REVIEW

Plant growth promoting rhizobacteria (PGPR) and their role in plant-parasitic nematodes control: a fresh look at an old issue

Ahmed A. A. Aioub1 · Ahmed E. Elesawy2 · Esraa E. Ammar3

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Abstract
The increasing demand for agricultural products can be met by maximizing production potential and reducing crop losses caused by common plant-parasitic nematodes. Chemical-based nematode management is a successful technique for mitigating damage and yield losses caused by nematode pests; however, inappropriate and irresponsible application of synthetic pesticides has negative impacts on fauna, bioflora, and natural enemies such as predators and parasites. The use of biocontrol agents is the most appreciated method for nematode control among farmers because it’s safe and reduces environmental pollution. There is increasing focus on the biological control of plant-parasitic nematodes using plant growth-promoting rhizobacteria (PGPR) as a biopesticide. Moreover, PGPR strains can promote plant growth by producing various secondary metabolites of these PGPRs. This review focuses on the direct (Nitrogen fixation, phytohormone formation, phosphate solubilization, Potassium solubilization, siderophores and ammonia production) and indirect mechanisms (Hyperparasitism, antibiosis, lytic enzyme production, induced systemic resistance) of action of PGPR in plant-parasitic nematodes management, and the future prospects of PGPR-based plant-parasitic nematodes biocontrol agents.

Keywords Biological control · Plant growth-promoting rhizobacteria · Alternative tool · Nematode

Abbreviations

| Abbreviation | Description |
|--------------|-------------|
| PGPR         | Plant growth promoting rhizobacteria |
| PPNs         | Plant-parasitic nematodes |
| BCA          | Biological Control Agent |
| RKN          | Root-knot nematodes |
| J2s          | Second-stage juveniles |
| GCs          | Giant cells |
| HCN          | Hydrogen cyanamide |
| ISR          | Induced Systemic Resistance |
| SOD          | Superoxide dismutase |
| PPO          | Polyphenol oxidase |
| PO           | Peroxidase |
| CAT          | Catalase |
| LOX          | Lipoxygenase |
| PAL          | Phenylalanine ammonia lyase |
| APX          | Peroxidase |
| JA           | Jasmonic acid |
| LPS’s        | Lipopolysaccharides |
| SA           | Salicylic acid |

Introduction
There are approximately 4000 plant-parasitic nematodes (PPNs) species known that may be found in all major biomes (Press and Phoenix 2005). Because of their inhabitation and parasitism behavior, it is more difficult to control plant-parasitic nematodes (Gillet et al. 2017). Plant-parasitic nematodes are polyphagous parasitic worms that cause extensive damage to important food crops, including maize, potato, and tomato (Nicol et al. 2011). Plant-parasitic nematodes control costs $173 billion per year to the global agriculture industry (Elling 2013). Species of Meloidogyne sp., Heterodera sp., Globodera sp., and Pratylenchus sp. are among the most economically significant due to the high levels of damage and infection they inflict, their vast host range, and interaction with the host plant. Root-knot nematodes (RKNs) inhibit not only plant growth and yield but also nodulation,
nitrogen fixation, and mineral nutrient absorption from the soil (Rehman et al. 2012). Root-knot nematode-infected plants exhibit symptoms both aboveground and belowground. The aboveground symptoms include poor development and fewer as well as smaller pale green leaves that wilt under high temperatures (Elnahal et al. 2022). Symptoms emerge as large galls on the roots that are two to several times the diameter of a healthy root and interfere with the plant’s ability to absorb and translocate water and dissolved nutrients. The nematode pests parasitize roots/other belowground plant parts, injuring them and allowing the entry of other soil-borne illnesses (Agrios 2005) (Fig. 1). Furthermore, there is an increasing demand for more food for the growing world population (FAO 2017). Therefore, PPN management is becoming increasingly popular throughout the world.

Several synthetic chemical nematicides such as fumigants are used to manage and control PPNs (Katooli et al. 2010). As population expansion demands an increased agricultural production and the efficacy of nematicides to protect crops against diseases and pests, the traditional method of nematode management is completely dependent on nematicides. Nevertheless, due to European Union (EU) regulations (EC No1107/2009), which state that pesticides are dangerous to human health and pollute the environment, pesticide use has considerably decreased, which has consequently increased the need for other effective nematode control methods (Zhang et al. 2017). Therefore, there exists a critical need for a nematode control method that is both ecologically acceptable and effective.

Plant-parasitic nematodes management strategies, including biocontrol methods, offer a safer and more practical option (Abd-Elgawad 2021). The term “biological control” (or biocontrol) refers to an ecologically sound and successful method for eliminating or suppressing plant-parasitic nematodes using naturally occurring species with pesticidal activity or manipulating the environment or introducing opponents (Landis and Orr 1996; Eldeeb et al. 2022). Moreover, a biological control agent is organism that adversely affects the biology and physiology (e.g., development, reproduction and respiration) and its and it is commonly referred to as a “biopesticide.” In general, biopesticides are defined as “products targeted at protecting plants and are produced from live organisms or natural compounds derived from species coevolution, rather than chemicals, and whose usage is suggested for controlling pests or bioaggressors for greater biocenosis and environmental safety” (Chandler et al. 2011).

