Review

Is the rhizosphere a source of applicable multi-beneficial microorganisms for plant enhancement?

Imane Chamkhi [a,b,*], Nasreddine El Omari [c], Abdelaali Balahbib [d], Naoual El Menyiy [e], Taoufiq Benali [f], Cherki Ghoulam [b,g]

[a] Geo-Biodiversity and Natural Patrimony Laboratory (GeoBio), Geophysics, Natural Patrimony Research Center (GEOPAC), Scientific Institute, Mohammed V University in Rabat, Morocco
[b] University Mohammed VI Polytechnic, Agrobiosciences Program, Lot 660, Hay Moulay Rachid, Benguerir, Morocco
[c] Laboratory of Histology, Embryology, and Cytogenetic, Faculty of Medicine and Pharmacy, Mohammed V University in Rabat, Morocco
[d] Laboratory of Zoology and General Biology, Faculty of Sciences, Mohammed V University in Rabat, Rabat, Morocco
[e] Faculty of Science, University Sidi Mohamed Ben Abdellah, Fez, Morocco
[f] Environment and Health Team, Polydisciplinary Faculty of Safi, Cadi Ayyad University, Safi, Morocco
[g] Cadi Ayyad University, Faculty of Sciences and Techniques, PO Box 549, Gueliz, Marrakech, Morocco

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ABSTRACT

The plant faces different pedological and climatic challenges that influence its growth and enhancement. While, plant-microbes interactions throught the rhizosphere offer several privileges to this hotspot in the service of plant, by attracting multi-beneficial mutualistic and symbiotic microorganisms as plant growth-promoting bacteria (PGPB), archaea, mycorrhizal fungi, endophytic fungi, and others...). Currently, numerous investigations showed the beneficial effects of these microbes on growth and plant health. Indeed, rhizospheric microorganisms offer to host plants the essential assimilable nutrients, stimulate the growth and development of host plants, and induce antibiotics production. They also attributed to host plants numerous phenotypes involved in the increase the resistance to abiotic and biotic stresses. The investigations and the studies on the rhizosphere can offer a way to find a biological and sustainable solution to confront these environmental problems. Therefore, the interactions between microbes and plants may lead to interesting biotechnological applications on plant improvement and the adaptation in different climates to obtain a biological sustainable agricultures without the use of chemical fertilizers.
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1. Introduction

The rhizosphere is the area of the soil influenced by plant roots, where plant roots and soil composition interact with each other (Lynch and de Leij, 2012). It represents a dynamic hotspot for interactions between roots and beneficial, as pathogenic soil microbes.

However, it is a gathering of several microorganisms such as bacteria, archaea, fungi, nematodes, protozoa, and other organisms that interact with each other, some are beneficial whereas others are harmful (Pathan et al., 2020). May be considered beneficial or neutral, or harmful to the plant, depending on the specific microorganisms and plants involved and on the prevailing environmental conditions (Jones and Hinsinger, 2008).

Roots exudates such as sugars, amino acids, organic acids, phenolic compounds, enzymes, phytohormones, and vitamin can attract several microorganisms, and can also act as signal molecules mediating interactions in the rhizosphere (Olanrewaju et al., 2019). The chemical signaling, between plant roots soil organisms, and the neighboring by plant roots may elicit dissimilar responses from different receivers (Canarini et al., 2019). Indeed, the chemical components of root exudates may deter some microorganisms, while attracting another organism, may be classified as either positive associations (mutualistic or symbiotic associations) or negative associations (competition, parasitism among plants or pathogenesis) (Bais et al., 2006).

In general, in the rhizosphere, the negative associations express virulence on only a limited number of host species and it is estimated that only about 2% of the known fungal species are able to colonize plants and cause diseases (Nihorimbere et al., 2011).

Otherwise, the microbial interactions in the rhizosphere are often of benefit to plants, improve soil fertility, enhance the degradation of toxic chemicals (Lynch and de Leij, 2012; Xiong et al., 2020) and the secondary metabolites induction of the plant (Chamkhi et al., 2021). However, root-associated microbiota in the rhizosphere play important roles and positively influence the health and the growth of their host plant through various mechanisms. The promotion of plant growth by microorganisms is based on a better acquisition of nutrients, hormonal stimulation and several direct or indirect mechanisms linked to plant growth, and could be involved in the reduction/suppression of plant pathogens (VelÃzquez et al., 2005; Berg, 2009).

Plant-beneficial microbial interactions can be roughly divided into four categories: (i) the microorganisms in association with plants, are responsible for its nutrition, (ii) the microorganisms that stimulate plant growth indirectly by preventing the growth or activity of pathogens, (iii) the microorganisms responsible for direct growth promotion, for example, by the production of phytohormones (Nihorimbere et al., 2011; Okon et al., 2015).

Indeed, the most root microbial associations in the rhizosphere are bacterial associations or rhizobacteria. They provide benefits to the plant resulting in its growth stimulation and are recognized as plant growth-promoting rhizobacteria (PGPR) (Bais et al., 2006; Okon et al., 2015). The PGPR can be divided into two groups according to their residing sites: first, symbiotic bacteria, which live inside the plant cells in produced nodules (Hayat et al., 2010) as rhizobia-legume interactions leading to establishment of atmospheric nitrogen fixing symbiose in root nodules as for *Sinorhizobium meliloti-* alfalfa and *Rhizobium leguminosarum-* faba bean (Bais et al., 2006; Masciarelli et al., 2014). On the other hand, the second group is free-living rhizobacteria, which live outside the plant cells and did not produce nodules. But still, prompt plant growth promotors such as *Azotobacter, Azospirillum, Bacillus*, and *Klebsiella* sp. are also used as biofertilizers to inoculate a large area of arable land in the world to enhance plant productivity (Dobbelaere et al., 2001; Vessey, 2003; Hayat et al., 2010). Indeed, the bacteria in the rhizosphere or rhizobacteria or plant promoting rhizobacteria (PGPR) can play an important role in the growth, the health, and in promoting nutrient acquisition by plants *via* several beneficial direct and indirect mechanisms (Singh et al., 2011).

Contrary to the rhizobacteria, the Archaea is much less in the rhizosphere. They were discovered especially in extreme environments, known to be essential actors in global processes, such as nitrification and ammonification in soils (Leininger et al., 2006). Furthermore, plant-fungal interactions include mycorrhizal fungi (MF) that interact in symbiosis with the roots of the plant and endophytic fungi that live inside living tissue of leaves, stems, or roots (Zeilinger et al., 2016). Likewise rhizobium bacteria, fungi can form symbiotic associations with plants, known as a mycorrhizal association, in which the interaction is between mycelial fungi and plants. Contrary to legume-rhizobia association, the mycorrhizal association is pervasive and can colonize nearly 80% of angiosperms and all gymnosperms plants. This mutualistic association can provide to the plant, phosphorus, water, and other micronutrient acquisitions by increasing the root surface. In return, the fungi receive fixed carbon from the host plant (Datta et al., 2020). On the other hand, endophytic fungi have been detected

in hundreds of plants and different studies demonstrated that they produce a large number of interesting secondary metabolites with interesting proprieties which can be used as a natural bioactive source (Aly et al., 2010; Chamkhi et al., 2018).

