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Mini Review

Bio Avengers: How do Endophytic Microorganisms Alter a Plant's Defense Mechanisms?

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Abstract

Endophytic microbes i.e. bacteria, fungi, and actinomycetes live inside the plant tissues without causing any harmful effect on them. Recently, research has been conducted on endophytic microbes to enhance agriculture and environmental sustainability. Endophytes stabilize a close association with their host, which leads to major changes in plant physiology. Endophytic microbes and pathogens use the same strategies for entering the host cell. This condition may create competition between the endophytes and the pathogen. Therefore, host plants develop strategies to allow the entry of specific microorganisms. Additionally, endophytic microorganisms may temper their own genetic structure to survive and avoid the host defence machinery. The plant-endophyte symbionts promote direct and indirect defences to host plants. This plays an essential role in modulating plant defences against various stresses, particularly biotic stress. In this minireview, we highlight the interaction of endophytic microbes with their host. As well as the role of endophytic microbes in the enhancement of plant defence systems

More Information

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Introduction

Plant endophytic microbes can colonize and establish their lives inside the inner sections of plants, including roots, stems, leaves, flowers, and seeds, without evidently harming the host plant [1]. Thus, endophytic bacteria are protected from external stress, suffer less competition from other microbes, and have better access to nutrients [2]. Therefore, endophytes have a more direct and strong effect on plants than rhizosphere and phyllosphere microorganisms. Plant intercellular gaps are favourable places for endophyte proliferation because they are rich in nutrients such as potassium, calcium, sulphur, phosphorus, chlorine, various amino acids, organic acids, and carbohydrates [3]. Endophytic microbes modules the plant's immune system by direct or indirect mechanisms. They directly benefit the plants by promoting their growth and development, while in an indirect way, they reduce the incidence of plant disease. Moreover, endophytes also improve the seedling growth and survival by providing resistance against biotic and abiotic stress. This minireview starts with the distribution of endophytic microbes and how they modulate the plant immune system during stress conditions.

Distribution of endophytic microbes on plant

Endophytic microbes can be present in different areas of plants such as the phyllosphere (above-the-ground part) and rhizosphere (below-the-ground part). The phyllosphere and rhizosphere both have different microbial communities, which modulate through the characters of each section. In the rhizosphere region, the microbial diversity modulates through several factors related to the soil microbial communities and the plant morphology. The microbial diversity inside the root tissue is lower as compared to rhizospheric soil [4]. According to Bulgarelli et, al. 2013 [5], the number of bacteria in the rot tissues was 10^4 – 10^8 cells/g of root tissues, while in the rhizosphere, it was 10^6 – 10^9 cells/g. This study concluded that roots act as biological filters, which restrict the entry and penetration of mesospheric microbes into the endospheric environment. Moreover, in the phyllosphere, endophytic microbes are lower as compared to epiphytic microbes, with an average of 10^6 – 10^8 cells/g of leaf material [6]. The phyllosphere is in continual touch with the environment, serving as an essential source of bacteria that interact with the plant surface [7]. Moreover, the distribution of endophytic microbes also depends on the physiological stages of the plants [8].

Besides all characters endophytic bacteria involved also do the quorum sensing for establishment of colonisation in host tissue. Bacterial Quorum Sensing (QS) is the mechanism that enables chemical signals to be sent between cells. This phenomenon happens in a particular bacterial habitat when there is a high enough cell density. It is now established that both Gram-positive and Gram-negative bacteria use this chemical communication mechanism. The synthesis and movement of signalling molecules into the intercellular space, referred to as Autoinducers (AI), are involved in this phenomenon. Autoinducers such as cyclodipeptides or N-Acyl Homoserine Lactones (AHL) are synthesized by gram-negative bacteria typically (Schenk and Schikora, 2015). Many genes regulated by QS, such as those involved in virulence, biofilm formation, chemotaxis, and many more, are activated or deactivated by the perception of QS molecules in bacteria [9].

