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Utilization of Plant Growth-Promoting Rhizobacteria (PGPR) for Managing Recently Reported Potato Cyst Nematodes, *Globodera* spp. in North Himalayan Regions of India

Vijeta Katoch[1] · Shavnam[1] · Saurabh Sharma[2] · Manisha Negi[2]

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Abstract

Globodera rostochiensis (Woll.) and *Globodera pallida* (Stone), two potato cyst nematodes (PCNs), are significant pests worldwide. The first PCNs from North Himalayan regions of India were detected in 2010 in Shimla, Himachal Pradesh (HP). Despite a domestic quarantine, succeeding surveys in the mountainous regions of North India have shown the presence of PCNs in numerous districts of HP, Jammu and Kashmir and Uttarakhand. The seed plot technique is utilized in North Himalayan regions of India to create virus-free seed and the state agricultural departments distribute it to farmers in other parts of the nation. Therefore, the entire nation should be concerned about the emergence of such a significant potato seed location as the primary sites for large PCN populations. Inorganic pesticide based nematode management is an effectual way to address this biotic stress but improper use of chemicals can have a negative impact on the environment. Therefore, the farming community must prefer the employment of potential biocontrol agents, this might aid in fending off regulatory and environmental pressure. Plant growth-promoting rhizobacteria (PGPR) enabled control of PCNs can be environmentally benign. In light of this, we undertook an extensive and thorough review of the available literature pertaining to PGPRs. Our analysis uncovered that PGPRs can greatly assist in enhancing plant resilience to various stressors that can impede their growth and yield. However, achieving these benefits will require successful development and commercialization efforts. Furthermore, before PGPRs can be widely employed, it is crucial to tackle the challenges related to their selectivity and restricted range of activity.

Keywords Enzymes · Hyperparasitism · Induced systemic resistance · Phytohormone

✉ Shavnam
shavnamthakur1467@gmail.com

[1] Department of Plant Pathology, Dr. YS Parmar University of Horticulture and Forestry, Nauni, Solan 173230, Himachal Pradesh, India

[2] Department of Soil Science and Water Management, Dr. YS Parmar University of Horticulture and Forestry, Nauni, Solan 173230, Himachal Pradesh, India

Introduction

Potato (*Solanum tuberosum*) is cultivated throughout the globe and is one of the most important crops for human nutrition (CIP 2020). It offers more protein and minerals than any other type of staple crop and it is abundant in carbohydrates (Beals 2019). Optimum pest and disease control are essential for the sustainable agricultural production following the rising demand from a growing global population. Plant parasitic cyst nematodes (PCN) namely *Globodera pallida* (Stone) and *G. rostochiensis* (Woll.) cause huge economic losses in potato crops (Aires et al. 2009). These are soil inhabitors, biotrophic sedentary endoparasites as pathogens specific to the *Solanaceae* family (Sabeh et al. 2019; Gartner et al. 2021). PCN are temperate species and attains high population densities in cool climates on the host plant. In warm or tropical areas, the PCN find it difficult to complete their life cycle because the annual egg mortality rate in warmer geographic areas is more than 75% as compared to 50% in temperate regions. As a result, temperate regions must be the main focus of PCN investigations.

These nematodes (worms) have a very severe negative impact on tuber production and quality (Brodie et al. 1993; Marks and Brodie 1998). The PCN are the most strictly controlled nematodes because of their capacity to form cysts that are passively transferred over great distances with contaminated or infected plant root remnants, tubers and soil debris (Sullivan et al. 2007). According to estimates, PCN can result in yield losses of 19 to 80%, based on the variety, seasonality and soil population of PCN (Turner and Evans 1998). Potato yields may fall short of the tonnes per hectare of the seed planted when PCN numbers are large in the field (Mai 1977; Whitehead and Turner 1998). According to Contina et al. (2020), PCN species may reduce potato output by up to 80% if left unchecked, resulting in significant financial losses for the global potato industry.

