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Bacteria as biocontrol agents of infectious diseases on horticultural crops (review)

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Abstract

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Plant protection against diseases with the aid of bioproducts based on bacteria is a promising strategy, which may be an alternative to some practices based on the usually applied synthetic fungicides and bactericides and is a subject of intensive research. The antagonistic bacteria show ability to suppress pathogens and prevent infections of various agricultural crops. The present review outlines the main modes of action of these microorganisms at their interaction with bacterial and fungal plant pathogens, including antibiosis through production of secondary metabolites with antimicrobial activity, competition for nutrients and space, and/or parasitism. Often some of the beneficial bacteria combine more than one mode of action. In addition to their adverse effect on the pathogens, certain bacterial biocontrol agents show a potential to promote the plant growth and induce plant resistance to infection and other stresses. The modes of action are supported with examples of more recent and some earlier research findings referring primarily to horticultural crops. Described are some commercial preparations based on bacteria, registered for practical use as protectors against bacterial and fungal diseases. The prospective for further studies and considerations on ecological issues are commented.

Keywords: biological plant protection; bacteria; antagonism; modes of action; biopreparations

Introduction

The microbiome of the plant environment is determined both qualitatively and quantitatively by the conditions in a given ecosystem. Most often it is dominated by commensals which have no detectable effect on plant growth or physiology. Among the mutualistic bacteria, microsymbionts of legumes and other bacteria promoting plant growth and yielding stand out. There are some bacterial pathogens that show an ability to exchange their primary host environments which means that plant disease-causing bacteria can infect humans and *vice versa* (Tyler & Triplett, 2008; Nadarasah & Stavrinides, 2011; Bonneaud et al., 2019; Kirzinger et al., 2011; Kim et al., 2020; Sobiczewski & Iakimova, 2022). From a practical point of view, bacteria that have positive effect on plant health deserve attention. The beneficial bacteria employ tools that allow direct and/or indirect control of the disease causal agents showing antagonistic activity towards them and possibly by inducing plant resistance to infection (Köhl et al., 2019; Collinge et al., 2022). The interactions between antagonistic bacteria and the pathogenic ones involve highly regulated chain of metabolic events both in the pathogen and in host plant. In this context, it is worth emphasizing that the compounds involved, such as signaling molecules, enzymes and various secondary metabolites are naturally produced at low concentrations (Köhl et al., 2019). More efficient inhibition of the pathogens has been observed at inoculation with higher density of the antagonists (Schmidt et al., 2004).

In similarity to plant bacterial pathogens, the antagonistic bacteria can inhabit the soil, the rhizosphere, the roots and the aerial part of the plants (Beneduzi et al., 2012). Often such bacteria have the capacity to live in a wide range of environments which gives them an advantage in adaptation to the new conditions. It is important to note that the risk of pathogens developing resistance to antagonists is very low (Heydari & Pessarakli, 2010).

In this review the basic modes of action of the antagonistic bacteria, their interaction with the pathogens and the effects on host plant are addressed. Some very recent and earlier examples for application of bacteria as protectors against bacterial and fungal plant pathogens, primarily of horticultural crops are described. The prospective for using bacterial antagonists as biocontrol agents is outlined and discussed in ecological point of view. The paper is aimed at wider readership of plant protection specialists, farmers and non-professionals.

Modes of Action of Antagonistic Bacteria

Bacterial antagonism to pathogens relies on three main types of interaction or combination of them: a) antibiosis; b) competition for nutrients and space and c) parasitism (Raaijmaker et al., 2002; Compant et al., 2005; Gamalero & Glick, 2011; Meena et al., 2017; Köhl et al., 2019; Collinge et al., 2022). Certain bacteria may also enhance the native resistance and stimulate plant defense reactions, including the production of reactive oxygen species, phytoalexins, phenolic compounds, pathogenesis-related proteins (PR-proteins) or the formation of physical barriers, e.g. in the epidermis (Wiesel et al., 2014).