Depending on their structure, AI molecules can move by active or diffusion from the cytoplasm to the outside of the cell. The conjugative transfer of plasmids by antibiotics, the replication of bacterial DNA, energy metabolism, enzyme synthesis, bioluminescence, and the motility of microorganisms are among the cellular processes that QS molecules control [10]. The ability to silence QS mechanisms also referred to as quorum quenching (QQ), is possessed by the QS system inhibitor (QSI), a synthetic or natural compound. There are various ways to achieve QQ, including blocking receptors that recognize AHL molecules, interfering with the synthesis of signalling molecules, enzymatically breaking down molecules, inhibiting gene expression, and using antibodies and macromolecules like cyclodextrins to intercept AIs [11].

Reshapes the plant's immune response

When discussing the relationship between a plant and a pathogen, the plant immune system is well characterized. While the model of immunity is less researched when considering bacterial commensalism. Endophytic microbes must overcome initial plant defences to colonize the surface of plant tissue and/or enter the endospheric region. Several studies have suggested that endophytic microbes possess Microbial-Associated Molecular Patterns (MAMPs) such as plant pathogens, to overcome the plant defence response [12]. The interaction of pathogen's MAMPs with plants develops different host responses, including the generation of reactive oxygen/nitrogen species, initiating transcriptional reprogramming, phosphorylation signalling, and synthesis of secondary metabolites during the MAMP-Triggered Immunity (MTI). However, in the case of endophytic microbes, the plant's signal during MTI may be different as compared to the pathogen entering. A study suggested that conserved MAMP flagellin (flg22) can be recognised differently through the plants in two different strains of bacteria such as *Bacillus phytofirmans* and *Xanthomonas campestris*. Among both *Bacillus phytofirmans* is a pathogenic bacteria while *Xanthomonas campestris* is a non-pathogenic bacterium [13]. Moreover, *Bacillus subtilis*, a beneficial bacteria produces an antibiotic subtilomycin. This antibiotic binds with its own producing flagellin protein, which escapes the plant immune response and at this condition, *Bacillus subtilis* easily colonised in plant internal tissue. The binding of subtilomycin with flagellin hides the full perception of the *Bacillus subtilis* and helps in avoiding the plant immune response [14].

Plant and endophytic microbes both modulate their gene expression related to entrance and colonisation during the symbiosis process. A study reveals that endosphere isolates of *Pseudomonas fluorescens* have more metabolic pathways than rhizosphere isolates, which can produce more metabolites for the plant for signaling events during plant-endophyte symbiosis [15]. Besides that, different miRNAs have a significant role during several pathogenic and mutualistic interactions [16]. Additionally, endophytes and plants both may modulate the expression of colonisation-related genes during the establishment of plant-endophyte symbiosis. Many pathways targeted by miRNAs for plant defense are suppressed or modulated during the establishment of symbiosis [17]. Most miRNAs that target plants that are infected with pathogenic symbionts seem to primarily function by triggering defence proteins or by focusing on detoxification pathways to eradicate the pathogen. In contrast, during the development of symbiotic endophytes, the host produces miRNAs that target hormone response pathways and innate immune activity, therefore strengthening plant immunity [18,19]. A miR172c, which promotes nodulation in some plants by inhibiting the translation of the ET-inducible translation factor APETALA2, is one example of miRNA during mutualistic interaction [20]. Upregulation of the miRNA- E4D3Z3Y01BW0TQ during AM fungal infection leads to disruption of the Gibberellic Acid (GA) signalling pathways, which is known to inhibit the reciprocal binding [21].

Different sets of gene expression can be stimulated by the host during the invasion process by distinct bacteria. For instance, most plant defence mechanisms that target miRNAs and would typically inhibit endogenous proliferation are prevented from establishing during symbiosis [22]. Lateral gene exchange has been crucial in acquiring traits and enhancing genetic variations for plant endospheric colonization and the production of secondary metabolites, which are vital for both partners [22]. Hemagglutinin, hemolysin, and iron/amino acid transporting genes are described as being present in endophytic Enterobacter sp., which are necessary for endophytic and plant communications [23].