Plant growth-promoting rhizobacteria (PGPR) are host-specific biological agents that can adversely impact on the development and survival of PPNs (Alberton et al. 2020). Plant growth-promoting rhizobacteria have been defined in different ways by different authors. For instance, Kloepper and Schroth (1981) defined PGPR as a type of soil bacteria that colonize the roots of plants after being inoculated onto seeds and help them thrive. Bishnoi (2015) defined PGPR as a wide collection of soil bacteria that are important components of soil-plant systems, wherein they interact actively and effectively in the rhizosphere, regulating plant development and yield through a variety of processes. Plant growth-promoting rhizobacteria are also termed as plant health-promoting rhizobacteria or nodule-promoting rhizobacteria (Hayat et al. 2010) and can be categorized into two groups based on their habitat, viz., iPGPR (i.e., symbiotic bacteria), which reside inside plant cells, generate nodules, and are confined to specific structures, and ePGPR (i.e., free-living rhizobacteria), which live outside plant cells, do not produce nodules, but nonetheless stimulate plant development (Gray and Smith 2005). In general, the function of PGPRs can be summarized in the following three ways: first, production of certain chemicals required for plants (Backer et al. 2018); second, increasing plant resistance (Çakmakçı et al. 2006); and finally, promoting the absorption of certain minerals from the soil (Saravanakumar et al. 2008). Bacillus, Paenibacillus, Brevibacillus, Pseudomonas, Serratia, Burkholderia, and Streptomyces species are typical PGPRs used as seed treatments because of their adverse effect
on disease microbes and antibiotic-producing properties (Kokalis-Burelle et al. 2006). Antibiotic synthesis, substrate competition, and induced systemic resistance in the host are some of the processes implicated in suppression of PPNs by PGPR (Nivya 2015). Moreover, numerous PGPR formulations have been reported to decrease the severity of disease caused by RKNs in experiments with muskmelon and watermelon (Kokalis-Burelle et al. 2003). Consequently, it has become more critical to explore innovative, ecologically acceptable methods, such as the use of PGPR, to control PPN populations.

Understanding the beneficial microorganism populations and their mechanisms of action in controlling PPNs at the molecular level will provide a foundation to enhance the pathogenic activity of potential biocontrol strains and develop modern biocontrol strategies in PPNs control. This review focuses on the usage of PGPR to control PPNs.

### Distribution of root-knot nematode in Egypt

*Meloidogyne* spp. cause important diseases affecting numerous plant crops in Egypt and hence has a significant economic impact. *Meloidogyne arenaria* Chitwood, *M. javanica* Chitwood, and *M. incognita* Chitwood are the most economically important species in Egypt (Ibrahim et al. 2000). They are particularly damaging in tropical, subtropical, and warm regions (Ibrahim et al. 2000). Root-knot nematodes are particularly significant disease-causing agents in Egypt, affecting numerous agricultural plants and food supplies due to their widespread distribution, broad host ranges, and association with disease-causing fungi and bacteria. There have been extensive investigations in this regard, and RKNs have been documented to infect a variety of crops in all regions of Egypt (Bakr et al. 2020). Table 1 shows the distribution of *Meloidogyne* spp. in Egypt.

#### Table 1 Distribution of various species of *Meloidogyne* spp. in Egypt

| Root-knot species | Host plant                                      | Government | Reference                      |
|-------------------|-------------------------------------------------|------------|--------------------------------|
| *M. incognita*    | Almond (*Prunus dulcis*), Apple (*Malus pumila*), Banana (*Musa paradisiaca*), Date palm (*Phoenix dactylifera*), Grape (*Vitis vinifera*), Guava (*Psidium guajava*) | Alexandria | Ibrahim and Mokbel (2009)      |
|                   | Pomegranate (*Punica granatum*), Strawberry (*Fragaria ananassa*), Banana (*Musa paradisiaca*), Grape (*Vitis vinifera*), Guava (*Psidium guajava*) | El-Behera  | Ibrahim and Mokbel (2009)      |
|                   | Citrus (*Citrus maxima*)                        |            |                                 |
|                   | Lantana (*Lantana camara*)                      |            |                                 |
|                   | Ngaio tree (*Myoporum pictum*)                  |            |                                 |
|                   | Table beet (*Beta vulgaris*)                     |            |                                 |
|                   | Field bindweed (*Convolvulus arvensis*)         |            |                                 |
| *M. arenaria*     | Banana (*Musa paradisiaca*), Common fig (*Ficus carica*), Grape (*Vitis vinifera*) | El-Behera  | Ibrahim and Mokbel (2009)      |
|                   | Date palm (*Phoenix dactylifera*)               | Matrouh    | Ibrahim (1994)                  |
|                   | Spanich (*Spinacia oleracea*)                   | Matrouh    | Ibrahim and Handoo (2015)       |
| *M. javanica*     | Olive (*Olea europaea*)                         | Matrouh    | Ibrahim (1994)                  |
|                   | Strawberry (*Fragaria ananassa*)                | El-Behera  | Ibrahim and Mokbel (2009)      |
|                   | *annual rabbitsfoot grass* (*Polypogon monspeliensis*) | Matrouh    | Ibrahim (1994)                  |
|                   | *Swiss chard* (*Beta vulgaris*)                 | El-Behera  | Ibrahim and Mokbel (2009)      |
|                   | *broad bean* (*Vicia faba*)                     |            |                                 |