Antibiosis

The bacterial biocontrol agents may produce secondary metabolites including antibiotics, often with a broad spectrum of activity. In certain cases the production of compounds with antimicrobial activity in beneficial bacteria may be influenced by abiotic (e.g. temperature, fluctuations in air composition, availability to sources of carbon, nitrogen and essential microelements) and biotic (e.g. the physiological state of plant host, the pathogen and the amount of producing strain) factors (Raaijmakers et al., 2002).

Antibiotics have been found in some bacterial species of the genera *Agrobacterium*, *Bacillus*, *Pantoea*, *Pseudomonas*, *Serratia*, *Stenotrophomonas* and *Streptomyces* (Braun-Kiewnick et al., 2000; Johnson & Stockwell, 2000; Shoda, 2000; Zhang et al., 2001; Nunes et al., 2002; Anjaiah et al., 2003; Yamunarani et al., 2019; Soenens & Imperial, 2020). Strains of the *Pseudomonas fluorescens*, producing pyrrolnitrin and pyoluteorin, proved to be effective antagonists of soil plant pathogens such as *Rhizoctonia solani*, *Thielaviopsis basicola*, *Verticillium dahliae*, *Alternaria* spp. *Pythium ultimum*, *Fusarium oxysporum, Macrophomina phaseolina* and *Pectobacterium carotovorum* (M'Piga et al., 1997; Karunanithi et al., 2000; Ganeshan & Kumar, 2005; Weller, 2007; Govindappa et al., 2010).

Antagonistic bacteria of some species of the genus *Bacillus* produce antifungal metabolites such as the lipopeptides iturins and surfactin and polypeptide bacillomycin (Fira et al., 2018). Of particular note is iturin A, which expresses strong activity against the plant pathogens *R. solani*, *P. ultimum*, *Sclerotinia sclerotiorum* and *F. oxysporum* (Fira et al., 2018). Among the examples is the antagonistic activity of *Bacillus* sp. strains against *Sclerotium rolfsii,* the causal agent of collar rot in gerbera (*Gerbera jamesonii*), tested in experimental systems *in vivo* and *in vitro* (Suneeta et al., 2016). In a crude extracts from bacterial strains, subjected to gas chromatography-mass spectroscopy (GC-MS) analysis, the authors identified several antimicrobial compounds belonging to the groups of terpenes, phenols and hydrocarbons, suggesting that they are responsible for the effectiveness of the strains in the inhibition of the fungus. Potential agents in biological protection of plants can be bacteria included in *Burkholderia cepacia* complex (Mahenthiralingam et al., 2005), producing antibiotic substances that are effective against various pathogens, including soil, foliar and fruit pathogenic agents causing storage diseases (Parke, 2000). Of practical importance is the soil bacterium *Agrobacterium radiobacter*, strain K84 that is antagonistic against *A. tumefaciens*, the causal agent of crown gall of fruit crops and roses. The antimicrobial activity of this bacterium occurs through production of the bacteriocin agrocin. The strain also is an efficient root colonizer (Shim et al., 1987).

