



REVIEW

Eco-Friendly Strategies to Combat *Botrytis cinerea* in Strawberry: Biological Control Agents, Natural Compounds, and Innovative Approaches

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ABSTRACT: Strawberry (*Fragaria × ananassa*) production is severely constrained by gray mold caused by *Botrytis cinerea*, a major pathogen responsible for significant pre- and postharvest losses worldwide. The increasing occurrence of fungicide-resistant populations and growing environmental concerns have intensified the search for sustainable disease management strategies. This review provides a comprehensive overview of the biology, epidemiology, and fungicide resistance of *B. cinerea*, with a particular focus on eco-friendly approaches for gray mold control in strawberry. It critically examines the effectiveness of cultural practices, biological control agents, including antagonistic bacteria, fungi and yeasts, as well as natural antifungal compounds such as botanical extracts and essential oils. In addition, recent advances in microbiome research, multi-omics technologies, nanotechnology, and formulation strategies are discussed as promising tools to improve the efficacy and reliability of biological control. Finally, the review points at the current challenges related to field performance, commercialization and regulatory approval, aiding the integration of these sustainable approaches within integrated disease management programs to reduce fungicide dependence and enhance the resilience of strawberry production systems.

KEYWORDS: Strawberry; gray mold; biological control; natural compounds; sustainable management

1 Introduction

Strawberry (*Fragaria × ananassa* Duch.) is one of the most economically important berry crops worldwide due to its nutritional value, sensory characteristics, and high market demand. The area under protected cultivation systems for the global production of fruits has increased significantly during the last few decades, specifically developed to extend the harvesting period and improve fruit quality [1]. However, strawberry fruit is among the most perishable fruits because of its thin epidermis, high water content, and intense metabolism activity [2], making it susceptible to fungal infections at both the pre- and postharvest periods.

Among the fungal diseases affecting strawberries, gray mold caused by *Botrytis cinerea* is considered the most destructive worldwide [3]. This necrotrophic pathogen has a wide distribution in nature and infects over 1400 plant species, making it one of the most serious threats to global food production systems. In strawberry cultivation, *B. cinerea* infects flower tissues and establishes latent infections during bloom, which later leads to fruit rot during ripening in strawberry production. Under favorable environmental conditions, particularly when relative humidity (RH) is >90%, and temperatures are moderate (15–25°C), disease can cause yield losses of 30–50%, especially in greenhouse and tunnel production systems [1,4].

The global epidemiologic success of *B. cinerea* is mainly due to its high genetic variability, copious sporulation, sclerotia formation and secretion of cell wall-degrading enzymes and phytotoxic metabolites [3]. Its exceptional adaptability enables rapid evolution under selection pressure by fungicides, resulting in the widespread development of resistant and multi-resistant populations in important strawberry-producing areas [4]. The main resistance mechanisms involve target-site mutation, increased efflux pump activity and metabolic adaptation, all of which substantially diminish the effectiveness of fungicides.

Conventional gray mold management has predominantly used repeated applications of synthetic fungicides, including dicarboximides, anilinopyrimidines, quinone outside inhibitors, and succinate dehydrogenase inhibitors. Intensive chemical use has led to decreased control effectiveness and environmental and regulatory issues, particularly in export-driven and organic production systems [5]. In addition, changes in temperature regimes, humidity patterns, and host–pathogen interactions due to climate change are predicted to alter disease dynamics by increasing the frequency and geographical spread of epidemics [6,7].

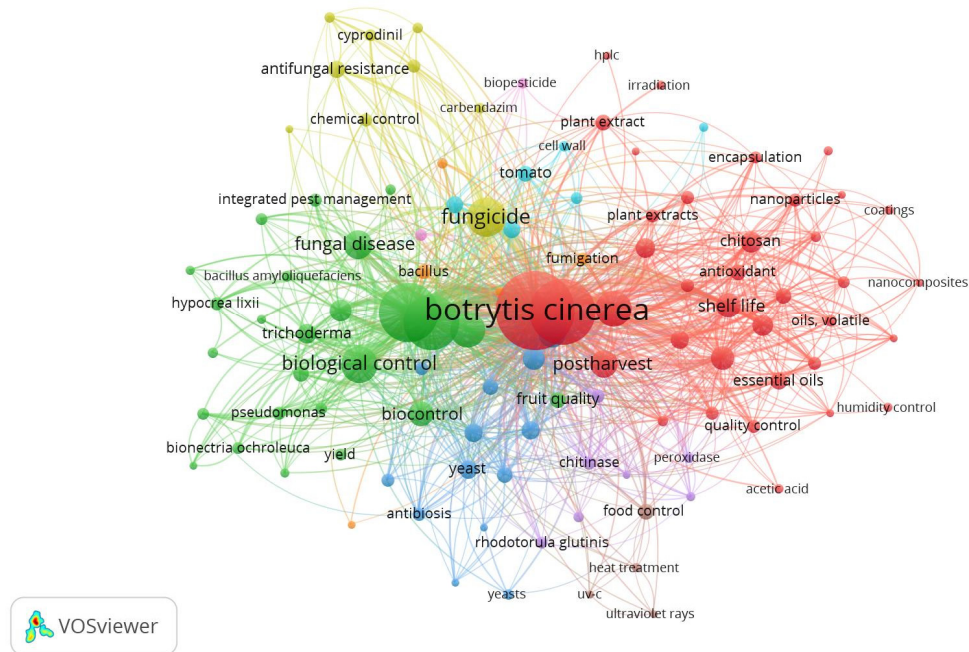
In response to these challenges, alternative eco-friendly solutions have attracted increasing attention. Biological control agents (BCAs), such as antagonistic fungi, beneficial bacteria, and yeasts, induce suppression of *B. cinerea* by mechanisms like competition, antibiosis, mycoparasitism, and induction of systemic resistance [8]. The development in the field of nanotechnology has also recently supported sustainable disease management for plants by improving stability, bioavailability, and targeted delivery of antifungal compounds or microbial agents [9]. Furthermore, genome-editing tools like Clustered Regularly Interspaced Short Palindromic Repeats/Cas9 technologies have brought new opportunities for enhancing the effectiveness and metabolic performance of fungal and bacterial biocontrol agents [10,11].

Despite these promising developments, significant challenges remain, including variability in field performance, formulation stability, economic viability, and regulatory constraints. Integrative strategies for achieving sustainable gray mold control in strawberry production systems will require the integration of diverse knowledge from pathogen biology, resistance monitoring, biological control, technology, and climate-adaptive management.

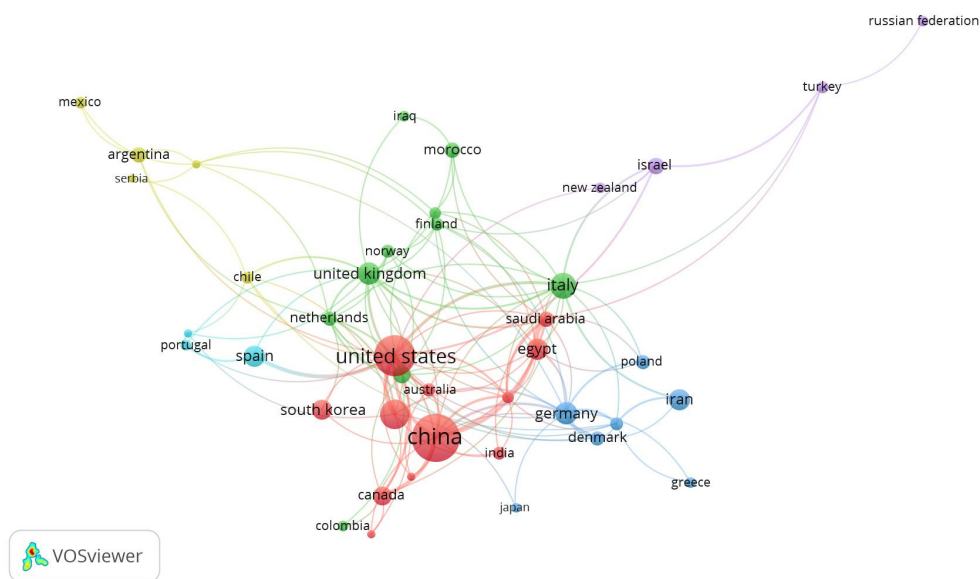
The objective of this review is to (i) give an updated overview of the biology and epidemiology of *B. cinerea* affecting strawberry; (ii) highlight limitations in chemical control and resistance development; (iii) discuss biological control agents and natural antifungal compounds for *B. cinerea* pathogens, with a focus on strawberry; (iv) summarize emerging technologies addressing diseases including *B. cinerea* in strawberries enabling long term diseases solutions; (v) describe field constraints and adoption challenges, and (vi) discuss current challenges and future perspectives.

In this review, bibliometric data were retrieved from 851 published articles on the management strategies and biocontrol against gray mold in strawberry cultivation, based on the Scopus database, using the keywords “Gray mold” OR “*Botrytis cinerea*” AND “strawberry” OR “strawberry plant” OR “*Fragaria ananassa*” AND “control” OR “management” OR “biological control” OR “innovative approaches” OR “integrated management” OR “antifungal compounds” OR “fruit quality” OR “bioformulation” were specifically used to gather bibliometric data from the database of SCOPUS (Available at: <https://www.scopus>).

com/, accessed on 11 May 2026) (Fig. 1). Fig. 1A illustrates the major research themes and keyword clusters in this field, whereas Fig. 1B highlights the global collaboration network among countries contributing to research on sustainable management of gray mold in strawberry. The VOSviewer processing software (v1.6.9, Leiden University, Leiden, The Netherlands) was used to create the bibliometric analysis. In Fig. 1, colors represent groups of linked terms; the label size of a term represents the number of publications, and the distance between two terms represents the degree to which they are associated.



(A)



(B)

Figure 1: Bibliometric analysis of 851 published articles about on the management strategies and biocontrol against gray mold in strawberry cultivation according to the Scopus database using specific keywords such as “Gray mold”

OR “*Botrytis cinerea*” AND “strawberry” OR “strawberry plant” OR “*Fragaria ananassa*” AND “control” OR “management” OR “biological control” OR “innovative approaches” OR “integrated management” OR “antifungal compounds” OR “fruit quality” OR “bioformulation”, the larger the circle, the more intense the scientific activity. (A) Keyword co-occurrence network generated using VOSviewer, illustrating the major research themes and their relationships. Each node represents a keyword, node size reflects its frequency of occurrence, colors indicate thematic clusters, and connecting lines represent co-occurrence relationships. (B) Country collaboration (co-authorship) network showing the scientific collaboration among countries contributing to this research field. Node size corresponds to publication output, colors indicate collaboration clusters, and links represent collaborative relationships between countries.

2 Biology of *B. cinerea*

The designation *B. cinerea* is derived from its morphology. The term *Botrytis* originates from the Greek word meaning “bunch of grapes,” referring to the grape-like arrangement of conidia on branched conidiophores, whereas *cinerea* refers to the characteristic gray sporulation [12,13]. *B. cinerea* represents the asexual (anamorphic) stage of the teleomorphic fungus *Botryotinia fuckeliana* (de Bary) Whetzel [12]. The genus *Botrytis* contains a total of 22 described species (with one hybrid) [14]. Although most species are host-specific, *B. cinerea* stands out for its exceptionally wide host range, infecting more than 200 dicotyledonous plant species worldwide [12,14].

Taxonomic identification historically relied on morphological characteristics, like conidiophore branching pattern and conidial morphology. *B. cinerea* produces erect, highly branched conidiophores bearing terminal clusters of hydrophobic macroconidia supported by a well-developed conidiogenous hypha, producing structures reminiscent of a grape bunch [12]. These conidiophores originate from a stroma that is cushion-like and develops underneath the host surface [2].

Macroconidia are unicellular, oval to ellipsoidal blastoconidia measuring approximately $\sim 8\text{--}14 \times 6\text{--}9 \mu\text{m}$ [2,12]. They are relatively dry and hydrophobic, promoting effective aerial dispersion. Once mature, the conidia are readily detached by air currents or rain splash, which constitute the principal modes of dissemination in agricultural systems [12]. The phylogenetic placement of *B. cinerea* generally reflects similar strategies for necrotrophic lifestyles, sclerotial survival, and aggressive infection mechanisms shared within the *Sclerotiniaceae*. Its global distribution and epidemiological success are explained by its wide host range, genomic plasticity and taxonomic complexity [15].

2.1 Disease Cycle and Infection Pathways of *B. cinerea*

The fungal pathogen *B. cinerea* overwinters primarily as sclerotia or latent mycelium within infected strawberry debris, mummified fruit, and senescent plant tissues. These survival structures serve as the primary inoculum reservoirs at the beginning of the growing season [13]. Overwintering persistence is also augmented in perennial and protected strawberry systems through crop residues infected within the canopy (Fig. 2).

During spring, when conditions are favorable (moderate temperatures and high relative humidity), the sclerotia germinate to produce mycelium as well as abundant conidiophores with macroconidia. The airborne conidia are the main source of primary inoculum for new infections [13]. Senescent reproductive parts, such as petals, calyces and stamens are especially prone to infection and act as entry courts of initial infections in strawberry crops. The release of conidia is induced by mechanical disturbances, vibrations or fast reduction in relative humidity. Upon release, conidia travel along air currents or by rain splash, allowing for rapid dispersal both within and between plant canopies [16]. The macroconidia form is extremely hydrophobic, improving its aerial dispersal effectively.

