The emerging role of *Yersiniaceae* bacteria in plant disease biocontrol

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Abstract

The immoderate application of agrochemicals worldwide has led to the need to find more strategies to control diseases that are safer for humans, animals, plants, and the environment. The use of microbial biocontrol agents answers this need well, and more efforts are needed to increase the number of microorganisms that could be developed as commercial biocontrol agents. A set of bacteria from the Yersiniaceae family has emerged as a beacon of hope, a viable option for commercial biocontrol agents that can be safely applied in agricultural fields. Genera like *Rahnella*, *Rouxiella*, and *Serratia* are not just showing biocontrol mechanisms but also direct plant growth promotion. On the other hand, other genera within the Yersiniaceae family have been scarcely evaluated. This review explores this microbial group's biocontrol capabilities, mechanisms, strengths, and areas of opportunity, highlighting the importance of ongoing research in this dynamic field.

Keywords: Biocontrol agents, Plant Growth-Promoting Bacteria, Plant Pathogens, Rhizosphere, *Rahnella*, *Rouxiella*, and *Serratia*

Introduction

The green revolution emerged in the latter part of the 20th century as a global strategy to increase agricultural production on a smaller area of arable land. Aspects such as the generation of new variants of vegetable crops (genetically modified or not) tolerant to adverse environmental conditions and synthetic agrochemicals (like pesticides, fertilisers, fungicides, etc.) led to a boom in the production of crops where these were applied. (Khaipho-Burch et al., 2023; John and Babu, 2021). However, the tendency to apply more and more agrochemicals to produce more was growing until it reached excessive use, which directed the green revolution towards an environmental problem. Some negative aspects that include synthetic agrochemicals are environmental pollution, such as the groundwater from which drinking water is obtained and the toxic effect on pollinating insects. In addition, there is evidence of certain diseases in humans and animals (Devi et al., 2022). Another adverse effect of some agrochemicals is their harmful effect on soil microbiota, a fundamental part of soil health (Thiour-Mauprivez et al., 2019).

Strategies have been sought to continue increasing crop production, but now sustainably and without affecting the environment and human and animal health. In addition to the strategy of manipulating the genome of plants to grow in harsh environments and under adverse environmental conditions or to be resistant to certain pests and plant pathogens (Khaipho-Burch et al., 2023; Raymond Park et al., 2011), there is the alternative of using plant growth promoting microorganisms (PGPM), including several species of bacteria (Plant Growth-Promoting Bacteria or PGPB) with multiple mechanisms that allow it to stimulate its development and production (Guzmán-Guzmán et al., 2023; Hyder et al., 2023; Patel et al., 2024; Santoyo et al., 2024). Such is the case of the PGPB of the genus *Pseudomonas*, which were one of the pioneer bacterial groups to be used as antagonists of fungal and bacterial plant pathogens (Hansen et al., 2022; Novinscak and Filion, 2020). Kloepper et al. in the early 1980s described the production of siderophores (iron chelating agents) as one of the first mechanisms that restricted the growth of plant pathogens since by occupying spaces and taking up iron, this element was limited to be taken up by plant pathogens (Kloepper et al., 1980). During the following decades, the increase in the isolation and characterisation of PGPB from the genus *Pseudomonas* increased substantially, encompassing an antagonism against plant pathogens such as *Alternaria* spp., *Botrytis* spp., *Colletotrichum* spp., *Fusarium* spp., *Puccinia* spp., *Rhizoctonia* spp., *Xanthomonas* spp., among others, causing various diseases in cereal, vegetable or fruit crops, to name a few (Guzmán-Guzmán and Santoyo, 2022; Khatri et al., 2023; Shi et al., 2024).

Another of the most studied bacterial groups, such as PGPB, are the species of the genus *Bacillus* (Etesami et al., 2023). Some members of the genus *Bacillus* have the advantage of being sporulating bacteria, which gives them an advantage to be used as bioinoculants and to be stored for longer, preserving their viability until they find better conditions (during application in the field) and germinate (Russi et al., 2024; Salazar et al., 2022). *Bacillus* species such as *B. amyloliquefaciens*, *B. cabrialesii*, *B. pumilus*, *B. subtilis*, or *B. velenzensis*, produce diffusible and volatile compounds involved in the regulation of hormonal synthesis in plants, resulting in the promotion of plant growth (Figueroa-Brambila et al., 2023; Russi et al., 2024; Song et al., 2024; Zeidan et al., 2024). Likewise, the production of cyclic lipopeptides is almost a common characteristic of bacilli with antifungal capabilities since their genomes present extraordinary antagonistic machinery to reduce the incidence of plant diseases (Balleux et al., 2025; Ramesh et al., 2024).

The genera *Bacillus* and *Pseudomonas* are just two examples of PGPB that have shown a constant in the laboratory or the open field, being efficient stimulators of plant growth and health. In fact, in multiple works, the co-inoculation of *Bacillus*-*Pseudomonas* species have shown synergism to improve plant growth (Kumari et al., 2016; Liu et al., 2023; Maheshwari et al., 2015; Rojas-Sánchez et al., 2024). Likewise, the interaction of *Pseudomonas* and *Bacillus* with other rhizosphere bacteria of species like *Serratia marcescens* and *Rahnella aquatilis* have shown positive results in controlling the Fusarium decline of chickpea (Palmieri et al., 2017)Bacillus and Pseudomonas are well-known for their biocontrol and plant growth-promoting properties, but they are far from the only genera with such capabilities. The search for new antagonistic bacterial genera remains a constant focus in current research, driven by the vast diversity of agroecosystems and crops across the globe. Given the tremendous biodiversity of plant pathogens, relying solely on a few biocontrol species is insufficient. There is, therefore, an urgent need to identify and apply new bacterial antagonists that can mitigate the harmful effects of plant pathogens without the adverse side effects often associated with synthetic agrochemicals, thus reducing economic losses worldwide. This urgency underscores the importance and relevance of our topic, making it a crucial area of study for researchers and professionals in the field. (Orozco-Mosqueda et al., 2021; Thiour-Mauprivez et al., 2019).

This review mainly focuses on genera from the recently described Yersiniaceae family (Adeolu et al., 2016), including *Rahnella* (*Ra.*) spp., *Rouxiella* (*Ro.*) spp., and *Serratia* spp., which are the most studied members of the family as biocontrol agents. It also highlights the necessity of exploring antimicrobial capacities in other genera (Calvo et al., 2007; Guo et al., 2016; Morales-Cedeño et al., 2021; Soenens and Imperial, 2020). Undoubtedly, bacterial members of the Yersiniaceae family, exhibiting multiple beneficial traits, are emerging as promising bioinoculants in the battle against plant pathogens.

