



## Endophytic microbes modulate plant responses to abiotic stresses: a review

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### Article info

### Abstract

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Many groups of microorganisms have been studied for their benefits towards humankind due to their capacity to produce natural compounds that can be valorized in many economic sectors such as agriculture. Due to the extensive use of chemicals pesticides and fertilizers, current agriculture systems facing several major problems such as emergence of resistant in pathogens and pests, soil infertility and bioaccumulation of toxic residues in the environment and particularly in foods which negatively affects human health. The use of natural products harmless to plants, humans and biodegradable constitute a promising way to overcome these problems. Modern agriculture systems are moving toward the use of beneficial microorganisms isolated from the soil, plant surfaces and inside tissues for developing eco-friendly products such as biofertilizers and biopesticides. Recent literatures show that colonization of plants by endophytes is the rule in nature and endophyte-free plant is a rare exception. Endophytes are microbes living inside plant tissues and supporting them in growth and development, as well as stresses tolerance without causing any apparent disease symptom. Abiotic stresses have a great impact on growth, production and health of plants. Many literatures show the role of endophytes in abiotic stress tolerance as well as mechanisms involved to cope with these constraints via the induction of stress-related genes and molecules. This review provides a summary of literature on how endophytes modulate plant growth and responses to abiotic stresses which may help to better understand their role in plant adaptation to environmental constraints and valorize their use in agriculture.

### 1. INTRODUCTION

The current agriculture system in the world must undergo a profound transformation if it has to meet the growing and interconnected challenges of food insecurity and climate change. According to forecasts, the world's population will increase from 7 to 9.2 billion in 2050 (FAO, 2010). Given trends in food consumption and population growth, a 60 % increase in world demand for agricultural products is expected by 2050. This challenge is even greater in developing countries, where economic development in rural areas is based on agriculture. Ensuring adequate food supplies in these areas will require faster growth in agricultural production than has been the case over the last decade (FAO, 2010). Although crop

production has increased globally, this is largely due to an expansion of cultivated area rather than productivity gains. The challenge of quickly boosting productivity is hindered by the current and projected impacts of climate change. Changes in precipitation and temperature are expected to reduce productivity and make production more irregular (Lobell et al., 2008). Climate models predict a reduction in precipitation and an increase and intensification of extreme events such as heat waves and drought in several parts of the world. These constraints could have a negative impact on natural resources, ecosystems and agricultural activities. Therefore, it is necessary to adopt a rational and sustainable agricultural productivity in order to guarantee the

improvement of food production under climatic change conditions. More sustainable farming systems need to take into account the scarcity of water and the depletion of natural resources used for the extraction of chemical fertilizers and their adverse effects on the ecosystem and human health. So, the agriculture system based on the exclusive use of chemical pesticides and fertilizers to increase plant production will not be the solution for these future challenges. Therefore, the modern agriculture system is moving toward the prospection and exploitation of renewable methods for example for energy as well as for irrigation, fertilization and disease management. The exploitation of natural resources that provide crop protection at lower ecological cost is a priority nowadays. Thus, the selection and formulation of biological agents that are able to promote plant growth and health is a promising approach for increasing crop production and resilience to environmental constraints.

Plants are colonized by a large number of microorganisms that can inhabit either the surface or the internal plant tissues, which is known as plant microbiome (Turner et al., 2013). Microbial endophytes are microorganisms occurring inside plant tissues without causing any apparent symptoms and have been detected in hundreds of plants, including many important agricultural crops (Larran et al., 2001), medicinal (Chowdhary and Kaushik 2015) and wild plants (Llorens et al., 2019). In addition, correlations to growth promotion of plants were observed with inocula levels that promoted endophyte populations (Pillay and Nowak 1997). Throughout the plant life cycle, endophytes may be transmitted vertically, growing within seeds, which are more likely to be mutualistic to the host, or horizontally, via shoots and roots, which tend to be more antagonistic (Aly et al., 2011). These endophyte microorganisms present a variety of benefits for their host, including reciprocal exchange of nutrients and/or protection from biotic and abiotic stresses (Rosenblueth and Martínez-Romero, 2006; Rodríguez et al., 2009). These endophytes can enhance the plant overall growth as well as stress tolerance ability (Suryanarayanan et al., 2004; Mei and Flinn, 2010). An increasing number of researchers showed that endophytes have a role in the outcome of plant-environment interactions through diverse mechanisms (Pal et al., 2019; Roberts et al., 2019). In addition, the efficient vertical transmission of these endophytes in a

manner similar to maternally inherited genetic characters (Schardl et al., 2004) will allow the production of infected seed at a commercial scale. Therefore, exploiting useful microorganism's properties is one of the novel ways prospected by public and private research laboratories to develop new bio-products to improve plant health and production. So, this review aims to provide an overview of the potential applications of endophytes particularly in the area of plant growth promotion and prevention from abiotic stresses toward better understanding of the role of these microbes in plant adaptation to environmental constraints and improve their use in a sustainable agriculture system.

## 2. Endophytes as a component of the plant microbiome

The plant microbiome has received substantial attention in the last decade because it can modulate plant health and productivity (Berendsen et al., 2012; Compant et al., 2019) and at a global scale biogeochemical cycles by affecting denitrification (Wrage et al., 2001) and methanogenesis (Conrad et al., 2006) into the rhizosphere. The plant microbiome represents the microbial component of the plant holobiont, i.e., all plant associated organisms in the rhizosphere, phyllosphere and endosphere, and it consists of different types of organisms including fungi, archaea and bacteria (Vorholt, 2012; Philippot et al., 2013; Taffner et al., 2018; Compant et al., 2019). The microbiome is strongly influenced by the plant genome and physiology, as well as environmental and cropping conditions (Turner et al., 2013; Materatski et al., 2019; Chen et al., 2019a).

The rhizosphere consists of root microbiota which is mostly acquired from the soil (horizontal transfer) and contains the large community and highly diverse populations of microorganisms. The community profiling utilizing 454 pyrosequencing of rhizosphere associated microorganisms of *Populus deltoides* roots showed that is dominated by Acidobacteria and Alphaproteobacteria for bacteria, whereas Pezizomycotina and Agaricomycotina groups were the most abundant fungi (Gottel et al., 2011). The external above-ground plant microbiota consists of the phyllosphere (the external leaf surface environment), the anthosphere (the external flowers environment), the spermosphere (the external of germinated seed environment) and the carposphere (the external fruit environment). Above-ground plant

associated microorganisms are mainly originate from soil, seed and air and their community composition is influenced by several factors including soil and environmental conditions (Bringel and Couée, 2015; Compant et al., 2019).