Some of the studies refer to biocontrol of the soil-borne pathogen *F. oxysporum* that is responsible for damages during the production and storage of flower crops of at least 20 genera of ornamentals including species such as asters, chrysanthemums, carnation, gypsophila, gerbera, lily, tulip, freesia, gladiolus, hyacinth, iris, daffodil, philodendron and other pre- and postharvest ornamentals (reviewed in Lecomte et al., 2016). Antagonistic bacteria belonging to genera *Pseudomonas, Bacillus* and *Streptomyces* for which is characteristic that can perform as well as plant growth-promoting rhizobacteria and protectors against abiotic stress are found efficient toward *Fusarium* sp. strains infecting various horticultural crops, including ornamental plants (Antoun and Prévost, 2006). For example, in experiments in *vitro* and *in vivo* Mihalache et al. (2018) documented an inhibitory activity of the lipopeptides fengycin, surfactin and mycosubtilin (produced by diverse strains of *B. subtilis*) on spore germination and mycelium growth of *F. oxysporum* f. sp. *iridacearum*, a cause of decay of the bulbs of *Iris* sp. *Fusarium* spp. cause stem rot and leaf wilting in gladiolus and carnation, damage gladiolus corms and severely reduce the quality of intact and cut flowers of these species. Recent trials *in vitro* have shown suppressive activity of *B. subtilis* and *P. fluorescens* on mycelium growth of *F. oxysporum* f. sp. *gladioli* (Vavre et al., 2021). Strains of *Pseudomonas* bacteria, tested *in vitro* and *in planta* have exerted inhibition of *Pythium cryptoirregulare* and *Rhizoctonia solani* that, among other crops, are as well causal agents of diseases in various ornamentals (Martin, 2017). The author established that *Pseudomonas chlororaphis* 48G9 and *Pseudomonas brassicacearum* Delaware were among the most efficient ones.

The potential of *Streptomyces* spp. to control *Fusarium* spp. and other fungal pathogens in various agricultural crops is to a great extend considered to rely on the bioactive secondary metabolites including the antibiotics kasugamycin, blasticidin-S, polyoxin, and streptomycin and enzymes such as peroxidases, chitinases and glucanases that have deleterious effect on pathogen growth (Sharma et al., 2020). *In vitro* trials with potato leaf disks have indicated inhibitory activity of *Pseudomonas* strains against the *Phytophthora infestants* and documented that antifungal action involves the release of volatile organic compounds (VOCs) such as sulfur-containing volatiles, dimethylsulfoxide and 1-undecene by the bacteria (Gfeller et al., 2022). Very recently reported results indicated that VOCs produced by lactic acid bacteria may efficiently inhibit the growth of *Aspergillus flavus* of red pepper (*Capsicum annum*). The GC-MS profiling revealed the volatiles 1-pentanol, glycidol, 1- hexanol and 1-heptanol that are suggested toxic to the fungus and to possess antioxidant properties in favor of the plant (Li et al., 2022).

Competition for nutrients and space

In the relationships between the pathogenic and antagonistic bacteria the mode of action based on a competition for nutrients and space plays an important role (Singh & Faull, 1988). An example can be postharvest fruits attacked by the so-called wound pathogens, e.g. *Penicillium expansum*, the causal agent of blue mold of apples and pears (Luciano-Rosario et al., 2020; Spadaro et al., 2004). In the fruit wounds, nutrients that are attractive both to the pathogen and the antagonist are released. However, the beneficial bacteria can be faster in the competition for food and thus prevent the infection and disease development (Di Francesco et al., 2016). The accumulation of beneficial bacteria exceeding the population of the pathogen can result in competition for space and access to nutrients in favor of the antagonist (Köhl et al., 2019).

Many bacteria produce siderophores – chelating compounds that can bind trivalent iron ions (Kado, 2010; Meena et al., 2017), which are components of nutrients essential for various microorganisms. Among the most explored siderophore-producing bacteria are *Pseudomonas fluorescens* and *Pseudomonas aeruginosa.* They can synthesize pyochelin and pyoverdine type of siderophores that may express antibiotic activity (Haas & Défago, 2005). The production of such compounds by rhizosphere bacteria is a tool helping to increase their competitive potential in inhibiting the growth of other microbes by limiting the iron source to the pathogens that cannot utilize the iron–siderophore complex and, on the other hand, to facilitate the iron nutrition for the plant (Glick et al., 1995; Shen et al., 2013; Meena et al., 2017).

