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EGE UNIVERSITY

Graduate School of Applied and Natural Science

PGPR-MEDIATED BIOCONTROL OF FUNGAL AND OOMYCETE PATHOGENS INFECTING POTATO AND TARO CROPS

MSc THESIS

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We hereby certify that this thesis entitled "**PGPR-MEDIATED BIOCONTROL OF FUNGAL AND OOMYCETE PATHOGENS INFECTING POTATO AND TARO CROPS**", conducted, prepared, and submitted for the degree of Master of Science in Plant Genomics and Improvement by **Bekele Gelena Kelbessa**, has been recommended for acceptance and approval for oral defense, as it conforms to both the "Ege University Graduate School Policies" and the "Ege University Graduate School of Natural and Applied Sciences'. This study is entirely adequate in scope and quality as a thesis for the degree of Master of Science and the candidate has been found successful and the thesis was unanimity/majority voting by the committee on ... / ... / 2021.

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DECLARATION

I hereby declare that this thesis entitled "**PGPR-MEDIATED BIOCONTROL OF FUNGAL AND OOMYCETE PATHOGENS INFECTING POTATO AND TARO CROPS**" is my work done after registering for the degree of Master of Sciences in Plant Genomics and Improvement at Ege University and that it has not been previously submitted to any higher institution for the purpose of obtaining any degree, diploma or other qualification. I further affirm that all information contained in this thesis has been obtained and presented in accordance with Ege University's academic rules and regulations, as well as ethical conduct. Finally, I affirm that all sources used in the preparation of this thesis have been properly referenced.

14/08/2021

Bekele Gelena Kelbessa

ABSTRACT

PGPR-MEDIATED BIOCONTROL OF FUNGAL AND OOMYCETE PATHOGENS INFECTING POTATO AND TARO CROPS

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MSc Thesis, Seed Science and Technology

Major supervisor: Assoc. Prof. Dr. Birsen ÇAKIR AYDEMİR
Co-supervisor: Assoc. Prof. Dr. Ramesh Vetukuri
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Potatoes and taro crops are important sources of food for nearly one billion people in the world. However, many economically important pathogens including, *Phytophthora infestans*, *Rhizoctonia solani*, and *Phytophthora colocasiae* have been threatening the production of these crops. Until now, synthetic pesticides have been used to control these filamentous pathogens. However, the use of fungicides has long-term negative effects on the environment, human health, and livestock. The aim of this study was to find alternative management strategies to overcome these problems by investigating the antagonistic effect of bacterial strains against filamentous pathogens affecting potato and taro crops. In this study, seven bacterial strains and their sixteen dual combinations that showed compatibility were tested against the pathogens in a dual culture assay. Our results showed that all strains tested reduced the growth of either *P. infestans*, *R. solani*, or *P. colocasiae* by at least 35%.

The mechanisms of action behind the antagonistic activity of the strains could be due to different lytic enzymes. We were screened strains-mediated production of lytic enzymes *in vitro* and most of the strains tested were positive for protease, cellulase, lipase, and chitinase, which together with other enzymes degrade the cell wall of the

pathogens. Leaf disk assays and greenhouse experiments were performed with the strains showing high antagonistic activity *in vitro* to evaluate their biocontrol activity *in vivo*. Our results showed that *Serratia plymuthica*, AS13; *S. rubidae*, 268 strains, and their combinations consistently reduced the growth of *P. colocasiae* in all experiments. While *S. rubidae*, 268; and its combination with 121 significantly reduced the mycelial growth of *P. infestans*. Interestingly, the tested strains also secreted various plant growth-promoting traits and improved the growth of both taro and potato plants. Overall, the current study shows that biocontrol bacterial strains can be used as an alternative to synthetic pesticides in the control of potato and taro diseases. However, further evaluation of their biocontrol against these pathogens should be carried out under field conditions.

Keywords: Potato and taro diseases, ***Serratia*** spp., ***Pseudomonas*** spp., **biofilm**, **lytic enzymes**, **plant growth-promoting traits**.

PREFACE

Potato is widely cultivated and plays an essential role in securing food for the rapidly increasing world population. It is a popular crop because of its remarkable essential nutrient such as carbohydrates, proteins, health-promoting minerals, and vitamins. Similarly, taro is the fifth most cultivated monocotyledonous root crop and an important staple food for peasant subsistence communities in humid tropical areas of the world. Although both crops contribute to global food security, they are attacked by a variety of pathogens. Among the economically important diseases, late blight, caused by *P. infestans*, and stem canker and black scurf, caused by *R. solani*, are the most devastating diseases of potato worldwide.

On the other hand, leaf blight caused by *P. colocasiae* is the major bottleneck to taro production in taro-producing regions of the world. Until now, the management of these filamentous pathogens rely heavily on the use of synthetic fungicides. However, the residue of synthetic fungicides has negative effect on human and environment. To overcome this problem, there is need to search alternative management strategy. The use of beneficial microbes is one such alternative strategy to suppress the growth of pathogens and maintain sustainable production of both potato and taro crops to ensure food security for the world's growing population.

14/08/2021 Bekele Gelena Kelbessa

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1 INTRODUCTION

Environmentally sustainable forms of crop production face the challenge of achieving high yields to meet the food needs of the world's rapidly growing population (Goswami *et al*., 2016; De Vrieze *et al*., 2018). It is estimated that 70% more production will be needed globally to feed the human population in 2050 (Sharma *et al*., 2017). However, both abiotic and biotic factors severely constrain agricultural production, making it insufficient to feed the rapidly growing global population (Goswami *et al*., 2016; Syed Ab Rahman *et al*., 2018). Biotic constraints leading to a reduction in agricultural yields are due to diseases caused by various pathogenic microbes in crops (Goswami *et al*., 2016). To this end, increasing agricultural production through a sustainable and environmentally friendly approach is a part of the global effort to overcome such constraints in food production (Duvaleix *et al*., 2020; Hannah *et al*., 2020; Czyżewski *et al*., 2021).

Potato (*Solanum tuberosum*) is one of the global crops, serving as the main stable food source for more than a billion people worldwide (Cray *et al*., 2016; Campos & Ortiz, 2019). It has different distribution patterns and is often grown in areas with high levels of hunger, malnutrition, and poverty (Obidiegwu *et al*., 2015). Taro (*Colocasiae esculenta*), similar to a potato, is one of the most widely cultivated root crops in the family Araceae and a staple food in many nations of the world, including Africa, Oceania, and South Asia. (Nath *et al*., 2014; Vetukuri *et al*., 2018). However, the production of these crops is threatened by the continuous emergence of pathogens and climate change (Yao *et al*., 2016; Abbas *et al*., 2020).

Among economically important pathogens, potato late blight caused by *Phytophthora infestans*, a hemibiotrophic oomycete is the most devastating pathogen of potato due to its rapid asexual life cycle and reproduces sexually, resulting in high genetic diversity (Chinchilla *et al*., 2019; Tzelepis *et al*., 2020; Vetukuri *et al*., 2020). The pathogen was also responsible for the historically famous Irish Potato Famine in the late 1840s and continues to cause more than seven billion dollars in yield losses annually worldwide (Yao *et al*., 2016; Morrison *et al*., 2017). It severely infects the leaf,

stem, and tuber and leads to the destruction of the potato field within a few days (Fry, 2008; Kamoun *et al*., 2015).

Rhizoctonia solani, the necrotrophic soilborne fungal pathogen is another devastating pathogen that causes stem canker and black scurf diseases of potatoes worldwide (Woodhall *et al*., 2007; Van den Brink & Wustman, 2014; Zrenner *et al*., 2020). The disease is initiated by seed or soil-borne inoculum and infects sprouts, young stolons, stems, and tubers of the potato plant (Van den Brink & Wustman, 2014; Zhang *et al*., 2016). It causes many deformations and cracks on the tuber surface and results in 30% of marketable yield loss (Woodhall *et al*., 2007; Tsror, 2010). Similarly, leaf blight and corm rot caused by *P. colocasiae*, a hemibiotrophic oomycete, is the major constraint on taro production in all taro-growing countries worldwide (Lin & Ko, 2008; Misra *et al*., 2008; Otieno, 2020). It is an economically important taro disease that can reduce yields by 25 to 95 % in growing regions (Misra *et al*., 2008; Otieno, 2020).

Currently, the successful methods of controlling plant diseases, such as potato and taro pathogens, rely heavily on the use of synthetic chemical fungicides (Misra *et al*., 2008; Tsror, 2010; Yao *et al*., 2016). However, fungicide residues have long-term negative consequences for human health, animals, beneficial microorganisms, insects, and the environment (Daayf *et al*., 2003; Yao *et al*., 2016). Therefore, a novel alternative method of potato and taro disease control is urgently needed to maintain the sustainable production of these crops (Guyer *et al*., 2015). One such alternative approach to controlling plant pathogens is the use of beneficial microbes as biocontrol agents (Slininger *et al*., 2007; Rosier *et al*., 2018).

Plant growth-promoting rhizobacteria (PGPR) belong to a group of beneficial microbes that can mediate plant growth and protection through different mechanisms (de Souza *et al*., 2015; Köhl *et al*., 2019). Rhizobacteria exert their direct beneficial effects on plant growth by fixing biological nitrogen, solubilizing phosphates, producing phytohormones and siderophore compounds (Timmusk, 2003; Mota *et al*., 2017; Nath Yadav, 2017; Köhl *et al*., 2019). They also mediate plant growth indirectly by counteracting and competing with harmful pathogens for nutrients and space through the synthesis of antibiotics, bacteriocins, and hydrolytic enzymes (Danielsson *et al*.,

2007; (Diallo *et al*., 2011; Caulier *et al*., 2018; Rodríguez *et al*., 2020). PGRP also induces systemic resistance to pathogen infection through mechanisms such as callose deposition (Rodríguez *et al*., 2020). Therefore, PGPR has shown a potential to promotes plant growth and combat plant stress and is a promising strategy to be used in the practice of sustainable agriculture (Goswami *et al*., 2016). However, the ways in which PGPR promotes plant growth and protection may differ across the host range as well as from strain to strain (Köhl *et al*., 2019). Over the years, numerous research findings have reported that a wide range of plant pathogens have been successfully controlled using various PGPR strains (Danielsson *et al*., 2007; Soenens & Imperial, 2020).

No studies are yet available on the biocontrol potential of *Serratia plymuthica*, S412; *S. plymuthica*, S414; *S. plymuthica*, AS13; *S. proteamaculans*, S4; *S. rubidae*, 119; *S. rubidae*, 268 and a *Pseudomonas fluorescens*, 121 strain to control filamentous pathogens (*P. infestans*, *R. solani*, and *P. colocasiae*) infecting potato and taro crops. Therefore, this study aimed to find alternative strategies to synthetic fungicides by evaluating the biocontrol potential of these strains against these filamentous pathogens. Elucidating the mechanisms of action behind the inhibitory effect of these bacterial strains was another aim of this study.

2 LITERATURE REVIEW

2.1 Potato and Taro Crops

Potato (*Solanum tuberosum*) is one of the most economically important staple food crops after wheat and rice and is grown in 80% of the countries in the world with a production of 378 million tons worldwide (Batool *et al*., 2020). It is distinguished from many other crops by its adaptability to different climatic conditions and remarkable phenotypic plasticity (Gao *et al*., 2013). Belonging to the *Solanaceae* family, potato originated in the Anders region of Southern Peru and was introduced to Europe in the 16th century, from where it spread to the rest of the world in the mid-17th century (Banaszkiewicz, 2013). Since then, a potato has been cultivated in temperate, subtropical, and tropical countries of the world and used as vegetables, food, and other processed products (Majeed *et al*., 2017). Earlier, the highest potato production was associated with developed countries, but currently, production has shifted towards developing countries in Africa, Asia, and Latin America (Axel *et al*., 2012).

The potato provides remarkable essential nutrients such as carbohydrates, proteins, health-promoting minerals (e.g., potassium, phosphorus, and magnesium), and vitamins (e.g., B1, B3, B6, and vitamin C) (Obidiegwu *et al*., 2015; Batool *et al*., 2020). In addition, the consumption of potatoes plays an essential role in the production of antioxidant defenses that help reduce various human diseases such as, cancer, heart disease, and hypertension (McGill *et al*., 2013; Obidiegwu *et al*., 2015). Although potato contributes to global food security (Devaux *et al*., 2014), its production is under attack from many diseases caused by pathogens such as bacteria, fungi, oomycetes, and viruses (Irshad, 2013; Rupp & Jacobsen, 2017; Caulier *et al*., 2018).

Like potatoes, taro (*Colocasia esculenta*) is another staple food crop widely cultivated in humid tropical areas of the world (Tarla *et al*., 2016; Renee Bellinger *et al*., 2020). Originally, the taro crop is domesticated from Southeast Asia, has spread to the rest of the world, and is now an important staple food for more than 50 million people in Africa, Asia, the Caribbean, and the Pacific (Singh *et al*., 2012; Simsek & Nehir El, 2015; Renee Bellinger *et al*., 2020). Globally, taro is the fifth most cultivated monocotyledonous root crop of the *Araceae* family and the main component of

subsistence farming communities in developing countries (Simsek & Nehir El, 2015; Renee Bellinger *et al*., 2020b). The corm is the most consumed part of the taro plant, contains a high nutritional value, and is rich in health-promoting substances that protect against a variety of human diseases such as tuberculosis, fungal infections, and pulmonary congestion (Singh *et al*., 2012; Charles Carnot, 2017; Pereira *et al*., 2018). Due to its richness in fiber and vitamin C, taro leaves are also consumed as a vegetable (Singh *et al*., 2012). Therefore, taro is a very important crop for food security, especially in many subsistence farming communities in developing countries (Singh *et al*., 2012; Abdulai *et al*., 2020). Although taro is a food security crop, it is threatened by various diseases and pests worldwide (Sriram & Misra, 2007; Singh *et al*., 2012).

2.2 Potato and Taro Diseases

2.2.1 Late blight

Late blight caused by *P. infestans* (Mont.) de Bary is the major biotic constraint on potato and tomato production (Caulier *et al*., 2018). *P. infestans* is a foliar pathogen, the most known, most studied, most aggressive, reemerging disease, and remains a challenge for potato growers around the world (Tsedaley, 2014; Dey *et al*., 2018; Lee *et al*., 2020; Tzelepis *et al*., 2020). In addition to potatoes and tomatoes, *P. infestans* uses bittersweet (*Solanum dulcamara*), hairy nightshade (*S. sarrachoides*), and petunia as alternative hosts in off-seasons (Golas *et al*., 2010; Golas *et al*., 2010; Vetukuri *et al*., 2020).

2.2.1.1 Origin and history

The origin of this devastating pathogen is still controversial with work suggesting either an Andean region in South Peru (Gómez-Alpizar *et al*., 2007) or an origin in central Mexico (Goss *et al*., 2014; Wang *et al*., 2017). Several study results suggest that Mexico is the center of origin of *P. infestans* due to the presence of two mating types, A1 and A2, which lead to sexual reproduction and genetic diversity (Cooke *et al*., 2012; Goss *et al*., 2014; Wang *et al*., 2017). On the other hand, research based on mitochondrial and nuclear loci supports the hypothesis for an Andean origin of *P. infestans* (Gómez-Alpizar *et al*., 2007; Martin *et al*., 2014).

Originally, outbreaks of potato late blight occurred in the United States, from where it migrated with remarkable speed to Europe and the rest of the world in the 19th century (Saville *et al*., 2016; Dey *et al*., 2018). Thus, the current global population structure of *P. infestans* results from a strong migration of clonal lineages (Saville *et al*., 2016; Wang *et al*., 2017). Furthermore, the population structure of *P. infestans* is constantly changing due to the emergence of new strains, which continues to threaten global food security (Whisson *et al*., 2016). The pathogen has co-evolved with potatoes in central and South America and then spread to the rest of the world via infected seed tubers (Tsedaley, 2014; Martin *et al*., 2014; Saville *et al*., 2016). It has caused many crop failures over the past 150 years remains a major threat to food security today, despite the efforts of potato breeders and fungicide manufacturers (Cooke *et al*., 2011; Goss *et al*., 2014; Hwang *et al*., 2014).

2.2.1.2 Taxonomy and biology

Phytophthora infestans belong to the oomycetes, the most destructive group of pathogens in both agriculture, and aquaculture and are taxonomically related to brown algae and diatoms (Derevnina *et al*., 2016; Whisson *et al*., 2016). *P. infestans* is one of the most notorious species and historically known for causing Irish Potato Famine in the mid-19th century (Fry, 2008; Derevnina *et al*., 2016). The pathogen has an intermediate lifestyle under both natural and agricultural conditions (Leesutthiphonchai *et al*., 2018). Initially, the pathogen enters into a biotrophic relationship with its host to establish a feeding structure (haustoria) but later switches to a necrotrophic phase as the infection progresses through secondary hyphae (Fawke *et al*., 2015; Ah-Fong *et al*., 2017; Leesutthiphonchai *et al*., 2018).

