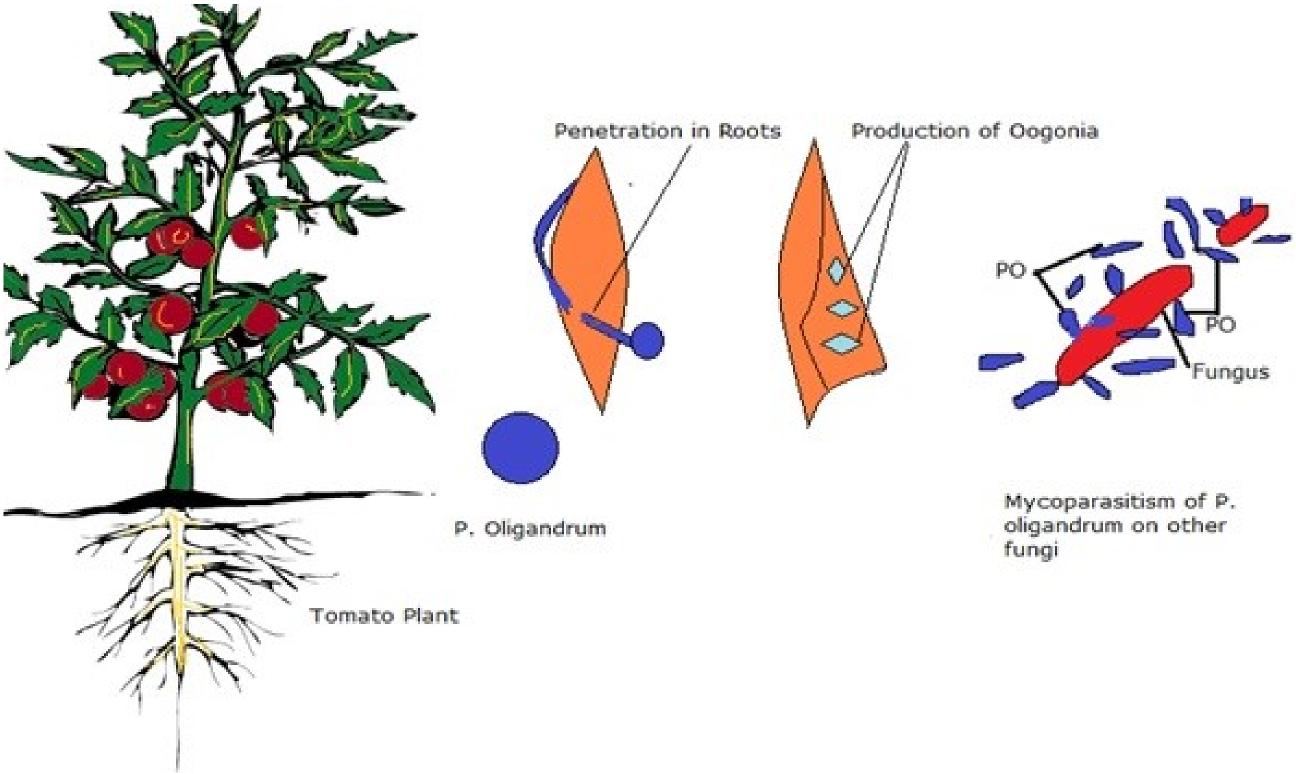

Figure 1: Artificial inoculation of tomato plants to observe the *P. oligandrum* mechanism of penetration in the root's epidermis. Hyphae abundantly colonize the cortex and on pathogen attack provides antagonism and development of host defense responses.

P. oligandrum provides protection to the plants from pathogen infection and induces resistance against bacterial, fungal and oomycetes pathogens. *P. oligandrum* mediated induced resistance in tomato against soilborne pathogen *Ralstonia solanacearum* i.e. a root pathogenic bacterium that causes lethal wilting disease (Genin and Denny, 2012). Increase in beta-1, 3-Glucanase and stilbene synthase transcripts, validates the *P. oligandrum* potential to activate the synthesis and accumulation of defense-related molecules. For example, the production of phenolics and pathogenesis related (PR) proteins which are responsible for reducing the pathogen viability (Abdel-Monaim *et al.*, 2017).

P. oligandrum competes in the rhizosphere with native soil microflora for space in root zone niche and nutrients (Takenaka, *et al.*, 2008). It was observed that the presence of *P. oligandrum* in the rhizosphere doesn't influence the indigenous microflora and fungal populations but reduces the pathogenic *P. dissotocum* population in tomato rhizosphere (Vallance *et al.*, 2009). *P. oligandrum* shifted the pathogenic bacteria in tomato rhizosphere, similarly as other biocontrol microorganisms and non-pathogenic fungal strains do without harming the diversity of non-target rhizosphere microbial groups. *P. oligandrum* is considered as a symbiotic microorganism and its behavior of protecting the plant roots in the rhizosphere is similar to *Trichoderma* species. This oomycete colonizes roots without damaging the host plant cells (Le Floch *et al.*, 2005) and promotes the plant growth and defense mechanism and may be considered as a plant growth promoting oomycetes.

Phytohormones and secondary metabolites synthesized by beneficial microorganisms is a well-documented phenomenon for the plant growth enhancement. *P. oligandrum* produced large amounts of tryptamine (TNH_2) an auxin like compound (Le Floch, *et al.*, 2003). *P. oligandrum* secrete slight but frequent TNH_2 in the rhizosphere which exerts a beneficial effect on plant physiology. TNH_2 secreted by the *P. oligandrum*, is likely to be taken up by plant roots and converted into indole acetic acid (IAA) that ultimately plays a significant role in root elogation.