For researchers working on sustainable agriculture, controlling PCN has become a difficult task. In the past, nematodes were controlled with a variety of synthetic chemical nematicides, including carbamates, organophosphates and fumigants. The demand for more effective nematode control strategies has increased as a result of the large decline in pesticide use caused by European Union (EU) rules (EC No. 1107/2009), which show that pesticides are detrimental for human health and the environment (Zhang et al. 2017). Chemical nematicides expanded agrarian and economic possibilities by boosting food and fibre production at the expense of human health and the environment (Akhtar and Siddiqui 2009). Plant growth-promoting rhizobacterial (PGPR) variants can operate as an effective nematode biocontrol agent (BCA) and environmentally friendly methods and also act as plant growth promoter for increased yield (Mhatre et al. 2018). Recognizing the communities of benevolent microorganisms and their modes of action for regulating PCNs will give a ground for enhancing the possible biocontrol strains' pathogenicity and create cutting-edge biocontrol methods for PCN management. This review aims in utilization of PGPR for management of PCN.

Occurrence

The cyst nematodes are the primary source of crop losses in the potato (*Solanum tuberosum* L.) industry (Van Riel and Mulder 1998). These are important quarantine pests worldwide originated from the Andean Mountains of South America. Hafez and coworkers (2007) for the first time reported the PCN species *G. pallida* in USA. Occurrence and distribution of *G. rostochiensis* (pathotype Rol) were the most abundant in Northern Ireland (Zaheer et al. 1993), whereas in England and Wales rather than *G. rostochiensis* another PCN species, i.e. *G. pallida,* was predominant (Minnis et al. 2000; Karnkowski et al. 2011). Similarly, in Algeria (Africa), the most divergent PCN species was *G. pallida* (Tirchi et al. 2016). However, both species were prevalent in Quebec, Canada, having high economic impact on the potato crop (Sun et al. 2007). In Japan, in the year 1972, PCN was earliest identified in Hokkaido region (Yamada et al. 1972). It was believed that PCN were introduced into Europe during 1850 along with the planting materials introduced for breeding to late blight resistance varieties; afterwards, their worldwide spread were recorded by the introduction of improved varieties developed in Europe (Evans and Stone 1977).

Their presence in India was first noted in the Nilgiri and Kodaikanal hills of Tamil Nadu (Fig. 1) in 1961 (Thangaraju 1983). Domestic quarantine was enforced in India to stop PCN from spreading outside of Tamil Nadu because the seed tubers are the main means of PCN transmission. However, PCN was afterwards recorded from Kerala, Himachal Pradesh and Karnataka. Being a quarantine pest, somehow,

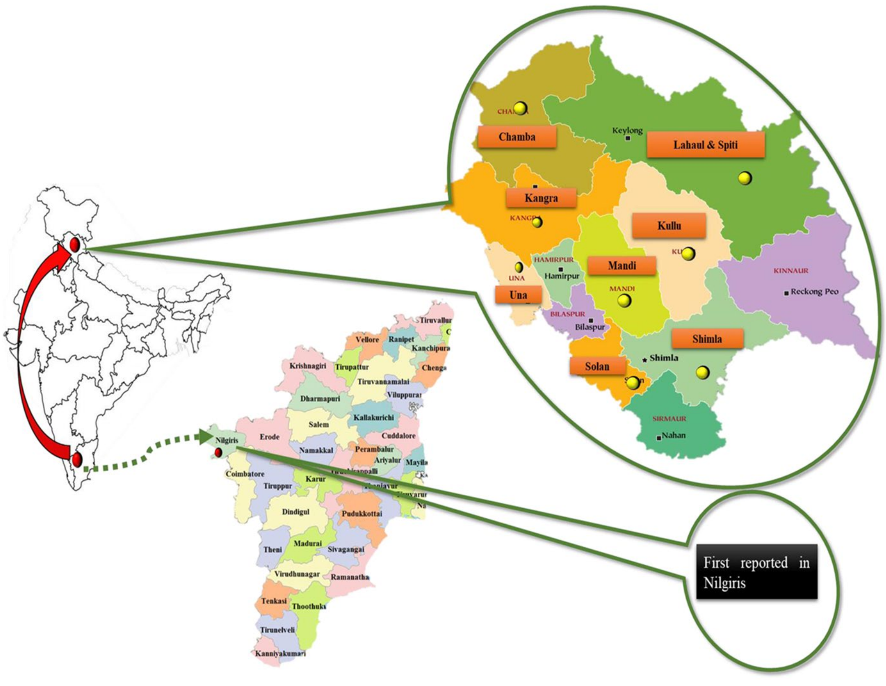

Fig. 1 Occurrence of PCN in India

in 2010, Shimla, Himachal Pradesh (HP) witnessed their first interception from North India (Ganguly et al. 2010). Despite the domestic quarantine against this nematode in place, later surveys of 2011–2019 conducted in the Himalayan regions of North India have shown the presence of PCN in a number of districts of HP, Jammu and Kashmir and Uttarakhand (Chandel et al. 2020). In the North Himalayan regions, the seed plot technique is frequently utilized to create virus-free seeds that are sown from October to January. State agricultural departments multiply these seeds and distribute it to farmers in other parts of the nation. Therefore, the entire nation should be concerned about the emergence of such a significant potato seed location as the primary sites for large PCN populations.