Many features make *P. infestans* a successful pathogen that rapidly overcomes host resistance, evolves new virulence strains, and even occasionally jumps to a new host (Jahan *et al*., 2015). For example, a flexible mating system is the main driving force that allows the pathogen to both gain allelic diversity and rapidly replicates, resulting in large population sizes (Jahan *et al*., 2015; Derevnina *et al*., 2016). Moreover, the *P. infestans* genome is characterized by a two-speed genome: gene-dense regions comprising mainly housekeeping genes and gene-sparse regions enriched for disease-

promoting effector proteins (Jahan *et al*., 2015; Knaus *et al*., 2019). Rapidly evolving pathogen effectors, including RxRL genes, play a significant role in the rapid adaptability of *P. infestans* to the host plant (Haas *et al*., 2009; Knaus *et al*., 2019). In addition, the *P. infestans* genome is one of the largest (240Mb), and complex among oomycetes, and a significant portion of it contains repetitive-rich sequences (Haas *et al*., 2009; Dey *et al*., 2018; Lee *et al*., 2020).

2.2.1.3 Lifecycle and infection stage

Phytophthora infestans is characterized by an asexual and sexual mode of reproduction (Majeed *et al*., 2017; Tzelepis *et al*., 2020). The pathogen reproduces sexually, with two compatible, opposite mating-type strains (A1 + A2), interacting with each other to produce oospores that serve as both a survival structure and a source of genetic variation (Fry, 2008; Wang *et al*., 2017; Dey *et al*., 2018; Tzelepis *et al*., 2020). However, in the absence of compatible mating types, the pathogen produces asexual reproductive structures such ass sporangia and zoospores that allow it to spread throughout the world as independent clonal lineages (Fry, 2008; Majeed *et al*., 2017). Under suitable conditions, the life cycle of the pathogen on leaves is completed about five days, and one lesion can result in thousands of sporangia (Fry, 2008; Compant *et al*., 2019).

Asexually reproducing structures are detached from the parent mycelium and spread by rainwater, wind, and mechanical means to produce new mycelium of the pathogen in infected host tissue (Majeed *et al*., 2017). This type of propagation can occur several times in a season depending on the presence of the host and the ideal environment (Axel *et al*., 2012). However, sporangia and zoospores are not persistent in the soil for many years like sexually produced oospores because their survival depends on the presence of the host plants (Cooke *et al*., 2011; Tsedaley, 2014).

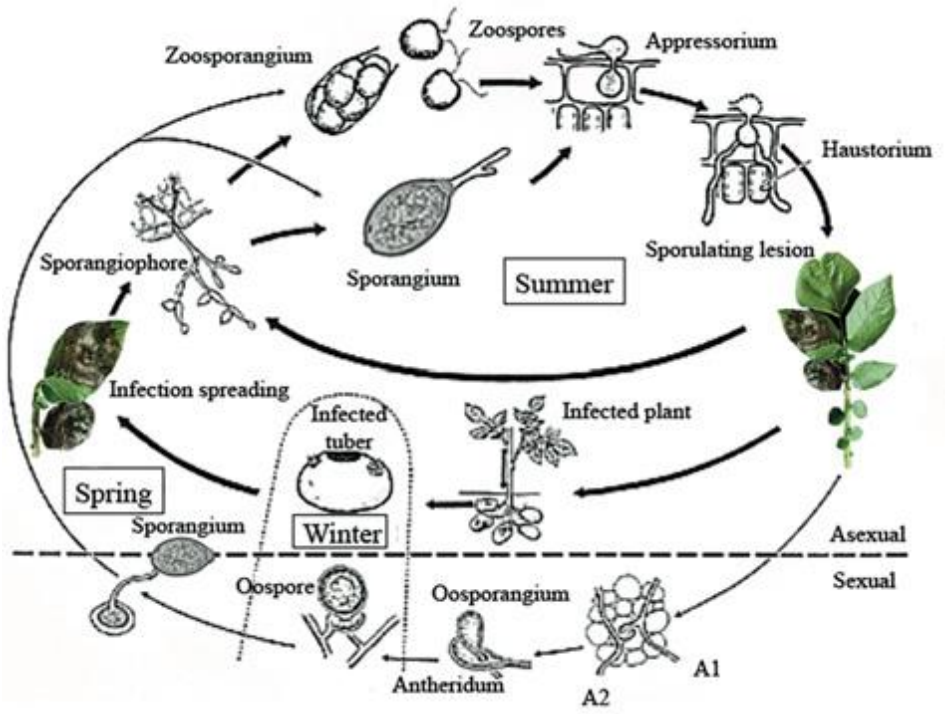

Figure 1: Lifecycle of *Phytophthora infestans*. (Adapted from Kessel & Förch, 2006)

Most infections during a season are initiated by asexual sporangia, which can germinate directly or indirectly through the formation of zoospores at an optimal temperature (18-24°C) (Fig. 2) (Axel *et al*., 2012; Whisson *et al*., 2016; Keskse, 2019). After direct penetration of the cuticle or epidermal cell wall by appressoria, *P. infestans* forms vegetative hyphae that grow intercellularly and introduce haustoria into host cells (Giraldo & Valent, 2013; Fawke *et al*., 2015). The haustorium of *P. infestans* serves to extract nutrients as well as a site of molecular exchange with the host for most of the disease cycle (Giraldo & Valent, 2013; Whisson *et al*., 2016). The final stage of *P. infestans* infection is associated with sporulation and host necrosis (Leesutthiphonchai *et al*., 2018).

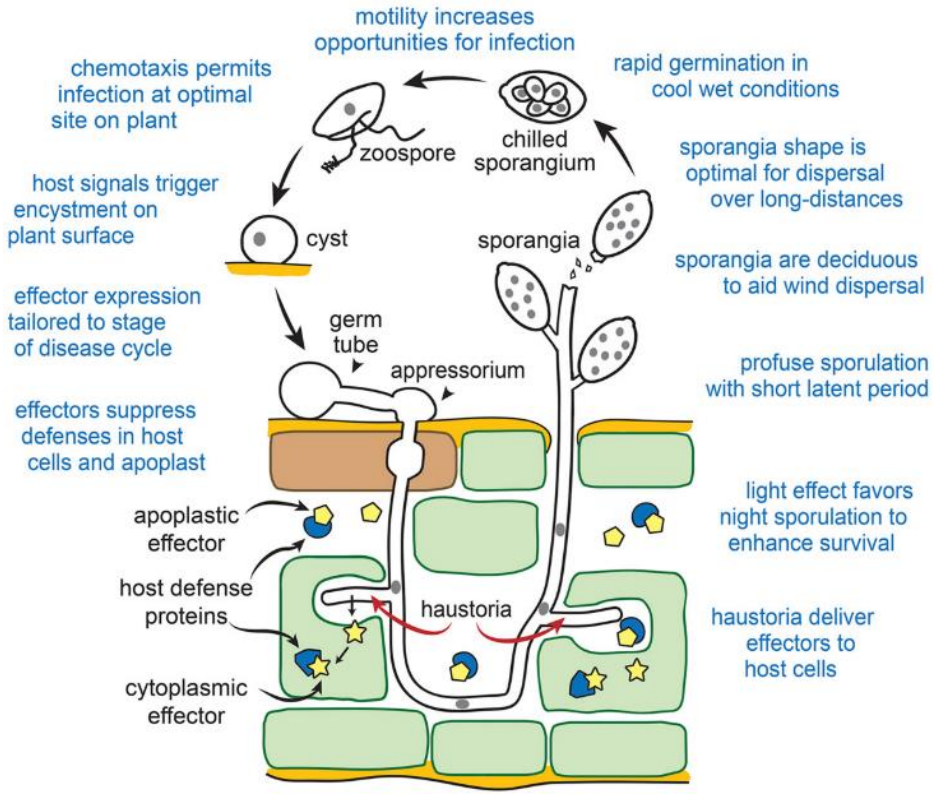

Figure 2: Disease cycle of *Phytophthora infestans* on foliage. Adapted from (Leesutthiphonchai *et al*., 2018)

Phytophthora infestans deliver two types of effector proteins that can act either externally (apo-plastic effectors) and internally (cytoplasmic effectors) disrupt each of these defense mechanisms (Jahan *et al*., 2015; Leesutthiphonchai *et al*., 2018; Lee *et al*., 2020). Apo-plastic effectors are secreted into the extracellular space of the plant and block plant enzymes such as serine proteases and cysteine proteases as a counter-defense (Ah-Fong *et al*., 2017). On the other hand, cytoplasmic effectors contain two families of proteins, namely amino acid motif near their N-terminus (RXLRs) and crinkle and necrosis (CRNs), which are translocated within the cells through haustorium, where they target different subcellular compartments (Haas *et al*., 2009; Jahan *et al*., 2015; Leesutthiphonchai *et al*., 2018). Once inside plant cells, these two effector proteins promote disease by blocking defense pathways or activating susceptibility factors (Boevink *et al*., 2016; Whisson *et al*., 2016; Lee *et al*., 2020).

2.2.2 Rhizoctonia solani

Rhizoctonia solani is another soilborne plant pathogenic fungus that causes Rhizoctonia disease complex in potatoes and leads to the occurrence of two diseases, namely stem canker and black scurf (Khaldi *et al*., 2015). In addition to potato crops, the pathogen has a worldwide distribution and affects many economically important crops such as maize, rice, soybean, tomato, and lettuce(Zrenner *et al*., 2020). The pathogen occurs in all areas where potatoes are grown and significantly affects both the quantity and quality of potato tubers (Van den Brink & Wustman, 2014; Zrenner *et al*., 2020).

2.2.2.1 History and origin

Rhizoctonia solani is the most studied pathogen within the genus *Rhizoctonia* and was originally described by Kühn (1858) from diseased potato tubers (Ajayi-Oyetunde & Bradley, 2018). The pathogen causes quantitative losses by infecting all underground potato plants, including stems, tubers, shoots, and the root, which directly affects the number and size of tubers (Tsror, 2010; Zhang *et al*., 2016). In addition, the pathogen causes qualitative losses through the development of malformed tubers and sclerotia on the tuber surface (Van den Brink & Wustman, 2014). According to Zrenner *et al*. (2020), Rhizoctonia potato disease causes tuber yield losses of up to 30%. However, the severity of the disease caused by *R. solani* depends on several factors including potato cultivar, *R. solani* strains, and environmental conditions (Woodhall *et al*., 2007; Zhang *et al*., 2016).

2.2.2.2 Taxonomy and biology

Rhizoctonia solani is a destructive soilborne pathogenic fungus and belongs to the phylum *Basidiomycota* (Zrenner *et al.*, 2020). The fungus is a species complex of different groups called anastomosis groups (AGs), in which isolates are further subdivided into subgroups according to the ability of their hyphae to anastomose (Van den Brink & Wustman, 2014; Zhang *et al*., 2016). In total, 14 different AGs of *R. solani* have been described, differing considerably in morphology, pathogenicity, aggressiveness, genetic characteristics, and host specificity (Ajayi-Oyetunde & Bradley, 2018; Zrenner *et al*., 2020). The best known and most problematic anastomosis groups

are AG-1, AG-2, AG-3, and AG-4 (Van den Brink & Wustman, 2014), while other AGs are less pathogenic to the potato at certain temperatures, but are generally less important as plant pathogens (Van den Brink & Wustman, 2014; Zrenner *et al*., 2020). Many reports indicate that *Rhizoctonia solani* AG-3 is the major pathogen of potato and causes the symptom characteristics of stem canker and black scurf of potato (Van den Brink & Wustman, 2014; Björsell *et al*., 2017).

2.2.2.3 Infection stage and lifecycle

Rhizoctonia disease complex of potato caused by *R. solani* is initiated by soil or seedborne inoculum and causes infection on all underground parts of the plant at any time during the growing seasons (Tsror, 2010; Khaldi, 2015). The pathogen occurs naturally as vegetative hyphae and sclerotia, as there are no conidia and hardly any sexual spores (Woodhall *et al*., 2007; Zhang *et al*., 2016). Sclerotia are dense clumps of hyphae that serve as both protective structures and dissemination mechanisms for the pathogen (Lehtonen, 2009). In addition to sclerotia, the fungus is mainly spread by contaminated planting material, water, and agricultural practices such as tillage (Neupane *et al*., 2015; Ajayi-Oyetunde & Bradley, 2018). Infection caused by *R. solani* is initiated when mycelia from a germinal sclerotium begin to grow towards potato plants as they attract host exudates (Van den Brink & Wustman, 2014). During the early growing period, *R. solani* causes necrosis and kills the shoot tip, resulting in symptoms of stem canker (Tsror, 2010). The late emergence of potato plants and reduced number of stems are also the common symptoms caused by stem canker infections under field conditions.

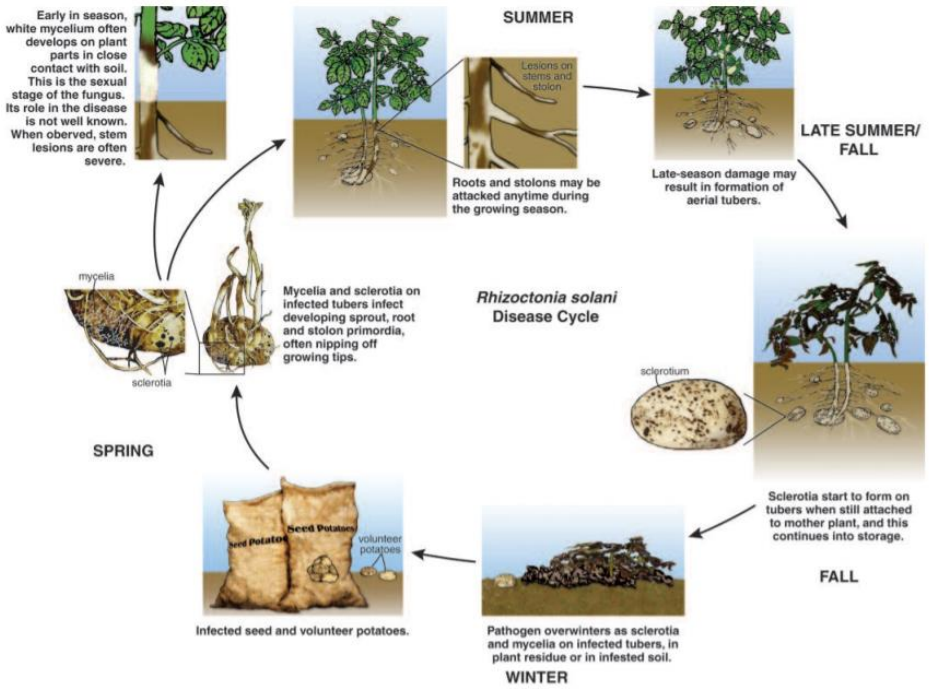

Figure 3: Disease cycle of *R. solani*, stem canker, and black scurf pathogen

2.2.3 Leaf blight

Among the taro diseases, leaf blight and corm rot caused by *P. colocasiae*, is the worst disease, and the major limiting factor for sustainable production of taro worldwide (Bandyopadhyay *et al*., 2011; Miyasaka *et al*., 2012). The pathogen is reported to destroy leaves and petioles within a few days after initial symptoms, leading to a reduction in photosynthesis and consequently a reduction in corm yield (Nelson *et al*., 2011). In addition to a reduction of corm yield in diseased plants, a corm rot can also occur, resulting in severe yield losses during storage (Vishnu Sukumari Nath *et al*., 2014; Devi *et al*., 2020). The devastating impact of the disease continues to affect the livelihood and food security of subsistence farmers and rural communities who depend on the crop (Singh *et al*., 2012; Tchameni *et al*., 2018). The pathogen present in all taro growing countries in the world, causes food insecurity, loss of genetic diversity of the crop, and harms national economies (Nath *et al*., 2014b; Renee Bellinger *et al*., 2020a).

Hence, the impact of *P. colocasiae* is a serious problem in taro-producing regions of the world, especially in South Pacific, Southeast Asia, and West Africa (Singh *et al*., 2012; Vetukuri *et al*., 2018). In Africa, this disease is more prevalent in the western

parts of Africa including, Nigeria, Ghana, and Cameroon, which are the major taro-producing regions (Bandyopadhyay *et al*., 2011; Singh *et al*., 2012; Otieno, 2020). In addition to *Colocasia* spp., the pathogen also infects other crops such as black pepper (*Piper nigrum*), castor bean (*Ricinus communis*), and elephant-foot yam (*Amorphophallus campanulatus*) (Singh *et al*., 2012).