Impact and diversity of plant pathogens in crop production

Plant pathogens can cause different percentages of losses in agricultural production, where global annual losses can amount to billions of dollars, affecting an estimated 10-16% of total crop production. In a review study, Savary et al. (2019) reported that approximately 137 plant pathogens and pests affect wheat, rice, maise, potato, and soybean, which are among the main crops that feed the global population. Production losses vary depending on the crop. For example, wheat losses range from 10.1% to 28.1%, rice from 24.6% to 40.9%, and maise from 19.5% to 41.1%. These percentages may fluctuate depending on the year and the region where the crops are grown. However, it has been observed that developing agricultural areas are more vulnerable. Due to inadequate technology and poor crop management, emerging plant pathogens can cause significantly more damage than in regions with advanced technologies, disease-resistant crop varieties, and better agricultural sanitation practices (Fischer et al., 2005; Vitousek et al., 2009). Additionally, there are indirect economic impacts on producers, as they need to purchase pesticides, fungicides, and other agrochemicals to repair the damage caused by plant pathogens. This situation has severe negative environmental consequences, including an increase in pathogen resistance and a rise in diseases associated with the use of these synthetic compounds (often in excessive amounts), affecting animal and human health (Khaipho-Burch et al., 2023; Raymond Park et al., 2011). These harmful effects of agrochemicals have been widely reported and documented for decades. Recent studies also show a significant impact of herbicides such as glyphosate on the bee microbiome, which causes a severe impact on these pollinators(Motta et al., 2024). Therefore, as we try to highlight in this work, it is necessary to explore the option of having multiple options for bioinoculants based on beneficial microbes, particularly from the Yersiniaceae bacteria.

The diversity of plant pathogens is incredibly high, affecting crops. For example, plant pathogens can include organisms such as viruses, bacteria, fungi, oomycetes, and nematodes, among others. One of the first lists of viruses that cause plant diseases was made in 2011 by Scholthof et al. and includes, in order of importance, Tobacco mosaic virus, Tomato spotted wilt virus, Tomato yellow leaf curl virus, Cucumber mosaic virus, Potato virus Y, Cauliflower mosaic virus, African cassava mosaic virus, Plum pox virus, Brome mosaic virus, and *Potato virus* which are also highly harmful to crops. Dean et al. (2012) also listed the top ten most important fungal plant pathogens, including *Magnaporthe oryzae*, *Botrytis cinerea*, *Puccinia* spp., *Fusarium graminearum*, *Fusarium oxysporum*, *Blumeria graminis*, *Mycosphaerella graminicola*, *Colletotrichum* spp., *Ustilago maydis*, and *Melampsora lini*. The above list is in order of importance by the degree of impact on production and the level of economic losses caused to crops worldwide. Later, Kamoun and coauthors (2015) also listed the 10 most lethal oomycetes for crops, which include *Phytophthora infestans*, *Hyaloperonospora arabidopsidis*, *Phytophthora ramorum*, *Phytophthora sojae*, *Phytophthora capsici*, *Plasmopara viticola*, *Phytophthora cinnamomi*, *Phytophthora parasitica*, *Pythium ultimum*, and *Albugo candida*, with some ties for second and eighth place for the number of votes received by experts in oomycete phytopathology. There is also a list of the most harmful to crops in the case of bacterial plant pathogens. This is the list in rank order: *Pseudomonas syringae* pathovars, *Ralstonia solanacearum*, *Agrobacterium tumefaciens*, *Xanthomonas oryzae* pv. *Oryzae*, *Xanthomonas campestris* pathovars, *Xanthomonas axonopodis* pathovars, *Erwinia amylovora* (Mansfield et al., 2012; Pedroncelli and Puopolo, 2023). It should be noted that the list is not complete, neither for fungi, oomycetes, or bacteria, since other groups of microorganisms can be a nuisance for farmers in specific regions or with more local damage to their crops.

Figure 1 presents an overview of the impact of some plant pathogens, mainly fungi, that affect crops and the main plant tissues. Additionally, it highlights how plants can become infected, the conditions required for an infection to occur, the potential of the associated Yersiniaceae bacteria to inhibit potential plant pathogens and pests, and some of their biocontrol mechanisms.

Overview of the *Yersiniaceae* family

The Enterobacteriales order encompasses a diverse group of Gram-negative bacteria characterised by facultative anaerobic metabolism, absence of spore formation, and rod-shaped morphology within the Gammaproteobacteria class. This versatile group ¨thrives across a spectrum of ecological niches, including soil, water, and symbiotic associations with various organisms such as plants, insects, animals, and humans¨ (Brenner and Farmer, 2005). Notably, several members of the Enterobacteriales order pose significant threats as plant pathogens to both humans and animals, with species like *Escherichia coli, Salmonella enterica*, and *Yersinia pestis* exemplifying this risk (Toth et al., 2006). Furthermore, certain species within this order, such as those belonging to the *Dickeya, Pectobacterium, Brenneria, Erwinia*, and *Pantoea* genera, wield considerable economic impact as plant pathogens(Hu et al., 2022; Islam et al., 2024).

The classification of the Enterobacteriales order underwent refinement in 2016 when Adeolu et al. (2016) proposed its division into seven families: Enterobacteriaceae, Erwiniaceae, Hafniaceae, Morganellaceae, Pectobacteriaceae, Thorselliaceae, and Yersiniaceae. The Yersiniaceae family now comprises eight genera, encompassing 67 species and three subspecies, as validated by Soutar and Stavrinides, 2020. Within the *Yersenia-Serratia* clade, genera include *Yersenia, Serratia, Rahnella, Ewingella, Hafnia, Cedecea,* and *Gibbsiella*, derived from phylogenetic analyses primarily based on the 16S rRNA gene. Molecular markers, such as core and ribosomal protein families, and multilocus sequence analysis fo genes like *rpoB, gyrB, dnaJ and recA fusA, pyrG, rplB, rpoB* and *sucA*, corroborated similar groupings within the *Yersenia-Serratia* Clade, albeit with minor variations (Hata et al., 2016; Naum et al., 2011). Figure 2 shows the phylogenetic relationships of representative members of the *Yersiniaceae* family resulting from 16S rRNA gene sequence analysis.

Modes of action of bacterial biocontrol agents

PGPB's biocontrol mechanisms often involve the production of antibiotic compounds (antibiosis), cell-wall degrading enzymes, and competition for nutritional resources, among other things. These biocontrol mechanisms are considered an indirect strategy used by beneficial microbes or PGPB to stimulate plant growth, as restricted pathogen growth prevents the development of diseases in crops.(Glick, 2012). In the following paragraphs, we describe some of these biocontrol mechanisms described in PGPM, including bacteria from the Yersiniaceae family.