**Life cycle of root-knot nematodes**

Root-knot nematodes can complete their entire life cycle in 20–40 days; however, its life cycle duration is influenced by soil moisture, temperature, and host species (El-Saadony et al. 2021). The life cycle of RKNs begins with an egg from which a second-stage juvenile (J2) hatches. With the aid of their chemosensory amphids, J2s travel across the vulnerable host roots and/or through the soil by sensing chemical gradients in root tissues (Vagelas et al. 2012). Physiologically, several gradients are found near active roots, such as carbon dioxide (CO₂), and it is possible that some of them operate as “long-distance attractants,” allowing the J2 to move to the root region (Banerjee and Hallem 2020). Besides CO₂, other attractants, including amino acids, carbohydrates, and metabolites, are equally effective in attracting RKN J2s (Tsai et al. 2019). After finding an appropriate host, RKN J2s readily perforate below the root’s protraction zone, migrate between cells toward the root tip, and pass the Casparian strip to reach the vascular tissue (Shukla and Barberon 2005).
The specific signals that govern the direction of J2s in the roots are uncertain, and only the role of CO2 as a significant attractant is known (Banerjee and Hallem 2020); however, pH can also influence the direction in which the J2s migrate (Kawanobe et al. 2020). Root-knot nematodes release a combination of enzymes that degrade the cell wall, which they use to transmit and split the soft, intermediate lamella connecting the root cells (Rai et al. 2015). A second-stage juvenile (J2) release a variety of enzymes from their subventral glands including cellulases (endoglucanases), polygalacturonases, pectate lyases, and endoxylanases (Rai et al. 2015). The J2s turns around (180 degrees).

A migrate in the opposite direction toward the vascular cylinder to settle in the differentiation zone for feeding. Then, 5–8 vascular cells are selected to form a feeding site, of which the cells undergo a series of metabolic and nutritional alterations before being transformed into giant cells (GCs). Moreover, hypertrophied cortical cells, proliferated pericycle cells, and xylem are significantly disturbed in the region of GCs, and the GCs are surrounded by complicated xylem tissues (Bartlem et al. 2014). Protophloem forms and spreads rapidly, surrounding the GCs (Absmanner et al. 2013) and resulting in the formation of a distinct pseudo-organ termed gall that contains the GCs. Meloidogyne spp. that form tiny or no galls in their host plant exhibit reduced hyperplasia surrounding tissues (Palomares-Rius et al. 2017). The life cycle of RKNs is depicted in detail in Fig. 2.

**Impact of PPNs on agriculture yield and productivity**

Root-knot nematodes are tiny roundworms that belong to the phylum Nematoda and are among the most numerous animals on the planet, with more than 4100 species discovered in a range of habitats (Krif et al. 2020). Root-knot nematodes reside in the moisture layer surrounding soil particles and plant roots for the most part of their life cycle (Krif et al. 2020). To gain access into root tissues, PPNs have protruding styles or mouth spears (Palomares-Rius et al. 2017). Root-knot nematodes are divided into two types based on their feeding environments, viz., endoparasites and ectoparasites (Smant et al. 2018). Ectoparasites feed on the exterior of root surfaces rather than inside the roots (Sato et al. 2019). Endoparasitic nematodes, on the other hand, can penetrate plant roots completely.
or partially during the infection process (El-Ashry et al. 2021; Aioub et al. 2021). This causes physical harm as well as the possibility of secondary damage from fungal and bacterial infection concurrently with PPN infection (Zasada and Ferris 2003). Endoparasitic nematodes are estimated to cause a worldwide annual loss of 13% ($216 billion) (Singh et al. 2015). For instance, it has been reported that *Meloidogyne* spp. were responsible for causing an annual global loss of $157 billion (Abad et al. 2008). Moreover, the loss due to *Rotylenchulus* spp. was approximately 26,000 bales of cotton, equivalent to a 3% yield reduction (Lawrence et al. 2014). Therefore, establishing an effective and long-term management program to combat PPNs is becoming a top priority across the world. Nevertheless, as PPNs are tiny and primarily target plant subsurface areas, the existing integrated PPN control strategies are limited compared to those used to control other pests (Bernard et al. 2017).

### Biological control

Biological control is currently a widely used approach for pest management across the world (Landis and Orr 1996). In biological control, there are four primary strategies that may be used as described in the following lines. (1) Introduction: this is a traditional strategy in which an exotic beneficial organism is introduced into a new territory and becomes completely established. This method is typically used against pests that have no natural enemies. (2) Augmentation: in vivo or in vitro reared individuals released in the natural environment to compensate for the inefficiency of existing or natural occurring microbial agents. Small numbers of native, natural enemies may be the reason for the lack of pest control. (3) Inoculation: an inoculative release is done at the start of the planting season when an indigenous microbial agent is not present or an exotic antagonist cannot persist indefinitely. This technique may have to be repeated for each subsequent growing season. (4) Inundation: this strategy involves bulk cultivation of a pathogen for application during crucial periods when rapid pest population control is required (D. L. Lee 2002). Root-knot nematode populations are regulated partially by biological control agents, and a variety of species, such as bacteria, exhibit antagonistic activity against them (Migunova and Sasanelli 2021).