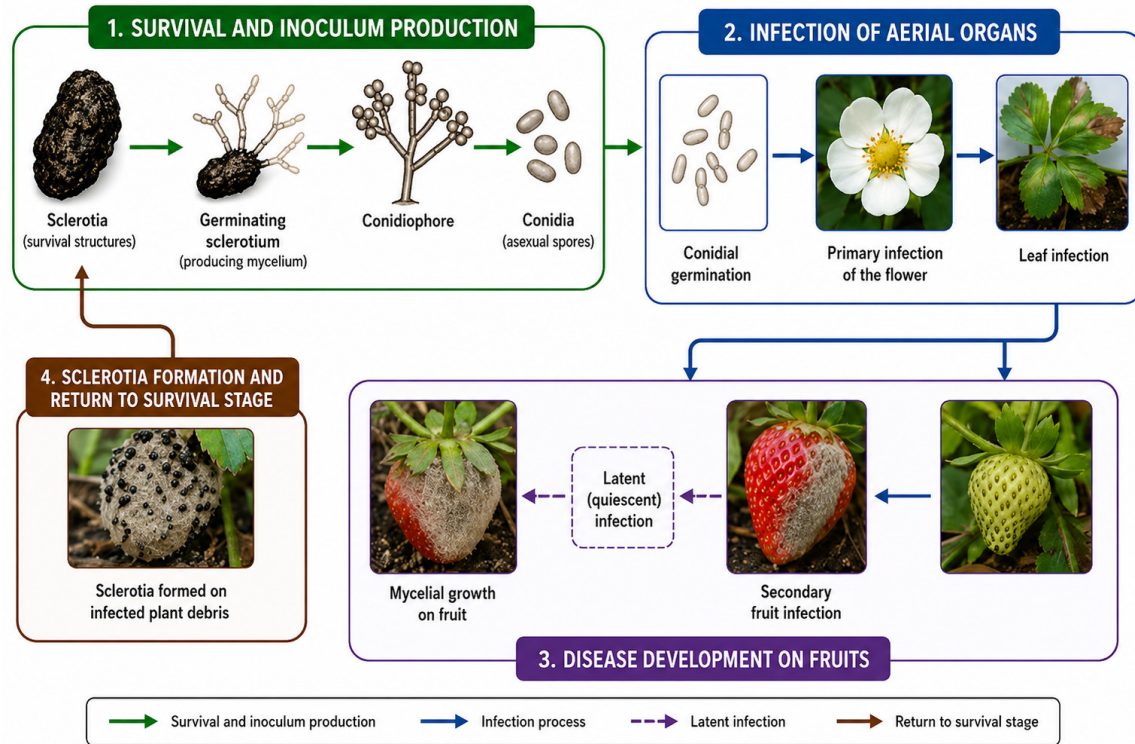


Figure 2: Disease cycle of *Botrytis cinerea*: from sclerotia survival to fruit infection in strawberries.

Conidia germinate on susceptible tissues in the presence of free moisture upon their deposition. Germ tubes immediately invaginated epidermis of strawberry, especially underneath petals, pistils and stamens, as microclimatic conditions under these regions are conducive to infection. *B. cinerea* has the ability to invade either directly through degrading enzymes, which can enable it to penetrate tissue, or indirectly via plant openings, such as stomata or pre-existing wounds [17].

A distinctive feature of *B. cinerea* epidemiology is its ability to establish latent infections in floral tissues. The pathogen can remain quiescent in developing fruits and resume active growth during ripening, when physiological changes such as increased sugar content, tissue softening, and reduced host defenses favor disease development [13]. Consequently, fruits may appear healthy at harvest but develop gray mold during storage and transportation. As berries mature, spore production increases and continues for the duration of the fruiting period, leading to secondary inoculum formation that prolongs polycyclic epidemics. *B. cinerea* can also skip quiescence and directly start necrotrophic development in the next infection cycles under highly favorable conditions [18].

2.2 Environmental and Epidemiological Factors Influencing Disease Development

Environmental and microclimatic conditions strongly influence the development and severity of gray mold, temperature is an important driver of pathogen activity. *B. cinerea* exhibits a broad thermal range, with growth occurring at temperatures close to 0°C, an optimal between 18 and 23°C, and an upper limit just below 30°C [12]. Recent investigations have shown that this broad thermal range enables the pathogen not only to attack strawberries in growing conditions but also to remain metabolically active during cold storage [2,18]. Climate-based modeling also indicates that increasing temperatures could change epidemic timing and increase disease pressure in temperate production systems [13].

High relative humidity (RH) and long leaf wetness duration are the most important environmental determinants of infection. Conidial germination generally occurs at RH levels above 90% and is dependent on the presence of free moisture on plant surfaces [13]. Both experimental and field studies show that successful penetration can occur after short wetness periods, in particular on floral tissues [8]. Protected cultivation systems, including those with greenhouses and high tunnels, often contribute to the formation of microclimatic niches defined by condensation-dependent conditions rather than a lack of ventilation or humidity, which further enhances disease risk [18]. Environmental factors during postharvest phase also play an important role in disease progression as latent infections can be established during flowering and will proceed asymptomatically until the fruit is placed in storage, where high humidity levels and small mechanical injuries may induce symptom expression [13].

In addition to local microclimates, global climatic change is predicted to affect the epidemiology of *B. cinerea*. Altered rainfall patterns, more frequent humid events and recurrent mild winters could improve the overwintering survival of sclerotia and thus increase their geographical spread [6,7]. The results of recent ecological analyses indicate that climate variability may also influence certain aspects of pathogen population dynamics and expressions of virulence [18].

3 Role of Cultural Practices in *B. cinerea* Management in Strawberry

Gray mold remains one of the most destructive diseases affecting strawberry production worldwide, particularly in regions characterized by moderate temperatures and high humidity [12,19]. Cultural practices alone rarely provide sufficient disease control but they play a fundamental role in integrated disease management by reducing pathogen population, modifying the crop microclimate and creating conditions that enhance the effectiveness of BCAs and other sustainable control strategies.

3.1 Role of Canopy Management in Regulating *B. cinerea* Epidemiology

Canopy architecture strongly influences the microenvironment surrounding strawberry leaves, flowers, fruits and indirectly affects the epidemiology of *B. cinerea*. Gray mold development is favored by high relative humidity and prolonged leaf wetness, which promote conidial germination and infection under favorable conditions [3,13]. Accordingly, field studies have shown that compact planting systems maintain longer periods of leaf wetness than open canopy structures, increasing the risk of disease development [20,21].

In Mediterranean strawberry production systems, the reduction of canopy density improves air circulation, lowers relative humidity and accelerates surface drying which thereby decreases gray mold incidence [22,23]. These findings demonstrate that crop architecture is an effective component of disease management [24]. On the other hand, canopy sanitation further contributes to disease suppression by removing senescent leaves, infected flowers and other plant residues that serve as important inoculum sources for *B. cinerea* [25,26]. Silviculture practices aim to disrupt the fungal life cycle by removing the source of the infected tissues, which indirectly limits the spread of the infection to the fruit [27,28]. These practices, aside from their direct role in reducing pathogen prevalence, they improve the microhabitat for the establishment and functioning of BCAs [29,30]. Because colonization of the microsites of flowers and fruits by antagonistic organisms requires a relatively stable and less competitive zone. Dense and poorly aerated environments lead to a rapid increase in pathogen spore production, which can outcompete BCAs before any competitive exclusion can occur, that is why improved ventilation limits excessive pathogen sporulation while enhancing the persistence of antagonistic microorganisms, thereby improving their ability to suppress *B. cinerea* through competition and antifungal activity [31,32]. As climate change is expected to increase the frequency of humid conditions, optimizing canopy architecture through appropriate plant

spacing and ventilation will remain an important strategy for reducing gray mold incidence in protected strawberry production systems [33–35].

3.2 Targeted Irrigation Practices

Irrigation management is a key cultural practice influencing the epidemiology of *B. cinerea* because conidial germination and host penetration require free water and prolonged leaf wetness [13,36]. Consequently, irrigation practices affect not only water supply but also the environmental conditions that favor pathogen infection. So basic overhead irrigation increases floral wetness and facilitates splash dispersal of conidia, leading to greater gray mold incidence [37,38]. Repeated wetting of dense canopies further prolongs moisture retention and enhances pathogen colonization, making irrigation management an important component of disease control rather than solely an agronomic practice [39].

In contrast, drip irrigation minimizes canopy wetness and consistently reduces disease incidence by limiting splash dispersal and lowering canopy humidity across different strawberry production systems [40–42]. The timing of irrigation is also as important the type, for instance, evening irrigation prolongs moisture availability and favors conidial germination [43], whereas morning irrigation allows plant surfaces to dry more rapidly under solar radiation, reducing infection risk [44]. Modern studies in precision agriculture, coupled with leaf wetness sensors and decision-support systems, have shown that microclimate-based irrigation scheduling in real-time can avoid increased water use while reducing gray mold [45]. Therefore, irrigation scheduling is a novel non-chemical approach to disrupting the timing of the pathogen's life cycle [46,47]. Appropriate irrigation management also supports the persistence and effectiveness of BCAs. Excessive overhead irrigation can wash antagonistic microorganisms from plant surfaces, dilute antimicrobial metabolites, and disrupt biofilm formation, thereby reducing their competitive ability against *B. cinerea* [48,49].

3.3 Use of Mulching and Ground Cover

Mulching is an important cultural practice that contributes to the management of gray mold by modifying the soil–plant interface and interrupting pathogen transmission pathways [12,13] (Fig. 3). Straw, plastic films, and biodegradable mulches reduce direct contact between developing fruits and the soil, thereby limiting fruit contamination and disease development [50]. In addition, mulch layers help to reduce soil particle mobilization and allow for better aeration in the fruiting zone [51,52]. Organic mulch increases soil micro flora and fauna, suppressing the saprophytic growth of the *B. cinerea* fungus and increasing competition for the remaining nutrients and decomposing residues [53,54]. Furthermore, by buffering temperature and moisture fluctuations, mulch layers create microhabitats that favor the persistence and activity of biological control agents, thereby enhancing the consistency of biological disease suppression [55,56].

3.4 Crop Rotation and Soil Health Management

Although *B. cinerea* primarily infects aerial tissues of strawberry plants, its long-term persistence depends largely on the survival of sclerotia and dormant mycelium in infected leaves, petioles, fruits, crop residues, and organic matter, where the pathogen can remain viable for extended periods [57,58]. The persistence of these survival structures in soil and plant debris constitutes an important source of inoculum for subsequent cropping seasons and contributes significantly to gray mold development [24,56,59].

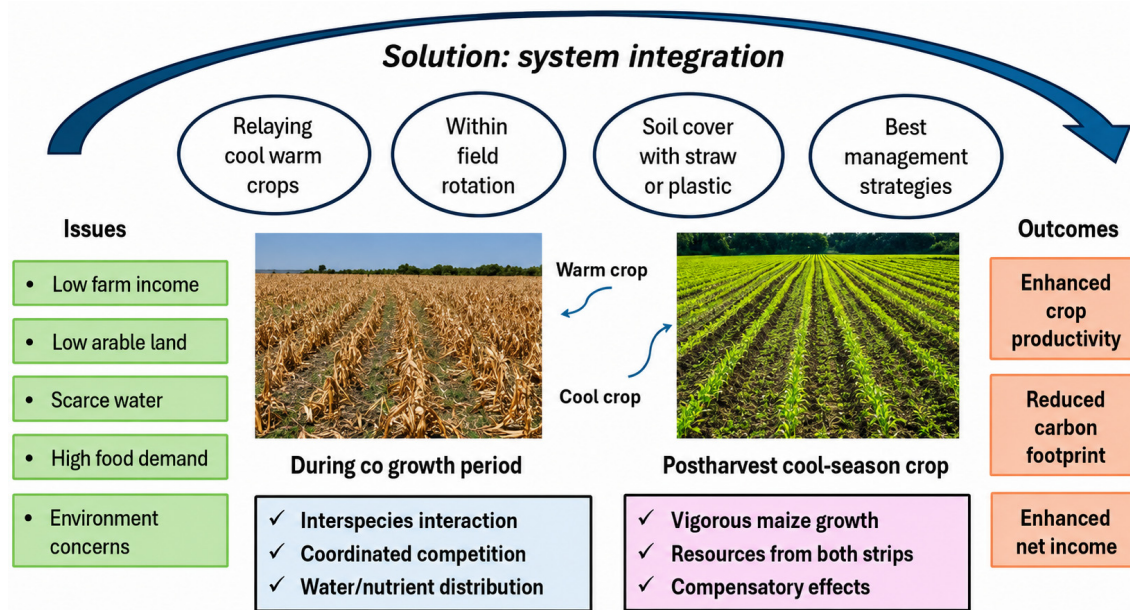


Figure 3: System-integrated mulching strategy to improve crop productivity and sustainability.

Crop rotation is an effective strategy for disrupting the disease cycle of *B. cinerea*. Although the pathogen has a broad host range, rotating with non-host or less susceptible crops reduces the accumulation of infected plant residues that support its saprophytic survival, thereby lowering pathogen populations in the field [60–62]. In addition to reducing pathogen reservoirs, rotational systems improve soil structure by enhancing aggregation, porosity and organic carbon dynamics, which promote better aeration and drainage while reducing the humid microsites that favor saprophytic survival of the pathogen [63–67]. These structural changes generally accompany the development of disease-suppressive soils owing to greater microbial diversity and functional redundancy.

Although cultural practices can significantly reduce disease pressure and enhance the effectiveness of biological control agents, they are often insufficient to provide complete protection under highly favorable environmental conditions. Consequently, commercial strawberry production has historically relied on fungicide-based programs to ensure acceptable levels of disease suppression.

4 Chemical Control and Resistance Development

4.1 Common Fungicides Used against *B. cinerea*

Chemical control remains one of the most widely used strategies for managing gray mold caused by *B. cinerea* in strawberry plantations, because the pathogen infects flowers, developing fruit and harvested berries, so the fungicide applications are often considered essential to reduce both pre- and postharvest losses [68,69]. Several studies describe strawberry gray mold management as highly dependent on fungicides, particularly under humid conditions favorable to disease development [70,71]. In this regard, the reliance is on a diverse range of fungicides, not one or two, and they belong to several chemical classes. The chemical management of gray mold in strawberries relies mainly on the application of site-specific fungicides belonging to different Fungicide Resistance Action Committee (FRAC) groups [72]. These fungicides are used extensively during flowering and fruit development stages because of their high efficacy in reducing both preharvest and postharvest infections. Over the past decades, several fungicide classes have become the cornerstone of gray mold management programs in commercial strawberry production systems [73]. Among

the oldest fungicides used against *B. cinerea* are dicarboximides, including iprodione, procymidone, and vinclozolin [74]. Table 1 represents major fungicides reported in studies from various strawberry-producing regions worldwide.

Table 1: Fungicides reported for the control of *Botrytis cinerea* in strawberry production systems worldwide.

