Disease management of powdery mildew using bacteria as biocontrol agents – A literature review on cucumber (*Cucumis sativus* L.) and strawberries (*Fragaria x ananassa*)

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Independent project • 15 credits
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Horticultural Management – Gardening and Horticultural Production 180 credits
Alnarp 2025

Disease management of powdery mildew using bacteria as biocontrol agents – A literature review on cucumber (*Cucumis sativus L.*) and strawberries (*Fragaria x ananassa*)

Bekämpning av mjöldagg via bakterier som biokontrollmedel – En litteraturstudie på gurka (Cucumis sativus) och jordgubbar (Fragaria x ananassa)

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Credits:	15 credits
Level:	G2E
Course title:	Independent project in Horticultural Science
Course code:	EX0844
Programme/education:	Horticultural Management – Gardening and Horticultural Production
Course coordinating dept.:	Department of Biosystems and Technology
Location of publication:	Alnarp
Year of publiction:	2025
Copyright:	All tables are made by the author. The photos used in this literature review are attained from other publications, which are credited in the respective figure text
Keywords:	Biological disease control, cucumber, *Cucumis sativus*, strawberry, *Fragaria x ananassa*, powdery mildew, *Podosphaera xanthii*, *Podosphaera aphanis*

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Abstract

Disease management with biocontrol agents (BCAs) is gaining more attention in recent times as pathogens evolve resistances to chemical treatments. For both cucumber and strawberry productions the fungal disease powdery mildew (PM) is a threat where resistances to several fungicides have been reported. Further PM is more severe in greenhouse environments, which are becoming increasingly common in berry productions. In order to examine the current state of bacterial BCAs on the market, as well as promising bacteria for future PM disease management in cucumber and strawberry, this literature review was conducted. Databases were utilized in order to understand which commercial bacterial BCAs are available and being investigated for their suppression as well as their mode of action against PM.

The results found that bacterial BCAs can act antifungal against PM through several mechanisms, including the production of antifungal compounds, iturin, fengycin, surfactin and prumycin; through secretion of enzymes; inducing the plants; promoting plant growth and through competition with the fungus for nutrients and space. Bacteria from the genera: *Bacillus, Pseudomonas Streptomyces* and *Enterobacter* show great potential as BCAs as they exhibit such traits.

The commercial products currently on the market have been shown to suppress PM. Among these *Bacillus subtilis* strain QST 713 (in commercial products Rhapsody and Serenade) gave varying results on PM inhibition, ranging from sufficient to no significant effect. Actinovate (*Streptomyces lydicus*) showed success in PM suppression on cucumber, whilst *Bacillus subtilis var. amyloliquefaciens* FZB24 (in products such as Taegro) gave poor results against PM on strawberries. Although some of the bacterial BCAs exhibit good suppression it is currently not viable as a sole treatment for PM in larger scale productions. The reason being that they require more frequent applications and do not provide enough effects against PM. Currently the bacterial BCAs can only give sufficient disease control when used in combination with conventional fungicides, reducing the overall chemical usage. However, in order to replace fungicides completely, more research must be conducted focusing on finding improved bacterial strains for better survivability on the phyllosphere environment as well as increased antagonistic interactions with PM.

Keywords: Biological disease control, cucumber, Cucumis sativus, strawberry, Fragaria x ananassa, powdery mildew, Podosphaera xanthii, Podosphaera aphanis

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Abbreviations

Abbreviations:	Description:
APPRIL	United States Environmental Protection Agency's Active Pesticide Product Registration Informational Listing
BCA	Biocontrol agent
ISR	Induced systemic resistance
PM	Powdery mildew
SAR	Systemic acquired resistance

1. Introduction

Globally the fungal disease powdery mildew (PM) can infect a wide variety of crops, leading to sever economic losses annually (Brandshaw et al. 2024). Combating PM is generally mainly done through the use of fungicides as well as choosing resistant cultivars (Berrie & Xu 2021; Rur et al. 2018). Although obstacles have become increasingly present as the fungi species have attained resistance to several commonly used fungicides. Because of the wittnessed adaptation to gain resistance, the effectiveness of said fungicides have declined and further highlights the importance of using a more cautious approach regarding the chemical usage, such as in integrated pest management (IPM).

1.1 Powdery mildew

Powdery mildew (PM) is caused by different parasitic fungi species, all producing symptoms that are expressed similarly on the host plants. Where hyphae are visible as white or gray spots that may look powdery, often present on the leaf surface initially (Mieslerová et al. 2022).

PM is among the most common fungal diseases that can infect a wide range of crops and causes losses in production worldwide in a short amount of time (Pérez-García et al. 2009; Berrie & Xu 2021). The fungi's success can be explained by its ability to undergo rapid evolutionary adaptations (Kusch et al. 2024). This mechanism is further attributed to the fungi's asexual reproduction, resulting in a fast generation time. Because it is quick to adapt, the development and spreading of resistances is of great concern. Contrary to the majority of fungi, the spores of PM can germinate in conditions with minimal moisture (Mieslerová et al. 2022).