Aantibiosis

Antibiosis

One of the most described biocontrol mechanisms is the production of antimicrobial compounds or antibiotics (Hamid et al., 2021). Some examples include compounds such as lipopeptides, such as iturin, surfactin and fengycin, as well as 2,4-diacetylphloroglucinol, agrocin 84, amphisin, bacillomycin, herbicolin, oomycin, phenazine-1-carboxylic acid, pyoluteorin, pyrrolnitrin, and viscosinamide, among others (Balleux et al., 2025; Balthazar et al., 2022; Hernández-León et al., 2015; Liu et al., 2021; Ramesh et al., 2024). Recent studies have suggested the regulatory role of RpoS in the production of antibiotics like pyoluteorin and 2,4-diacetylphloroglucinol in species like *Pseudomonas* in the rhizosphere (Zhang et al., 2022). PGPB can also produce low molecular weight compounds that are defined as volatile organic compounds (VOCs), which can be of the type alcohols, aldehydes, aromatics, sulfides and ketones(Cortazar-Murillo et al., 2023). Three examples of VOCs are hydrogen cyanide (HCN), dimethyl disulfide or dimethylhexadelamine, produced by bacteria such as *Arthrobacter*, *Microbacterium*, and *Pseudomonas* (Anand et al., 2023; Hernández-León et al., 2015; Velázquez-Becerra et al., 2013). Volatile compounds such as dimethyl disulfide have been reported in different species of *Serratia*, helping to control diseases such as damping off in tomatoes (Abreo et al., 2021).

Competition for resources and nutrient deprivation through siderophores

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The rhizosphere is a highly competitive microenvironment. All microorganisms in the rhizosphere want to access the best microsites where they can obtain nutritional resources such as root exudates(Chepsergon and Moleleki, 2023). Root exudates can contain amino acids, vitamins, organic compounds, and sugars. Therefore, those who are more competitive will have access to this source of nutrients(Afridi et al., 2024). Likewise, it has been considered that the root exudates of each plant can vary and be highly selective with specific groups of PGPB and, therefore, function as chemo-attractants. For example, 2,4-dihydroxy-7-methoxy-1,4-benzoxazine-3-one (DIMBOA), which is produced by corn plants (*Zea mays* L.), inhibits the growth of potential plant pathogens such as *Ralstonia solanacearum* but stimulates the growth of beneficial bacteria(Guo et al., 2016).

Being competitive in the rhizosphere is essential for plant growth-promoting rhizobacteria (PGPR)(Hassan et al., 2019). If PGPR can compete for space and nutrients in the rhizosphere, they can benefit the plant. In some cases, they will even be able to colonise the spaces of the root endosphere and exert a closer relationship with their plant host (Compant et al., 2024). Characteristics such as the production of exopolysaccharides or biofilm, as well as rapid growth, antioxidant activities, motility and chemotaxis, and evasion and suppression of plant immune system, are some of the determinants that will make a PGPR highly competitive in the rhizosphere and an excellent bioinoculant in the open field (Santoyo et al., 2021).

The Fe^{+3} ion is a fundamental element for the growth of the rhizosphere microorganisms, and despite being highly abundant in nature, it is surprisingly insoluble (Harrison et al., 2008). PGPR produce Fe^{+3} chelating compounds such as siderophores, some with high affinity for this element. Once a siderophore-Fe complex is formed, releasing it into the rhizosphere is almost impossible. Still, they can facilitate it to their plant host. Although it has been proposed that bacteria cannot assimilate it "easily", PGPR have an outer cell membrane receptor that allows them to internalise the complex and release the Fe inside the cell (Kramer et al., 2019). Studies have shown that bacteria of the genus *Pseudomonas* that produce siderophores can inhibit the growth of plant pathogens through this mechanism (Srivastava et al., 2022). Even the abundance of these species in the rhizosphere is associated with "disease-suppressing" soils (Mendes et al., 2011). Other species of the *Yersiniaceae* family, such as *Hafnia* spp*., Rouxiella badensis, Serratia* spp., or *Rahnella bruci*, also produce siderophores, so their role as antagonists is relevant as they are inhabitants of the rhizosphere (Awolope et al., 2021; Eze et al., 2023; Morales-Cedeño et al., 2021). Of course, this mechanism may not be effective if there is an excess of this element in the medium, and therefore, it continues to be available for potential plant pathogens. Thus, more studies are required to reveal other strategies by PGPR to deprive plant pathogens of other essential elements.

Hydrolytic enzymes, mycoparasitism and predation

Mycophagy is a mechanism by which certain bacterial (or fungal, such as *Trichoderma*) species can obtain nutrients from a fungus (Ferreira and Musumeci, 2021; Guzmán-Guzmán et al., 2023). Strictly speaking, mycoparasitism is a mycophagic behaviour, as it involves obtaining nutrients by penetrating the host cells. Some reports of mycophagous bacteria include *Paenibacillus*, *Streptomyces*, or *Pseudomonas*, although the fungal host they attack is not necessarily a plant pathogen(Leveau and Preston, 2008). Therefore, it would be interesting to study this bacterial strategy in more detail as a biocontrol mechanism in the strict sense.

The cell wall of fungal plant pathogens is targeted by some lytic enzymes such as chitinases, β-glucanases, and proteases, which can be produced by various bacterial biocontrol agents, including *Bacillus*, *Paenibacillus*, *Pseudomonas*, and *Streptomyces*(Riseh et al., 2024). The mode of action of these enzymes primarily involves weakening compounds like chitin, glucans, and structural proteins that are essential components of the fungal pathogen membrane. Chitinases hydrolyse chitin, while β-glucanases aim to break down the glycosidic bonds of glucans. Finally, proteases lyse structural proteins without a direct target. The action of these enzymes is the weakening of the cell wall potential, leading to lysis and cell death (Reddy et al., 2022).

In the case of bacteria like *S. marcescens*, it has been observed that chitinases are relevant for the biocontrol of the plant pathogen *Sclerotium rolfsii*. This species can synthesise two types, including chitinase A (ChiA) and chitinase B (ChiB) (Brurberg et al., 1996; Ordentlich et al., 1988). More recent studies have also shown that species of *Serratia* and *Rahnella* exhibit genes in their genomes responsible for the synthesis of other β-glucanases and cellulases (Abo-Elyousr et al., 2010; Trejo-López et al., 2022).

Induction of plant immune responses and modulation of ethylene production

Sensing attack by plant pathogens, plants respond in a coordinated manner to turn on the production of pathogenesis-related or “PR” genes. The PR genes code for various proteins with antimicrobial activity (García-Cristobal et al., 2015). As part of the plant's response to infection by plant pathogens, some of which cause tissue necrosis, it increases the production of salicylic acid (SA). SA is an important phytohormone that plays a vital role in a series of physiological responses but also includes plant defence, particularly systemic acquired resistance (SAR) (Peng et al., 2011).