2.2.3.1 History and origin

Initially, taro leaf blight was described in Java by Raciborski in 1900 (Hallyer, 1990), who named its causal pathogen Racib. Although the information on the origin of *P. colocasiae* is limited and the area of origin undetermined, previous reports speculated that the pathogen may have originated from Southeast Asia (Tyson, 2003). Another research report also supports Asia as the origin of *P. colocasiae* due to the coexistence of cultivated and wild taro species in the region (Vishnu Sukumari Nath, Hegde, et al., 2014). It is postulated that the pathogen spread from Java to Taiwan and subsequently to Japan and Hawaii in the early 1920s (Lebot *et al*., 2003). Since then, *P. colocasiae* has spread through infected tubers, sporangia, and zoospores in tropical Asia, South Pacific, and Africa, where it has had disastrous effects on food security and farmer welfare (Lebot *et al*., 2003; Misra *et al*., 2008; Singh *et al*., 2012).

2.2.3.2 Taxonomy and biology

Like *P. infestans, P. colocasiae* is also one of the oomycetes, the most destructive pathogens in a wide range of plants (Nelson *et al*., 2011; Vetukuri *et al*., 2018). To form oospores (the sexual stage), the pathogen requires two opposite mating types (A1 and A2) (Lin & Ko, 2008; Nelson *et al*., 2011). However, only A1 types occur in most taro-growing areas of the world (Misra *et al*., 2011). Sexually formed oospores have thick walls suitable for overwintering propagules in the absence of taro cultivars and also contribute to the genetic variability of the pathogens through possible new gene recombination (Nelson *et al*., 2011; (Sukumari Nath *et al*., 2016). In the absence of sexually produced oospores, the pathogen persists as an asexual clone in the infected tuber and produces numerous sporangia that spread to the new hosts by wind and rain-splashes (Sukumari Nath *et al*., 2016). Asexually produced sporangia germinate directly and infect host tissues through germ tubes (Nelson *et al*., 2011).

2.2.3.3 Infection stage and lifecycle

P. colocasiae infects the leaves of the plant and leads to the formation of brownish water-soaked circular spots on both young and mature leaves (Nath *et al*., 2014). As the infection by the pathogen progresses, the spots enlarge, and rotting of the entire leaves occurs (Singh *et al*., 2012). The disease life cycle of *P. colocasiae* depends on environmental factors and host genotypes (Singh *et al*., 2012). Under suitable weather conditions, the entire taro field is devastated within a few weeks of the onset of infection, causing yield losses of 30 to 50% (Lebot *et al*., 2003; Nath *et al*., 2014). Sporangia is the primary multiplication and dissemination unit of the pathogen, but *P. colocasiae* also produces chlamydospores and occasionally oospores (Lebot *et al*., 2003; Nelson *et al*., 2011). The pathogen requires optimal temperature (20-22°C) at 100% relative humidity for sporulation (Lebot *et al*., 2003; Nath *et al*., 2014). The sporangia spread within and between plants via rain splash and wind (Lebot *et al*., 2003; Bandyopadhyay *et al*., 2011).

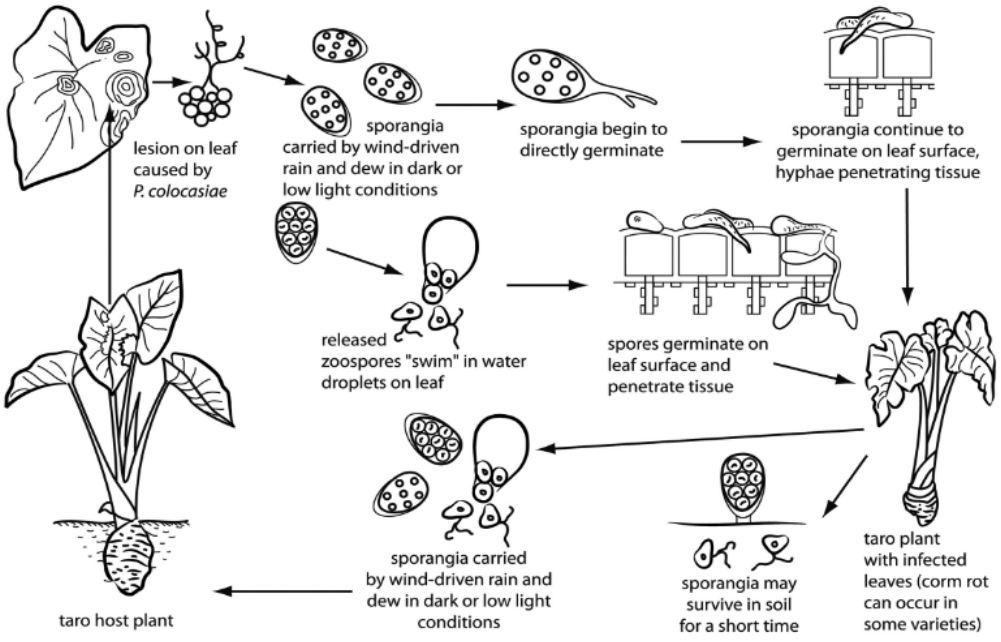

Figure 4: Sporangia of *P. colocasiae* germinating directly and produce zoospores.

2.3 Management of Potato and Taro Diseases

Various crop protection strategies including, cultural practices, host resistance, synthetic chemicals, and biological control have been used worldwide to control plant pathogens including, potato and taro diseases (Tsedaley, 2014; Cohen & Rubin, 2020). However, effective and sustainable management of plant diseases requires an understanding of morphological and genotypic diversity in pathogen populations, pathogen biology, mechanisms underlying disease development, survival strategies, spread mechanism, and sensitivity to fungicides (Vishnu Sukumari Nath *et al*., 2014; Huot *et al*., 2017)

2.3.1 Cultural practices

Plant diseases including, oomycetes and fungal pathogens that infect potato and taro crops can be controlled to some extent by cultural practices (Gao *et al*., 2019). Crop rotation practices significantly reduce the build-up of inoculum of overwintering pathogens (Tsror, 2010). Moreover, shifting planting dates in such a way that the critical stages of crop growth and favorable environmental conditions for disease development do not coincide also helps in reducing the incidence of potato and taro diseases (Tarla *et al*., 2016; Keskse, 2019). In addition, mixed cropping and control of contaminated sources such as infected tubers and secondary hosts help to reduce the severity of late blight, Rhizoctonia diseases, and taro leaf blight (Tsror, 2010; Tsedaley, 2014; Tarla *et al*., 2016). Removal of infected leaves, use of healthy tuber, and wide spacing between plants are also recommended for taro leaf blight diseases control (Misra *et al*., 2008; Singh *et al*., 2012). However, individually, the individual cultural practices are not effective in protecting potato and taro crops from these devastating diseases, but together they can play an essential role in an integrated disease management strategy.

2.3.2 Host resistance

Similar to other crops, disease management with a resistant variety is an important strategy and an environmentally friendly approach to reducing the spread of pathogens in both potato and taro crops (Arafa *et al*., 2017; Elnahal *et al*., 2020; Wang *et al*., 2020).

Plants have two layers of active defense, namely pattern-triggered immunity (PTI), and effector-triggered immunity (ETI) to protect themselves from pathogen damage (Saijo *et al*., 2018; Köhl *et al*., 2019). In first-layer defense, the presence of pathogen-associated molecular patterns (PAMPs) is detected by a pattern-recognition receptor (PRRS) (Dangl *et al*., 2013; Giraldo & Valent, 2013) and then activate PTI defenses against the pathogens (Leesutthiphonchai *et al*., 2018). However, many plant pathogens including, *P. infestans*, secrete effector proteins as a counter-defense to block the host defense response (Giraldo & Valent, 2013; Whisson *et al*., 2016). In turn, the intracellular NLR receptors recognize effector molecules as counter-counter defense and activate ETI, resulting in programmed cell death (Whisson *et al*., 2016; Leesutthiphonchai *et al*., 2018).

For more than a century, enormous breeding efforts have been made by potato breeders to produce new varieties with improved resistance (Golas *et al*., 2010; Jahan *et al*., 2015). Initially, a dominant resistance gene against *P. infestans* was identified from a wild species, *Solanum demissum*, and crossed into cultivated potatoes (Golas *et al*., 2010; Yang *et al*., 2017). In the 1960s, 11 R genes were identified from *S. demissum* and introduced into potatoes (Golas *et al*., 2010). However, this strategy was largely neglected after the 1970s when it was observed that a major R-gene was soon overcome by new virulent races in response to selection pressure (Cooke *et al*., 2011; Yang *et al*., 2017).

Subsequent breeding efforts emphasized the introduction of quantitative resistance by combining multiple R-genes to overcome the short shelf-life of qualitative resistance genes (Beketova *et al*., 2006; Jahan *et al*., 2015). However, breeding for quantitative resistance is difficult because the mechanisms behind resistance are unknown and many genes are involved (Rietman *et al*., 2012; Pilet-Nayel *et al*., 2017). The majority of European potato production remains susceptible to *P. infestans* infection (Cooke *et al*., 2011). Similarly, some breeding efforts have been made to develop taro leaf blight-resistant cultivars (Miyasaka *et al*., 2012; Renee Bellinger *et al*., 2020b). However, the development of host resistance to this pathogen is limited due to the lack of other

desirable economic and market traits and the occurrence of the virulent strains (Nath *et al*., 2014b; Wang *et al*., 2020).

2.3.3 Chemical fungicides

Fungicidal sprays have been the most effective strategies for preventing plant diseases including, pathogens of potato and taro, for many decades (Majeed *et al*., 2017; Cohen & Rubin, 2020). More than thirty-six fungicides and fungicidal mixtures with different modes of action are registered in Europe for foliar and tuber treatments of potatoes against late blight (Cohen & Rubin, 2020). This type of strategy is effective, fast, and has the potential to inhibit the zoosporangia and mycelium of the pathogen (Majeed *et al*., 2017). However, fungicides used to control potato late blight and taro leaf blight (TLB) may not be 100% effective due to the emergence of fungicide-resistant strains, especially in pathogen populations with higher evolutionary potential (McDonald & Linde, 2002; Daayf *et al*., 2003; Yao *et al*., 2016). Moreover, the continued use of these fungicides to control these diseases harms humans, animals, and the environment (Pérez-García *et al*., 2011; Sharma *et al*., 2017). In addition, the presence of a waxy coating on the leaf lamina of the taro plant renders fungicides ineffective and makes them an uneconomical strategy to control leaf blight caused by *P. colocasiae* (Vishnu Sukumari Nath *et al*., 2013).

Currently, there is increasing consumer demand for organically produced food and, therefore, farmers use copper-based products as an alternative to fungicides in organic potato and taro production to protect these crops from these diseases (Pérez-García *et al*., 2011; De Vrieze *et al*., 2018). However, due to its low degradability, the copper-based product is accumulated in the soil and is toxic to soil fauna (Du Plessis *et al*., 2005; De Vrieze *et al*., 2018). Hence, there is a need to search for alternative strategies that can replace chemical fungicides to control these devastating diseases (Rodríguez *et al*., 2020). Biocontrol by beneficial microorganisms is a new alternative strategy for sustainable disease management practices (Ongena & Jacques, 2008; Rodríguez *et al*., 2020).

2.3.4 Biocontrol

Currently, the use of chemical pesticides to control plant pathogens, including those that cause potato and taro diseases, is declining due to increasing food safety and environmental concerns (Axel *et al*., 2012; Pertot *et al*., 2015). In this context, the use of microorganisms as biological agents are a promising tool for the sustainable management of plant diseases (Mota *et al*., 2017; Syed Ab Rahman *et al*., 2018). Microbes associated with the plant rhizosphere and phyllosphere play an essential role in suppressing abiotic and biotic stresses in plants, leading to better plant production (Raaijmakers *et al*., 2009; Kudoyarova *et al*., 2019). Among them, PGPR possesses several plant growth-promoting traits and is used directly or indirectly to alleviate the effect of harmful pathogens (Guyer *et al*., 2015; Juanjuan Wang *et al*., 2020). In general, interest in PGPR as a biocontrol of plant diseases has gradually increased as current advances in microbial and molecular techniques provide new insights into the underlying mechanisms by which introduced beneficial bacteria function (Choudhary & Johri, 2009; Syed Ab Rahman *et al*., 2018).

2.3.4.1 Biocontrol Bacteria

Over the years, several PGPR strains from the genera *Bacillus*, *Pseudomonas*, and *Serratia* have been isolated and evaluated as potential biocontrol agents against soilborne fungal and oomycete pathogens, and in some cases, their mode of action has been elucidated (Danielsson *et al*., 2007; Pliego *et al*., 2011; Morrison *et al*., 2017). Serratia is a Gram-negative, widespread facultative anaerobic bacteria belonging to the family *Enterobacteriaceae*, and have various ecological functions, including antagonistic, mutualistic, and pathogenic (Martínez *et al*., 2018). Several species belonging to the genus *Serratia* are known as PGPR (Neupane *et al*., 2015; Soenens & Imperial, 2020). Plant-associated rhizobacteria strains improve the growth and health of their hosts in multiple ways (de Souza *et al*., 2015). They may be directly involved in plant growth by synthesizing growth-stimulating phytohormones that regulate plant development at different stages (Kudoyarova *et al*., 2019). In addition, PGPR directly affects plant growth by increasing the availability of essential nutrients to plants (For example, nitrogen, phosphorus, and iron (Diallo *et al*., 2011; Sharma *et al*., 2017; Tshikantwa *et*

al., 2018). Indirect mechanisms mediated by PGPR may include the production of antibiotics or other deleterious molecules that are harmful to infection by a pathogen (Oleńska *et al*., 2020). PGPR can also stimulate plant growth indirectly through the synthesis of salicylic acid, which makes plants more tolerant to pathogens by activating systemic acquired resistance (Diallo *et al*., 2011; Köhl *et al*., 2019). However, the way PGPR promotes plant growth and suppresses harmful pathogens differs among species and strains (De Souza *et al*., 2015).

2.3.5 Direct plant growth promotion

2.3.5.1 Phytohormone production

Rhizobacteria directly affect plant growth and development through the production of growth-stimulating phytohormones or intermediates (Diallo *et al*., 2011; Köhl *et al*., 2019). PGPR are reported to produce and secrete phytohormones that directly promote plant growth, increase root surface area, and enhance plant adaptability to a variety of abiotic and biotic stresses (Juanjuan Wang *et al*., 2020). Beneficial bacteria produce indole-related compounds such as phytohormone auxin, which are of great relevance to bacteria-plant interactions (Kuan *et al*., 2016). However, the biosynthesis of an indole-related compound in bacteria depends on the presence of a precursor (L-tryptophan) in root exudates (Spaepen & Vanderleyden, 2011; Oleńska *et al*., 2020). Several studies have shown that other growth-stimulating phytohormones such as ethylene, cytokinin, and abscisic acid are also largely produced by bacterial strains associated with plants (de Souza *et al*., 2015; Oleńska *et al*., 2020).

2.3.5.2 Nitrogen fixation

All plants require nitrogen for the synthesis of amino acids, nucleosides, phospholipids, and chlorophyll (de Souza *et al*., 2015). However, the main source of nitrogen in nature, atmospheric nitrogen (N_2) is not accessible to plants (Juanjuan Wang *et al*., 2020). Nitrogen-fixation by beneficial microbes has emerged as one of the biological alternatives to N-fertilizers and could lead to ecologically sustainable crops production (Raaijmakers *et al*., 2009; Mpanga *et al*., 2019). PGRP reduces atmospheric N_2 to ammonia (NH_3) with the help of their nitrogenase enzyme complex and thus supply for plants (Rilling *et al*., 2018). Hence, nitrogen fixation by bacteria helps plants

to obtain nitrogen directly from the atmosphere and meet their nutrient requirements (Kuan *et al*., 2016; Rilling *et al*., 2018). Some members of the genera *Bacillus*, *Pseudomonas*, and *Serratia* colonize various plant niches such as the rhizosphere and endosphere of plants and contribute to meeting the N requirement of non-leguminous plants (Bhattacharyya & Jha, 2012; *Kuan et al., 2016; Weselowski et al., 2016).*

2.3.5.3 Phosphorus solubilization

Like nitrogen, phosphorus is an essential macronutrient for plant growth. Despite its availability in soil, it is not available to plants due to its insolubility properties (Lucke *et al*., 2020). Beneficial bacteria dissolve various forms of organic phosphorus such as aluminum phosphate and rock phosphate into inorganic forms that can be readily taken up by plants through the secretion of organic chelators such as citric, gluconic, and malic acid upon utilization of sugar present in root exudates (Alori *et al*., 2017; Nath Yadav *et al*., 2017). Organic acid secreted by beneficial microbes plays an important role in lowering soil pH and producing bioavailable HPO_4^{-2} (Adnan *et al*., 2017). Several studies have shown that some strains of the genera *Bacillus*, *Pseudomonas*, and *Serratia* secrete organic acid that solubilizes phosphorus and increases its bioavailability to plants (Ben Farhat *et al*., 2009; Alori *et al*., 2017).

