frontiers | Frontiers in Horticulture

TYPE Mini Review
PUBLISHED 31 May 2024
DOI 10.3389/fhort.2024.1401147

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OPEN ACCESS

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RECEIVED 14 March 2024
ACCEPTED 10 May 2024
PUBLISHED 31 May 2024

CITATION
Palmisano A, Parrado L and Quintanilla M (2024) "Exploring the synergistic relationship between *Pratylenchus penetrans* and *Verticillium dahliae* in potato cropping systems: recent developments and research gaps". *Front. Hortic.* 3:1401147.
doi: 10.3389/fhort.2024.1401147

"Exploring the synergistic relationship between *Pratylenchus penetrans* and *Verticillium dahliae* in potato cropping systems: recent developments and research gaps"

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The plant parasitic nematode species *Pratylenchus penetrans* has been known to form a synergistic relationship with the fungal plant pathogen *Verticillium dahliae* in potato cropping systems across North America. The results of this interaction can be devastating; with plants suffering from choloris, wilting, and premature death or complete yield loss in infected fields. Many studies have been conducted in order to understand how this symbiotic connection is occurring; whether that be from competition within the soil microbial community, through the development of amendment-induced suppressive soils, or from other interactions caused by nematode activity. While the mechanisms behind the hostile interaction between *V. dahliae* and *P. penetrans* are undetermined, the purpose of this review is to compile recent developments relating to this symbiotic relationship, the effects the soil microbial community has on said relationship, as well as identify potential gaps in research.

KEYWORDS

plant pathogen interaction, plant parasite nematode, potatoes (*Solanum tuberosum L.*), *Verticillium*, potato early dying disease, root lesion nematode

Introduction

Potatoes have been a dietary staple for millions of Americans for generations, and their importance to the nation's agriculture sector cannot be overstated. According to recent estimates, the potato industry has contributed over $101 billion to the US economy in 2021 (Ellis, 2023). However, this vital crop is not without its challenges. Potatoes host several species of plant parasitic nematodes, however *Pratylenchus penetrans* (commonly referred to as root-lesion nematode) is frequently associated with significant yield loss and the potato early die disease complex in North American cropping systems (Powelson and Rowe, 1993) due to its ability to form a synergistic relationship with the plant pathogen *Verticillium dahliae* (Robinson et al., 2007).

Root-lesion nematodes present a significant threat to a broad variety of mainly vascular host plants, including corn, cereal crops, and potatoes (Jones and Fosu-Nyarko, 2014). These migratory endoparasitic pests can inflict small wounds on a plant's fine roots, rendering it vulnerable to pathogenic pressure, as they feed, reproduce, and live out their life cycles within the plant's root system (Orlando et al., 2020). Migratory endoparasitic nematodes, like all plant parasitic nematodes, are equipped with a stylet that secretes proteins into plant cell walls as the nematode feeds (Hussey, 1989). While the migratory behavior of nematodes such as *P. penetrans* can be destructive to the plant's cells, it is important to note that the feeding behavior and subsequent secretions of the nematode into host cells are more often connected to severe pathological disturbances (Hussey, 1989). To safeguard plants against these pests, agriculture professionals have started adopting preventive measures, such as implementing crop rotation strategies and developing transgenic resistant plant varieties (Jones and Fosu-Nyarko, 2014) in order to be proactive in their management of these nematodes. However, the most effective method of control is chemical fumigation or commercially available nematicides, which has historically been the more popular and cost-effective approach (Orlando et al., 2020). Root lesion nematodes exhibit clustering behavior within fields (Orlando et al., 2020), so economic thresholds are difficult to determine. Therefore, growers focus their management on limiting the reproduction rate of the pests prior to planting their crops (Orlando et al., 2020).

A symbiotic relationship

Potato early die (PED) complex is an economically important disease associated with two species of *Verticillium* that occur in different geographical locations across the United States; *V. albo-atrum* and *V. dahliae* that can cause choloris, wilting, or even premature death within infected fields (Powelson & Rowe, 1993). In the northern central states and Pacific Northwest, *V. dahliae* is more prevalent and affects an extensive host range of trees, shrubs, and vegetable crops, including potatoes; however, recent findings suggest that different populations can exist within a species and exhibit varying levels of pathogenicity (Powelson & Rowe, 1993). Growers in long-standing (multiple, consecutive, growing seasons) potato fields may overlook the slow-moving disease, mistaking it for early maturation. According to reports from researchers Holgado, Oppen Skau, and Magnusson in 2009, the disease has a noticeable effect on the appearance of plants, but yield loss is often difficult to quantify. PED can be troublesome to manage effectively, which is proliferated by the fact that the microsclerotial resting structures by *V. dahliae* can overwinter and survive in soil from anywhere between 10–20 years (Huisman and Ashworth, 1976). The methods of control against this pathogen include soil fumigation and the application of fungicides (Collins et al., 2005; Orlando et al., 2020). However due to high costs, supply chain disruptions, and increasing environmental concerns, growers have been exploring alternative methods of control through the application of green manures (Robinson et al., 2007) in hope of developing suppressive soils.