#### Plant growth promoting rhizobacteria (PGPR) as biocontrol agents

Several bacterial species live in the “rhizosphere” of a plant’s roots and stimulate plant development by enhancing plant growth regulators. These bacteria are known as PGPR (Kumar et al. 2015). Plant growth promoting rhizobacteria are bacteria that live in the “rhizosphere” of a plant’s roots and promote plant regulators and boost nutrient availability (PGPR) (Turan et al. 2021). In the soil, diverse microorganisms such as *Rhizobium* sp., *Xanthomonas*, *Bacillus* sp., *Arthrobacter* sp., *Bradyrhizobium* sp., *Frankia* sp., *Enterobacter* sp., *Proteus* sp., *Klebsiella* sp., *Flavobacterium* sp., *Pseudomonas* sp., *Serratia* sp., *Microbacterium* sp., and *Erwinia* sp. thrive as widespread rhizosphere elements that completely colonize the rhizosphere (Teymouri et al. 2016; Abad et al. 2008). *Bacillus*, *Azospirillum*, and *Pseudomonas* are some of the most well-known colonized rhizobacteria genera. The use of bacteria in the rhizosphere plays a significant role as a biofertilizer and psychostimulant and in developing disease resistance and heavy metal cleanup, but it is dependent on colony formation in the rhizosphere. Rhizosphere-based microorganisms can improve plant growth through production of a set of plant growth compounds and conferring resistance to nematode infection and development (Basu et al. 2021). Moreover, PGPR have been identified as potential agents for reducing the damage caused by PPNs, resulting in improved effective PPN management (Subedi et al. 2020). The use of PGPR has a significant impact on plant development and can cause the death of PPNs. Therefore, PGPR represent an excellent tool for improving agriculture practices and are a critical component of nematode control (Backer et al. 2018). Several PGPR strains are known to display a reduction in gall number of RKN species, including *Bacillus firmus* T11, *B. cereus* N10w, *B. aryabhattai* A08, *Paenibacillus barcinonensis* A10, and *P. alvei* T30 (Viljoen et al. 2019). A greenhouse experiment conducted on cucumber with the strains *Pseudomonas fluorescens* and *Serratia marcescens* resulted in a significant decrease in gall index and egg mass of RKN species compared with the untreated control group, and these strains are now considered biocontrol agents compared with *M. incognita* (Ali et al. 2021). Examples of PGPR shown in Table 2 are used as biological control agents for PPN suppression.
Table 2  Plant growth-promoting rhizobacteria act as biocontrol agents for the management of plant-parasitic nematodes

| PGPR                  | Target PPN                                                                 | Mode of action                                                                 | Reference                                                                 |
|----------------------|---------------------------------------------------------------------------|--------------------------------------------------------------------------------|---------------------------------------------------------------------------|
| Pasteuria penetrans  | Aphelenchoides besseyi, Globodera rostochiensis, Meloidogyne incognita, Pratylenchus penetrans, Radopholus similis | Parasitism                                                                     | Ciancio (2018) Abd-Elgawad and Askary (2018) Tian et al. (2007)            |
| Agrobacterium radiobacter (G12) | Meloidogyne spp.                                                      | Induced systemic resistance                                                   | Nikoo et al. (2014)                                                       |
| Bacillus cereus      | Meloidogyne javanica, Meloidogyne incognita,                               | Induced systemic resistance                                                   | Jiang et al. (2020)                                                       |
| B. amyloliquifaciens | Meloidogyne incognita                                                   | Induced systemic resistance and systemic acquired resistance                  | Xie et al. (2018)                                                         |
| B. amyloliquifaciens FR203A | Xiphinema index                                                               | Lipases                                                                                 | Köhl et al. (2019)                                                        |
| B. thuringiensis     | Meloidogyne incognita                                                   | Bt crystal protein (toxin protein), Thuringiensin (exotoxin)                   | Mohammed et al. (2008)                                                    |
| B. thuringiensis     | Meloidogyne hapla                                                         | Cry6Aa2 protoxin                                                                | Radhakrishnan et al. (2017)                                               |
| B. thuringiensis     | Meloidogyne spp.                                                          | Cry5B                                                                            | Ghahremani et al. (2020)                                                  |
| B. thuringiensis     | Bursaphelenchus xylophilus                                                | Cry1Ea1                                                                         | Nascimento et al. (2013)                                                  |
| B. firmus            | Meloidogyne incognita                                                   | Sep 1 protease Secondary metabolites                                            | Geng et al. (2016)                                                       |
| B. coagulans         | Meloidogyne incognita                                                   | Hydrolytic enzymes                                                             | Xiang et al. (2018)                                                       |
| B. licheniformis     | Bursaphelenchus xylophilus                                                | Protease, Chitinase                                                            | El-Nagdi et al. (2019)                                                    |
| B. subtilis          | Meloidogyne javanica                                                      | Lipopeptide antibiotics, Hydrolytic enzymes, Secondary metabolites             | Basyoni and Abo-Zaid (2018)                                               |
| B. panulis           | Meloidogyne incognita                                                   | Induced systemic resistance and systemic acquired resistance                  | Lastochkina et al. (2017)                                                 |
| B. mojavensis        | Meloidogyne incognita                                                   | Induced systemic resistance                                                    | Xiang et al. (2017)                                                       |
| Bacillus sp.         | Meloidogyne javanica                                                      | antibiotics, siderophores, changes in root exudates, and induced resistance    | Turatto et al. (2018)                                                     |
| Pasteurias penetrans | Meloidogyne spp.                                                          | Predation                                                                       | Bhuiyan et al. (2018)                                                     |
| *Pseudomonas fluorescens* | Meloidogyne incognita                                      | Sphingosine, Antibiotic production, Chitinase, Protease                       | Abd El-Aal et al. (2021)                                                  |
| *P. fluorescens*     | *Globodera rostochiensis*                                                | 2,4 diacetylphloroglucinol (DAPG)                                              | Siddiqui and Shaukat (2004)                                               |
| *P. aeruginosa*      | *Meloidogyne javanica*                                                    | Induced systemic resistance and systemic acquired resistance                  | Fatima and Anjum (2017)                                                   |
| *P. fluorescens*     | *Meloidogyne incognita*                                                  | Sphingosine, Antibiotic production, Chitinase, Protease                       | Ali et al. (2021)                                                         |
| *P. patida*          | Meloidogyne incognita                                                   | Induced systemic resistance                                                    | Almaghrabi et al. (2013)                                                  |
| *P. fluorescens*     | Meloidogyne incognita                                                   | Antibiosis, nematicidal toxins, parasite of nematode eggs and adult females, nematode juvenile inside the egg is destroyed by the rapidly growing hyphae | Bharali et al. (2019)                                                    |
| P. stutzeri          | Meloidogyne incognita                                                   | Hydrogen cyanide (HCN)                                                         | Khan et al. (2016)                                                        |
| P. Fluorescens       | Meloidogyne javanica                                                      | antibiotics, siderophores, changes in root exudates, and induced resistance    | Turatto et al. (2018)                                                     |
| P. aeruginosa        | Meloidogyne incognita, Meloidogyne javanica                               | HCN                                                                             | Singh and Siddiqui (2010)                                                 |
| *P. fluorescens* Wood1R | Meloidogyne incognita                                                | 2,4-diacetylphloroglucinol (DAPG)                                              | Timper et al. (2009)                                                      |
| Serratia marcescens  | Meloidogyne incognita                                                   | Induced systemic resistance                                                    | Almaghrabi et al. (2013)                                                  |
| S. marcescens        | Meloidogyne incognita                                                   | Sphingosine, Antibiotic production, Chitinase, Protease                       | Ali et al. (2021)                                                         |
| S. marcescens        | Meloidogyne incognita                                                   | ISR                                                                             | Almaghrabi et al. (2013)                                                  |
| S. marcescens        | Meloidogyne javanica                                                      | Volatile metabolites, Prodigiosin                                              | Rahul et al. (2014)                                                       |
Mode of actions of PGPR