Plant-bacteria interactions

The microbial population that exists in the rhizosphere depends on root exudates for survival (Whipps, 1990). Due to the presence of such diverse population, this zone is very important from plant growth point of view. A diverse bacterial population is present in the rhizosphere that interacts with the plants. These interactions may be positive or negative ones. All these interactions cause significant impact on plant growth and development. These interactions are based on complex exchanges between both partners i.e.; microbes and plant. The beneficial and harmful nature of these relationships is all regulated by complex molecular signaling (Dardanelli *et al.*, 2010; Zhang *et al.*, 2017).

Plant beneficial bacteria

The plant growth promotion depends upon positive plant-microbe interactions. Among the diverse microbial populations occurring in the rhizosphere, plant growth promoting rhizobacteria (PGPR) are considered to be one of the major organisms owing to their ability to promote plant growth by virtue of their number of growths promoting traits (Mehmood *et al.*, 2018). Among these growth promoting traits, production of hormones, solubilization of nutrients, production of siderophores and exopolysaccharides, nitrogen fixation and presence of very important enzymes like chitinase and ACC-deaminase are well documented in the literature (Nadeem etl. 2010; Glick *et al.* 2014). PGPR belong to some important genera such as *Pseudomonas*, *Bacillus*, *Serratia*, *Enterobacter*, *Erwinia*, *Beijerinckia*, *Klebsiella*, *Flavobacterium*, *Burkholderia* and *Gluconacetobacter* (Podile and Kishore 2006). Some examples of plant growth promotion by bacteria have been presented in Table 3.

These beneficial bacteria not only improve plant growth under normal conditions but also protect the plant from negative impacts like stresses. These bacteria mitigate the stress induced impact by the activity of their ACC-deaminase enzyme, exopolysaccharides production and enhancing the activity of antioxidant enzymes and regulating the nutrient uptake (Glick *et al.*, 2007; Nadeem *et al.*, 2010a). For example, under stress conditions like salinity and drought, a significant increase in ethylene concentration is recorded that causes negative effect on plant growth by inhibiting root growth (Nadeem *et al.*, 2010b). This negative impact of stress-induced ethylene can be minimized by inoculating with PGPR containing ACC-deaminase activity (Glick *et al.*, 2007). Similarly, PGPR having ability to produce exopolysaccharides can be used effectively for protecting the plant from desiccation under water-limited environment (Sandhya *et al.*, 2009). Phosphate and potassium solubilizing bacteria play key role for increasing the availability of phosphorus and potassium to the plant (Archana *et al.*, 2012; Panhwar *et al.*, 2014). In addition to these, the availability and uptake of other macronutrients like Ca, also improves when plants are inoculated with PGPR (Lee *et al.*, 2010).

These PGPR also protect the plant from deleterious impacts of various plant pathogens. This can be achieved either by decreasing the availability of certain nutrients to the pathogen or degrading the cell wall of pathogens. The former is achieved by the production of siderophores that binds iron and makes it unavailable to the pathogen (Bhattacharyya and Jha, 2012). The PGPR can also protect the plant from diseases by degrading the cell wall of the pathogen by the activity of their chitinase enzymes (Beneduzi *et al.*, 2012). Such biocontrol bacteria can lyse a portion of the cell walls of many pathogenic fungi by producing enzymes like chitinases, cellulases, glucanases, proteases, and lipases. They can also mitigate the negative impact of pathogen by enhancing plant resistance against diseases by a mechanism called induced systemic resistance (ISR) (Saravana Kumar *et al.*, 2007). Components of bacteria that can activate ISR include lipopolysaccharides (LPS), salicylic acid, and siderophores (Lugtenberg and Kamilova, 2009). In plant-bacteria interactions, the introduced bacteria initiate a reaction in plant root that results in transfer of signals throughout the plant. This activates the plant defense mechanisms against the pathogen attack. These mechanisms include strengthening cell wall, synthesis of pathogen related proteins and production of anti-microbial phytoalexins (Van loon, 2007).

Plant pathogenic bacteria

Plant growth enhancement is a well-known aspect of the rhizosphere bacteria. However, certain studies show the negative effect of these bacteria on plant growth and development (Saharan and Nehra, 2011; Su slow and Schroth, 1982). This negative impact might be due to production of compounds that are harmful for plant or overproduction of certain growth regulators. Auxin is a well-known hormone that enhances plant growth; however,

Table 3: Effectiveness of plant growth promoting rhizobacteria on plant growth under normal and stress conditions