Country/Region	Fungicides	Fungicide Groups	References
USA, eastern states	Thiophanate-methyl, pyraclostrobin, boscalid, cyprodinil, fenhexamid, iprodione, fludioxonil	Benzimidazole, Quinone outside inhibitors (QoI), succinate dehydrogenase inhibitors (SDHI), anilinopyrimidines (AP), hydroxyanilide, dicarboximide, phenylpyrrole	[75]
USA, southern states	Thiophanate-methyl, pyraclostrobin, boscalid, cyprodinil, fenhexamid, iprodione, fludioxonil	Benzimidazole, QoI, SDHI, AP, hydroxyanilide, dicarboximide, phenylpyrrole	[73]
USA, California	Benzimidazoles, dicarboximides, SDHI, anilinopyrimidines, QoI, phenylpyrroles, hydroxyanilides; resistance monitored in 888 isolates from strawberry fields	Boscalid, cyprodinil, fenhexamid, fludioxonil, fluopyram, isofetamid, penthiopyrad, iprodione, pyraclostrobin, thiophanate-methyl	[76]
Brazil, Paraná	Carbendazim, procymidone, iprodione, boscalid, pyraclostrobin, fenhexamid, cyprodinil, fludioxonil	Benzimidazole, dicarboximide, SDHI, QoI, hydroxyanilide, AP, phenylpyrrole	[77]
China, Hubei	Procymidone, zoxamide	Dicarboximide, benzamide	[78]
China, Shanghai	Fluxapyroxad	SDHI	[79]
China, Sichuan	Boscalid, pyraclostrobin, iprodione and related fungicide-resistance markers	SDHI, QoI, dicarboximide	[80]
Germany	Boscalid, pyraclostrobin, fenhexamid, fludioxonil, cyprodinil and others	SDHI, QoI, hydroxyanilide, phenylpyrrole, AP	[81]
Germany	Benzimidazoles, dicarboximides, SDHI, anilinopyrimidines, QoI, hydroxyanilide: Complex resistance pattern to multiple fungicides in one strawberry field	Carbendazim Iprodione Boscalid Cyprodinil Pyraclostrobin Fenhexamid	[82]
Denmark	Boscalid, pyraclostrobin, fenhexamid; high multiple resistance reported	SDHI, QoI, hydroxyanilide	[83]
Switzerland	Fenhexamid, boscalid, pyraclostrobin, fludioxonil, cyprodinil	Hydroxyanilide, SDHI, QoI, phenylpyrrole, AP	[84]
Spain, Huelva	Benomyl, carbendazim, vinclozolin, procymidone, iprodione	Mainly dicarboximides, APs and other botryticides	[85]
Spain	Fenpyrazamine resistance and cross-resistance with fenhexamid	Keto-reductase inhibitor/hydroxyanilide-related	[86]
Italy, southern Italy	Anilinopyrimidines, fludioxonil, fenhexamid, boscalid, QoIs	AP, phenylpyrrole, hydroxyanilide, SDHI, QoI	[87]

Table 1: *Cont.*

Country/Region	Fungicides	Fungicide Groups	References
Greece	Cyprodinil, boscalid, fenhexamid; multidrug resistance involving several fungicide classes	AP, SDHI, hydroxyanilide	[88]
Korea	Benomyl, procymidone, vinclozolin; later benzimidazole resistance monitoring	Benzimidazole, dicarboximide	[89]
Korea	Carbendazim, Procymidone, Boscalid, Fluopyram, Pyrimethanil, Pyraclostrobin, Fenhexamid	Benzimidazole, dicarboximide, SDHI, anilinopyrimidine, QoI (strobilurin)	[90]
Argentina	Carbendazim, procymidone	Benzimidazole, dicarboximide	[91]
Egypt	QoI and DMI fungicides evaluated against <i>B. cinerea</i> on strawberry	QoI, DMI	[92]

Despite regional differences in fungicide registration and management practices, succinate dehydrogenase inhibitors, quinone outside inhibitors, anilinopyrimidines, hydroxyanilides and, phenylpyrroles constitute the core of contemporary gray mold control programs worldwide. Notably, resistance has been reported for nearly all major fungicide classes, indicating that the continued introduction of new active ingredients has not prevented the progressive adaptation of *B. cinerea* populations [93]. These compounds interfere with fungal osmotic signal transduction and membrane-associated processes and were historically very effective against gray mold.

Anilinopyrimidines (APs), mainly cyprodinil and pyrimethanil, were introduced as important alternatives for gray mold control. These fungicides inhibit methionine biosynthesis and the secretion of hydrolytic enzymes required for fungal infection [94]. Cyprodinil is frequently used in mixture formulations with fludioxonil, such as Switch®, to improve efficacy and resistance management [95]. Despite their effectiveness, resistant isolates of *B. cinerea* have been increasingly reported in strawberry production systems [70].

Succinate dehydrogenase inhibitors (SDHIs) constitute another major fungicide class widely applied against strawberry gray mold [96]. Fungicides such as boscalid, fluopyram, fluxapyroxad and pydiflumetofen inhibit the SDH enzyme involved in fungal mitochondrial respiration and are characterized by strong protective and curative activities, and are commonly integrated into spray programs because of their broad-spectrum efficacy [97]. Boscalid-based mixtures, particularly boscalid + pyraclostrobin formulations, have been extensively used in strawberry cultivation [98].

Known as strobilurins, quinone outside inhibitors (QoIs) represent a different category of fungicides that can target *B. cinerea* [99]. Three of the most common strobilurins include pyraclostrobin, azoxystrobin and, trifloxystrobin, all of which inhibit the cytochrome bc1 of the mitochondrial electron transport chain in fungi [100]. Because of their systemic nature and high activity at low doses, QoIs are considered very useful fungicides with broad-spectrum activity [101]. Especially the capability to induce resistance, which has now been recorded in multiple pathogenic fungi, including *B. cinerea*, due to mutations in the mitochondrial *cytB* gene [99,102].

Strawberry gray mold management relies on a few additional fungicide classes, like phenylpyrroles such as fludioxonil and hydroxyanilides like fenhexamid [103]. Fludioxonil remains one of the most effective *B. cinerea* fungicides, with resistance issues [104]. Fenhexamid has excellent activity on gray mold, and resistance has been documented [105].

The first problem with the listed fungicides is the duration of their protection. Fungicides lose efficacy in production regions, documented in benzimidazoles and dicarboximides [106,107]. Resistance to thiophanate-methyl and procymidone was documented in 93% and >50% of Brazilian strawberry isolates, respectively [108]. Similarly, Resistance to anilinopyrimidines has become increasingly prevalent in strawberry-associated *B. cinerea* populations following prolonged field exposure in Sicily [109]. In addition, studies conducted in the United States, Germany and, Asia have reported widespread resistance to pyraclostrobin and cyprodinil, often occurring within multidrug-resistant populations, highlighting the strong selective pressure imposed by repeated applications of these site-specific fungicides [70,73,82,88,110–112]. Conversely, fludioxonil maintains a position as one of the most effective compounds, with reports on reduced sensitivity being sporadic [103]. Among the compounds used in the management of gray mold, SDHIs are considered the most dominant. However, the rising frequency of alterations in the *sdh* genes illustrates that the prolonged use of SDHIs may also be questionable [113]. Therefore, the effectiveness of fungicides is no longer determined solely by their intrinsic pharmacological properties but also by the pathogen populations' resistance characteristics in a given locality [114].

4.2 Drawbacks of Chemical Control

Due to the capacity for extensive genetic variability and adaptation, most modern management strategies for strawberry diseases recommend fungicide rotation and alternation of FRAC groups to slow down resistance and conserve fungicide efficacy [115]. The ongoing and extensive use of fungicides imposes several agronomic, environmental and toxicological challenges [116]. Modern strawberry production systems mostly rely on frequent applications of multiple fungicides during the growing season and especially during the flowering and fruit maturation stages. This results in significant selection pressure on the fungal population and raises sustainability and efficacy concerns [117].

One of the main challenges of fruit protection with fungicides is the accumulation of pesticide residues in fruit and also in the ecosystem. Strawberries are largely sold fresh and are very perishable; therefore, fungicide residue is a major food safety issue regarding this aspect [118]. In the same regard, several studies show fungicide residue on strawberries and the potentially severe health effects from chronic exposure and the need for international standards on permissible residue levels [119–122].

The effect of repeated applications may result in persistent environmental contamination and runoff that further drives soil and water pollution [123–125]. In this case, it is well documented that fungicides have adverse effects on nontarget organisms, plant health, function and, on beneficial soil microbial communities [126–129]. There is a broad spectrum of negative impacts of fungicide use on soil-dwelling biota, natural pest control, pollination and other organisms that are vital to the health and integrity of the ecosystem [130]. Such disturbances may alter microbial biodiversity and reduce ecosystem stability within agricultural soils.

Another important limitation concerns the increasing regulatory restrictions imposed on fungicide use [131]. Several active ingredients previously used against *B. cinerea*, including certain dicarboximides and benzimidazoles, have faced restrictions or withdrawal in different countries because of environmental persistence, toxicological risks or resistance-related concerns [110,132]. Regulatory agencies increasingly encourage the reduction of pesticide inputs and promote safer and more sustainable disease management strategies [133]. However, the repeated use of site-specific fungicides accelerates the development of fungicide-resistant *B. cinerea* populations [134,135].

Cases of multidrug resistance have been reported in several strawberry-producing regions worldwide, severely limiting available chemical options [4]. In addition to resistance emergence, chemical control

strategies may create dependence on continuous fungicide applications to maintain acceptable disease suppression [114]. This dependency can increase economic burdens on growers due to the rising costs of fungicides, repeated spraying operations, and resistance management programs [136]. Consequently, concerns regarding environmental safety, public health, fungicide resistance and sustainable agriculture have intensified the search for alternative and integrated approaches for gray mold management in strawberries.

4.3 Resistance Mechanisms Developed by *B. cinerea*

B. cinerea is considered one of the fungal pathogens with the highest capacity to develop resistance to fungicides [74]. It's remarkable that genetic variability, short reproductive cycle, abundant sporulation, and adaptability to environmental stress have enabled the rapid emergence of resistant populations in strawberry production systems worldwide [137]. Repeated exposure to site-specific fungicides exerts strong selection pressure on fungal populations, favoring the survival and proliferation of resistant isolates [138]. As a result, resistance to multiple fungicide classes has become a major challenge in the chemical management of gray mold [139].

One of the most common resistance mechanisms in *B. cinerea* involves mutations occurring at fungicide target sites [74]. These mutations alter the structure of the targeted protein, thereby reducing its binding efficiency while maintaining normal cellular function. On the other hand, resistance to QoIs is commonly associated with mutations in the mitochondrial *cytB* gene, particularly the G143A substitution [140], which prevents fungicide interaction with the cytochrome bc1 complex involved in mitochondrial respiration [141]. This mutation has been widely detected in resistant *B. cinerea* isolates from strawberry fields [70]. Similarly, resistance to SDHIs is associated with mutations in genes encoding subunits of the SDH complex, especially *sdhB*, *sdhC*, and *sdhD* [142,143]. Among these, mutations such as H272R and H272Y in the *sdhB* gene are frequently reported and significantly reduce sensitivity to boscalid and other SDHI fungicides [144]. These mutations impair fungicide binding while preserving enzyme activity, allowing fungal survival under fungicide exposure [139].

Resistance to hydroxyanilides, particularly fenhexamid, has also been documented in *B. cinerea*. This resistance is mainly linked to mutations in the *erg27* gene encoding the 3-keto reductase enzyme involved in ergosterol biosynthesis [145]. Alterations in this target enzyme reduce fungicide affinity and consequently decrease fungicidal activity [145]. In addition to target-site mutations, *B. cinerea* can develop multidrug resistance through the overexpression of membrane-associated efflux transporters. These transport systems actively export fungicide molecules outside fungal cells, thereby reducing intracellular fungicide accumulation [146]. Two major transporter families are involved in this mechanism: ATP-binding cassette (ABC) transporters and major facilitator superfamily (MFS) transporters [147]. Overexpression of genes such as *atrB* has been associated with multidrug resistance phenotypes affecting several unrelated fungicide classes simultaneously [88].

Cross-resistance represents another important phenomenon observed in *B. cinerea*. In this case, resistance to one fungicide confers reduced sensitivity to other fungicides belonging to the same chemical group or sharing similar modes of action [138]. Cross-resistance has been reported among several SDHI fungicides as well as among anilinopyrimidines and QoIs [74]. This phenomenon further complicates resistance management because the effectiveness of multiple fungicides may be compromised simultaneously [131].

The increasing limitations associated with chemical fungicides have intensified the search for ecological and sustainable alternatives for the management of gray mold caused by *B. cinerea* in strawberries [148]. Although fungicides remain important tools for disease suppression, their long-term effectiveness is progressively declining due to the emergence of resistant pathogen populations, environmental concerns,

and growing regulatory restrictions [149]. Consequently, modern plant protection strategies increasingly emphasize reducing dependence on synthetic fungicides while maintaining effective disease control [150]. Another important reason for developing ecological alternatives is the rapidly developing resistance of *B. cinerea* to fungicides [74]. The extensive use of site-specific fungicides creates a considerable selection pressure that eventually will result in a population of *B. cinerea* resistant to that specific fungicide. The more resistant strains there are, the less effective the fungicide becomes. This results in an increasing frequency of application and higher costs of production [114]. This creates a cycle that is both economically and environmentally unsustainable.

The emergence of alternative methods to managing plant diseases has also been affected by environmental and public health considerations [150]. The continuous use of fungicides resulting in a residue of fungicides on strawberries, the contamination of soil and water and the detrimental effects on organisms that are not the target of fungicides have all contributed to a booming market for safer and more environmentally conscious agricultural methods and production. To adapt to market demands, government and international agricultural policies are moving toward the reduction of pesticide use and are increasingly supporting more sustainable pest management practices [151].

Biological control agents may provide one of the most effective eco-friendly strategies against *B. cinerea* [152]. There are many ways to control gray mold, which include *Bacillus*, *Pseudomonas*, and *Trichoderma*, along with some antagonistic yeasts. These employ antibiosis, competition for nutrients, mycoparasitism, and the induction of plant defense mechanisms [152–154]. A variety of microbial biocontrol agents have been shown to significantly diminish the symptoms of the disease in both field and greenhouse experiments [117]. Aside from these microbial antagonists, much interest has been given to non-synthetic, user-friendly substances such as plant-based compounds, natural extracts, essential oils and products of modern application of the basic principles of nanotechnology [155]. According to Dwivedi et al. [115], sustainable strawberry production has been influenced by integrated disease management strategies. Strategies that include cultural practices, resistant cultivars, biological control agents and fungicide reduction have promoted sustainability. These strategies reduce selection pressure on the fungal population, reduce the ecological hazards associated with high chemical levels, and promote alternative ecological strategies. The long-term sustainable management of strawberry gray mold has been supported by environmentally friendly strategies [115].