2.3.6 Indirect plant growth promotion

2.3.6.1 Antibiosis

Antibiosis is a secondary metabolite and is produced by a variety of microorganisms, including beneficial microbes (Sharma *et al*., 2017). Several study results reported that bacterial strains from the genera Pseudomonas and Serratia produce a wide range of antibiotic compounds, including bacteriocins, cyclic lipopeptides, hydrogen cyanide, and oomycin, which affect the growth and metabolic activity of harmful pathogens (Köhl *et al*., 2019; Soenens & Imperial, 2020). In addition to antibiotics, PGPR can synthesize a wide range of lytic enzymes, including protease, lipase, chitinase, amylase, and beta-1,3-glucanases, which affect the growth of phytopathogens and further improve their biocontrol efficiency. According to the results of Compant *et al*. (2005), *Serratia plymuthica* secretes cell wall hydrolases (chitinase)

that inhibit spore germination and germ-tube elongation of phytopathogens. PGPR also indirectly influence plant growth by forming a biofilm that serves as a protective layer against harmful pathogens (Weselowski *et al*., 2016) or as an improved surface for nutrient uptake from the surrounding plant rhizosphere (Lucke *et al*., 2020).

2.3.6.2 Competition for nutrients and space

Along the root surface and surrounding rhizosphere of plants, various nutrient-rich niches attract a wide variety of microorganisms, including harmful phytopathogens (Beneduzi *et al*., 2012). To grow and multiply on the surface of roots, PGPR compete with pathogenic microbes for nutrients such as C- and N-containing compounds and for the site of growth (Choudhary & Johri, 2009; Neupane *et al*., 2015). During the nutrient competition, PGPR secretes secondary metabolites that aid in the suppression of fungal and oomycete pathogens (Lucke *et al*., 2020).

2.3.6.3 Production of siderophore

As with other essential nutrients, the scarcity of bioavailable iron in the soil increases energetic competition between PGPR and pathogenic microbes due to the low solubility of Fe^{+3} ions (Sharma & Johri, 2003; Adnan *et al*., 2017). To acquire iron competitively, PGPR produces low molecular weight compounds called siderophores such as carboxylates, catecholates, and hydroxamates in iron-limited soils (Patra *et al*., 2018). Due to its high affinity for iron, a siderophore produced by microbial strains can be used as a biocontrol by competing with pathogens that produce a lower amount of siderophores with a lower affinity for iron (Backer *et al*., 2018; Lucke *et al*., 2020). Siderophores also enhance the ability of PGPR to colonize roots by suppressing phytopathogens (Beneduzi *et al*., 2012; Backer *et al*., 2018). However, siderophores produced by different bacterial strains differ in their ability to sequester iron under iron deficiency conditions (Patel *et al*., 2018).

2.3.6.4 Induce systemic resistance (ISR)

The induction of resistance in host plants to both root and foliar pathogens is another recognized mechanism of PGPR-mediated biocontrol (Choudhary & Johri, 2009; Köhl *et al.*, 2019). Several study results showed that PGPR strains protect plants against

deleterious pathogens by inducing systemic resistance without causing symptoms themselves (Choudhary & Johri, 2009). Activation of induced resistance by various stimulators increases the expression of natural defense mechanisms of plants against biotrophic and hemi-biotrophic pathogens (Backer *et al*., 2018). Recently, the study of mechanisms of induced resistance in plants against a variety of pathogens is gaining attention due to their effectiveness, sustainable, and environmentally friendly strategies to control plant diseases (Köhl *et al*., 2019; Rodríguez *et al*., 2020). Induced resistances activated by elicitors in the host plant are not only expressed locally in the infected tissue but also spread systematically, preparing plants for future pathogen attacks (Romera *et al*., 2019).

Plants develop either local or systematically spreading responses from infected tissues to uninfected parts to cope with biotic challenges caused by biological agents, such as phytopathogens (Bakker *et al*., 2013; Romera *et al*., 2019). Systematically common responses of plants against pathogenic microbes include systemic acquired resistance (SAR) and induced systemic resistance (ISR) (Choudhary *et al*., 2007; Conrath *et al*., 2015). SAR is induced by pathogens and is associated with the accumulation of pathogenesis-related protein and salicylic acid (SA) throughout the plant (Conrath *et al*., 2015; Köhl *et al*., 2019). On the other hand, ISR is induced by plant-associated beneficial microbes (Romera *et al*., 2019) and regulated by interconnected signalling pathways in which phytohormones such as jasmonate and ethylene play important regulatory roles (Choudhary *et al*., 2007; Bakker *et al*., 2013). PGPR-mediated ISR alters host physiology and metabolic response, leading to increased synthesis of plant defense chemicals when attacked by pathogenic microbes. Many PGPR species from the genera Bacillus, Pseudomonas, and Serratia have been reported to induce ISR (Bakker *et al*., 2013; Romera *et al*., 2019; Oleńska *et al*., 2020). However, ISR is effective against harmful pathogens that are sensitive to ethylene and jasmonate-dependent defenses including, necrotrophic pathogens and insect herbivores (Colling *et al*., 2013).

3 MATERIAL AND METHODS

3.1 Chemical and Culture Media

LB broth was prepared by dissolving 25 g L^{-1} in sterilized dH_2O and used for culturing bacterial strains. Rye agar (RA) was prepared by simmering 60 g L^{-1} rye grains in tap water overnight and then the filtered liquid (1.5 mm mesh) was filled up to a volume of 1 L with dH_2O and sucrose, 20 g L^{-1} was added. Subsequently, the pH of RA was adjusted at pH 5.8, supplemented with agar, 15 g L^{-1}, and used to cultivate *P. infestans* 88069. Vietnamese strain 7290 of *P. colocasia* was grown on V8-media [$CaCO_3$, 1.5 g L^{-1}, veg juice, 100 g L^{-1}, and agar, 15 g L^{-1}) while *R. solani* AG4-HG II, was cultured on potato dextrose agar (PDA), which was prepared by dissolving PDA 19.5 g L^{-1} and supplemented with agar, 7.5 g L^{-1}. This study conducted at the Swedish University of Agricultural Sciences, Alnarp Campus in 2021.

3.2 Antagonistic Assay

The antagonistic activity of seven bacteria, six strains of *Serratia* (*Serratia plymuthica*, S412; *S. plymuthica*, S414; *S. plymuthica*, AS13; *S. proteamaculans*, S4; *S. rubidae*, 119; *S. rubidae*, 268) and a *Pseudomonas strain* (*Pseudomonas fluorescens*, 121) obtained from the culture collection of the laboratory of Dr. Ramesh Vetukuri (Assoc. Professor), the Swedish University of Agricultural Sciences, Sweden. A 4 mm diameter mycelial disk of each pathogen was taken from progressing hyphae growing on RA (*P. infestans*), PDA (*R. solani*) and V8 (*P. colocasiae*) and inoculated with a sterile cork borer into the center of a 9 mm diameter Petri dish containing freshly prepared RA (*P. infestans*), PDA (*R. solani*) and V8 (*P. colocasiae*). For this purpose, the bacterial strains were cultured overnight in LB broth at 28°C and 220 rpm, the density was adjusted to (OD600 = 0.3), and the strains then streaked in a straight pattern on both sides of 9-mm Petri plates, 2 cm from the center. The plates were incubated at 28°C, 220 rpm, and the inhibitory activity of the strains against the pathogens was evaluated after 3 days (*R. solani*), 7 days (*P. colocasiae*), and 14 days (*P. infestans*).

The diameter of the zone of pathogen mycelium growth inhibition was calculated as [diameter of pathogen growth in the absence of strains (untreated control) (mm) –

diameter of pathogen growth in the presence of bacterial strains (mm) / diameter of pathogen growth in the absence of strains (untreated control) (mm)] X 100 (Saha *et al*., 2012; Wang *et al*., 2019). As a negative control, RA (*P. infestans*), PDA (*R. solani*), and V8 (*P. colocasiae*) medium were used. The dual culture assay was conducted with six replicates and repeated twice.

3.3 Compatibility Assay

To determine whether these bacterial strains coalesce or inhibit each other, we examined the compatibility of all strains. Briefly, the bacterial strains were cultured overnight in LB broth at 28°C and 220 rpm. After measuring the optical density of each bacterial strain and setting the density to (OD = 0.3), one strain was streaked perpendicularly onto the freshly prepared TSA plates and incubated for 24 hours at 28°C and 220 rpm. Then, the second strain was inoculated at a 90° angle starting from the colony of the first strain and incubated for another 94 hours at 28°C, 220 rpm. After incubation, we took photographs showing the zone of inhibition and the synergistic effect at the junction of the paired strains. We also tested the antagonistic effect of the compatible bacterial strains against all pathogens. Based on the *in vitro* inhibitory activity of the strains against either *P. infestans*, *R. solani*, or *P. colocasiae*, all the tested single and their nine dual combinations were selected for further experiments. The assay was carried out with six technical replicates and repeated twice.

3.4 Biochemical and enzyme activity test

3.4.1 Biofilm production test

Biofilm production of selected strains was assessed using the microplate assay method described by (Pratt and Kolter, 1998). 10 µL of either single (OD600=0.3, for single strains) or combined strains (OD600=0.15, for combined strains) were transferred into 96-well polystyrene microtiter plates filled with 150 µL of LB broth and incubated for 48h at 28°C, 220 rpm. To detect biofilm production, loosely associated bacteria were removed from the wells, rinsed three times with sterilized dH_2O, air dried, and then stained with 0.2% crystal violet (170 µL). After 30 min incubation at room temperature, the crystal violet was discarded, and the wells were again washed three times with

sterilized dH_2O and stained with 96% ethanol (200 µL). Then 100 µL from each well was transferred to a new microtiter plate and absorbance was measured at 595nm using a spectrophotometer. The biofilm assay was performed twice, with octuplicates per strain, and LB broth was used as a control. The results obtained were adjusted for background staining by subtracting the value for crystal violet bound to the untreated controls and treated statistically.

3.4.2 Lytic enzymes production

3.4.2.1 Protease activity

Protease activity of selected strains was assayed on skim milk (SM) agar [skim milk, 28 g L^{-1}; dextrose, 1 g L-1; casein hydrolysate, 5 g L^{-1}; yeast extract, 2 g L^{-1}; agar, 15 g L^{-1}] at pH 7±0.2 according to the method of (Caulier *et al*., 2018). 10 µL of either single (OD = 0.3) or combined strains (OD = 0.15) were pipetted onto the above medium and incubated for two days at 28°C, 220 rpm. Thereafter, the appearance of a clear zone around the bacterial colony was assessed and the protease index was calculated as [(diameter of the clear zone (mm) - diameter of bacterial colony/diameter of the bacterial colony) X 100] (Pertiwiningrum *et al*., 2017). The protease assay was performed with six replications per strain and treated statistically.

3.4.2.2 Amylase activity

Amylase production of selected strains was assessed on TSA plates (TSA, 40 g L^{-1}, and soluble starch, 2 g $L^{-1)}$ following the method described by (Pascon *et al*., 2011) with some modifications. 10 µL of either single (OD = 0.3) or combined strains (OD = 0.15) were spotted onto TSA plates containing soluble starch and incubated for 48h at 28°C and 220 rpm. The plates were then flooded with an iodine solution (1 % potassium iodide and 0.1 % iodine) for 5 minutes, and amylase activity was assessed by the starch degradation zone formed on the purple background (Pascon *et al*., 2011). The experiment was performed with six replications per strain and repeated twice.

3.4.2.3 Cellulase activity

Cellulase-producing strains were assessed using the method described by (Ariffin *et al*., 2006) on carboxy-methyl cellulose (CMC) agar [KH_2PO_4, 1 g L^{-1}; $MgSO_4.7H_2O$, 0.5 g L^{-1}; NaCl, g L^{-1}; $FeSO_4.7H_2O$, 0.01 g L^{-1}; NH_4NO_3, 0.3 g L^{-1}; CMC, 10 g L^{-1}; agar, 12 g L^{-1}] at pH 7±0.2. 10 µL of the individual or combined strains were spotted onto CMC-agar and incubated at 28°C and 220 rpm for five days. Subsequently, the cellulase-degrading ability of the strains was confirmed by super-fusing the plates with 0.1% Congo red for 15 min followed by 1M NaCl (Ferbiyanto *et al*., 2015). The cellulase assay was performed with six technical replicates and repeated twice.

3.4.2.4 Lipase activity

Lipase-producing strains were tested on a peptone agar medium. The peptone agar medium [peptone, 10 g L^{-1}; NaCl, 5 g L^{-1}; $CaCl.2H_2O$, 0.1 g L^{-1}; agar, 16 g L^{-1}] was prepared according to (Kumar *et al*., 2015) at pH 6 and supplemented with 1% separately sterilized Tween 20. A 10 µL of either single (OD = 0.3) or combined strains (OD = 0.15) were pipetted onto peptone agar medium and incubated for five days at 28 °C and 220 rpm. Then, the clear zone formed around a colony was used as an indicator of the lipase activity of the strains. This assay was performed with six replicates per bacteria strain.

3.4.2.5 Hydrogen cyanide

For qualitative screening of hydrogen cyanide-producing bacterial strains, the approach described by (Lorck, 1948) was used. Bacterial strains were cultured overnight in LB medium, and their density was adjusted to (OD = 0.3, for single strains) and (OD = 0.15, for combined strains). 10 µL of the single or combination strains were spread on TSA plates supplemented with 4.4 g L^{-1} glycine. The top of the Petri plate was covered with No. 1 Whatman filter paper after being dipped in 0.5% picric acid and 2% sodium carbonate w/v. The plates were then inverted, sealed with parafilm paper, and incubated at 28 °C and 220 rpm for two days. The intensity of the color change from yellow to orange or red indicates the production of hydrogen cyanide by the bacterial strains. *Pseudomonas choloraphis* 294, which produces hydrogen cyanide, was used as

a positive control. The test for hydrogen cyanide production was performed with six replicates per strain and repeated twice.

3.4.2.6 Chitinase

To detect chitinase-producing bacterial strains, colloidal chitin was prepared according to the method previously described by (Roberts & Selitrennikoff, 1988) with some modifications. Briefly, 5 g of powdered chitin (Sigma-Aldrich) was dissolved in concentrated HCL (100 mL) and stirred at 220 rpm and 10 °C until the chitin dissolved (2 h). The chitin- HCL mixture was then filtered with eight layers of cheesecloth, and the filtrate obtained was poured into 1 L of Milli-Q water and stored overnight at 4 °C in a refrigerator. Afterward, the white cake-like chitin solution was centrifuged at 4200 x g for 20 min and the chitin pellets were repeatedly washed with cold Milli-Q water until the pH of the obtained filtrate reached 5. For the detection of chitinase-producing selected bacterial strains, 10 µL of either single (OD = 0.3) or combined strains (OD = 0.15) were pipetted onto colloidal chitin (CC) agar [$NH_4H_2PO_4$, 1 g L^{-1}, KCl, 0.2 g L^{-1}; $MgSO_4.7H_2O$, 0.2 g L^{-1}; CC, 10 g L^{-1}, agar, 20 g L^{-1}] at pH 6 ± 0.2 and incubated at 28 °C for five days. This assay was performed with six technical replicates per strain.

3.4.3 Plant growth-promoting traits

3.4.3.1 Siderophore production assay

Siderophore secretion strains were tested using modified chromazurol S (CAS) agar [10 ml $FeCL_3.6H_2O$, 27 mg/100 mL HCl 10 mM; 50 mL CAS, 1.2 g L^{-1}; 40 mL hexadecyltrimethylammonium bromide (HDTMA), 1.82 g L^{-1}] as previously described from (Neilands, 1981; Louden *et al*., 2011) at pH 6.8±0.2. A 10-µL drop of either single (OD = 0.3) or combined strains (OD = 0.15) of overnight bacterial culture in LB medium was pipetted onto CAS agar and incubated for 72h at 28°C, 220 rpm. After the incubation, the formation of an orange halo zone was observed in the strains treated CAS agar medium. This assay was performed with six technical replicates and repeated twice.