As mentioned earlier, the rhizosphere is a hotspot gathering of several organisms such as protozoa and nematodes, that can play an important role complementary to the role of bacteria and fungi, as the remobilization of nutrients from consumed bacterial biomass, the nutrient mineralization in soil, and enhanced plant N uptake, and offered a strong stimulation of lateral root growth in presence of protozoa (Bonkowski and Clarholm, 2012).

This review focuses on the rhizosphere, particularly microbe and root interactions, the principal interactions that could play a very important role in the growth and the health of the plants and their applications, including some examples of how these interactions can be affected and used to improve crops of sustainable agriculture.

2. The rhizosphere : Derived from close soilplant association

The interaction of soil physicochemical properties and plant root exudates can determine the composition of microbial communities associated with roots in the rhizosphere (Fig. 1), and can also be selecting a specific microbial composition by creating niche environments. Although, soil pH and nutriments availability affect the abundance of crop pathogenic bacteria, fungi, and nematodes as well as beneficial microbes (Dumbrell et al., 2010). In addition, soil interactions with plant root exudates can create a rhizosphere environment that gradually alters the soil biome to promote the establishment of a rhizobiome and affect the composition of rhizosphere communities depending on soil types and plant species (Tkacz et al., 2015).

The compounds of plant root exudates alter soil chemistry and provide nutrient sources for microbes in the rhizosphere (Miransari, 2013), that create a selective environment for those microbes which, due to further adaptation, have evolved mechanisms to colonize the plant root or to live in the rhizosphere (Bever et al., 2012). Predominantly, plant-derived compounds can modify the bacterial diversity by stimulating or inhibiting different community members, which indicate that particular types of exudates attract or repel specific microbes (Berendsen et al., 2012). Thus, the rhizosphere is an area of recruit beneficial microbes of the plants by using root exudates to attract mutualistic interactions to enhance plant protection against pathogens or improve the growth through nutrient acquisition abilities (Oldroyd, 2013).
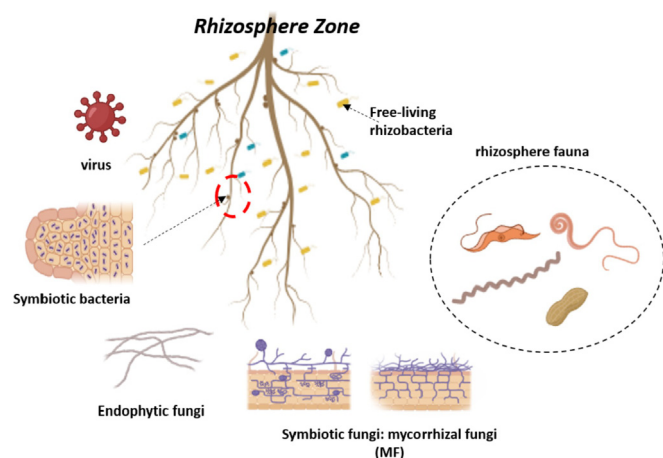

Fig. 1. Microbial community of rhizosphere.

3. Bacteria- plant interactions in the rhizosphere

In the rhizosphere, plantbacterial interactions, allow roots to recruit beneficial soil bacteria, from divers range of genera (*Azotobacter, Klebsiella, Streptomyces, Bacillus megaterium* (*B. megaterium*) and *Pseudomonas* spp) due to their important functions to enhance plant growth and development (Rudrappa et al., 2008)., Indeed, bacteria such as PGPR species have been applied to soils to specifically enhance the plants through divers beneficial mechanisms such as solubilizing inorganic phosphates, producing phytohormones (auxins, cytokinins, and gibberellins), fixing atmospheric nitrogen, increasing iron nutrition through chelators (siderophores) and also production of antibiotics to suppress antagonistic pathogens, competition for space and nutrients, the induction of systemic resistance in plants against a broad spectrum of leaf pathogens, and the reduction populations of root pathogens and other harmful microorganisms in the rhizosphere (Solano et al., 2008; Nihorimbere et al., 2011; Bhattacharyya and Jha, 2012; Kang et al., 2014; Goswami et al., 2016). Generally, all PGPR actions have an observable effect on the different parameters of plant health and growth (yield of cultivated plants, and fruits) (Bais et al., 2006; Singh et al., 2011; Jha and Saraf, 2015; Xiong et al., 2020).

3.1. Beneficial effects of PGPR application on the plant

3.1.1. Plant growth and development

Nutrient uptake

The function of biofertilizers is to promote plant growth by supplying nutrients to the host.

The absorption of mineral nutrients is mainly carried out by the roots *via* exchanges with bacteria from the rhizospheric soil. In 1995, researchers were interested in studying the interactin (Belimov et al., 1995) on effect between mixed cultures of nitrogen-fixing bacteria (*Arthrobacter mysorens* and *Azospirillum lipoferum*) and phosphate-solubilizing bacteria (*Agrobacterium radiobacter*) on the nutrition and yield of two barley cultivars (Belimov et al., 1995).

Hence, the combined inoculation recorded an increase in grain yield and an accumulation of nitrogen and phosphorus fertilizer in both plants, which provided balanced nutrition, confirmed by the investigation of the effect of rhizobacterium *Variovorax paradoxus* effect on pea plants (*Pisum sativum*) inoculated in drying soil. Consequently, the strain improved the roots length and the efficiency of water use in droughted peas (1620%) *via* nodulation and systemic and local hormonal signaling (Belimov et al., 2009).

Thereafter, in the rhizosphere of *Anthyllis cytisoides*, between three types of microorganisms (PGPR, Arbuscular mycorrhizal fungi (AMF), and *Rhizobium* spp.) isolated from an area with a semi-arid Mediterranean ecosystem, the double and the triple inoculations of the different microbial groups were assayed by evaluating P and N absorption, nitrogen fixation, root system efficiency, and biomass production. Indeed, the combinations tested were effective in promoting plant performance through nitrogen fixation, nutrient absorption, and root development (Requena et al., 1997).

Moreover, to improve the growth of sea oats (*Uniola paniculata* L.), *Klebsiella pneumoniae* (*K. pneumoniae*) was chosen as inoclum. Consequently, *K. pneumoniae* increased the growth of shoots and roots, and also that of the plant with the presence of high phosphorus (P) content in the sand (Will and Sylvia, 1990).

As its known, root nodulation is necessary for legume plants growth particularly under nitrogen deficiency. The implication of synergistic PGPR in this process has been reported. Indeed, the fre-

quency of *Pisum sativum* root nodulation was importantly increased after inoculation with *Streptomyces lydicus* (Tokala et al., 2002). Furthermore, this colonization increased the size of the nodules and improved the vigor of the nodular bacteroids which assimilate Fe and other soil inorganic nutrients, subsequently promoting the growth of pea plants (Tokala et al., 2002). Likewise, the genus *Burkholderia* used phytate (Na-IHP) to ensure a P supply for *Lotus japonicus* plants (Unno et al., 2005) and the researchers found that some isolates used Na-IHP as a source of carbon (C) and some others improved plant growth, with a strain (FpRpG4) that increased shoot length, P content, and plant dry weight.

Promoted uptake

It has been shown that the interaction between *Vibrio campbeilii* (*V. campbelli*) and *Listonella anguillarum* (*L. anguillarum*), two new N₂-fixing bacteria isolated from the roots of mangrove plants, with a non-diazotrophic bacterium (*Staphylococcus* sp.) increased the ability of *L. anguillarum* (17%) to fix nitrogen and decreased that of *V. campbellii* (15%) (Holguin et al., 1992). This indicated that the N₂-fixing activity observed in the rhizosphere of mangroves is attributed to the combination of interactions between the different strains of the rhizosphere community.