1.2 Biological disease control against powdery mildew

The utilization of microorganisms for plant protection against powdery mildew (PM) is a method that is used commercially in present times. A broad range of alternatives are commercially available as several biocontrol agents (BCAs) consisting of different species of fungi or bacteria. Yet more strains are continuously being evaluated and patented for commercial use (APPRIL 2025-04-24). The BCAs aim to be used as an alternative to chemical treatments against diseases such as PM. The importance of limiting the chemical usage against PM is connected to the increase in PM fungi acquiring resistances against them (Hafez et al. 2018).

The fungal BCAs are generally more dependent on high humidity, whilst commonly used bacteria species are more tolerant towards a broader range in environments (Németh et al. 2023; Rur et al. 2015). Such adaptability is beneficial in phyllospheric environments with great fluctuations. Another beneficial trait of bacterial BCAs is that they are able to survive and remain active for a longer period without the presence of the pathogen, as opposed to mycoparasitic fungal BCAs (Rur et al. 2015), making preventative applications more successful. As such this study will focus on exploring the bacterial BCAs further.

1.3 Powdery mildew on cucumber

Cucumbers, *Cucumis sativus* L., are a popular crop grown commercially worldwide both outside in fields and in greenhouses, especially in colder climates. According to Från Sverige (2025) cucumber harvests are 43 000 metric tonnes annually in Sweden. Because of its economic importance and large growing areas, sustainable production and reduction in fungicide costs are of most interest (Pérez-García et al. 2009).

PM is one of the most common diseases on Cucurbitaceae, including cucumbers (symptoms shown in figure 1), severely reducing the yield by around 40% (Wang et al. 2024). Two fungi species are the main causes of PM on cucumbers: *Golovinomyces cichoracearum* (DC.) Heluta (synonymous with *Erysiphe cichoracearum*) and *Podosphaera xanthii* (Castagne) U.Braun & Shishkoff (formerly *Sphaerotheca fuliginea* and synonymous with *P. fuliginea* and *P. fusca*) (Rur et al. 2018). Both are present in greenhouse environments as well as in fields and can colonize simultaneously or independently. The pathogenic fungi *G. cichoracearum* is present under cooler climates while *P. xanthii* have a higher optimum, enabling a broader range of which the cucumber plants can be infected.

The main methods of combating PM in cucumbers are by using chemical treatments, working preventatively and choosing suitable varieties. Several varieties have been developed for PM resistance but are generally not preferred by the growers since these varieties perform worse than susceptible varieties (Rur et al. 2015).

Figure 1: Powdery mildew infected cucumber leaves. Source: Zeng et al. 2023

1.4 Powdery mildew on strawberries

Strawberry, *Fragaria × ananassa* (Weston) Duchesne ex Rozier, is a crop of commercial interest that is grown worldwide in tunnels as well as out in fields (Berrie & Xu 2021; Hernández-Martínez et al. 2023). Market trends to have strawberries available year-round has shifted the growing system towards annual production in tunnels or greenhouses rather than perennial, in order to meet the demand (Berrie & Xu 2021).

The fungus causing PM in strawberries is *Podosphaera aphanis* (Wallr.) U. Braun & S. Takam (synonymous with *Sphaerotheca macularis*), infected leaves are shown in figure 2. (Berrie & Xu 2021) The disease is especially predominant and challenging in protected environments, such as high tunnels and greenhouses, due to the lack of rain which otherwise can damage hyphae (Berrie & Xu 2021, Pertot et al. 2008; Svensson 2005). The fungus is favored by temperatures around 20°C and high relative humidity. (Berrie & Xu 2021). The fungus is predominantly a problem on cultivars for late harvest or during later parts of the season in remontant cultivars, also known as everbearing or day neutral. There are resistant varieties, however in some parts of the world, such as in the UK, the market tends to prefer the commercial varieties that are susceptible to PM. While in other countries the varieties with good resistance are predominant (Hushållningssällskapet 2021).

