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Review

Purpureocillium lilacinum as an Agent of Nematode Control and Plant Growth-Promoting Fungi

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Abstract: Plants support numerous microorganisms within their tissues and the rhizosphere, and these microorganisms, known as the microbiota, can influence plant growth and health. Up to 40% of a plant's photosynthetic metabolism may be invested in the rhizosphere. The microbiota is considered an extra genome that can be modulated to meet plant needs. Researchers have identified a set of genes from these microorganisms, known as the microbiome, which can be manipulated to enhance plant growth and health, improve nutrient absorption, reduce the need for chemical fertilizers, increase resistance to pathogens and pests, and increase stress tolerance. In particular, fungi exhibit large genetic and metabolic diversity and are often used to promote plant growth. For example, the fungus *Purpureocillium lilacinum* has been employed primarily as a biocontrol agent to manage nematodes, but some studies have suggested that it may also promote plant growth by increasing the efficiency of the plant in absorbing nutrients from the soil and providing phytohormones to plants. Therefore, the current review aims to summarize the existing literature on the use of this fungus in agriculture as nematodes control, and discuss its potential as a plant growth-promoter.

Keywords: phosphorous solubilizing; yield increasing; tobacco virus; tomatoes

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1. Introduction

The rhizosphere refers to the area of soil surrounding the roots, which is subject to the nutritional influence of the roots. Notably, the microbial population in the rhizosphere can vary from 10 to 1000 times than that in the bulk soil. Additionally, the microbial composition in the rhizosphere can fluctuate depending on the developmental stage of the plant, whereas the microbial composition of the bulk soil remains constant [1,2].

Depending on the specific needs of the plant, certain microorganisms from the rhizosphere and phylosphere (the surface of the plant) may be required. These microorganisms possess unique abilities and characteristics that enable plants to absorb nutrients from the soil and to withstand abiotic and biotic stresses [3,4].

The formation of the microbial community in the rhizosphere is affected by the plant's root architecture, soil composition, and environmental conditions. The capacity of plants to regulate the release of various compounds, such as proteins, amino acids, and organic acids, in conjunction with microbial populations, is a crucial aspect of their ability to selectively benefit from microbes present in their environment [5,6].

In relation to microorganisms associated with plants, certain microorganisms are found in high taxa, and they are not limited to the soil or the environment in which the plant is located. These microorganisms are referred to as the core microbiomes. The core microbiome is formed as a result of evolutionary processes that selected for functional genes in the finesse of the plant holobiont. In contrast, taxa with low abundance are referred to as satellite taxa, which have been demonstrated to play a crucial role in preventing undesirable microbial intrusion into soil communities. These microbes are primarily responsible for the generation of volatile organic compounds (VOCs), which help decrease soil-borne pathogens [7].

The ability of plants to sustain microorganisms from the rhizosphere through photosynthetic metabolites leads to the selection of microorganisms that can thrive in this environment. Although the microbial density is higher in the rhizosphere than in bulk soil, the microbial diversity is typically lower. This finding suggests that there is a selection of microorganisms that can survive in the rhizosphere, and that these microbes offer benefits to plants [8,9].

The effects of rhizospheric microbes on plant growth can be classified into two categories: direct and indirect. Direct effects result from the direct action of microbes on the plant, such as enhancing nutrient availability, improving the efficiency of roots in absorbing water and nutrients, and increasing the photosynthetic efficiency and chlorophyll content. Indirect effects are observed when microbes reduce harmful effects that hinder plant growth, such as reducing the incidence of pathogens, controlling pests, and enhancing the tolerance of plants to abiotic factors [10,11]. Numerous microorganisms in the rhizosphere serve as carriers of various abilities related to plant growth. These microorganisms hold great promise for reducing reliance on chemical fertilizers, pesticides, and herbicides, thereby decreasing input dependence and minimizing environmental impacts without compromising productivity [12–14].