The endosphere microbiota consists of plant associated microorganism living inside underground and aboveground plant tissues (Fig. 1). These microorganisms colonize all plant organs i.e., roots, vegetative and reproductive parts. Gottel et al., (2011) showed substantial differences between microbial communities in the rhizosphere and endosphere which let them to conclude that root endophytic communities are distinct assemblages rather than opportunistic subsets of the rhizosphere. In addition, the structural analysis of phyllosphere or carposphere microbiota of the grapevine showed also substantial differences in terms of bacteria genera in comparison to endophytes of grape berries (Campisano et al., 2014). Only a fraction but diverse microorganisms of the phyllosphere and rhizosphere are able to colonize the inner tissues of plants (Gaiero et al., 2013; Dong et al., 2019). Indeed, in *Populus deltoids* the root endophytic bacterial richness was highly variable and 10-fold lower than in rhizosphere (Gottel et al., 2011) and in tomato the most abundant associated community phyla belongs to Proteobacteria with the lowest richness occurred in the endosphere composed mainly by the genera *Acinetobacter*, *Enterobacter*, and *Pseudomonas* in the roots, stems and leaves (Dong et al., 2019).

### 3. Definition, abundance and diversity of endophytes

The term endophyte *stricto sensu* signify "inside the plant" which includes all organisms that can inhabit the inner tissues of plants such as fungi, bacteria, plants and even insects. Taken literally, it can include avirulent microorganisms as well as opportunistic pathogens and virulent pathogens in the early infection stages (Schulz and Boyle, 2006). Although there are diverse uses for the word endophytes, but commonly they are defined as endosymbiotic group of microorganisms that spend most or part of their lives in the internal tissues of their healthy host without causing harmful effects (Schulz and Boyle, 2005). So, we will use the term "endophytes" to describe microorganisms, mainly bacteria and fungi that can be detected at a particular moment within the tissues of plants without causing any visible disease symptoms. Endophytes can be classified into three main

categories based on plant-colonizing strategies (1) obligate endophytes are unable to propagate outside of plant tissue and are likely transmitted via seed rather than originating from the rhizosphere (Hardoim et al., 2008), (2) facultative endophytes are free living in soil but colonize the plants at appropriate conditions and (3) passive endophytes which does not actively colonize the plant, but do so spontaneously through open wounds along the plant organs (Verma et al., 2004; Hardoim et al., 2008).

Several studies have demonstrated that environmental conditions (humidity, rain, temperature...), the growing season, the phenological stage, the organ of plants, the plant cultivar and the disease infection, can influence the abundance and diversity of the endophytic communities (Materatski et al., 2019). For instance, more endophytic fungi were isolated during the rainy season compared to dry season in the leaves of *Rhizophora apiculata* and *Rhizophora mucronata* (Suryanarayanan et al., 1998). Also, Bulgari et al., (2011) reported the seasonal influence, as well as the effects of phytoplasma infection, on endophytic bacteria diversity in grapevine. The distribution of endophytes depends also from the altitude, for example Rojas-Jimenez et al., (2016) showed that in tropical wet forests of Costa Rica the richness of fungal endophytes decreases as elevation increases.

The plant organ has an influence on endophyte communities in plants. Dong et al., (2018) showed that the compositions of the bacterial endophytes of *Panax notoginseng* from aboveground parts (flower, leaf, and stem) differed from that of underground parts (root and fibril). In addition, da Silva et al. (2020) found that the diversity of the endophytic microbiota differed more between plant organs than between common bean varieties. In *Glycine max* the fungal endophytes *Ampelomyces* sp., *Cladosporium cladosporioides*, *Colletotrichum gloeosporioides*, *Diaporthe helianthi*, *Guignardia mangiferae* and *Phoma* sp. were more abundant in leaves compared to roots, whereas the fungal species *Fusarium oxysporum*, *Fusarium solani* and *Fusarium* sp. were only found in roots (Fernandes et al., 2015). The phenological stage influence on endophytic diversity was reported by Shi et al. (2014). The analysis of endophytic bacterial communities of sugar beet (*Beta vulgaris*) revealed differences in the endophytic diversity during different growth periods, with

the greatest diversity occurring during tuber growth and rosette formation (Shi et al., 2014).

### 3.1. Bacterial and Archaeal endophytes

A growing number of literatures describe the diversity of bacterial endophytes in plants, especially in crop species (Rosenblueth and Martínez-Romero 2006; Romero et al., 2014; Santoyo et al., 2016). In tomato (*Solanum lycopersicum*) leaves, endophyte communities were mainly composed of Proteobacteria (90%) with other minor phyla such as Actinobacteria, Planctomycetes, Verrucomicrobia and Acidobacteria (Romero et al., 2014). In sugar beet, the most abundant division was also Proteobacteria (98 %) with the endophyte community being composed of Enterobacteriales, Rhizobiales, Pseudomonadales, Xanthomonadales, Sphingomonadales, Flavobacteriales, Burkholderiales and Actinomycetales (Shi et al., 2014). Overall, the studies of bacterial endophytes diversity report that the Phylum of Proteobacteria ( $\beta$ ,  $\alpha$ , and  $\gamma$ -Proteobacteria) is the most dominant. The members of the Firmicutes and Actinobacteria are consistently found and other classes such as Bacteroidetes, Planctomycetes, Verrucomicrobia and Acidobacteria are rarely reported. The most commonly found genera of bacterial endophytes are *Pseudomonas* spp., *Bacillus* spp., *Burkholderia* spp., *Agrobacterium* spp., *Micrococcus* spp., *Pantoea* spp., *Enterobacter* spp., and *Microbacterium* spp. (McInroy and Kloepper, 1995; Cao et al., 2004; Rosenblueth and Martínez-Romero, 2006; Romero et al., 2014; Shi et al., 2014; Santoyo et al., 2016; Dong et al., 2018).

In the last decade many research studies had identified Archaea as a significant component of the plant, animal and human microbiomes (Janssen and Kirs 2008; Nkamga et al., 2017; Taffner et al., 2018), whereas their functions still poorly understood. Within plants, Archaea had often been found in the rhizosphere and endosphere but rarely in the phyllosphere, probably due to the difference in microenvironments conditions of these habitats (Chelius and Triplett, 2001; Müller et al., 2015). In general, plant roots and rhizosphere provide microinches of oxygen-limited conditions which probably allow colonization of Archaea in high abundances like methanogenic and ammonium-oxidizing Archaea (Chelius and Triplett, 2001; Herrmann et al., 2008). Archaea were found to have the potential to interact with plants by

plant growth promotion through auxin biosynthesis, nutrient supply, and protection against abiotic stress (Taffner et al., 2018). At a global level, plant associated Archaea were also found to influence nitrogen and carbon biogeochemical cycles by affecting denitrification and methanogenesis into the rhizosphere of several plant such as rice (Graeme and Schleper, 2006; Pump et al., 2015).

### 3.2. Fungal endophytes

Unlike mycorrhizal fungi which are rhizospheric and colonise only roots, fungal endophytes reside and grows within plant tissues and sporulate at host-tissue senescence (Stone et al., 2004). Fungal endophytes are abundant and colonize plants in various natural ecosystems. Statistical species richness and molecular phylogeny analyses indicate that the observed species numbers described in literature are only a fraction of the effective endophyte richness of a host plant (Unterseher, 2011). This highly diverse group has been identified in all plant tissues such as roots, stems, leaves, flowers, and fruit. Research into the exploitation of endophytic fungi has increased due to their beneficial impacts on plant communities and sustainable crop production (Lugtenberg et al., 2016). Two major endophytic groups, the clavicipitaceous endophytes and the nonclavicipitaceous endophytes, are reported based on their phylogeny and life history traits. Rodriguez et al., (2009) showed that nonclavicipitaceous endophytes represent three distinct functional groups based on host colonization and transmission, in planta biodiversity and fitness benefits conferred to hosts which differentiate endophytes into four functional classes. The fungal taxa of *Alternaria*, *Colletotrichum*, *Phoma*, *Phomopsis*, *Cladosporium*, *Fusarium*, *Leptosphaerulina*, *Penicillium* and *Stemphylium* were the dominant fungal endophytes found in different plants species such as medicinal plants (Huang et al., 2008) and olive tree (Materatski et al., 2019).