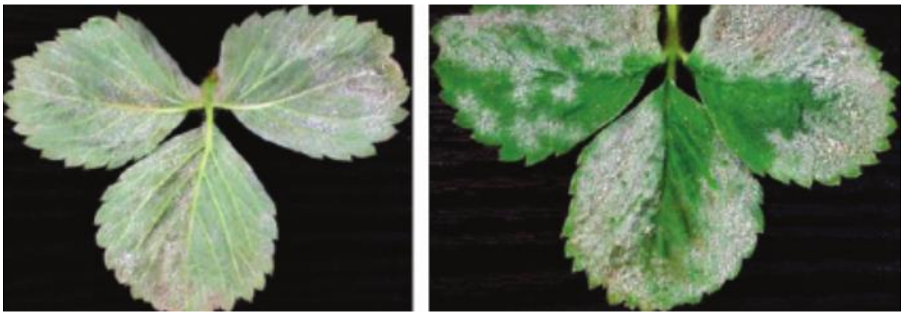

Figure 2: Powdery mildew on the leaves of strawberries.The underside (abaxial) leaf is shown to the left. The upper side (adaxial) is seen to the right. Source: Lifshitz et al. 2007

Both vegetative parts of the plant as well as generative can be infected by PM (Pertot et al. 2008). This severely affects fruit quality by causing deformation, hindering proper ripening and flavour development, causing fruit splitting, as well as negatively impacting storability post-harvest (Pertot et al. 2008). The mycelia on fruits are visible in the picture below (figure 3), which compares different genotypes of strawberries in their ability to resist PM.

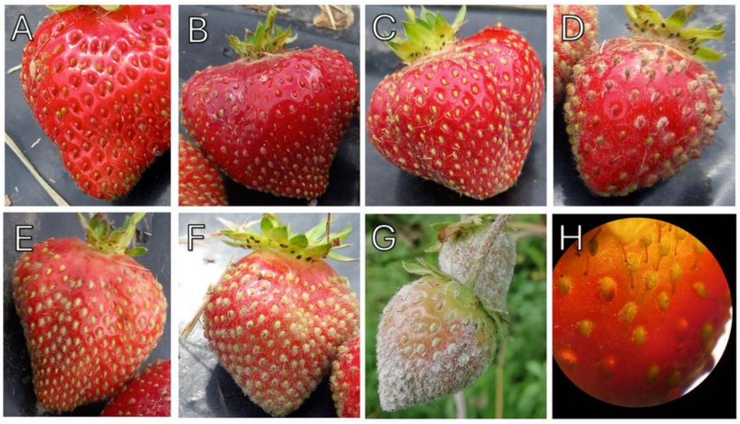

Figure 3: Different strawberry genotypes that exhibit varying degrees of resistance to PM, where it is visually represented on the fruit A-G. H depicts the fruit, which has low degree of PM, under the microscope. Source: Lynn et al. 2024.

1.5 Aim and purpose

This literature review aims to recognize different BCAs that are currently approved and used for biological disease control of PM on cucumber and strawberry plants. Bacteria species that are not currently approved for commercial use, but shown to exhibit promising qualities, are also evaluated as potential future BCAs

1.6 Research questions

This study will answer the following questions:

(i) What antifungal traits against powdery mildew makes bacterial disease control effective?

(ii) Which commercially available products, containing bacteria as their active ingredient, exist for use against powdery mildew on cucumber and strawberry?

(iii) Which bacteria are of interest that are not currently used commercially, in application against powdery mildew on cucumber and strawberry?

Two limitations for this study were implemented. Firstly, only commercial products were listed from North America and Europe, due to the availability of databases and the language barrier. Secondly, only products with foliar application were of relevance, as PM inhabits the above ground parts of the plant.

2. Method

This work is a literature review which is based on previous studies and other sources of information. The relevant information was found using search engines Google scholar and Web of Science as well as from the reference lists on articles within the subject. When using the search engines the input of one or multiple keywords, listed below, were used in different combinations.

To acquire information regarding strains approved for usage the databases EU Pesticides Database v3.3 and United States Environmental Protection Agency's Active Pesticide Product Registration Informational Listing (APPRIL) last updated 24/4 2025 were used for their respective regions. In APPRIL the input information was:

Site(s): Cucumbers (Foliar Treatment), Cucumbers (Greenhouse-Foliar Treatment), Cucurbits (Foliar Treatment), Cucurbits (Greenhouse-Foliar Treatment), Berry Plantings (Foliar Treatment) and Berry Plantings (Greenhouse-Foliar Treatment)

Pest(s): Powdery mildew

The information was collected from the two databases 2025-04-25.

2.1 Keywords used in search engines

Biological disease control, cucumber, *Cucumis sativus*, strawberry, *Fragaria x ananassa*, powdery mildew, mjöldagg, *Bacillus subtilis*, *Bacillus subtilis* strain QST 713, *Bacillus amyloliquefaciens*, *Pseudomonas, Streptomyces*, *Golovinomyces cichoracearum, Erysiphe cichoracearum, Podosphaera xanthii, Sphaerotheca fuliginea, Podosphaera fuliginea, Podosphaera aphanis*, phyllosphere, microbiota, foliar application, Serenade, Rhapsody, Taegro, Sonata, Actinovate

3. Results

3.1 Mechanisms behind powdery mildew disease control

Studies have identified several antifungal mechanisms of which bacteria can inhibit PM. The mechanisms can be divided depending on the antifungal substance produced (enzymes or other compounds) or how they reduce the plants' susceptibility (enhancing plant defense, competing with the pathogen for resources or promoting plant health).