The investigation of these microorganisms requires numerous studies conducted at various stages. Initially, these microorganisms must be isolated, which can be accomplished by obtaining them from rhizospheric soil or plant tissue, which they inhabit as endophytes. Subsequently, these microorganisms must be screened to confirm their capabilities. Commonly, microorganisms are screened for their ability to fix nitrogen, solubilize phosphorus, produce phytohormones, synthesize siderophores, and produce 1-aminocyclopropane-1-carboxylate (ACC) deaminase [15–19]. Following this screening process, it is essential to apply these microorganisms to plants. Subsequently, the parameters related to plant growth were compared with the control to determine the impact of microbial inoculation on the plant. Microorganisms are usually identified to ensure that they do not pose a threat to plants and animals. Intriguingly, the evaluation of microorganisms for their ability to promote plant growth often yields inconsistent results [12–14]. At times, isolated microorganisms are unable to promote plant growth, and this may be due to several reasons. First, exogenous microbes may not be adapted to the soil or environment, whereas indigenous microbes may be adapted, which can lead to the elimination or inability of exogenous microbes to colonize the rhizosphere or plant tissues. Second, the dosage of the microbial inoculant plays a critical role in determining its ability to colonize and compete with other microorganisms [20,21]. A lower dosage may result in the inhibition of microbial inoculant growth owing to unfavorable conditions or the presence of other microorganisms. Additionally, dosage may influence the physiology of the microbial inoculant, potentially affecting its ability to colonize. Therefore, it is essential to carefully consider the dosage of microbial inoculants used in agricultural applications. Third, several factors affect the colonization of the introduced microorganisms in the crop, with plant species and genotypes being the most significant. Typically, plant breeding programs focus on characteristics that promote increased yield rather than those related to interactions between the plant and the microbial inoculant [22–24]. When a microbial inoculant is applied to a plant that has not been selected for its positive interaction with microbes, there is a high likelihood that the plant species or genotype will not interact with the introduced microbes, which may result in microbes failing to colonize the rhizosphere or plant tissues. The current plant genotypes exhibited lower microbial diversity than their wild progenitors. This indicates that certain genes were chosen during the breeding process, whereas the others were eliminated. As a result, domesticated microbiomes have emerged. This has two primary consequences. The genes that were lost could be crucial for the introduced microbial inoculant to colonize the plant, making it impossible for the inoculant to do so. The other effect is that the domesticated microbiome does not provide the plant with the same level of protection as the wild microbiome. Consequently, humans must compensate for this shortcoming using chemical fertilizers, pesticides, and herbicides [25–27].

The relationship between plants and fungi is prevalent and well-documented. Evidence confirms that endophytes and mycorrhizas have coexisted with plants for over 400 million years, beginning when plants first colonized the soil [28]. This long-standing partnership suggests that fungi have played a significant role in the evolution of plant life [29].

Sustainable agriculture is the driving force behind recent scientific studies, and improving sustainable agriculture practices can mitigate the negative impacts on the environment and protect it for future generations [30].

In the context of sustainable production, *Purpureocillium lilacinum* (previously known as *Paecylomices lilacinum*) interact with plants and offer numerous benefits. These fungi can decompose organic matter and release essential nutrients such as nitrogen, phosphorus, and potassium, which become more easily accessible to plants in the soil and secrete phytohormones that stimulate the growth of roots and shoots, resulting in increased soil exploration and photosynthetic efficiency in plants [31,32]. Most studies have indicated that this fungus is effective for controlling nematodes. Its effectiveness in this regard is attributable to its ability to synthesize several enzymes, including chitinase and proteases. However, this fungus also exhibits characteristics related to plant growth, which has been the focus of only a few studies. The objective of the present review is to synthesize recent and significant research findings on the use of *P. lilacinum* as a nematode control agent and plant growth promoter, to emphasize the importance of future investigations in this field, and to highlight this fungus as a promising microorganism that can be used for sustainable food production. Table 1 addresses the ability of *P. lilacinum* to reduce nematode populations and promote plant growth.

Table 1. *Purpureocillium lilacinum*'s abilities to control phytopathogen fungi, secondary metabolites production and plant growth promotion.

Effect	Results	References
Plant Growth	In soybean, stimulated root growth and nutrient absorption	[19]
Plant Growth	Increased the availability of P and N and promoted the growth of maize, beans and soybean	[30]
Plant Growth	Promoted significant increases in plant dry biomass in cotton crop	[33]
Plant Growth	Improved soil nutrient availability in common bean growth	[9]
Nematode Control	Suppressed nematode *Meloidogyne incognita* population in a tomato–cucumber rotation in a greenhouse	[34]
Nematode Control	The fungus was effectively applied as a biocontrol agent of phytoparasitic nematodes in tomatoes under variable agroecological conditions	[35]
Nematode Control	The fungus showed maximum egg mass inhibition of *Meloidogyne incognita*	[36]
Nematode Control	The fungus controlled root-knot nematodes infecting eggplant	[37]