Life Cycle

PCN nematodes complete one life cycle with each crop. During maturation, *G. rostochiensis* female nematodes attain yellow colour from white and later develop a cyst of brown colour; however, the female of *G. pallida* becomes “brown” from “creamy white” (Wainer and Dinh 2021). In soil, PCN cysts are dormant and a stony deceased body of female nematode protects the egg inside. Root exudates of a host plant stimulate the eggs to hatch, leading to spread of infective juvenile second stage (J2) nematodes in the soil. These get entered into roots by puncturing the cells around the root tip and move to the interior cortical layers (Perry 2002; Varandas et al. 2020). During migration of juveniles via the outer root tissues, fast and vigorous stylet insertion takes place which causes the cell death due to liberation of effector proteins, cell wall modification and dissolution proteins (Cotton et al. 2014; Palomares-Rius et al. 2017). Modification of plant cells by establishing a feeding site, which is source of nutrients for the nematode, results into poor root system and also reduced productivity (Wainer and Dinh 2021). Afterwards, molting of the nematode takes place from third (J3) and fourth (J4) stages up to maturity. Fully developed females become sedentary while matured males are movable in nature and leave the root attracted towards the females, and when they produce sexual pheromones, fertilization takes place (Ali et al. 2015). The female produces 300–500 eggs that she keeps inside her body after the male fertilizes them in the soil. The female perishes along with the root, but her skin hardens and changes to create a cyst (Fig. 2) that protects the eggs (Stanton 1987).

Symptoms

Above ground, PCN infestation symptoms are frequently vague and difficult to identify. In the farm, poor growth patches that exhibit yellowing, necrosis and withering of leaves are common symptoms (Wainer and Dinh 2021). These species harm potatoes by piercing and entering inside the tissues of roots, which results in nutrient and water shortage that manifests as chlorosis and withering of the leaves. They may also cause poor growth, dwarfism and the multiplication of small lateral roots, which reduce yield. These symptoms are not specifically produced by PCN nematodes

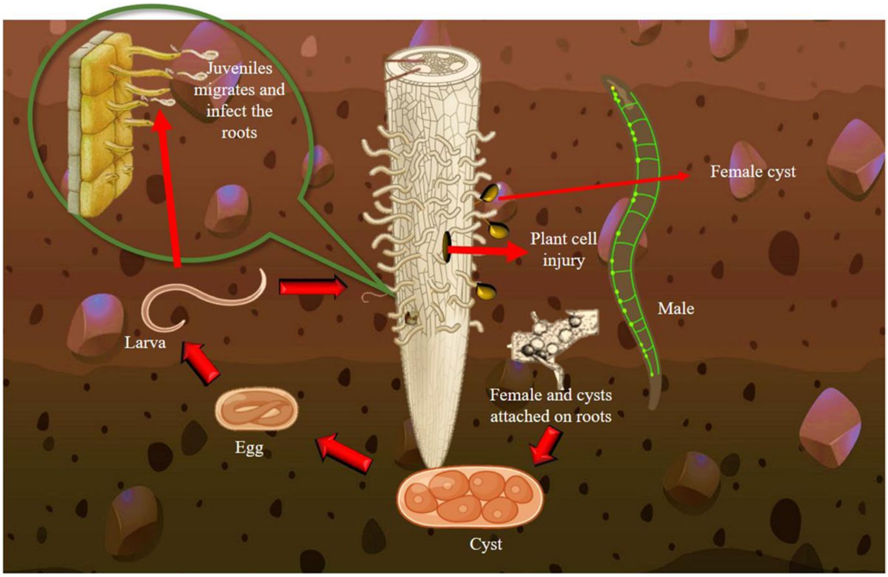

Fig. 2 Life cycle of PCN

but may be caused by any other plant pathogen such as fungi, bacteria and viruses including other nematodes. By uprooting the infected plants, young female and with the naked eye, cysts appear as tiny white, yellow or brown nitwits on the surface of the root. This method is possible for a short period of time as the female gets mature into a cyst which can be simply lost with uplifting and it also takes a long time (EPPO 2017) (Fig. 3).