3.1.1 Antifungal compounds

Table 1: Compounds and how they are antifungal against PM. The bacteria associated with each compound is also listed

Compound	Mode of action	Bacteria	Source
Lipopeptides: iturin, fengycin & surfactin	Distorts fungal cell membrane	*Bacillus spp.*	Sreedaharan et al. 2023; Romero 2007; Fridlender et al. 1993
Amino sugars	Degrades fungal cell wall	*Bacillus pumilus*	Serrano et al. 2013
Prumycin	Hinders protein synthesis	*Bacillus amyloliquefaciens*	Tanaka et al. 2017
Wuyiencin	Disrupts fungal cell membrane	*Streptomyces albulus*	Yang et al. 2021

Several bacteria species have been found to produce compounds that exhibit antifungal properties, listed in table 1. One such category of compounds are lipopeptides. These include iturin, fengycin and surfactin which can disrupt the fungal cell membrane and subsequently hinders the germination of conidia, distorting hyphae and limits fungal activity (Sreedaharan et al. 2023; Romero 2007). Other compounds are amino sugars, which hinder the fungal cell wall formation (Serrano et al. 2013) and the antibiotic prumycin has been shown to disrupt fungal protein synthesis as well as hindering germination of PM conidia (Tanaka et al. 2017). In particular members within the *Bacillus* genera have been identified for producing such antifungal bioactive compounds, specifically iturin, fengycin, surfactin, prumycin as well as amino sugars (Sreedaharan et al. 2023;

Tanaka et al. 2017; Romero 2007). This is visible as most studies which investigates the production of antifungal compound have mainly observed on *Bacillus* spp., seen in table 1. However recent studies have identified the compound wuyiencin produced by *Streptomyces albulus* to have antifungal effects on *P. xanthii* (Yang et al. 2021). Wuyiencin distorts the fungal cell membrane as well as enhances plant defense.

3.1.2 Enzymes

Table 2: Overview of enzymes produced by the given bacteria.

Enzyme	Mode of action	Bacteria	Source
Chitinase & β-1,3 glucanase	Degrades fungal cell wall components	*Bacillus* spp., *Pseudomonas* spp. & Streptomyces spp.	Legein et al. 2020; Fridlender et al. 1993; Mansour et al. 2010
Superoxide dismutase	$O^{2\cdot}-$ into H_2O_2	*Bacillus* spp., *Pseudomonas* spp. & Streptomyces spp	Li et al. 2015; Legein et al. 2020; Fridlender et al. 1993; Yang et al. 2021
Phenylalanine ammonia lyase	Involved in the biosynthesis of salicylic acid	*Bacillus* spp., *Pseudomonas* spp. & Streptomyces spp	Li et al. 2015; Legein et al. 2020; Fridlender et al. 1993; Yang et al. 2021

Many bacteria produces enzymes in response to PM infection, though the different enzymes can either be antifungal or aid through enhancing the plants' defense. The different enzymes as well as which bacteria produces them can be seen in table 2.

Plant enzymes that are associated with resistance are often synthesized in order to improve plants' defensive capabilities. (Li et al. 2015) Such enzymes include superoxide dismutase and phenylalanine ammonia lyase. Superoxide dismutase hydrolyses superoxides ($O^{2\cdot}-$) into hydrogen peroxide (H_2O_2), which is a major component in plant protection against diseases. Phenylalanine ammonia lyase enhances several secondary plant products, one of which is salicylic acid needed for the activation of plant defense (Legein et al. 2020).

Chitinase and β-1,3 glucanase are two lytic enzymes that degrade components of the fungal cell wall, chitin and β-1,3 glucan respectively (Fridlender et al. 1993).

3.1.3 Enhancing plant defense

Systemic acquired resistance (SAR) is present by the plant's defense mechanism being triggered by pathogen infections or the BCA simulating such a response. (Li et al. 2015) The protective properties are long lasting and are effective against a broad spectrum of pathogens. It can activate genes responsible for the coding of antimicrobial proteins, pathogenesis related (PR) proteins. Salicylic acid (SA) acts as a signaling molecule for the activation of the PR genes.

Induced systemic resistance (ISR) is also a defense response in plants from pathogen stimulation. (Sreedaharan et al. 2023) The signaling hormone is mainly jasmonic acid (JA) and ethylene. The bioactive metabolites surfactin, iturin, fengycin and wuyiencin have also been found to be able to induce ISR (Sreedaharan et al. 2023; Yang et al. 2021). The bacteria that are able to activate SAR and ISR respectively can be seen in table 3.