Direct mechanisms

Plant growth promoting rhizobacteria help plants cope with nematode stress by producing phytohormones (cytokines, abscisic acid, auxins, and ethylene) and improving nutrient availability and uptake through phosphate and potassium solubilization, nitrogen fixation, and organic compound mineralization.

Nitrogen fixation

Nitrogen is a critical macronutrient required for plant development and growth; it is essential for protein synthesis and photosynthesis and is a substantial macronutrient of nucleic acids in the form of nitrogenous bases (Elrys et al. 2019, 2021a). Constant loss of nitrogen results in its low levels in agricultural soil. However, plants are unable to directly use atmospheric nitrogen (Cocking 2000; Elrys et al. 2021b). Plant growth promoting rhizobacteria are important for nitrogen fixation and nutrition supplementation in this situation. These nitrogen-fixing bacteria may be divided into two types as follows: symbiotic or free-living nitrogen-fixing bacteria (Raymond et al. 2004). Nitrogen-fixing PGPR strains with nematicidal activity play a significant role in sustainable agriculture as they provide both a nitrogen source and a nematode-free environment for the host plant (Vejan et al. 2016; Liao et al. 2021). In particular, Bradyrhizobium, Rhizobium, Frankia, Mesorhizobium, and Sinorhizobium are PGPR genera that can fix atmospheric nitrogen and supply it to plants, promoting plant development (Dash et al. 2017). Aggangan et al. (2013) also demonstrated that banana plants treated with nitrogen-fixing bacteria had suppressed populations of M. incognita and Radopholus similis, resulting in increased banana growth. Similarly, Paenibacillus polymyxa, a nitrogen-fixing bacterium, promotes plant development and exhibits nematicidal activity (El-Hadad et al. 2011).

Phytohormone formation

The diversity of PGPR strains may result in the production of plant growth-promoting chemicals such as phytohormones and plant growth regulators such as auxins (indole butyric acid, indole acetic acid, and phenylacetic acid), cytokines (trans-zeatin ribose, isopentenyl adenine riboside, isopentenyl adenosine, and zeatin), abscisic acid, gibberellic acid, ethylene, brassinosteroids, polyamines, jasmonates, strigolactones, salicylic acid, and other plant growth regulator compounds (Tsukanova et al. 2017) that have a direct impact on plant development and metabolism. Indole acetic acid is the most prevalent phytohormone. Phytohormones produced by PGPR are considered to promote plant development and plant–bacterial interactions (Chandra et al. 2018). The primary function of microbial phytohormones is to improve plant development by promoting elongation, cell division, tissue expansion, and other favorable effects on plant development (Khan et al. 2009). Moreover, the inclusion of bacteria that produce indole acetic acid may improve plant development and generate disease resistance (Chakraborty et al. 2006). Phytohormones produced by PGPR have been shown to protect against the negative effects of different environmental stressors (Glick 2010). Plant growth and nematode biocontrol can be improved by introducing phytohormones that produce PGPR to the field via seed application (Backer et al. 2018). For instance, Myo et al. (2019) reported that indole acetic acid production by the strain Streptomyces frae lique NKZ-259 enhanced plant growth and reduced pest population. Similarly, the strain Pseudomonas simiae MB751 produces indole acetic acid that plays a role in M. incognita control and improves plant growth (Sun et al. 2021). Therefore, any direct effect of bacteria on phytohormone synthesis may have an impact on their phytostimulating effectiveness.

Phosphate solubilization

Phosphorus is another important element required for plant development (Malhotra et al. 2018). It is involved in various aspects of plant growth, including nucleic acid formation,
protein synthesis, tissue growth, cell division, and complex energy conversion (Mahler 2004). However, phosphate compounds are available in an insoluble form in agricultural settings. Plant growth promoting rhizobacteria isolated from soil use chelation, organic acid generation, and acidification to transform inaccessible phosphorus into available forms (Alori et al. 2017), influencing host plant development and nutrient uptake. Several PGPR genera such as Arthrobacter, Bacillus, Enterobacter, Flavobacterium, Microbacterium, Pseudomonas, Rhizobium, Rhodococcus, and Serratia have been previously reported to act as phosphate solubilizers (Raj et al. 2014; Bechtaoui et al. 2019; Maldonado et al. 2020). Guang-Can et al. (2008) demonstrated that the bacterial species P. syringae, B. megaterium, B. cereus, P. cichorii, and B. caryophylli possess both phosphate solubilization and mineralization capacity, resulting in increased phosphate bioavailability. Furthermore, the phosphate-solubilizing bacterium B. firmus was found to suppress M. incognita populations in tomato roots (Terefe et al. 2009). Consistently, Seenivasan et al. (2007) reported that P. fluorescens, P. lilacinus, and T. viride caused a reduction in Globodera rostochiensis and G. pallid cyst populations in potato (Solanum tuberosum). Similarly, inoculating tomato plants with B. megaterium led to improvement in growth parameters and Nitrogen, Phosphorus and Potassium contents as well as reduction in M. incognita J2 populations (El-Hadad et al. 2011).

