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Review

Bacterial endophytes: The hidden actor in plant immune responses against biotic stress

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Abstract: Bacterial endophytes interact closely with plant tissues and constitute an essential part of the plant microbiome. These interactions can promote plant growth and elicit specific defense responses against abiotic stresses and pathogen attacks. In this paper, we review the role of endophytic bacteria in modulating defenses of the host rendering the entire plant more resistant to pathogens and pests. The endophyte-induced resistance will probably introduce a new factor when considering plant-pathogen interactions. The impact of the bacterial endosymbionts on the host leading to the priming state is also discussed since it confers a specific adaptation of the plant to the biotic threat.

Keywords: Priming, Endophytic bacteria, ISR, Pathogens, Signalling

1. Introduction

Plant endophytes are described as microorganisms that inhabit the internal parts of a plant and gain entrance into the root stem, leaf, flowers and seeds and they are not causing apparent harm to the host plant [1]. Conventionally, endophytes are isolated from surface-sterilized plant tissue and cultivated in nutrient-rich medium [2]. But in recent years, with the metagenomics studies development, many endophyte communities have been studied through culture-independent approaches such as the sequencing of the 16S rRNA gene and internal transcribed spacer regions (ITS1 and ITS2), the whole genome sequencing or through shotgun metagenomics studies [3-5].

Endophytic bacteria are considered a subclass of rhizospheric bacteria that have acquired the ability to invade and colonize different parts of plant tissues [2]. They play an imperative role to maintain the health of their host, as they can confer tolerance/resistance to the host plants from abiotic and biotic stresses and help in enhancing growth and yields [6-10]. Plant-Endophyte associations were the subject of study for many years. However, a complete understanding of the mechanisms utilized by plant endophytic bacteria to mitigate the negative effect of different environmental stressors remains unclear. What seems clear is that plants may recognize and select their specific microbiota with which enter in intimate association [8,11,12]. In these mutualistic interactions, the plant host provides diverse protective niches for the microbial partner, and endophytes may produce useful metabolites and signals [13,14], which can increase nutrient uptake and promote plant growth [15], induce resistance against pathogens [16-18], and insects herbivores [19], and increase plant tolerance to salinity [20], low temperature [21], heavy metals [22], contaminated chemicals [23], and other abiotic factors.

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To be able to invade, colonize and translocate in the plant's endosphere, endophytic bacteria should be equipped with specific and necessary traits [24]. Several genomic studies showed differences between endophytes and rhizosphere colonizing bacteria. Endophytes may contain genes responsible for the endophytic lifestyle [20]. A list of genes with possible roles in endophytic behavior was identified by [20,25] by comparing the complete genomes of several endophytes. Up to now, only some of those genes have been experimentally shown to be involved in endophytic colonization and it is not yet known the role of specialized genes designated for the endophytic lifestyle [26].

To establish stable mutualistic interaction with plants, endophytes produce or induce the host plant to produce metabolites that promote plant growth and help them to adapt better to the environment [14, 27]. Endophytes play an imperative role to maintain the health of their host as they interact directly with the plant system than the rhizospheric and phyllospheric bacteria [9,28,29]. The abilities of bacterial endophytes to protect against plant pathogens occurs because of either direct or indirect mechanisms. Direct mechanisms are related to the ability of endophytes to release antimicrobial compounds including siderophores, antibiotics, hydrolytic enzymes, and other secondary metabolites. On the other hand, indirect mechanisms are related to their competing relation with pathogens for space and nutrients and their ability to modulate plant defense responses [2,30].

To date, most of the research has been done assuming that the interaction of endophytes with the host plant is similar to the plant growth-promoting bacteria (PGP) present in the rhizosphere. However, a new appreciation of the difference of the rhizosphere environment from that of internal plant tissues is gaining attention [26]. This review aims to analyze the impact of the bacterial endosymbionts on the host leading to the priming state, as well as to highlight the strategies used by these microorganisms in interaction with plants, which result in physiological and biochemical changes, triggering the plant protection.

2. Biodiversity of bacterial endophytes

Several reports have described the diversity of bacterial endophytes in multiple plant species, particularly those with agronomical interest [31,32]. The diversity can be modulated by different factors related to the soil microbial communities and the host factors. The microbiome composition in the root interior is significantly less diverse than the microbiomes in the rhizosphere or in the soil [8]. The number of bacterial cells in the rot internal tissues reaches 10^4–10^8 cells per gram of root tissues, while in the rhizosphere, it is around 10^6-10^9 bacterial cells per g [33]. This suggests that roots act as a biological filter, restricting the penetration of mesospheric microbes to the plant endosphere [34]. Additionally, the plant endophyte population also depends on many other variables such as shush as plant tissue, plant growth stage, plant health, and nutritional state of the plant [11].

Proteobacteria including α, β, and γ classes, are reported to be dominant in diversity analysis of bacterial endophytes, although members of the *Firmicutes* and *Actinobacteria* are also among the classes most consistently found in the plant endosphere [2,3]. Other classes such as *Bacteroidetes*, *Planctomycetes*, *Verrucomicrobia* and *Acidobacteria* are less commonly reported as endophytes [8]. The most found genera of bacterial endosymbionts are *Pseudomonas*, *Bacillus*, *Burkholderia*, *Stenotrophomonas*, *Micrococcus*, *Pantoea*, *Microbacterium*, *Enterobacter*, *Azospirillum*, and *Serratia* [16,35-40]. All these genera, described as bacterial endophytes, are also common inhabitants of the rhizosphere. Therefore, it has been suggested that the endophyte microbiome may be a subpopulation of the rhizosphere inhabiting bacteria [8].