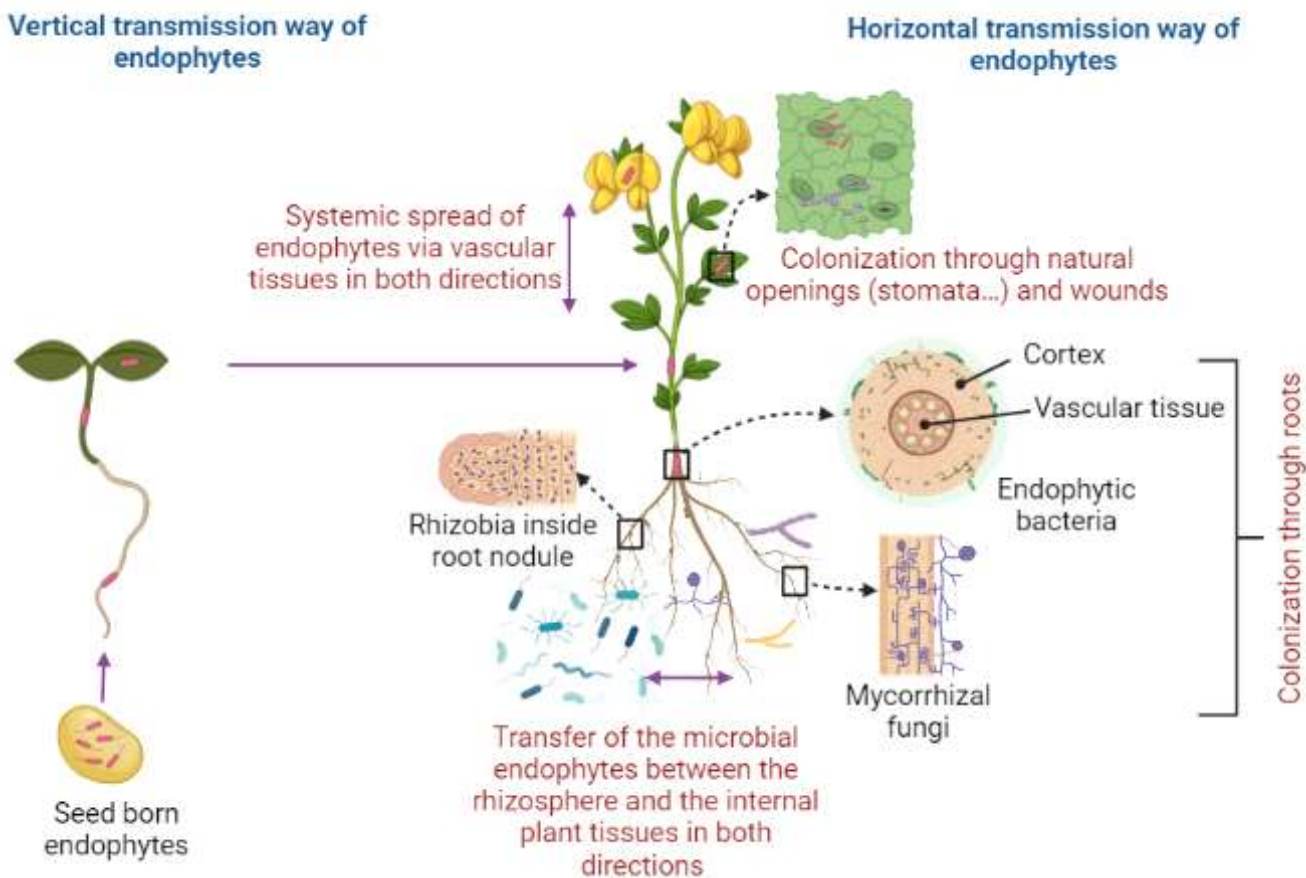
## 4. Colonization and distribution of endophytes

Endophytic microorganisms have been shown to inhabit an enormous number of wild and crop plants (Hallmann et al., 1997; Larran et al., 2001; Chowdhary and Kaushik, 2015; Llorens et al., 2019). It is important to note that plants may contain a mixture of colonizing endophytes, and not just a single species. Endophytes can be transmitted to plants through vertical and

horizontal transmission ways (Fig. 1). The vertical transmission occurred through seeds from generation to another as known in *Epichloë* species, which represent exclusively systemic

metabolites which includes various amino acids and organic acids (Canny et al., 1993).

The colonization of plants by endophytic bacteria is a complex process that implies



**Fig. 1.** Colonization and distribution of endophytes within plant tissues. The endophytic microorganisms colonize underground and aboveground internal plant tissues without causing any symptoms. Two way of transmission of endophytes are described here i.e. vertical transmission within seeds, and horizontal transmission via shoots and roots.

biotrophs of graminoid hosts (White et al., 2000). The second way of transmission is by horizontal transmission, which imply the entry of fungal and bacterial endophytes into plants through different modes such as open wound sites or breaks in the root tissues or via other natural openings in plant tissues (stomata). It was suggested that endoglucanase and endopolygalacturonase produced by bacterial endophytes were involved in degradation of localized cell wall, supporting bacterial entry through cuts at root emergence sites or the root tip (Compant et al., 2005). Endophytes predominantly colonize the intercellular spaces as these spaces are rich in minerals, containing potassium, calcium, sulphur and phosphorus, as well as various sugars and non-carbohydrate

different steps including (1) detection of exudates and motility towards roots, (2) adhesion to the root surface, (3) biofilm formation, (4) penetration in the outer root tissues, and (5) invasion of the inner plant tissues (Pinski et al., 2019). In order to invade the plant tissues, endophytic bacteria produce various molecules related for example to chemotaxis, motility, adhesion and biofilm formation, as well as cell wall degrading enzymes in order to establish a successful interaction. The colonization process is mediated by plant receptors and regulated by the interconnection of plant hormone-signaling pathways such as ethylene, jasmonic acid and salicylic acid (Pinski et al., 2019).

The distribution of endophytes within the plants depends upon the colonizing ability of

endophytes as well as site of colonization. After initial colonization, some endophytes can move to other areas of the plant by entering the vascular tissues and spreading systemically (Compant et al., 2005; Johnston-Monje and Raizada, 2011). Indeed, maize stem injection of GFP-tagging endophytes showed that several seed endophytes could spread systemically through the plant and even reaching the rhizosphere for a particular isolate of *Enterobacter asburiae* (Johnston-Monje and Raizada, 2011), which demonstrate possibly that bacterial endophytes are in permanent movement between the rhizosphere and the internal plant tissues in both directions (Gaiero et al., 2013).