The method described by (Devi *et al*., 2016) was used to estimate the siderophore concentration to confirm the synthesis of siderophores by the strains. For this purpose,

the bacterial strains were cultured overnight at 28 °C and 220 rpm in LB broth and then centrifuged at 4200 x g for 10 min to extract 1 ml supernatant which was combined with 1 mL CAS reagent [10 mM HDTMA, 1 mM $FeCl_3$, and 2 mM CAS solution]. Subsequently, the absorbance was measured at 630 nm compared to the control (1 mL uninoculated LB broth + 1 mL CAS reagent). The amount of siderophore in all samples was measured in % siderophore units (SUs) as [(Ar -As) x Ar^{-1}) x 100], where Ar = untreated control absorbance at 630 nm and As = strains absorbance at 630 nm (bacterial supernatant + CAS reagent).

3.4.3.2 Auxin (IAA) production assay

The potential of the bacterial strains to form indole compounds was investigated following the method previously used (Martínez *et al*., 2018). For this purpose, the strains were cultured in LB broth with 100 µg mL^{-1} or without L-tryptophan and incubated for 48 h at 28 °C, 220. After incubation, the strain suspension was centrifuged at 4200 x g for 10 min to collect 1 mL of supernatant, which was then added to 96-well white-bottom plates with 200 µL of Salkowski reagent [15 mL 95-97 % H_2SO_4, 0.75 mL 0.5 M $FeCl_3$.6H0, and 25 mL dH_20]. Absorbance at 530 was measured spectrophotometrically to determine the amount of IAA produced by the strain by comparing it to the IAA standard curve generated using a known concentration of IAA (Sigma-Aldrich). Sterile LB medium (containing L-tryptophan or without L-tryptophan) was used as a control. The concentration of indole-related compound at 530 nm of the control was subtracted from the concentration of indole-related compound at 530 nm of the bacterial strains to obtain the background subtraction concentration.

3.4.3.3 Ammonia production

To detect ammonia production, all selected strains were grown in 4% peptone water broth and incubated for two days. After the incubation period, 0.5 mL of Nessler's reagent was added to the strain suspension and the development of brown to yellow color indicates that the bacteria produce ammonia (Bhattacharyya *et al*., 2020). Absorbance was determined at 450 nm using a spectrophotometer compared to the control (4% peptone broth).

3.4.3.4 Phosphorus solubilization

The phosphorus solubilizing potential of the tested strains was evaluated according to the procedure previously described by Mehta & Nautiyal (2001). Briefly, selected strains were cultured on National Botanical Research Institute Phosphate (NBRIP) agar medium [glucose, 10 g L^{-1}; $Ca_3(PO_4)_2$, 0.5 g L^{-1}; MgCl2, 0.5 g L^{-1}; $(NH_4)_2SO_4$, 0.1 g L^{-1}; $MgSO_4$. $7H_2O$, 0.25 g L^{-1}; KCl, 0.2 g L^{-1}; agar, 15 g L^{-1}]. Subsequently, the NBRIP media inoculated with the strains were incubated at 28°C for three days and the formation of a distinct halo zone around the colony was observed and the phosphorus solubilization index of each strain was calculated.

3.4.4 Leaf disk assays

To evaluate the biocontrol ability of the strains in *planta* against *P. infestans* and *P. colocasiae*, a leaf disk assay was performed with selected strains that showed promising antagonistic effects in the *in vitro* dual culture test. Potato tubers of the susceptible cultivar 'Desiree' and taro tubers were planted in 2-L pots containing sterilized compost and grown in Bitron at 20°C and 72% relative humidity for one month. After one month of growth, the 3rd and 4th leaves of both potato and taro cultivars were harvested and cleaned with sterilized dH2O. Bacterial strains were grown overnight in LB broth at 28 °C and 220 rpm, and the density was adjusted to (0.3, for single strains) and (0.15, for combination strains). Leaves were pretreated with the adjusted bacterial strains (20 µL) one day before pathogen inoculation. The next day, the spore density of *P. infestans* and *P. colocasiae* were calculated using a hemocytometer and the suspension was standardized to obtain a final sporangia concentration of $2x10^4$ spores/mL for both pathogens, which was inoculated onto the underside of potato and taro leaves. Treated leaves were then incubated for five days (*P. colocasiae*) and ten days (*P. infestans*) at 22 °C and 72 % relative humidity (appropriate growth temperature and relative humidity for both pathogens).

The necrotic part of the taro leaf was incised with a cork borer (1.8 cm diameter) and stained with trypan blue for one hour after exposure to *P. colocasiae* for five days. Trypan blue was then removed, and a leaf disc was kept overnight in absolute ethanol

(99.7%) and treated with 30% glycerol before images were taken using ImageJ software. Potato leaves were subjected to a similar process after being exposed to *P. infestans* for ten days. Four treatments were included: (1) leaves + water; (2) leaves + pathogen; (3) leaves + single strains + pathogen; and (4) leaves + combination strains + pathogen. The leaf disk assay was performed three times with six technical replicates.

3.4.5 Biotron experiments

Biotron experiments were conducted to evaluate the potential biocontrol and plant growth-promoting ability of selected strains. For this purpose, the strains that showed the highest antagonistic activity in the leaf disk assay were selected, cultured overnight, and centrifuged at 4200 x g for 20 min to collect the cells. The density of the collected bacterial cells was adjusted with 1X PBS to (OD = 0.3, for single strains) and (OD = 0.15, for combined strains) and used to treat the same potato and taro tubers used in the leaf disk assays. Bacteria-treated taro and potato tubers were planted in 1.5-L pots containing sterilized compost and grown in the Biotron at 20°C and 72% relative humidity for one month. The same bacterial strains used in the tuber treatments were carefully poured (30 mL/pot) into the root level of the potato and taro plants after one and two weeks of emergence. In the third week of plant growth, the same strains (50 mL/plant) were sprayed on the leaves of the potato and taro plants. Finally, the same strains (50 mL/plant) were sprayed on both plant leaves one day before inoculation with the pathogen. Then, the same amount of the final sporangia suspension of each pathogen ($2x10^4$ spores/mL) used in the leaf disk test was used to infect the leaves, and the plants were maintained at 20 °C and 85% relative humidity (appropriate temperature and relative humidity for both pathogen infections). The daily development of mycelial growth on the leaves of potato and taro plants was monitored to the untreated control.

Also, the effect of the strains on both plants was evaluated by measuring plant height, chlorophyll content, fresh weight, and dry weight. Biotron experiments were conducted with four treatments: a) plant + water only, b) plant + pathogen, c) plant + single or combined strains, d) plant + single or combined strains + pathogens. The experiments were conducted with ten biological replicates for each treatment in a completely randomized design.

3.5 Statistical analysis

All data were subjected to one-way analysis of variance (one-way ANOVA) using the software program R x 64 3.2.3 and mean differences were compared using Duncan's multiple ranges at $P \leq 0.05$.

4 RESULTS

4.1 *In vitro* Antagonistic Assays

Seven single and sixteen of their dual combinations were tested for their inhibitory activity against two different potato pathogens: the oomycete *P. infestans* and the fungus *R. solani*, and one taro pathogen: the oomycete *P. colocasiae* in the dual culture assay. The result showed that the presence of an individual or combined strains were exhibited antagonistic activity against the tested pathogens. It was observed that the mycelial and sclerotia growth of pathogens was reduced in the presence of bacterial strains as compared to the untreated control (Figure 5 and Figure 6A, B, and C). However, the extent of antagonistic activity of the individual or combination of strains depends on the targeted pathogen and the strains themselves (Figure 6A, B, and C).

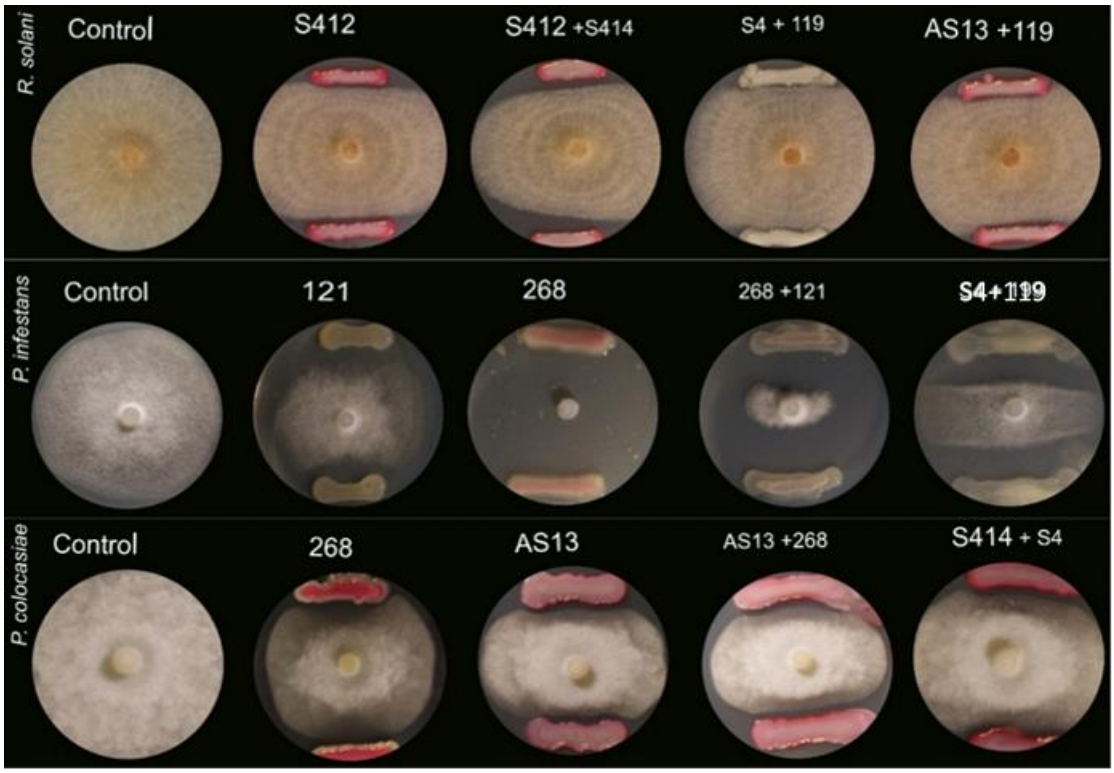

Figure 5: Mycelial growth inhibition of pathogens (*P. infestans*, *R. solani*, and *P. colocasiae*) in dual culture assay. The diameter of the zone of pathogen mycelium growth inhibition was calculated by comparing the diameter of pathogen growth in the absence of strains.

The highest mycelial inhibition (40-46%) of *R. solani* was observed in the presence of single or combined strains, S4 + 121, S412, S414 + S412, and S4 +119 (Figure 6A). In

contrast, the presence of strain 268 and its combination with strain121 inhibited the growth of *P. infestans* the most (74.4-97.6%), followed by S4 +119, which reduced mycelial growth by 62.8% compared to the control (Figure 6B). The highest growth reduction (40-50%) of *P. colocasiae* was also observed when inoculated with single or combined strains S4, AS13, S4 + 119, S414 + S4, and AS13 + 268. Of the strains tested, all the single strains (S412, S414, S4, AS13, 268, 119 and 121) and some of the combined strains (S414 + S412, S414 + S4, S412 + 121, S4 + 119, S4 + 121, AS13 + 119, AS13 + 268, 268 + 121 and 119 + 121) showed the highest inhibitory activity against *R. solani*, *P. infestans* or *P. colocasiae in vitro* and were therefore selected for further experiments.

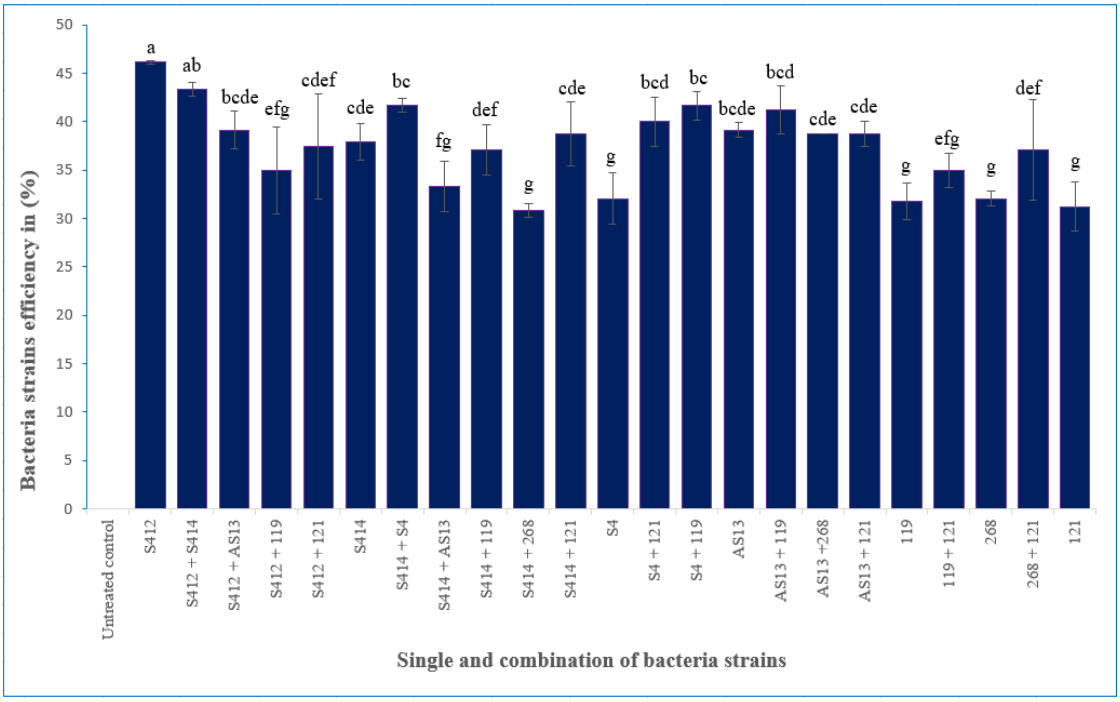

Figure 6A: Inhibition of mycelial growth of *R. solani* when challenged with single or combined strains in the dual culture assay. Data are the mean ± standard deviation (SD) of six technical replicates. Means with the same letter show non-significant differences ($P \leq 0.05$) between single and combined bacterial strains based on Duncan's multiple range tests.

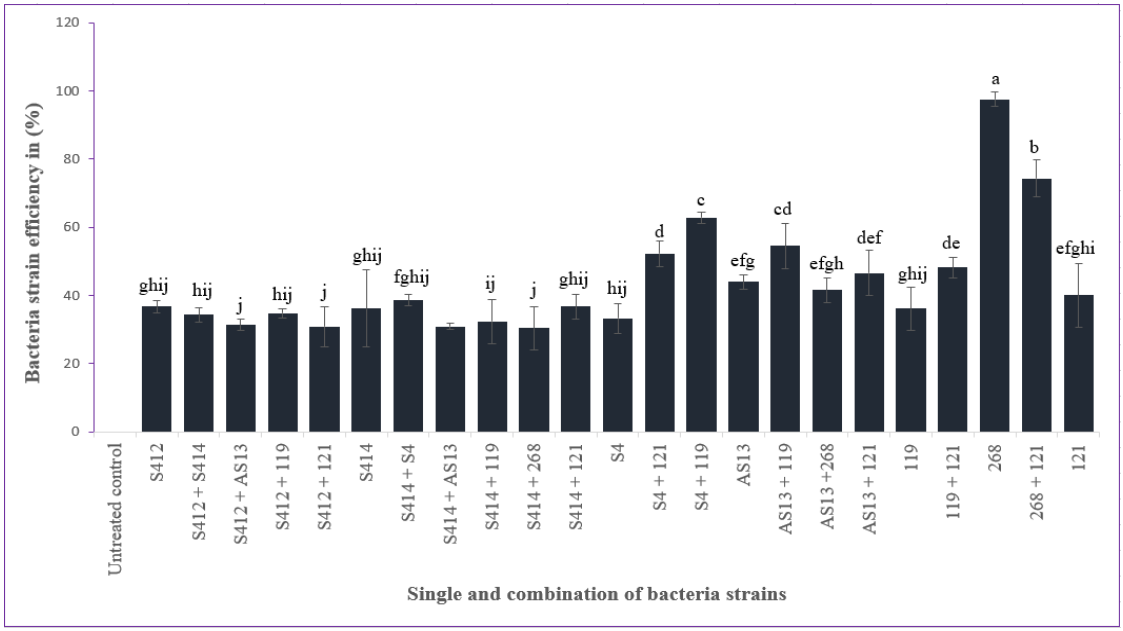

Figure 7B**:** Inhibition of mycelial growth of *P. infestans* when challenged with single or combined strains in the dual culture assay. Data are the mean ± standard deviation (SD) of six technical replicates. Means with the same letters show non-significant differences between tested strains according to Duncan's multiple range test at $P \leq 0.05$.