Table 1. *Cont.*

Effect	Results	References
Nematode Control	Control of root-knot nematodes in tomatoes	[38]
Nematode Control	Potential control against cotton aphids	[39]
Nematode Control	Control of *Meloidogyne javanica* in commercial pineapple	[40]
Nematode Control	Controlled the insect *Thrips palmi* in orchid farms	[41]

2. Nematode Control

Root-knot nematodes are a significant source of damage and crop reduction in numerous plant varieties, including tomato, potato, soybean, and maize [42,43]. The primary effect of nematodes is root galling, which impairs nutrient and water absorption [44–46]. *Meloidogyne* spp. is the primary culprit behind this reduction in root function, leading to a decrease in plant energy and ultimately, a reduction in the energy available for plant production.

The most important of these are root-knot nematodes, *Meloidogyne javanica*, and *M. incognita*, which cause significant reductions in yields worldwide, along with other important species, *Rotylenchulus reniformis* and *Pratylenchus brachyurus* [36,47–49].

Concerns regarding environmental conservation and food security have led to the prohibition of the use of various nematicides for nematodes control. Consequently, it is essential to investigate alternative and secure approaches to maintaining plant production [44,50]. Biological Control Agents (BCA) have been shown to be efficient alternatives to crop production due to their economic and environmental benefits in reducing nematode damage [51,52]. Integrated nematode control management programs can benefit from the use of entomopathogenic fungi as an eco-friendly biopesticide. These fungi are more effective than other microorganisms in mitigating the adverse effects of nematodes that often result in significant harm to plant production [37,53–55].

The efficacy of introducing a fungus for biocontrol in an outdoor setting is heavily influenced by its capacity to endure and proliferate in the soil, which can be affected by fluctuations in the temperature and moisture levels. The potential of fungi to serve as biological control agents is noteworthy due to their extensive genetic and metabolic diversity. These organisms possess the ability to produce a plethora of secondary metabolites that are effective in controlling a wide range of nematodes that attack the roots of plants [56,57].

The application of *P. lilacinum*, a fungus, in tomato cultivation was explored to curb *M. incognita* infestations. These results demonstrate that the fungus effectively reduced the nematode population and concurrently boosted crop productivity. Moreover, this application opens up promising prospects for integrating biological and chemical control measures, thereby enhancing the efficiency of chemical control in mitigating nematode infestations in tomato crops. The interesting characteristic of *P. lilacinum* is that it attacks nematode eggs, thereby preventing the birth and growth of new nematodes [58].

The effectiveness of *P. lilacinum* in controlling tomato nematodes through the production of proteases was verified in tomato plants. Proteases target the cuticle of nematodes, breaking down their protein components, which are essential for nematode survival. These mechanisms can directly kill nematodes or render them more susceptible to other threats, making *P. lilacinum* a promising biological control agent for managing tomato nematodes [35].

The effectiveness of control exerted by *P. lilacinum* can vary depending on the substrate on which the fungus grows. A study was conducted to evaluate the effectiveness of *P. lilacinum* in controlling nematodes in tomato plants grown on two different substrates: a traditional substrate based on wheat and the Karanja substrate. Karanja deoiled cake (KDC) is a nitrogen-rich substrate made from the residue left after extracting oil from Karanja (*Pongamia pinnata*) seeds, which has been further processed to reduce its oil content. The results show that Karanja deoiled cake mixed with sundried biogas slurry resulted in a higher inhibition of nematode egg mass hatching (96.8%) than the traditional wheat-based substrate, which only inhibited 68.72% of egg mass hatching. These results can be attributed to the higher protease activity (376.65 U/g) observed with the Karanja-based substrate, indicating a stronger nematicidal effect against the nematodes, unlike the lower activity observed with the wheat-based substrate. The results of this study highlight the significance of protease production by *P. lilacinum* in effectively controlling nematodes [59].

