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Pseudomonas fluorescens in plant growth promotion and biocontrol: A focus on secondary metabolites, IAA, and siderophores

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Abstract: Pseudomonas fluorescens, a Gram-negative bacterium abundant in soil, plays a critical role in promoting plant growth and controlling pathogens, demonstrating remarkable biocontrol capabilities. This review explores the utility of P. fluorescens and its ability to produce secondary metabolites, IAA (Indole-3-acetic acid), and siderophores, addressing agricultural challenges under the strains of climate change. It emphasizes its role as a plant growth-promoting bacterium (PGPB), synthesizing recent findings on its contributions to enhancing plant resilience, pathogen resistance, and sustainable agricultural practices. The production of secondary metabolites, IAA, and siderophores by P. fluorescens is examined for its effectiveness in biocontrol, nutrient mobilization, and hormonal regulation. These functions are critically analyzed through diverse research methodologies, including laboratory and field trials, underscoring the bacterium's pivotal role in advancing agricultural sustainability and productivity. As the agricultural sector increasingly focuses on bio-products and the exploration of soil microorganisms, P. fluorescens emerges as a promising solution to enhance farming resilience in the face of climatic adversities.

Keywords: Biocontrol; Nutrient mobilization; Plant growth-promoting bacteria; Siderophores; Sustainable agriculture.

Introduction

Plant growth-promoting bacteria (PGPB) encompass a diverse array of microorganisms widely recognized for their beneficial effects on plant growth and productivity (Ngalimat et al., 2021). Pseudomonas fluorescens, a Gram-negative bacterium prevalent in soil, has been extensively studied for its comprehensive plant growth-promoting attributes, including nutrient mobilization, hormonal regulation, and biocontrol of plant pathogens (Guzmán-Guzmán and Santoyo, 2022).

Recent studies have clarified the mechanisms underlying the plant growth-promoting effects of P. fluorescens. These effects are primarily due to the bacterium's production of a variety of secondary metabolites that interact with both plants and their associated microbes (Mayrodi et al., 2021; Dimkić et al., 2022; Wang et al., 2022; Raio 2024). These metabolites, including pyoluteorin, pyrrolnitrin, and 2,4-diacetylphloroglucinol, have been demonstrated to inhibit the growth and development of a wide array of plant pathogens, such as Fusarium oxysporum, Botrytis cinerea, Ralstonia solanacearum, and Phytophthora infestans (Bhetwal et al., 2021; Soesanto et al., 2023).

In addition to its biocontrol attributes, P. fluorescens has been documented to enhance plant growth and yield across various crop species, including maize (Jakhar et al., 2022), wheat (Khezri et al., 2021), soybean (Singh et al., 2021), and tomato (Prakash et al., 2021). These beneficial effects are facilitated by the bacterium's ability to solubilize and mobilize essential nutrients such as phosphate, iron, and zinc, as well as by its production of plant growth-promoting hormones, including indole acetic acid and gibberellins (Nagpal et al., 2021; Ayub et al., 2024).

Due to its extensive plant growth-promoting properties, P. fluorescens is increasingly recognized as a valuable asset in integrated pest management (IPM) strategies. IPM is an ecologically oriented approach that integrates multiple tactics for managing pests and diseases, aiming to minimize environmental impact. Biocontrol agents derived from P. fluorescens have been developed and implemented in IPM programs, proving effective against a broad spectrum of plant pathogens (Dey et al., 2021; Shanmugam et al., 2022; Rashad et al., 2024).

In recent years, the importance of soil sustainability and innovation in agriculture has become increasingly prominent. Soil sustainability refers to the soil's ability to maintain its productive potential while minimizing adverse environmental impacts, such as erosion, nutrient depletion, and contamination. Innovation, on the other hand, entails the development and adoption of new technologies, practices, and business models that improve the efficiency, sustainability, and profitability of agricultural operations (Sofo et al., 2022; Lamichhane et al., 2023). The use of P. fluorescens in agricultural practices aligns well with these goals, enhancing soil health and reducing dependence on chemical pesticides. Furthermore, it offers potential for developing new biocontrol agents and advancing precision agriculture technologies.

In this review, we present a synthesis of the most recent advancements over the past four years concerning research on Pseudomonas fluorescens and its viable applications in the agricultural sector. Our focus is particularly on the bacterium's secondary metabolites, emphasizing their crucial roles in promoting plant growth and suppressing diseases, alongside the underlying mechanisms that enable the bacterium to enhance nutrient uptake and mobilization. Furthermore, we explore the latest developments in the utilization of Pseudomonas fluorescens-based biocontrol agents and their integration within Integrated Pest Management (IPM) strategies, reflecting on their burgeoning potential for sustainable agriculture.