Other rhizosphere strains affiliated with *Agromyces, Streptomyces, Flavobacterium, Serratia, Janthinobacterium,* and *Pseudomonas* showed the ability to enhance the absorption of heavy metals by willows (*Salix caprea* (*S. caperea*)). This phenotype involves the capacity of these bacterial strains to synthesize ACC deaminase, IAA, and siderophores as well as to tolerate Zn, Cd, and Pb (Kuffner et al., 2008). In the same investigation, the tested bacteria have exhibited significant resistance to high concentrations of Zn with an ability to produce siderophores and IAA, and to mobilize Zn and Cd extracted from contaminated soil. Moreover, *Agromyces* AR33 strain doubled the extractability of both metals and improved the growth of *S. caprea* seedlings. Otherwise, *Streptomyces* AR17 improved the metals uptake (Kuffner et al., 2008). It is known that Zn is essential for the formation of auxins (regulator of plant growth). The contents of Zn are under regulation of layered double hydroxides (LDH) intercalated with phosphate (LDH-P) and nitrate (LDH-N) (Shafigh et al., 2019). It has been shown that some PGPR as *Pseudomonas fluorescens* (*P. fluorescens*) P52, *P. putida* P19, and *Pseudomonas* sp. A5 induce Zn accumulation of maize plants and promote their growth. Indeed, three strains tested showed an accelerated increase in the cumulative Zn content over time in the presence of PGPR. In plants treated with LDH-N, the strains increased the Zn concentration, while no significant effect was noted in those treated with LDH-P (Shafigh et al., 2019).

Phytohormone-producing

Moreover, the major part of PGPRs were classified as phytostimulators. Indeed, the ability of rhizobacteria, as *Azotobacter chroococcum*, *B. megaterium*, and *B. mucilaginosus* to synthesize phytohormones such as indole acetic acid (IAA) and cytokinins (CKs) can regulate plant growth (Blom et al., 2011; Sokolova et al., 2011).

Phytohormones production by the rhizobacteria raised plant growth characteristics due to the elevation of the IAA and CKs content that influences the elevation in the root mass as well as to the stimulation of seed germination, especially during the vegetative period (M≈ller et al., 1989; Sokolova et al., 2011). Inoculation of cucumber (*Cucumis sativus* L.) plants increased the content of CKs and IAA in them by 35.6 and 21.3%, respectively, that caused growth stimulation through and stimulated seed germination and increased the growth rate, the biomass of shoots, the number of lateral roots, and the root hair area, which ensured better plant nutrition (Sokolova et al., 2011).

In addition, plant growth-promoting traits like the production of ammonia, hydrogen cyanide (HCN), IAA, solubilization of inorganic phosphate, and production of bioactive metabolites (siderophore, biosurfactant, and phenazine) recognized in certain bacteria as *Pseudomonas* spp. MCC 3145 for wich the inoculation stimulated the germination of mung bean (*Vigna radiata*) seeds and increased root length with a marked tolerance against agricultural contaminants such as metals, salt, pesticides, and herbicides. Additionally, this organism produced phenazine-1-carboxylic acid (PCA) with fungicidal (against phytopathogens) and anticancer activities (Patil et al., 2017)

On the other hand, salinity is an abiotic constraint negatively affecting plants development and limits their productivity. However, the presence of salt-resistant bacteria in saline environment could improve growing conditions and plant health giving more importance to inoculation with well adapted rhizobacteria. Thus, many studies have aimed at selection of salt tolerant bacteria through the evaluation of their tolerance capacity to different level of salinity (Shukla et al., 2012; Nautiyal et al., 2013). Halotolerant PGPR include several strains as *Agrobacterium tumefaciens*, *Zhinguelliuella*, *Brachybacterium saurashtrense*, *Vibrio*, *Brevibacterium casei*, and *Haererohalobacter* (Shukla et al., 2012), and *B. amyloliquefaciens* (Nautiyal et al., 2013). These salt-tolerant bacteria increased plant growth and expression of about 14 genes having a significant effect in salt stress adaptation. Eventually, improving the salt stress in rice required modulation of the differential transcription of 14 genes, an increase in ACC deaminase activity and chlorophyll content, an accumulation of proline, as well as a stimulation of osmoprotectant utilizing rhizosphere microflora. Moreover, the increase of soil salinity leads to a decrease in its water availability and subsequently to the plant drought, which negatively affects their yield and growth.

Indeed, under drought stress, the PGPR inoculation considerably improved the various parameters negatively altered by this constraint such as membrane integrity, water status, growth parameters, and modification of the expression of genes sensitive to stress. Consequently, the inoculation effect of PGPRs strains (*Flavobacterium* sp., *Enterobacter ludwigii*, and *Klebsiella* sp.) improved drought tolerance in wheat by enhancing plant recovering and reducing transcript levels (Gontia-Mishra et al., 2016).

3.1.2. Plant protection

In their environment, plants effectively resist pathogens *via* several mechanisms including communication with bacteria in their rhizospheres and rarely develop severe symptoms of the disease. Therefore, rhizospheric bacteria could be exploited as a strategy for protecting crops against pathogens. Indeed, like *P. fluorescens* (Quadt-Hallmann et al., 1997). Other *Pseudomonas* sp. increased the resistance of inoculated tomato plants, against *Verticillium dahliae* (Sharma and Nowak, 1998). Furtheremore, *P. chlororaphis* PCL1391 and *P. fluorescens* protect the same plant species against *Fusarium oxysporum* f. Sp. *Radicis-lycopersici* (FORL), which attacks the roots causing serious damage (Bolwerk et al., 2003). The protection mechanism involves the reduction of FORL's pathogenicity *via* phenazine-1-carboxamide (PCN) produced by the strain *P. chlororaphis* (Bolwerk et al., 2003).

Similarly, the PGPR strains including *P. aeruginosa* and *B. cereus*, recording of important activities of defense against *Fusarium udum* that infecting the root vessels *via* the production of two enzymes (polymethyl galacturonase and -1,3-glucanase). Indeed, the lifespan of plants with the combined inoculation of Rhizobium and PGPR was greater than the individual inoculation, with recording of important activities of defense-related enzymes, namely, polyphenol oxidase (PPO), peroxidase (POX), and L-phenylalanine ammonia lyase (PAL). Similarly, both *B. cereus* strain and *P. aeruginosa* strain drastically reduced the production of the pathogen's enzymes. Overall, the combined treatment of these strains has

induced systemic resistance against pigeon pea (*Cajanus cajan* L.) wilt (Dutta et al., 2008).