Studies conducted in northern or midwestern regions of the United States have shown that fields infected with both *V. dahliae* and the root lesion nematode species *P. penetrans* can accelerate symptom development at population levels that would not have significantly impacted the field had each species been present individually (Bowers et al., 1996). In potato cropping systems, even low populations of both *P. penetrans* and *V. dahliae* have been found to cause a synergistic interaction between plant top and tuber weights, along with the progression of stem length and plant wilting symptoms (Martin et al., 1982, Rowe, 1985). However, according to a study conducted by Martin, Ridel, and Rowe in 1981, this synergistic effect was lost as inoculum populations increased.

Exactly how the *Verticillium-Pratylenchus* interaction impacts potato early die (PED) is up for much debate. However, it is hypothesized that when nematodes feed on roots, it can cause damage that allows fungal pathogens to enter the stele, which can bypass the host's natural defenses against fungal infections, leading to potential damage and decreased crop yields (Powell, 1971).

Nematodes are highly equipped for parasitization. Along with their stylet, PPN's (plant parasitic nematodes) have three large and complex esophageal secretory glands, one dorsal and two sub-ventral (Hussey, 1989). The sites where two distinct gland ducts discharge into the nematode's esophageal lumen may play a role in the onset of certain plant diseases. The dorsal gland secretions are released into the esophageal lumen close to the stylet's base, rendering them easily injectable into plant tissue through the stylet (Hussey, 1989). This phenomenon has been observed in the feeding behavior of various nematodes, where dorsal gland secretions are injected into plant cells (Hussey, 1989). Both the dorsal and subventral glands of the nematode contain a large lobed nucleus with a prominent nucleolus. They also contain abundant Golgi complexes, strands of rough endoplasmic reticulum, free ribosomes, and secretory granules. These are typical organelles found in glandular cells. Nerve processes and neurosecretory cells oppose the cytoplasmic extension and ampulla of the glands. This suggests that the nematode's nervous system regulates the release of glandular substances (Hussey, 1989). Researchers have observed that juvenile endoparasitic nematodes utilize their stylets to puncture and slit cell walls, allowing them to move inside cells and penetrate adjacent ones (Hussey, 1989). While migrating, the subventral glands of these young nematodes are filled with secretory granules, which are not released through the stylet. Once they reach the vascular tissue, the juveniles stop migrating and begin intensely probing several cells around their head with stylet thrusts. After the stylet penetrates a cell wall, it remains protruded within the cell, followed by twitching of the metacorpus and the accumulation of secretory granules in the ampulla of the dorsal gland (Hussey, 1989). It is possible that the development of disease in infected plants is connected to the way cells react to the secretions of nematodes that feed on them or it could be a result of an imbalance in growth processes triggered by the plant's systemic response to the parasitic activity of the nematodes (Hussey, 1989). It is also possible that both these factors contribute to the development of disease in infected plants (Hussey, 1989).

It's interesting to note that chemical changes in soil microbial communities may have an impact on the relationship between *Verticillium*, *Pratylenchus*, and PED. Changes could play a role in the infection affecting potatoes either positively creating biocontrol against the fungus, or falling ill to the disease (Larkin et al., 2010).

Control methods

Further research has been conducted on the alterations in the soil microbiome caused by various treatments like commercially available nematicides, as well as green manures or compost that may change the composition of the microbiome (Molina et al., 2014). The health and makeup of the soil microbiome, including its abundance, diversity, and structure, are closely connected to soilborne diseases. This structure can be changed through various soil management practices; such as fumigation, crop rotation, and the application of green manures (Li, 2021). Green manuring is a farming technique that involves incorporating plant material, or organic amendments like manure or composts, into the soil while it's still green or after it has matured (Fageria, 2007), providing nutrients to crops and boosting soil quality. In fact, studies have shown that green manures or composted amendments have a more rapid and significant effect on the soil microbial communities by increasing biomass and the amount of organic matter than just crop rotation alone (Larkin et al., 2011a). Green manures affect the soil through biofumigation, which refers to the process of breaking down plant metabolites in soil to create volatile compounds that can be harmful to various soil microorganisms, including nematodes, however many field trials have shown that the efficacy is closely linked to particular soil and environmental conditions (Larkin et al., 2011b). Research studies have demonstrated varying levels of efficacy in the use of organic amendments for the formation of suppressive soils against *V. dahliae* and *P. penetrans*. This is achieved by stimulating the growth of microbial communities, including copiotrophic and oligotrophic bacteria, which act against *V. dahliae* (Termorshuizen et al., 2006). Studies have indicated that the effectiveness of fumigation treatments may be reduced, which could be linked to soil type and structure. Research has shown that treatments yield varying results in soil with higher levels of organic carbon and nitrogen, and that more fungi survive fumigation in fine-textured soils compared to coarse-textured ones (Collins et al., 2006). This suggests that the fumigant may not penetrate as deeply in the fine-textured soil, fungal structures may be protected by the heavier soil matrices, bioactive compounds may degrade, or the fumigant may be absorbed and rendered inactive by soil constituents (Warton et al., 2001).