## 5. Endophytes modulate plant responses to abiotic stress

In this section the main mechanisms of tolerance to various abiotic stresses induced by endophytic microorganisms in plants are included and resumed in supplementary table 1.

### 5.1. Drought stress tolerance

Drought stress is the most common constraint limiting plant growth and production all over the world. Plant express drought stress at deficient water supply related to the absence of rainfall and/or irrigation or when the transpiration rate is high under arid and semi-arid climates (Anjum et al., 2017). The responses of plants to drought stress dependent from the interaction of climatic, edaphic and biological factors including the intensity and duration of the stress, the nature of soil, and the plant genotype and microbiome (Cairns et al., 2011; Fleta-Soriano et al., 2016; Santos-Medellín et al., 2017). Drought stress has many adverse effects on plants including a decrease in fresh and dry weights, leaf area and pigmentation, relative water content and affects negatively the function of the photosynthetic apparatus (Zhou et al., 2017). Bacterial and fungal endophytes have been prospected to alleviate the adverse effects of drought stress in plants (Khan et al., 2014; Gagné-Bourque et al., 2016; Ma et al., 2017) (Fig. 2). The endophytic *Bacillus subtilis* B26 enhanced the net photosynthesis and stomatal conductance and increased the osmolyte accumulation in roots and shoots of *Phleum pratense* in comparison to non-inoculated plants. The melatonin producing *Bacillus amyloliquefaciens* SB-9 endophyte increased grapevine plant growth and was able to counteract the adverse effects of drought-

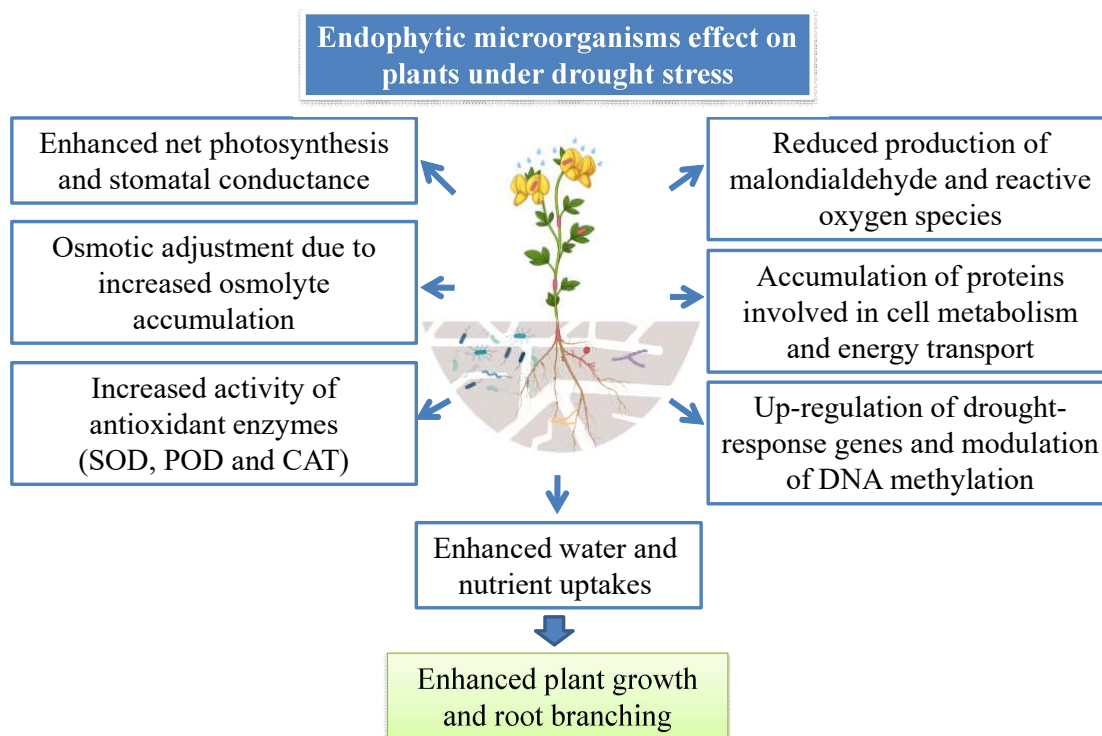
induced stress by reducing the production of malondialdehyde and reactive oxygen species (ROS) in roots (Jiao et al., 2016). Aslam et al., (2018) showed that carbonic anhydrase (CA; EC 4.2.1.1)-containing endophytic bacteria strains *Bacillus marisflavi* (WR2), *Bacillus thuringiensis* (WS11) and *Bacillus subtilis* (WL19) enhance photosynthesis and biomass of wheat seedlings under water-deficit conditions.

A proteomic analysis of the effect of endophytes on plant tolerance to drought stress showed that the relative tolerance of *Piriformospora indica*-inoculated barley plants under drought stress was explained by the detection of proteins involved in oxidative stress defense (isoform of carbonic anhydrase), in photosynthesis (Rubisco activase) and in cell metabolism and energy transport (5-methyltetrahydropteroyltri-glutamate homocysteine methyl transferase) (Ghabooli et al., (2013). The *Bacillus subtilis* B26 strain affected the whole growth cycle of *Brachypodium distachyon*, accelerating its growth rates, shortening its vegetative period, and alleviating drought stress effects by the upregulation of drought-response genes, DREB2B-like, DHN3-like and LEA-14-A-like and the modulation of the DNA methylation genes, MET1B-like, CMT3-like and DRM2-like (Gagné-Bourque et al., 2015). The *Bacillus subtilis* strain DHK induced a significant increase in plant biomass under moderate water deficit by decreasing ROS and increasing activity of antioxidant enzymes including superoxide dismutase, peroxidase, and catalase in *Zea mays* (Sood et al., 2020). Drought tolerance was also procured by *Neotyphodium coenophialum* in *Festuca arundinacea* through the accumulation of organic solutes that may play a role as cellular protectant in leaves and roots (Nagabhyru et al., 2013) and by *Ochrobactrum* sp. EB-165, *Microbacterium* sp. EB-65, *Enterobacter* sp. EB-14 and *Enterobacter cloacae* strain EB-48 consortium via the up-regulation of drought related genes like *sbP5CS2* and *sbP5CS1* in *Sorghum bicolor* (Govindasamy et al., 2020).