5 Principles and Mechanisms of Biological Control

In contrast with synthetic fungicides that operate by targeting specific biochemical pathways, BCAs use other ways of management which are more like multiple ecological interactions that includes stimulation of plant defense reaction, competition over nutrient and space and direct antagonism via antibiosis or even mycoparasitism when it comes to benefic fungi like *Trichoderma* species [8], Fig. 4 summarize the main mechanisms of action that microbial biocontrol agents use in the biocontrol process against *B. cinerea*. In order to choose effective BCAs, the selection needs to be based on the mechanisms of action that way it helps improving the formulation aspect and application is strawberry production [156].

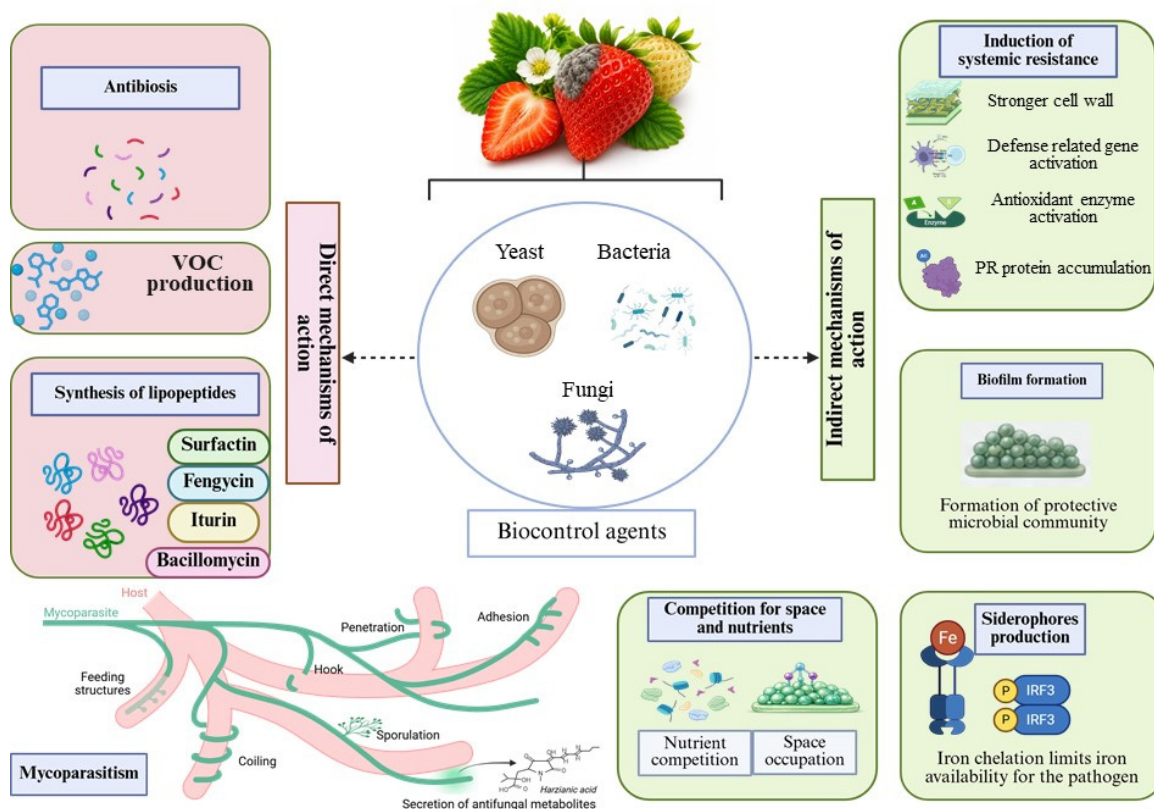


Figure 4: Mechanisms of action from microbial biocontrol agents against *Botrytis cinerea* on strawberry.

5.1 Competition for Nutrients and Space

Competition for nutrients and ecological niches represents one of the most widespread mechanisms of biological control against *B. cinerea*. It is a mechanism that involves beneficial and harmful organisms so BCA do compete over nutrients and space in addition to other direct antagonistic mechanisms like antibiosis and mycoparasitism. In any plant environment, competition has been observed for trace elements like manganese, zinc, copper and iron [157]. Additionally, microorganisms compete with one another for favorable locations as well as soluble and bioavailable iron in the soil decreases [158,159]. Early studies on strawberry already showed that microbial antagonists could reduce *B. cinerea* on leaves and fruit, but their efficacy was closely linked to their ability to colonize the treated tissue and persist at the pathogen entry site [160,161]. In postharvest cultures, yeasts can rapidly colonize wounds and fruit surfaces, consume amino acids, soluble sugars and physically occupy sites required for pathogen germination [162]. Especially in the case of *B. cinerea*, commonly known to initiate infection through senescent floral organs rich in exuded nutrients and wounded tissues, this is where rapid occupation of these sites by antagonistic microorganisms can significantly reduce pathogen establishment [163]. In this regard, fast colonization of leaves, flowers and fruit surfaces by beneficial microorganisms restricts pathogen access to essential resources required for spore germination and mycelial development [164]. Nutrient competition and spatial exclusion operate together rather than as separable mechanisms and it has been observed in several yeast-*Botrytis* systems, where attachment to pathogen structures and rapid occupation of wounds contributed to biocontrol efficacy [165,166]. It involves the solubilization and mobilization of essential elements such as phosphorus, potassium, and iron [167], especially iron because it is a limited resource in most soils and its bioavailability is often controlled by microbial siderophores. In this regard, *Bacillus* spp. also produce

siderophores, iron (Fe^{3+}) chelating molecules that play an essential role in competition for nutrients in the environment of the plant and give *Bacillus* an ecological advantage over pathogens that are unable to produce such complex agents [168,169]. Many species of the genus, such as *B. subtilis*, *B. pumilus*, *B. cereus*, *B. licheniformis*, *B. amyloliquefaciens*, *B. velezensis*, *B. thuringiensis* and *B. mojavensis*, are known to synthesize siderophores with notable antifungal properties [170]. This competition for mineral resources is the main cause of fungistasis that lowers spore germination [159]. The effectiveness of this mechanism depends largely on microbial growth rate, adaptation to environmental conditions, and persistence on plant surfaces.

5.2 Antibiosis and Production of Antimicrobial Metabolites

Antibiosis by fungal biocontrol agents involves the production and secretion of antifungal secondary metabolites that directly inhibit or kill target pathogens through diffusion into their growth medium [171], these compounds can damage fungal membranes, inhibit spore germination, disrupt cellular metabolism, or reduce mycelial growth [171]. The potential to produce gliotoxin has been observed in *T. virens* strain GV-29-8, isolated from cotton rhizosphere soil in Texas, USA, rendering it highly effective in suppressing the growth of *B. cinerea* [172]. Earlier studies showed that *T. longibrachiatum* synthesizes viridin, a steroidal antibiotic with strong activity against fungal pathogens [171,173]. *Trichoderma* species produce diverse antibiotics like gliotoxin that impairs DNA synthesis [174], viridin that blocks sterol biosynthesis and respiration [175], peptaibols which forms membrane pores and 6-pentyl- α -pyrone that disrupts hyphal integrity effectively suppressing *B. cinerea* [176]. Yeasts such as *Aureobasidium pullulans* and *Metschnikowia pulcherrima* emit volatile organic compounds (VOCs) like 2-phenylethanol, which inhibit spore germination and mycelial growth in postharvest pathogens. *Chaetomium globosum* secretes chaetoglobosins that target *Fusarium* and *Alternaria* via microtubule disruption [177]. Bacteria isolated from strawberry tissues is known to be well suited to the crop environment. For instance, de Moura et al. [178] isolated endophytic bacteria from strawberry roots and leaves and selected five *Bacillus* isolates and one *Pantoea* isolate with strong activity against *B. cinerea*, diffusible compounds from these strains reduced mycelial growth by more than 80%, while VOCs were about 90%, the isolates lowered gray mold incidence on harvested fruit.

One of the main groups of metabolites that are used in antibiosis are lipopeptides, which mainly include surfactins, iturins, and fengycins, *Bacillus* lipopeptides act by disrupting lipid bilayers and reducing the surface tension of pathogen cell membranes, leading to pore formation, osmotic imbalances, and ultimately cell lysis [179]. Among these molecules, Iturine A stands out for its ability to destabilize fungal plasma membranes, thereby limiting infections while extending the shelf life of agricultural products [180]. Surfactins, on the other hand, promote the formation of protective biofilms that limit microbial proliferation on plant surfaces, while fengycins have broad-spectrum antimicrobial activity, targeting both bacteria and fungi [181]. In addition, *Bacillus* spp. secrete various lytic enzymes, including chitinases, β -glucanases, and proteases, degrade the cell walls of phytopathogenic fungi [182]. These enzymes hydrolyze the glycosidic or peptide bonds that provide the strength of cells walls, breaking down pathogenic cells [183]. These enzymes also enhance the competitiveness of *Bacillus* and can stimulate plant defense responses through the production of phytoalexins. Thus, *B. amyloliquefaciens* FS6 produces a β -1,3-1,4-glucanase active against *B. cinerea* [184].

5.3 Mycoparasitism and Direct Pathogen Attack

When two different, unrelated species interact in a way that one is a parasite that takes advantage of a host organism, this interaction is called parasitism [185], regarding fungal biocontrol agent, many studies

reported the efficacy of *Trichoderma* fungus against various pathogenic nematodes and microorganisms. In its nature, it is a non-pathogenic and opportunistic fungus that is highly antagonistic against pathogenic microbes [186]. The mechanism behind is called mycoparasitism and it starts when *Trichoderma* wraps around the pathogen hyphae and begins to procedure appressoria, this step prevents the growth and spread of pathogenic fungi [187]. Mycoparasitism by fungal biocontrol agents like *Trichoderma* spp. involves a multi-step process where the antagonist detects, attaches to, and degrades the host pathogen's hyphae. This mechanism directly suppresses *B. cinerea* and soilborne fungi through enzymatic lysis and nutrient parasitism [188], the multi-step process involves three stages, host recognition via oligochitins, appressoria formation by hydrophobins, and degradation using lytic enzymes. *Trichoderma* species like *T. atroviride* and *T. virens* show conserved genes for these traits [189]. First, host recognition occurs via chemosensory cues like oligochitins and hydrophobins from the pathogen's cell wall, triggering G-protein-coupled receptors (GPCRs) and signaling pathways such as cyclic adenosine monophosphate (cAMP) and mitogen-activated protein kinase (MAPK). The mycoparasite forms appressoria-like structures and coils around hyphae, mediated by Tmk1 MAP kinase and Ste12 transcription factor for infection structure development [190]. On the other side, secretion of cell wall-degrading enzymes (CWDEs) chitinases, β -1,3-glucanases, proteases-lyses the host cell wall, allowing nutrient absorption while producing reactive oxygen species (ROS) for additional damage. Secondary metabolites like peptaibols and gliotoxin enhance lysis and inhibit host recovery [191]. G α subunits regulate CWDE production, infection structure formation, and secondary metabolism, deletions impair coiling and lysis. Cross-talk between cAMP, MAPK, and light response pathways fine-tunes antagonism under environmental stress. These integrate with indirect effects like competition and induced resistance for robust biocontrol [192].

5.4 Induction of Plant Defense Responses

Induced systemic resistance (ISR) represents an indirect mode of action by which some biological control agents reduce gray mold severity without necessarily inhibiting *B. cinerea* directly [31]. Unlike direct antibiosis or competition, ISR depends on the capacity of beneficial microorganisms or their metabolites to prime host defenses, allowing a faster or stronger response after pathogen challenge [193]. Classical ISR is generally associated with jasmonic acid (JA) and ethylene (ET) signaling, whereas systemic acquired resistance (SAR) is more closely linked to salicylic acid (SA) and Pathogenesis-Related proteins (PR protein) accumulation; however, these pathways interact, and their contribution may vary according to the host, antagonist and pathogen lifestyle. This distinction is particularly important for *B. cinerea*, a necrotrophic pathogen, because effective resistance often involves JA/ET-regulated defenses, controlled ROS production, callose deposition, antioxidant activity, phenylpropanoid metabolism and cell-wall reinforcement. Several microbial signals can act as ISR elicitors, including Microbe-associated molecular patterns (MAMPs), cyclic lipopeptides, siderophores, volatile compounds, cell-wall-degrading enzyme products and elicitor proteins from *Trichoderma* or bacterial antagonists [194]. Study of Yu et al. [195] showed that *Bacillus cereus* AR156 reduced gray mold, slowed fruit senescence by increasing defence-related enzyme activity and antioxidant, the study also evoked induced transcriptional responses linked to salicylic acid signalling and flavonoid metabolism. Consequently, biological control involves at the same time preservation of cellular integrity and strengthening fruit defences, which could delay the activation of quiescent infections [196,197]. Still, the mechanistic evidence is partly correlational because higher expression of defence-related genes like pattern recognition receptors (PRRs), proteins PR and resistance (R) genes and also higher antioxidant accumulation are consistent with induced resistance, but they do not show that these responses are

required for disease suppression [198]. Experiments using pathway inhibitors, deficient plant material or time-resolved measurements of defence activation and pathogen growth would provide a stronger test.

Recent strawberry-specific studies show that induced resistance against *B. cinerea* is highly dependent on genotype, elicitor type and application method. In *Fragaria vesca*, Badmi et al. used RNA-seq to analyse leaf responses after β -Aminobutyric acid (BABA) treatment and *B. cinerea* challenge. Contrary to the usual assumption that BABA uniformly primes resistance, soil-drench application increased susceptibility in leaves, with higher fungal colonization and larger necrotic lesions, while foliar application had only a weak positive effect [199]. Transcriptomic analysis showed that infection induced broad reprogramming of defense-related genes, including genes associated with pathogen recognition, defense signalling, oxidoreductase activity, terpene and phenylpropanoid metabolism, while genes related to photosynthesis and auxin responses were downregulated. This study is therefore important because it demonstrates that elicitor-induced resistance in strawberry is not automatically beneficial and may depend on the treated organ and the balance between defense activation and physiological cost. In cultivated strawberry, Murena et al. [200] further showed that induced resistance is cultivar-specific: repeated applications of BABA and (R)- β -homoserine (RBH) reduced *B. cinerea* lesion size in the cultivars Rowena and Soraya, whereas Durban did not respond. Untargeted metabolomics indicated that RBH in Rowena cultivar and BABA in Soraya cultivar triggered the strongest priming-associated metabolic reprogramming, especially in amino acid, nucleotide, flavonoid and phenylpropanoid pathways, without reducing plant growth, flowering or fruit set. Consequently, ISR-like protection in strawberry should not be presented as a simple activation of defense genes, but as a context-dependent priming state whose outcome depends on host genotype, elicitor chemistry, application route and the necrotrophic lifestyle of *B. cinerea*. In this framework, reports that *B. amyloliquefaciens* enhances strawberry defense responses after *B. cinerea* challenge are relevant, but they should be interpreted cautiously unless direct antifungal effects are experimentally separated from host-mediated resistance.