Secondary metabolites produced by *P. fluorescens*

Secondary metabolites produced by Pseudomonas fluorescens play a pivotal role in plant-microbe interactions, endowing the bacterium with remarkable growth-promoting and biocontrol properties. These complex chemical substances, which transcend the basic survival needs of the bacterium, are crucial for interspecies communication, pathogen suppression, and the enhancement of plant health. This segment explores the diversity and functions of P. fluorescens' secondary metabolites, examining their contributions to the bacterium's efficacy in agricultural settings, particularly in enhancing disease resistance and promoting plant growth.

Pseudomonas fluorescens, a key player among plant growth-promoting rhizobacteria (PGPR), produces a rich array of secondary metabolites, including DAPG, hydrogen cyanide, lipopeptides, phenazines, pyoluteorin, pyrrolnitrin, siderophores, and the volatile organic compound 2R, 3R-butanodiol (Mishra and Arora, 2018; Singh et al., 2021; Raio, 2024). This arsenal enables the bacterium to navigate and thrive within the rhizosphere's complex ecology, effectively competing with pathogens and other microbes (Gupta et al., 2023), and providing robust plant protection under environmental stressors like nutrient scarcity (Ding et al., 2024).

Of particular note, 2R, 3R-butanodiol plays a critical role in triggering systemic resistance within host plants, illustrating the nuanced communication P. fluorescens establishes with plant immune systems for enhanced disease resistance (Raio, 2024). Furthermore, the biosynthesis of DAPG and phenazines underlines the bacterium's significant antifungal and antibacterial prowess, contributing to disease suppression and rhizosphere health (Serafim et al., 2023; Cui et al., 2022).

Moreover, the production of siderophores and indoleacetic acid (IAA) by P. fluorescens not only supports iron mobilization and root development but also represents its strategic approach to promoting plant growth and health. The integration of such bioactive compounds, including 2R, 3R-butanodiol, into Pseudomonas' metabolic repertoire exemplifies its role in advancing sustainable agriculture by improving soil vitality and reducing dependency on chemical interventions.

In summary, Pseudomonas spp.'s diverse metabolic capabilities affirm its invaluable contribution to enhancing plant defense mechanisms and underpinning sustainable and innovative farming practices. Through fostering healthier soils and leveraging natural microbial processes, Pseudomonas highlights a path towards achieving eco-friendly and resilient agricultural systems.

Pseudomonas fluorescens as a tool for biocontrol of pathogens

As agricultural practices evolve towards more sustainable models, the exploration of eco-friendly alternatives to chemical pesticides has gained critical importance. In this quest for greener solutions, biological control methods, which capitalize on the natural antagonistic relationships between microorganisms and plant pathogens, have emerged as a promising avenue for disease management. Among the various biological agents, P. fluorescens stands out as a formidable ally. Recognized for its comprehensive ability to suppress plant diseases through the production of antifungal and antibacterial compounds and by inducing systemic resistance in plants, P. fluorescens serves as a cornerstone in biocontrol strategies. Its use not only represents an effective and sustainable approach to reduce reliance on chemical pesticides, thereby mitigating environmental and human health risks associated with their use (Nagrale et al., 2023; Lopes-Ferreira et al., 2022), but also highlights its role in pioneering advancements in agriculture. This section delves deeper into the deployment of P. fluorescens as a biocontrol agent, underscoring its efficacy against a broad spectrum of pathogens and its contribution to the advancement of sustainable agricultural practices.

P. fluorescens is extensively investigated for its potential to suppress plant diseases through the production of antifungal and antibacterial compounds, in addition to inducing systemic resistance in plants. Moreover, P. fluorescens can outcompete other microorganisms in the rhizosphere,