Plant Growth-Promoting Rhizobacteria (PGPR)

Various free-living bacteria present in soil, known as plant growth-promoting rhizobacteria (PGPR), invade the rhizosphere and promote plant development, which raises agricultural crop yields (Kumar et al. 2016). *Azospirillum*, *Pseudomonas* and *Bacillus* are the most studied root dwelling microbes among the rhizobacterial genera. The triumph of the PGPR has been employed for a variety of advantageous reasons, including phytostimulation, biofertilization, bioremediation and biological control, all of which depend on their colonization in the root system (Mhatre et al. 2018). PGPR have also been found to be possible agents for reducing plant parasite damage (Table 1). Nematodes and their interactions have been intensively researched in order to effectively manage phytopathogenic nematodes (Tabatabaei and Saeedizadeh 2017; Rashad et al. 2015). When compared to traditional management techniques, recent research has suggested that biocontrol can be a more cost-effective strategy to deal with PCN. Particularly, PGPR have shown promise as BCA contenders (Siddiqui and Mahmood 1999; Wani 2015).

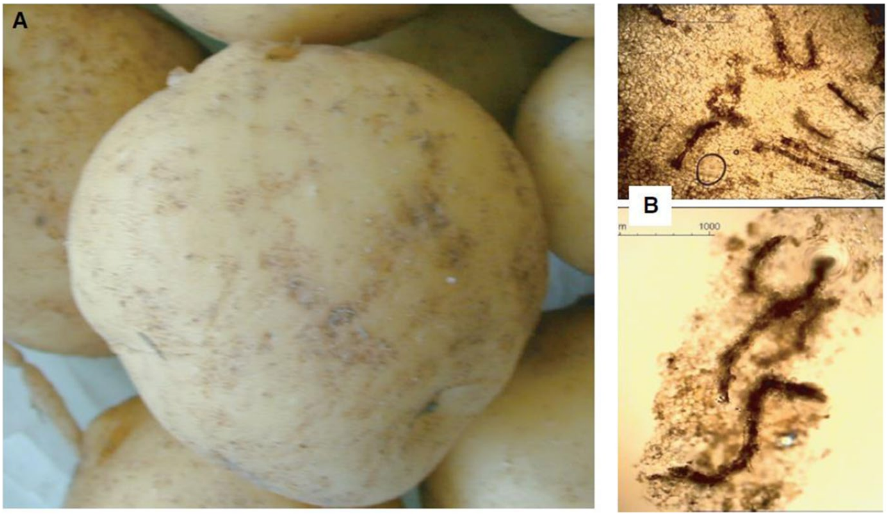

Fig. 3 Skin diseases caused by *Globodera pallida* (**A** whole tuber and **B** second stage juveniles (J2s) in the cuticle) (Mugniery and Phillips (2007) with permission of © (2007) Elsevier)

Non-pathogenic bacteria called PGPR have indeed been shown to increase plant growth under both stress-free and stressful situations through both direct and indirect approaches (Lugtenberg and Kamilova 2009). The direct and indirect approaches define PGPR being a bio-fertilizer that generates organic chemicals which in turn enhances soil nutrient absorption/uptake boosting plant development, creation of antibiotics, chelates of Fe (also known as siderophores) and exterior cell membrane disintegrating enzymes (such as chitinase and glucanase) that may hydrolyze the cell wall of pathogens (Van Loon et al. 1998). According to this scenario, it has been shown that numerous PGPR, regularly belonging to the genus *Agrobacterium*, *Bacillus* and *Pseudomonas*, can lower PCN population size through several different mechanisms, such as parasitism, the generation of hydrolytic enzymes and antinematicidal metabolites and by inducing systemic resistance (Lugtenberg and Kamilova 2009). PGPRs can have both direct and indirect approaches in reducing the population of PCN.