The gibberellins producing fungal endophyte *Penicillium resedanum* LK6 increased plant growth, fruit yield and capsaicin contents of *Capsicum annuum* under drought stress by reducing ROS production while increasing antioxidant enzymes (Khan et al., 2014). The inoculation of *Citrus reticulata* with *Penicillium citrinum*, *Aurobassium pulluntis*, *Dothideomycetes* sp. under drought constraint reduced the accumulation of ROS by increasing

the redox state of ascorbate and glutathione and promotion of antioxidant enzymes activities like ascorbate peroxidase (APX), superoxide dismutase (SOD) and glutathione reductase (GR) (Sadeghi et al., 2020). The dark septate endophytes (DSE) fungi (Paraconiothyrium strains, Phialophora sp., and Embellisia chlamydospora) isolated from xerophyte plants and inoculated to *Ammopiptanthus mongolicus* under drought stress enhanced root branching and biomass which facilitate water and nutrient uptakes (potassium and calcium) from soil, which are required for osmotic adjustment in plants (Li et al., 2018).

effective mitigation strategies are used to cope with salt stress. However, there is a need to develop simple, rapid and low-cost biological methods for salinity stress management (Shrivastava and Kumar, 2015). The use of microorganisms showed a significant role in salt stress mitigation in plants due to their properties such as high salinity tolerance, synthesis of compatible solutes, production of plant growth promoting hormones and inducing systemic tolerance in plants (Kaushal and Wani, 2016; Metoui-Ben Mahmoud et al., 2017; 2020). The use of endophytes to promote plant growth under salt stress has been studied by several researchers (Fig. 3). Tomato plants treated with 75 mM NaCl showed a decrease in growth



**Fig. 2.** Main mechanisms of drought stress tolerance induced by endophytic microorganisms in plants. CAT catalase, POD peroxidase and SOD Superoxide dismutase.

## 5.2. Salt stress tolerance

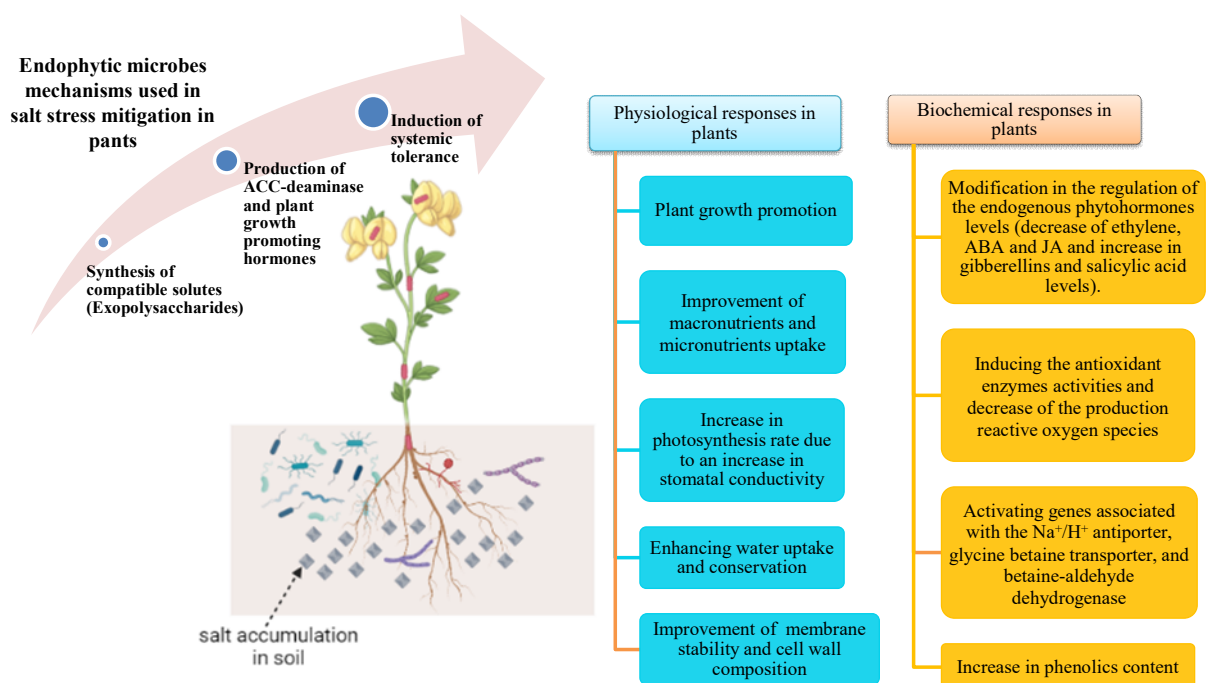
Salt stress constitutes one of the major abiotic threats for plant production worldwide. It has been estimated that 20 % of total cultivated and 33 % of irrigated lands are affected by high salinity in the world (Pitman and Läuchli, 2002). Salt stress is due to the accumulation in soil and water of electrical mineral solutes in concentrations (an electrical conductivity in the root zone exceeding 4 dS m<sup>-1</sup> at 25 °C) that reduce crops yield (Shrivastava and Kumar, 2015). A wide range of long term and cost-

parameters, photosynthesis rate due to a decrease in stomatal conductivity and transpiration at 21 days of treatment, however plants inoculated with the endophyte *Pseudomonas* spp. strain OFT5 showed an increase in plant growth due to an improvement of the uptake of macronutrients (P, K, and Mg) and micronutrients (Mn, Fe, Cu, and Zn) under moderate salt conditions by reducing stress-related ethylene levels (Win et al., 2018). The endophytic bacterium *Bacillus amyloliquefaciens* SB-9 producing melatonin increased plant

growth of *Vitis labruscana* and counteract the adverse effects of salt-induced stress by reducing the production of malondialdehyde and ROS in roots of grapevine (Jiao et al., 2016). While salt stress intensifies ethylene content in plants which inhibit significantly their growth. The use of the endophytes *Pseudomonas fluorescens* YsS6, *Pseudomonas migulae* 8R6 producing 1-aminocyclopropane-1-carboxylate (ACC) deaminase which degrades ACC, a precursor molecule of ethylene, thereby reducing the ethylene in host plant which enhanced biomass, chlorophyll contents and flowers and buds number in inoculated tomato plants in comparison to those inoculated with deficient ACC deaminase mutant strains and non-inoculated plants treated with 165 mM and 185 mM of NaCl (Ali et al., 2014). The use of *Pantoea alhagi* NX-11 enhanced salt tolerance of rice through secreting exopolysaccharides which adsorb cations such as Na<sup>+</sup> due to their negative charges and by increasing the activities of some antioxidant enzymes including, superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT) (Sun et al., 2020). Some studies focused on the sequencing of the genome of some halotolerant endophytes to understand their mechanism of salt tolerance. For example, *Bacillus flexus* KLBMP 4941 strain is a

halotolerant endophyte isolated from the halophyte *Limonium sinense* harbor multitude genes responsible for high salinity tolerance, like genes associated with the Na<sup>(+)</sup>/H<sup>(+)</sup> antiporter, glycine betaine transporter, and betaine-aldehyde dehydrogenase (Wang et al., 2017).