Parasitism

Many bacteria representing various taxonomic groups exhibit parasitism which refers to their ability to grow at the expense of pathogens. This mode of action engages, *inter alia*, the secretion of hydrolytic enzymes that break down the cell wall of pathogens which in many fungi is made of chitin. The ability to secrete chitinases is considered an important factor in the action of antagonistic bacteria of the genera *Bacillus*, *Vibrio* and *Serratia* against various soil and foliar pathogens (Swiontek Brzezinska et al., 2004). It should however be noted that the antagonists are characterized by a narrow range of hosts and their activity depends on the environmental situation including factors determining the possibility of growth and reproduction (Köhl et al., 2019). The study of Bryk et al. (2004) demonstrated that by parasitism, the strains B194 and B224 of *Pseudomonas* spp. limited the development of *Botrytis cinerea* and *Penicillium expansum*, respectively the causal agents of gray mold and blue mold of apple and pear. Many of the antagonists release lytic enzymes, the production of which is regulated by signals from the pathogen, meaning that they are specific and dependent on the substrate available in the pathogen (Köhl et al., 2019). Antagonistic activity of fluorescent pseudomonads toward *F. oxysporum* f. sp. *dianthi* has been established based on the production by the bacteria of chitinases that express mycolytic activity (Ajit et al., 2006).

Antagonists with Multiple Modes of Action

Remarkable are the beneficial bacteria that in the same time may exhibit at least two types of modes of action and positive effect on plant: inhibition of pathogens and plant growth promotion (plant growth promoting bacteria, PGPB) (Antoun & Prévost, 2006; Meena et al., 2017). Such activity was demonstrated, for example, by lactic acid bacteria (*Lactobacillus amylovorus* and *L. brevis*) in control of fusarium head blight of barley (Byrne et al., 2022). Some of the tested isolates limited the growth of the disease causal agents *in vitro* and showed the ability to inhibit their sporulation on barley leaves. When applied protectively on plants, they reduced disease severity and the production of mycotoxin by the pathogen. A positive effect of lactic acid bacteria on the expression of defense-related marker genes has been observed (Byrne et al., 2022).

Studies on the use of bacteria in the protection of barley and wheat against infection by *Fusarium graminearum*, *Zymospetoria tritici* and *Pyrenospora teres* have shown the protective abilities of some strains from the genera *Bacillus*, *Pseudomonas* and *Burkholderia* (Dutilloy et al., 2022). Although few mechanisms of action of above strains have been described, the *Bacillus* and *Pseudomonas* strains, showing direct antagonism and the ability to induce plant resistance against infection by the mentioned pathogens, deserve more emphasis. Valuable information was provided by Ghazala et al. (2022) who detected antagonistic activity against *F. verticillioides*, *F. graminearum*, and *Rhizoctonia solani* of VOCs emitted from *B. mojavensis*. The exposure of *Arabidopsis* plants to these VOCs promoted the plant growth, increased the biomass production and chlorophyll content. The antagonistic strains of fluorescent *Pseudomonas* spp. are of double benefit for the plant organism: on one hand by reducing the viability of fungal pathogens by exerting adverse effect on their life and on the other hand by enhancing the defense response of the plant against the pathogen and inducing systemic resistance (Bakker et al., 2007). It is found that strains of *Pseudomonas* spp. producing 2,4-diacetyl-phloroglucinol (DAPG), an antibiotic with high activity against diverse plant pathogens, show a high ability to colonize the root system, effectively compete for nutrients, and may induce defense responses in plants to stresses of biotic origin (Bangera & Thomashow, 1999). Several *Pseudomonas* bacteria have been screened for suppressing activity against *Pythium cryptoirregulare* and *Rhizoctonia solani* that, among other crops, are pathogenic also to various ornamentals (Martin, 2017).