5.5 Biofilm Formation and Microbial Establishment

The persistence of biological control agents on strawberry flowers, leaves and fruit surfaces is a critical but often under-examined determinant of gray mold suppression [201,202]. In the strawberry-*B. cinerea* pathosystem, antagonists must remain active on highly exposed and nutritionally discontinuous surfaces, where UV radiation, desiccation, rainfall, fluctuating humidity and competition with resident microbiota can rapidly reduce population density [203]. The role of biofilm formation in this persistence is letting microbial cells adhere to plant tissues and become fixed in extracellular matrices that are built from proteins, polysaccharides and extracellular DNA [204,205]. In bacteria from the genus *Bacillus*, this mechanism is important because motility, sporulation and lipopeptide production are all ecological traits that are interconnected not isolated from each other, for instance, surfactin is not only involved in antimicrobial activity but also related to biofilm development and surface motility, this aspect influence all *Bacillus* bacteria in their capacity to maintain antagonistic populations and colonize plant surface [206]. This is an evidence to explain why some *Bacillus* strains perform better when they combine stable establishment with antiobiosis. As an example, recent epiphytic *Bacillus* isolates such as *B. amyloliquefaciens* MR7, which suppressed *B. cinerea* on detached fruit and under greenhouse conditions [153]. Nevertheless, *in vitro* biofilm formation should not be equated to effective colonization *in planta* because a bacteria may form persistent biofilms on abiotic surfaces but can probably fail to adhere on flowers or fruit, while another one may establish efficiently through rapid growth, adhesion, nutrient acquisition or stress tolerance without forming a biofilm. Moving to yeasts, they are also known by protecting strawberry but differently and are

particularly useful after harvest [207,208]. This is mainly because they are known by colonizing wounds quickly and consuming sugars and other nutrients, this is another kind of pressure they apply to the pathogen before becoming established without directly killing *B. cinerea* [209]. For instance, *Aureobasidium pullulans*, a yeast-like fungus tested against strawberry gray mold. Iqbal et al. found that *A. pullulans* reduced the development of *B. cinerea* on detached strawberry leaves, fruit, and whole plants [210]. Later work showed that this activity is linked to several traits, including rapid growth, extracellular enzyme production, antifungal metabolites, and strong colonization of host surfaces [211]. Its biocontrol effect therefore appears to involve more than direct antagonism. By establishing itself on fruit or floral surfaces, *A. pullulans* may limit the nutrients and infection sites available to *B. cinerea*. Other studies before showed the same effect for *Galactomyces candidum* JYC1146 despite this strain is particularly associated with the production of VOCs but commercial use of it would require measurements of VOCs in actual packages or storage facilities, tests for sensory effects and evidence that inhibitory concentrations can be maintained without reducing fruit quality. On the other hand, the strain efficacy fits also with rapid establishment on the fruit surface that way it can restrict the resources and infection space available to *B. cinerea* [212]. In the same way, *Yarrowia lipolytica* MBC25 has shown activity both before and after harvest, suggesting that some yeasts may act at several points in the disease cycle [213]. Still, a result from one cultivar or controlled environment cannot establish performance across production systems. As with other yeast-based antagonists, this type of protection is likely to work best when applied preventively, before the pathogen penetrates the tissue or resumes growth from latent infections. Once *B. cinerea* is established inside host tissues, a surface-acting antagonist is less likely to provide curative control [214]. Therefore, microbial establishment should be considered a functional component of biocontrol, but it requires direct evidence, such as population monitoring, microscopy, reporter-tagged strains or recovery assays from treated tissues.

6 Diversity of Biological Control Agents

6.1 Antagonistic Fungi

Among the effective studied microorganisms as BCAs, fungal antagonists particularly *Trichoderma* species and *Clonostachys rosea*, have been investigated for their effects against *B. cinerea*. *Trichoderma* spp. are filamentous fungi that live in soil and are known for their role as opportunistic symbionts of plants [215]. *Trichoderma* is an important genus due to its strong capacity and potential in the control of phytopathogens [216]. Certain studies have reported the effective potential of *Trichoderma* species in the management of *B. cinerea* both in pre- and post-harvest of strawberries. According to Fan et al. [217] *T. asperellum* T7 inhibited the germination of conidia and the mycelial growth of *B. cinerea* through damaging the integrity of cell membranes. The VOCs produced by this strain were the main cause of its antagonistic effect, as these molecules showed a biocontrol efficacy of 76.9% on strawberries. In another study, *T. harzianum* have been shown a reduction of the mycelial growth of *B. cinerea* *in vitro* by 51.3% [218]. Also, the assay on strawberry fruits showed that this strain had a higher reduction effect on disease incidence (75%). In a study conducted by Balode [219], it was reported that the treatment with aqueous solution (300 L/ha) of the Biomikss containing two *Trichoderma* strains (*T. harzianum* 7-t and *T. viride* A-L) at a concentration of (10^7 – 10^9 CFU/mL) resulted in a significant decrease in disease incidence of gray mold under field conditions. Awad & Al-Shennawy [220] reported that the pulverization of pre-inoculated strawberry fruits with the culture filtrates of *Trichoderma* spp., *T. harzianum* (isolate 1), and *T. hamatum* (2 isolates), significantly decreased the infection on the four tested cultivars. Alizadeh et al. [221] studies the effect of *T. koningii* (T21) on the mycelial growth of *B. cinerea* *in vitro*. The finding revealed that this strain inhibited the pathogen growth effectively through branching at the end of *B. cinerea* hyphae, coiling,

lyses and vacuolization of pathogen hyphae. Moreover, the greenhouse trial demonstrated an important antagonistic effect of *T. koningii* (T21) by reducing the disease severity of gray mold by 56% [221].

Fungi of the genus *Clonostachys* are widely distributed in soil and play an essential role in plant decomposition [222]. Due to its ability to suppress sporulation of phytopathogenic fungi (mycoparasitic lifestyle), colonize senescent and dead tissue, induce plant resistance, and promote plant growth, *Clonostachys* has gained importance as a valuable multifunctional BCA [223,224]. *C. rosea* (syn. *Gliocladium roseum*) is particularly distinguished as a necrotrophic mycoparasite of several phytopathogenic fungi, including *B. cinerea*. For instance, Cota et al. [225] applied *C. rosea* under field condition over two consecutive growing seasons. It was demonstrated that *C. rosea* effectively colonizes strawberry leaves, which increased colonization levels by up to 80% with twice-weekly applications. This colonization significantly suppressed the sporulation of *B. cinerea* by approximately 70% on leaves, decreased the incidence of gray mold on flowers by 50%, and on fruits by 45%, compared to untreated controls. These disease reductions corresponded with a significant increase in strawberry yield, improving fruit production by 35% [225]. Nobre et al. [226] reported that *C. rosea* isolates decreased the sporulation of *B. cinerea* on leaves of strawberries by 96.8%. Similarly, it was reported that the culture filtrate of *C. rosea* strains (NCR19/F, NCR60/F, NCR61/F and NCR62/F) significantly inhibited the mycelial growth and conidial germination of *B. cinerea* compared to the untreated control [227].

6.2 Beneficial Bacteria

As with fungi, there are numerous researches investigated the application of beneficial bacteria for the management of plant pathogens [228]. It is easy to obtain bacteria as control agents because they are abundant in nature. Interestingly, antagonistic bacteria can be isolated from the surface of plant tissues, roots, soil, as well as plant rhizosphere [229,230]. Moreover, endophytic bacteria are in high demand as BCAs since they can colonize plant tissues to form internal defenses against pathogens [231].

The *Bacillus* genus is the most studied genus of bacteria, as it has the ability to produce multiple sources of antimicrobial (antibiotics) and non-antimicrobial (enzymes and lipopeptides) molecules, in addition to the capacity to induce systemic resistance [232]. Species of this genus are considered safe and are used in agriculture due to their beneficial effects, as well as to the endospore property of this species because it allows to survive under unfavorable conditions like drought and heat [233,234]. There are many studies until now that examined the antagonist ability of *Bacillus* species to control *B. cinerea*. Hang et al. [235], for example, reported that the strain *B. subtilis* S1-0210 inhibited the mycelial growth of *B. cinerea* *in vitro* (80%). The results showed that when it was applied as a wettable powder, the strain S1-0210 showed a reduction in the incidence of gray mold on strawberries to less than 5%, and that's in comparison with the untreated controls (70%). In addition, the greenhouse experiment revealed that *B. subtilis* S1-0210 has been very effective in the control of gray mold incidence (85–89%) and that pretreatment was more effective than post-infection application. Furthermore, the results of field trial revealed a reduction of the disease by approximately 70%.

The result of the study conducted by Hassan et al. [236] revealed that the B3 strain of *B. safensis* was very effective in the suppression of the mycelial development of *B. cinerea* Str5. Further, this strain was able to reduce the severity of the disease by 86.52% on the strawberry fruits. Hassan et al. [236] explained these results by the ability of *B. safensis* Str5 to secrete the lytic enzymes (protease, lipase, and chitinase). According to Wang et al. [237] the treatment with *B. halotolerans* KLBC XJ-5 was found to be effective in the inhibition of the growth of *B. cinerea* mycelia *in vitro* with an inhibition rate of 73%. Also, the strain decreased the severity of gray mold after 4 days of incubation in strawberries compared to untreated

controls. The sequencing of KLBC XJ-5 genome allows the identification of genes with antimicrobial and chitin degradation properties. Interestingly, *B. halotolerans* KLBC XJ-5 had no negative affect on the nutritional quality of the fruits in terms of ascorbic acid, titratable acidity, and total soluble solids [237].

Toral et al. [238] studied the effect of the strain XT1 of *B. velezensis* and demonstrated that it had a dual effect as a plant growth-promoting rhizobacteria (PGPR) and as an effective BCA. Indeed, the application of XT1 to the foliage and roots of strawberry plants showed an increase in the biomass of plants and development of root system. Treatment with XT1 reduced the incidence of disease by 50% and its severity by 60%. Also, *B. velezensis* XT1 caused deposition of callose, which enhanced the defense mechanism of the plants against the pathogen. The biocontrol activity of *B. velezensis* XT1 has been attributed to the effect of phytohormonal regulation that involves jasmonic acid (JA) and ethylene that stimulate the immune system of the plant [238]. Other strains like *B. amyloliquefaciens* RS-25 and *B. subtilis* Z-14 have been also demonstrated to be effective in the suppression of postharvest gray mold by the production of lipopeptides, VOCs (esters), and enzymes (protease and cellulase) and also in the formation of biofilms that attach to the surfaces of fruits [239].

Pseudomonas spp. is another well-documented bacterium with biocontrol properties and widely used in agricultural settings [240]. Several strains have been evaluated in strawberry systems, both *in vitro* and *in vivo*, which proved their effect as biocontrol agents. For instance, *P. fluorescens* UM270 significantly reduced postharvest gray mold incidence in strawberries, achieving approximately 55% disease reduction while also maintaining fruit firmness compared to untreated controls [241]. The antagonistic effect was due to the capacity to produce diffusible antifungal molecules and VOCs such as 2,4-diacetyl phloroglucinol, auxins, fengycins, siderophores, and N, N-dimethyl-hexadecyl amine, among others. In *in vitro* conditions, *P. protegens* ML15 inhibited the growth of *B. cinerea* [242]. Genomic analysis revealed that this strain is enriched with 18 distinct genetic regions with the capacity for the production of secondary metabolites, known for their crucial role in biocontrol responses against phytopathogens.

In addition to the extensively studied *Bacillus* and *Pseudomonas* species, Actinomycetes have also demonstrated significant potential as biocontrol agents against *B. cinerea* in strawberries. For example, *Streptomyces* species, particularly *Streptomyces* sp. sdu1201, have shown important antifungal activity through the production of actinomycin D, which inhibits *B. cinerea* with an EC₅₀ value of 7.65 µg/mL and reduces disease severity on strawberry leaves by 78.77% within three days. The study of Silva et al. [243] revealed that *Streptomyces araujoniae* ASBV-1 produced a multiantibiotic complex with ionophoric properties that effectively controlled the gray mold disease caused by *B. cinerea*. They reported that the complex includes actinomycins and ionophorous antibiotics that inhibited the mycelial growth of the pathogen and reduced disease severity on strawberry fruits and leaves, with control efficiencies exceeding 45%. Similarly, Lyu et al. [244] demonstrated a strong antifungal effect of the metabolites reveromycins A and B produced by *Streptomyces* sp. 3–10 against *B. cinerea* and other plant pathogenic fungi. In fact, reveromycin A at 50 and 100 µg/mL completely suppressed *B. cinerea* *in vitro* and in a strawberry food model system, showing efficacy comparable to commercial fungicides without phytotoxic effects on strawberry plants.

Bacillus and *Pseudomonas* species remain the most extensively investigated bacterial antagonists against *B. cinerea*, recent studies indicate that lactic acid bacteria also represent promising food-grade biopreservation agents for postharvest strawberry protection. In particular, probiotic *Lactiplantibacillus plantarum* strains have demonstrated significant antagonistic activity by reducing fungal growth on strawberries while preserving fruit nutritional quality and improving sensory attributes. Moreover, the application of LAB through fermented strawberry juice offers an innovative and sustainable strategy that

combines biological control with enhanced food safety and functional quality, highlighting the potential of LAB as complementary biocontrol agents for postharvest disease management [245].

6.3 Antagonistic Yeasts

Yeasts have also been investigated as promising BCAs, particularly in fruit systems [246]. Compared to bacteria, they offer various advantages, including simple nutritional needs, rapid growth, and the capacity to persist on the surface of dry plants for long periods [247]. Moreover, yeasts are generally considered environmentally safe, because they do not produce harmful metabolites that could pose toxicological risks; sometimes this limitation is associated with certain bacterial strains [248]. Also, the efficacy of yeasts is enhanced by the diverse mechanisms through which they can suppress pathogens.

