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Pathway analysis of beneficial bacteria in suppression of plant immunity

Sihan Chen

Department of Art & Science, University of Toronto, Toronto M5S 1A1, Canada

veronica.chen@mail.utoronto.ca

Abstract. Plants, much like animals, possess immune mechanisms that help protect them against harmful microorganisms and pathogens. Research studies have provided evidence that various detrimental microorganisms can target the immune system of plant roots in the soil, leading to plant diseases. At the same time, recent studies have shown that beneficial microorganisms can also suppress the plant's immune system and form a mutually beneficial relationship with the plant, promoting the colonization of beneficial bacteria and helping the plant to defend itself against other harmful microorganisms. This paper provides a summary of the concept that beneficial bacteria hinder root immunity by inhibiting various downstream reactions within the plant's immune system, based on the understanding of plant root immune mechanisms. The authors also highlight the existing gaps in research on non-invasive microbe-plant interactions and raise questions regarding the intricate interplay between immunity and symbiotic signaling.

Keywords: beneficial bacteria, pathways, plant immunity, immune mechanisms.

1. Introduction

It is widely recognized that the soil harbors a rich diversity of bacteria [1]. Plants, thriving within the expansive natural petri dish of soil, are subject to intricate and diverse interactions between their root systems and a multitude of microorganisms. These interactions play a significant role in modifying the physiological state of plants and reshaping the microbiota residing in the inter-root region [2]. During such interactions, harmful microorganisms, such as pathogens, can attack the immune system and prevent healthy plant growth by controlling the metabolism of plants, even killing the plant [3]; simultaneously, beneficial microorganisms have been recognized for their ability to prevent plant diseases and support vital physiological functions by enhancing microbial activity [4]. However, a growing number of studies have shown that beneficial microbes can also suppress the plant's immune system and establish a mutually beneficial relationship with the host [5] This symbiotic relationship not only enables the beneficial bacteria to thrive within the plant's root zone but also empowers the plant to defend itself against detrimental bacteria [6]. Moreover, the beneficial bacteria can assist the plant in self-protection through the secretion of proteins that serve as elicitors and effectors [7]. This article aims to provide a comprehensive review by organizing the existing literature from two perspectives: (1) the pathway of the plant root immune mechanism, and (2) the inhibitory and regulatory effects of probiotics on the plant root immune mechanism.

2. Immune mechanisms in plant roots

The innate immune response serves as the mechanism through which plants defend themselves against pathogen attacks. This immune response comprises two distinct layers, each playing a crucial role in protecting the plant from pathogens [8]. The initiation of these two layers of the innate immune system requires a cell surface-localized pattern recognition receptor (PRR) and an intracellular nucleotide-binding domain leucine-rich repeat sequence receptor (NLR), respectively, and leads to pattern-triggered immunity (PTI) and effector-triggered immunity (ETI), respectively [9]. Despite their differences, these two layers of the innate immune system share numerous downstream reactions and engage in complex interactions [9]. Common downstream reactions in the plant innate immune system include the activation of the mitogen-activated protein kinase (MAPK) cascade [10], the generation of reactive oxygen species (ROS) burst, the influx of ions (such as calcium flux), transcriptional reprogramming, and the enhanced synthesis of plant defense hormones [11]. These downstream reactions collectively contribute to the establishment of a robust immune mechanism in plants [9]. Importantly, these immune mechanisms are not limited to specific plant parts, but are applied throughout the entire plant. Specifically, the root system, which is submerged in the soil, is also capable of initiating a pattern recognition receptor (PRR)-mediated immune response [12]. The underlying principle is that pattern recognition receptors (PRRs) in plant roots have the ability to detect the presence of abundant microorganisms in the soil by recognizing specific microbial-associated molecular patterns (MAMPs). In response to this recognition, the PRRs can trigger an immune response or activate defense genes, leading to various outcomes such as the induction of cellular damage at the root site and the initiation of a localized immune response [1, 12, 13].*Immunosuppression of plants by beneficial bacteria*

After reviewing immune mechanisms in the plant root system, it is noteworthy that beneficial microorganisms can elicit responses in plants that closely resemble those triggered by pathogens [13, 14]. In other words, beneficial bacteria possess microbial-associated molecular pattern (MAMP) analogs that allow them to interact with and activate pattern recognition receptors (PRRs) in plant roots, leading to the stimulation of immune signals [13, 14]. Moreover, in the later stages of interaction between beneficial bacteria and plant roots, symbiotic bacteria can block plant defence mechanisms and thus remain in the plant root interiors [14].

It is known from the immune pathways of plants that diverse downstream responses are essential to ensure the immune mechanisms of plants [9]. Therefore, it is reasonable to speculate that beneficial bacteria have the capability to suppress plant immunity by inhibiting or modulating these downstream reactions.