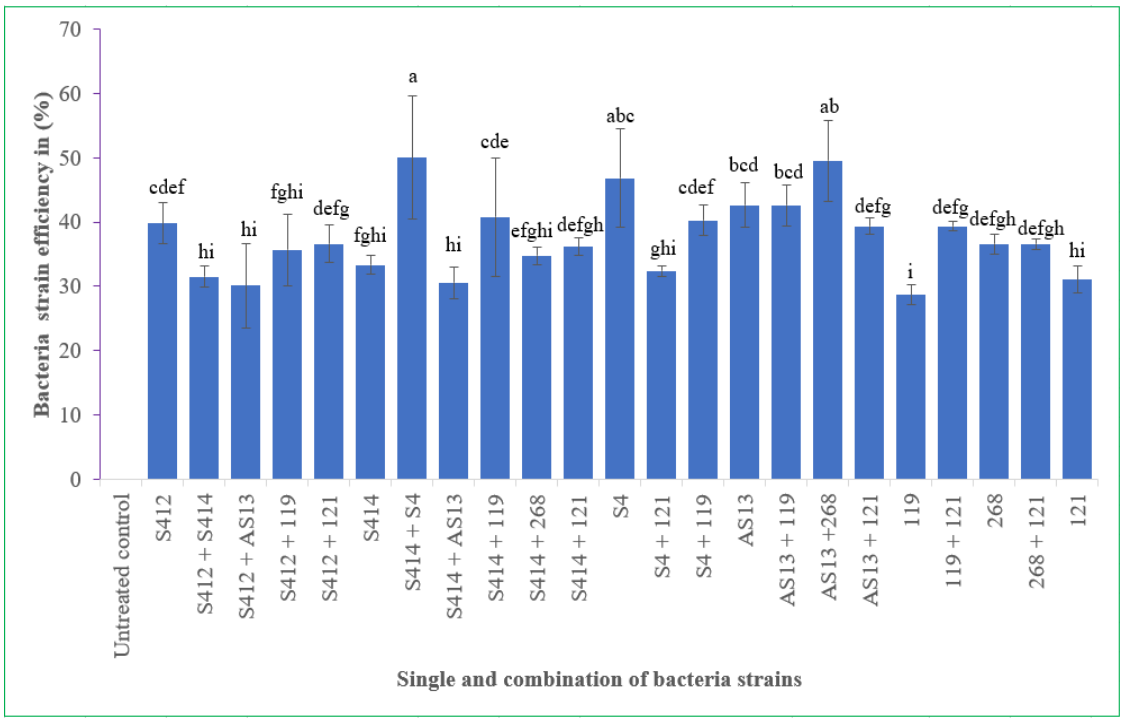

Figure 8C: Inhibition of mycelial growth of *P. colocasiae* when challenged with single or combined strains in the dual culture assay. Data are the mean ± standard deviation (SD) of six technical replicates. Means with the same letters show a non-significant difference from each other according to Duncan's multiple range test at $P \leq 0.05$.

4.2 Compatibility Assay

To enhance the antagonistic effect of the tested strains, we performed the compatibility assay on TSA plates. Our result showed that out of 21 possible dual combinations of strains, sixteen of them are compatible while five of them inhibit each other in a center where the strains intersect (Figure 7). Bacterial consortia containing compatible strains produced high lytic enzymes and plant growth-promoting properties, thereby inhibiting the mycelial growth of pathogens as compared to the single strain, although some strains do not allow generalization of these observations (Figure 6A, B, and C).

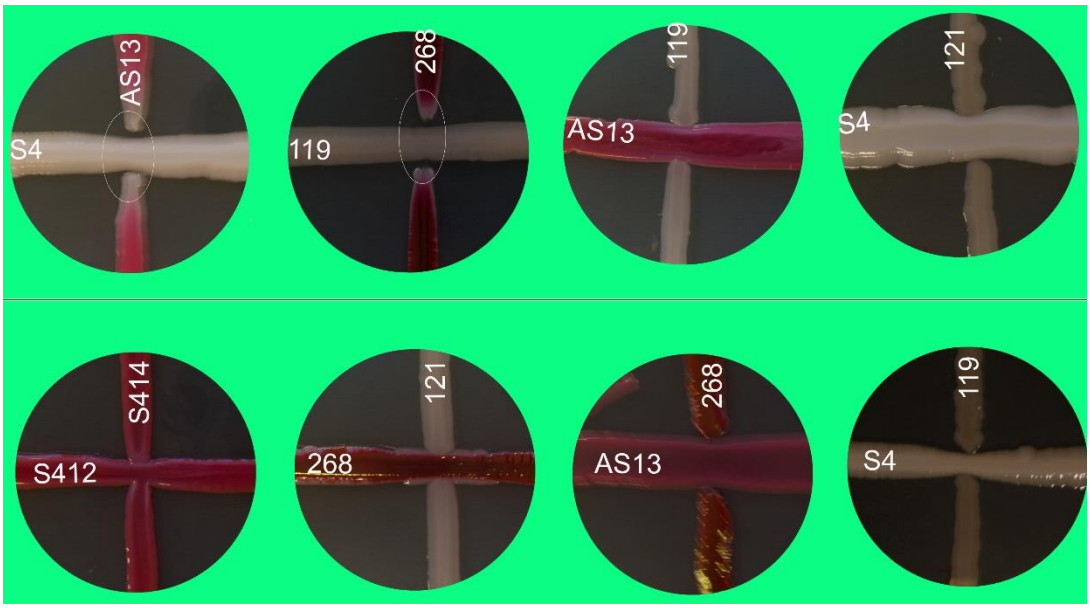

Figure 9: Compatibility assay between co-inoculated strains. Each of the strains was streaked perpendicularly and the photo showing their synergistic effect and zone of inhibition was taken after four days of incubation.

4.3 Production of Biofilm and Lytic Enzymes

To understand the mechanisms behind the inhibitory effect of strains against the mycelial growth of pathogens, the biochemical and enzymatic activity of selected strains on specific media was functionally investigated. Biofilm formation by the strains was studied on 96-well microtiter plates. Among the strains tested, *S. rubidae*, 268, and its combination with *S. plymuthica* showed significant biofilm formation on a microtiter plate and optical density measurements were 0.64 and 0.47, respectively, at 595 nm

(Figure 8). Other strains tested also showed varying degrees of biofilm formation ability as shown in (Figure 8).

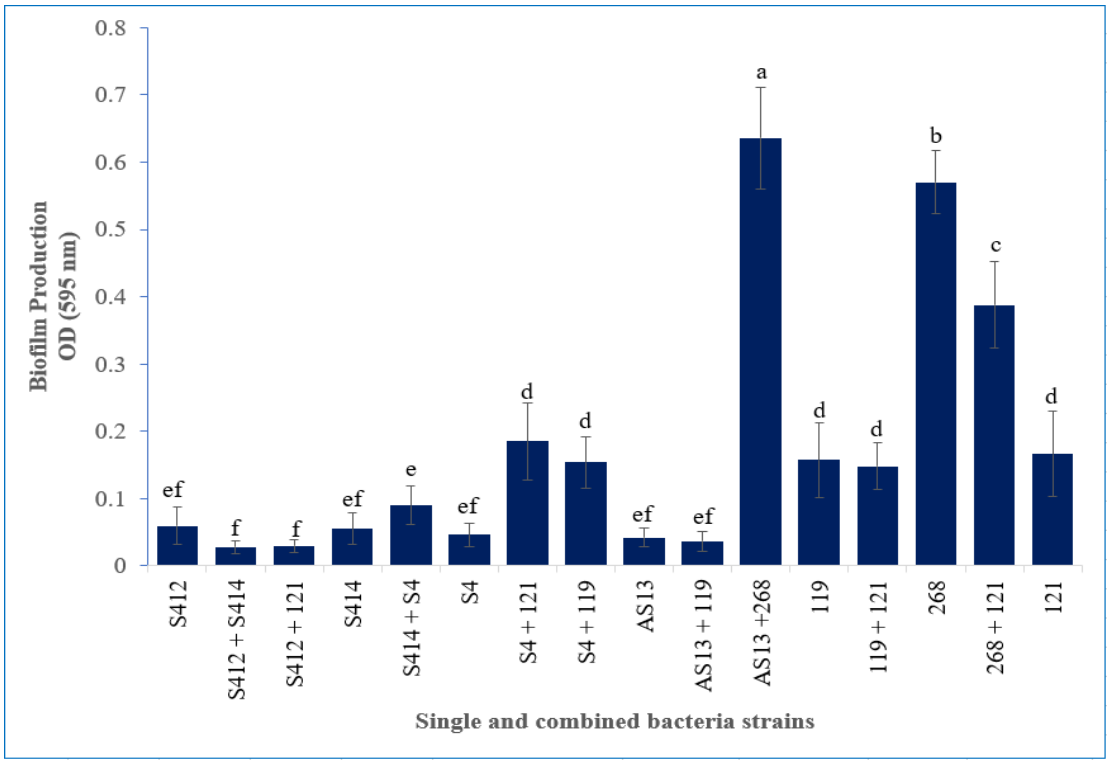

Figure 10: Biofilm formation of selected strains *in vitro*. Data are the mean ± standard deviation (SD) of octuplicates per strain. Means with the same letters show a non-significant difference between strains according to Duncan's multiple range test at $P \leq 0.05$.

Similarly, the production of various lytic enzymes (protease, cellulase, amylase, chitinase, lipase, and hydrogen cyanide) secreted by the strains was evaluated. The result showed that all the strains tested were positive for protease and lipase and most of them were also positive for cellulase. In contrast, almost half of the strains tested (119, 268, 121 and their dual combinations) were negative for amylolytic and chitinase enzymes (Table 1). We also tested the production of hydrogen cyanide secreted by the strains, but the results were negative for all strains tested (Table 1).

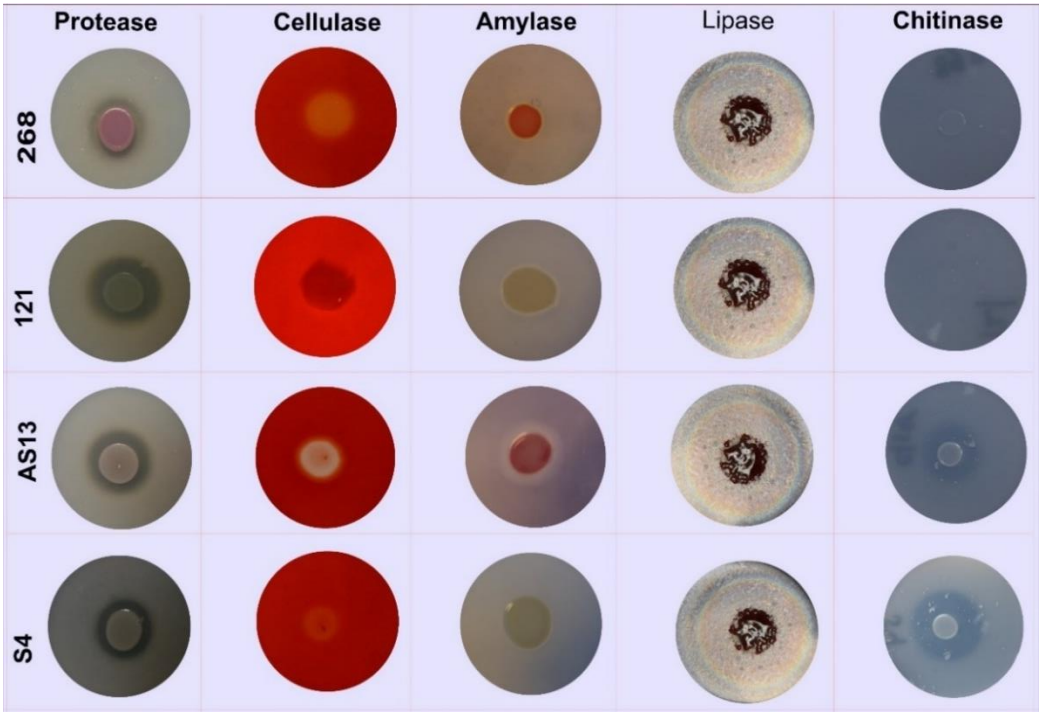

Figure 11: *In vitro* production of different lytic enzymes by bacterial strains.

Table 1: Screening of bacterial strains-mediated *in vitro* production of lytic enzymes.

SINO	Strain	Protease (cm dia.)	Cellulase (cm dia.)	Amylase	Lipase	Chitinase	Hydrogen cyanide
1.	S412	0.61 ± 0.08^{bcd}	+	+	+	+	-
2.	S414	0.63 ± 0.08^{bcd}	+	+	+	+	-
3.	S4	0.46 ± 0.08^{cd}	+	-	+	+	-
4.	119	0.65 ± 0.11^{bcd}	-	-	+	-	-
5.	121	0.77 ± 0.05^{ab}	-	-	+	-	-
6.	268	0.38 ± 0.09^{d}	+	-	+	-	-
7.	AS13	0.49 ± 0.3^{cd}	+	+	+	+	-
8.	S412+ S414	0.48 ± 0.18^{cd}	+	+	+	+	-
9.	S412 + 121	0.48 ± 0.17^{cd}	+	+	+	+	-
10.	S414 + S4	0.52 ± 0.11^{bcd}	+	+	+	+	-
11.	S4+121	0.48 ± 0.17^{cd}	+	-	+	+	-
12.	S4 + 119	0.54 ± 0.14^{bcd}	+	-	+	+	-
13.	AS13 + 119	0.91 ± 0.35^{ab}	+	-	+	+	-
14.	AS13 +268	0.59 ± 0.15^{bcd}	+	+	+	+	-
15.	119 + 121	0.72 ± 0.09^{abc}	-	-	+	-	-
16.	268 + 121	0.63 ± 0.19^{bcd}	+	-	+	-	-

Data are the means ± standard deviation. Means with the same letters shown a non-significant difference between the treatments according to Duncan's multiple ranges at $P\leq0.05$.

4.4 Production of Plant Growth-Promoting Traits

Plant growth-promoting properties such as indole acetic acid, siderophores, ammonia, and phosphorus solubilization ability of all tested strains were evaluated *in vitro*.

4.4.1 Indole-acetic acid (IAA) production

Strains-mediated production of IAA was detected by both qualitative and quantitative assays. The qualitative assay confirmed the production of IAA by the color change of the supernatant from yellow to pink after the addition of Salkowski reagent. IAA was also quantitated in all tested strains in LB broth supplemented with L-tryptophan and the concentration of IAA was measured at 530 nm using a spectrophotometer. The result showed that all tested strains were able to produce different amounts of IAA in the presence of L-tryptophan (Table 2).

4.4.2 Siderophore production

Siderophore production of selected strains was evaluated on chromazurol S (CAS) agar medium. The qualitative test confirmed the production of siderophores by bacterial strains by the formation of orange halo zone in Chromazurol S (CAS) agar medium. The formation of the halo zone in chromazurol S (CAS) agar is due to the production of siderophores that remove iron from the dye complex, which changes the color of the medium from blue to orange. The siderophores synthesized by the strains were also confirmed by a quantitative CAS assay, measuring absorbance at 630 nm. Our data showed that all strains tested synthesized siderophores in the range of 79.55-89.27% siderophore units (Table 2).

4.4.3 Ammonia production

Bacterially mediated ammonia formation is another important property associated with the promotion of plant growth. Our qualitative test indicated that all strains tested produced ammonia, as evidenced by the change in color of the inoculated peptone broth to yellow after the addition of Nessel's reagent. Furthermore, the quantification of results showed that ammonia production by the bacterial strains ranged from 0.1 to 1 (Table 2).

4.4.4 Phosphate solubilization

The ability of selected strains to solubilize $Ca_3(PO_4)_2$ was investigated on the NBRIP medium. According to a previous report, the presence of a distinct halo zone surrounding the colony of the strain was considered a positive (Mehta and Nautiyal, 2001). All strains examined in this study were able to solubilize phosphate in an NBRIP agar medium. The formation of these halo zones around the colony of bacterial strains suggests the secretion of organic acids or enzymes into the surrounding medium that solubilizes $Ca_3(PO_4)_2$. Therefore, our results suggest potential for use as plant growth promoters, although they do not necessarily imply phosphate solubilization in nature. The solubilization index of each strain tested was calculated as follows: Phosphorus solubilization index (PSI) = (diameter of halo zone + diameter of colony) / diameter of colony) (Table 2).

Table 2: Screening of plant growth-promoting properties of bacterial strains *in vitro*.