At present, various studies have reported the important antifungal effect of different yeast genera in the context of the biocontrol of *B. cinerea*. For instance, the strain JYC1146 of *Galactomyces candidum* exhibited strong inhibition of the proliferation of *B. cinerea* both *in vitro* and *in vivo* by the production of VOCs that suppressed the development of the fungi on the surface of strawberry fruits. This strain significantly reduced the severity of the infection under controlled conditions, but its biological control effect decreased at refrigerated storage temperatures (4°C), which makes its post-harvest application under refrigerated conditions limited [212]. Qin et al. [249] reported that the *Hanseniaspora uvarum* strain inhibited mycelial growth and spore germination of *B. cinerea* *in vitro*. In the same study, the *in vivo* assay revealed that the strain significantly reduced the severity of gray mold on strawberries through the production of VOCs. In addition, the treated fruits maintained their appearance, total soluble solids content, and firmness compared to the positive control. The yeast strain *Yarrowia lipolytica* MBC25 significantly reduced the severity of gray mold on strawberries by around 60% under pre-harvest and post-harvest conditions [213]. They revealed that the biocontrol effect of this strain was achieved through multiple mechanisms, including competition for nutrients and space, the production of antifungal metabolites, and the possible induction of resistance in the host. Furthermore, the application of *Y. lipolytica* MBC25 at a concentration of 10^8 CFU/mL was effective in suppressing the growth of the pathogen without altering the quality of fruits and helped maintain the shelf life of strawberries after harvest.

Overall, the biological control agents evaluated against *B. cinerea* differ considerably in their mechanisms of action, efficacy, ecological adaptability, formulation potential, and degree of commercial development. Table 2 provides a comparative overview of the principal fungal, bacterial, and yeast-based antagonists investigated for gray mold management in strawberry.

Table 2: Comparative overview of the principal biological control agents evaluated against *Botrytis cinerea* in strawberry.

Biological Control Agent	Strain/Isolate	Experimental Context	Principal Mechanisms	Reported Efficacy	Main Advantages	Current Limitations	Commercial Availability	References
<i>Trichoderma asperellum</i>	T7	<i>In vitro</i> and postharvest strawberry fruit	VOC production, membrane disruption, inhibition of conidial germination and mycelial growth	76.9% biocontrol efficacy on strawberry fruit	Multiple antagonistic mechanisms; potential fumigant application; may extend shelf life	VOC composition and effective concentration require standardization; field validation remains limited	Experimental strain; commercial <i>Trichoderma</i> -based products exist, but not necessarily this strain	[217]
<i>Trichoderma harzianum</i>	Study-specific isolate	<i>In vitro</i> and strawberry fruit	Antibiosis, competition, lytic enzymes, possible mycoparasitism	51.3% inhibition of mycelial growth and 75% reduction in disease incidence	Broad-spectrum activity; multiple modes of action; well-established formulation potential	Performance may vary with strain, temperature, humidity, and colonization capacity	Commercial products based on <i>T. harzianum</i> strains exist; availability and registered uses vary geographically	[218]
<i>T. harzianum</i> + <i>T. viride</i>	7-t and A-L, Biomikss	Field application	Competition, antibiosis, mycoparasitism, establishment on plant surfaces	Significant reduction in gray mold incidence under field conditions	Evidence of field applicability; combination may broaden functional traits	Exact contribution of each strain and consistency across seasons require clarification	Product/formulation reported in the study; regional availability should be verified	[219]
<i>Trichoderma harzianum</i> and <i>T. hamatum</i>	Culture filtrates from three isolates	Postharvest fruit and multiple cultivars	Secreted antifungal metabolites and hydrolytic enzymes	Significant reduction of infection across four strawberry cultivars	Cell-free metabolites may simplify storage and application	Metabolite stability, dose standardization, toxicological assessment, and field persistence require investigation	Experimental	[220]
<i>Trichoderma koningii</i>	T21	<i>In vitro</i> and greenhouse	Hyphal coiling, lysis, vacuolization, and mycoparasitism	56% reduction in disease severity under greenhouse conditions	Direct attack on pathogen hyphae; strong mechanistic evidence	Older study; limited recent field and formulation data	Experimental	[221]
<i>Clonostachys rosea</i>	Field-applied isolate	Two-season field study	Colonization of senescent tissues, competition, mycoparasitism, suppression of sporulation	Approximately 70% reduction in leaf sporulation, 50% reduction on flowers, 45% reduction on fruit, and 35% yield increase	Strong field evidence; suppresses inoculum and disease at multiple crop stages	Requires frequent preventive application and successful tissue colonization	Available, strain-specific products such as PRESTOP/LALSTOP contain <i>C. rosea</i> J1446; registration varies by country	[225]

Table 2: Cont.

Biological Control Agent	Strain/Isolate	Experimental Context	Principal Mechanisms	Reported Efficacy	Main Advantages	Current Limitations	Commercial Availability	References
<i>Clonostachys rosea</i>	Selected Brazilian isolates	Strawberry leaves	Mycoparasitism, competition, and suppression of pathogen sporulation	Up to 96.8% reduction in <i>B. cinerea</i> sporulation	Very strong suppression of secondary inoculum	Isolate-dependent activity; disease reduction on fruit and commercial-scale consistency require confirmation	Experimental isolates; commercial availability exists for other strains	[226]
<i>Clonostachys rosea</i>	NCR19/F, NCR60/F, NCR61/F, NCR62/F	<i>In vitro</i>	Diffusible antifungal metabolites	Significant inhibition of mycelial growth and conidial germination	Potential source of bioactive metabolites and cell-free products	Active compounds, stability, safety, and formulation remain insufficiently characterized	Experimental	[227]
<i>Bacillus subtilis</i>	S1-0210	<i>In vitro</i> , fruit, greenhouse, and field	Antibiosis, competition, enzymes, biofilm formation, and preventive colonization	80% <i>in-vitro</i> inhibition; disease incidence below 5% versus 70% in controls; 85–89% greenhouse control; approximately 70% field reduction	Strong evidence across multiple experimental scales; endospore formation favors formulation and shelf life	Preventive treatment was more effective than curative application; strain-specific environmental performance	Experimental strain; commercial <i>Bacillus</i> products exist, including QST 713-based Serenade formulations	[235]
<i>Bacillus safensis</i>	B3	<i>In vitro</i> and strawberry fruit	Protease, lipase, chitinase, and direct antagonism	86.52% reduction in disease severity	High fruit-level efficacy and production of several lytic enzymes	Limited field evidence, formulation studies, and ecological persistence data	Experimental	[236]
<i>Bacillus halotolerans</i>	KLBC XJ-5	<i>In vitro</i> and postharvest fruit	Antimicrobial metabolites, chitin degradation, and pathogen growth inhibition	73% inhibition of mycelial growth and reduced fruit disease severity	Did not adversely affect ascorbic acid, acidity, or soluble solids	Field efficacy, shelf life, and formulation performance remain unknown	Experimental	[237]
<i>Bacillus velezensis</i>	XT1	Strawberry foliage, roots, and disease assays	Induced resistance, callose deposition, JA/ET-related signaling, PGPR activity, and direct antagonism	50% reduction in disease incidence and 60% reduction in severity	Combines disease suppression with plant-growth promotion	Outcome may depend on cultivar, application route, and environmental conditions	Experimental strain; commercial products based on other <i>B. velezensis</i> / <i>B. amyloliquefaciens</i> strains exist	[238]

Table 2: *Cont.*

Biological Control Agent	Strain/Isolate	Experimental Context	Principal Mechanisms	Reported Efficacy	Main Advantages	Current Limitations	Commercial Availability	References
<i>Bacillus amyloliquefaciens</i> and <i>B. subtilis</i>	RS-25 and Z-14	Postharvest fruit	Lipopeptides, VOCs, protease, cellulase, and biofilm formation	Effective suppression of postharvest gray mold	Multiple mechanisms and strong formulation potential due to endospores	Comparative field efficacy and strain persistence require further study	Experimental strains; commercial products exist at the species/strain-group level	[239]
Endophytic <i>Bacillus</i> spp. and <i>Pantoea</i> sp.	Five <i>Bacillus</i> isolates and one <i>Pantoea</i> isolate	<i>In vitro</i> and harvested fruit	Diffusible compounds and VOCs	Diffusible compounds inhibited mycelial growth by >80%; VOC-mediated inhibition reached about 90%; fruit incidence was reduced	Strawberry-adapted endophytes may colonize the crop more effectively than non-native strains	Taxonomic resolution, biosafety, formulation, and field validation are needed	Experimental	[178]
<i>Pseudomonas fluorescens</i>	UM270	Postharvest strawberry	Diffusible metabolites, VOCs, siderophores, competition, and possible auxin-mediated effects	Approximately 55% reduction in gray mold incidence; fruit firmness maintained	Strong metabolic diversity and potential fruit-quality preservation	Gram-negative bacteria may present greater formulation and shelf-life challenges than endospore-forming <i>Bacillus</i>	Experimental strain	[241]
<i>Streptomyces</i> sp.	sdu1201	<i>In vitro</i> and strawberry leaves	Actinomycin D production	EC ₅₀ of 7.65 µg/mL; 78.77% reduction in disease severity after three days	Potent defined metabolite and strong leaf-level efficacy	Antibiotic-related residue, resistance, toxicological, and regulatory considerations require assessment	Experimental	[117]
<i>Streptomyces araujoniae</i>	ASBV-1	Strawberry fruits and leaves	Multiantibiotic complex containing actinomycins and ionophoric metabolites	Control efficiencies exceeding 45%	Multiple active compounds may broaden antifungal activity	Complex composition complicates standardization, safety assessment, and registration	Experimental	[243]

Table 2: Cont.

Biological Control Agent	Strain/Isolate	Experimental Context	Principal Mechanisms	Reported Efficacy	Main Advantages	Current Limitations	Commercial Availability	References
<i>Streptomyces</i> sp.	3–10	<i>In vitro</i> and strawberry food-model system	Reveromycins A and B	Reveromycin A at 50–100 µg/mL completely inhibited <i>B. cinerea</i> and showed activity comparable to commercial fungicides	Strong activity with no reported phytotoxicity in the evaluated system	Food-model findings require validation on commercial fruit, residue assessment, and formulation development	Experimental	[244]
<i>Galactomyces candidum</i>	JYC1146	<i>In vitro</i> and postharvest strawberry	VOC production and rapid surface establishment	Strong disease suppression under controlled conditions	Non-contact fumigation potential	Reduced activity at 4°C; VOC dose, sensory effects, and package-scale performance require validation	Experimental	[212]
<i>Hanseniaspora uvarum</i>	Study-specific strain	<i>In vitro</i> and postharvest strawberry	VOC production; inhibition of mycelial growth and spore germination	Significant reduction in disease severity while preserving appearance, firmness, and soluble solids	Good compatibility with fruit-quality preservation	Cold-storage performance, formulation, and consistency require further assessment	Experimental	[249]
<i>Yarrowia lipolytica</i>	MBC25	Preharvest and postharvest strawberry	Nutrient and space competition, antifungal metabolites, and possible induction of host resistance	Approximately 60% reduction in disease severity at 10 ⁸ CFU/mL	Active at more than one stage of the production chain and preserved fruit quality	High inoculum requirement; field-scale reproducibility and shelf-life data remain limited	Experimental	[213]
<i>Aureobasidium pullulans</i>	Study-specific beneficial isolate	Detached leaves, fruit, and whole strawberry plants	Competition for nutrients and infection sites, extracellular enzymes, metabolites, and rapid surface colonization	Reduced disease development across several strawberry assay systems	Strong epiphytic fitness and suitability for preventive applications	Surface-active protection is mainly preventive; isolate-specific performance and environmental dependence remain concerns	Yes at species/strain level: BOTECTOR contains DSM 14940 and DSM 14941, although these are not necessarily the same isolate evaluated in the manuscript	[210]

7 Natural Substances and Plant-Based Antifungal Compounds

In the last years, researchers have shown great interest to the use of essential oils and extracts derived from plants because of their effectiveness against several pathogens [250–252].

Essential oils (EOs) are mixtures of volatile and lipophilic phytochemical extracted from aromatic plants. Much research has been conducted on their effect in the management of gray mold [253]. For example, de Albuquerque Sousa et al. [254] revealed that, at a minimal concentration of 0.85 mg/mL, the essential oils of cinnamon, clove, and lemongrass have been inhibited completely (100%) the mycelial growth of the pathogen. This effect was related to their richness with important compounds, which included citronellal, β -citral, eugenol, and cinnamaldehyde. In their study, Gebel and Magurno [255] reported that the treatment of strawberry fruits with EO of thyme at a dilution of 500 $\mu\text{L mL}^{-1}$, suppressed fungal infection for seven days, while the control group showed a high level of infection. In addition, the treated strawberries retained better firmness and color than the untreated fruit [255].

Also, some research has studied the application of EOs in vapor phase. In fact, Tančinová et al. [256] demonstrated that the application of certain essential oils (lavender, lemongrass, litsea, peppermint, and thyme) in vapor phase inhibited completely the growth of *B. cinerea* strains at a concentration of 625 $\mu\text{L/L}$. Between these treatments, essential oil of peppermint was the only one to prevent the development of lesions at the lowest concentration, which was 125 $\mu\text{L/L}$, on inoculated fruit. However, sensory evaluation revealed that lemongrass and litsea EOs maintained better profiles of taste and aroma at this concentration. A study conducted by Yan et al. [257] found that vapor of thyme and oregano essential oils significantly reduced mycelial growth *B. cinerea* by damaging fungal cell membranes and causing leakage of nucleic acids, proteins, and sugars. When applied in packaging of strawberries, the disease index reduction reached 53.85% and 57.69%, respectively for thyme and oregano treatments. Also, oregano EO preserved strawberry fruit quality by preventing weight loss and soluble solid degradation. The vapor phase method has the advantage of reducing direct contact with oils, thus minimizing possible alterations to the taste and aroma of the fruit, and offers better diffusion within the packaging environment [258].

Although the antifungal effect of various EOs has been proven against *B. cinerea*, their mode of action remains poorly understood [259]. Current evidence suggests that essential oils primarily target the cytoplasmic membranes of microbial cells. Maissa and Walid [260] demonstrated that the antifungal effect of tea tree EO against *B. cinerea* attributed to modifications in the permeability of membrane cells and in a loss of the function of cellular organelles. In fact, the antifungal effect is primarily attributed to the presence of monoterpenes and phenolic compounds such as thymol, carvacrol, camphor, and eugenol, which compromise the fungal plasma membrane and increase permeability, leading to cytoplasmic leakage and cell death [261,262]. Due to their hydrophobic nature, essential oils can integrate into the fungal lipid bilayer where they can disrupt its integrity [263]. In addition, certain essential oils may activate mechanisms of plant defense; for example, oil of thyme induced resistance in apple fruit by the activation of defense responses against *B. cinerea* [264]. These mechanisms could also work in strawberries, helping to enhance their resistance.