4. Archaeal-plant interactions in the rhizosphere

According to the literature, archaea are not widely found in soils at the level of the rhizosphere compared to other bacteria which colonize it in a significant way. This is mainly due to the origin of archaea which dates back to 1977. Indeed, these microorganisms are associated with extreme environments and they are considered as engines of reactions for the environmental recycling of certain atoms between the organic and mineral forms. These phenomena include anaerobic digestion (Erkel et al., 2006), nitrification in the ocean (Wuchter et al., 2006). and ammonification in soils (Leininger et al., 2006). At the level of the rhizosphere, the presence of archaea had remained largely unknown until the 90s. Indeed, when researchers started to use molecular hybridization techniques, certain research groups have confirmed the presence of archaea, in particular *Crenarcheoata* and *Euryarcheota*, at the rhizosphere ground level using amplification and hybridization of the 16S rRNA gene (Bintrim et al., 1997;Borneman and Triplett, 1997; Jurgens et al., 1997). Subsequently, other studies have reported the presence of Archaea genomic sequences, in the rhizosphere, in the roots of certain plants. This is the case for example of *Crenarcheota* non thermophilic found by (Simon et al., 2001) in tomato roots with a percentage of 4 and 16%. In addition, other Archaea genomic sequences have been identified (only 0.16%) in the rhizosphere in the roots of *Festuca ovina* (Ochsenreiter et al., 2003).

4.1. Beneficial effects of archaebacteria on plants

Although that the role of archaea in the rhizosphere, in association with plant roots, is not yet known. Some studies showed that they can contribute in the renewal of nutrients and maintenance of important ecological functions in the plants roots. Moreover, Archaea colonization of rhizosphere depends on several factors, especially on biotic and abiotic factors (Taffner et al., 2018). In fact, Archaea constitute a substantial component of the plant microbiome without causing negative effects on these host plants. Their effects (negative or beneficial) on the host, and/or on abiotic and biotic factors conditioning the composition of the community at the level of the rhizosphere, remains largely unknown.

4.1.1. Effects on plants growth and development

Few studies are available on archaea as plant growth promoting, which includes Indole acetic acids production, nitrogen fixation by methanogens, siderophore production, and phosphorus solubilization by *Haloarchaea* (Yadav et al., 2015; Yadav et al., 2017). In the domain of agriculture, archaea have been used in nitrogen cycle, especially ammonia oxidation and global methane cycle (Nettmann et al., 2010). Moreover, Taffner and collaborators revealed recently that archaea colonize importantly alpine. Indeed, the authors showed that these archaea species interact with host plants at the rhizosphere and exhibit different functions such as promotion of plants growth *via* the stimulation of auxin biosynthesis and nutrient supply (Taffner et al., 2018).

4.1.2. Effects on plant protection

In the rhizosphere of rice plants, ammonia-oxidizing archaea (AOA) were found to be dominant and indicate a profound plant-archaea interaction (Chen et al., 2008). In fact, AOA, known as major drivers of ammonia oxidation (Radax et al., 2012), present interactions based essentially on syntrophic nitrogen cycling (Treusch et al., 2005; Francis et al., 2007). Because of their evolutionarily adaptation to different extreme environmental stress,

archaea contribute also to mediate the resistance to stress in host plants (van de Vossenberg et al., 1998; Valentine, 2007). Moreover, it has recently been shown that the presence of different archaea in the rhizosphere induced the protection of alpine plants against abiotic stress *via* the regulation of oxidative stress and osmotic pressure (Taffner et al., 2018). On the other hand, the interaction of Archaea with host plants in the rhizosphere can induce the resistance against other microorganisms including bacteria. Indeed, Song et al., (2000) studied, for the first time, the interaction between soil archaea and *Arabidopsis thaliana*. Results demonstrated that soil archaea promote plant growth and trigger induced systemic resistance (ISR) against the necrotrophic bacterium *Pectobacterium carotovorum* subsp. *Carotovorum* SCC1 and biotrophic bacterium *P. syringae* pv. tomato DC3000. An increase of resistance against both pathogenic species *via* salicylic acid-independent signaling pathway was caused by AOA on *Nitrosocosmicus oleophilus* MY3 cells colonization of the root surface of *Arabidopsis* plants (Song et al., 2000).

5. Fungal-plant interactions in the rhizosphere

Rhizosphere fungal communities play a key role in terrestrial and agricultural ecosystems due to their several interactions with different plants (Medina et al., 2020). They are major decomposers and recyclers of different organic matter and they can interact in the rhizosphere with plant roots or in above-ground with plant components (Zeilinger et al., 2016). The plant-fungal interactions are complex and the results are diverse. They range from parasitism to mutualism associations (Medina et al., 2020).

5.1. Beneficial effects of fungi on plants and their applications

5.1.1. Symbiotic fungi: Mycorrhizal fungi (MF)

Mycorrhization is a mutualistic interaction, which has a net benefit for both parts through different nutritious biological activities; maily bio-fertilisation, bioprotection, and a bio-regulation of plant development (Chen et al., 2018).

Dissolution, acquisition of mineral nutrients, and absorption of water

Mycorrhizae play a very important role in the acquisition of mineral nutrients in the soil and can also actively release nutrients from mineral particles and rock surfaces across low molecular weight organic acids (Gryndler et al., 2005). However, plants alone are unable to optimize the uptake of mineral elements from the soil by the roots, such as phosphorus and nitrogen (Lambers et al., 2008). The fungal mycelial network can, therefore, have access to additional resources of mineral elements, which are then transmitted to the host plant (Jansa et al., 2014), under different agricol practices (Chamkhi et al., 2019).

In addition, mycorrhizae are known for their high water absorption function by the vast network of hyphae, which prospect the soil by exploiting a surface much larger than that traversed only by the plant roots (Govindarajulu et al., 2005). Moreover, the mycorrhization improves nitrogen, phosphorus, potassium, and calcium woody nutrition. Improvements are observed in the ability to acquire iron, magnesium, and manganese by mycorrhized *Jacaranda*, which showed higher leaves and stem dry weights (Zaouchi et al. 2015).

Increase in resistance to biotic and abiotic stresses

In the desert regions, drought and salinity cause serious damage, making any agricultural activity difficult or impossible. Therefore, the use of MF is one of the promising biological means. MF have a range of effects that help improve various types of stress experienced by their host plants, including metal toxicity, oxidative stress (Abdel Latef and Chaoxing, 2011; Liu et al., 2014), tem-

perature stress (Zhu et al., 2010; Pavithra and Yapa, 2018), and the effects of soil acidification (*via* the production of chelating agents) (Ouledali et al., 2018), regulation of genes that protect against Oxygen reactive species, protection against oxidative stress induced by toxic metals (Yan et al., 2019), and tolerance to water stress (Ruiz-Lozano et al., 2016; Abdel-Salam et al., 2018).

Drought stress

Several studies suggest that increased tolerance to water deficit in mycorrhized plants may involve the modulation of drought-induced plant genes and this may play a role in enhancing tolerance to water and salt stress (Finlay, 2008; Santander et al., 2019), by controlling stomatal conductance and osmotic adjustment of the plant by the fungus under water stress (Ruiz-Lozano, 2003). On the other hand, it has been shown that AMF inoculated Ephedra foliate showed improved nitrogen metabolism by positively regulating nitrate and nitrite reductase activity, which results in greater ammonium availability for the synthesis of amino acids (Al-Arjani et al., 2020).

Inoculation with AMF also increased antioxidant enzyme activities, ascorbic acid contents, and reduction in glutathione level. Notably, the inoculated soybean (*Glycine* max L.) plants with MF revealed that fungi are able to increase plant stress tolerance by increasing the leaf proline concentration, photosynthetic rate, and growth parameters (leaf area index and relative growth rates) of soybean under drought stress (Pavithra and Yapa, 2018). Investigations on olive trees reported that the incolulation of fungi with AMF immediately alleviate drought impact, improve mineral uptake (K, N, Zn, and Fe), and increased turgor potential (p) (Ouledali et al., 2018).