The strain JCK-6131 of *Streptomyces* sp. is reported to express a broad spectrum of antagonistic activity against various phytopathogenic bacteria and fungi (Le et al., 2021). This strain has been effective in reducing disease severity on host plants: e.g. apple fire blight (caused by *Erwinia amylovora*), tomato bacterial wilt (caused by *Ralstonia solanacearum*) and cucumber fusarium wilt (caused by of *F. oxysporum*). It produces antimicrobial compounds, three of which have been identified as streptothricin E acid, streptothricin D and 12-carbamoyl streptothricin D. Based on the results obtained from experiments the authors assumed that the strain may increase the resistance to tomato bacterial wilt because in the treated tomato plants an induction of gene expression of several PR-proteins (PR1, PR3, PR5, and 12), that are involved in the simultaneous activation of defense signaling pathways depending on salicylic acid (SA) and jasmonic acid (JA) was detected (Le et al., 2021). Efficient inhibition of *F. oxysporum* f. sp. *dianthi* and *F. oxysporum* f. sp. *gladioli*, has been observed in presence of an isolate from *Streptomyces* (Vaidya et al., 2004).

The research of Mikiciński et al. (2016) and Mikiciński et al. (2020) with strains of bacterial species with biocontrol activity against fire blight (*Erwinia amylovora*) showed for the first time that the novel strain 49M *P. graminis* expressed good protective activity against the disease in organs of apple and pear trees. Several potential mechanisms of action of this strain were determined *in vitro*, showing, *inter alia*, its ability to produce siderophores, form a biofilm and inhibit the growth of the disease agent. This strain possesses the regulatory gene *gac*A influencing the production of several secondary metabolites including antibiotics. Interestingly, the genes *prn*D (encoding for pyrrolnitrin), *plt*C, *plt*B (pyoluteorin), *phl*D (2,4-diacetyl-phloroglucinol), *phz*C and *phz*D (and their homologues *phz*F and *phz*A encoding for phenazine), described in antagonistic fluorescent pseudomonads were not detected (Mikiciński et al., 2016). For other strains of the same group of bacteria it was found that the strain L16 (*P. vancouverensis*), characterized by the highest antagonistic activity, showed the ability to produce siderophores, a biosurfactant, hydrogen cyanide (HCN), SA, indole-3-acetic acid (IAA) and to breakdown nicotinic acid. Among the tested bacteria, the strain 43M (*Enterobacter ludwigii*) expressed the lowest activity, producing only IAA and degrading nicotinic acid. A study of the detection of genes encoding antibiotics characteristic of pseudomonads showed the presence of *prnD* and *gacA* in the strain 3M (*P. chlororaphis* subsp. *aureofaciens*) and *phlD*, *pltB*, *pltC* and *gacA* in 59M (*P. protegens*). However, none of the genes sought were detected in the L16 strain (Mikiciński et al. unpublished work). The antagonism of *Streptomyces* spp. is assumed to combine the modes of action antibiosis, lysis of cell wall, competition for nutrients and hyperparasitism (Mohammadi, 1992). The possible simultaneous occurrence of these mechanisms is suggested in the base of the effect of treatment of daffodil (*Narcissus* spp.) bulbs with preparation Mycostop, comprising a strain of *S. griseoviridis* that has prevented the development of basal rot caused by *F. oxysporum* f. sp. *narcissi* but the inhibition of fungal growth was noticed in some and not in all cultivars tested (Hiltunen et al., 1995).

Summarizing the examples for the effects of antagonistic bacteria, it is of importance to stress that a part of the results is obtained in *in vitro* studies that may be helpful for the indication of contribution of some metabolic pathways and gene expression to antagonistic activity, which may be of great practical importance, but it should be taken into account that through *in vitro* tests it is not possible to clearly determine how a given strain will behave at treatment of various plant organs in natural conditions. Laboratory tests only indicate the existence of potential modes that may or may not operate in the certain case. An important issue is also the possibility of interaction between the various modes of antagonism, especially in the context of synergism between them to achieve the greatest possible efficiency. The success of the application of beneficial bacteria depends largely on various factors in the specific environment, including the capacity of adaptation of these bacteria and their potency for utilization of nutrients.