Beyond EOs, extracts from medicinal plants, aqueous preparations, ethanol-based preparations, or preparations based on other solvents derived from botanical materials [265], have attracted growing interest as an alternative strategy for controlling gray mold in strawberries. These extracts contain complex mixtures of bioactive compounds (phenolics, flavonoids, alkaloids, saponins, sulfur compounds, etc.) and generally have low toxicity, biodegradability, and, for many of them, compatibility with food crops [266,267]. The synergistic action of these metabolites contributes to the inhibition of plant pathogens through various

mechanisms, such as disruption of cell membrane integrity, interference with spore germination, inhibition of mycelial growth, and in some cases induction of host defense responses [268,269].

Indeed, several studies reported the inhibitory potential of plant extracts against *B. cinerea*. For instance, Priya et al. [202] reported that neem extract (15% w/v) showed a higher antifungal effect with an inhibition rate of the mycelial growth of *B. cinerea* of 76.66%. Similarly, Šernaitė et al. [270] demonstrated that clove extract exhibited strong antifungal activity, inhibiting *B. cinerea* mycelial growth by more than 80% at a concentration of 200 $\mu\text{L/L}$ and achieving complete (100%) inhibition at 600–2000 $\mu\text{L/L}$ *in vitro*. Daniel et al. [271] reported that aqueous extract of garlic demonstrated a higher antifungal activity against *B. cinerea* in *in vitro* condition, with a total inhibition of mycelial growth and spore germination. The extract of neem that was obtained from leaves or seeds of *Azadirachta indica*, also has an important antifungal property [272]. Ali et al. [272] revealed that the efficacy of this extract against *B. cinerea* is the result of the synergistic action of triterpenoids and limonoids, including azadirachtin, which interfere with cell division and metabolism of the fungi. Eucalyptus leaf extract, which is rich in tannins and phenolic compounds, has been shown to suppress fungal growth and delay the development of gray mold symptoms on strawberries [273].

Although EOs and plant extracts represent important biological alternatives for the control of *B. cinerea* in strawberries, several constraints limit their practical application. The high volatility and low persistence of EOs and many plant extracts are a major challenge to their effectiveness under ambient conditions. As documented by Chang et al. [263], the majority of EOs are highly volatile, suffer from low water solubility, and are rapidly lost under storage or field conditions, which limits their long-lasting efficacy. The instability and variable composition of these compounds represents another important limitation. In fact, the chemical composition of essential oils varies depending on plant cultivar, conditions of harvest, the technique used for the extraction, and the conditions applied for their storage. The variation of all these criteria leads to inconsistent antifungal effects [253]. Furthermore, some EOs or extracts may cause phytotoxicity or alteration of the organoleptic properties of the fruits if used at high doses; for example, the sensory evaluation of strawberries treated with certain EOs revealed decreased taste, aroma and overall quality even at effective antifungal concentrations [256]. Additionally, the lipophilic and volatile nature of these compounds necessitates the development of advanced technologies for their formulation (nanoemulsions, encapsulation, coatings) to improve their release and stability, and to adhere effectively to fruit surfaces. Without improvements to the formulation, use in real-world field conditions or post-harvest may yield poor results. Therefore, as Chang et al. [263] highlighted, the development of standardized and effective delivery systems for essential oils in horticultural applications remains a crucial research priority.

Natural products evaluated against *B. cinerea* differ substantially in their chemical composition, mode of application, antifungal efficacy, persistence, and effects on fruit quality. Table 3 summarizes the principal essential oils, botanical extracts, and naturally derived antifungal compounds investigated for gray mold management in strawberry.

Table 3: Comparative overview of natural products evaluated against *Botrytis cinerea* in strawberry.

Natural Product	Principale Source or Active Compounds	Application or Experimental Context	Main Mechanisms of Action	Reported Efficacy	Main Advantages	Current Limitations	Commercial Availability	References
Cinnamon essential oil	<i>Cinnamomum</i> spp.; cinnamaldehyde	<i>In vitro</i> direct-contact assays	Membrane disruption, increased permeability, cytoplasmic leakage, interference with fungal metabolism	Complete inhibition of mycelial growth at 0.85 mg/mL in the cited comparative study	Strong antifungal activity at relatively low concentrations; suitable for encapsulation and vapor delivery	High volatility, low water solubility, possible sensory effects and phytotoxicity at elevated doses	Essential oil is commercially available, but standardized strawberry gray-mold products are not clearly established	[254]
Clove essential oil	<i>Syzygium aromaticum</i> ; eugenol	<i>In vitro</i> assays	Membrane destabilization, leakage of cellular constituents, inhibition of spore germination and mycelial growth	Complete inhibition at 0.85 mg/mL in one study	Potent broad-spectrum activity; eugenol is a well-characterized antifungal constituent	Strong aroma may affect fruit acceptability; composition varies with origin and extraction	Commercially available as an essential oil; crop-protection registration varies	[254]
Lemongrass essential oil	<i>Cymbopogon citratus</i> ; citronellal and citral isomers	Direct-contact and vapor-phase assays; postharvest strawberry	Disruption of fungal membranes and cellular leakage	Complete mycelial inhibition at 0.85 mg/mL; complete vapor-phase inhibition at 625 µL/L in another study	Strong antifungal activity; vapor delivery reduces direct fruit contact	Volatility, compositional variability and possible aroma transfer	Commercial essential oil available; no strain- or crop-specific antifungal registration should be assumed	[256]
Thyme essential oil	<i>Thymus vulgaris</i> ; thymol and carvacrol	Direct fruit treatment, vapor phase and package atmosphere	Membrane disruption, cytoplasmic leakage, inhibition of respiration; possible induction of host defenses	Suppressed infection for seven days at the reported dilution; vapor treatments also reduced disease development	Strong antifungal activity; compatible with vapor, coating and nanoemulsion systems	Strong odor, potential sensory alteration, rapid volatilization and inconsistent persistence	Essential oil commercially available; standardized postharvest formulations remain limited	[255]
Oregano essential oil	<i>Origanum</i> spp.; carvacrol and thymol	Vapor treatment in strawberry packaging	Membrane damage, leakage of nucleic acids, proteins and sugars	Disease-index reduction of 57.69% in the cited packaging study	Effective through indirect vapor exposure; preserved soluble solids and reduced weight loss	Aroma intensity, dose optimization, package standardization and volatility	Essential oil commercially available; specialized gray-mold products are not widely established	[257]

Table 3: Cont.

Natural Product	Principale Source or Active Compounds	Application or Experimental Context	Main Mechanisms of Action	Reported Efficacy	Main Advantages	Current Limitations	Commercial Availability	References
Peppermint essential oil	<i>Mentha piperita</i> ; menthol and menthone-rich mixtures	Vapor-phase treatment of inoculated strawberries	Membrane and metabolic disruption; inhibition of germination and mycelial development	Prevented lesion development at 125 $\mu\text{L/L}$ in the cited study	Effective at a lower vapor concentration than several oils tested	Possible transfer of mint aroma and flavor; efficacy may depend on headspace volume and temperature	Commercial essential oil available	[256]
Lavender essential oil	<i>Lavandula</i> spp.; linalool and linalyl acetate-rich mixtures	Vapor-phase <i>in vitro</i> evaluation	Membrane perturbation and inhibition of fungal growth	Complete growth inhibition at 625 $\mu\text{L/L}$ in the cited study	Volatile application allows broad distribution within packages	Lower potency than peppermint in the fruit assay; aroma effects require evaluation	Commercial essential oil available	[256]
Litsea essential oil	<i>Litsea cubeba</i> and related species; citral-rich oil	Vapor-phase treatment	Membrane disruption and inhibition of fungal growth	Complete inhibition at 625 $\mu\text{L/L}$; acceptable sensory profile at the lower tested concentration	Favorable aroma profile relative to some other essential oils	Limited field and commercial-package validation	Commercial essential oil available	[256]
Tea tree essential oil	<i>Melaleuca alternifolia</i> ; terpinen-4-ol-rich oil	Mechanistic <i>in vitro</i> studies against <i>B. cinerea</i>	Alteration of membrane permeability and impairment of cellular organelles	Antifungal activity demonstrated, but no directly comparable strawberry disease-reduction value is provided in the manuscript	Well-characterized antimicrobial action	Strong aroma, potential phytotoxicity and insufficient strawberry-specific efficacy data	Commercial essential oil available	[260]
Neem extract	<i>Azadirachta indica</i> leaves or seeds; limonoids and triterpenoids, including azadirachtin	<i>In vitro</i> assays against <i>B. cinerea</i>	Interference with fungal metabolism and cell division; inhibition of mycelial growth	76.66% inhibition at 15% w/v in one cited study	Biodegradable botanical source; multiple bioactive constituents	Extract composition depends on plant part, solvent and preparation; comparatively high application concentration	Neem-based agricultural products exist, but efficacy and registration against strawberry gray mold are product-specific	[202]
Clove extract	<i>S. aromaticum</i> botanical extract	<i>In vitro</i> assay	Phenolic-mediated membrane damage and inhibition of mycelial growth	>80% inhibition at 200 $\mu\text{L/L}$ and complete inhibition at 600–2000 $\mu\text{L/L}$	Strong <i>in-vitro</i> activity; preparation may be simpler than purified compounds	High effective concentrations, sensory effects and absence of field validation	Experimental for this use	[270]

Table 3: Cont.

Natural Product	Principale Source or Active Compounds	Application or Experimental Context	Main Mechanisms of Action	Reported Efficacy	Main Advantages	Current Limitations	Commercial Availability	References
Garlic aqueous extract	<i>Allium sativum</i> ; sulfur-containing compounds such as allicin-related constituents	<i>In vitro</i> assay	Inhibition of spore germination and mycelial growth; disruption of fungal metabolism	Complete inhibition of mycelial growth and spore germination in the cited <i>in-vitro</i> study	Low-cost source and strong activity	Chemical instability, strong odor and absence of direct strawberry-fruit validation in the cited study	Experimental for strawberry gray mold	[271]
Eucalyptus leaf extract	<i>Eucalyptus</i> spp.; tannins, phenolics and other secondary metabolites	Postharvest application to strawberry	Direct fungal suppression, antioxidant effects and preservation of fruit physiology	Suppressed fungal development and delayed gray-mold symptoms while maintaining physicochemical quality	Combines antifungal action with fruit-quality preservation	Extract standardization, residue characterization and sensory evaluation are needed	Experimental	[273]
Citrus essential oils	Citrus peel oils; commonly limonene-rich, with composition depending on species	<i>In vitro</i> and postharvest strawberry assays in recent literature	Membrane disruption, oxidative imbalance and inhibition of fungal development	Recent work reported approximately 90–97% inhibition of <i>B. cinerea</i> growth for selected citrus oils, although performance varied by species and dose	Abundant agro-industrial by-products; suitable for circular-economy formulations	Highly volatile, poorly water-soluble and chemically variable; limonene-rich oils may require encapsulation	Raw oils are commercially available; standardized disease-control products are limited	[274]
<i>Ferula gummosa</i> essential oil	<i>F. gummosa</i> volatile phytochemicals	Isolation and antifungal study involving <i>Botrytis</i> isolates from diseased strawberry	Direct inhibition of fungal growth	Recent research demonstrated activity against strawberry-associated <i>Botrytis</i> isolates, but the retrieved source does not provide a sufficiently detailed field-efficacy value for direct comparison	Expands the diversity of botanicals tested against strawberry isolates	Limited replication across cultivars, field conditions and postharvest systems	Experimental	[275]

Table 3: *Cont.*

Natural Product	Principale Source or Active Compounds	Application or Experimental Context	Main Mechanisms of Action	Reported Efficacy	Main Advantages	Current Limitations	Commercial Availability	References
Methyl anthranilate	Naturally occurring volatile aromatic compound found in several plants and fruits	Vapor treatment during strawberry storage	Volatile inhibition of fungal growth and establishment	Extended strawberry shelf life from six to nine days and maintained better firmness and color in a recent study	Non-contact treatment; may avoid direct coating residues	Effective headspace concentration, odor thresholds, consumer acceptance and regulatory status require clarification	Experimental for gray-mold con	[276]

8 Emerging Technologies and Innovations

8.1 Strain Enhancement by Biotechnology

The enhancement of bacterial strains through biotechnological and genomic analyses has been a significant advance in contemporary biocontrol (Fig. 5). The use of high-throughput sequencing, transcriptomics, and genome-editing tools, such as the CRISPR-Cas9 system, has enabled researchers to target genes responsible for various traits, including the production of antifungal metabolites, colonization ability, and stress resistance [277,278].

This has been achieved by targeted genetic enhancement in *Trichoderma harzianum* for increased secretion of hydrolytic enzymes, such as chitinases and glucanases, and secondary metabolites, which have antifungal activity against *B. cinerea*, thus leading to higher suppression rates under variable environmental conditions [279]. Similarly, strains of *Bacillus subtilis* have been improved through adaptive mutagenesis and metabolism pathway optimization to increase lipopeptide production, which are the main agents in antibiosis and biofilm development [280].

In addition, multi-omics research, which integrates genomics, proteomics, and metabolomics, has achieved a systems-level understanding of interactions between plants and microorganisms and pathogens, thus facilitating the identification of superior strains of biological control agents suitable for application in the rhizospheric environment of the strawberry [281].

8.2 Advanced Formulations

In general, environmental stressors such as UV radiation, desiccation, and nutrient depletion are the most common limiting factors for BCAs in terms of stability, shelf life, and delivery efficiency. To minimize such limitations, advanced formulation technologies have emerged (Fig. 5), among which are microencapsulation, nanoformulation, and polymer-based delivery systems [282–284].

Encapsulation in biodegradable matrices, such as alginate, starch, or chitosan, may physically protect the microbial cells and allow controlled release mediated by humidity and temperature fluctuations. Chitosan-based nanoparticles were reported to exhibit a dual role of both a carrier that protects the bioactive molecules and an antifungal agent itself through membrane disruption and induction of host resistance [285]. Moreover, biopolymer coatings improve adhesion to strawberry leaves and prolong persistence on the phyllosphere.

Recent advances in microencapsulation and nanocarrier technologies indicate that biodegradable polymers and nanoscale delivery systems can improve the protection, storage stability, adhesion, and controlled release of microbial propagules and natural antifungal compounds. However, strawberry-specific field evidence remains limited, and formulation performance should be validated under commercial production conditions before broad conclusions regarding efficacy and shelf life can be drawn [286,287].