The role of AMF in protecting host plants under drought stress was not well understood. However, some recent investigations suggested that inoculation of tomato with AMF for example alleviates the negative effects of drought by altering the hormonal profiles as well as plant physiology and development (Ruiz-Lozano et al., 2016). Moreover, on damask rose (*Rosa damascena* Mill.), it was suggested that AMF colonization can mitigate deleterious effects of drought stress by enhancing growth, flower quality, and adaptation of rose plants *via* improving their water relations and photosynthetic status (Abdel-Salam et al., 2018).

Temperature stress

Under low temperature induced stress, the AMF, *Glomus etunicatum*, improved water status of maize plants through decreasing water loss rate (Zhu et al., 2010). Moreover, *Glomus mosseae* colonization alleviated the damage caused by this stress on tomato plants by decreasing membrane lipid peroxidation, elevating the photosynthetic pigments, accumulation of osmotic adjustment compounds, and increasing antioxidant enzyme activities (Abdel Latef and Chaoxing, 2011). Including, AMF inoculation significantly decreased NADPH oxidase activity that is involved in H_2O_2 production and increased the ATPase activity, ATP concentration, and plasma membrane protein content in the roots of cucumber plants under low temperature (Liu et al., 2014). In additon to decrease of ROS activities and their generating system, AMP can also exhibit an antioxidant effect. Indeed, some investigations reported that the association of AMF, (*Glomus fasciculatum)* G. fasciculatum with cyclamen (*Cyclamen persicum* Mill.) plants alleviated heat stress damage through increased antioxidative activity and significantly enhanced temperature stress tolerance which promoted plant growth and elevated the host biomass under heat stress (Maya and Matsubara, 2013).

Symbiotic AMF relationship increased also grain number in wheat under heat-stress, altered nutrient allocation, and tiller nutrient composition (Cabral et al., 2016). Indeed, AMF also improved photosynthetic efficacy and led to higher production in biomass of plants for combat high temperature stress conditions (Mathur et al., 2018).

Salt stress

The effect of AMF on the plant's tolerance to salt stress is also studied in several works (Giri et al., 2007; Hajiboland et al., 2010; Sheng et al. 2011; Hashem et al., 2015; Hashem et al., 2018; Santander et al., 2019). Indeed, it has been reported that arbuscular mycorrhiza (*G. fasciculatum*) improved tolerance of *Acacia nilotica* to salt stress inducted by different salinity levels (1.2, 4.0, 6.5, and 9.5 dS m^1) (Giri et al., 2007). The authors attributed this effect to the improvement of P nutrition and K/Na ratios in root and shoot tissues of AM-inoculated plants that may be protected disruption of K-mediated enzymatic processes under salt stress conditions.

Mycorrhization alleviated also salt induced reduction of P, Ca, K uptake, Ca/Na, and K/Na ratios in tomato plants (*Solanum lycopersicum* L.) (Hajiboland et al., 2010). It also improved the net assimilation rates through both elevating stomatal conductance and protecting photochemical processes of PSII against salinity. AMF-inoculated *Panicum turgidum* alleviate salinity induced negative effects on the plant growth and nutrient uptake by altering photosynthetic and decreasing the oxidative damage through strengthening of the antioxidant system under saline conditions (Hashem et al., 2015).

Recently, the same group research reported that AMF-inoculation of cucumber improves the negative impact of salinity stress by enhancing the biomass and activity of antioxidant enzymes as well as by accumulation of phenols and proline and enhancing of jasmonic acid, salicylic acid, and several important mineral elements (K, Ca, Mg, Zn, Fe, Mn, and Cu) in AMF-inoculated plants (Hashem et al. (2018). Moreover, AMF-inoculated lettuce had higher biomass production, with increased proline synthesis, elevated N uptake, and noticeable changes in ionic relations than those in non-mycorrhizal plants under stress conditions (Santander et al., 2019). In addition, mycorrhizal associations enhance the accumulation of organic solutes in leaves and increase the production of betaine resulting in up-regulation of the osmoregulation process in plants growing in saline soil (Sheng et al. 2011).

Metals stress

Several researches have demonstrated that the association between the fungi and the host plants improves the resistance of plants to metal stress and alleviation capability on contaminated soils (Yan et al., 2019). AMF association with Pot Marigold (*Calendula officinalis* L.) improved growth, yield, and phytoremediation performance of the plant in heavy metal stressed condition [0, Pb (150 and 300 mg/kg) and Cd (40 and 80 mg/kg)], by increasing heavy metals accumulation in the plant organs (Tabrizi et al., 2015). Moreover, *Glomus coronatum* enhances the copper tolerance of *Tagetes patula* through the sorption and barrier mechanisms of AMF intraradical hyphae resulting reduced Cu toxicity in the roots of the plant and eventually enhanced the plants Cu tolerance (Zhou et al. 2017). Also, *Rhizophagus irregularis* inoculation improve the growth and photosynthesis of *Phragmites australis* under copper stress (Wu et al. 2020). The strong effects of AMF (*Glomus mosseae* BEG167) on maize (*Zea mays* L.) plant development and growth under metals stress devalued using zinc, cadmium, and phosphorus at different levels, the mycorrhizal inoculation increases plant growth with improved P nutrition and lead to higher soil solution pH after harvest which can decrease the availability of the metals for plant uptake, and reduced the concentrations of soluble Zn and Cd in the soil solution (Shen et al., 2006). However, AM fungal inoculation significantly decreased the translocation factor of trigonella plants and increased malondialdehyde content and antioxidant enzyme activities. It also increased growth parameters, chlorophyll, and protein contents in the host plant under Cd stress (Abdelhameed and Metwally, 2019).

Effect on soil structure and aggregate stability

The mycorrhizal fungal hyphae develop a complex and branched network in the surrounding soil until 30 m of fungal hyphae per gram of soil, this network can constitute up to 50% fungal mycelium in the soil. This mycelial network can contribute to soil structure improvement (Gianinazzi et al., 2010). In addition, AMF produce a glycoprotein, glomalin hydrophobic, and sticky protein substances, that contribute to soil stability and water retention. The combination of an extensive hyphal network and glomaline secretion is considered to be important to help stabilize soil aggregates, structural stability, and the quality (Miller and Jastrow, 2000). A reduction in fungal biomass will negatively affect soil stability and therefore increase the risk of soil erosion. The study of Bearden and Petersen, (2000) demonstrated that AMF contribute significantly to the stabilization of soil aggregates in a vertisol, while the effect was significant after only one growing season, associated with both AM hyphae and the stimulation of root growth by AMF.

5.1.2. Other endophytic fungi

The different groups of fungi can have an impact on the ecology, physical form, and shape of plant communities, conferring resistance to abiotic (temperature, pH, osmotic pressure), and biotic (bacteria, fungi, nematodes, and insects) (Bano et al., 2016). In addition, endophytes fungi are able to synthesize bioactive compounds, which can be used by plants for defense against pathogens and motivate plant growth (Pavithra et al., 2012).