Improvement in plant growth under normal condition		
Crop	**Response**	**Reference**
Straw Berry (*Fragaria ananassa*)	Inoculation significantly increased fruit yield, plant growth and leaf P and Zn contents of organically grown straw berry	Esitken *et al*., 2010
Potato (*Solanum tuberosum*)	Rhizobacterial strains caused significant impact on potato however showed variable response regarding their ability to promote plant growth	Dawwam *et al*., 2013
Maize (*Zea mays*)	A multi-strain bacterial consortium enhanced the maize growth by increasing the availability of P and K.	Abou-el-Seoud and Abdel-Megeed, 2012
Tomato *(Solanum lycopersicum)*	Application of P and K solubilizing bacteria caused significant effect on tomato growth	Lynn *et al*., 2013
Okra (Abelmoschus esculentus)	Inoculation of bacteria enhanced the root and shoot growth of bacteria.	Prajapati *et al*., 2013
Tobacco (Nicotiana tabacum)	Tobacco growth significantly improved that was due to efficient uptake of K and N in the presence of inoculating bacteria.	Zhang and Kong, 2014
Wheat (*Triticum aestivum*)	Bacteria in combination with biofertilizer enhanced the growth, productivity and net return of wheat	Hussain, 2016
Century plant (*Agave americana*)	Inoculating bacteria caused significant impact on plant growth and sugar content of Agave Americana L. through nutrient solubilizing and phytohormone production ability	Torre-Ruiz *et al*., 2016
Growth enhancement under stress condition		
Tomato *(Solanum lycopersicum)*	Inoculated strains enhanced the root and shoot growth of tomato under salinity stress.	Tank and Saraf, 2010
Mustard Greens (*Brassica juncea*)	Improvement in phytoremediation efficiency of inoculated plant has been observed	Qui *et al*., 2014
Pearl millet (*Pennisetum glaucum*)	Protected the plant from Zn toxicity, temperature and salinity stress by the production of phytohormones and enhancing availability of phosphorus	Misra *et al*. 2012
Wheat (*Triticum aestivum*)	Under salinity stress PPGPR inoculation significantly improved wheat growth by reducing the availability of Na through the production of exopolysaccharides	Upadhyay *et al*., 2011
	An endophytic strain *Burkholderia phytofirmans* PsJN improved wheat growth under drought by improving ion balance	Naveed *et al*., 2014
Maize (*Zea mays*)	Enhanced maize growth by reducing the stress-induced ethylene through their ACC-deaminase activity	Ahmad et al., 2014
Cucumber (*Cucumis sativus*)	Inoculated plant showed better growth under salinity stress compared to uninoculated plants	Nadeem *et al*., 2016
	Inoculated bacteria regulated the growth by altering the level of abscisic acid, jasmonic acid and salicylic contents	Waqas *et al*., 2012
	Improved drought stress tolerance by improving the efficacy of antioxidant system	Wang *et al*., 2012

its positive and negative role is related to its concentration. At low concentration, it improves plant growth (Patten and Glick, 2002) while at high concentration, it inhibits the growth due its negative impact on plant root (Xie *et al.*, 1996). Certain bacterial strains produce cyanide that has inhibitory effect on plant growth and development (Agbodjato *et al.*, 2015). *Pseudomonas aeruginosa* is a well-known strain that have the ability to degrade contaminants; however, it is also an opportunistic pathogen (Mahajan-Miklos *et al.*, 1999). Microbial volatiles are organic compounds that are produced by all microorganisms as part of their normal metabolism. These volatile compounds make a good contribution to the plant-microbe interactions than non-volatile ones. Volatile compounds released by microorganisms may cause inhibitory or stimulating effect (Tirranen and Gitelson, 2006). Weise *et al.* (2013) reported the emission of ammonia that caused the alkalization of the medium and reduced growth of *A. thaliana*. Similarly, the production of dimethyl disulfide, 2-phenylethanol and hydrogen cyanide by bacterial strains acts as phytotoxic volatiles (Blom *et al.*, 2011; Wenke *et al.*, 2012,).

Mechanisms of action used by pathogenic microbes

Fungi

To obtain food for growth, fungi interact with the host plant cell wall that contains substances like minerals, simple sugars, nucleotides and amino acids used by fungi for their growth (Tonukari, 2003). Interaction of fungi with host plant involves their physical contact, followed by different mode of penetration into the host cells. Some fungi apply mechanical force on their host plant surface for penetration. For this purpose, they have to adhere to the host surface with the help of mucilaginous substances present on fungi hyphae. In addition to this, spores of some fungi also contain adhesive substances on their surface which on hydration help to be attached to host surface (Bastmeyer *et al.*, 2002). Tip of hyphae form bulb like structure appressorium that increases the area of attachment and a fine growing point (penetration peg) is developed from appressorium which moves into the cuticle and cell wall. In powdery mildew fungi, turgor pressure of 2-4 MPa is developed in appressoria which is sufficient for penetration into host cell (Agrios, 2005). In some fungi like *Magnaporthe*, *Colletotrichum*, *Alternaria*, *Gaeumannomyces*, *Verticliium* and *Cochliobolus* penetration only takes place if the melanin accumulates in appressorium (Agrios, 2005).

Fungal pathogens are also assisted by specific enzymes like cutinases, lipases, pectin methyl esterases, pectinases, pectin lyases, xylanases, and polygalacturonases to overcome penetration barriers present on site of host (Laluk and Mengiste, 2010; Lionetti *et al.*, 2012). Fungus penetration tube has narrow diameter and thread like structure which when passing through cuticle its diameter increases. Function of these enzymes is to soften the host cell wall or even helps to dissolve host cell wall which makes its penetration easier (Cantu *et al.*, 2008; Tundo *et al.*, 2015). It has been observed that two cellulases enzymes one at the tip of primary germ tube and other at the appressorial germ tube were present that facilitated this penetration (Pryce-Jones *et al.*, 1999).