SINo	Strains	Plant growth-promoting traits			
		IAA production	Siderophore units	Ammonia production	PSI
1.	S412	0.01 ± 0.002^{i}	88.80 ± 0.70^{a}	-	3.46 ± 0.2^{def}
2.	S414	0.01 ± 0.00^{1j}	86.15 ± 0.27^{c}	-	3.21 ± 0.19^{efg}
3.	S4	0.03 ± 0.001^{c}	89.26 ± 0.29^{a}	+	2.79 ± 0.48^{g}
4.	119	0.04 ± 0.00^{a}	80.74 ± 0.78^{ef}	-	3.28 ± 0.44^{efg}
5.	121	0.01 ± 0.001^{h}	82.89 ± 0.22^{d}	-	4.02 ± 0.42^{abcd}
6.	268	0.01 ± 0.001^{h}	83.75 ± 0.21^{d}	+	3.81 ± 0.29^{bcde}
7.	AS13	0.03 ± 0.001^{c}	89.27 ± 0.16^{a}	-	3.44 ± 0.25^{def}
8.	S412 + S414	0.02 ± 0.00^{e}	87.87 ± 0.17^{ab}	-	2.90 ± 1.04^{fg}
9.	S412 + 121	0.02 ± 0.00^{g}	86.65 ± 0.29^{bc}	-	3.67 ± 1.07^{cde}
10.	S414 + S4	0.03 ± 0.00^{b}	86.15 ± 0.19^{c}	+	3.22 ± 0.08^{efg}
11.	S4+121	0.02 ± 0.001^{g}	83.14 ± 0.76^{d}	+	4.58 ± 0.66^{a}
12.	S4 + 119	0.01 ± 0.00^{ij}	83.85 ± 0.51^{d}	+	4.34 ± 0.22^{ab}
13.	AS13 + 119	0.02 ± 0.002^{f}	88.53 ± 0.39^{a}	-	4.54 ± 0.69^{a}
14.	AS13 +268	0.02 ± 0.00^{e}	81.07 ± 0.35^{e}	+	4.25 ± 0.25^{abc}
15.	119 + 121	0.03 ± 0.00^{c}	83.49 ± 0.54^{d}	-	3.97 ± 0.14^{abcd}
16.	268 + 121	0.03 ± 0.001^{d}	79.55 ± 5.69^{f}	+	3.75 ± 0.47^{bcde}

4.5 Leaf Disk Assays

Leaf disk assays were conducted to evaluate the biocontrol potential of selected strains *in planta*. Our data showed that necrotic lesions on potato and taro leaves were significantly reduced when pretreated with either single or combined strains compared to the untreated control where only *P. colocasiae* or *P. infestans* was applied (Figure 9A, and B). However, there was a significant difference in the ability of the pre-applied strains to prevent the development of necrotic lesions by *P. infestans* and *P. colocasiae* on potato and taro leaves (Figure 10A, and B). Compared to the other strains, 268, 121, S4, 119 and their dual combinations (268 + 121 and S4 + 119) reduced the development of *P. infestans* symptoms on potato leaves (Figure 9A). Whereas AS13, 268, S4, S414, and their dual combinations (AS13 + 268 and S414 + S4) showed stronger antagonistic activity against necrotic lesions induced by *P. colocasiae* on taro leaves than the other strains examined (Figure 9B). No lesion was observed in the control water treatment for both pathogens tested (Figure 9A and B).

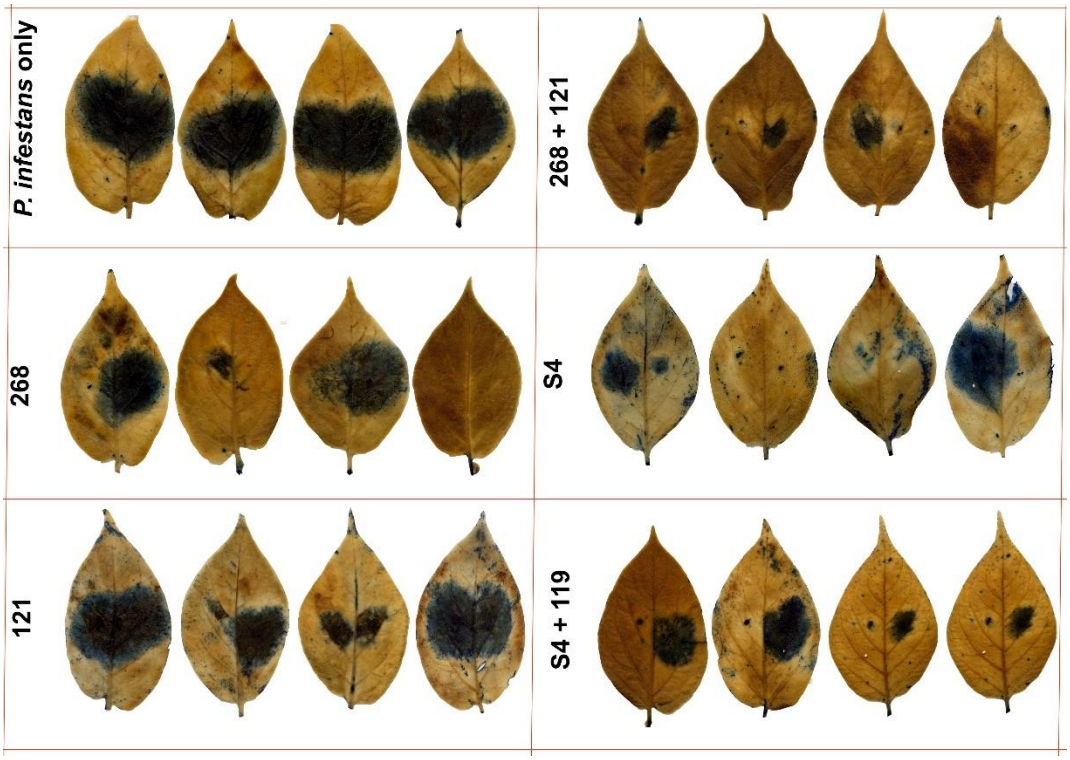

Figure 12A: Trypan blue staining of detached potato leaves showing antagonistic activity of selected strains against *P. infestans*

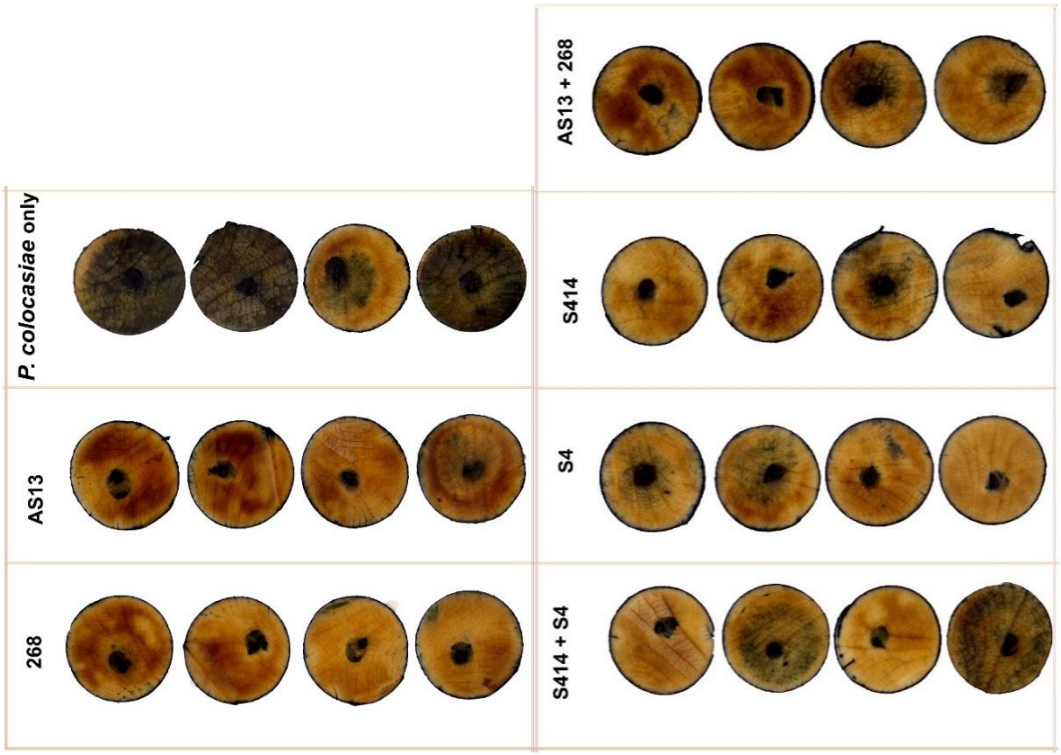

Figure 13B: Trypan blue staining of detached taro leaves showing inhibitory activity of selected strains against *P. colocasiae*.

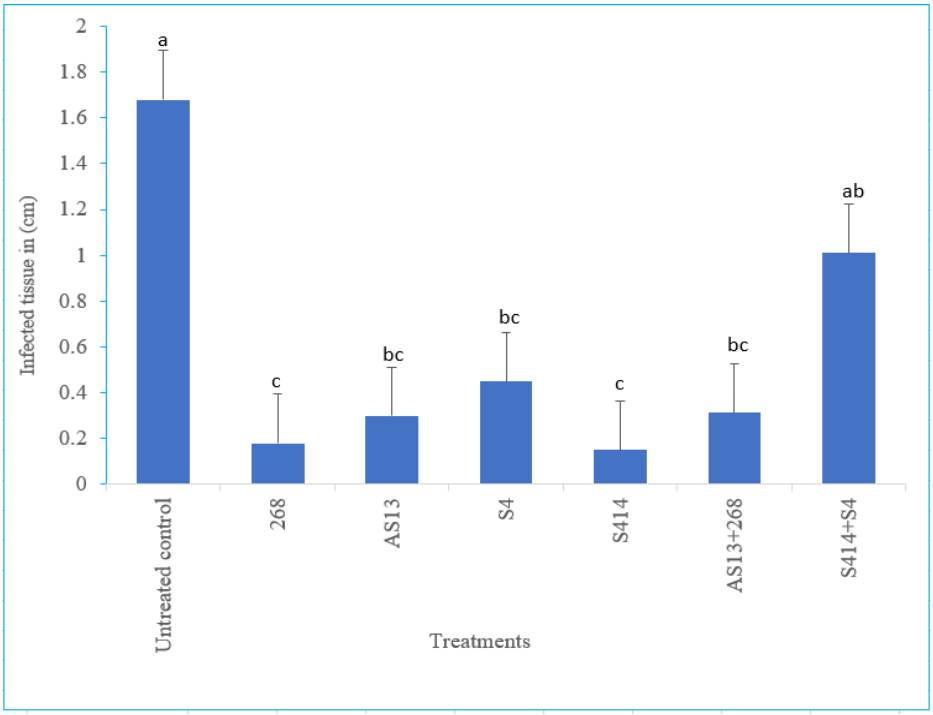

Figure 14: Antagonistic test of bacterial strains on detached taro leaves against *P. colocasiae*. Data are the means ± standard deviation. Means with the same letters shown a non-significant difference between the treatments according to Duncan's multiple ranges at $P \leq 0.05$.

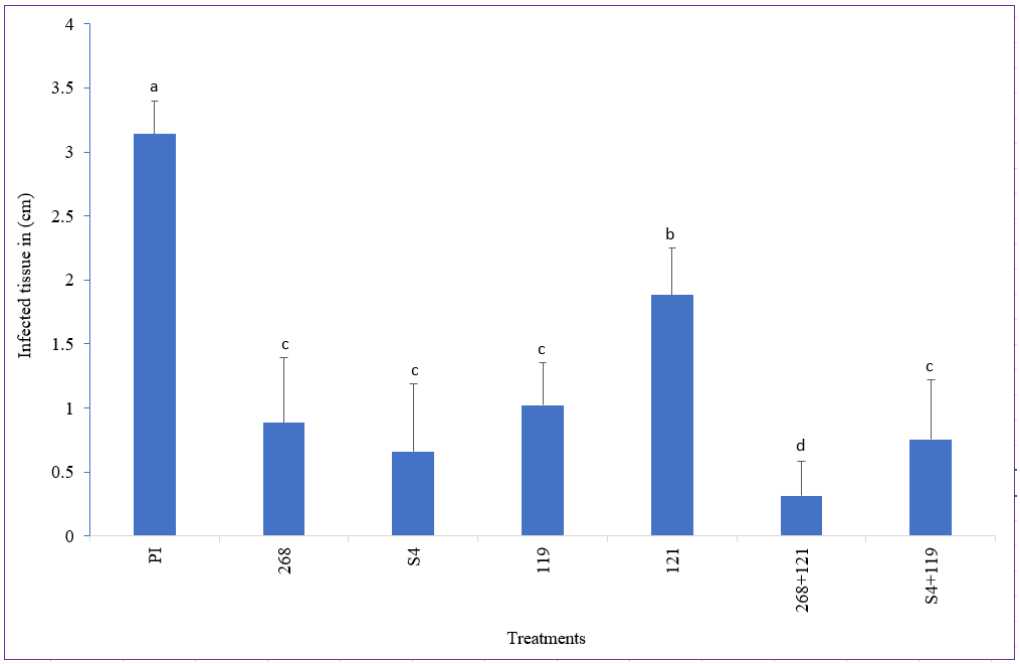

Figure 15: Antagonistic test of bacterial strains on detached potato leaves against *P. infestans*. Data are the means ± standard deviation. Means with the same letters shown a non-significant difference between the treatments according to Duncan's multiple ranges at $P \leq 0.05$.

4.6 Biocontrol Ability of Strains in Biotron Conditions

The experiments done under sterile conditions to evaluate the biocontrol potential of bacterial strains under Biotron conditions. Bacteria treated potato and taro plants were infected with *P. infestans* and covered with plastic bags to maintain humid condition and kept in biotron conditions under normal light and temperature conditions (light:160µmol m^{-2} s^{-1}, temperature 20°C, and RH: 85%). A set of plants treated with water were used as controls. The plants were arranged in a completely randomized block design with ten biological replicates (six leaves per plant) for each disease assessment. After five days of inoculation, the disease scoring was conducted by measuring the area of infected of the leaves of both potato and taro plants using the following scale: 0 = no disease symptoms, 1 = 0-2cm; 2 = 2-4cm; 3= 4 cm-6cm; 4 = completely dead leaves. Disease index (DI) was calculated as follows: DI = (sum of individual rating / number of plants assessed * maximum scale) * 100.

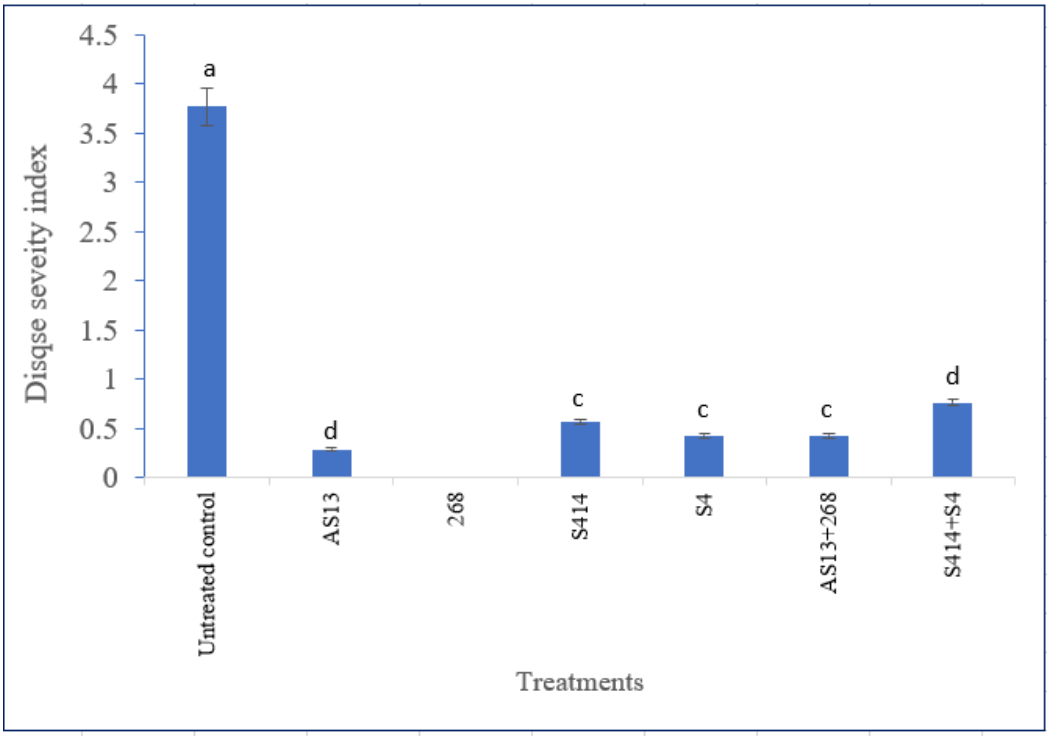

Figure 16: In vivo bioassay to evaluate the biocontrol potential of selected bacterial strains against *P. colocasiae* on taro plants. Data are the means ± standard deviation. Means with the same letters shown a non-significant difference between the treatments according to Duncan's multiple ranges at *P≤0.05*.