Increase of resistance to abiotic stresses

The plants are exposed to several abiotic stresses during their growth and development such as drought, metal, cold, hot temperature, and salinity (Venugopalan and Srivastava, 2015), which are able to modulate genetic regulation of cellular pathways that result from the reactive oxygen species accumulation, as well as imbalance in hormone and membrane dysfunction. However, endophytic and MF can increase stress tolerance in their host plants across additional defensive mechanisms on the plant immune system *via* influencing the direct antimicrobial metabolites such as alkaloids to indirect phytohormones as jasmonic acid, or salicylic acid (Yan et al., 2019).

Drought stress

Several experiments revealed that inoculation of maize and rice with the fungus help the plants to resist better to drought conditions using different mechanisms (Hosseini et al., 2018; Pandey et al., 2016a). Hosseini et al. (2018) reported that maize roots colonized by an endophytic fungus *P. indica* were better adapted to drought stress induced by PEG 6000 solution with osmotic potentials of 0.3 and 0.5 MPa, and mechanical stress by placing weights on the surface of the sand medium. The inoculated plants had greater root volume, leaf area, relative water content, leaf water potential, and proline content under stressful conditions. It also revealed lower CAT and APX activities in comparison with non-inoculated plants which show that they experienced less oxidative stress. Fungal association increase seedling biomass, the uptake of phosphorus, and zinc that are functional elements for the growth under drought stress. It also improved the total antioxidant activity in leaves, as well as increasing the production of proline by upregulated activity of the Pyrroline-5-carboxylate synthase (P5CS) (Saddique et al. 2018). It has been also shown that endophytic fungus as *Trichoderma harzianum* Th-56 improved drought stress in rice by upregulated aquaporin and dehydrin, modulated proline metabolism, superoxide dismutase level, and lipid peroxidation product (Pandey et al., 2016b). On the other hand, Zhang et al. (2018) revealed that endophytic fungus *Piriformospora indica* improved the oxidative potential of maize roots by rebalancing the carbonsulfur surplus and by activating genes for hormone mediated signaling pathways including those which respond to abscisic acid, auxin, salicylic acid, and cytokinins.

Salinity stress

Salinity stress is an increasing environmental problem that undermines plant growth by affecting vegetative development and stimulating the generation of reactive oxygen species (Begum et al., 2019). Several studies have reported the efficiency of plant-fungal association in the increased salinity stress tolerance of plants, the plant growth and yield enhancement (Waller et al., 2005; Giri et al., 2007; Hajiboland et al., 2010; Sheng et al. 2011; Hashem et al., 2015; Li et al., 2017; Hashem et al., 2018; Santander et al., 2019; Gul Jan et al., 2019; Farias et al., 2020). Moreover, under salinity stress conditions endophytic fungi enhanced the length and fresh weight of plants and mitigated the adverse effects of this constraint by limiting lipid peroxidation and accumulating proteins, as well as decreasing levels of abscisic acid and increasing salicylic acid levels in stressed plants (Radhakrishnan et al., 2013). Endophytic fungi able to alleviates salinity stress *via* accumulation of osmoprotectant, stimulating the expression of defense-related genes, and antioxidant enzymes (Li et al., 2017). On the other hand, under salt stress, endophytic fungi interaction with plants improved nutrition with N and P favoring the growth and rate of liquid photosynthesis in the plants (Farias et al. 2020). As reported, the *Yarrowia lipolytica* inoculation ameliorated also the negative impact of salt stress in maize. It significantly promoted plant growth through controlled metabolism and hormonal secretions (ABA and IAA) under salinity stress (Gul Jan et al., 2019).

Metals stress

The capacity of endophytic fungi to increase the resistance of host plants to metals stress is also reported in several studies (Wang et al., 2016; Gong et al., 2017; Lalancette et al., 2019; Hou et al., 2020). Indeed, fungal endophytes populations promote plant growth and increased their tolerance to Cu, Ni, Zn, and As induced stress (Lalancette et al., 2019), improved root growth and tolerance to cadmium stress by altering the soil Cd concentration and facilitating plant growth and survival under Cd stress (Hou et al., 2020). As reported, endophytic fungus *Exophiala pisciphila* has been associated with maize (*Zea mays*) under also increased soil cadmium stress (0, 10, 50, 100 mg kg^1) and the result showed a marked tolerance to Cd, with a significant reduction in Cd phytotoxicity and a significant increase in maize growth by stimulating antioxidant systems, altering metal chemical forms into inactive cadmium, and repartitioning subcellular cadmium into the cell wall (Wang et al., 2016). Moreover, Gong et al. (2017) reported that endophytic fungus *Purpureocillium* sp. A5 protect mangrove plant *Kandelia candel* under copper stress by decreasing uptake of Cu in *K. candel* and changes the pH characterization of soil. It also increased the concentration of Cu complexes in soil and enhanced the concentration of carbonate-bound Cu, MnFe complexes Cu, and organic-bound Cu in soil.

Temperature (high and low) stress

Heat-stress is one of the major destructive stresses among abiotic ones that can lead to detrimental effects on plant growth and development (Begum et al., 2019). Indeed, fungus-inoculated plants revealed better growth under heat stress compared with the non-fungus inoculated ones (Zhu et al., 2010; Abdel Latef and Chaoxing, 2011; Liu et al., 2014; Waqas et al., 2015; Cabral et al., 2016; Ismail et al., 2018; Ismail et al., 2019). Moreover, mutualistic fungal endophytes can protect rice plants from heat-stress by decreasing the endogenous level of stress-signaling compounds such as abscisic and jasmonic acids, and by increasing total protein content (Waqas et al., 2015). The endophytic fungus as *Aspergillus japonicas* improved heat stress by negotiating the activity of abscisic acid, catalase, and ascorbic acid oxidase as well as nutritional quality such as phenolics, flavonoids, soluble sugars, proteins, and lipids in comparison to endophyte-free plants (Ismail et al. 2018). Moreover, in high temperature induced stress, endophytic

fungi promote growth by increasing the levels of abscisic acid (ABA), proline, and decreasing the levels of phenols, flavonoids, catalase, and ascorbic acid oxidase. It also decreased chlorophyll, root-shoot length, and dry weight (Ismail et al., 2019).

Increase in resistance to biotic stresses

Fungi induce several beneficial effects on their host plants including the resistance to biotic stresses from pathogens and herbivores (Khare et al., 2018; Yan et al., 2019). Indeed, endophytic fungi inhibited fungal pathogens as *Panax notoginseng* Yao et al. (2017), *Moniliophthora roreri*, *Phytophthora palmivora, Monilioph-thora perniciosa* (MejÚa et al., 2008), *Heterobasidion parviporum*, *Phytophtora pini*, and *Botrytis cinerea* (Terhonen et al. 2016). The authors reported that this fungus increased resistance to pathogen damage in *Theobroma cacao* leaves by the upregulation of host defensive genes (Tc00g04254). On the other hand, Siddaiah et al. (2017) reported that endophytic fungus *Trichoderma hamatum* UoM 13 produce resistance by significant overproduction of endogenous SA and the overexpression of PR proteins, HRGPs, and defense enzymes in plants, which showed mounted systemic immunity against downy mildew pathogen.