During the interaction of fungi with host plants different substances are secreted by the fungi i.e.; toxins, polysaccharides, enzymes and growth regulators. The contribution of these substances in pathogenicity varies depending upon the nature of the disease. In soft rots of fruits and vegetables, enzymes affect protoplast components, enhance break down of structural components and inert food substances in cell (Jayani *et al.*, 2005). *Bipolaris* blight disease of Victoria oats is caused by the toxin produced by the pathogen which affects the permeability of cell membranes and protoplast components (Wolpert *et al.*, 2002). Similarly, growth regulators can also enhance the virulence of fungi and such virulence is generally occurring at high concentration of growth regulators (Gohlke and Deeken, 2014).

Most of the time fungi interact with their host at plant surface which is covered with waxy layer. Study at molecular level showed that some fungi like *Puccinia hordei* and *Pestalotia malicola* produce enzymes which degrade cuticular waxes (Hardham, 2007). For the breakdown of cutin, fungi produce cutinases which reduces polymers to monomers and oligomers of the component fatty acid derivatives. These monomers enter the fungi cell and cause triggering of cutinase genes. In response to this, fungi cell produces thousand times more cutinase as compared to earlier (Kim and Rhee, 2003). Several facts showed the involvement of cutinase in fungi penetration via cuticle (Li *et al.*, 2003; Morid *et al.*, 2009). It is also evident from the work of Agrios (2005) that no virulence was observed due to infection of mutant fungi i.e. deficient in cutinase whereas reverse was happening when cutinase was provided on host surface. Cutinase activity increases as the fruit matures ultimately fungus penetrates the fruit. Also, virulent isolate showed more cutinase as compared to avirulent isolate. *Cryphonectria parasitica* which causes chestnut blight also showed that cutinase production is more in virulent strain as compared to hypovirulent strain (Varley *et al.*, 1992). Some fungi require a single cell wall degrading enzyme (CWDE) while others require several CWDEs

(Kubicek *et al.* 2014). *Botrytis cinerea* produces cutinase and lipase enzymes which play crucial role in cutin break down (Choquer *et al.*, 2007) whereas virulence caused by *Fusarium solani* on potato was due to cutinase activity (Morid *et al.* 2009).

Some fungi produce enzymes that degrade pectic substances i.e. major portion of middle lamella. These enzymes are pectin methyl esterases, pectinases, pectin lyases and polygalacturonases. Anthracnose diseases caused by *Colletotrichum gloeosporioides* in avocado fruit occurs due to the production of pectin lyase which is a key virulent factor (Yakoby *et al.*, 2001). *Aspergillus flavus* pathogenicity increases on cotton boll which is controlled by pectinase genes (Shieh *et al.*, 1997). Similarly, endopolygalacturonase enzyme produced by *Botrytis cinerea* cause virulence on tomato host (ten Have *et al.*, 1998). Endopolygalacturonase is also essential factor in pathogenecity of *Alternaria citri* on citrus plants (Isshiki *et al.*, 2001). Plant pathogenic fungi also produces cellulases i.e. cellulose degrading enzymes that help in softening and disintegration of host cell wall which results in penetration of fungi into the host cells and results in disease production (Wilson, 2009). Hemicellulases enzymes (arabinase, galactanase, mannanase, endoglucanase, and xylanase) produced by fungal pathogens that breakdown the hemicellulose and results in fungi penetration within the host plant (Brito *et al.*, 2006). Fungi belonging to ascomycetes and basidiomycetes fungi produce lignin decomposing compounds which enable them to cause disease (Dashtban *et al.*, 2010). Similarly, several fungi produce amylases for starch breakdown, lipases and phospholipases for lipids breakdown (Gurung *et al.*, 2013; Saleem and Ebrahim, 2014). Virulence of *Fusarium compactum* on broomrape infection is enhanced with addition of cellulolytic and pectinolytic enzymes which help the fungi in host penetration (Babalola *et al.*, 2010).

Table 4: Toxin production by plant pathogenic fungi

Fungi	Toxins	Hosts	References
Alternaria alternata	Tentoxin	Brassica chinensis	Pusztahelyi *et al.*, 2015
Cercospora zeae-maydis, *Cercospora zeina*	Cercosporin	Corn, Zinnia	Benson *et al.* 2015
Pyricularia grisea	Pyricularin	Rice	Pooja and Katoch, 2014
Ophiostoma ulmi	Ceratoulmin	Dutch elm	Khoshraftar *et al.*, 2013
Fusicoccum amygdali	Fusicoccin	Almond, Peach	Michalak *et al.*, 2005
Cochliobolus victoriae	Victorin/HV toxin	Oat	Friesen *et al.*, 2006
Cochliobolus carbonum	HC toxin	Maize	Wight *et al.*, 2013
Cochliobolus heterostrophus race T	T toxin	Maize	Wu *et al.*, 2012
Alternaria alternata pathotypes	AAL toxin	Tomato	Akagi *et al*, 2009
Alternaria alternata pathotypes	ACRL toxin	Rough lemon/Citrus	Chung, 2012
Alternaria alternata pathotypes	AM toxin	Apple plant/ European pear	Harimoto *et al.*, 2007
Alternaria alternata pathotypes	AK toxin	Japanese pear fruit	Shimizu *et al.*, 2006
Pyrenophora tritici-repentis	Ptr toxin	Wheat	Day *et al.*, 2015
Stemphylium vesicaarium	SV toxin	European pear	Puig *et al.*, 2014
Rhizopus stolonifer	Fumaric acid	Almond	Teviotdale *et al.*, 2001
Cryphonectria parasitica	Oxalic acid	Chestnut	Chen *et al.*, 2010