By limiting the damages caused by the pathogens on the plant organs, the antagonists help for improving the growth and development of plants during the production cycle and to sustain the post-harvest quality. In addition to biocontrol ability, the beneficial effect of antagonists on the plant itself is another important trend of research. Generally the mechanisms for plant growth stimulation by PGPB include antibiosis, competition with the potential pathogens for nutrients and ecological niche, production of enzymes facilitating the utilization of nutrients by the plant and compounds, positively contributing to plant growth and resistance to infections (Compant et al., 2005; Gamalero & Glick, 2011). Some of activities related to improvement of plant growth by the beneficial rhizobacteria involve processes such as phosphate solubilization, nitrogen fixation, iron sequestration (production of siderophores), production of phytohormones (e.g. the auxin indole acetic acid (IAA), cytokinins and gibberellins), and control over ethylene level. The particular PGPB may show more than one of these activities (Gamalero & Glick, 2011; Meena et al., 2017). Antagonistic bacteria possess also ability to enhance plant tolerance to abiotic and biotic stresses (Meena et al., 2017). For example, by stimulating the antioxidant defense machinery *Bacillus cereus* strain Pb25 has improved the resilience of mung bean (*Vigna radiata)* to salt stress (Islam et al., 2016a). *P. stutzeri*, *B. subtilis*, *Stenotrophomonas maltophilia* and *B. amyloliquefaciens*, isolated from the rhizosphere of cucumber have been proven to restrict the crown rot caused by *Phytophthora capsici*, to produce IAA and promote the germination of cucumber seeds (Islam et al., 2016b) Alleviation of consequences of water stress on chickpea (*Cicer arietinum*) is reported in presence of *P. putida* that induced molecular and biochemical defense events including the expression of stress responsive genes and genes encoding for SA and jasmonate (Tiwari et al., 2016). Inoculation with *Burkholderia phytofirmans* strain PsJN of wheat has led to increased resilience to drought stress by improving the chlorophyll content, carbon dioxide assimilation, photosynthetic rate and the efficiency of water use, resulting in increased grain yield (Naveed et al., 2014). Of practical significance is the possibility for applying PGPB as biofertilizers (Antoun & Prévost, 2006).

Examples of Practical Use of Antagonistic Bacteria

In plant protection the use of preparations containing bioagents is known from many years and especially nowadays is progressing as a promising alternative to chemical-based products. However the number of bioproducts comprising antagonistic bacteria as active ingredients is still relatively limited. Their registration is often difficult because it requires extensive and multidirectional research proof both for the efficacy in the control of plant diseases and the behavior of the given bioagent in natural conditions. It should be also a concern about the potential for harmfulness of such bioagent to humans and eventual contamination of the environment with its possibly toxic metabolites. Moreover, preparation containing a full *dossier* of the bioproduct is expensive and the process for legislation is takes time (Meena et al., 2017; Collinge et al., 2022; Palmieri et al., 2022).

Based on the A506 *P. fluorescens* strain, the preparation “BlightBan® A506” was registered in the United States for the protection of apple orchards against frosts and fire blight. For control of pome fruit and citrus fruits against storage diseases the products “Bio-Save® 10LP” and “Bio-Save® 11L” are recommended. The preparations comprise as active ingredients, respectively the strains ESC-10 and ESC-11 of the species *P. syringae* (Stockwell & Stack, 2007). The strain K84 and its genetic modification K1026 of *A. radiobacter* are components of biopreparations for the protection of fruit trees and rose shrubs against crown gall (*A. tumefaciens*) e.g. “NOGALL®™”and “Galltroll” (Kerr & Bullard, 2020). On the basis of this strain, the pharmaceutical factory ‘Polfa’ in Pabianice, Poland produced the preparations “Polagrocyna SL” and “Polagrocyna PC” (Sobiczewski et al., 1995). A great advantage of *A. radiobacter* is its ability to survive as saprotroph in the rhizosphere, even for several years. The presence of this bacterium in the soil of apple orchard increased the number of other beneficial bacteria, including non-symbiotic nitrogen-fixing bacteria (Catska, 1993).