3. Interaction of bacterial endophytes with the host

During millions of years of coevolution with plants, bacteria have developed different traits that enable them to translocate and colonize the plant's interior [8]. Advanced metagenomic studies have revealed important findings regarding the genome of bacteria in the plant endosphere [3,24]. For instance, a genomic analysis of the endophytic

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bacterium *Verrucomicrobia* showed a reduction in genome size by almost half comparing to other soil bacteria [41]. This reduction in the genome of the obligate endosymbiotic bacteria present an adaptation to dependency on hosts for several activities [42] and can be explained by the presence of a large expansion of insertion sequences (IS) in endophytes genomes [43].

Endophyte penetration into their host plant may be mediated by a passive or active process. The passive penetration occurs mostly at the site of emergence of lateral roots or in the lesions created by deleterious organisms [11], whereas active penetration may be achieved through the attachment of bacterial endophyte to the plant cells using their flagellum and via production of several metabolites that help in penetration process. Those metabolites include mostly, exopolysaccharides (EPS), cell wall degrading enzymes and many other quorum-sensing molecules [24,44]. The presence of bacterial flagellum may mediate endophytic competence by enabling bacterial chemotactic movement and anchoring to plant surfaces [45]. [46] showed that only the endophytic bacteria containing the entire flagella machinery can colonize wheat roots efficiently while flagella-deficient mutant was hampered in colonization abilities. Genes encoding cell-wall degrading enzymes including cellulases, xylanases, cellobiohydrolases, and endoglucanase were detected in high copy numbers in the metagenome of several endophytic bacteria [46,47]. For example, the endoglucanases were shown crucial for *Azoarcus* sp to colonize inside rice roots [48]. To facilitate their entrance to the intracellular compartment and translocate within the symplast, endophytic bacteria may also secrete pectinases that degrade the middle lamella between plant cells. [49], showed that pectinase production is crucial in modulating early infection of rice by the *Bradyrhizobium* sp.

Plant microbiota may be classified in many forms such as pathogenic, epiphytic, saprotrophic, and endophytic based on the type of colonization and their roles [14]. Only a few microorganisms such as endophytic bacteria and mycorrhiza fungi can exceptionally find their way into the inner tissues of a plant. They exhibit a mutualistic association with tissues of most plants and sometimes can be slightly obligate. These endophytic microbes have been identified in many varieties of plants some of which have an agricultural interest such as rice, wheat, tomato, cowpea, maize, strawberry, chickpea, mustard, sugarcane, chili, citrus, soybean, cotton, pearl millet, and sunflower [26,50], and several wild plants [51,52].

Additionally, several studies suggest that plant genotypes have also a significant influence on the microbiome in the plant endosphere [53,54]. In certain cases, depending on the host plant genotype the endophytes may have an asymptomatic endophyte lifestyle or pathogenic [55]. For example, *Ramularia collo-cygni*, during crop development, lives as an asymptomatic endophyte, but later in the growing season can switch to be necrotrophic pathogen [56].

3.1. Metabolites implicated in the interaction host-bacterial endophyte

The entry and colonization of endophytic bacteria into the host plant is a complex phenomenon that involves a series of events starting with the crosstalk of signal molecules changed between the endophytes and their host [24]. Root exudates are rich in organic substrates such as carbohydrates, lipids, phenolics, amino acids, phytosiderophores, and flavonoids, which attract or are recognized by mutualistic microbes [57]. Microbes can use these compounds as carbon- and energy sources for growth and development. Also, some molecules from root exudates may act as signals and alter gene expression patterns in the microbe, which might influence its interaction with the host [58,59]. Flavonoids are one best described of these chemoattractants, which play an important role in the interaction with the root hair especially legume roots with rhizobia [60]. However, flavonoids are also reported to play a role in non-rhizobial endophytes, and it was showed that in the presence of these metabolites, the colonization of root in rice by the endophytic bacterium Serratia sp. was far more effective [61]. Recently, several other root exudates including sugars, amino acids, organic acids, phenolic compounds, and other secondary metabolites are reported as signal molecules secreted by plant roots, which selectively invite the

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mutualistic microbes, particularly the endophytes [24,62]. For instance, the presence of citric acid in cucumber exudates was shown to recruit *Bacillus amyloliquefaciens* SQR9 and to induce biofilm formation [63]. In another study, [64] showed that *Burkholderia phytofirmans* strain defective in oxalate utilization were observed in significantly fewer numbers compared to the wild type of strain in both maize and lupine plants that secrete moderate and low levels of oxalate, respectively.