But plants also respond to the presence of beneficial bacteria or other non-harmful organisms in the soil, however, they are usually distinguished by the roots of the plant through specific receptors; but they do not stimulate (in most cases) the synthesis of SA, but rather jasmonic acid (JA), and this in turn, the synthesis of ethylene (ET). This resistance induced by PGPM is called systemic induced response (ISR) (Kamle et al., 2020; Yadav et al., 2024). An interesting component that participates in the signaling of both pathways, SA (SAR) and SA/ET (ISR) is NPR1 (Non-expressor of Pathogenesis-Related genes) (Dong, 2004). Interestingly, npr1 mutants in plants such as *Arabodopsis* exhibit a blockage of ISR activation by non-pathogenic rhizobacteria, as well as failure to express PR genes after SAR induction, caused by necrotic plant pathogens (Choudhary and Johri, 2009).

ISR can be triggered by various quorum sensing molecules, as well as the production of rhamnolipids, lipopeptides, antibiotic compounds, siderophores, exopolysaccharides, among others, which are produced by PGPM (Aznar and Dellagi, 2015; Carezzano, 2023; Helman and Chernin, 2015). By stimulating ISR in plants by beneficial microorganisms, including bacteria such as *Serratia.* Such is the case of the CDP-13 strain of *S. marcescens*, which could induce ISR in wheat plants and confer protection against the plant pathogen *F. graminearum*. Additionally, this strain managed to confer a cross-response in wheat plants, by stimulating their tolerance to salinity through the production of antioxidant enzymes such as superoxide dismutase, catalase, and peroxidase (Singh and Jha, 2016).

The phytohormone ET is essential to regulate certain physiological and growth processes in plants. ET is known as the stress hormone, that is, under conditions of abiotic stress (e.g. soil salinity, heavy metal contamination, drought, cold, extreme temperatures) or biotic stress (e.g. infection by plant pathogens) its production is stimulated, which, in high levels cause defoliation, stimulate senescence, inhibition of growth, among other cellular damages that lead the plant to have low production performance(Moon and Ali, 2022; Orozco-Mosqueda et al., 2020). A precursor to ethylene synthesis is 1-amino cyclopropane-1-carboxylic acid or ACC. ACC can be degraded by the action of the ACC deaminase enzyme, which when present in microorganisms associated with the plant, can lower ET levels under biotic stress (and in certain conditions also in developing plants) (Gupta and Pandey, 2019; Naing et al., 2021). ACC deaminase activity is widely distributed in PGPM of soil and rhizosphere, as well as in inhabitants of the endosphere and phyllosphere (Orozco-Mosqueda et al., 2022). This mechanism has been widely reported in different experimental conditions, ranging from the laboratory to the field (Nascimento et al., 2012; Peng et al., 2019), in ACC deaminase mutants (Ali et al. 2014), as well as through phylogenetic studies that show that said activity is widely distributed in beneficial fungi (such as *Trichoderma*)(Blaha et al., 2006; Nascimento et al., 2012), as well as in PGPB, which includes species like *S. marcescens* and *Ra. aquatilis*. Several studies have shown the importance of ACC deaminase coding genes in heavy metal resistance and plant growth-promotion (He et al., 2013; Kong et al., 2022; Yuan et al., 2014).

***Serratia* species as biocontrol agents**

Among the different bacterial genera in the family Yersiniaceae, the genus *Serratia* includes various species such as *Serratia marcescens*, *Serratia inhibens*, *S. rubidaea*, *S. surfactantfaciens*, *S. ureilytica*, and *S. plymuthica*. These species have been reported as antagonists or biocontrol agents against different crop plant pathogens, which cause severe diseases and economic losses (Alijani et al., 2022; Cao et al., 2023; Clements et al., 2019; Hennessy et al., 2020; Müller et al., 2009). As of the writing of this article, 43 species and 4 subspecies of the genus *Serratia* are reported on the portal "https://lpsn.dsmz.de/search?word=serratia"; however, not all have been "validated." In fact, a literature search with keywords such as "biocontrol" for each of the genera presented in Figure 3 shows that *Serratia* is the genus in the Yersiniaceae family with the most publications related to this topic, compared to other bacterial groups like *Rahnella*, *Rouxiella*, *Hafnia*, among others. This underscores the need to continue isolating and characterizing new biocontrol agents that might present novel mechanisms for controlling plant diseases.

The antagonistic mechanisms against plant pathogens exhibited by the genus *Serratia* are diverse. For example, the production of biosurfactants, which may include compounds such as lipopetides. Lipopetides are molecules that contain a short chain of amino acids (peptide) attached to a chain of fatty acids (lipid), and their amphipathic structure allows them to interact with cell membranes, making them useful as antimicrobials. Lipopetides have been widely characterised in PGPB like *Bacillus* and *Pseudomonas*, but there is still much to discover in genera like *Serratia*. The application of biosurfactants produced by *Serratia* bacteria has also had various uses beyond agriculture, including in the pharmaceutical, medical, and oil industries (Clements et al., 2019).

Some studies, such as those by (Nalini and Parthasarathi (2014), have demonstrated that biosurfactants produced by a strain of *S. rubidaea* SNAU02 can control plant pathogens such as *F. oxysporum*, *Colletotrichum gloeosporioides*, and *Pythium aphanidermatum*. The authors evaluated this activity using the agar well diffusion method. Gas chromatography–mass spectrometry (GC–MS) analysis of the compounds produced by strain SNAU02 revealed the presence of a rhamnolipid as responsible for the antifungal action. Interestingly, this surfactant was also found to be non-toxic to plants, making it an excellent candidate for use in biocontrol against these fungal plant pathogens.

In another study, it was reported that an endophytic strain of *S. rubidaea* Mar61-01 produces a pigment with antifungal action against the plant pathogen *C. nymphaeae*, the causal agent of anthracnose disease in strawberry crops. Through *vitro*, *in vivo*, and greenhouse tests, *S. rubidaea* Mar61-01 showed consistent antagonistic results against *C. nymphaeae*. The study also reports the purification of the pigment, named prodigiosin, through thin layer chromatography, and its chemical structure was characterised by FT-IR and NMR (400 MHz) spectra, suggesting great potential for controlling diseases like anthracnose in economically important crops such as strawberries worldwide(Alijani et al., 2022).

Another study by Trejo-López et al (2022) also found that *Serratia* strains produce the same pigment, prodigiosin, which may be involved in antagonism against plant pathogens such as *C. siamense* and *Alternaria alternata*. The authors evaluated this antifungal activity *in vitro* and in mango fruits; they also explored the production of chitinases, glucanases, and cellulases in these strains, suggesting that these lytic enzymatic activities might be involved in inhibiting the growth of the evaluated plant pathogens. Finally, the authors propose that *Serratia* strains could be a good option for controlling anthracnose in fruits like mangoes, which suffer significant economic losses due to plant pathogens like *C. siamense* and *A. alternata*.