Growth of host plants

Fungi inoculation could promote the growth of their host plants by several mechanisms such as increasing hormones and absorption of useful nutrients for plants (Guo, and Wang, 2001; Sheramentei et al., 2005; Chen et al., 2011; Waqas et al., 2015; Jia et al., 2016; Metwally and Al-Amri, 2020). The inoculation with endophytic fungi as *Penicillium citrinum* and *Aspergillus terreus* promoted plant biomass and other growth characteristics such as stem diameter, shoot fresh/dry weight, shoot length, and photosynthetic function by increasing the levels of endogenous Jasmonic acid and Salicylic acid of the host plant (Waqas et al., 2015). Also, the production of indole acetic acid reported to increases seed germination and enhances yield of the host plant (Guo, and Wang, 2001), positively influence the plant growth by increasing size of roots and amount of chlorophyll (Chen et al., 2011). At the molecular level, endophytic fungus *Piriformospora indica* promotes the growth of *Arabidopsis* and tobacco roots by stimulating gene expression for nitrate reductase and the starch degrading enzyme (glucan-water dikinase) (Sheramentei et al., 2005). The inoculation of onion (*Allium cepa*) plants by AM fungi in combination with biocontrol fungus (*Trichoderma viride*) significantly increased onion growth parameters (fresh and dry weights, root and shoot lengths and leaf area) and also improved chlorophyll, carotenoids, and total pigments in onion leaves (Metwally and Al-Amri, 2020).

Production of plant secondary metabolites

Several studies reported that a special relationship found with endophytes and their host plants that influencing the production of bioactive metabolites in plants (Wang et al., 2006; Gao et al., 2011; Pandey et al., 2016; Yuan et al., 2019; Zhang et al., 2020; Teimoori-Boghsani et al., 2020). Association of endophyte fungi and medicinal herb produced sesquiterpenoids accumulation by increasing the photosynthesis, expanding the glycolysis and tricarboxylic acid cycle, and enhancing the metabolic sesquiterpenoids biosynthesis pathway (Yuan et al., 2019). Moreover, endophytic fungi inoculation improve the accumulation of total flavonoid, rutin, isorhamnetin, and cyanidin-3-glucoside chloride contents and promoted their growth and development (Zhang et al., 2020). In addition, it has been showed that Fungi such as *Coetotrichum gloesporioides* fungi induce the biosynthesis of terpenoid (such as isoeuphpekinensin and euphol), defense-related enzymes, and biomass (Gao et al., 2011) (Wang et al., 2006).

Pandey et al. (2016) reported that colonization of opium poppy *Papaver somniferum* L. by endophytes improved plant productivity and benzylisoquinoline alkaloid (BIA) biosynthesis. Moreover, endophytic fungi *Penicillium canescens*, *Penicillium murcianum*, *Paraphoma radicina*, and *Coniolariella hispanica* isolated from *Salvia*

abrotanoides plants are producers of cryptotanshinone which is a main bioactive compound of the host plant (Teimoori-Boghsani et al., 2020).

6. Effects induced by other living organisms or microorganisms on plant-microbes interactions in the rhizosphere

6.1. Effect of saprophytic fungi on plants

Saprophytic fungi are a group of macro-fungi that use the nutrition from the debris of plant or animals. The degradation of these bodies requires the presence of specific enzymes, in Saprophytic fungi, which digest the cellulose, lignin, and chitin in these plants or animals into simple soluble molecules (Saldajeno et al., 2008). These compounds can be absorbed by plants and saprophytic fungi as nutrients. Despite, there are no several studies which investigated the effects of saprophytic fungi on plants, some studies suggested that the presence of saprophytic fungi is beneficial for plants growth; they can therefore induce the accumulation of essential nutrients (carbon and nitrogen) in plants. Indeed, some saprophytic fungi like plant growth promoting fungi (PGPF) are non-pathogenic soil inhabitants and able to promote growth of several plants such as wheat (Shivanna et al., 1996), and cucumber (Shivanna et al., 2005). Moreover, it has been shown that several phyto-pathologies are controlled by these fungi. These plant diseases include *Rhizoctonia damping* off, *Fusarium crown* and root rot in tomatoes Pythium, take-all disease of wheat, and brown patch diseases (hyakumachi, 2004; Horinouchi et al., 2007). On the other hand, the indirect effect of Saprophytic fungi on plants can be mediated indirectly by their effects on Arbuscular Mycorrhizae. Indeed, *in vitro* and *in vivo* investigations revealed that the interaction between Arbuscular Mycorrhizae and saprophytic fungi can stimulate the germination and the growth of Arbuscular Mycorrhizae (Saldajeno et al., 2008).

6.2. Interactions of rhizosphere fauna with beneficial microorganisms

Nematodes, earthworms, and protozoa are very abundant, living in interaction with plants and other rhizosphere microorganisms. These relationships can be symbiotic or non-symbiotic (Wardle et al., 2004).

However, numerous studies reported recently that some parasites, by their interactions with plants in the rhizosphere, are beneficial for plants. In fact, they can induce the growth and development of host plants, reinforce plant defense, and stimulate secondary metabolites synthesis. Such as protozoa, nematodes, earthworms

In this context, protozoa play an important role at the soil-root interface by accelerating the mineralization of microbially immobilized nutrients (Elliott et al., 1979). They also strongly stimulate the mineralization and turnover of bacterial N (Kuikman and Van Veen, 1989) and enhanced N absorption (Koller et al., 2013). In addition, the presence of protozoa significantly enhanced soil nitrogen mineralization (Ekelund et al., 2009), plant nitrogen uptake, and plant growth, which is facilitated by a mucilage-border cells-complex (Somasundaram et al., 2008). Moreover, in interaction with AMF, protozoa increased plant N and P uptake, increased the root (Bonkowski et al., 2001), and leaves surface (Koller et al., 2013). Furthermore, amoebas (protozoa) are involved in a mechanism known as microbial loop in soil, they mobilize the N pool locked up in bacterial biomass, and results in a marked increase in plant growth (Bonkowski, 2004), and also can rapidly change bacterial community composition in the rhizosphere (Kreuzer et al., 2006; Rosenberg et al., 2009).

Thus, a decrease in plant stress levels due to changes induced by protist-induced shifts in microbial communities, is a prominent effect of microbial predatorprey interactions in the rhizosphere (Kuppardt et al., 2018). Furthermore, phagotrophic protists have modified bacterial functioning by improving the genes of secondary metabolites suppressing pathogens (Xiong et al., 2020). A very recent study showed that heterotrophic protists increase plant growth and nitrogen uptake, with a great impact on plant biomass (Asiloglu et al., 2020).

Otherwise, Nematode-plant relationships may be modified by plant variety and age, nematode species, and environment. Certain nematodes like *Meloidogyne* spp. can have positive effects on the legume-rhizobium association by increasing the number of nodules and the amount of nitrogen fixed (Baldwin et al., 1979). Similarly, nematodes (*Heterodera trifolii*) can increase plants growth (Wardle et al., 1995). Furthermore, plant-nematode interaction, in the rhizosphere, is mostly mediated by chemicals present in root exudates (Bais et al., 2004). In response to plant-released volatiles that attract nematodes; a soil nematode (*Caenorhab ditiselegans*) mediated the interaction between the roots of the legume *Medicago truncatula* and the rhizobia, leading to nodulation (Horiuchi et al., 2005).

Nematodes may stimulate plant growth by secreting small molecules. In this context, numerous studies showed that several genera of phytoparasitic nematodes have the capacity to produce ascr#18, the main ascaroside (Manosalva et al., 2015), functioning as a small-molecule signature that elicits plant immune responses (Manosalva et al., 2015), and which is responsible for the plant's defense response (Vercauteren et al., 2001). According to Manosalva et al., (2015), these small molecules increased the resistance of Arabidopsis, tomato, potato, and barley against viral, bacterial, oomycete, fungal, and nematode infections.