3.2. Perception of bacterial endophytes and modulation of plant immune system

The plant immune system is well defined when describing the plant-pathogen interaction but when facing bacterial commensalism, the model of immunity is less studied. Bacterial endophytes must circumvent initial plant defenses to colonize the surface of the plant tissue and/or entry into the endosphere. Different approaches have shown that bacterial endophytes, unlike phytopathogens, can emit their microbial-associated molecular patterns (MAMPs) to avoid an overresponse of plant defenses [65]. MAPMs are known to generate different host responses such as the production of reactive oxygen species (ROS), phosphorylation cascades, and initiate transcriptional reprogramming and synthesis of secondary metabolites, through the MAMP-triggered immunity (MTI). But when endophytes enter in communication with the plant, these signals might be different. For instance, [66] showed that the conserved bacterial MAMP flagellin (flg22) can be differently recognized by the plant from two different strains of bacteria, one pathogenic (*Bacillus phytofirmans*) and other pathogenic (*Xanthomonas campestris*). It has been discovered that beneficial bacteria *Bacillus subtilis* produces subtilomycin, an antibiotic peptide, that binds its self-produced flagellin, avoiding strong plant response probably because of a non-full perception of the bacteria [67]. Additionally, the protein secretion system (SS) used by bacteria for introducing their effectors in the plant cell is also different. While pathogenic strains use type III and IV SS to deliver their virulent proteins inducing effector-triggered immunity in plants, endophytic bacteria do not use this SS or in a very low abundance [8]. Another important factor in perception and signaling in plant defense is the production and regulation ROS. These ROS might be also controlled by some bacterias by producing antioxidant enzymes like superoxide dismutases (SOD), catalases (CAT), and glutathione-S-transferases (GSTs) among others at the transcriptional level [3,68]. All these bacterial strategies are framed in the evasion of the plant response by MAMP divergence, by developing variants from the same MAMP; or degradation, by secreting other compounds that can digest somehow their MAPMs [69].

During the establishment of symbiosis between plants and their endophytes, both may modulate the expression of some genes related to the colonization processes [7,49,70]. Advancements in mutualistic symbioses research indicate that plants via nutrient monitoring plants can identify whether the invading microbe is beneficial or a parasite [70]. In a comparative genomic study, [71] showed that endosphere isolates of P. fluorescens have significantly more metabolic pathways for utilization of plant signaling compounds and an increased metabolic range that includes utilization of energy-rich nucleotides and sugars than rhizospheric isolates. Recently several works have evidenced the role of different miRNA during different pathogenic and mutualistic interactions [72,73,74]. When plants are challenged by pathogenic symbionts, the majority of miRNAs appear to either induce defense proteins or target plant detoxification pathways, thereby supporting a toxic method of killing off the pathogen. Whereas, the role of miRNAs induced in the host during the establishment of symbiotic endophytes target hormone-response pathways, protein methylation, and innate immune function [72,73,75]. A specific example of miRNA during mutualistic interaction includes the miR172c that, promotes nodulation in several plants by suppressing the translation of the ET-inducible transcription factor APETALA2 [76,77]. In general, during the establishment of symbiosis, the majority of pathways targeted by miRNAs for the plant defense system are turned off that would otherwise have obstructed the proliferation of endophytes [70].

4. Extension of plant immunity by endophytes

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Benefits derived from the microbiome present in the phyllosphere have been described already in the literature. Recently, it has been defined two concepts regarding the modification/amplification of plant immunity due to the microbiome. Considering the holobiome as an entity, the two types of extended immunity that have been proposed are direct and indirect immunity [78].

4.1. Direct interactions in the holobiont

The diversity of microorganisms in the phytosphere may influence pathogens independently of the plant immune system. Endophytes may adopt several strategies to attenuate the negative impacts of pathogens and pests on their host [2,26,65]. Those activities may be achieved by direct inhibition of pathogens since they share with them similar colonizing patterns and being in intimate contact with plants. Direct inhibition of pathogens is mainly mediated by the synthesis of inhibitory allelochemicals including siderophores, antibiotics, cell wall degrading enzymes, and volatile organic compounds, alkaloids, steroids, quinines, terpenoids, phenols and flavonoids [79-83] (Table 1) or by a quenching signal QS of pathogens [84].

Lipopeptides are among the most important classes of antimicrobial compounds produced by endophytic bacteria, which are formed by cyclic or short linear peptides linked to a lipid tail or lipophilic molecules. *Bacillus* and *Paenibacillus*-related lipopeptides are the most studied lipopeptides [85], whereas several *Bacillus amyloliquefaciens* strains have been recognized as higher lipopeptides producers [86]. The endosymbiont, *Pseudomonas viridiflava* was reported also to produce antimicrobial compound nominated Ecomycins, a lipopeptide containing unusual amino acids including homoserine and β-hydroxy aspartic acid [87]. In addition to lipopeptides, several endophytic isolates were reported also to produce other antibiotic compounds such as polyketides (surfactin, bacillomycin, fengycin, iturin, lichenysin, mycosubtilin, plipastatin, pumilacidin) produced by *B. subtilis*, polymyxins (a cyclic cationic lipopeptide) synthesized by *Paenibacillus polymyxa* [88] and many other metabolites reviewed recently such as flavonoids, quinones, alkaloids, phenols, steroids and terpenoids [89] (Table 1).