Meloidogyne javanica and *M. incognita* are two types of nematodes that cause significant damage and decreased productivity in a number of crops, including tomatoes. Inoculation with *P. lilacinum* reduces the population of these nematodes. Previous studies have compared the effects of inoculation with *Steinernema feltiae* and *Xenorhabdus bovienii* with *P. lilacinum*. *Steinernema feltiae* is a roundworm nematode that belongs to the family Steinernematidae. It is an entomopathogenic nematode that parasitizes insects. *Xenorhabdus bovienii* is a bacterium that lives symbiotically with *Steinernema feltiae*. This bacterium resides inside the nematode and is released into the insect host when it infects it. The bacterium then kills the insects by producing toxins. Notably, *P. lilacium* demonstrated a significant reduction in nematode infestation compared to *S. feltiae* and *X. bovienii*, which proved to be advantageous for tomato growers in terms of effectiveness and economic benefits [38]. *Purpureocillium lilacinum* demonstrated a notable reduction in the infestation of *M. javanica* on pineapple plants by decreasing the number of nematode eggs and galls on the roots. However, this reduction was less pronounced than that in *Trichoderma atroviridae*. *P. lilacinum* exhibits a particular affinity for infecting the eggs and females of nematodes, effectively disrupting their reproductive cycle and ultimately resulting in a reduced nematode population and reduced damage to the plants [40].

Purpureocillium lilacinum may be used, together with some bacteria, such as *Bacillus amyloliquefaciens*, to increase the efficiency of control. The combination of *P. lilacinum* and *B. amyloliquefaciens* significantly reduced the number of harmful nematode eggs and root galls in cucumber plants, showing a much better result than when each microorganism was used alone. This mixture also increased toxicity against the nematode juveniles and inhibited their eggs from hatching, suggesting that the combined action of these microorganisms disrupts the nematode's life cycle more effectively than individual applications. Additionally, the combination with these two microorganisms made cucumber root exudates repellent to nematodes, altering their behavior and preventing them from attacking the plants, which indicates a strategic advantage in using a mixture of biocontrol agents [60]. These results indicate that this fungus can be used in combination with other microorganisms to improve nematode control. Although the outcomes have been favorable, it is crucial to exercise prudence when blending *P. lilacinum* with other microorganisms. In one study, the effects of *P. lilacinum* and *Funneliformis caledonium* were assessed to minimize the prevalence of *Phytophthora capsici*, the pathogen responsible for diseases in pepper plants. The findings reveal that incorporating *P. lilacinum* did not enhance plant well-being or productivity compared with the use of *F. caledonium* individually. This outcome suggests that the fusion of these fungi may not be advantageous for controlling *P. capsici* in pepper plants [61].

Several investigations have indicated that *P. lilacinum* can be employed as a nematode control agent, leading to a decrease in the damage caused by this disease. Additionally, this fungus can be utilized in conjunction with other microorganisms and chemicals, resulting in a synergistic effect that reduces dosage, production costs, and environmental impact [30,32,62].

3. Plant Growth

Most studies have demonstrated the efficacy of *P. lilacinum* as a means of controlling nematodes [58,60]. However, few studies have highlighted its potential as a plant growth-promoting agent owing to its ability to solubilize phosphorus and produce phytohormones and secondary metabolites, which are characteristics associated with plant growth. This section presents studies that support the notion that *P. lilacinum* is a promising plant growth-promoting agent.

Globally, more than 25% of citrus fruits are lost during the postharvest period [63]. The primary cause of these losses is postharvest decay, primarily caused by *Penicillium digitatum* (green mold), the leading postharvest pathogen affecting citrus crops [64]. This pathogen is responsible for significant losses worldwide [65] and in Morocco [66]. Infection occurs through injuries and wounds sustained during harvest and subsequent handling [67]. Although synthetic fungicides remain the primary method for controlling postharvest diseases [68], these chemical products pose a toxicological risk due to the excessive use of certain systemic fungicides, which has led to the development of *P. digitatum* resistance [66]. *Purpureocillium lilacinum* secretes a substance that effectively inhibits the proliferation of *Penicillium digitatum*, a fungus that causes green mold on oranges. Disrupting the cell walls of harmful fungi and preventing spore formation completely hinders their growth, resulting in the death of the fungus and the prevention of sporulation, ultimately reducing the incidence of this disease [69].