Soybean associated with the fungal endophyte *Aspergillus flavus* CSH1 under salt stress conditions (400 mM) showed a modification in the regulation of the endogenous phytohormones levels, manifested by significant increase in gibberellins, but a decline in the levels of abscisic acid (ABA) and jasmonic acid (JA) compared to control (Asaf et al., 2018). The same authors showed that *A. flavus* CSH1 induced plant ROS homeostasis by inducing high level of antioxidant enzymes like superoxide dismutase (SOD) and catalase (CAT) compared to non-inoculated plants under salt condition (Asaf et al., 2018). As well, Waller et al., (2005) and Baltruschat et al., (2008) showed that the root endophyte *Piriformospora indica* induced barley plant growth and attenuated the effect of NaCl-stress by activating the glutathione-ascorbate cycle and increasing the antioxidant enzymes system. Further investigations have been carried out on the effects of salinity on soybean using several endophytic fungi specifically, *Aspergillus flavus* that lead to ABA



**Fig. 3.** Main mechanisms of salt stress mitigation via endophytic microorganisms, along with plants physiological and biochemical responses to endophytes inoculation under salt stress. ACC-deaminase 1-aminocyclopropane-1-carboxylate deaminase, ABA abscisic acid, JA Jasmonic acid.



and JA reducing level in parallel with polyphenoloxidase, CAT, SOD and POD elevation (Asaf et al., 2018). Endophytic fungal pre-treatments of soybean plants by *Fusarium verticillioides* and *Humicola* sp. alleviates salinity stress effects by increasing salicylic acid and reducing abscisic acid levels (Radhakrishnan et al., 2015). The endophyte *Penicillium funiculosum* LHL06 enhanced plant growth of soybean by isoflavone biosynthesis under salt stress (Khan et al., 2011). *Aspergillus ochraceus* reduced the harmful effects of seawater on barley growth by improving chlorophyll b, total chlorophyll, and carotenoids contents in plants (Badawy et al., 2021). Under saline conditions, *Chenopodium quinoa* plants inoculation with the fungal endophytes *Talaromyces minioluteus* and *Penicillium murcianum* improved SOD, APX, and POD activity over 50 % and phenolic content by about 30 % (González-Teuber et al., 2022). Endophytic fungi can influence the concentration and profile of osmolytes in plants as a mechanism of salt stress tolerance, which increase water absorbing capacity (Pang et al., 2007), scavenging ROS, stabilizing enzymes and maintaining membrane integrity (Chen et al., 2019b).

### 5.3. Temperature stress tolerance

A temperature stress is caused by a change in the thermal state of an organism exposed to elevated (heat) or low temperatures (chilling and freezing) which induce physiological and metabolic disturbance in particular stimulate the production of ROS in plants that can cause injury or death in excessive conditions (Żróbek-Sokolnik, 2012; Muneer et al., 2016). There is a growing literature reporting a significant impact

of endophytes on plants subjected to temperature stress (Fig. 4). The inoculation of tomato plants by *Paraburkholderia phytofirmans* strain PsJN induced growth parameters along with chlorophyll content and gas exchange at both normal (25 °C) and high temperatures (32 °C) compared to non-bacterized plants with a better acclimation at 32 °C (Issa et al., 2018). Stritzler et al., (2018) characterized a novel type of extracellular polyhydroxy butyrate polymerase secreted by *Pseudomonas fluorescens* FR1 strain involved in *Triticum aestivum* growth adaptation to cold stress.

The endophytic fungal *Curvularia protuberata* strain Cp4666D isolated from panic grass growing in a non-geothermal habitat was sensitive to heat in vitro, but in association with the grass plants increase tolerance to heat confirming that tolerance to temperature stress is “habitat-adapted symbiosis” (Rodriguez et al., 2008). In addition, Chen et al. (2016) demonstrated that the inoculation of *Achnatherum inebrians* with the fungal endophyte *Epichloë gansuensis* induced positively the germination rate under low temperature (10 °C) compared to non-inoculated plants. The same authors showed differentially expressed genes involved in low temperature response, such as genes participating in the biosynthesis of alkaloids and unsaturated fatty acids in plants infected with the fungal endophyte and subjected to low temperature (Chen et al., 2016). The inoculation of barley plants by the fungal endophyte *Piriformospora indica* improve the time taken to reach flowering and maturity as well as the dry grain weight at low temperature (Murphy et al.,