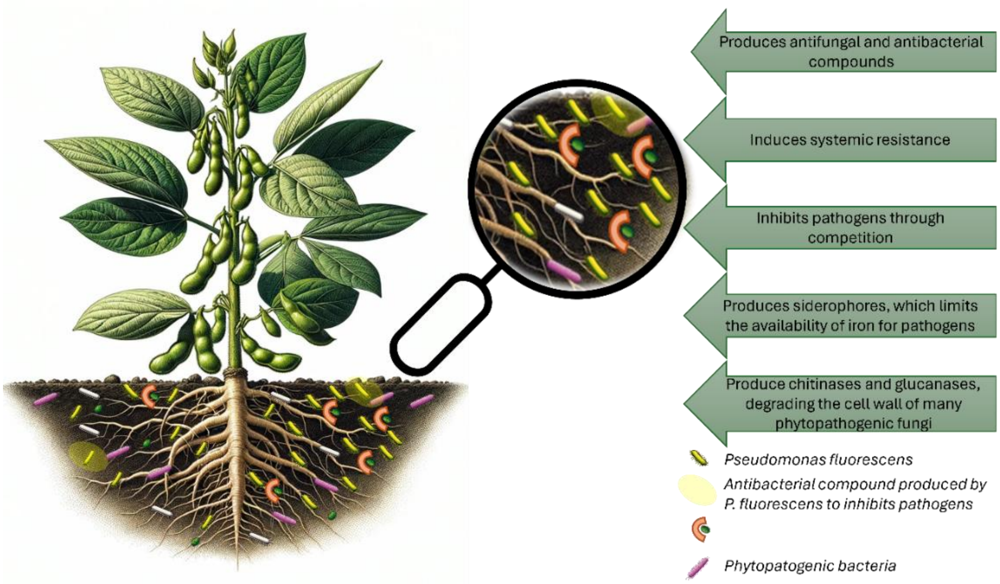

Figure 1. Demonstration of the rhizosphere in soybean cultivation, showing the mechanisms by which Pseudomonas fluorescens promote biocontrol of pathogens

claiming a critical ecological niche that reduces disease incidence by creating an unfavorable environment for plant pathogens (Figure). Specifically, the strain CFBP2392 has been recognized for its antifungal activity against pathogens such as Alternaria sp., Pythium ultimum, Fusarium oxysporum, and Rhizoctonia solani, thanks to specialized biosynthetic gene clusters similar to those producing lokisin and corpeptin (Riera et al., 2023). This capability is part of what makes P. fluorescens a valuable ally in biocontrol. A long-term study by Khatri et al. (2023) comparing organic and conventional soils over 19 years further demonstrated the biocontrol potential of Pseudomonas species, showing a higher community presence in organic soils and emphasizing the role of these bacteria in sustainable agriculture.

The utilization of P. fluorescens as a biocontrol agent provides a sustainable approach to managing plant diseases, with significant benefits for both agricultural productivity and the environment. Several studies have demonstrated the potential of P. fluorescens strains in controlling major pathogens in agricultural settings, including Phytophthora sp. (Nysanth et al., 2022), Rhizoctonia sp. (Singh et al., 2021), Xanthomonas sp. (Jat et al.2022) and Fusarium sp. (Singh et al.,2021b). Additionally, Singh et al. (2021a) reported the efficacy of P. fluorescens in controlling Meloidogyne incognita juvenile 2 and inhibiting 75% of the hatching of its eggs. P. fluorescens can also improve post-harvest quality, as evidenced by the reduction in the incidence and size of lesions caused by Penicillium italicum in citrus when applied preventively (Wang et al., 2020). Suresh et al. (2022) investigated the induction of systemic resistance in tomato seedlings inoculated with Ralstonia solanacearum using P. fluorescens, which was evaluated by the production of defense enzymes such as peroxidase, polyphenol-oxidase, lipoxygenase, and phenylalanine-ammonia-lyase by the plants. The results of the study revealed the significant contribution of P. fluorescens in controlling R. solanacearum. Johnson et al. (2022) investigated the efficacy of P. fluorescens in inhibiting fungal mycelium growth of tomato pathogens in vitro. The application of the bacterium resulted in enhanced germination, vigor, and accumulation of enzymes associated with resistance induction. These findings suggest that P. fluorescens can be used as a biocontrol agent in tomato cultivation to suppress pathogenic fungi.

In addition, the use of P. fluorescens as a biocontrol agent can be integrated into a precision agriculture system, aimed at optimizing the application of biocontrol agents to obtain maximum benefits (Mourouzidou et al., 2023). By identifying specific areas of the field with a high incidence of plant pathogens, biocontrol agents can be targeted, reducing the amount of product required and increasing the effectiveness of control (He et al., 2021). This can result in significant savings in time and money for the producer, as well as reducing the environmental burden associated with the use of chemical pesticides. Precision agriculture practices can also provide a more sustainable and efficient approach to farming, by reducing the amount of inputs required while maintaining or improving crop yields (Monteiro et al., 2021). The integration of P. fluorescens as a biocontrol agent in precision agriculture practices can be a powerful tool for sustainable and effective plant disease management.