Siderophores and ammonia production

Living organisms require iron for biological functions such as electron transport, respiration, photosynthesis, and as a cofactor for numerous enzymes (Proença et al. 2019). Iron exists in an insoluble form in soil under aerobic conditions, making it difficult for living organisms to obtain it. Plant growth promoting rhizobacteria have developed unique methods to bind the insoluble form of iron by producing low molecular weight siderophores in environments with low iron bioavailability (Schwabe et al. 2020). Aeromonas, Azadirachta, Azotobacter, Azospirillum, Bacillus, Burkholderia, Enterobacter, Pseudomonas, Rhizobium, Serratia, and Streptomyces sp. are among the PGPR that aid in the synthesis of siderophores that carry iron into the cells of plants and promote their development (Bapiri et al. 2012; van Beelen and Fleuren-Kemíla 1997). Similarly, Enterobacter spp., Pseudomonas spp., and Bacillus spp. possess numerous properties related to plant development, as well as nematicidal activity (El-Sayed et al. 2014). Plant growth promoting rhizobacteria strains have a direct effect on plant development by triggering cell division, physiological and biochemical metabolisms, and tissue development (Oleńska et al. 2020); however, PGPR help the host plant deal with nematode infection by providing additional assistance.

Potassium solubilization

Plants also require potassium as a macronutrient. Potassium is essential for plant development, both biochemically and physiologically (Hasanuzzaman et al. 2018). However, the majority of potassium-containing minerals exist in the soil in a permanent form that is difficult for the plant to exploit (Khanna et al. 2019a). Some rhizospheric microorganisms, such as phosphate-solubilizing bacteria, solubilize the insoluble form of potassium and release it in a form that plants may use for their own development and production (Wang et al. 2020). For potassium solubilization, PGPR use a variety of processes, including chelation, organic acid excretion, reduction, acidolysis, and exchange (Wang et al. 2020). Bacillus edaphicus, Acidithiobacillus ferrooxidans, Burkholderia spp., B. mucilaginosus spp., Pseudomonas spp., and Paenibacillus spp. are among the microbial species involved in potassium solubilization (Han and Lee 2006). In addition, the inoculation of potassium-solubilizing bacteria has a favorable effect on tomato (Solanum lycopersicum) development and nematicidal activity (El-Hadad et al. 2011).

Indirect mechanism

Hyperparasitism

Hyperparasitism is the most effective and direct type of antagonism (Pal and Gardener 2006). Hyperparasitism entails the trophic growth of the biocontrol agent toward the target organism, coiling, ultimate assault, and disintegration of the target pathogen’s cell wall or membrane through enzyme activity (Singh et al. 2017). Pasteuria penetrans exhibits excellent activity against G. rostochiensis, Apehlenchoides besseyi (Tian et al. 2007), M. graminicola, M. incognita, M. arenaria, M. hapla (Ciancio 2018), R. similis, and Pratylenchus penetrans (Abd-Elgawad and Askary 2018).

Antibiosis

Antibiotics are bacteria-produced chemical compounds with a low molecular weight. Through competition and parasitism, they play an important role in the biological control of a variety of pests (Arseneault and Filion 2017). Antibiosis is a crucial aspect of luminous pseudomonad disease control. Enzymes, metabolic by-products, and toxins are released by several PGPR to control PPNs. This prevents hatching of nematode juveniles, growth, survival, and reproduction (Subedi et al. 2020). Ammonia is generated by ammonifying bacteria through the decomposition of nitrogenous organic compounds and helps decrease root-parasitic nematode
populations (Norton and Ouyang 2019). *Pseudomonas fluorescens* also produces secondary metabolites, such as 2,4-diacetylphloroglucinol, which has been found to suppress *M. incognita* populations on pepper (*Capsicum annum*) (Meyer et al. 2009). Also, some rhizobacteria have been shown to produce chemicals such as hydrogen cyanide, which kills nematodes in the rhizosphere and aids in plant growth (Abd El-Rahman et al. 2019). Furthermore, *P. fluorescens* delays nematode development (Rizvi et al. 2012). *Azospirillum*, *Azotobacter*, and *Rhizobium* have also been demonstrated to significantly decrease root galling by *M. javanica* in root of chickpea (*Cicer arietinum*) (Siddiqui and Mahmood 2001).