Toxins affect the host plant cell's protoplast, by disturbing cell membrane permeability, inhibiting enzymes production and various biochemical and metabolic reactions taking place in the host cell (Daub *et al.*, 2005). Toxins that affect a specific host species are called host specific/selective toxins, while those affecting non-host plants are called non-host specific/selective toxins (Lee, 2010; Tsuge *et al.*, 2013). Host selective toxins are one of the prerequisites for the microorganism to cause the infection. A number of fungi (*Alternaria, Phyllosticta, Hypoxylon, Periconia, Corynespora* and *Cochliobolus*) are able to produce host specific toxins. Some important toxins produced by the fungi have been presented in Table 4. *Alternaria alternata* produces tentoxin which causes chlorosis and spots in host plants (Ramm *et al.*, 1994). Tentoxin affects the protein which is important for energy transfer into chloroplast. Phosphorylation in which ADP is converted into ATP is also inhibited by tentoxin. Tentoxin inhibits the function of polyphenol oxidase which plays significant role in resistance mechanisms of host plants. *Alternaria alternata* also produces host selective toxins, which target the four sites of cellular components i.e. metabolically important enzymes, mitochondrion, chloroplast and plasma membrane (Tsuge *et al.*, 2013). Cercosporin is a toxin which is activated with light absorption and then reacts with oxygen molecule and produce oxygen reactive species that reacts with nucleic acids, lipids and proteins of the cells and enhance the virulence. *Cercospora* and other fungi produce cercosporin (You *et al.*, 2008) that causes blight and leaf spot diseases like gray leaf spot of corn and Cercospora leaf spot of zinnia. Victorin or HV-toxin produced by *Cochliobolus victoria*, affects the oat variety Victoria (Friesen *et al.*, 2006). Primary target of the toxin is plasma membrane where it binds with proteins and affects its synthesis. It also accelerates the respiration, modified cell wall structure and causes loss of cellular electrolytes.

HC-toxin is produced by the race 1 of *Cochliobolus carbonum* fungus that causes two important diseases in maize crop i.e. ear rot and northern leaf spot. T-toxin is produced by fungus *Cochliobolus heterostrophus* race T (Wu *et al.*, 2012). Toxin was named as T toxin because of its production by only race T. This race is different from other races of *C. heterostrophus* because only this race produces T toxin. Toxin affects the ATP synthesis and mitochondria. Interesting fact about this fungus is that it attacks only maize varieties having Texas male-sterile cytoplasm (Horwitz *et al.*, 2013). Similarly, fungus also produces other toxic compounds which are host specific. For example, HS toxin against sugarcane crop, AAL toxin against tomato crop producing stem canker symptoms (Akagi *et al.*, 2009), ACRL toxin on rough lemon which causes metabolite leakage, disturb mitochondrial function, interfere with oxidative phosphorylation and posttranscriptional RNA splicing (Akimitsu *et al.*, 1989; Ohtani *et al.*, 2002). AK toxin that causes black spot on Japanese pear (Okada *et al.*, 2000) and AM toxin that causes loss of electrolytes by affecting the cell wall and plasma membrane of apple plant (Harimoto *et al.*, 2007) is other examples of toxins produces by fungi.

Growth regulators like cytokinins, auxins, gibberellins, abscisic acid (ABA) and ethylene are naturally occurring compounds produced by both plant and microorganism. These are required in a minute amount and any hormonal imbalance causes a serious change in plant growth patterns. Like plant, fungi also produce host specific substances that may accelerate or inhibit the host's normal growth. Plant pathogenic fungi cause number of plant diseases either due to disruption in host's growth regulators production or hormones produced by the fungi themselves (Carris *et al.*, 2012). Host shows different abnormal response like, phyllody, leaf epinasty, stunting, stem malformation, rosetting, and excessive root branches.

Diseases like corn smut (*Ustilago maydis*), pine western gall rust, cedar apple rust (*Gymnosporangium juniper-virginianae*), azalea leaf and flower gall (*Exobasidium azalea*), banana wilt (*Fusarium oxysporum* f. sp. *cubense*), lime anthracnose (*Colletotrichum acutatum*) occur due to disturbance in the indole acetic acid (IAA) level in their hosts. This disturbance sometimes results due to inhibition of IAA oxidase, which ultimately results in increase in IAA level (Yin *et al.*, 2014; Ludwig-Muller, 2015). *Magnaporthe grisea* produces IAA on rice infection and causes the host to produce its own IAA which induce the expansins (cell wall loosening protein) production, that ultimately loses the cell wall and other host barriers for microorganism (Jing *et al.*, 2011).

Pathogenic fungi like *Ustilago maydis, Fusarium oxysporum, F. chlamydosporum, Botryodiplodia theobromae* produce gibberrellins during their infection process (Tsavkelova *et al.*, 2006). *U. maydis* induces tumours due to gibberrellins on vegetative and inflorescence parts (Schirawski *et al.*, 2006; Brefort *et al.*, 2009). *Sporisorium reilianum* produces gibberellin and causes head smut of sorghum (Ghareeb *et al.*, 2011). Cytokinins like zeatin and isopentenyl adenosine are also found in plants. Different plant pathogenic fungi from genera *Taphrina, Uromyces* and *Schizophyllum* also produce cytokinins (Tsavkelova *et al.*, 2006). An increase in cytokinins level rust and smut galls and in bean leaves infected with rust was observed (Stirk*et al.*, 2006; Connor *et al.*, 2012). However, low cytokinin level in cotton plants infected with *Verticillium* wilt has also been observed (Xu *et al.*, 2011).