Defense responses to stimuli may include physiological changes, such as plant cell wall strengthening; enhanced production of lytic enzymes, reactive oxygen species and antimicrobial substances (Sreedaharan et al. 2023).

Table 3: The two different defense mechanisms of plants and which bacteria they are associated with.

Defense mechanism	Signaling molecule	Bacteria	Sources
Systemic acquired resistance	Via salicylic acid	*Bacillus* spp., *Pseudomonas* spp. & *Enterobacter* spp.	Li et al. 2015; Romero et al. 2004; Sreedaharan et al. 2023; Vergnes et al 2020; Asha, et al. 2021
Induced systemic resistance	Via jasmonic acid and ethylene	*Bacillus* spp., *Pseudomonas* spp., *Streptomyces* spp. & *Enterobacter* spp.	Li et al. 2015; Romero et al. 2004; Sreedaharan et al. 2023; Vergnes et al 2020; Yang et al. 2021; Asha, et al. 2021

3.1.4 Competition and plant growth promotion

Competition for space, nutrients and carbon sources can act suppressive on pathogens, which can be viewed as a form of biological control (Innerebner et al. 2011). Plant growth promotion (PGP) can increase plant health and make them less susceptible to infection or decrease disease symptoms. BCAs can increase the plants’ gibberellic acid and auxin production as well as improve available nutrients. All bacteria genera presented in this study have been reported to promote plant growth (Asha, et al. 2021; Vergnes et al 2020; Kämpfer et al. 2005).

3.2 Commercial bacterial biocontrol agents used towards powdery mildew in cucumber and strawberry cultivations

Several biocontrol agents of bacterial origin are commercially available and include the bacteria from different genera, listed in table 4 seen below.

Table 4: The table describes the bacterial biofungicides' commercial names, in what region they are approved (EU and/or USA). The active ingredient in the for given product is also listed, by the bacterial species and strain.

Bacteria	Strain	Product	Approval
Bacillus amyloliquefaciens	D747	AMYLO-X, Cx-9030 & Cx-9032	USA & EU
	ENV503	Companion Maxx	USA
	MBI 600	Subtilex Ng & Integral li A	USA & EU
	PTA-4838	Zorda Wg & Varnimo Wsp	USA & pending EU
Bacillus mycoides	Isolate J	Lifegard Lc & Bmj Wg	USA
Bacillus pumilus	QST 2808	Sonata Aso	USA
Bacillus subtilis	AFS032321	Theia	USA
	CX-9060	Bacillus Subtilis Cx-9090	USA
	IAB/BS03	AVIV, Mildore, Milagrum Plus, Fungisei & Bacix	USA
	QST 713	Minuet, Serenade, Rhapsody Aso & Qrd 146	USA & EU
Bacillus subtilis var. amyloliquefaciens	FZB24	Taegro & Taegro 2	USA & EU
Bacillus velezensis	11604	Crimson alternatively AMARA	USA
Gluconobacter cerinus	BC18B	BC18-WG alternatively PROSORTIA	USA
Hanseniaspora uvarum	BC18Y	BC18-WG alternatively PROSORTIA	USA
Methylorubrum populi	NLS0089	Ts601	USA
Pseudomonas chlororaphis	AFS009	Howler	USA
Streptomyces lydicus	WYEC 108	Actinovate	USA

Bacillus spp. are the most common active ingredient among commercial bacterial BCAs. Examples of such products include: Rhapsody, Serenade, Sonata and Taegro. The products are available as "ready-to-use solutions" and "wettable powder" (APPRIL 2025-04-25). All products listed are intended for use against a broad spectrum of pathogens, where PM may be one of many.

Four other BCAs that are not related to *Bacillus* spp. are found in: Actinovate (*Streptomyces lydicus*), Howler (*Pseudomonas chlororaphis*), Ts601 (*Methylorubrum populi*) and BC18-WG (*Gluconobacter cerinus*).

The products are available as "ready-to-use solutions" and "wettable powder" (APPRIL 2025-04-25). All products listed are intended for use against a broad spectrum of pathogens, where PM may be one of many.

3.2.1 Effects of the commercial bacterial biocontrol agents on cucumber and strawberry

Ni and Punja (2021) found that Rhapsody (*Bacillus subtilis* strain QST 713) effectively reduced *P. xanthii* on cucumbers in a greenhouse environment. Weekly applications for 4 weeks resulted in PM leaf coverage of 65% with water treatment, compared to 8% using the recommended Rhapsody dosage. They also found that preventive application contributed to better protection.

Cerkauskas and Ferguson (2014) evaluated different treatments of PM on cucumbers grown in the greenhouse. They found that Serenade (*Bacillus subtilis* strain QST 713) did not suppress PM, contrary to Ni and Punja (2021), whilst Actinovate (*Streptomyces lydicus*) provided significant control, slightly less than the effects of chemical fungicides in the study.