Treatments effect on the soil microbiome

Monitoring changes occurring in the soil microbiome following treatment with fumigants or green manures is essential to gain insight into the underlying mechanisms of the disease complex, especially for long-term management. Beneficial microbes play a critical role in inhibiting pathogen growth through the secretion of antibiotic metabolites into the soil or by parasitizing pathogens (Perez et al., 2007; Dicklow & Madeiras 2018; Nihorimebere et al., 2011). Additionally, they facilitate the decomposition of organic soil matter, which promotes plant growth by facilitating the absorption and release of nutrients, and reduces heavy metal contamination (Li, 2021). A study conducted by Larkin et al., 2011a revealed that only fumigation treatment led to a substantial reduction in *V. dahliae* populations in the soil, while green manure treatments, although reducing disease, did not decrease populations of *Verticillium* spp. The fumigant treatment appears to work primarily by reducing the pathogen inoculum (Larkin et al., 2011b).

Microbial communities produce volatile fatty acids (VFAs) during the decomposition process of manure-based composts, which act as a mechanism of control (Cole et al., 2020). Studies have demonstrated that even small concentrations of VFAs found in liquid swine manure can have lethal effects on *V. dahliae* and nematodes (Cole et al., 2020). Unfortunately, the majority of VFAs do not exhibit long-term persistence within composts or manures, due to their rapid breakdown by microorganisms, degradation, or absorption, which significantly reduces their antagonistic properties over time (Cole et al., 2020). Incorporating green manure into soil may not lead to a significant decrease in pathogen count or their survival rate, particularly in highly infested fields (Perez et al., 2008), however, it has been found to promote the growth of microorganisms with the potential to combat these harmful pathogens by releasing pesticidal agents or ITCs from the amendment and into the soil (Molina et al., 2014). One proposed explanation for *V. dahliae* suppression is that incorporating composted amendments into field soil can promote microbial competition, which helps boost a plant's natural growth hormones, subsequently increasing yield (Davis et al., 2010). A study focusing on using biocontrol against *V. dahliae* infections discovered a novel endophytic bacterium in a specific potato cultivar that not only promotes plant function and growth but is also antagonistic against *V. dahliae* (Ambwani, 2019). Incorporating these antagonistic microbes into disease management and understanding their impact on root-lesion nematode populations may represent the future of biocontrol for PED.

Conclusion and future prospects

Monitoring the soil microbiome and understanding the variability of composts is crucial for developing effective disease management strategies against PED. However, broad-spectrum compost treatments for PED disease management are challenging to recommend due to the diverse feedstocks and micro fauna populations of composts, as well as native field soil diversity. Thus, a comprehensive analysis of the soil microbiome and nematode diversity is necessary to devise sustainable disease management approaches. Green manures and composted amendments have been found to have a significant effect on microbial activity, which is inversely related to the incidence of *Verticillium* and PED. In order to overcome the limitations in effectiveness and truly understand the impact of treatments on soil microbiome and nematode populations, further research is absolutely essential. By delving deeper into the factors that affect the efficacy of treatments and the underlying mechanisms by which they interact with the soil, we can develop more effective and sustainable solutions for managing soil health and boosting crop yields. It is crucial that we also consider the long-term effects of these treatments on soil fertility and the wider ecosystem, including beneficial soil organisms. Identifying specific beneficial or antagonistic microbes, VFAs, and ITCs could be plausible mechanisms for nematode and *V. dahliae* reduction, and should be studied further. The synergistic relationship between *P. penetrans* and *V. dahliae* is the largest culprit for the spread and severity of the disease. Therefore, studying and subsequently disrupting this interaction without the reliance on fumigation or other damaging chemicals should take precedence for further research proposals. This will facilitate the development of sustainable soils with long-term suppression of PED and nematode pests, while still respecting potato growers and other stakeholders' productivity goals.

Author contributions

AP: Writing – original draft, Writing – review & editing. LP: Writing – review & editing. MQ: Writing – review & editing.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. This article was funded in part by the Michigan Potato Industry Committee.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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