**Lytic enzyme production**

Another mechanism of action of PGPR is the production of enzymes, for example, phenylalanine ammonia lyase, \( \beta \)-glucanase, chitinase, lipase, dehydrogenase, protease, peroxidase, and phosphatases that enhance plant growth (Won et al. 2021). *Corynebacterium paurometabolous* has been found to generate chitinase and hydrogen sulfide, both of which impede hatching of nematode juveniles (Mena et al. 2002). *Pseudomonas fluorescens* and *S. marcescens* were found to decrease nematode populations in roots of cucumber (*Cucumis sativus*) (Ali et al. 2021). On testing a strain of *Lysobacter capsici* newly isolated from Korean soil (Lee et al. 2015) for its biocontrol activity against root-knot nematodes in tomato (*Solanum lycopersicum*), this strain was found to express both chitinase and gelatinase activities. The amount of these enzymes released increased significantly following the addition of eggs and J2 of *M. incognita* to the culture medium. The lower numbers of galls and egg masses found in tomato roots inoculated with this PGPR, compared to those occurring in untreated plants, was found to be a consequence of the synthesis of these enzymes. Moreover, Li et al. (2019) revealed that inoculation of tomato plants with strain *B. cereus* (BCM2) increased the release from the bacterium of nematode-inhibitory molecules, especially 2,4-di-tert-butylphenol and 3,3 dimethyloctane. Subsequently, it has been demonstrated that a crude protein extract of BCM2, also contained chitosanase, alkaline serine protease, and neutral protease, and induced 100% mortality in second-stage juveniles of *M. incognita*.

**Induced systemic resistance (ISR)**

Induced resistance refers to a plant’s improved capacity to defend itself against a diverse variety of pests after being appropriately stimulated (Kamal et al. 2014). Systemic acquired resistance (SAR) refers to the enhanced defense response caused by an inducing substance following infection by a pathogen or pest (Wendehenne et al. 2014). Induced systemic resistance can be induced by PGPR, whereas SAR refers to the resistance generated by other microorganisms. Both generated resistances protect against a wide spectrum of diseases, including those caused by fungi, nematodes, bacteria, insects, and viruses (Beneduzi et al. 2012). Numerous defense enzymes are linked to systemic resistance, such as superoxide dismutase, polyphenol oxidase, peroxidase, catalase, lipoxygenase, chitinase, phenylalanine ammonia lyase, \( \beta \)-1,3-glucanase ascorbate, peroxidase, and proteinase (Pokhare et al. 2012). These enzymes initiate the resistance-inducing process by generating phenolic chemicals and phytoalexins (Mohammadi et al. 2020). Extensive research has demonstrated that PGPR reduce the population of plant-parasitic nematodes by increasing the plant’s systemic resistance (Khanna et al. 2019b). This induced tolerance is achieved through cell wall intensification, callose sedimentation, phenolic compound accumulation, and upregulation of biochemical compounds such as jasmonic acid, pathogenesis-related (PR) proteins, lipopolysaccharides, phytoalexin, siderophores, chitinase, and salicylic acid (Khanna et al. 2019b). Another study showed that *B. cereus* significantly decreased *M. incognita* and *M. javanica* populations in roots of *Arabidopsis* through the development of systemic resistance (Jiang et al. 2020). Hackenberg et al. (1999) found that *Agrobacterium radiobacter* (G12) plays an essential role in preventing *Globodera* spp. juveniles from penetrating potato (*S. tuberosum*) roots. Interestingly, tomato roots (*S. lycopersicum*) treated with *P. fluorescens*, Pf128 plus *Bacillus subtilis*, Bbv57, showed increased activity of enzymes and decreased *M. incognita* populations (Meena et al. 2012). This demonstrates the possible function of PGPR in establishing systemic resistance to nematodes by animating and compiling defense enzymes such as polyphenol oxidase, peroxidase, and phenylalanine ammonia lyase. The overall mechanisms of action of PGPR as nematode biocontrol agents are presented in Fig. 3.

**Fig. 3** Schematic view of direct and indirect mechanisms of plant growth-promoting rhizobacteria
Challenges in PGPR application

The capacity of microbial inoculations to compete with native microbial populations and environmental conditions is critical for their application in phytoremediation, bioremediation, as biofertilizers, and as biocontrols. Major problems with microbial survival arise under naturally occurring, field conditions circumstances. The physical and chemical qualities of the soil, the biological activity of indigenous microbes, and agricultural management strategies such as crop rotation all influence the microbial inoculation of crop plants. Most inoculants are successfully based on the basis of first come, first served. So, what are the reasons, and which are the critical areas where new inputs are required in order to increase commercialization of PGPR products? The selectivity of PGPRs is one of the key factors preventing them from becoming more widely used. The majority of conventional agrochemicals are broad-spectrum compounds that affect a wide range of organisms. Plant growth promoting rhizobacteria, on the other hand, tend to be highly targeted. This can result in variable quality and efficacy under field conditions.

Applications of PGPR as multifunctional agents

The other advantages of inoculating plants with PGPR include drought resistance, as shown for the strains *P. fluorescens* DR11 and *Enterobacter hormaechei* DR16 (Ilyas et al. 2020), tolerance to salinity stress, as shown for *Bacillus pumilus* and *Achromobacter piechaudii* (Sagar et al. 2020), tolerance to biotic stress as demonstrated for *Paenibacillus xylanexedens* and *Bacillus amyloliquefaciens* (Reshma et al. 2018), increased nutrient absorption, as shown for *P. poly- myxa* (Chen and Liu 2019), seed germination enhancement, shown for *S. marcescens* and *P. fluorescens* (Almaghrabi et al. 2014), biostimulation by phytohormone production, as demonstrated for *Azospirillum lipoferum* and *B. subtilis* (Kalam et al. 2017), soil fertility enhancement, described for *B. subtilis* and *B. cereus* (Jang et al. 2017), bioremediation of pollutants, as shown by *P. fluorescens* and *S. marcescens* (Romeh and Hendawi 2017), and amendment of plant secondary metabolites, demonstrated for *B. subtilis* and *Azoto- bacter chroococcum* (Ordookhani et al. 2011).