Lytic enzymes produced by the endophytes hydrolyze a wide variety of polymeric compounds, including chitin, cellulose, proteins, and lipids [8]. When endophytes colonize on the plant surface, they produce enzymes to hydrolyze plant cell walls. As a result, these enzymes also could alter the structural integrity of the fungal cell wall and thereby inhibit or kill the pathogens. These include β-1,3-glucanase, chitinase, cellulase, and protease [90]. Chitinase mediates the degradation of chitin, which is the major cell wall component of fungus. Along with other enzymes, it is active against various phytopathogens. For instance, the chitinase enzymes produced by endophytic *Streptomyces hygroscopicus* were found to inhibit the growth of different strains of fungi or fungus-like such as *Ralstonia solani*, *Fusarium oxysporum*, *Alternaria alternata*, *Aspergillus niger*, *Aspergillus flavus*, *Sclerotinia sclerotiorum*, *Hyaloperonospora parasitica*, *and Botrytis cinerea* [91]. The endophytic strain *B. cereus* 65 producing chitinase enzyme was showed to protect the cotton seedlings from root disease caused by *R. solani* [92] (Tables 1).

Endophytic bacteria are also able to produce volatile organic compounds (VOCs), another group of antimicrobial compounds with a broad-spectrum activity against phytopathogenic bacteria, fungi, and nematodes [26,93] (table 01). [94] reported that black pepper-associated endophytic *Pseudomonas putida BP25* inhibits various phytopathogens such as *Phytophthora capsici*, *Pythium myriotylum*, *Gibberella moniliformis*, *Rhizoctonia solani*, *Athelia rolfsii*, *Colletotrichum gloeosporioides*, and plant-parasitic nematode, *Radopholus similis*, by several volatile substances. In addition to the antimicrobial activity, the advantage of VOCs is their ability to facilitate interactions between physically separated microorganisms. VOCs occur as alcohols, nitrogen compounds, aldehydes, ketones, alkanes, olefins, phenols, acids, and esters [95-97]. Some of the VOCs produced by endophytes processing

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as antifungal are benzothiazole, cyclohexanol, n-decanal, dimethyl trisulfide, 2-ethyl-1-hexanol, nonanal, and pyrazine [95,98].

An additional mechanism for direct action against pathogens is the quenching of the quorum sensing (QS) required for the survival of most microbes including pathogens. The QS is responsible for the regulation of physiological activities such as cell-cell crosstalk, reproduction, biofilm formation, adaptation, mutualism, and pathogenesis [99]. Several endophytes were reported to disrupt signaling pathways of phytopathogens by quorum quenching approach [84,100]. For instance, the endophytic bacteria harbored in *Cannabis sativa L* have been found to disrupt the cell-to-cell communication of *Chromobacterium violaceum* [100]. Additionally, *Stenotrophomonas maltophilia*, *Pseudomonas aeruginosa,* and *Rhodococcus corynebacterioides* isolated from the xylem of eggplant (*Solanum melongena L.*), chili pepper (*Capsicum annuum L.*), and wild eggplant (*Solanum torvum Sw*) was also found able to degrade the 3-hydroxy palmitic acid methyl ester (3OH-PAME), a quorum-sensing molecule of *Ralstonia solanacearum* and reducing bacterial wilt in eggplant [101].

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Table 1 : Antimicrobial compounds produced by the bacterial endophytes

	Endophytes	Plant host Class	Activity	Compounds	Chemical classes	References
Antibiotics	*Pseudomonas viridiflava*	Grasse	Antifungal	Ecomycin	Peptide	[87]
	B. subtilis 168	-	Antifungal	Bacilysocin	Phospholipid	[102]
	B. thuringiensis	-	Insecticidal	β-exotoxin	Polypeptide	[103]
	Streptomyces sp. strain NRRL 30562	*Kennedia nigriscans*	Antifungal / Antibacterial	Munumbicins A, B, C, and D,	Peptide	[104]
	Streptomyces sp. strain NRRL 30566	*Grevillea pteridifolia*	Antibacterial	Kakadumycin A	Peptide	[105]
	Verrucosispora maris AB-18-032	*Sonchus oleraceus*	Antibacterial	Proximicin	Peptide	[106]
	Streptomyces sp. HK 10595	Kandelia candel	Antibacterial	Xiamycin B, Indosespine and Sespenine	Entacyclic indolosesquiterpine	[107]
	Streptomyces sp.	marine mudflat-derived actinomycete	Antibacterial	Harmaomycin	Peptide derivatives	[108]
	B. substilis		Antibacterial	Subtilin	Peptides	[109]
	Bacillus atrophaeus, Bacillus mojavensis	Glycyrrhiza uralensis	Antifungal	1,2-bezenedicarboxyl acid, Methyl ester, Decanodioic acid, bis(2-ehtylhexyl) ester	Polyketides	[110]
	Lysinibacillus,Staphylococcus ,Enterobacter, Pseudomonas, and Bacillus species	Combretum molle	Antibacterial	-	-	[111]
	Bacillus subtilis strain 1-L-29	*Camellia oleifera*	Antifungal	-	-	[112]
	Nodulisporium sp	*Myroxylon balsamum*	Antifungal	phenylethyl alcohol. alkyl alcohols alkyl alcohols (1-butanol-3-methyl, 1- propanol-2-methyl, 1- pentanol, 1-hexanol, 1-heptanol, 1- octanol, 1-nonanol	esters, ketones, benzene derivatives, a terpenoids, hydrocarbons.	[113]