Direct Approaches

Animosity between PGPR and PCN

Direct antagonism of PGPR can prevent egg incubation and/or the growth and reproduction of PCN by predating and the release of allergens or hydrolytic enzymes. Ammonifying bacteria release ammonia during the degradation of nitrogenous organic compounds, which is harmful to nematodes and aids in the control of worm populations. The population of cyst nematodes was reportedly decreased by *Pseudomonas fluorescens* all the way through synthesis of secondary metabolites like DAPG (Siddiqui and Shaukat 2003). Additionally, according to Rose et al. (2012), *Pseudomonas*

Table 1 Effects of PGPR application on nematodes

PGPR used	Mode of action	Observation	References
Pseudomonas fluorescens F113	2,4-Diacetylphloroglucinol (DAPG)	The improvement in hatch ability and the decrease in juvenile mobility were both driven by DAPG	Cronin et al. (1997)
Bacillus flexus and *B. pumilus*	The specific activity of the protease and chitinase differed significantly among the isolates	Observed 98% egg mortality (*B. pumilus*) and 96.4% (*B. flexus*)	Widianto et al. (2021)
P. putida and *P. aurantiacea*	Produced certain metabolites that can prevent nematode eggs from hatching	Decreased nematode proliferation with *P. putida* 3 and *P. aurantiacea* 13 by 40.7–42.2% compared to the control, respectively	Trifonova et al. (2014)
B. subtilis and *P. fluorescens*	Production of antibiotics and protease enzyme in case of *Bacillus* while in *Pseudomonas fluorescens* production of cell wall-degrading enzymes such as β1, 4-gluconase and siderophore as biocontrol agents as well as antibiotics including phenazine 1-carboxylic acid, fenazine 1-caboxamide, pirolnithrine and pilotheorine	*B. subtilis* and *P. fluorescens* highest antagonistic activity and caused 78.74% and 76.54% mortality	Nikpay and Khodakaramian (2013)
Agrobacterium radiobacter and *B. sphaericus*		Root infection was significantly reduced by 24–41% when *Agrobacterium radiobacter* and *Bacillus sphaericus* were present at concentrations of 9.7 10^8 and 3.16 10^9 cfu ml^{-1}, respectively	Racke and Sikora (1992)
Agrobacterium radiobacter G12	Exopollysaccharids (EPS) and lipopolysaccharides (LPS)	Caused a significant decline in nematode penetration: 77% with *B. sphaericus*	Hasky-Gunther et al. (1998)
Pasteuria penetrans	Hyperparasitism		Ciancio (2018)
B. sphaericus	Induced systemic resistance (ISR)		Xiang et al. (2018)
Pasteuria nishizawae	Predation		Sayre et al. (1991)

fluorescens reduces the rates at which nematodes proliferate and it performed better in conjunction with neem cake. Numerous PGPR from the families of *Bacillus* and *Pseudomonas* generate nematicidal substances. For instance, many strains of *Pseudomonas fluorescens* reduce the levels of PCN (*Globodera* spp.) and root knot nematodes (*Meloidogyne incognita*) in soil conditions and/or in vitro by producing DAPG, a phenolic anti-phytopathogenic metabolite (Subedi et al. 2020). In comparison to mutant strains that disrupted DAPG manufacturing, the wild-type bacteria may inhibit the activity of adolescent PCNs by 85% (Cronin et al. 1997).

Synthesis of Enzymes (lytic)

The creation of certain enzymes is another way that PGPR works such as dehydrogenase chitinases, phenylalanine ammonia lyase, lipases proteases, peroxidase and so on. *Corynebacterium paurometabolous* was identified to generate hydrogen sulphide and chitinase, both of which impede the hatching of worm eggs (Mena and Pimentel 2002). PGPR-produced hydrolytic enzymes can hinder the production and preservation of cell membranes and walls, as well as the creation of cellular organelles (Maksimov et al. 2011). Chitinases and distinct proteolytic enzymes generated by *Bacillus cereus*, *Bacillus licheniformis*, *Bacillus megaterium* and *Bacillus subtilis*, as well as *Corynebacterium paurometabolous*, are known to contribute for hindering the proliferation of certain cyst nematodes (Subedi et al. 2020).