Commercialization of PGPR

The use of PGPR as nematode biocontrol agents and for plant growth promotion, soil fertility improvement, and phytopathogen biocontrol supports sustainable agriculture by providing environmentally benign alternatives to synthetic agrochemicals such as chemical fertilizers and pesticides. A protocol for the development and commercialization of PGPR-based biocontrol agents is shown in Fig. 4. Although various strains of PGPR are currently available on the market as biological nematicides, a simple question (i.e., repeatability) remains to be answered before PGPR may be commercialized (Table 3). However, the efficacy of these products must be evaluated further. PGPR products must have a wide range of applications, a long shelf life, be safe to use, have a viable market, be readily available, be consistent in terms of their efficacy and have a low investment cost to be economically successful.

Future prospects

Future research into improving the growing conditions, safety, broad-spectrum activity, shelf life, and stability of PGPR products is critical to their commercialization success. The agricultural revolution has increased worldwide agriculture productivity and prompted the introduction of synthetic chemical fertilizers to enhance yield and preserve crops. Excessive agrochemical usage is becoming a serious concern to animals, humans and the environment, and consequently, numerous chemicals have been prohibited across the world. Meeting the growing food demands of the
world’s population is a huge challenge that may be addressed by enhancing agricultural output through adequate safe and productive strategies. These conditions may be achieved using a single yet complex method, i.e., the application of PGPR, which helps increase crop safety, soil fertility, and plant development and lead to sustainable agriculture. This

| Commercial products | PGPR Strain(s) | Mode of action | Market Region | References |
|---------------------|----------------|----------------|---------------|------------|
| BioNemaGon™         | *Bacillus firmus* | Produces secondary metabolites and toxins like cyclodextrin glycosyltransferase that is toxic to *Meloidogyne arenaria* and *M. javanica* which aid in killing it | India         | Tranier et al. (2014) |
| Nemaxxion Biol®     | *Bacillus subtilis* | It is a liquid-formulated large-spectrum product that is active against nematodes, composed of *Bacillus subtilis* and extracts that are active against *Meloidogyne incognita* | Mexico       | Tranier et al. (2014) |
| REM G®              | *Bacillus spp. and Pseudomonas spp.* | It is supplemented with chitinolytic, proteolytic and lipolytic enzymes to specifically target the nematodes’ walls such as *Meloidogyne incognita* | Italy        | Tranier et al. (2014) |
| BioYieldTM          | *Bacillus amyloliquefaciens* | Controlling of second-stage juveniles of *Meloidogyne incognita* in tomato (*Solanum lycopersicum*), strawberry (*Fragaria ananassa*), and bell pepper (*Capsicum annuum*) | Mexico       | Li et al. (2015) |
| Econem              | *Pasteuria penetrans* | *Pasteuria penetrans* for control of *Meloidogyne incognita* on tomato (*Solanum lycopersicum*) and cucumber, and *M. arenaria* on snapdragon (*Antirrhinum majus*) | USA          | Kokalis-Burelle (2015) |
| Stanes Sting        | *Bacillus subtilis* | Reduction in second-stage juveniles of *Meloidogyne arenaria* in soil and roots of potato (*Solanum tuberosum*) | Egypt        | Ismail et al. (2014) |
| VOTiVO              | *Bacillus firmus* GB-126 | Reduction in number of eggs and juvenile life stages of *Rotylenchulus reniformis* on cotton (*Gossypium hirsutum*) | Germany      | Castillo et al. (2013) |
| Bio-Arc             | *Bacillus megaterium* | Reduction in second-stage juveniles and egg masses of *Meloidogyne incognita* on tomato (*Solanum lycopersicum*) | USA          | Raddy et al. (2013) |
| Onix                | *Bacillus methylotrophicus* | Management of *Meloidogyne javanica* on tomato plants (*Solanum lycopersicum*) | Brazil       | Lopes et al. (2019) |
| Nemaless            | *Serratia marcescens* | Reduction in second-stage juveniles, egg masses, egg numbers of *Meloidogyne incognita* on tomato (*Solanum lycopersicum*) | Egypt        | Raddy et al. (2013) |
| Micronema           | *Serratia spp., Pseudomonas spp.* | Significant reduction in second-stage juveniles, galls and egg masses of *Meloidogyne incognita* on sugar beet (*Beta vulgaris*) | Egypt        | Youssef et al. (2017) |
| Equity              | *Bacillus sp.* | Significant reduction in *Meloidogyne incognita* eggs, juveniles and galls on tomato (*Solanum lycopersicum*) | USA          | Burkett-Cadena et al. (2008) |
technique is well recognized as a safe method of insect management and plant growth enhancement across the world. The application of genetic engineering to improve PGPR technology, and other innovations, would ensure agroecosystem productivity and stability, resulting in an optimal and sustainable agricultural system.

Conclusion

Increased yield with improved crop protection and higher soil fertility using an environmentally feasible technique is critically needed. For the optimal use of efficient PGPR strains for sustainable agriculture it is necessary to gain in-depth knowledge of the PPNs population and their colonization. Moreover, genetic engineering technologies may be used to enhance the biocontrol efficiency of PGPR by synergistically overexpressing multiple anti-phytopathogen characteristics for effective pest management. The complete potential of the consortium of efficient bacterial strains for reducing the detrimental effects of different biotic stressors on plant growth can be exploited. Commercialization of PGPR-based biopesticides should receive further attention.

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Author’s contributions

A. Aioub collected and summarized the results. A. Elesawy has conducted the systematic literature review. E. Ammar has participated in writing the manuscript. The authors read and approved the final manuscript.

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Data availability

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest

The authors declare no competing interest.

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