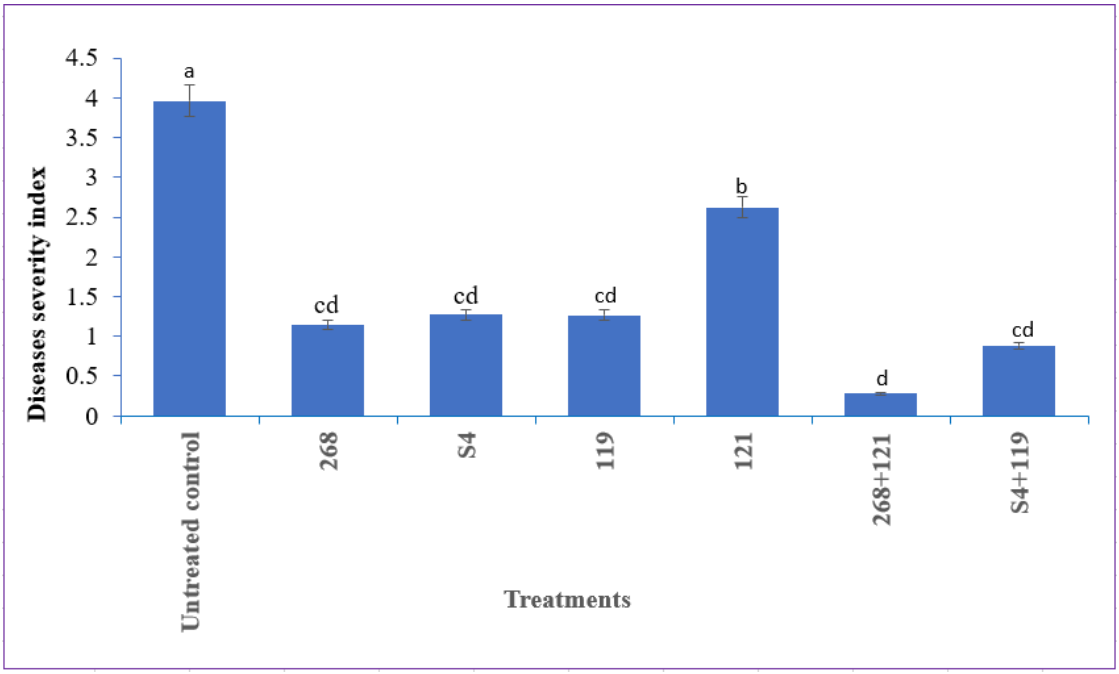

Figure 17: In vivo bioassay to evaluate the biocontrol potential of selected bacterial strains against *P.infestans* on taro plants. Data are the means ± standard deviation. Means with the same letters shown a non-significant difference between the treatments according to Duncan's multiple ranges at P≤0.05

Evaluation of plant growth-promoting activities of selected strains

In Biotron, the assays of potato and taro plants were conducted to evaluate the effect of the strains to plant growth. Following the treatments, both potato and taro plants were harvested to evaluate the effect of bacterial strains on plant growth (Table 3). Plant height, fresh weight, dry weight, and root weight were increased significantly for potato plants treated with bacterial strains (Table 3). Similarly, plant height, fresh weight, and root weight of taro plants were increased significantly as compared to untreated control (Table 3). However, no significant differences in dry weight were observed in taro plants co-cultured with the strains in comparison to untreated control. To evaluate the effect of the strains on potato and taro photosynthetic tissue, the chlorophyll content was determined using Apogee chlorophyll concentration meter with units of (µmol m^{-2}). Our study results indicated that potato and taro plants treated with bacterial strains showed higher levels of chlorophyll content with respect to untreated control (Table 3).

Table 3: Effect of Bacteria strains on growth of potato and taro plants

	Potato growth parameter					
SI No	Strains	Height (cm)	Fresh weight (g)	Dry weight (g)	Root weight (g)	Chlorophyll content
1.	Untreated Control	45.5 ± 6.79^{d}	112 ± 22.86^{c}	9.25 ± 1.98^{b}	7.25 ± 2.71^{c}	41.12 ± 2.25^{c}
2.	268	53.2 ± 4.52^{bc}	116.8 ± 21.26^{abc}	9.38 ± 1.69^{ab}	7.13 ± 2.93^{c}	44.92 ± 3.27^{abc}
3.	121	57 ± 9.32^{ab}	123.3 ± 31.64^{abc}	$11,25\pm1.83^{a}$	10.38 ± 3.20^{abc}	44.19 ± 1.91^{bc}
4.	268+121	49 ± 5.98^{cd}	119.6 ± 23.23^{abc}	9.89 ± 1.13^{ab}	12.5 ± 5.88^{a}	44.63 ± 4.57^{bc}
5.	S4	52.8 ± 6.48^{bc}	119 ± 27.38^{abc}	9.38 ± 1.77^{ab}	10 ± 4.59^{abc}	42.79 ± 3.66^{bc}
6.	119	50.2 ± 6.84^{cd}	113.7 ± 10.70^{bc}	9.5 ± 1.60^{ab}	8.0 ± 4.0^{bc}	46.56 ± 4.24^{ab}
7.	S4 + 119	57 ± 6.22^{ab}	136.2 ± 16.78^{a}	10.63 ± 1.06^{ab}	11.38 ± 3.74^{ab}	48.91 ± 4.73^{a}
8.	S412	62.3 ± 4.76^{a}	134.9 ± 32.47^{ab}	11.25 ± 3.28^{a}	10.13 ± 3.18^{abc}	46.16 ± 4.97^{ab}

	Taro growth parameter					
SI No	Strains	Height (cm)	Fresh weight	Dry weight (g)	Root weight (g)	Chlorophyll content

1.	Untreated control	41.71±1.87^{b}	53.38±11.87^{c}	6.43±1.27^{a}	8.14±1.80^{c}	41.64±3.67^{d}
2.	268	53.43±7.48^{a}	62.39±13.05^{a}	7.86±2.79^{a}	11.0±3.27^{bc}	49.89±10.58^{bc}
3.	AS13	46.11±6.09^{b}	57.76±21.69^{ab}	8.86±2.91^{a}	16.0±4.55^{a}	60.48±5.50^{a}
4.	268+AS13	42.5±4.03^{b}	62.67±11.34^{a}	7.71±2.14^{a}	12.71±3.73^{ab}	53.49±5.90^{ab}
5.	S414	44.21±8.72^{b}	53.37±7.97^{c}	6.71±3.49^{a}	8.26±1.67^{c}	44.60±9.28^{cd}
6.	S4	43.07±7.20^{b}	50.77±17.42^{c}	8±2.08^{a}	13.43±5.71^{ab}	45.08±2.38^{cd}
7.	S414+ S4	41.79±4.83^{b}	55.68±17.16^{bc}	7.43±1.72^{a}	12.86±2.12^{ab}	56.16±7.65^{ab}

5 DISCUSSION

Nowadays, the use of beneficial bacteria as biocontrol agents seems to be an alternative to synthetic fungicides to control plant diseases including, potato and taro pathogens (De Vrieze *et al*., 2018). To this end, many rhizobacterial strains have been isolated and evaluated as potential biocontrol agents against phytopathogens in the last two decades (Pliego *et al*., 2011). But only a few strains have been successful and are now commercially available for use as biocontrol agents. Screening potential candidates with possible PGPR properties *in vitro* is an important first step, as we did in the current study against *P. infestans*, *R. solani*, and *P. colocasiae*. Our results showed that the mycelial growth of all tested pathogens was reduced by at least 35% in the presence of either single or combined strains in the dual culture assays (Figure 5 and Figure 6A, B, and C). However, the effect of the strains on mycelial growth varied depending on the target pathogen and the strains themselves. Various *Serratia* and *Pseudomonas* strains have also been reported to reduce the growth of pathogens in potato, oilseed rape, and tea (Khaldi, 2015; Purkayastha *et al*., 2018).

The compatibility assay was conducted *in vitro* to evaluate the synergistic effect of the strains on pathogen growth reduction and plant growth-promoting effect. Out of the 21 possible combination strains, sixteen of them showed compatibility (Figure 9). Most of the combined strains resulted in a higher reduction of targeted pathogen growth *in vitro*, although some of the combined strains did not necessarily reflect the same trend *in planta* or even under Biotron conditions.

The mechanisms behind the antagonistic activity could be correlated with antifungal metabolites secreted by the strains. Our results showed that most of the strains were positive for protease, cellulase, lipase, and chitinase enzymes. However, some of the strains tested did not produce amylase and chitinase (Table 1). It has been previously reported that the production of chitinase along with other lytic enzymes is considered crucial for antagonistic activity. In our case, 268 that did not produce chitinase exhibited higher inhibitory activity against *P. infstans* and *P. colocasiae*, suggesting that chitinase may be a part of multicomponent mechanisms of rhizobacteria in the environment. *Serratia* and *Pseudomonas* strains have been reported to be antagonistic to many soil-

borne pathogenic fungi through the secretion of chitinase and other lytic enzymes that are involved in cell wall degradation. In contrast, none of the strains studied produced hydrogen cyanide (HCN) (Table 1), which is believed to be a desirable trait in PGPR strains due to HCN limiting plant growth by intermediating cytochrome oxidation (Bakker & Schippers, 1987; Purkayastha *et al*., 2018).

Our results showed that the strains that exhibited the highest *in vitro* activity were also the most efficient in inhibiting necrotic lesions of *P. infestans* and *P. colocasiae* on potato and taro leaves during the leaf disk assay, although the very few strains in this study do not exhibit generalization of this observation (Figure 10A and B). Of the strains tested, 268 + 121 resulted in a higher inhibition against the development of necrotic lesions on potato leaves in the in-leaf disk assay (Figure 10A). The successful protective effect of 268 + 121 could be explained by their different mechanisms of action. Although 268 was an effective antagonist of *P. infestans in vitro* but did not show a consistent protective effect during the leaf disk assay. On the other hand, AS13, 268, and their combination were significantly reduced the growth of *P. colocasiae in vitro* and resulted in significant inhibition of necrotic lesion in leaf disk assay (Figure 10B).

Application of bacterial strains significantly reduce severity of leaf blight disease under biotron conditions compared to untreated control where only *P.colocasiae* was applied (Figure 16). Interestingly, application of single or combination of the strains delay the development of *P. colocasiae* disease on taro plants. In this study, application of strain 268 effectively control the development of leaf blight of taro under biotron conditions. Indeed, our results on the biocontrol of *P. colocasiae* exhibited consistent protective effect with the observed *in vitro* antagonism. Similarly, application of bacterial strains delays the development of late blight on potato plants as compared to untreated control. Our result revealed that there is significance difference between treatments.

Many rhizobacterial strains are not only capable of suppressing plant diseases caused by soil-borne pathogens, but can also promote plant growth (Raaijmakers *et al*., 2009; Oleńska *et al*., 2020). In this study, bacteria-mediated plant growth-promoting properties were screened *in vitro* and their effect on growth promotion of taro and potato

plants was evaluated under Biotron conditions. Most of the strains tested were able to produce biofilm, IAA, siderophores, ammonia, and solubilize phosphorus, although the level of production varied between strains tested (Table 2).

The formation of biofilms by PGPR strains is considered a common way of life in natural environments and protects a variety of abiotic and biotic stresses (Ansari and Ahmad, 2018). Interestingly, in our case, all strains tested can form biofilm *in vitro* (Figure 8), possibly enhancing the colonization of the strains in the rhizosphere and thereby promoting plant growth by suppressing plant diseases. There is evidence that inoculation with biofilm-forming rhizobacteria strains promotes plant growth better than non-biofilm-forming strains (Müller *et al*., 2009; Ansari and Ahmad, 2018).

IAA is a plant hormone that plays essential role in various stages of plant growth development and is thought to be important in the beneficial effects of PGPR on plant growth. In our case, all tested strains were able to produce IAA between 0.01 and 0.04 µg IAA/ml in LB tryptophane-enriched LB culture medium. Despite all tested strains produce IAA *in vitro*, this property alone cannot indicate the difference in growth promotion by the strains. For instance, the strains, 121 showed the lowest level of IAA (Table 2) but promote higher growth than strains with high IAA content. Of course, the secretion of IAA *in vitro* by strains does not necessarily show the ability to alter hormone levels in the plants (Jasim *et al*., 2013). This clearly indicated that the effect of strains on potato and taro growth cannot be explained solely by the alternation of crop hormone homeostasis. However, we also detected some strains producing this compound in the absence of L-tryptophan. It has been reported that PGPR strains can synthesize indole-acetic acid compounds in the presence and absence of L-tryptophan (Purkayastha *et al*., 2018).

Previously, it was reported that bacterial IAA can promote root growth or root hairs, but evidence suggests that IAA production does not necessarily have positive effects on root growth and that IAA production and root growth are not necessarily correlated (Juanjuan Wang *et al*., 2020). So, the outcome of the interaction between plants and bacteria is highly dependent on the plant and bacteria species. But how the bacteria we tasted for growth promotion interfere with the complex hormone signalling network and

why only certain strains of the *Serratia* species tested here exert this influence requires further analysis. Particularly, *in vitro* measurement of bacterial IAA production and determination of hormonal signalling activity in root cells would be helpful for a detailed understanding of bacterial effects. To investigate the complex interactions between plants and bacteria that lead to direct plant growth promotion, it is crucial to find PGPR that are naturally associated with the model plant Arabidopsis. PGPR have been shown to exert specific effects on their host plants (i.e., the plants from which they were originally isolated) that differ from the general effects of these bacteria on other plants.

Siderophore-producing PGPR, including *Bacillus*, *Serratia*, and *Pseudomonas* strains, increase plant production and competitively inhibit soil pathogens by sequestering essential iron in iron-deficient environments (Beneduzi *et al*., 2012; Patra *et al*., 2018). In the current study, all strains tested are capable of producing siderophores between 79.55-89.27% siderophore units (Table 2). Moreover, PGPRs are important players in the natural phosphorus cycle as they solubilize different types of phosphorus in different soils in a pH-dependent manner (Ben Farhat *et al*., 2009; Adnan *et al*., 2017; Alori *et al*., 2017). In the current work, all strains tested were found to efficiently solubilize tricalcium phosphate in NBRIP medium (Table 2), indicating potential for use as plant growth promoters. However, strain S4 showed weak phosphate solubilizing ability compared to the other strains tested (Table 2). The production of ammonia by PGPR is also one of the most important traits related to the promotion of plant growth. Ammonia-producing PGPR strains have been shown to supply nitrogen to their host plants and promote root and shoot elongation in general (Bhattacharyya *et al*., 2020). Strain 268, S4, and their combination produce ammonia. However, the amount of ammonia produced was different among the tested strains.

In summary, our results showed that screening of seven individual and their sixteen combinations led to the observation that some strains showed a strong and consistent protective effect, either when used alone or in combinations. Interestingly, strains 268, 121, S4, 119 and their dual combinations suppressed the growth of *P. infestans* and promoted the growth of potato plants under bitron conditions. On the other hand, strains AS13, 268, S414, S4 and their double combinations inhibit the growth of *P. colocaasiae*

and promote the growth of taro plants compared to the untreated control. Therefore, these strains could be used as potential biocontrol agents against *P. infestans* and *P. colocasiae*. However, further evaluation of these strains under field conditions is required to assess their biocontrol ability for the development of a successful biocontrol strategy. Also, the use of dual combination of strains should be encouraged to increase their biocontrol efficacy and plant-growth promoting properties.

6 CONCLUSION AND RECOMMENDATION

In this study, the biocontrol ability of seven single bacterial strains and their sixteen dual combinations against filamentous (*P. infestans*, *R. solani,* and *P. colocasiae*) pathogens infecting potato and taro crops were investigated. Indeed, all tested strains inhibited pathogen growth to some extent *in vitro,* but only a few bacterial strains showed consistent activity *in vitro*, leaf disk, and whole plant against the tested pathogens. Most of the tested strains are positive for protease, cellulase, lipase, and chitinase, which are the mechanisms of action behind their antagonistic activity. In addition, most of the strains tested are also positive to produce various plant growth-promoting properties such as indole acetic acid, ammonia, siderophores, and phosphate solubilization. Therefore, the biocontrol strains tested in this study can be used as an alternative to synthetic pesticides for disease control in potato and taro crops. However, further experiments should conduct to understand their biocontrol potential and their plant growth-promoting properties at molecular level.

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