Ethylene production by fungi also affects the root growth and causes root infection. *Fusarium oxysporum, Pythium ultimum,* and *Penicillium cyclopium* inhibit the root elongation and produce disease symptoms due to production of ethylene in rhizosphere region (El-sharouny, 1984). It is suggested that ethylene acts as germination inducing factor for conidia of the *B. cinerea* (Chague *et al.*, 2002). Similarly, ABA plays important role in the mycelial growth acceleration of the fungi and therefore, play crucial role in fungi development on host plant (Janitor *et al.*, 2002). Abscisic acid (ABA) is produced by a number of pathogenic fungi including *Aspergillus niger, Botrytis cinerea, Cercospora spp. Cladosporium cladosporioides, Schizophyllum commune* act as plant growth inhibitor (Siewers *et al.*, 2004; Tsavkelova *et al.*, 2006; Hartung, 2010).

Oomycetes

The mechanism of pathogenesis of oomycetes is not fully understood as the interaction of oomycetes with plant roots occurs in soil, however, few studies have revealed the possible mechanism of pathogenic interactions of oomycetes with plants. These interactions include penetration within plant cells, re-differentiation of host cells to establish intracellular interfaces for nutrients and exchange of information with coded effectors proteins. Similarly, as AM fungi is surrounded by peri arbuscules membrane spiked with phosphate transporter and haustoria of *Phytophthora* enveloped by extra haustorial membrane. Haustoria of pathogenic *Phytophthora* facilitate the deployment of pathogen-encoded effector proteins. A chemical talk of *P. palmivora* and host plant roots is developed. Host plant produces cutin-derived signal for the interaction of both *P. palmivora* and AM fungi. Both microbes germinate and form the attachment and penetration structures, appressorium and hyphopodium, respectively. In case of AM fungi, intracellular hyphae are supported by a plant-derived pre-penetration apparatus. Specialized intracellular interfaces, haustoria and arbuscules formed within plant root cells in *Phytophthora* and AM fungi, respectively. *P. palmivora* and AM fungi follow the analogues mechanism of roots interaction under the soil (Figure 2). But *P. palmivora* pathogen-encoded factors enables colonization on host roots which in turns leads to the cell death, *Phytophthora* species are considered as necrotrophs.

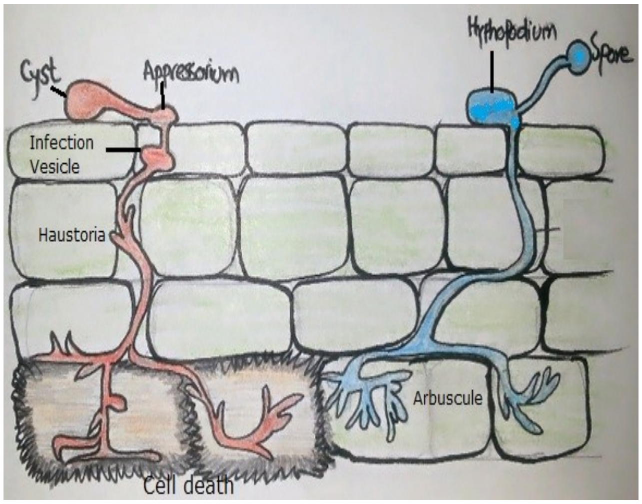

Figure 2: *Phytophthora palmivora* and arbuscular mycorrhizal (AM) fungi analogous mechanism to establish a root interaction with host plant

Pythium infection is mainly limited to meristematic tips, epidermis, cortex of roots and fruits, but occasionally deeper into the plant tissues and reaches the vascular system. *Pythium* species produce variety of propagules including oospores, sporangia, hyphal swellings, motile zoospores and zoospores cysts in regulatory control of plant root exudates. Some species are not able to produce all stages while some can produce all of these stages (Van der Plaats-Niterink, 1981; Kuznetsova *et al*., 2018). Along with oospores, sporangia are the most persistent in rhizosphere, even in host absence for a long period. Root exudate in rhizosphere attracts different spp. of *Pythium* as other pathogenic or beneficial microorganisms do. *Pythium* spp. in turn rapidly produce oospores or zoopores and infect the plant root tissues after penetration through their germ tubes on roots of the host plants. A key requisite step in *P. ultimum* is thinning of oospores, enhance the formation of germ tube which leads to early root infection. Unsaturated fatty acids present in seed exudates are primary elicitors of *P. ultimum* in soil for sporangium germination, which stimulate the pathogenesis of *P. ultimum* against the seeds, roots and root exudates. Sporangium releases zoospores which are attracted to glutamic acid of roots and accumulate in the root hair region and zone of cell elongation just behind the root cap and germinate within minutes. All these oospores, sporangia, cysts and zoospores increase the inoculum potential on roots for infection. Once infection starts, it proceeds rapidly on roots or seeds and colonizes the whole infected surface.