The first avenue of exploration focuses on the MAPK cascade. Previous studies have shed light on the inhibitory effects of nodule exoprotein L (NopL), a type III effector produced by the symbiotic bacterium Rhizobium, on plant innate immunity [15]. Notably, NopL is regarded as a crucial virulence factor in plant-pathogen interactions [15]. Experimental evidence from tobacco (Nicotiana tabacum) reveals that the expression of NopL can impede the full induction of pathogen-associated (PR) defense proteins, thus effectively suppressing the plant's innate immune response [16]. In a more targeted experiment, the influence of NopL on the MAPK cascade was investigated using Agrobacterium-mediated transient transformation of tobacco. The results demonstrated that co-expression of NopL and SIPK (salicylate-inducible protein kinase) in tobacco led to a noticeable reduction in cell necrosis within the leaf region, which is typically associated with the overexpression of the MAPK SIPK gene [17]. This observation strongly suggests that the co-expression of NopL and SIPK disrupts MAPK signaling pathways. Moreover, additional investigations revealed that the presence of SIPK DD (a mutant form of SIPK) directly triggers cell death [17]. These experimental results suggest that NopL from beneficial microorganisms has a repressive effect on the function of MAPK proteins and their downstream transcription factors [17].

The second concept revolves around the regulation of reactive oxygen species (ROS) bursts, as exemplified by the effector PIIN_08944 derived from the beneficial microorganism Piriformospora indica (P. indica) [18]. P. indica is a tamerobacterium that colonizes the roots of various plants as a beneficial bacterium [19]. To investigate the impact of PIIN_08944 on ROS burst in plants, experimental procedures involved the use of quantitative polymerase chain reaction (qPCR) to confirm the expression of PIIN_08944 in plant roots. Subsequently, transgenic barley plants fused to PIIN_08944 and GFP (HvPIIN_08944OE plants) with peptide flg22 and titin to measure the production of ROS in the plant. It was obtained that overexpression of PIIN_08944 significantly reduced the conclusion that flg22 and tylosin-induced ROS burst in HvPIIN_08944OE [18].

In addition, the modulation of hormonal signaling is recognized as an essential mechanism to suppress plant immunity. To explore the regulation of plant immunity through hormonal signaling, researchers conducted an investigation focusing on the promoters of flg22-triggered plant defense. Specifically, they examined the response of CYP71A12, MYB51, and WRKY11 promoters in plants with root treatments of the beneficial bacterial rhizobacterium FB17[20]. The results indicated a significant inhibition of these promoters in plants treated with FB17, suggesting that FB17 suppresses the flg22-induced root defense responses that are typically activated by microbial-associated molecular patterns (MAMPs) [20].

2.2. *Beneficial bacteria colonize the root system*

According to the pathway mentioned above of immunosuppression of plants by beneficial bacteria, it is not difficult to find that some beneficial bacteria promote plant root colonization in this process. For example, in the P. indica effector PIIN_08944 mentioned above, experiments have concluded that PIIN_08944 promotes fungal colonization of barley roots by using PIIN_08944-deficient mutants grown on medium and comparing the colonization of plant roots in the standard group [18]. Moreover, beneficial rhizobia FB17 performed rhizobia inoculation of Arabidopsis wild-type plant leaves by spraying with MAMPS, stimulating the colonization and quantification of FB17, indicating that plants can recruit beneficial rhizobia underground [20].

3. Discussion

The aforementioned examples provide compelling evidence for the immunomodulatory strategies employed by beneficial microbes during their invasion of host roots. These studies highlight the effectiveness of suppressing plant root immunity through the inhibition of downstream signals in the immune machinery. The inhibition of MAPK, ROS burst, and hormone signalling molecules are exemplified for the downstream responses of plant immunity. It is shown that colonization of plant roots by beneficial bacteria can be achieved in these pathways, thus recruiting other fungi or microorganisms to protect the plant better. At the same time, existing studies have shown that non-invasive beneficial microbes can also modulate plant immunity. For example, beneficial Pseudomonas can suppress multiple downstream flg22-dependent root immunity by acidifying the environment [21], and another example is the use of high-throughput transposon sequencing (Tn-Seq) to search for genes in Pseudomonas _ WCS365 that prevent the formation of dense biofilms in roots to evade plant defence mechanisms [22]. Furthermore, these studies also affirmed that these pathways could promote the colonization ability of microorganisms [21,22]. Nevertheless, in the context of the diverse and intricate immune interactions between plant roots and the myriad microorganisms present in the soil, it is imperative to explore the potential interplay between these different pathways. Specifically, understanding whether invasive beneficial bacteria and non-invasive microorganisms exhibit antagonistic or synergistic effects on each other represents a crucial and intriguing area for future investigation.

4. Conclusions

In conclusion, this study has provided insights into the diverse mechanisms through which beneficial bacteria can suppress plant immunity. By elucidating these mechanisms, the paper highlights the ability of plants with suppressed immune systems to still defend themselves against harmful microbes. This symbiotic relationship between beneficial bacteria and plants allows for the colonization of plant roots and provides enhanced protection. While this article offers a comprehensive literature review on the diverse mechanisms by which beneficial bacteria influence plant immunity, its limitations lie in the absence of empirical validation. It is crucial for future research to prioritize experimental studies and utilize alternative methodologies to gather firsthand data, allowing for a more in-depth exploration of this subject. By incorporating empirical evidence, researchers can delve further into the specific interactions and molecular mechanisms that underlie the suppression of plant immunity by beneficial bacteria. This will contribute to a comprehensive understanding of complex plant-microbe interactions and establish a solid foundation for the development of practical applications in the fields of agriculture and environmental management.

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