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VOCs	*Enterobacter aerogenes*	*Maize*	Antifungal	2,3-butanediol	-	[114]
	Pseudomonas putida BP25	-	Antifungal/antiparasitic	-	-	[94]
	Bacillus velezensis ZSY-1,	Chinese catalpa	Antifungal	2-tridecanone, pyrazine (2,5-dimethyl), benzothiazole, and phenol (4-chloro-3-methyl)	ketones, alcohols, and alkanes	[115]
	Bacillus spp	-	Antifungal	1-Hexadecanol, Hexacosyl acetate, Tryphenylphosphine oxide , 1,3-Propanediol, 2-methyl, dipropanoate, 1,4-Pentadiene , Hydroxyurea , Decyl trifluoroacetate ,Pentadecane , 4-Ethyl-1-octyn-3-ol, Tridecane Benzothiazole, N,N-Dimethyldodecylamine , 1,3-Butadiene, Dodecane, 2-Undecanone IR-(+)-a-pinene	-	[116]
	Bacillus subtilis DZSY21	Eucommia ulmoides	Antifungal	2-Methylbutyric acid, 2- heptanone, and isopentyl acetate	-	[117]
Enzymes	*B. cereus* 65	mustard	Antifungal	chitinase	-	[92]
	Lysobacter enzymogenes	Antifungal	Antifungal	1, 3-glucanase	-	[118]
	Streptomyces hygroscopicus			chitinase	-	[91]
	Bacillus pumilus JK-SX001	*Populus*	Antifungal	cellulases and protease	-	[119]
	Bacillus sp., Micrococcus sp., and P. polymyxa	*Panax ginseng- and Plectranthus tenuiflorus*	Antbacterial	amylase, esterase, lipase, protease, pectinase, xylanase, and cellulase	-	[120]
	Paenibacillus sp and *Bacillussp*	***Lonicera japonica***		cellulase and pectinase	-	[121]

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4.2. Indirect interactions in the holobiont

Indirect interactions associated with microbiota comprise the induction of plant defenses. This induction is performed by stimulation of defenses through induced systemic resistance (ISR) or more accurately proposed in De Kesel et al 2021 [122], endophyte-induced resistance (E-IR). Each interaction or group of interactions can develop different strategies inducing resistance depending on the pathosystem.

In general, the priming process depends on either JA, SA, ET, or a combination of these signaling pathways [17]. Two types of induced defenses were proposed, ISR and SAR depending on the hormone implicated and the type of the elicitor [123] (Pieterse et al., 1998). Accordingly, ISR is elicited by rhizobacteria or other non-pathogenic microorganisms, while SAR is elicited by pathogens or chemical compounds [124]. Further, the signal transduction pathway of ISR is regulated by the JA/ET and is associated with the expression of the gene encoding plant defensin 1.2 (PDF1.2), while SAR is controlled by the SA-dependent signaling pathway and characterized by the expression of genes encoding pathogenesis-related (PR) proteins, including many enzymes, such as 1, 3-glucanases and chitinases [125-128]. Besides this, numerous studies showed that ISR triggered by endophyte and other rhizobacterial strains may be dependent on SA and dependent or not on JA/ET. Dependence on both SA- and JA/ET-signaling pathways was reported by Niu et al., (2011) [129], the ISR mediated by Bacillus cereus strain AR156 requires both the SA and JA/ET signaling pathways and NPR1. Whereas the treatment of tobacco roots with *P. fluorescens* CHA0 triggers the accumulation of SA-inducible PR proteins (chitinase and b-1, 3 Glucanase) in the leaves [130]. In another study, [18], showed that the ISR mediated by the root endophytic bacterium Mi*cromonospora* against *B. cinerea* is dependent only on JA/ET pathway (Table 02).

The modulation of signaling and defense components during endophytic colonization may result in the activation of the enhanced resistance. Besides, the communication of endophytic communities with the host plant can activate some silent gene clusters leading to the synthesis of novel secondary metabolites [26, 131-133]. The ability of endophytes in enhancing plant defenses can be assigned to the interaction of the host plant with the bacterial cell themselves or their metabolites [134]. A numerous study indicated that ISR can be trigged through several compounds produced by endophytes such as phytohormones, lipopeptides, pyocyanin, siderophore, and VOCs [135-138]. ISR triggered by endophytic bacteria can protect the host against a wide range of pathogens including soilborne pathogenic fungi [139-141], biotrophic pathogens [142,143], viruses [144-146], nematodes [147], and insect herbivores [148,149].

The potentiated responses induced by bacterial endophytes include a variety of defense strategies [150]. These strategies include different mechanisms as illustrated in Figure 1 and discussed below.

4.2.1. Induction of Pathogenesis-related proteins (PRs) and antioxidant enzymes

Pathogenesis-related proteins (PRs) are well known for their role in acquired resistance that is induced in association with necrotic lesions in plants [151,152]. Different studies evidenced the ability of some bacterial endophytic strains also to induce PR activity and eventually increase resistance against a wide range of pathogens [153-155]. Among them, β-1,3-glucanases (PR-2 family) and chitinases (PR-3 family) are the most described [140]. [156] showed that the endophytic strain *Bacillus pumilus* SE34 triggered ISR in tomato plants by a sequence of steps starting with the elaboration of structural barriers, and production of toxic substances such as phenolic compounds and β-1,3-glucanases. The endophytic bacteria B. amyloliquefaciens strain TB2 showed an excellent control effect on litchi downy blight disease caused by Peronophthora litchi through the production of 1,3-glucanase and chitinase [153]. In another study, the endophytic actinobacteria isolated

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from wheat tissues up-regulates defense genes like PR-1 and PR-4 as well as PDF1.2 and Hel genes of the jasmonic acid/ethylene (JA/ET) pathway in Arabidopsis thaliana in response to *Erwinia carotovora* subsp. Carotovora challenge [157]. Recently, endosymbiotic bacteria *Bacillus* spp. was reported to produce antifungal lipopeptides (iturin and fengycin) and induce pathogenesis-related genes, including PR-1 and PR-4 in maize [134] (Table 2).