Reflecting the significant advancements in the understanding and application of P. fluorescens in agriculture, the Ministry of Agriculture, Livestock, and Supply (MAPA) in Brazil has documented a remarkable growth in the registration of microorganisms for agricultural use. Just two years ago, there was only a single microorganism based on P. fluorescens registered. Now, recent data highlights that out of 560 products registered for pest control, three include P. fluorescens in their formulation, all in synergy with other microorganisms. Additionally, among 531 inoculants registered, nine feature P. fluorescens, specifically tailored for various crops: one for rice, four for corn, five for soy, and one for Ruziziensis grass (MAPA, 2023). This surge in registrations underlines the expanded acceptance and integration of P. fluorescens in Brazilian agri-products.

The landscape is further enriched by the active efforts of numerous companies in the process of product registration, alongside a growing trend among farmers to utilize on-farm amplified microorganisms (Faria et al., 2023; Goulet, 2023). This evolving scenario opens a plethora of questions and opportunities for exploration, revealing a substantial, yet untapped potential for P. fluorescens in biocontrol. Despite its recognized efficacy as a biocontrol agent, the Brazilian market has seen a limited presence of P. fluorescens-derived products, indicating a notable commercial exploitation gap. With the initial registration breakthrough and ongoing farmer adoption through On Farm systems, the scope for P. fluorescens as cornerstone biocontrol agent is immense. These developments are pivotal for steering future research and development efforts towards harnessing the full spectrum of advantages offered by this biocontrol agent within precision agriculture frameworks.

IAA synthesis by P. fluorescens: A potential strategy for enhancing crop productivity under abiotic stress

Pseudomonas fluorescens, as briefly reported earlier, can synthesize indole acetic acid (IAA), a plant hormone that acts as a modulator of plant growth and development. The production of IAA by P. fluorescens is regulated by different environmental factors, such as the presence of aromatic amino acids, the concentration of dissolved oxygen, and the availability of nutrients (Patten and Glick, 2002; Khalid et al., 2019), as well as abiotic stresses such as drought (Nishu et al., 2022) and salinity (Rojas-Solis et al., 2023).

Considering agriculture as one of the most important production systems, constantly facing adverse climatic conditions that are exacerbated by global warming, this microorganism can be an important ally. By releasing IAA in response to stresses such as drought and salinity, significant advantages can be obtained in the presence of these factors. A recent study showed that P. fluorescens aided the growth of tomato plants under normal conditions. However, when subjected to salt stress, the plants grew and developed more, as the inoculation of P. fluorescens released a greater amount of IAA in this condition (Rojas-Solis et al., 2023). Another study extracted P. fluorescens from Codonopsis pilosula and evaluated the bacterium's ability to promote growth and development in the same medicinal plant, in a greenhouse experiment. This study showed that stressed and inoculated plants had an increased ability to survive and develop under water stress conditions (Zhu et al.,2022). A similar result was found in Melissa officinalis also under water stress (Mohammadi et al.,2021). The ability of P. fluorescens to synthesize IAA is highly valuable, as it can be used as a plant growth promoter in various agricultural crops, ultimately enhancing the sustainability and productivity of the agricultural sector, especially in the face of climate change and global warming.

Siderophores: key agents in iron solubilization

Iron (Fe), while abundant in terrestrial ecosystems, predominantly exists in an insoluble state, thereby curtailing its bioavailability to plants. In this context, the significance of plant growth-promoting rhizobacteria (PGPRs) cannot be overstated, as they play a pivotal role in solubilizing iron and thus, abating its deficiency in plants (Singh et al., 2017).

Siderophores, biogenic compounds synthesized and secreted by bacteria, have demonstrated a unique capacity to bind iron present in the soil environment stably. The binding of siderophores to iron culminates in the formation of soluble complexes, facilitating their subsequent reabsorption by bacterial cells. This production of siderophores is triggered by the paucity of iron within the rhizosphere (Kraemer et al., 2015). A key strategy employed by PGPRs to stimulate plant growth involves the synthesis of secondary metabolites, including siderophores (Chandran et al., 2021).

As low molecular weight secondary metabolites, siderophores possess ligands characterized by their high affinity for ferrous ions, which enables the transport of these ions across bacterial cell membranes (Ghssein and Ezzeddine, 2022). Various microbial communities, including rhizobacteria, synthesize siderophores. These compounds are further classified into distinct categories based on the number of oxygen atoms they donate to the iron ion. These categories encompass carboxylates, hydroxamates, catecholates, and mixed types and are predicated on their structural and functional attributes (Egbers et al., 2023).