Overall, most of the pathways that miRNAs target for plant defense are turned off during symbiosis establishment, which facilitates the entrance of the beneficial endophyte [24].

Furthermore, bacteria employ a distinct protein Secretion

System (SS) to transfer their effectors into plant cells. Type III and IV stem cells (SS) are employed by pathogenic strains to transfer their virulent proteins and induce effector-triggered immunity in plants. In contrast, endophytic microbes either do not use this SS or only use it very rarely [25]. Another essential aspect of plant defense sensing and signaling is ROS generation and control. Certain endophytic microbes can also regulate these ROS by transcriptionally generating antioxidant enzymes such as Glutathione-S-Transferases (GSTs), Superoxide Dismutase (SOD), and catalases (CAT) [26]. All these endophytic tactics are based on evading the plant reaction through MAMP divergence or creating variants from the same MAMP, or degradation, which involves secreting additional substances that can digest their MAPMs [27]. These strategies allow endophytic microbes to successfully dodge the plant response and remain in the host environment.

Extension of plant immunity by endophytes

Currently, two types of immunity have been proposed by several researchers in plants during the endophytic microbe's interaction [28]. These two types of immunity are direct and indirect immunity.

Direct immunity: Plant immune system resistance to infections may not be affected by the great diversity of endophytes in the phyllosphere. Endophytes have a variety of strategies at their disposal to reduce the harm pests and diseases cause to their host [29,30]. Since infections and plants have close interaction and similar colonization tendencies, these actions can be accomplished by directly inhibiting pathogens.

The major mechanisms through which infections are directly inhibited include quenching signals from the pathogens or inhibitory allelochemicals such as quinines, terpenoids, phenols, siderophores, antibiotics, enzymes that break down cell walls, volatile organic compounds (VOCs), alkaloids, and steroids. These pathogen-quenching signals or inhibitory allelochemicals are essential for defending plants against infections [31]. Some antimicrobial compounds produced by endophytic microbes are given in Table 1.

Indirect immunity: The development of plant defense is a result of indirect interactions linked to microbiota. The process of inducing resistance is known as induced systemic resistance (ISR) or, more precisely, endophyte-induced resistance (E-IR) [32]. The interaction between plants and endophytes can depend on the pathosystem and it can develop different strategies such as resistance, and defense. Basically, two types of induced systems are reported in plant systems. First is induced systemic resistance (ISR) and second is systemic acquired resistance (SAR), and both systems depend on the type of elicitor and hormone production [33]. The induced systemic resistance (ISR) is initiated by rhizobacteria or non-pathogenic microorganisms, while SAR is induced by pathogens or chemical compounds. Moreover,

Table 1: Antimicrobial compounds produced by endophytic microbes and their host plant.