When evaluating BCAs for *P. aphanis* suppression on strawberries, Sylla et al. (2013) observed poor results from application of *Bacillus subtilis var. amyloliquefaciens* FZB24, a bacteria in products such as Taegro. For context the study was conducted on detached leaves, therefore the authors noted that the effects may not reflect applications in greenhouse or fields study.

Fiamingo et al. (2007) found some suppression of PM on strawberries under greenhouse conditions with *Bacillus subtilis* QST 713 application. The bacteria is commercially branded as Serenade, Rhapsody etc. Though they only observed significant results when the BCA was applied at the same time as the inoculation of PM.

3.3 Bacteria genera and their potential to suppress powdery mildew on cucumber and strawberry

Several studies have investigated the inhibition of PM using bacteria that are not presently used commercially. Though they are commonly isolated by researchers from the soil or phyllosphere. As such, the specific strains are unique to the study and/or research institution. Because of this the relevance of specific strains that are studied may not be as relevant compared to an overall overview of the different genera of bacteria, as well as why they are promising in PM suppression.

3.3.1 *Bacillus spp*.

Many strains of *B. subtilis* species are currently being used commercially (Legein et al. 2020). This can be attributed to their ability to be stored for longer periods as spores. Further they can tolerate a broad range in environmental factors, enabling them to inhabit many different places (Tanaka et al. 2017).

Strains from *B. subtilis, B. amyloliquefaciens, B. velezensis* and *B. cereus* produce the bioactive metabolites that have antifungal effect (Romero 2007; Sreedaharan et al. 2023), as well as enzymes corresponding to plant protection against disease stress and lytic enzymes (Li et al. 2015; Legein et al. 2020). *B. pumilus* produces amino sugars (Serrano et al. 2013). Furthermore they have been linked to initiation of plants defensive responses (Romero et al. 2004). The results on PM suppression have been shown to be comparable with commonly used fungicides (Șovărel & Hogea 2023; Ni and Punja 2021). Because of their exhibited effects on diseases, many strains of the genus are often considered as BCAs.

Multiple *Bacillus* spp. have been shown to suppress *P. xanthii* including: *B. chitinosporus, B. megaterium, B. polymexa B. licheniformis* and *B. aerius* for example (Hafez et al. 2018; Abo-Elyousr et al. 2022).

3.3.2 *Pseudomonas* spp.

Pseudomonas spp. are used commercially due to their ability to produce antagonistic lytic enzymes, acting antifungal against PM (Sreedaharan et al. 2023; Fridlender et al. 1993). Further they play a role in the activation of the plants' defense. These characteristics make them widely used as BCAs commercially at present (Legein et al. 2020).

3.3.3 *Streptomyces* spp.

Members of the genus are currently in use for PM treatment (Actinovate SP). *Streptomyces* spp. is associated with the production of plant growth promoting hormones and the antifungal compound wuyiencin (Vergnes et al 2020; Yang et al. 2021). The bacteria genera have also been known for its ability to induce plant defense systems.

3.3.4 *Enterobacter* spp.

Isolated strain D5/23, identified as *E. radicincitans*, have been investigated for its ability to produce plant growth promoting hormones, fix nitrogen and induce the ISR defense response (Asha, et al. 2021; Kämpfer et al. 2005). Sylla et al. (2013) found that the strain also inhibited PM successfully on detached strawberry leaves.

4. Discussion

Currently several bacterial BCAs exist for PM treatment, however their evaluated effectiveness varies between the studies found in this literature review. Though in practice, bacterial BCAs are not sufficient for PM control on a larger scale in cultivation of cucumber and strawberries as frequent applications are necessary to maintain proper protection (Cerkauskas & Ferguson 2014). Improvements in the BCAs ability to survive and colonize the phyllosphere, along with better antifungal interactions, may therefore help reduce the number of applications necessary.

4.1 Varying antifungal effects and environmental conditions

In this study several commercial biofungicides were mentioned as well as relevant research regarding their effect against PM on cucumber and strawberry. The findings showed that the evaluated products varied greatly in their qualities to protect plants. The range included products with results comparable to commonly used fungicides (Ni & Punja 2020), to no significant control (Cerkauskas & Ferguson 2014). Similarly, results with great variation on *P. xanthii* suppression have been found on other Cucurbitaceae species (for example Șovărel & Hogea 2023; Matheron & Porchas 2013). Even when studies were performed using the same bacterial strain, *Bacillus subtilis* QST 713, the difference in its evaluated effectiveness differed between significant to non-significant (Ni & Punja 2020; Cerkauskas & Ferguson 2014)

Many explanations exists for the conflicting results found in the different studies. Firstly it could be due to the activity of the bacteria, i.e. how the products have been stored and the vitality of the bacteria. Secondly the studies differed in how they were conducted and what environmental factors were present. This is important since high humidity favors the bacterial BCAs (Rur et al. 2018; Romero et al. 2007.). The method for application is also affecting the successfulness of the BCAs as good coverage should be ensured, as per the label of Howler biofungicide. Lastly it is worth mentioning that the same bacterial strain can be present in different commercial products. As such it is speculated that these products differ in composition in terms of the other ingredients, though such information is omitted from the labels which could be due to patents. Further studies may investigate what ingredients can aid in increasing the survival of the bacteria when stored.