Induced Systemic Resistance (ISR)

The improved defense system for plants known as induced resistance is acquired with the proper stimulation in opposition to a variety of diseases and pests. Induced systemic resistance (ISR) or systemic acquired resistance (SAR) describes the elevated defensive reaction induced by a substance subsequent to pathogen infection (Van Loon 2000). Rhizobacteria have been shown in several studies to decrease the impact of nematodes by fostering systemic resistance in plants (Ramamoorthy et al. 2001; Pieterse et al. 2002). ISR resembles SAR phenotypically; SAR is the phenomena wherein a plant develops resistance to successive challenge inoculations by the same pathogen and different diseases and, in some cases, even insects (Van Loon and Bakker 2006). Treatment with biocontrol agent initiates systemic resistance and ISR is induced by PGPRs depending on jasmonic acid and ethylene as signal. Reitz et al. (2002) revealed that the development of systemic resistance in roots of the cyst nematode *Globodera pallida* is cell membrane lipopolysaccharide of *Rhizobium etli* strain G12. This demonstrates how PGPR may contribute to systemic resistance against nematodes by concentrating and regulating defense enzymes.

Indirect Approaches

Nitrogen Fixation, Phosphorus and Potassium Solubilization

In addition to being crucial for both photosynthesis and for protein biogenesis, nitrogen (N) is a crucial major nutrient for plants. Furthermore, it contributes significantly to nucleotides in the form of N bases (Elrys et al. 2019, 2021). Due to frequent N loss, agricultural soils are deficient in N. Since plants cannot utilize air nitrogen directly, therefore, in this situation, PGPR is essential for N fixation and food replenishment. These N-fixing bacteria are divided into two categories, including symbiotic and free-living N-fixers (Gopalakrishnan et al. 2017). As they supply the host plant with both a source of N and an environment free of nematodes, N-fixing PGPR strains having nematode-fighting activity are significantly crucial for agriculture on sustainable basis (Vejan et al. 2016). Utilizing PGPR containing N-fixers as biological pest controllers for plants parasite nematodes has been confirmed particularly for sugar beet and PCN by Sikora (1992) and Nagachandrabose (2020).

Both biochemically and physiologically, phosphorus (P) and potassium (K) are necessary for plant growth (Hasanuzzaman et al. 2018). But the bulk of minerals having P and K may be found in the soil in a fixed state that the plant finds arduous to utilize (Khanna et al. 2019). PGPR from soil such as *Bacillus*, *Beijerinckia*, *Erwinia* and so on, combine chelation, release of organic acid and acidification to convert fixed forms of P to available ones, influencing target plant growth and nutrient availability (Gulati et al. 2010). The microbial species *Pseudomonas syringae*, *Bacillus megaterium*, *Bacillus cereus*, *Pseudomonas cichorii* and *Bacillus caryophylli* are known to have the potential to both solubilize and mineralize phosphate, resulting in improved phosphate bioavailability. Furthermore, by offering additional aid, PGPR helps the host plant deal with nematode infestation. According to Seenivasan et al. (2007), *Pseudomonas fluorescens* and *Pseudomonas lilacinus* reduced *Globodera rostochiensis* and *Globodera pallida* cyst levels in potato. Some rhizospheric microorganisms convert insoluble K in an available form for crop development and productivity, much like P-solubilizing bacteria do. For K solubilization, PGPRs uses a variety of processes, including excreting organic acid, chelation, reduction, complexolysis, exchange and acidolysis (Meena et al. 2016). Additionally, the growth and nematicidal activity in tomato (*Solanum lycopersicum*) were found to be benefited by the inoculation of K-solubilizing bacteria (El-Hadad et al. 2011).

Hyperparasitism and Production of Phytohormone

Hyperparasitism involves tropic development of the biological control toward the target cell, coiling, final attack and membrane or cell wall destruction by enzyme activity (Mavrodi et al. 2017). Excellent efficacy has been shown by *Pasteuria penetrans* against *G. rostochiensis* (Tian et al. 2007).

Many phytohormones are produced by PGPR, including auxins (IAA, IBA and phenylacetic acid), cytokinins (isopentenyl adenosine, isopentenyl adenine riboside, transzeatin ribose and zeatin), gibberellic acid, abscisic acid, ethylene, polyamine, etc. which can have an influence on the metabolism and growth of plants (Gopalakrishnan et al. 2015). It is believed that phytohormones generated by PGPR facilitate plant growth and interactions with microorganisms (Chandra et al. 2018). Additionally, the addition of bacteria that create IAA may promote disease resistance (Chakraborty et al. 2006) and nematode biocontrol is also improved when phytohormones generating PGPR are introduced to the rhizosphere (Khan et al. 2012). Consequently, any direct impact of microbes on phytohormone creation may influence the potency of these hormones as phytostimulants. It has been demonstrated that the class of phytohormones known as strigolactones, which Arabidopsis roots secrete, actively contributes to host attraction during cyst nematode parasitism (Martinez et al. 2019).