Another biocontrol mechanism presented by the genus *Serratia* is quorum sensing (QS), which is regulated by molecules such as N-acyl homoserine lactones (AHLs). AHLs are essential in bacterial population communication, including *Serratia* in microecosystems like the rhizosphere, and they are also relevant for biocontrol, as demonstrated by Müllerand et al. (2009). In this study, the authors generated two mutants in AHL production in the rhizosphere-associated bacterium *S. plymuthica* HRO-C48. One mutant produced residual levels of AHLs (*S. plymuthica* HRO-C48 AHL-4), while the other mutant did not produce detectable levels of AHLs (*S. plymuthica* HRO-C48 pME6863). Interestingly, both mutants showed impaired effects on the control of *Verticillium dahliae*. Therefore, this study demonstrated years ago that the QS system is relevant in the biocontrol of rhizosphere *Serratia* strains.

Some *Serratia* strains have not been exclusively isolated from soil, the rhizosphere, or as endophytes but also from aquatic environments, which contain *Serratia* species with biocontrol potential. For example, Pereira et al. (2023) recently isolated the strain *S. marcescens* B8 from a mangrove in Brazil, which, along with a strain of *Bacillus sp.*, showed antagonistic action against plant pathogens such as *F. solani*, *F. oxysporum*, and *Rhizoctonia solani*. *Serratia marcescens* BKACT, isolated from an island near India, exhibited antagonism against various *Fusarium* species. The authors isolated and proved that 2,4-ditert-butylphenol was the compound responsible for the inhibition of plant pathogen growth caused by *S. marcescens* BKACT. 2,4-ditert-butylphenol has been isolated and characterised not only from bacterial sources but also from other organisms, such as the fungus *Marasmiellus* sp. (PUK64), whose antifungal action has been evaluated against plant pathogens such as *Aspergillus oryzae*, *Curvularia lunata*, and *F. verticillioides* (Reference). Other compounds produced by a *Serratia* (and *Bacillus*) bacteria, including austinoneol, Phe-

Pro, N-acetyl-l-leucine, Leu-Gly, Ile-Leu, Phe-Pro, 2,5-piperazinedione, 3-(1H-indol-3-methyl)-6-methyl-cyclo(d-Trpl-Pro), and cholic acid, have been characterised for their antifungal action against *Magnapothe oryzae* and *Bipolaris oryzae* (Kushveer et al., 2023). Some fungal plant pathogens attack agricultural species and tree species, affecting forests. In an interesting study, various strains of the genus *Serratia* were isolated, but two of them, identified as *S. proteamaculans* and *S. grimesii*, showed the ability to inhibit plant pathogens such as *Annulohypoxylon stygium* and *Daldinia eschscholtzii*, which cause defoliation in different pine species(Gutiérrez-Flores et al., 2023). Therefore, these *Serratia* species may have applications beyond agriculture, and in forestry, they could also be an excellent option as antagonists.

Another example of novel biocontrol *Serratia* spp. strains was reported by Garbeva et al. (2012), who identified *S. inhibens* as a new species and presented it as a novel inhibitor of plant pathogens such as *Rhizoctonia solani*. Interestingly, in this study, it was found that *S. inhibens* S40, isolated from potato rhizosphere, had radial growth inhibition percentages of *R. solani* comparable to the biocontrol agent *S. inhibens* PRI-2C (Garbeva et al., 2012). Unfortunately, no subsequent studies (to our knowledge) have explored this strain's metabolic or functional capabilities. Moreover, no reports have emerged about isolating other *S. inhibens* species in different regions of the world.

Dual activities in *Serratia* strains

Some PGPB, as previously reviewed, can exhibit dual activities that benefit their plant hosts, including both plant growth promotion and plant pathogen biocontrol, mechanisms described as direct and indirect plant growth promotion. Such activities have also been observed in *Serratia* species. For instance, Hamane et al. (2023) searched endophytes in root nodules of *Sulla flexuosa* L., a plant from northern Morocco used to prevent soil erosion due to its robust root architecture. In this plant, 19 bacterial endophytes were isolated, some of which were assigned to the *Serratia* genus. These *Serratia* spp. strains exhibited plant growth promotion and antifungal activities against plant pathogens such as *Botrytis cinerea*, *Aspergillus ochraceus*, and *F. oxysporum*. However, despite the broad potential of these strains as dual action bioinoculants (promotion and biocontrol), much remains to be understood about their modes of action.

Similarly, Li et al. (2023) reported that *S. plymuthica* MM exhibits dual action by promoting the growth of watermelon plants (variety Jingxin No. 1) and antagonizing *F. oxysporum* f. sp. *niveum* (FON), which affects the same plant host. Although *S. plymuthica* MM secreted various extracellular enzymes, such as protease, chitinase, glucanase, and cellulase, its antifungal mechanism remains unknown; interestingly, the authors found that the *S. plymuthica* MM could increase the production of antioxidant and defence enzymes in watermelon plants by upregulating genes such as LOX, POD, PAL, ClPR3, and C4H.

Phosphorus is one of the essential elements for plant nutrition and is considered the second most important nutrient. Additionally, this element helps plants absorb other nutrients like nitrogen and magnesium, making its availability crucial in agriculture. Unfortunately, phosphorus is not available in many soils for plants, requiring the aid of phosphorus-solubilizing organisms (Bargaz et al., 2021; Etesami et al., 2023). A recent study described that *S. marcescens* Pt-3 exhibited excellent phosphorus-solubilizing activity. *Serratia marcescens* Pt-3, isolated from tea rhizosphere in a province of China (species not reported), demonstrated multiple functions in solubilizing insoluble phosphate, promoting corn seedling growth, and producing abundant VOCs. In addition to promoting plant growth and phosphate solubilisation, *S. marcescens* Pt-3 showed antagonism against *Magnaporthe oryzae*, *B. cinerea*, *Aspergillus flavus*, *A. fumigatus*, *Colletotrichum graminicola*, and *A.*

alternata. Individual evaluation of some VOCs revealed that dimethyl disulfide was important for inhibiting the germination of *A. flavus* by destroying its mycelial cell structures. The authors suggested that this strain could be an excellent plant growth promoter and biocontrol agent, making it promising as a biofertiliser and biofungicide (Gong et al., 2022). Another study published by Méndez-Santiago et al. (2021) showed that an endophytic strain of *Serratia* sp. exhibited mechanisms such as phosphate solubilisation, siderophore production, and auxin production, like indole acetic acid, which could be involved in plant growth promotion. Unfortunately, the effect of the strain on plants was not evaluated to confirm its role as a PGPB. Still, its antagonism was assessed *in vitro* against plant pathogens such as *Rhizoctonia solani*, *Bipolaris* sp., *Alternaria raphani*, *A. brassicicola*, and *F. oxysporum*, managing to inhibit the mycelial diameter of some of them. The strain also showed nematicidal activity against species such as *Nacobbus aberrans* and *Haemonchus contortus*. In contrast, symbiotic associations between *S. nematodiphila* species and nematodes (*Heterorhabditidoides chongmingensis*) have been reported. Interestingly, this *S. nematodiphila* species shows a close phylogenetic relationship with *S. marcescens*, suggesting that further investigation into the genomic-ecological aspects of such antagonistic and symbiotic interactions would be valuable (Zhang et al., 2009).