Purpureocillium lilacinum produces several secondary metabolites that can control some pathogens, and the production of phytohormones can promote plant growth. Promoting the growth of roots and total dry mass in soybean plants, *P. lilacinum* demonstrated its ability to enhance the physical growth and nutrient absorption capacity of the plants. Notably, when root growth was stimulated by *P. lilacinum*, the capacity of the plant to absorb water and nutrients increased, allowing it to manage water stress better and become more efficient in the use of nutrients. Consequently, it may be possible to reduce the dosage of chemical fertilizers [30]. However, the possibility of reducing chemical fertilization with *P. lilacinum* inoculation is controversial. Moreno-Salazar [70] conducted an evaluation of the impact of *P*. *lilacinum* on *Capsicum chinese* in relation to two levels of chemical fertilization, 100% and 75%. Their findings suggest that the fungus requires high levels of soil fertilization to fully realize its potential in promoting plant growth. Another study demonstrated the impact of *P. lilacium* on the development of roots and shoots. Although some studies have shown the ability of this fungus to solubilize certain nutrients in the soil [30,51], such as phosphorus, strong evidence indicates that its impact is on the plant rather than on the soil. Specifically, it enhances the capacity of plants to absorb nutrients [33]. The aforementioned fungus has demonstrated its capacity to enhance iron content in plants. This is accomplished through its role as a carrier of siderophores, which facilitates the transport of iron to the plant and contributes to plant growth, as evidenced by a study involving *C. chinense*. Interestingly, in this study, the *P. lilacium* strain produced high levels of phytohormones that could engage in mutualistic interactions, enhancing the growth of host plants [71].

The use of the fungus *P. lilacinum* was found to promote the growth of cotton plants. Treated plants exhibited increased dry biomass and more nodes than untreated plants, as well as a higher number of developing flowers (squares). This suggests that the fungus may have a positive effect on the reproductive success of cotton plants. Although the study examined the impact of the fungus on reducing the damage caused by the insect *Helycoverpa zea*, the specific effect of the fungus on the plant was associated with plant growth promotion [39].

4. Control of Other Pathogens

Along with the abilities to control nematodes and promote plant or fungal growth, the fungus *P. lilacinum* can also control other pathogens. A study has shown that *P. lilacinum* has the ability to enhance plant resistance by activating its induced systemic resistance. Research has shown that it can effectively combat the tobacco mosaic virus by triggering a defense mechanism that directly damages the virus particles and causes them to clump together, thereby preventing the virus from spreading further within the plant. Additionally, this compound stimulates a hypersensitive reaction (HR), which is a rapid response mechanism employed by plants to contain the spread of infection. Through the activation of defense-related enzymes such as peroxidase (POD), catalase (CAT), and phenylalanine ammonia-lyase (PAL), this compound fortifies plant defense against pathogens. Furthermore, it induces the overexpression of pathogenesis-related (PR) proteins and the upregulation of salicylic acid (SA) biosynthesis genes, which are essential for building systemic acquired resistance (SAR) in plants. This heightened resistance allows the plant to be better equipped to withstand future attacks [62]. These findings present promising possibilities to employ this fungus to boost plant resilience, with the ultimate goal of decreasing the demand for pesticides and fungicides as well as diminishing the reliance on plant varieties resistant to viruses. Another study on tobacco showed that the application of *P. lilacinum* decreased the abundance of soil microbes between tobacco roots and reduced the pathogenic fungi in tobacco leaves, suggesting an antagonistic effect of *P. lilacinum* against pathogenic fungi [41].

Purpureocillium lilacinum serves as a beneficial biocontrol agent in the fight against harmful fungi such as *Verticillium dahliae*, which causes *Verticillium* wilt in eggplants. By producing substances that directly inhibit the growth of this harmful fungus, *P. lilacinum* reduces the impact of disease on eggplants. Additionally, it promotes plant growth by increasing seed germination, bud growth, chlorophyll content, and root activity, making them more resistant to diseases such as *Verticillium* wilt. The application of *P. lilacinum*, grown in fermentation broth, to the soil or directly onto eggplant roots has been proven effective in decreasing the incidence and severity of *Verticillium* wilt under both greenhouse and field conditions, demonstrating its efficacy as a biocontrol agent [34].

The fungus *Penicillium digitatum* is a major cause of green mold in oranges, leading to significant economic losses during storage, transport, and marketing, accounting for up to 90% of the orange losses in some regions. *P. lilacinum* produces a secondary metabolite that, when applied in oranges, can completely stop the growth of the harmful fungus *P. digitatum* by breaking down its cell walls and preventing its spores from growing. Interestingly, the use of *P. lilacinum* reduced the use of fungicides to avoid the presence of mold [69]. Figure 1 shows different steps regarding the isolation, identification, and characterization of the fungus *P. lilacinum* from the soil. Figure 2 shows the mode of application of this fungus in crop production.