Bacteria

Bacteria can cause plant infection by multiple ways. Infection may take place passively where bacteria can enter through natural plant opening like stomata or hydathodes. Entry of bacteria into plant can also take place through abrasion and wounds on roots, stem or on leaves. Entry of bacteria also takes place by placement of specific feeding insects and by seed immersion into inoculum. After entry of bacteria, the attachment of bacteria to the host cell takes place. Adhesion of bacteria to host surfaces is a crucial aspect of host. Polymeric hair like organelles called pili are involved in the adhesion of bacteria to the host. In addition to pili, certain bacterial surface factors with adhesive properties also play role in bacterial binding with host (Pizarro-Cerda and Cossart. 2006; Kline *et al.*, 2009). Nutrient conditions in plant favor or inhibit the multiplication of bacteria in plant parts. After colonization, disease symptoms appear in the form of wilts, spots, blights, cankers and galls. Bacterial infection is caused by both types of bacteria including proteobacteria and actinobacteria. Virulence factors which determine disease severity are the most important characteristics of the bacterial pathogens. The major virulence factors include type I to VI secretion system, extracellular enzymes, polysaccharides, plant hormones and toxins. The use of these virulence factors varies with bacterial species. For example, *Pseudomonas* and *Xanthomonas* usually do not use the plant hormones as virulence factors whereas *Xanthomonas* secrete exopolysaccharides (EPS). It was observed that mutants of *Xanthomonas* which lack the ability to produce EPS usually lose their virulence function (Frederick *et al.*, 2001). Pathogenic Gram-negative bacteria use the T3SS and exopolysaccharides are secreted by both Gram-negative and Gram-positive bacteria. For effective infection, some bacteria secrete extracellular enzymes to degrade plant cell wall that is the first barrier of protection against pathogen attack. *Erwinia carotovora* use cell wall-degrading enzymes as the main virulence factors. Toxins produced by pathogenic bacteria are secondary metabolites that affect physiology and biochemistry of host plant. Leaf scald disease of sugar cane caused by *Xanthomonas albilineansis* is due to a toxin i.e. albicidin that is major pathogenicity factor in *X. albilineans*.

The secretion system is a distinct pathway that pathogenic bacteria use to secrete protein involved in virulence across the membrane. Currently six classes of secretion system type I to type VI (T1SS to T6SS) have been identified. In T1SS, bacteria export molecules form cytosol to external environment without periplasmic step (Deleperaire *et al.*, 2004) while in T2SS, proteins translocate across the inner membrane to the periplasm and then external environment. Gram negative and Gram-Positive bacteria use T1SS and T2SS pathway, respectively. T3SS system that is used by many bacterial species directly translocates toxin protein into cytoplasm of host plant (Lindeberg *et al.,* 2012). The T4SS present in Gram positive and negative transport pathogenicity factor from inner bacterial cell to external environment or directly to host cell (Judd *et al.,* 2005). The type V secretion system is the simplest secretion pathway that is widely present in Gram negative bacteria (Tseng *et al.,* 2009). In this pathway, the protein is transferred in two steps. First step is mediated by secondary translocator across the inner membrane and in second step transportation occur through outer membrane by forming a protected module (Van Sluys *et al.,* 2002). T6SS is a new system which ejects effector protein directly into the host cell or in the extracellular mileu (Tseng *et al.*, 2009; Pukazki *et al.*, 2007).

Mechanism of infection caused by the bacterial toxins is different from T3SS in a way that no host specificity is required in case of toxin virulence (Appelmelk *et al.*, 1996). Exopolysaccharides protect the bacteria from environmental stresses and cause pathogenicity by altering the accessibility of antimicrobial compounds and blocking the xylem (Denny, 1995).

Plant defense against pathogenicity

When pathogens come in physical contact with host, specific signals are received by the host plant indicating the presence of pathogens. These signals are very important for host in activation of its defense system. In order to protect themselves from pathogens, plants have self-defense mechanism consisting of chemical and biochemical substances which are produced when pathogen interact with plant. Certain defense substances are already present prior to infection so called pre-existing defense chemicals. For example, toxic exudates are present in sugar beet and tomato leaves against *Cercospora* and *Botrytis* spores (Agrios, 2005). Red scale onion contains catechol and protocatechuic acid against fungus *Colletotrichum circinans* that causes onion smudge disease (Lubaina and Murugan, 2013). These substances cause the bursting of conidia after spore entry. Dienes, tanins and several phenolic compounds exist in high concentration in seeds, fruits and leaves of plants which offer resistance against phytopathogens like *Botrytis*. Catechin is present in strawberry leaves which protects host from *Botrytis cinerea* (Puhl and Treutter, 2008). Similarly, avenacin in oats (Owatworakit *et al.*, 2013), dehydrotomatine, and alpha-tomatine in tomato (Nobuyuki *et al.*, 2004) and saponins in different monocotyledons (Yang *et al.*, 2006) are antifungal compounds. Plants surface also contain hydrolytic enzymes like glucanases and chitinases which breaks down fungi cell wall components (Patil *et al.*, 2000; Van den Burg *et al.*, 2006).