Particularly noteworthy is the species *Pantoea agglomerans*, some strains of which, isolated and tested in various countries, have shown high effectiveness against plant diseases caused by bacteria and fungi, especially against apple and pear fire blight (Braun-Kiewnick et al.. 2000; Dutkiewicz et al., 2016; Johnson & Stockwell, 2000; Nunes et al., 2002). In some countries, including the United States and New Zealand, the biopreparations "Blossom Bless™" and "Bloomtime Biological™", containing various strains of *P. agglomerans* have been registered, but their registration in Europe encounters constrains because this bacterium is mainly considered an occasional human pathogen. EU Directive 2000/54/EC4 covers the bacteria *Enterobacter* spp. (taxon which also includes *P. agglomerans*) that are currently classified in biosafety level 2 (BL-2) which means that they can cause disease in humans and can be dangerous in the workplace. Comparative studies of strains isolated from plants and clinical conditions, aimed at searching for genomic markers differentiating them, showed that most of the clinical strains are incorrectly classified as *P. agglomerans*. The obtained result was based on the multi-field phylogenetic analysis and the fluorescence polymorphism of the length of the amplified fragments (fAFLP) (Rezzonico et al., 2009). The authors believe that it is related to, *inter alia* , previous changes in the taxonomy of *P. agglomerans* / *E. herbicola* complex and its grouping in the species *P. agglomerans*. It should be emphasized that in this species no separate marker has been identified for clinical strains and strains intended for biological plant protection. The putative marker fAFLP has only been detected in the latter group of strains and may be useful in determining biosafety. It may also be helpful to test the pathogenicity of the strains in accordance with Koch's postulates, but the problem is not only in this group of bacteria.

To the beneficial bacteria belongs also *P. aeruginosa*. Studies conducted in India with the PNA1 strain of this species, isolated from the rhizosphere of chickpeas, showed their high effectiveness against diseases caused by *F. oxysporum* f. sp. *ciceris* and *Fusarium udum* (Anjaiah et al., 2003). In a study in Belgium the 7NSK strain has been reported antagonistic to *Pythium* sp. on tomatoes (Buysens et al., 1996). A biopreparation containing the wild strain of *P. aeuruginosa* and its mutants, developed and patented in the United States (Patent No. 5762928, 1998) is recommended to protect cultivated mushrooms against green mold caused by the fungus *Trichoderma harzianum*. On the basis of the QST 713 *B. subtilis* strain, the biopreparation Serenade ASO has been registered in several European countries, including Poland, intended to control fire blight on apple and pear trees, bacterial canker and brown rot on apricots, peaches, sweet and sour cherries and plums, gray mold and powdery mildew on chokeberry, highbush blueberry, blackberry, raspberry, cranberry, black and colored currant and gooseberry, as well as against gray mold and powdery mildew of strawberries and grapevines. The active ingredients of Amylo-X WG, Serifel and Taegro preparations (registered in Poland) are strains D747, MB1600 and FZB 24 of *B. amyloliquefaciens*, recommended for protection of strawberry black current, gooseberry and blueberry against gray mold and powdery mildew (www.certiseurope.pl; www.agro.basf.pl; www.novozymes.com). Commercial formulations containing bacteria as active ingredient have been approved as low risk substances and authorized for use in several European countries (EU Pesticides Database, 2022); European and Mediterranean Plant Protection Organization, List of registered plant protection products (PPPs) in the EPPO region; Current situation and trends of biopesticide regulations in EU) (2022). For example, *B. amyloliquefaciens* strain FZB24 based bioproduct is approved in EU member states (AT, BE, BG, CY, CZ, DE, EL, ES, FR, HU, IT, NL, PL, RO, SI, SK) and UK for biocontrol of fungal diseases such as downy mildew, late blight and grey mold on horticultural crops including potatoes, cucumbers, courgettes, grapes, melons and various ornamentals. *Bacillus subtilis* strain IAB/BS03 based preparation is recommended as biofungicide for field lettuce, orchards and protected cucurbits, and approved in ES, FR, IT (Arena et al., 2018). Another is *Streptomyces* strain K61 based preparation (originally registered in Italy in year 2000 as product Lalstop K61 WP) that has been approved and authorized under different names in all EU countries as fungicide on fruiting, leafy, root and bulb vegetables, ornamental plants and aromatic herbs (Anastassiadou et al., 2020).