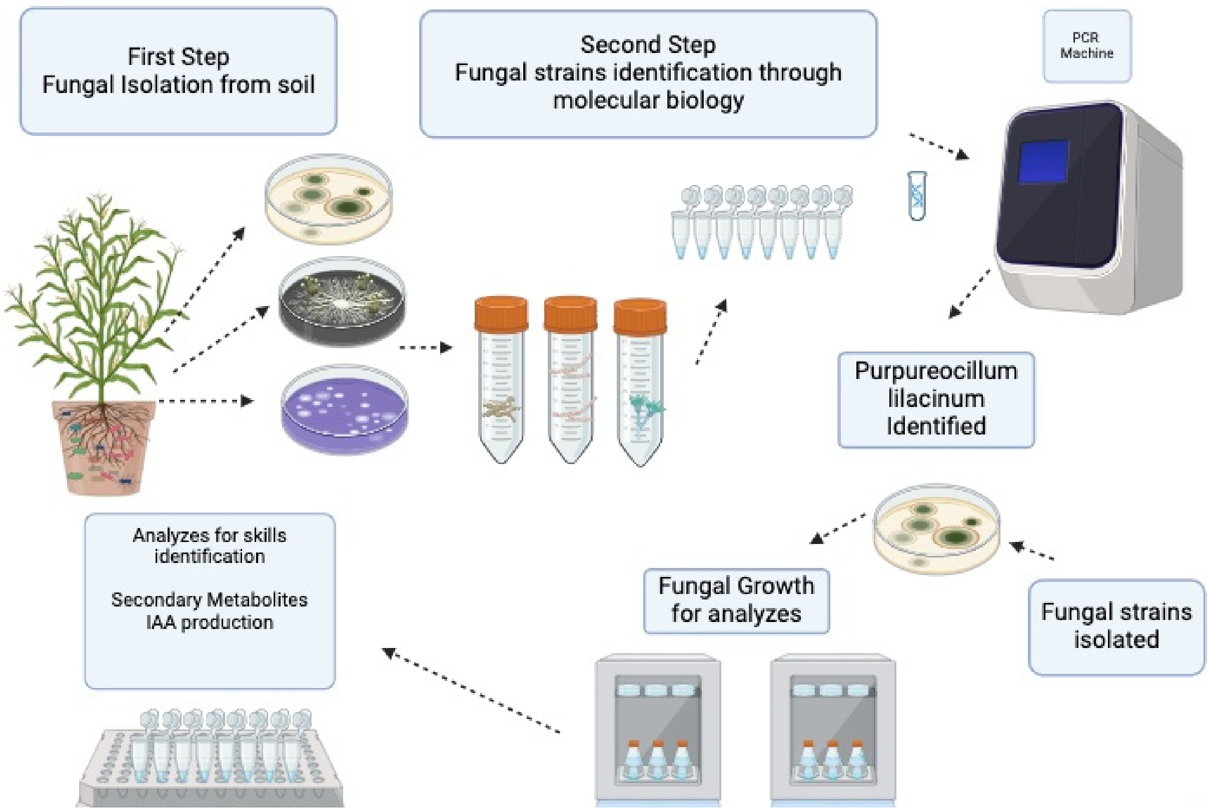

Figure 1. Isolation, identification, and characterization of the fungus *P. lilacinum* from the soil.