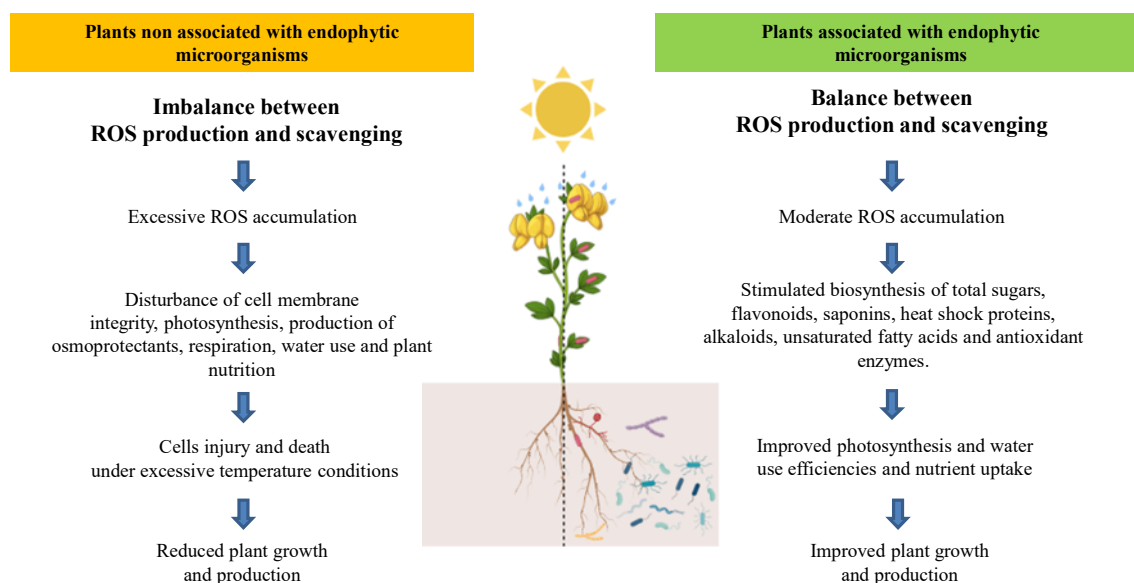


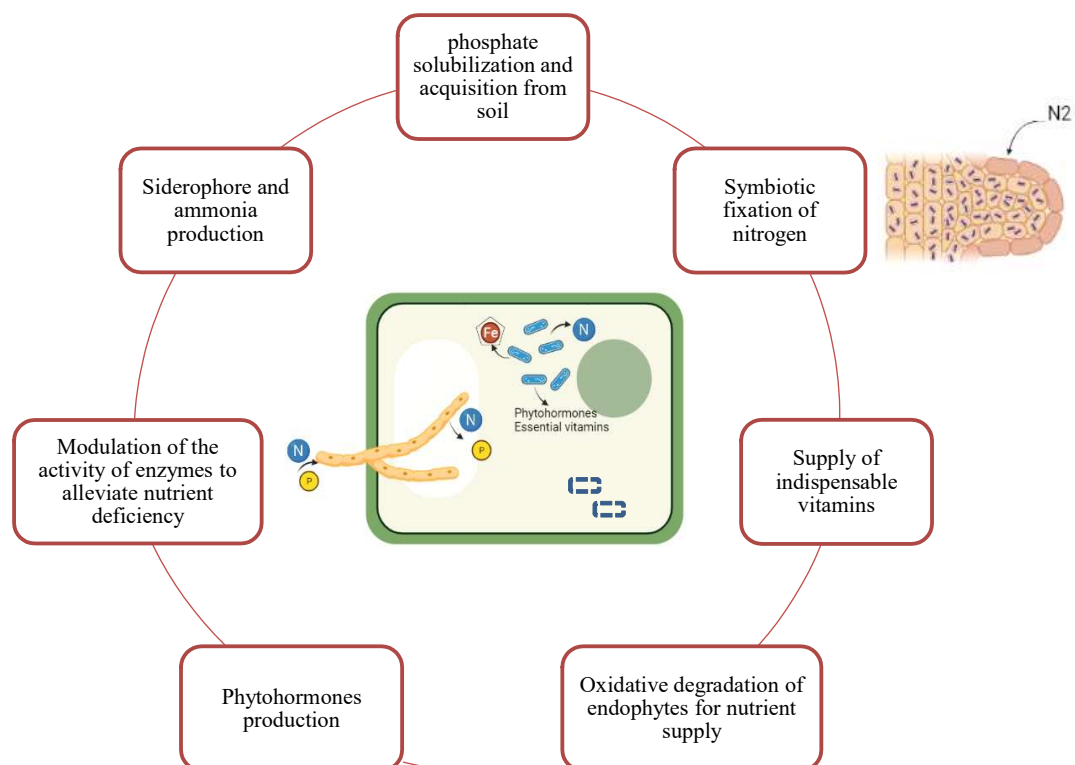
Fig. 4. Main mechanisms of temperature stress mitigation in plants through endophytic microorganisms. ROS reactive oxygen species

2014). Ali et al., (2018) showed that the interaction between *Thermomyces* sp. and cucumber plants eliminates the adverse effects of heat stress on plants by maintaining the maximum quantum efficiency of photosystem II, photosynthesis rate, water use efficiency and increase root length and induced the significant accumulation of total sugars, flavonoids, saponins, soluble proteins and antioxidant enzyme activities relatively to untreated plants. Recently, Bilal et al., (2020) showed the up-regulation of heat shock protein 90 (GmHsp90A2 and GmHsp90A1) gene expression of *Glycine max* inoculated with *Paecilomyces formosus* LHL10 and *Penicillium funiculosum* LHL06 under heat stress.

#### 5.4. Nutrient stress tolerance

Plants face particular challenges in absorbing sufficient mineral nutrients for their growth and development but at the same time dealing with toxic levels of these minerals. Nutrient stress is defined as deficiency or excess in both micronutrients and macronutrients supply in plants which seriously affects their growth, yield and quality of production. Endophytes are well known to support plant nutrition by phosphate

solubilization and mineralization, siderophore and indole acetic acid production, and the supply of indispensable vitamins (Jha et al., 2011) (Fig. 5). The well-known example of the contribution of endophytic bacteria to support plant nutrition is the example of the symbiotic association between endophytic bacteria (Rhizobiaceae) and legumes initiated by nitrogen starvation of the host plant. The biological nitrogen fixation is the conversion of atmospheric di-nitrogen (N<sub>2</sub>) by the endophytic rhizobia to ammonia (NH<sub>3</sub>), a form that can be used by legumes for growth and in return the photosynthates (C<sub>4</sub>-dicarboxylic acids as carbon and energy source) from the host are delivered to the symbiotic nitrogen-fixing bacteria (Poole and Allaway, 2000; Wang 2019). Another mechanism of nitrogen nutrition of plants supported by endophytic bacteria was elucidated by Beltran-Garcia et al., (2015). This research group demonstrated the organic nitrogen transfer from <sup>15</sup>N-labeled endophyte bacteria *Bacillus tequilensis* to the chlorophyll of *Agave tequilana* by a process that appears to involve oxidative degradation of the bacteria which support the hypothesis that some plants under nutrient limitation may degrade and obtain nitrogen from endophytic microbes.



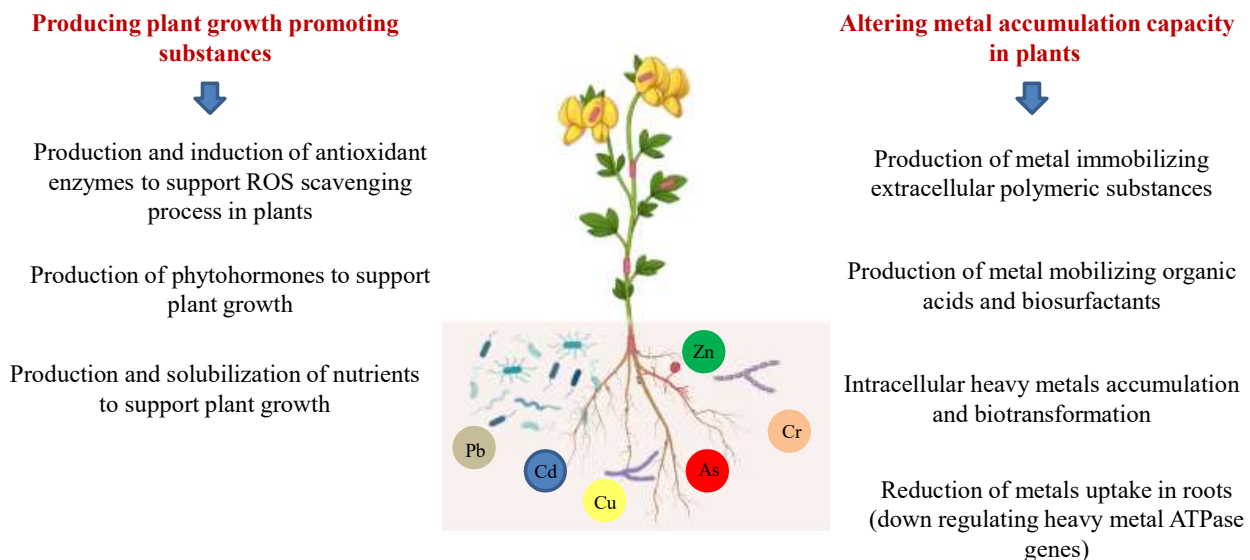
**Fig. 5.** Main mechanisms of plant nutrition support by endophytic microorganisms under nutrient deficiency. In the centre, a plant cell colonized by endophytic microorganisms that supply and synthesis a panoply of substances that support plant growth and nutrition. At the right a nodule colonized with rhizobia fixing nitrogen.