Recently, a study showed that both monocot and dicot plants converted ascr#18 to shorter side-chained ascarosides acting as chemical signals when excreted in the rhizosphere to regulate the early stages of plant-nematode interactions (Manohar et al., 2020). Moreover, bacterial-feeding nematodes (*Cephalobus* sp. and *Mesorhabditis* sp.) stimulated the activity of IAA-producing bacteria that promoted *Arabidopsis thaliana* growth, nitrogen mineralization in the soil, plant growth (root architecture, shoot dry weight, and plant nitrogen), and the expression of two IAA-responsive genes (IAA3 and IAA13) (Jiang et al., 2020).

Several studies have reported the effectiveness of the plant-earthworm interaction in improving root biomass, carbon content, and plant growth and yield (Scheu and Parkinson, 1994; Hudson and Floate, 2009). Indeed, Kooch and Jalilvand, (2008) found that the feeding activities of earthworms significantly enhance the mineralization of macronutrients, especially nitrogen, from birch litter and humus in coniferous forest soil. Similarly, the earthworm *Dendrobaena octaedra* (Savigny) enhanced the shoot biomass of the grass *Agropyron trachycaulum* (Link) Malte (Poaceae) and increased the shoot-to-root ratio during early plant growth (Scheu and Parkinson, 1994). Besides, the presence of earthworms (*Aporrectodea caliginosa*) increased the root biomass and the carbon content of *Cardamine hirsuta* shoots (Wurst and Jones, 2003). Earthworms have also facilitated nitrogen mineralization and increased root biomass and carbon content, thereby stimulating plant growth and development (Hudson and Floate, 2009).

7. Viral-plant interactions: Virus as an elicitor/inductor of host plant metabolites

Indeed, the presence of virus in plants can lead to remarkable interactions *via* signaling pathways inducing thus several positive phenotypes in plants. Among these phenotypes, it has been shown that virus mediate signaling pathways involved in the immune system of these plants (Pellati et al., 2011). Moreover, some plant viruses induce a hypersensitive response using coat, movement, and replicase proteins (GarcÚa and PallÃs, 2015).

Under drought stress, Xu et al., (2008) revealed that four different RNA viruses, Brome mosaic virus (BMV), Cucumber mosaic virus (CMV), Tobacco mosaic virus, and Tobacco rattle virus improved the tolerance to abiotic stress of various plant species inoculated by increasing osmoprotectant as well as antioxidant levels in these virus-infected plants. This result was confirmed by (Westwood et al., 2013), who studied *Cucumber mosaic virus* (CMV) associated with *Arabidopsis thaliana* plants, and showed the virus is able to increase plant stress tolerance by aiding susceptible hosts to survive periods of environmental stress. In another study, the infection of Arabidopsis (*Arabidopsis thaliana*) plants with *Cucumber mosaic virus* (CMV) rendered seeds with improved tolerance to deterioration when compared to the non-inoculated plants in the biotic stress (Bueso et al., 2017). Moreover, Khankhum and Valverde, (2018) reported that PvEV-infected Common bean (*Phaseolus vulgaris*) had faster seed germination, longer radicle, lower chlorophyll content, higher carotene content, longer pods, and higher weight of 100 seeds. More recently, (Fukuhara et al., 2020) revealed that the latent infection of tomato plants (*Solanum lycopersicum*) with Southern tomato virus (STV) increased the production of fruit and the germination rate of seeds more than STV-free plants.

The viruses play also a beneficial role in plantherbivore interactions and protected their hosts by decreasing herbivore infestation rates. Indeed, van Molken et al., (2012) demonstrated that white clover mosaic virus infection can reduce the attractiveness of stoloniferous herb *Trifolium repens* (white clover) for fungus gnat females. This effect may be due to -caryophyllene compound which was exclusively detected in the headspace of virus-infected plants. (Thaler et al., 2010) studied the effects of Tobacco mosaic virus infection in *Spodoptera exigua* caterpillars and showed that virus increased growth of *Spodoptera* when feeding on infected tomato plants. Moreover, Shapiro et al., (2013) showed that the infection of *Cucumis sativa* by zucchini yellow mosaic virus (ZYMV) decreased the attraction of the cucumber beetle, which can transmit the bacterial wilt pathogen *Erwinia tracheiphila*. Recently, Safari et al., (2019) showed also a positive relationship between *Pepper cryptic virus 1* and Jalapeþo pepper plants by protecting the plants from the vector of acute viruses and reducing aphid herbivory.

8. Rhizospheric microorganisms: Perspectives for a biological agriculture

Agriculture underwent fundamental changes all over the world. In the past, the main objective was to increase the yield potential of crops and their productivity, while today, the dynamism of productivity is increasingly combined with the demand for sustainability. This would meet human needs while maintaining the quality of the environment and conserving natural resources for the future.

Improving agricultural sustainability requires the optimal use and management of soil fertility and its physicochemical properties. This implies management practices that improve the biological activity of soils and their biodiversity (Egamberdieva et al., 2015). The study of biodiversity patterns is a crucial step to achieve one of the main objectives of ecology particularly the understanding of the distribution of organisms (Lubchenco et al., 1991). Environmentalists are increasingly interested in the relationship between productivity and diversity (Claire Horner-Devine et al., 2003).

The use of microorganisms and the exploitation of beneficial plant-microorganisms interactions offer promising and environmental friendly strategies for conventional and organic farming worldwide (Berg, 2009). Although microbiologists have studied the impact of microbial diversity on the stability of ecosystem function since the 1960s (Hairston et al., 1968). There is now an increased interest in the effect of the diversity of microbial communities on ecological function and resilience to disturbances in soil ecosystems. The use of beneficial microorganisms has proven to be an environmentally sound option for increasing crop yields. Microorganisms are fundamental for maintaining essential soil functions. They participate in key processes such as soil structure, decomposition of organic matter, elimination of toxins, suppression of diseases, and play a key role in carbon, nitrogen, phosphorus, and sulfur cycles (Garbeva et al., 2004). Microorganisms maintain plant growth and therefore have primary effects on soil and crop quality (Garbeva et al., 2004). A wide range of advantages is possible depending on their predominance and their activity at any time, intending to obtain a maximum high-quality agronomic yield, without the use of artificial fertilizers, herbicides, insecticides, and pesticides (Singh et al., 2011).

9. Conclusion and future perspectives

The relationship between microorganisms and plants in the rhizosphere has been well understood recently. Differ

ent microorganisms such as bacteria, fungi and archaea exert direct and/or indirect benefic effects on host plants. These beneficial effects include the improvement of plant growth and development, the enhancement against abiotic stresses, and the increase of resistance to biotic stresses. This positive association between these microorganisms and plants plays an important role in balancing the rhizosphere. However, the molecular mechanisms involved in these beneficial interactions are not well understood. Therefore, further investigations are required to establish molecular pathways by which microorganisms induce phenotypic changes in host plants and the use of these associations for improving the culture of plants as well as their adaptations to different conditions. In addition the study of quorum sensing mediators as molecular communication between plants and microbes could be a key element to understand these interactions and therefore to use them as biotechnological tools.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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