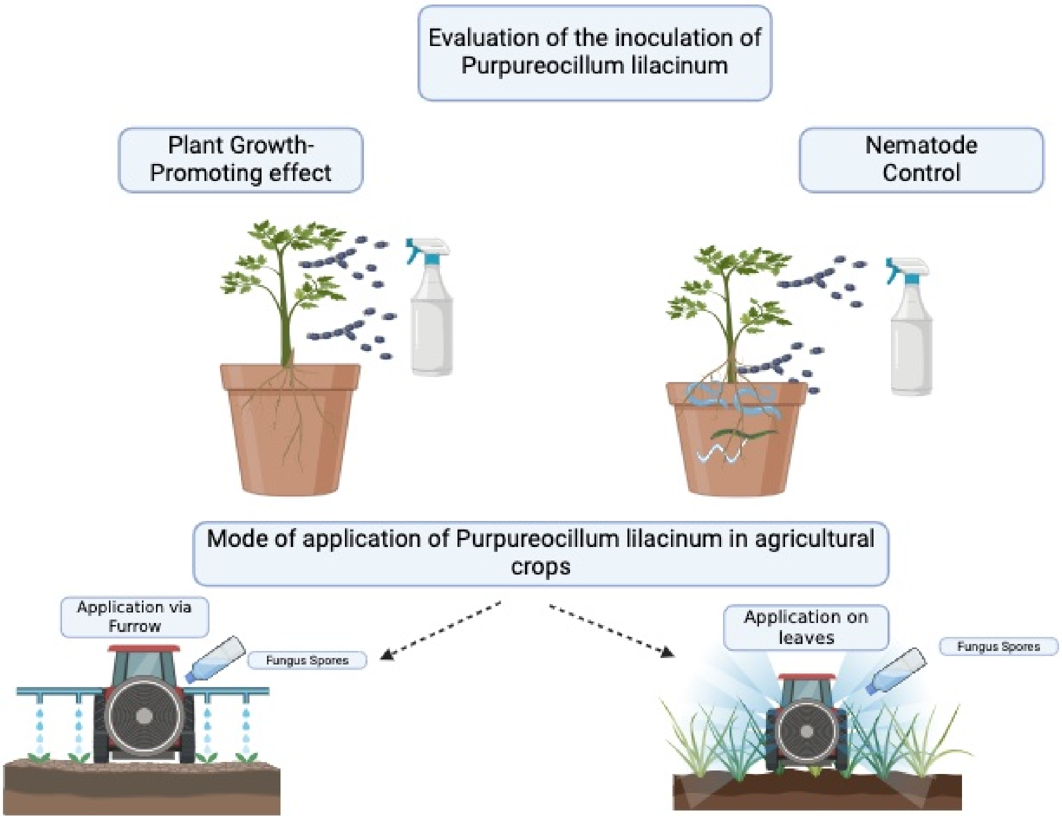

Figure 2. Mode of application of *P. lilacinum* to crop production.

5. Conclusions

Purpureocillium lilacinum, a fungus with several abilities related to plant growth promotion, has been widely studied for its use in nematode control. The production of enzymes such as proteases allows this fungus to digest the bodies of nematodes, accounting for its effectiveness in nematode control. However, *P. lilacinum* also possesses other important characteristics such as phosphorus solubilization, siderophore production, and phytohormone production, which make it a valuable plant growth-promoting agent. Few studies have demonstrated that this fungus promotes root and shoot growth, improves the efficiency of plant exploration in the soil, induces systemic resistance, and increases yield while reducing the need for pesticides and fungicides. *Purpureocillium lilacinum* is a promising fungus for use in sustainable plant production, as it can help reduce production costs and environmental impact.

6. Futures and Perspectives

The use of *P. lilacinum* as a carrier for various plant growth-promoting capabilities has been previously discussed. However, most studies have focused on its potential use as a nematode-control agent. Further research is required to fully understand its potential to induce systemic resistance, which could lead to a reduction in the use of agrochemicals. This fungus also produces several phytohormones that promote increased root and shoot growth, enhancing the ability of plants to explore soil and absorb water and nutrients, potentially reducing the need for chemical fertilization. In addition, it may improve the photosynthetic efficiency. Some studies have demonstrated its potential as a phytopathogenic control agent. In addition, the selection of plant genotypes that interact with fungi is vital for their inclusion in breeding programs. It is crucial to select plants that are highly productive and have the ability to interact with microorganisms. By selecting such plants, there is a greater likelihood of achieving success in terms of sustainable production. The goal was to incorporate this into a breeding program. Previous studies that have assessed the impact of fungi on plant growth have typically used plants that are highly productive and do not interact with microorganisms. However, selecting plant genotypes that are capable of interacting with the fungus and possess several characteristics that promote plant growth would significantly increase the chances of achieving sustainable production. Lastly, no study has investigated the influence of inoculation with *P. lilacinum* on the plant microbiome. The plant microbiome plays a critical role in maintaining plant fitness and health. Therefore, it is essential to understand how inoculation with *P. lilacinum* affects the plant microbiome, especially because this fungus has been shown to promote plant growth. Further research is needed to elucidate these phenomena and to enhance our understanding of the role of *P. lilacinum* in sustainable production in the near future.

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