The symbiotic relationship between plants and microorganisms is a cornerstone of plant health and soil fertility. In the rhizosphere, bacteria can produce siderophores, thereby boosting plant growth by rendering iron readily available to the plant roots. Concurrently, these bacterial siderophores limit the access of plant pathogens to iron, making it preferentially available to the plants (Jha and Saraf, 2015). This iron sequestration impedes the propagation of phytopathogens (Beneduzi et al., 2013). Pseudomonas fluorescens bacteria are recognized for their notable siderophore production capacity (Hungria et al., 2021).

In a study that elucidated the role of two bacterial strains, Geobacillus sp. (RHBA19) and Pseudomonas fluorescens (RHBA17), both noted for siderophore production, in promoting Codonopsis pilosula growth and development. The application of these bacteria resulted in significantly enhanced plant growth, root development, and photosynthesis. It was observed that siderophore production was instrumental in triggering beneficial physiological changes and stress-resistance mechanisms in the plants, particularly when the strains were mixed (Zhu et al.,2022). In a subsequent study, cucumber seeds subjected to a treatment regimen with a suspension of P. fluorescens NK4 displayed induced siderophore activity within the plant system. This biochemical response was correlated with enhanced survival rates, augmented vegetative and root growth, and suppressed populations of P. viridiflava within the plant host, underscoring the biocontrol efficacy of siderophore-producing P. fluorescens (Al-Karablieh et al., 2022).

It is worth noting that siderophore production incites a competitive response among microorganisms, thereby reducing the prospect of a singular competitor exploiting this resource. Consequently, strategies for iron acquisition mediated by siderophores are dynamic and liable to fluctuations (Kramer et al., 2019).

In conclusion, siderophores synthesized by P. fluorescens and other rhizobacteria are instrumental in enhancing iron availability to plants, thereby promoting their growth and wellbeing. The employment of siderophores produced by beneficial microorganisms signifies a promising method.

Future perspectives

Beneficial microorganisms, long harnessed in agricultural practices, have seen their potential progressively tapped into with the advent of advanced technologies such as mass spectrometry and genomic sequencing. Prominently, Pseudomonas fluorescens has shown significant promise as a versatile ally in sustainable agriculture, serving multiple roles from biocontrol agent and growth promoter to phosphate solubilizer across diverse crops. Yet, the adoption of P. fluorescens in agriculture is not without its challenges. The commercial realm currently sees a limited diversity of strains utilized, and there is a noticeable knowledge gap regarding the potential of secondary metabolites. However, with the ever-increasing pressure to shift towards sustainable farming practices in the wake of looming climate change and growing demand for effective biological solutions, this presents a unique opportunity for a deeper exploration into P. fluorescens. Future research will likely focus on discovering and characterizing new strains of P. fluorescens, assessing their potential as biocontrol agents and growth enhancers. With sophisticated tools like proteomics and metabolomics, we can unveil new metabolites and the adaptive pathways microorganisms deploy under specific stress conditions. The understanding thus gained will be instrumental in developing new biological products that harness specific secondary metabolites, and employing genetic transformations to mass produce these key components. Hence, there's an urgent need to escalate research into P. fluorescens and other beneficial microorganisms to unlock their immense potential in promoting sustainable agricultural practices. In bridging the existing knowledge gaps, we move one step closer to a sustainable future for agriculture that is both eco-friendly and resilient in the face of global challenges

Conclusion

Despite extensive exploration of Pseudomonas fluorescens within the Pseudomonas genus, the emergence of novel strains remains a fledgling area of scientific scrutiny. Traditionally, molecular taxonomic strategies, primarily reliant on 16S ribosomal DNA sequencing, have been the mainstay of strain identification. However, the advent of sophisticated metagenomic approaches predicates an impending surge in the discovery of new strains belonging to this species. The incorporation of P. fluorescens as a plant growth-promoting rhizobacterium (PGPR) in agricultural systems is gathering momentum, though it remains an incipient branch of research. Existing investigations have predominantly aimed to elucidate the potential applications of this microbe, with scant emphasis on the identification, extraction, and exploitation of its secondary metabolites. Within the realm of secondary metabolites, siderophores have been the subject of substantial attention due to their vital role in enhancing plant growth and biocontrol of pathogens. Despite this, the broader spectrum of secondary metabolites synthesized by P. fluorescens is yet to be exhaustively investigated and fully characterized. In sum, to fully harness the agricultural potential of P. fluorescens, additional rigorous research is warranted. This necessitates the identification of novel strains, comprehensive characterization and utilization of secondary metabolites, and the exploration of diverse strategies to incorporate this bacterium in the advancement of sustainable agricultural practices.

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