Previous studies show that various *Serratia* species are excellent biocontrol agents for plant pathogens, but they can also act as biofertilisers by improving plant nutrition and stimulating growth through phytohormone production (Table 1). However, their use needs to be extended and field studies expanded, as most reported work is *in vitro*. Evaluating other aspects, such as rhizosphere or endophytic colonisation under optimal or abiotic stress conditions (*e.g.*, salinity, drought, flooding, heavy metal contamination) remains to be fully explored.

Rahnella species as biocontrol agents

Rahnella is another bacterial genus that has recently been included within the Yersiniaceae family, which comprises 13 recognised species (Adeolu et al., 2016) (https://lpsn.dsmz.de/genus/rahnella). The species *Ra. aquatilis* is the most well-known and was also the first species described within this genus. Initially, the first isolates were classified as enterobacteria (Enterobacteriaceae) by Gavini et al. in 1976 at Institut Pasteur (Lee et al., 2019), and later, (Izard et al., 1979) and collaborators (1979) proposed the new genus *Rahnella*, including *Ra. aquatilis* as the type species. Years later, some *Rahnella* species were isolated from the rhizosphere of plants like maize and wheat and characterised as nitrogen-fixing bacteria (Berge et al., 2011). Since then, several *Rahnella* species have been extensively reported as biocontrol agents against various plant diseases for decades, including the bacterial plant pathogen *Xanthomonas campestris*, where *Rahnella* was identified as an important antagonist (Calvo et al., 2007; Chen et al., 2007; El-Hendawy et al., 2005; Sallam, 2011).

Currently, strains such as *Ra. aquatilis* MEM40, a PGPR isolated from rice rhizosphere, have shown antagonism against devastating plant pathogens like *M. oryzae* and *F. graminearum*, with its genome revealing certain characteristics relevant for plant protection. Other strains, like *Ra. aquatilis* ZF7, have also sequenced genomes, revealing beneficial capabilities such as antibiotic and biosurfactant production for biocontrol. Furthermore, growth-promoting and stress-resistance traits in this genome have been evaluated, including auxin (e.g., IAA) production, phosphate solubilisation, formation of Se nanoparticles, and organic acid biosynthesis (Yuan et al., 2014).

In another recent study, the genome of *Ra. aceris* strain ZF458 was analyzed, containing three replicons: one chromosome and two circular plasmids. The authors compared the genome of this species with other *Ra. aquatilis* strains, finding similar genes encoding essential functions for antagonism and plant growth promotion. They also evaluated *in vitro* antagonism of strain ZF458 against fungal plant pathogens like *Stemphylium solani*, *Corynespora cassiicola*, *Ascochyta citrullina*, *Colletotrichum* sp., *Phytophthora capsici*, *F. oxysporum*, and bacteria such as *Acidovorax citrulli*, *Pectobacterium brasiliense*, *Pseudomonas amygdali*, *Pseudomonas syringae* pv. *tomato*, *Ralstonia solanacearum*, *Xanthomonas campestris* pv. *campestris*, *Clavibacter michiganensis*, and *Agrobacterium tumefaciens*. Good antagonistic activity with varying degrees or inhibition percentages was determined among these plant pathogens (Xu et al., 2022).

Interestingly, Type I, II, III, and IV secretion systems were present in several sequenced *Rahnella* strains, a common feature in these strains. Secretion systems are relevant for the secretion of molecules and effector proteins that interact with plants and plant pathogens (Lucke et al., 2020). For example, the Type I protein secretion system (TISS) in nitrogen-fixing bacteria like *Rhizobium* is responsible for biofilm formation (Poole et al., 2018). Type III secretion systems (T3SS) and Type IV secretion systems (T4SS) in various PGPB are relevant for secreting effectors that can regulate proteins and induce plant immune responses, enhancing resistance to potential plant pathogens. In fact, Type I, III, IV, and VI secretion systems (T1SS, T3SS, T4SS, T6SS) are capable of directly translocating proteins across both the inner and outer membranes of Gram-negative bacteria in a single step, bypassing the periplasm. In contrast, Type II and V secretion systems (T2SS, T5SS) operate in two steps: first transporting proteins into the periplasmic space, then transferring these proteins to the outer membrane. T2SS uses a pilus-like structure to push proteins through the outer membrane, while T5SS, also known as the autotransporter system, involves the protein forming a β-barrel structure that inserts into the outer membrane, allowing its own secretion (Gamalero et al., 2022).

In another recent study, two bacterial genomes were sequenced and analysed: one from *Ra. perminowiae* S11P1 and another from *Variovorax* sp. S12S4, isolated from the rhizosphere of *Crocus sativus* L. (saffron). Functional characterization determined that they are plant growth promoters and possess genes involved in plant pathogen biocontrol. Some of these genes include *cobOST*, involved in cobalamin (vitamin B12) biosynthesis; *phzF*, *lysR*, involved in phenazine biosynthesis; *metH*, encoding methionine synthase, an enzyme that acts as a resistance inducer; *rhlBE*, involved in rhamnolipid biosynthesis (antimicrobial compounds); *srfAC*, involved in surfactin biosynthesis (antimicrobial and antifungal lipopeptides); *alsS, ilvNG*, encoding the large and catalytic subunits of acetolactate synthase, involved in volatile organic compound (VOC) production, among others.

Volatile organic compounds have attracted attention for their antagonistic activity against various fungal plant pathogens and for stimulating induced systemic resistance in various crop species. Volatiles may have certain advantages over other antimicrobial or protein compounds due to their low molecular weight, low polarity, lipophilicity, and ability to be transported over long distances while maintaining functionality (Sharifi and Ryu, 2020). In the case of *Rahnella* bacteria, strains like JZ-GX1 of *Ra. aquatilis* produce volatiles such as 3-methyl-1-butanol and 2-phenylethyl methyl that can inhibit mycelial growth and germination in plant pathogens like *C. gloeosporioides*. Interestingly, volatiles from JZ-GX1 reduced anthracnose disease spots on leaves of *Liriodendron chinense* x *tulipifera*, highlighting their role as biocontrol agents (Kong et al., 2022).