S.N.	Endophytes	Host plant	Compounds	References
		Antifungal activity		
1	Pseudomonas viridiflava	Grass	Ecomycin	Miller, et al. 2001 [31]
2	Streptomyces sp. strain NRRL 30562	Kennedia nigriscans	Munumbicins A, B, C, and D,	Castillo, et al. 2002 [39]
3	Bacillus atrophaeus, Bacillus mojavensis	*Glycyrrhiza uralensis*	1,2-bezenedicarboxyl acid, Methyl ester, Decanodioic acid, bis(2-ehtylhexyl) ester	Mohamad, et al. 2018 [40]
4	Nodulisporium sp.	Myroxylon balsamum	phenylethyl alcohol. alkyl alcohols alkyl alcohols	Mends, et al. 2012 [41]
5	Bacillus pumilus JK-SX001	Populus	Cellulases and protease	Ren, et al. 2013 [42]
6	Enterobacter aerogenes	Maize	2,3-butanediol	DAlessandro, et al. 2014 [43]
7	Bacillus velezensis ZSY-1,	Chinese catalpa	2-tridecanone, pyrazine (2,5-dimethyl), benzothiazole, and phenol (4-chloro-3-methyl)	Gao, et al. 2017 [44]
8	Bacillus subtilis DZSY21	Eucommia ulmoides	2-Methylbutyric acid, 2-heptanone, and isopentyl acetate	Xie, et al. 2020 [45]
9	*Paecilomyces sp.*	*Moringa oleifera*	cis-13-Octadecenoic acid, methyl ester, 1-Heptacosanol	Hawar, et al. 2023 [46]
10	*Epicocum nigrum*	*E. milii*	2, 2, 3, 3, 4, 4-Hexadeutero Octadecanal, 2, 2-Dideutero Octadecanal, and Isochiapin B	Ali et al., 2024 [47]
		Antibacterial activity		
11	Streptomyces sp. strain NRRL 30566	Grevillea pteridifolia	Kakadumycin A	Castillo, et al. 2003 [48]
12	Verrucosispora maris AB-18-032	Sonchus oleraceus	Proximicin	Fiedler, et al. 2008 [49]
13	Streptomyces sp. HK 10595	Kandelia candel	Xiamycin B, Indosespine and Sespenine	Ding, et al. 2011 [50]
14	Streptomyces sp.	Marine mudflat-derived actinomycete	Harmaomycin	Bae, et al. 2015 [51]
15	Bacillus sp., Micrococcus sp., and P. polymyxa	Panax ginseng- and Plectranthus tenuiflorus	Amylase, esterase, lipase, protease, pectinase, xylanase, and cellulase	El-Deeb, et al. 2013 [52]
16	Neurospora tetrasperma	Cordyline fruticose	4-hydroxy-5-phenylpenta-1,3-dien-1-yl acetate and ergosterol	Elfita, et al. 2019 [53]
17	Bacillus subtilis strain EP1	*Boswellia sacra*	(4-(4-cinnamoyloxy)phenyl)butanoic acid), (cyclo-(L-Pro-D-Tyr)), (cyclo-(L-Val-L-Phe)), and (cyclo-(L-Pro-L-Val))—	Numan, et al. 2022 [54]
18	Stenotrophomonas maltophilia and Alcaligenes faecalis	*Moringa oleifera*	Octadecanoic acid, hexadecanoic acid, linoleic acid ethyl ester	Haseem, et al. 2023 [55]

the ISR pathway's signal is regulated by the Jasmonic acid/ Ethylene (JA/ET) pathway and involves the expression of the *DEFENSIN 1.2 (PDF1.2)*. On the other hand, the SAR is initiated by a Salicylic Acid (SA) dependent pathway and involves the expression of pathogenesis-related (PR) proteins [34,35].

Some studies suggest that endophyte-triggered ISR may be dependent on SA or not dependent on the JA/ET pathway. Niu, et al. 2011 [36] describe that *B. cereus* strain AR156 mediated ISR dependent on both SA- and JA/ET-signaling pathways. Additionally, *P. fluorescens* CHA0 triggered the accumulation of PR proteins in the tobacco leaves, which was induced by SA [37]. Moreover, a root endophytic bacterium *Micromonospora* against *B. cinerea* mediate ISR is dependent only on the JA/ET pathway [38]. The host plant's contact with the bacterial cell or its metabolites is responsible for endophytes' capacity to strengthen plant defense [56-60].

Conclusion

These days, it's common to think of plant immunology as a comprehensive system that involves the activity and interaction of microorganisms, in which microbes inside the plants might work together to prepare the product when exposed to biotic stress. We have updated the ways that endophytes support plant health in the current study. Additionally, highlights the role of endophytes in plant immunity boost especially, their role in priming defense. Since research on this topic is expanding, the processes involved in the cooperative action of plant endophytes against biotic stressors are still being investigated, owing to the difficulties of working with one specific endophyte strain separately from others that share the same niche. This minireview may serve as a guide for future biocontrol strategy development, considering the intricate interactions between plants, endophytes, and potential microbe vectors (like insects). Furthermore, endophytes can create metabolites that aid in biocontrol methods or more sustainable agricultural practices. How to combine priming defense with plant-growth stimulation is another unanswered subject. Future research may be centred on a potential connection between these two events.

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