Besides PPRs, several other defense-related enzymes including antioxidant enzymes such as superoxide dismutase (SOD), peroxidase (POD), polyphenol oxidase (PPO), phenylalanine, and ammonia-lyase were shown important in the induced resistance of several endophytes [143,158-160]. [143] showed a significant increase in antioxidant enzymes including superoxide dismutase, catalase, peroxidase, and PPO 24 hours after inoculation of the endophytic bacterium *B. subtilis* in tomato plants. The inoculation of banana plantlet with the endobacterium *S. marcescens* strain UPM39B3 induced the production of host defense enzymes such as peroxidase, PPO, PAL, total soluble phenols, and lignothioglycolic acid and protect against *Fusarium* wilt disease [161].

4.2.2. Stimulation of plant secondary metabolism

During the plant-endophyte interactions, significant changes appear in the secondary metabolism of both plant and microsymbiont and these changes could be because of (a) the induction of host metabolism by the endophyte, (b) the induction of endophyte metabolism by the host, (c) host and endophyte partially share parts of a specific pathway (d) the host metabolizes products from the endophyte and (e) the endophyte can metabolize secondary compounds from the host [162,163].

Phytoalexins are a group of plant antimicrobial molecules with a low molecular weight [128], and contain many substances, some of which are terpenoids and flavonoids among many others. Almost of studies have concentrated on the production of phytoalexins when triggered by pathogens [164]. The production of phytoalexins moderated by endophytes is still a new research area. Findings revealed that mycorrhizal and rhizobacterial root colonization impact significantly phenolic compounds, alkaloids, terpenoids, and essential oils composition in plants [165-167]. [167] demonstrated that flavonoids, phenolics, and anthocyanins were the modified secondary metabolites associated with delayed postharvest fungal growth on blackberries treated with the *Rhizobacterium* N17.35. Other secondary metabolites such as camalexin and glucosinolates were also quantitatively changed in Arabidopsis plants associated with *Pseudomonas fluorescens* SS101 [168]. In maize, significant changes in benzoxaninones were observed in plants associated with rhizobacterial colonization. Root inoculation with *P. putida* KT2440 induced metabolic changes and the early responses were via JA- and ABA-dependent pathways. Lastly, benzoxaninones were differentially abundant in roots 3 days after treatment [169].

The abilities of bacterial elicitors like peptides, glycoprotein, lipopolysaccharides and to trigger plant defense mechanisms and increase secretion of plant secondary metabolites were reported in several studies. In potato tuber cells, fengycin treatments resulted in activation of phenylpropanoid pathway metabolism [170]. Moreover, N-acyl-homoserine lactones (AHLs), quorum sensing molecules of several bacterial groups were also reported to stimulate an accumulation in phenolic compounds, oxylipins and SA in several plant species [171,172].

Numerous findings have demonstrated that endophytes assist the host plants in controlling the amount of ROS and defend the plants from the harmful consequences of ROS. This may be explained by the ability of endophytes to produce several metabolites in particular antioxidants enzymes and phytohormones [173,174]. For instance, *Festuca arundinacea*, *Festuca rubra* and *Elymus dahuricus* under different stress conditions were all reported to contain higher levels of antioxidants and phenolic compounds than endophyte-

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free plants [175]. A high number of genes encoding enzymes involved in ROS-scavenging were detected in the genome of several bacterial endophytes including *Enterobacter sp*. 638 [176], *Gluconacetobacter diazotrophicus* [68], and *Serratia marcescens* RSC-14 [177]. Also, auxins that could be considered as relevant compounds that mediate plant cells' responses to ROS were produced by several endophytes [2,174,178]. For instance, indoleacetic acid (IAA) and other related compounds have been isolated from different bacterial endophytes including *Pseudomonas spp., Ochrobactrum* spp., *Bacillus spp*., *Arthrobacter, Enterobacter,* and *Klebsiella spp.* [179-182]. Nevertheless, there is scarce knowledge regarding the role of auxins and auxin-related compounds produced by endophytic microbiomes to support plant growth or defense and influence plant-endophyte interactions.

The endophytic microbiome may also metabolize specific plant-synthesized compounds [183] and induces the accumulation of other chemical compounds [184]. For example, ethylene is considered a gaseous plant growth regulator that may influences plant growth and responses to environmental signals [185-187]. Bacterial endophytes help to alleviate and enhance the resistance of plants to abiotic stress indirectly by lowering ethylene levels, especially during stress, when ethylene concentration increases [8,11]. Some bacterial endophytes use 1-aminocyclopropane-1-carboxylate (ACC), the immediate precursor of ET, as a carbon and nitrogen source by producing ACC deaminase, thereby preventing ethylene signaling [188].