In this subsection, we highlight the potential of *Rahnella* species as biocontrol agents for plant diseases. However, not all *Rahnella* species exhibit beneficial interactions with plants. For instance, *Ra. victoriana*, along with *Enterobacter hormaechei* subsp. *hoffmannii* and *Citrobacter braakii*, has been associated with walnut decline disease (Hajialigol et al., 2023), and has also been reported in diseased onion bulbs (*Allium cepa*) cultivated in the United States and Norway (Asselin et al., 2019). Therefore, caution should be exercised when proposing new biocontrol agents, and in vivo tests, preferably in greenhouses or semi-controlled environments, should be conducted to ensure the safety of these strains for plants, animals, and humans before use. Finding potentially plant-pathogenic strains for crops is quite common; for example, *Pseudomonas* species, which are favourites as promoters and biocontrol agents, also include plant-pathogenic species like *P. syringae* (Xin et al., 2018). Therefore, while there is no need for excessive concern, it is a topic that should not be overlooked but instead discussed and evaluated with rigour. Table 1 includes reviewed works here including *Rahnella* species and their controlled plant plant pathogens.

Rouxiella **species as biocontrol agents**

The genus *Rouxiella* has the fewest described species among the main ones analyzed in this work as biocontrol strains, which include *Ro. chamberiensis*, *Ro. aceris*, *Ro. silvae*, and *Ro. badensis* (https://lpsn.dsmz.de/genus/rouxiella). The species *Ro. chamberiensis* was the first described as the Type species when proposed as a new genus by Flèche-Matéos (2015), and *Ro. aceris* and *Ro. silvae* were subsequently described by Fléche-Matéos et al. (2017). The species *Ro. aceris* was proposed by Lee et al. (2021) through a polyphasic taxonomy approach.

However, to our knowledge, none of these species had been characterised as biocontrol agents until 2021 when Morales-Cedeño et al. isolated *Ro. badensis* SER3 from the phyllosphere of *Fragaria* × *ananassa* and discovered that it exhibited strong *in vitro* antagonism towards multiple post-harvest fungal plant pathogens, including species from the genera *Alternaria*, *Botryosphaeria*, *Botrytis*, *Fusarium*, *Geotrichum*, *Mucor*, and *Penicillium*. The antagonism exerted by *Ro. badensis* SER3 towards the plant pathogens was through diffusible compounds, where there was direct contact, as well as through volatiles, in divided Petri dishes. More detailed analyses of the compounds excreted by the SER3 strain showed that they distorted the morphology of the mycelium of fungi like *Botrytis* and *Fusarium*. Sequencing the 16S rRNA gene showed similarity with strains of *Rahnella* and *Serratia*, but obtaining the genome of the strain and performing phylogenomic analyses and OGRIS (average nucleotide identity or ANI and a genome-to-genome distance calculator or GGDC) grouped it with the newly described species *Ro. badensis* by Fléche-Matéos et al. (2017). In fact, it showed 100% 16S rRNA gene identity, 99.69% (ANI), and 98.20% (GGDC) with *Ro. badensis* strain DM 100043T. Therefore, the strain was designated as *Ro. badensis* SER3.

Annotation, genome mining, and metabolite prediction with the AntiSMASH program (Blin et al., 2021) for *Ro. badensis* SER3 revealed various interesting functions related to plant growth promotion and biocontrol, such as thiopeptides, non-ribosomal peptide synthetases (NRPS), and polyketide synthases (PKS), siderophores, and arylpolyene compounds (Morales-Cedeño et al., 2021). Thus, this was the first study to demonstrate the potential of a *Rouxiella* strain as a biocontrol agent, opening the possibility of finding these functions in other species of the genus.

Another recent study isolated various strains with potential plant growth-promoting traits, as well as antagonistic activity against bacterial canker disease from the phyllosphere and endosphere of *Prunus* spp. in Iran, including some strains of *Rouxiella*, which were evaluated for their ribosomal gene and showed some similarity to *Ro. chamberiensis* (99.15%). Unfortunately, no such activities were found among the strains screened by the authors, but they were found in other isolated strains (Vasebi et al., 2023).

Recently, Guzmán-Guzmán et al. (2024) reported that the *Ro. badensis* SER3 strain could enhance antifungal and plant-beneficial responses of the mycoparasitic fungus *Trichoderma atroviride* by upregulating its effector genes, such as *epl1*, *tatrx2*, and *tacfem1*, in tripartite interactions with the plant pathogen *F. brachygibbosum*. Additionally, *Ro. badensis* SER3 inhibited the growth of *Fusarium* mycelium, either individually or in interaction with *T. atroviride*. Using transgenic lines of *A. thaliana* PR1 and LOX2 to analyze salicylic acid (SA) and jasmonic acid (JA)-mediated defence responses, a synergistic action between *Ro. badensis* SER3 and *T. atroviride* was observed, stimulating LOX2 expression more than 10 times. This was interesting because, with other strains like *P. fluorescens* UM270 and two strains of *Bacillus*, *Trichoderma* did not respond similarly or stimulate JA-mediated defence responses in *Arabidopsis*. Thus, the effector functions of *Trichoderma* were enhanced by interaction with beneficial bacteria like *Ro. badensis*. This work highlights that *Ro. badensis* SER3 could be part of a synthetic community (SynCom) with other beneficial fungi for agriculture like *Trichoderma*, as they showed no antagonism between them but did exhibit antagonism against plant pathogens like *Fusarium* (Table 1).

Predicting biocontrol metabolites in Yersiniaceae bacteria

Understanding the biocontrol potential of bacteria involves identifying and predicting the metabolites they produce, which can play a crucial role in their antagonistic activities against plant pathogens. Thus, the antiSMASH program is instrumental in predicting the potential production of antimicrobial metabolites (Blin et al., 2021). Table 2 shows a prediction analysis of metabolites from the different bacterial genomes of members of the Yersiniaceae family sequenced up to the writing of this work, including species and strains such as *Ro. badensis* SER3, *Ro. badensis* DSM 100043, *Ro. badensis* WG36, *Ro. badensis* DAR 84756, *Ro. silvae* 213, *Ro. silvae* Leaf50, *Ro. chamberiensis* 13033, *Ro. aceris* SAP-1, *Ra.bruchi*

DSM 27398, *Ra. woolbedingensis* DSM 27399, *Ra. inusitata* DSM 30078, *Ra. variigena* CIP 105588, *Ra. victoriana* DSM 27397, *Ewingella americana* CCUG 14506, *S. liquefaciens* ATCC 27592, *S. proteamaculans* CCUG 14510, *S. quinivorans* NCTC 11544, *S. grimesii* NCTC 11543, *S. ureilytica* HNU47, *S. ureilytica* C7, *S. ureilytica* 10436wE5, *Obesumbacterium proteus* DSM 2777, *Hafnia paralvei* ATCC 29927, *H. alvei* NCTC 8105, and *Cedecea davisae* DSM 4568.