4.2 BCAs effectiveness and combining with fungicides in order to minimize the risk of resistance development

One method that several studies have suggested is to use both BCAs and chemical fungicides. This is advantageous by providing the same or better protective effects whilst a lower dosage of chemicals is applied (Hadimani & Kulkarni 2017; Zhang et al. 2011; Gilardi et al. 2008). This principle has been successfully implemented in rotational programs for *P. xanthii* suppression (Matheron & Porchas 2013). The synergistic effects between BCAs and fungicides has been observed through alternating applications of. Serenade (*B. subtilis* QST 713) with the fungicides Procure 480SC (Triflumizole) and Quintec 250SC (Quinoxyfen) (Matheron & Porchas 2013). Similar results were found when alternating Companion (*Bacillus amyloliquefaciens* strain ENV503) as well as Actinovate (*Streptomyces lydicus* strain WYEC 108) respectively with Procure 480SC. Though it is also observed when mixed together before application, using *B. subtilis* QST 713 with the fungicide azoxystrobin (Gilardi et al. 2008).

4.3 Combinations of different BCAs for powdery mildew inhibition

The usage of multiple BCAs could enable PM suppression without supplementation with chemical fungicides. Sylla et al. (2013) found *B. subtilis* strain FZB24 to perform better against *Podosphaera aphanis* when combined with the bacteria *Enterobacter radicincitans* and the fungi *Ampelomyces quisqualis* (commercially in AQ10). Though negative interactions between *B. subtilis* and *Trichoderma harzianum* T58. Contrary to their results, Romero et al. (2007) observed less PM suppression when alternating between *B. subtilis* strains and AQ10 as well as the fungi *Lecanicillium lecanii* (Mycotal). The bacterial BCAs against PM harbours antifungal properties which might explain the antagonistic effects on the fungal BCAs. Because of the varied results when combining bacterial and fungal BCAs, it can be theorized that the environmental factors, application methods used and selected BCAs are all important factors to consider. One example of a commercial product which successfully combines fungal and bacterial BCAs is BC18-WG alternatively named PROSORTIA, containing the fungus *Hanseniaspora uvarum* strain BC18Y and the bacteria *Gluconobacter cerinus* strain BC18B. Therefore, a better understanding of successful combinations of BCAs could greatly increase the usage of biocontrols in cultivations of cucumber and strawberry. The method of which they are applied is likely also an important factor and studies could observe if alternations or simultaneous applications are best suited for the given microorganisms.

4.4 The impact of regulations on bacterial BCAs and what consequences it brings for farmers

As with every treatment, BCAs must be evaluated in order to be permitted and ensure safe usage. As a result, they are highly regulated with an extensive registration process before releasing the products to the market (Strauch et al. 2011). Globally many different strains are approved and in use, however the European Union has a generally stricter policy and as such, fewer products containing BCAs exist on the market and often require a lengthier time before approval. This results in consequences for both the manufacturers of the biofungicides and the commercial growers. In European agriculture this leads to suboptimal biofungicides available compared to other countries, making them less economically viable as they require more frequent application and/or provide less protection. In order to overcome such an obstacle it may be important to implement financial support for growers, making treatments with BCAs more viable.

The BCA-manufacturers are also affected by the stricter regulations in the EU and the lengthier time before approval. As it is a costly process, sometimes the predicted economical outcome is a net loss when taking the approval time into consideration (Strauch et al. 2011). One of the reasons for such a lengthy time to reach a decision is because the EU commission consists of multiple member states. As such the use and development of new BCAs, within the EU, would greatly benefit if the system were to be reworked and implementing a special organ for such matters that can both evaluate the risks and make a final decision. The result would lead to a stronger market for BCAs with more products available and increased economic viability for the growers leading to a reduction in chemicals used for plant protection.