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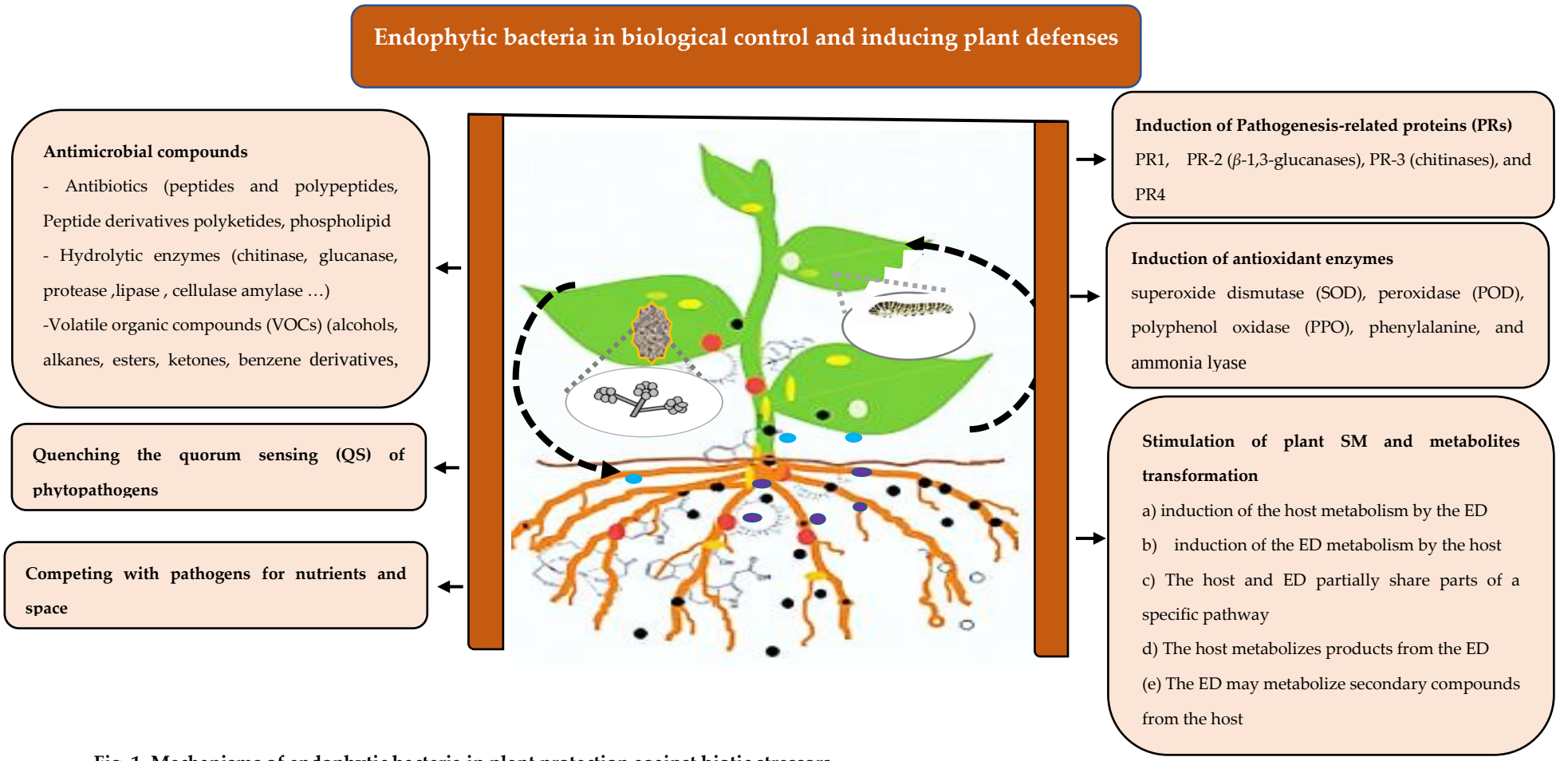

Fig. 1. Mechanisms of endophytic bacteria in plant protection against biotic stressors.

Endophytic bacteria may protect their host both directly, by producing amicrobial compounds including antibiotics hydrolytic enzymes and volatile organic compounds , or indirectly, by inducing plant defenses such as induction of pathogenesis related proteins (PR-1,PR-2,PR-3, and PRR-4 families),antioxidant enzymes and stimulation of the secondary metabolisms of both the host and the bacterial endophyte .ED:endophyte,SM; Secondary metabolism