Fungi produce different nonspecific elicitors like proteases, toxins, pectic enzyme, fatty acids, glycoproteins, carbohydrates and specific elicitors like suppressor molecules, *avr* gene products, *hrp* gene product which play role in pathogen and host recognition (Van Loon and Van Strien, 1999). During host pathogen interaction, elicitors from pathogen interact with specific molecules in host called as receptors. So, disease is established when plants having receptor sites recognized by the pathogen elicitors and plants lacking such sensitive sites remain disease free. For example, in wheat powdery mildew caused by *Blumeria graminis* f. sp. *tritici* produces carbohydrate which acts as elicitor and thaumatin like proteins act as receptor molecule, and *PmHNK* gene of wheat is involved in host resistance (Li *et al.*, 2013). After the recognition of elicitors and receptors, series of biochemical and structural modifications occur in plant cells. These changes act as signal for different genes to be activated in this response. Molecules involved during intracellular signal transduction are ethylene, ATPases, protein kinase, hydrogen peroxide, calcium ions, phospholipases, and phosphorylases (Stone and Walker, 1995; Tuteja and Mahajan, 2007). These changes finally determine whether host acts as resistant or susceptible against that specific pathogen. Ethylene, jasmonates, fatty acids, salicylic acid, jasmonic acid, oligogalacturonides and systemin are involved in systemic signal transduction in plants (Turner *et al.*, 2002; Savatin *et al.*, 2014; Wang *et al.*, 2018; Cortleven *et al.*, 2019). Hormone levels of plants are adjusted in response to the microbial colonization and propagation. Phytohormones have also been found interacting with various endophytic microbes including endophytic fungi. Recently the role of phytohormones including auxins, cytokinins, giberellins, ethylene, abscisic acid, jasmonates and brassinosteroids in the interaction of *Piriformospora indica* with higher plant species has been reviewed (Xu *et al.*, 2018). Phytohormones act as key players in plant defense against pathogens, revealed by the studies in model plants such as *Arabidopsis thaliana.* Co-evolution of phytohormone signaling pathways and the phytocolonization of land suggests a likely requirement for plant adaptations to an environment which included pathogens as well (Berens *et al*., 2017). Regulated amount of these hormones in plant cells is the key factor responsible to halt an infection (Tezuka *et al*., 2019). Elevated levels of auxins or auxin signaling in infected host tissues promote various pathogenesis related processes including colonization of epiphytic microflora, hyperplasia (e.g. gall formation), inhibition of host defenses and spread of pathogen in host tissues (McClerklin *et al*., 2018; Kunkel and Harper, 2018). Ye *et al*. (2019) have recently found that the balance between root growth of maize and stalk rot disease is managed by an auxin regulated protein *ZmAuxRP1*.

Plants that have structural defense owing to thick and hard cuticle, waxes, and spines form defense structures after host recognition like, cell wall defense structures (Van Kan, 2006; Mendgen and Hahn, 1996), cytoplasmic defense reaction, and histological defense structures (Okubara and Timothy, 2005; Amil-Ruiz *et al.*, 2011). During cell wall structures callose papillae deposits on cell wall inner side, cell wall thickening along infusion with phenolic compounds (Jacobs *et al.*, 2003; Ton and Mauch-Mani, 2004). In cytoplasmic defense reaction, nucleus either breaks into two or enlarges, protoplast disappears, cytoplasm enlarges, and become granular (Abdel-Fattah *et al.*, 2011). Histological defense structures include formation of corky layers around point of infection. e.g. potato tuber infected with *Rhizoctonia*, formation of abscission layers, tyloses formation in xylem, gum deposition in stone fruits (Kitin *et al.*., 2010).

Secondary metabolites that are toxic to fungi are produced after infection. Ferulic acid, sinapic acid, curcuminoids, caffeic acid, chlorogenic acid, coumarins, stilbenes, hydroxybenzoic acid are phenolic compounds toxic to fungi (Abad *et al.*, 2007; Huang *et al.*, 2009). *Monilinia fructicola* infection in peach brown rot disease is inhibited by chlorogenic acid (Lee and Bostock, 2007). Sinapic acid, *p*-hydroxybenzoic acid, ferulic acid, and *p*-coumaric acid in date palm inhibit *Fusarium oxysporum* infection (Modafar and Moustani, 2001). During *Mycosphaerella fijiensis* infection of banana phenylalanine ammonia lyase (PAL) is produced by resistant plants and inhibits infection (Alvarez *et al.*, 2013). Phenol oxidizing enzymes oxidize phenols to quinones that is more severe than phenolic compounds. Phytoalexins are toxic compounds against fungi produced after pathogen infection or by chemical and physical injury. Pisatin in pea against *Ascochyta pisi* (Morkunas *et al.*, 2013), gossypol in cotton against roots infecting fungi (Mellon *et al.*, 2010), glyceollin in soybeans against *Phytophthora sojae, Macrophomina phaseolina,* and *Sclerotinia sclerotiorum* (Lygin *et al*, 2010) are other examples of toxins produced by plant against pathogens.

Conclusion and future prospects

The above discussed review examines the interactions taking place among the microbial community as well as with the plant. It is evident from the above discussed review that these interactions may be parasitic, mutualistic, commensal and/or pathogenic. These interactions cause significant impact on plant growth. The understanding about these interactions is very important from plant growth point of view. The present review indicates that the most microbial communities are complex and consisting of a number of species those interact with each other and also with other microbial population existing in the environment. In addition to interactions among microbial community, many insects also interact with microbes and play significant role in nutrient acquisition. Due to complex nature, validation of microbial interaction is very difficult if not possible. The literature shows that none of the mechanisms are necessarily exclusive and exhibited by a single strain. A microbial strain may be benefited in one environment can show negative behavior in other environment or when interact with some other microbes. The understanding of these interactions as well as mechanism of action is very important for getting benefits and sustainability of environment system. Based on above discussion it came to know that microbial infection, virulence and pathogenicity is a multi-factorial phenomenon.

In order to gain better understanding about microbial interactions, there are still many aspects that need to be explored. For effective control of microbial pathogenicity, the nature of pathogen, its virulence factors as well as its interaction with host defense mechanism needs to be explored. Further study of virulence factors at molecular level is required to know their contribution in plant pathogen interaction. There is also a need to explore how interactions influences ecosystem processes.

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