4.5 Production systems and how it affects powdery mildew as well as BCAs

In northern countries the production under protection, i.e. greenhouses and high tunnels, is necessary for growing certain crops and prolonging the season. For example, in order to meet the demands for strawberries the cultivation is shifting more and more towards annual production in such environments (Berrie & Xu 2021). Consequently, PM grows better in those types of productions, (Berrie & Xu 2021; Sylla 2013). One reason why these environments favor PM is due to the absence of rainfall, which otherwise can destroy PM mycelia (Wei et al. 2016). Other factors in production systems in greenhouse environments are also beneficial for PM development, such as high temperature and high relative humidity, depending on the strain and species of PM (Berrie & Xu 2021). As such, the trend in shifting production systems will lead to cultivations that rely more heavily on fungicide use.

The frequent chemical application in such greenhouse environments is further increased by the selection of cultivars. In cultivations of both cucumbers and strawberries the growers tend to prefer susceptible varieties. The reason being that they are more productive and generally preferred on the market (Berrie & Xu 2021; Rur et al. 2015). Further the pathogen's rapid evolution is faster than the development of resistant cultivars, which poses challenges for breeding programs (Vielba-Fernández et al. 2020). As such, these production systems rely on heavy usage of fungicides, making the impact of alternations with BCAs greater.

Although greenhouse environments promote PM growth, many BCAs are often also promoted by the high humidity (Rur et al. 2018; Romero et al. 2007). This applies to both bacteria, *B. subtilis*, for example, and mycoparasitic fungi. As such, BCAs may be more commonly utilized as cultivation in such environments becomes increasingly more common.

4.6 What role the natural phyllospheric bacteria may bring for disease control

Greenhouse environments, and other environments that are limited in microbial abundance, could greatly benefit from the application of BCAs and naturally occurring bacteria in order to increase diversity and strengthen plant health. This is witnessed by Mehlferber et al. (2023) who applied a mixture that tried to mimic naturally occurring bacteria on to greenhouse grown tomatoes. It resulted in an increase in yield and decreased the presence of the pathogenic *Pseudomonas syringae*. It is therefore suggested that an abundant phyllospheric bacterial community can enhance the plants' health and increase disease resistance, for example by competing with pathogens for carbon and nutrients and promoting plant growth. This could, in theory, be seen as a parallel to human gut microflora which is vital for human health. However, more studies need to be conducted in order to gain a better understanding of naturally occurring microorganisms' relationship with the crops.

4.7 Objectives for further studies

Further isolation and examination of different bacteria species should be carried out to find more strains for PM control. As PM undergoes rapid adaptations toward resistances against fungicides the presence of viable alternatives is vital for halting its development.

Bacteria species which have strains that are already active ingredients in products on the market are likely candidates for finding additional BCAs, since more is known regarding their beneficial attributes. Among the BCAs that are used commercially the *Bacillus* species are predominant. This is an effect from being well studied, adapted for various environments and harboring several antifungal properties (Tanaka et al. 2017). Therefore finding more suitable *Bacillus* strains may further improve their effectiveness and survivability on the phyllosphere. However great potential may also lie in the currently lesser studied bacteria genera, which could contribute to an array of new mechanics for combating PM in the future. Further, it is also being used alongside existing BCAs for a broader range of mechanics to combat PM.

The endosphere, inside plant tissues, hosts an environment for microorganisms, some of which are related to plant growth promotion and induction of defense mechanisms (Gayathry et al. 2024). In the rhizosphere the benefits endophytic bacteria bring are well recognized however the effects of endophytic bacteria inhabiting the phyllosphere are far less known. Due to the limited information available, scientists have recently begun to investigate such relationships. Some relatively new findings reveal that phylloendophytic bacteria may act as plant growth promoters. For example Madhaiyan et al. (2015) found *Methylobacterium* sp. that exhibited nitrogen fixation properties. Such findings indicate that phylloendophytic bacteria may play a bigger role in plant health than previously thought. Therefore future studies may explore the use of phylloendospheric bacteria as BCAs and begin to uncover what potential benefits these can bring for agriculture.

5. Conclusion

In summary a wide variety of bacterial BCAs are currently used for disease management of PM and many promising strains are continuously being discovered. Among the bacterial species *Bacillus* spp. remains the most widely used bacterial genera in commercial products against PM, due to its members exhibiting desirable traits. In practice, BCAs alone doesn’t provide enough protection against PM to be satisfactory in most cases currently. As such it is necessary to use in alternation with fungicides, which nets an overall lower chemical usage. Much is left to explore in order to utilize BCAs better and increase their effectiveness, especially how they can be adapted for cultivation in greenhouse environments. Further the importance of the relationship between the host plant and its native bacteria, including endospheric, is relatively unexplored. Once better understood they may be utilized in agriculture as novel BCAs. Finally, this literature review suggests that use of bacterial BCAs will be a continued important tool for production systems in particular in greenhouse environments, as PM fungi acquiring resistances to fungicides remains a constant threat. However, in order to achieve this within the EU, the regulations of BCA-products on the market must aim to shorten the approval time and decrease the cost associated with it.

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