The predicted compounds with varying similarity percentages found in the respective bacterial genomes correspond to NRPS, siderophores, thiopeptides, aryl polyene, T1PKS, T3PKS, transAT-PKS, Hserlactone, transAT-PKS-like, thioamides, terpenes, beta lactones, ladderane, pyrrolnitrin, NRP-metallophone, among others. It is noteworthy that this table includes the genomes of *Obesumbacterium proteus* DSM 2777, *Hafnia paralvei* ATCC 29927, *H. alvei* NCTC 8105, and *Cedecea davisae* DSM 4568, which do not have been reported to our knowledge, antagonistic, antimicrobial, or antifungal functions against plant pathogens. However, these genomes do present a broad metabolic potential for exploring such antimicrobial functions, as well as others like plant growth promotion, including the production of siderophores. Siderophores can have dual functions and act as iron scavengers from the soil, improving plant nutrition through iron and other elements, restricting fungal growth, as well as molecules eliciting ISR responses in agricultural crops. Recent studies have highlighted the presence of iron in the soil and its fundamental role in microbial interactions that allow PGPR to coexist in the rhizosphere (Du et al., 2024). Therefore, the production of siderophores is crucial in the complex microbial communications that occur in this microenvironment, and the roles of bacterial members of the Yersiniaceae family remain unexplored.

Other unexplored Yersiniaceae genera as antagonists

The principal biocontrol agents of the Yersiniaceae family are *Serratia* and *Rahnella*, confirmed as the most studied in this new bacterial family (Alijani et al., 2022; Calvo et al., 2007; Cao et al., 2023; Chen et al., 2007; Clements et al., 2019; El-Hendawy et al., 2005; Hajialigol et al., 2023; Hennessy et al., 2020; Müller et al., 2009; Sallam, 2011). After *Rouxiella*, with two studies where *Ro. badensis* exhibits antagonism against post-harvest fungal plant pathogens and its synergistic interaction with *Trichoderma* (Guzmán-Guzmán et al., 2024; Morales-Cedeño et al., 2021), a well-known mycoparasitic and beneficial fungus (Mukherjee et al., 2022). However, there are no clear studies evaluating other members such as *Hafnia*, *Obesumbacterium*, and *Cedecea*. Except for some studies like the one by Silva et al. (2012), who isolated approximately 200 bacterial strains as endophytes from healthy-looking *Coffea arabica* L. and *Coffea robusta* L. plants, including a strain 119G that might correspond to *Cedecea davisae*. This strain 119G exhibited a certain degree of biocontrol severity of leaf rust disease in coffee seedlings caused by *Hemileia vastatrix*. However, the authors did not provide further descriptions of this endophytic species.

Another strain of *Cedecea lapagei* KU14 in co-inoculation with *Bacillus subtilis* KU2 showed beneficial effects on the sustainable production of *Rosmarinus officinalis*, although no beneficial biocontrol effects against any plant pathogens were reported (Sharma et al., 2023).

Regarding *Hafnia*, there is a short report from 1985 published by Sneh et al. showing the biocontrol potential of *S. liquefaciens* and *Hafnia alvei* strains in carnations, protecting them from infection by *F. oxysporum* f. sp. *dianthi*. The authors concluded that *Serratia* was a better controller than *Hafnia* (Sneh et al., 1985).

In the case of the genus *Obesumbacterium*, we did not find literature showing its activity as a biocontrol agent of plant pathogens. Still, there is a recent study exploring its plant growth-promoting activities, where the rhizobacterium *O. proteus* KH8 exhibited certain PGP traits, such as phosphate solubilisation, production of siderophores, volatiles like HCN and ammonia, protease, chitinase, and cellulase activity. Unfortunately, experiments exploring its potential in plant interactions or interactions with plant pathogens were not conducted (Bhardwaj et al., 2023). The scarcity of functional, biochemical, or genomic studies of these three genera represents a significant opportunity to assign beneficial functions associated with plants, whether through direct or indirect plant growth promotion, such as biocontrol.

Conclusions and new challenges

With the current global warming, which is more pronounced in some regions than in others, new plant pathogens emerge that must be fought with microbial biocontrol agents. Biological control has multiple advantages over pesticides, such as its zero toxic effects on the environment. Therefore, new biocontrol agents, such as bacteria from the Yersiniaceae family, need to be searched for and characterised. These genera, which have been described previously, despite being close relatives of opportunistic human pathogens, have proven to be highly safe for both human and animal health, offering the same or even better biocontrol mechanisms than commonly studied or marketed strains like *Bacillus*, *Pseudomonas*, or even fungi like *Trichoderma*. In fact, with the new everyday genomic sequencing techniques, it is quite safe to perform genomic comparison analysis with plant pathogenic bacterial strains and detect possible plant pathogenicity islands or other virulence factors that could be harmful to human health. In fact, this should be routine for all microbial biocontrol agents: the non-detection of genetic factors with possible virulence/pathogenicity.

Another aspect to investigate in the future is the compatibility of Yersiniaceae family strains with known biocontrol agents, or whether they complement functions not found in other bacterial strains. This would help design synthetic communities or consortia for the development of more effective biopesticides under open field conditions, as well as in environments where abiotic factors may be extremely variable.

Additionally, it is recommended that the impact of inoculating Yersiniaceae family agents on the native microbial communities of crops be studied. Studies have shown that the introduction of new microbial agents to the rhizosphere can impact the structure and composition of microbial communities and, as a result, modify interactions with the plant host, affecting growth, metabolism, function, and, ultimately, agricultural production.

Recently, the role of other microbiota groups in the rhizosphere, such as protists, has been observed, and as far as we know, there are no studies demonstrating beneficial interactions between these eukaryotic microbes and bacteria from the Yersiniaceae family. Therefore, it would be helpful to conduct long-term microcosm studies to understand the interactions that may arise between these soil microorganisms, whose activity is crucial when interacting with plants. Recently, Asiloglu et al. (2024) discovered that protists may impact microbial communities in the rhizosphere and those that colonise the plant's internal tissues. Therefore, the impact of these interactions may go beyond the underground and have an aboveground effect.

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Figure legends

Figure 1. Role of biocontrol bacteria belonging to the Yersiniaceae family as part of the rhizospheric, endophytic, and phyllospheric microbiomes. Mechanisms such as competition, antibiosis, production of lytic enzymes, and induction of systemic resistance (ISR) have been detected in these bacterial members. Genera such as *Rahnella*, *Rouxiella*, and *Serratia* and their species have shown biocontrol activity against various pathogenic fungi, oomycetes, and nematodes in different crops. See the text for additional details.

Figure 2. Neighbor-joining phylogenetic tree of representative members of the Yersiniaceae family based on 16S rRNA gene sequence analysis. The 16S ribosomal DNA sequences were obtained from GenBank. Alignment was performed using MUSCLE, and the Neighbor-joining statistical method was applied. A total of 1000 bootstrap replicates were used. *Morganella morganii* ATCC 25830T (CP034944) was used as an outgroup.

Figure 3. Publications indexed in Scopus (https://www.scopus.com) related to biocontrol by genera within the Yersiniaceae family. See the text for further details.