Generation of Siderophores

Living beings demand iron for a variety of biological processes, including electron transport, respiration, photosynthesis and as an enzyme cofactor (Proenca et al. 2019). In circumstances with poor iron bioavailability, PGPR have created novel strategies to attach iron's insoluble form by creating siderophore of lower weight (Schwabe et al. 2020). *Enterobacter* spp., *Pseudomonas* spp. and *Bacillus* spp. have a variety of plant growth traits coupled with nematicidal behavior (El-Sayed et al. 2014). Ruanpanun et al. (2010) revealed siderophores synthesis and anti-nematode action of *Streptomyces* sp. Likewise, *Azadirachta*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Enterobacter* and *Pseudomonas* sp. are amongst the PGPR that contribute to the generation of siderophores, which bring iron into plant cells and encourage growth (Cornelis 2010).

Complications Related to PGPR Application

Most traditional agrochemicals are broad-spectrum substances that have an impact on a variety of species. Therefore, a single agrochemical can be used for a variety of pathogens and species. However, this quality is lacking in PGPR and limiting it from being utilized more broadly. Another issue related to use of PGPR is even if some strains of PGPR are offered as biological nematicides in the market, there is still a basic issue of commercialization to be resolved. PGPR products need to have a diverse range of uses, a prolonged keeping quality, be secure for using, have a profitable market, be easily accessible, be reliable and having a low capital cost in order to be financially prosperous. The partnership between multidisciplinary scientific organizations and private enterprises, as well as its expansion to the stakeholders, will result in the success of PGPR commercialization. Unlike other potent PGPR species like *Pseudomonas* spp., *Bacillus* spp. are the most common species of marketed PGPR because of their resoluteness. They are regarded as good choices since they can easily create endospores, rapidly proliferate and colonize plants in adverse situations. However, additional research is needed to evaluate their mode of operation as BCAs of PCN in order to determine more efficient procedures.

Conclusions and Future Thrusts

Potato is staple food crop grown worldwide and is infested by plant parasitic nematodes, amongst cyst nematode namely *Globodera rostochiensis* and *G. pallida* which cause huge economic losses up to 80%, when proper management practices are not followed. Globally, potato cyst nematode is an important quarantine pest, and to prevent the spread of PCN, Government of India kept quarantine guidelines in Tamil Nadu and Madras. In spite of strict legislative regulations, their prevalence was recorded in northern hills of India viz., Jammu and Kashmir, Uttarakhand and Himachal Pradesh. It is imperative to increase production while enhancing crop protection and soil fertility with an environmentally sustainable method. Recent findings have suggested the potential and sustainable benefit of PGPR as BCAs in controlling PCN. This approach is widely accepted around the world as one of the safest ways to manage nematodes and encourage plant development. By using genetic engineering to advance PGPR methodology, consortium applications and other advancements will guarantee the productivity and stability of agro-ecosystems, resulting in an agricultural system that is both optimal and sustainable. Through a direct or indirect mechanism, several strains of PGPR appear to effectively inhibit PCN infestation and proliferation in plants and fields. PGPRs will be considerably aided in improving plants' ability to survive in the face of varied ecological restrictions without compromising yield potential if they are successfully developed and commercialized.

The success of PGPR products' commercialization depends on future research into enhancing their growth circumstances, security, all-purpose action, keeping quality and permanence. The conditions for successful use of effective strains of PGPR for sustainable crop production include a thorough knowledge of the rhizosphere community and colony formation by them. In order to increase the effectiveness of an integrated nematode management strategy, a use of both molecular and biotechnological methods with conventional methods will help to better control of PCN. Furthermore, by overexpressing a variety of anti-phytopathogen features synergistically for effective PCN management, scientific know-how of genetic engineering may be employed to augment the biocontrol effectiveness of PGPR.

Declarations

Competing Interests The authors declare no competing interests.

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