Table 2 : different mechanisms of defenses induced by Endophytic bacteria

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Endophyte	Signalling pathway	Induced defenses	Plant pathogens	Host plant	Reference
B. pumilus SE34	-	Elaboration of structural barriers, production phenolic compounds and β-1,3-glucanases.	*Fusarium oxysporum* f. sp. *radicis lycopersici*	Tomato	[156]
Serratia plymuthica	-	Enlarged callose-enriched wall appositions at sites of potential pathogen penetration and accumulation of an osmiophilic material in the colonized areas	*Pythium ultimum*	Cucumber	[139]
B.mycoides	-	Increased activity of B-1,3-glucunase, chitinase, peroxidase and pathogenesis related proteins.	*Cercosporonbeticola Sacc*	*Sugar beet*	[189]
Bacillus subtilis GB03 and *Bacillus amyloliquefaciens* IN937	ET pathway	-	*Erwinia carotovora* subsp. carotovora	*A. thaliana*	[136]
Actinobacteria	JA/ET pathway	Up-regulation of defense genes , *PR-1* , *PR-4* as well as *PDF1.2* and *Hel* genes.	*E. carotovora subsp. Carotovora*	*A. thaliana*	[157]
B. amyloliquefaciens strain TB2		Increase PPRs production including 1,3-glucanase and chitinase	*Peronophthora litchi*		[153]
Bacillus cereus AR156	Simultaneous activation of SA- and JA/Et-Dependent signaling pathways	Activation of some defense-related genes including *PR1*, *PR2*, *PR5*, and *PDF1.2*	*Pseudomonas syringae pv.tomato*	Tomato	[129]
Bacillus B014	-	Increase in the activities of the defense-related enzymes phenylalanine ammonia lyase, peroxidase and polyphenol oxidase when challenged with the pathogen	*Xanthomonas axonopodis pv. dieffenbachiae*	Anthurium	[190]
Enterobacter radicincitans DSM 16656	Both SA- and JA/Et-Dependent Signaling Pathways	Accumulation of PR1, PR2, PR5, and PDF1.2 transcript 24 h after treatement with the endophyte	-	*A. thaliana*	[191]
Bacillus spp	-	Up-regulation of pathogenesis-related genes	-	Maize	[134]
B. amyloliquefaciens S499	-	Induction of lipoxygenase pathway (accumulation of transcripts of genes corresponding to the two isoforms, *Tom LOXD* and *Tom LOXF*	*Botrytis cinerea*.	Tomato	[192]
Pseudomonas fluorescens PICF7	-	Induction of olive genes potentially coding for lipoxygenase 2, catalase, 1-aminocyclopropane-1-carboxylate oxidase, and phenylananine ammonia-lyase.	Verticillium wilt	Olive	[193]

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B. amyloliquefaciens strain FZB42	-	Higher expression of PDF 1 and 2	*R.solani*	Lettuce	[194]
B. amyloliquefaciens strain Blu-v2	-	Produces lipopeptides that elicits ISR in plants against fall armyworms	*Spodoptera fruigiperda*	Hosta	[148]
Micromonospora spp.	JA/ET pathway	Induction of jasmonate-regulated defenses (PINII and Lox A)	*B. cinerea*	Tomato	[18]
P. fluorescens WCS417r	JA/ET	Increased expression of LOX2 , PDF1.2 and HEL	chewing herbivores	*A.thaliana*	[195]
P. simiae WCS417r	JA/ET	Elicits higher expression of the JA/ET dependent ORA59-branch than the JA-dependent MYC2 branch, and enhances the synthesis of camalexin and aliphatic glucosinolates (GLS)	leaf-chewing herbivores	*A. thaliana*	[196]
Bacillus sp	JA	Higher levels of JA, an octadecanoid-derived, defense-related phytohormone and JA-related genes	beet armyworm *Spodoptera exigua*	Cotton	[197]
Streptomyces spp	-	Upregulation of PR10, NPR1, PAL and LOX2	-	-	[198]
B.pumilus	-	High expression levels of different genes including PR protein1, PR protein10, chitinase class III, phenylalanine ammonia lyase, stil-bene synthase, chalcone synthase, antranilate synthase, callose synthase, Glutathione S-transferase, and b-1,3 glucanase.	*P. chlamydospora*	Grapevine	[199]
B. subtilis	-	Increase in antioxidant enzymes including superoxide dismutase, catalase, peroxidase, and PPO	*Xanthomonas campestris* pv. *vesicatoria*	Tomato	[143]
Bacillus amyloliquefaciens strain MBI600	SA pathway	Induction of the SA signaling pathway in tomato after MBI600 treatment, and discrete gene expression patterns in plant response to TSWV and PVY infection.	*Tomato spotted wilt virus and Potato virus Y*	Tomato	[145]
Azospirillum sp. B510	ET signaling is required for endophyte-mediated ISR	Induces systemic disease resistance in rice without accompanying defense-related gene expression	-	Rice	[74]
Bacillus cereus	JA	Increase JA contained in leaves and roots of	*Ralstonia syzigiisub sp.*	Tomato	[200]

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Serratia nematodiphila TLE1.1		tomato significantly until 12 days after pathogen innoculations			

5.Conclusions and perspective

Nowadays, plant immunity is prone to be considered in terms of a whole system including the action and interaction of a complex holobiome, in which plant and microbes in the phytosphere may prepare the final output when facing biotic stress. In the present study, we have revised the actions exerted by bacterial endophytes in protecting plant health. Moreover, we would like to attract attention to the function of the bacterial endophytes as actors of the ISR and more specifically, in priming defenses. It is known that primed defenses generate exceptional protection with low physiological cost in the plant. Although the studies around this subject is increasing, the mechanisms involved in the joint action of plant-endophyte against biotic stressors are still ongoing, due to the difficulty in working with one specific endophyte strain separately from others sharing the same niche. Several issues are now open in this new field of research. One of these is the choice of studying the action of one endophyte or the combination of several endophytes (which indeed may be closer to the real situation in nature) in induced resistance against biotic stressors. Or perhaps isolate one strain that can improve plant immunity in different plant species. This can be considered as a three-way interaction study (endophyte-plant-pathogen/pest), gaining more complexity to the experimental system, since it is needed to know the specific interaction with the plant as the place where the microbes converge.

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