Several bioproducs containing beneficial bacteria and applicable to combat *F. oxysporum* and/or improve the growth performance of ornamental plants are listed in Lecomte et al. (2016). Among them are the products of Bayer Crop Science "Yield Shield" containing *B. pumilus* strain GB34, "Kodiak" (with *B. subtilis* strain GB03) and "Rhapsody" (*B. subtilis* strain QST), "Subtilex" (*B. subtilis* MBI 600 from BASF, "Taegro" (*B. subtilis* FZB 24, a product of Novozymes and Syngenda), "Intercept" (*Pseudomonas cepacia* NM, company Soil Technology), "ArEze" (*P. chlororaphis* 63-28 from EcoSoilSysytems, "Actinovate SP" (*Streptomyces lydicus* WYEC 108, product of Novozymes. Interesting is the biofungicide, produced by Premer Tech Horticulture, containing a mix of *B. subtilis*, *B. pumilus* and the antagonistic soil fungus *Glomus intraradices*. The development of biopesticides comprising a mixture of antagonistic microbes (the so called "microbial consortia") appears as a promising tendency (Xu et al., 2011; Palmieri et al., 2022; Ram et al., 2022). Mazzola & Freilich (2017) formulated the opinion that efficient strategy for elimination of soil-borne diseases would be the application of "omics" technology for development of preparations with beneficial bacteria that naturally colonize 'tired' soil (which may result in replantation disease), by modifying the environment in such a way that it stimulates their reproduction and activity.

Considerations on Environmental Issues

It should be taken into account that bacteria belonging to the same species can be both plant and human pathogens, and also agents of biological protection against diseases. Even the same strains can exert a positive effect on plants and in the same time pose a threat to the environment (Sobiczewski and Iakimova, 2022). Therefore in some cases, the differences between beneficial and harmful bacteria are not yet quite clear and, which is worth noting, as a result of possible horizontal gene transfer (HGT), unfavorable features may be transferred between bacteria, e.g. pathogenic capacity (Soucy et al., 2015; Arnold et al., 2022). For example, documented cases of HGT have shown acquisition of pathogenic ability by nonpathogenic bacteria belonging to the genus *Agrobacterium* (Platt et al., 2014) or development of resistance to antibiotics of bacteria from genera *Pseudomonas, Erwinia* and *Xanthomonas* (Sundin & Wang, 2018). Comparative analysis of genomic sequences showed that some bacteria share certain common genomic structures, suggesting a possibility of changing their way of life in a specific ecological niche and potential host (Bulgari et al., 2019). From this point of view, the use of bacteria to control plant pathogens can result in disease worsening and even the emergence of new pathogens. An issue that is not to be ignored is the possibility the toxic for the plant pathogens metabolites released by the antagonists to contaminate to certain extent the environment which may expose to danger the life of other species in the nearby biosphere.

Concluding Remarks

In plant environment there are bacteria that show an ability to act as antagonists of plant pathogens. Moreover, these bacteria may exert a beneficial effect on plant growth and yield. They possess mechanisms that enable direct and/or indirect control of disease agents and also can potentiate plant resistance to infection and other stresses. Biological plant protection is a promising prospect in agrosystems, but the application of bacterial antagonists as biocides requires additional profound research by employing modern 'omics' technologies (genomics, proteomics, metabolomics) for deeper understanding of the interactions between antagonistic plant bacteria, pathogens and plants. The issues related to the assessment of possible threats to environmental safety and harmful effects on other organisms, including humans, also require more attention.

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