Under nitrogen deficiency, the interaction between the fungal endophyte *Neotyphodium lolii* and the perennial ryegrass showed that inoculated plants recorded significant tillers growth, less dead leaves, and they maintained their photosynthetic level compared to the non-inoculated plants (Ravel et al., 1997). Wang et al., (2018) studied also the effect of *Epichloë gansuensis* to enhance *Achnatherum inebrians* growth under nitrogen deficiency, they demonstrate that this fungal endophyte up-regulate the Glucose-6-phosphate dehydrogenase activity to alleviate the adverse effect of nitrogen deficiency. In peanut, the application of *Phomopsis liquidambari* improved growth parameters, nitrate reductase activity and micronutrient (iron and molybdenum) nutrition (Su et al., 2019). For nitrogen uptake, Christian et al. (2019) showed that *Colletotrichum tropicale* (endophyte)-inoculated *Theobroma cacao* plants have significantly greater nitrogen-15 (<sup>15</sup>N) uptake than endophyte-free plants with a significant enrichment of younger leaves. In addition, these authors showed that endophyte-*Phytophthora palmivora* (pathogen) co-infection increased plants biomass and leaves <sup>15</sup>N content compared to plants inoculated only with the pathogen (Christian et al., 2019). For phosphate solubilization the fungal genera *Penicillium*, *Aspergillus*, *Piriformospora*, *Curvularia*, and the class of symbionts arbuscular mycorrhizal fungi are well known to sustain plant phosphate nutrition (Mehta et al., 2019). At the agronomical level, the application of encapsulated *Metarhizium brunneum*, an entomopathogenic fungal endophyte, under nutrient poor conditions enhanced the biomass, leaf area, nitrogen and phosphorus contents in potato indicating fungal nutrient mobilization and transfer and was correlated with significantly improved quantum yields of photosystem II (Krell et al., 2018).

### 5.5. Heavy metal stress tolerance

Heavy metals are metallic chemical elements that have a relatively high density and are toxic to living organisms at low concentrations such as arsenic, cadmium, chromium, lead, and mercury (Sheetal et al., 2016). They are released in the environment as a consequence of the industrial, domestic and agricultural activities. Heavy metals affect plant growth and production by disturbing a plenty of vital responses via the generation of ROS. In fact, they alter the most vital process in plants i.e. photosynthesis by lipid

peroxidation of cell membranes, affecting chlorophyll biosynthesis as well as disturbing electron transport in light reactions (Rai et al., 2016). Plants developed several mechanisms to counteract heavy metal toxicity by forming phytochelatins or metallothioneins metal complex at the intra- and intercellular level for the removal of heavy metals from sensitive sites (Emamverdian et al., 2015). In addition, plants have enzymatic and non-enzymatic intracellular antioxidant systems that strengthen their metal detoxification capacity (Emamverdian et al., 2015). Several studies showed that the associations of plants with endophytes improve their resilience capacities against heavy metals toxicity through mainly two mechanisms (Fig. 6) (i) by producing plant growth beneficial substances (solubilization of mineral nutrients, production of phytohormones, siderophores and hydrolytic enzymes) and (ii) by altering metal accumulation capacity in plants (producing metal immobilizing extracellular polymeric substances, metal mobilizing organic acids and biosurfactants) (Abadi et al., 2016; Ma et al., 2016). In addition, several studies showed that bacterial and fungal endophytes exhibited an important in vitro resistance against heavy metals. For example, a high proportion of endophytic bacteria isolated from *Spartina maritima* tissues (a heavy metal bio-accumulator plant) showed in vitro resistant toward one or several heavy metals and metalloids including As, Cu, and Zn (Mesa et al., 2015). The same authors demonstrated that the inoculation of *Spartina maritima* by an endophytic consortium composed of *Micrococcus yunnanensis*, *Vibrio sagamiensis* and *Salinicola peritrichatus* enhanced its growth in heavy metals contaminated soil. Zribi et al., (2012) showed that the endosymbiotic *Sinorhizobium* sp. strains nodulating *Medicago sativa* were able to grow in soils containing up to 2.5 mM Zn, 0.3 mM Cd, 1 mM Cu and 2 mM Pb allowing normal growth of this plant legume through their bioaccumulation process of heavy metals. In their study, Guo et al., (2010) showed that heavy metal bioremediation by an endophytic bacteria strain L14 isolated from the cadmium hyperaccumulator *Solanum nigrum* have high levels of divalent heavy metals uptake exceeding 75 % for Cd (II) and Pb (II). Bacterial endophytes isolated from *Oxalis corniculata* of the species *Pantoea agglomerans*, *Agrobacterium tumefaciens*, *Bacillus pumilus* and *Kocuria rhizophila* showed highest resistance against heavy metals such as Cu, Ni, Pb and Cr and were positive for phosphate



**Fig. 6.** Main mechanisms of heavy metal stress mitigation in plants through the association with endophytic microorganisms.

solubilization, IAA, catalase activity and ammonia production demonstrating their multiple plant growth promoting traits (Mufti et al., 2015). Recently, the transmission electron microscopy (TEM) analysis showed the accumulation of metals in the intracellular environment of *Methylobacterium radiotolerans*, which was due to the expression of proteins that encode heavy metal detoxification including nickel-responsive transcriptional regulator protein NikR, cobalt-zinc-cadmium resistance protein CzcA, and copper resistance A (Photolo et al., 2021).

The fungal endophyte *Mucor* sp. decrease the negative effect of heavy metals in *Brassica campestris* plants by removing metals through biotransformation and/or accumulation in its hyphae (Zahoor et al., 2017). In addition, the isolate HEF3 of *Lasiodiplodia theobromae* isolated from *Boswellia ovalifoliolata* leaves showed high tolerance to heavy metals concentration up to 600 ppm (Aishwarya et al., 2017). Bilal et al., (2019) studied the stress-mitigating effects of *Penicillium funiculosum* LHL06 on soybean in responses to combined heavy metal (Ni, Cu, Pb, Cr, and Al) toxicity. The inoculation by this fungal endophyte reduced metals uptake in roots and shoots by down regulating heavy metal ATPase genes, inducing higher antioxidant activity and transcript accumulation of glutathione S-transferase compared to non-inoculated plants which decreased metal-induced ROS (Bilal et al., 2019).

## 6. Conclusion and future prospects

The demand of novel and effective compounds to improve crop health and production for human food and animal feed is ever growing. Microorganisms have a great diversity, a multitude of functions and produce various compounds that can be exploited for enhancing plant resilience in stressful environments. Endophytic microorganisms living inside plants throughout their life cycle have been explored for their role and potential exploitation in agriculture. Overall, the multitude of studies reviewed showed that endophytes play an important role in plant growth and development and in particular in their adaptation to various biotic stresses. Indeed, these endophytes modulate different and vital processes in plants such as photosynthesis, ROS homeostasis through modulating antioxidant system, water and nutrient uptake as well as plant phytohormones production that control plant development and reaction to environmental conditions. Microbial endophytes are increasingly examined for their ability to produce novel bioactive compounds that can be used in different fields such as agriculture, industry as well as medicine.

Plants harbor a multitude of endophytes, so it is important to understand their interactions in planta in order to better select those that cope and establish within preexisting plant microbiome for successful application in the field. Several research studies showed that many

opportunistic plant and human pathogens can be isolated from healthy plants, which constitute a challenge for the selection of safe endophytic strains. This can be managed by additional studies that decipher the mechanisms by which microorganisms can switch from their pathogenic behavior, via opportunism, to their beneficial mutualistic life style. Another, important point for the selection of valuable endophytes is to study their effect in planta in different environmental conditions to ensure their efficacy as mutualistic endophytes and avoid selecting opportunistic ones. The formulation of endophytes is another critical issue that must be mastered to overcome the challenges for the commercialization of these microorganisms. Indeed, the formulation must ensure long life period for the endophyte and facilitate its release in the environment and colonization of inner plant tissues.

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