Recent formulation strategies aim to protect microbial cells and volatile natural compounds from environmental degradation, improve adhesion and persistence on plant or fruit surfaces, and enable controlled release. The principal innovative formulation and delivery systems relevant to strawberry gray-mold management are compared in Table 4.

Table 4: Innovative formulations and delivery technologies developed or proposed for biological control agents and natural antifungal compounds against *Botrytis cinerea*.

Formulation or Delivery Technology	Active Agent or Payload	Carrier or Formulation Matrix	Intended Function	Reported Performance	Principal Advantages	Current Limitations and Knowledge Gaps	Development Status	References
Microencapsulation of fungal conidia	<i>Trichoderma longibrachiatum</i> conidia	Protective microcapsule matrix	Improve conidial viability, storage stability and controlled release	Recent work showed that microencapsulation could prolong viability and shelf life of <i>T. longibrachiatum</i> conidia	Protects propagules from desiccation and environmental stress; facilitates handling and application	Must demonstrate release, colonization and efficacy on strawberry under field conditions; production cost and scale-up remain uncertain	Experimental; not strawberry-specific in the cited formulation study	[282]
Alginate-based microbial encapsulation	Bacterial or fungal BCAs	Calcium alginate or alginate-based beads	Protect cells and permit moisture-mediated release	General evidence supports improved survival and controlled delivery, but the manuscript provides no strawberry-specific quantitative result	Biodegradable, relatively inexpensive and compatible with live microorganisms	Bead size, drying, release kinetics, application through sprayers and shelf stability require optimization	Experimental to pre-commercial depending on organism	[286]
Starch-based encapsulation	Microbial propagules or natural compounds	Starch matrices	Protection during storage and gradual environmental release	Proposed as a biodegradable formulation strategy; strawberry-specific efficacy is not established in the manuscript	Renewable, low-cost carrier	Moisture sensitivity, batch consistency, microbial compatibility and release control	Experimental	[282–284]
Chitosan-based nanoparticles	Natural antifungal compounds, microbial metabolites or other bioactive agents	Chitosan nanoparticles	Protect payload while providing additional antifungal and resistance-inducing activity	Chitosan nanoparticles are described as having dual carrier and antifungal functions	Biodegradable; positively charged surface may improve adhesion; intrinsic antimicrobial activity	Particle-size standardization, phytotoxicity, residue behavior and regulatory classification require evaluation	Experimental	[285]
Essential-oil nanoemulsion	Thyme and mint essential oils	Oil-in-water nanoemulsion with surfactants	Increase water dispersibility, protect volatile compounds and improve contact with fruit surfaces	Nanoemulsions were more effective than non-formulated oils, reduced decay and microbial load, and better maintained firmness, vitamin C and antioxidant activity; thyme nanoemulsion at 0.5% performed particularly well	Improves solubility, stability, uniform distribution and fruit-quality preservation	Surfactant safety, sensory effects, droplet stability, cost and commercial-scale production require evaluation	Advanced experimental postharvest system	[288]
Rosemary essential-oil nanoformulation	Rosemary essential oil	Nanoemulsion or related nanoscale carrier	Enhance antifungal activity and prolong postharvest protection	Recent strawberry research reported reduced gray mold and effects on shelf-life preservation	Natural active ingredient with improved dispersion and persistence	Complete formulation composition, sensory thresholds and performance under commercial storage must be validated	Experimental	[289]

Table 4: Cont.

Formulation or Delivery Technology	Active Agent or Payload	Carrier or Formulation Matrix	Intended Function	Reported Performance	Principal Advantages	Current Limitations and Knowledge Gaps	Development Status	References
Cinnamon essential-oil nanoemulsion	Cinnamon essential oil	Tea-saponin nanoemulsion	Improve stability and antimicrobial dispersion	A recent formulation extended strawberry shelf life to seven days at room temperature and reduced mildew and weight loss relative to controls	Uses a plant-derived emulsifier; strong antimicrobial effect; improved aqueous dispersion	Room-temperature shelf-life evidence does not establish efficacy under commercial cold-chain conditions; sensory effects need testing	Experimental	[290]
Cinnamon essential-oil nanoemulsion coating	Cinnamon essential oil	Wild sage seed gum nanoemulsion coating	Combine controlled delivery with moisture and gas barrier properties	Reported particle size of 148.5 nm, encapsulation efficiency of 86%, and superior preservation of coated strawberries compared with conventional coating	Edible carrier, high encapsulation efficiency and combined antimicrobial/barrier effects	Study primarily assessed shelf life; direct standardized disease efficacy against inoculated <i>B. cinerea</i> requires confirmation	Experimental	[291]
Chitosan-essential-oil nanoemulsion coating	<i>Ocimum gratissimum</i> essential oil	Chitosan nanoemulsion edible coating	Improve antifungal activity and reduce postharvest deterioration	Recent work evaluated this formulation for strawberry shelf-life extension and antifungal preservation	Combines chitosan activity, essential-oil activity and a physical coating barrier	Dose, flavor effects, coating thickness, reproducibility and regulatory assessment require further work	Experimental	[292]
Lemon essential-oil nanocoating	Sicilian lemon essential-oil nanoemulsion	Chitosan- and pectin-based coating	Reduce microbial contamination and moisture loss	Coatings were developed to protect strawberries from spoilage and microbial contamination	Renewable biopolymers; valorizes citrus by-products; combines barrier and antimicrobial functions	It may be difficult to separate effects on <i>B. cinerea</i> from general spoilage reduction; sensory and scale-up studies are needed	Experimental	[293]
Polymer nanocapsule multisystem coating	<i>Lippia graveolens</i> essential oil	Polymer nanocapsules incorporated into a coating	Controlled release and prolonged preservation	A recent study reported that the multisystem coating could preserve strawberry for longer storage periods	Controlled release and reduced direct exposure to concentrated oil	Antifungal efficacy should be quantified against defined <i>B. cinerea</i> inoculum; polymer biodegradability and cost require consideration	Experimental	[294]
Carboxymethylcellulose-essential-oil coating	<i>Lippia sidoides</i> essential oil, rich in thymol	Carboxymethylcellulose edible coating	Improve retention of the volatile oil and provide a protective fruit barrier	The formulation showed preventive and curative activity against <i>B. cinerea</i> and was assessed during 18 days of refrigerated storage	Integrates antifungal action with postharvest quality and sensory evaluation	Results may depend on coating thickness, initial inoculum, storage humidity and consumer acceptance	Experimental	[295]

Table 4: *Cont.*

Formulation or Delivery Technology	Active Agent or Payload	Carrier or Formulation Matrix	Intended Function	Reported Performance	Principal Advantages	Current Limitations and Knowledge Gaps	Development Status	References
Cinnamaldehyde solid-lipid nanoparticles	Cinnamaldehyde	Solid lipid nanoparticles	Slow volatilization and provide sustained antifungal release	Treatment reduced strawberry decay without producing excessive weight loss and supported antioxidant-related quality parameters	Protects cinnamaldehyde and enables slower release	Lipid composition, release kinetics, residue analysis and comparison with free cinnamaldehyde require further study	Experimental	[296]
Sustained-release cinnamaldehyde active film	Cinnamon essential oil or cinnamaldehyde	Non-contact nanostructured active film	Release antifungal vapor gradually within packaging	A 2025 study reported sustained release and increased resistance of stored strawberry to <i>B. cinerea</i> without direct food contact	Minimizes direct contact, provides prolonged headspace exposure and may reduce sensory hotspots	Packaging volume, release rate, temperature dependence, migration and disposal must be standardized	Experimental active packaging	[297]
Pegylated mesoporous-silica nanoparticles	Citrus peel essential oil	PEG-modified mesoporous silica nanoparticles	Encapsulate volatile citrus oil and regulate release	The manuscript cites a 2025 study specifically targeting postharvest <i>B. cinerea</i> in strawberry	High loading capacity and tunable release; valorizes citrus waste	Silica residue, food-contact safety, biodegradability, manufacturing cost and regulatory acceptance require evaluation	Experimental	[287]
Nano-coating containing essential oil and nerolidol	<i>Baccharis dracunculifolia</i> essential oil and nerolidol	Nano-coating matrix	Provide antifungal and antioxidant protection	A 2025 study evaluated the formulation on postharvest strawberries against spoilage including <i>B. cinerea</i>	Combines antifungal, antioxidant and coating effects	Recent evidence requires independent replication, sensory testing and commercial-scale validation	Experimental	[298]
Biopolymer coating for microbial BCAs	<i>Bacillus</i> , <i>Trichoderma</i> or other microbial agents	Chitosan, alginate or other adhesive biopolymer	Improve adhesion to foliage, reduce wash-off and prolong phyllosphere persistence	The manuscript proposes improved adhesion and persistence, but does not provide a verified strawberry-specific quantitative trial for each system	Potentially improves survival under rainfall, irrigation and desiccation	Compatibility between polymer, microbial viability and spray equipment must be demonstrated	Emerging experimental strategy	[286,287]
Volatile-release packaging	Essential oils or natural volatile compounds	Sachets, films, pads or package headspace systems	Maintain inhibitory vapor concentration without direct fruit contact	<i>Thyme</i> , <i>oregano</i> , methyl anthranilate and cinnamaldehyde systems have reduced decay and prolonged shelf life in strawberry studies	Uniform treatment of packaged fruit and reduced direct oil contact	Requires precise control of package volume, temperature, release rate, sensory threshold and worker exposure	Experimental to emerging commercial packaging concept	[297]

The formulation studies summarized in Table 4 indicate that nanoemulsions, encapsulation systems, edible coatings, and active packaging can address several inherent weaknesses of biological control agents and natural compounds, particularly volatility, poor aqueous solubility, limited persistence, and sensitivity to environmental stress. Nevertheless, most systems remain at the laboratory or pilot postharvest stage. Direct comparison remains difficult because formulation composition, particle size, loading efficiency, release kinetics, pathogen inoculation, storage conditions, and fruit-quality endpoints are rarely standardized. Future studies should compare formulated and non-formulated active ingredients, include commercial biological and chemical controls, quantify residues and sensory effects, and assess economic feasibility under realistic cold-chain and field conditions. Regulatory evaluation must also consider both the active ingredient and the carrier material, especially for nanoparticles intended for direct food contact.

8.3 Smart Detection and Precision Application Tools

Digital technology integration in precision agriculture has become increasingly relevant to optimizing biocontrol, it does not directly suppress *B. cinerea*, it enhances the efficiency of sustainable disease management by enabling earlier disease detection, more accurate disease forecasting and targeted application of biological control agents and natural compounds, To begin with, smart sensors, artificial intelligence models, and hyperspectral imaging technology can be utilized to monitor the microclimatic conditions of the crops, the dynamics of pathogens, and soil-plant interactions in a real-time process [299]. It is possible to determine the risk of infection related to temperature, humidity levels, and canopy density using predictive algorithms to target the application of BCAs for optimal *B. cinera* infection conditions [300,301]. Additionally, technology for spraying and autonomous drones is being developed to ensure the optimal delivery of microbe suspensions, thereby reducing wastage and achieving maximum pathogen inhibition [302]. These smart technologies not only increase the effectiveness and economy of biological products (Fig. 5), but are also useful in planning data-driven IPM strategies, which align with sustainable systems of strawberry cultivation [303,304].

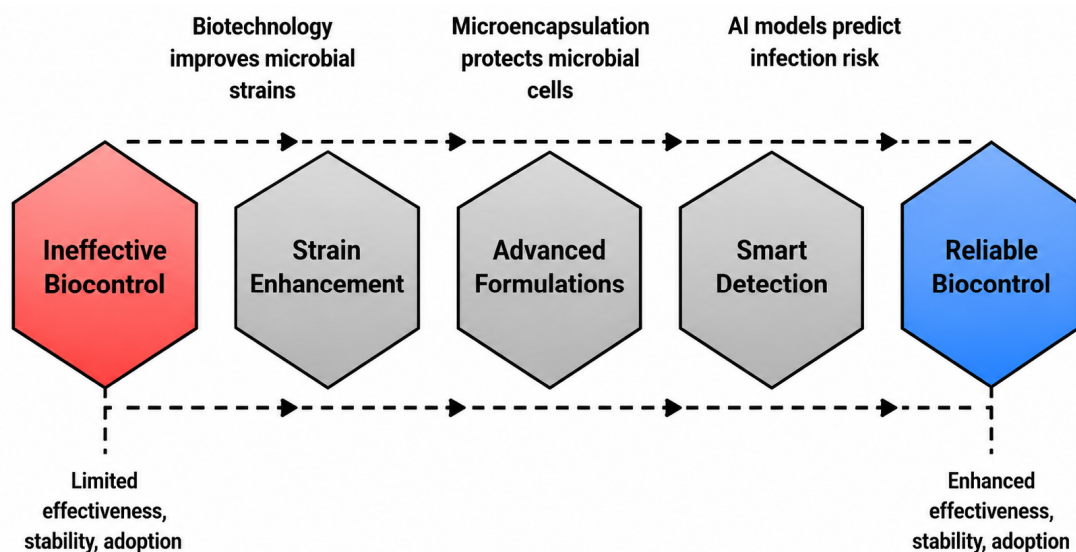


Figure 5: Enhancing biocontrol with advanced technologies.

Beyond disease detection, decision support systems (DSS) are emerging as valuable tools for integrating weather forecasts, pathogen biology, crop phenology, and historical disease records into practical

management recommendations [305,306]. Rather than relying on fixed application schedules, these systems estimate infection risk and recommend the optimal timing for biological control applications, thereby improving their effectiveness while reducing unnecessary treatments [307]. Such predictive approaches are particularly relevant for *B. cinerea*, whose infection is strongly influenced by temperature, relative humidity, leaf wetness duration, and canopy microclimate. Integration of DSS with biological control programs therefore represents an important step toward precision IPM [308]. Recent advances in computer vision and hyperspectral imaging have also enabled the detection of pathogen-induced physiological changes before visible symptoms appear. Early identification of infected plants or localized infection hotspots allows site-specific application of biological control agents, thereby minimizing product use and reducing disease spread within the crop [309].

Despite their considerable potential, most smart detection and precision agriculture technologies remain at the experimental or pilot stage for strawberry gray mold management. Their widespread adoption is still limited by the high cost of imaging equipment and sensor networks, the need for large, well-annotated datasets to train artificial intelligence models, variability among cultivars and production systems, and the lack of standardized validation under commercial field conditions [310]. Moreover, prediction models developed in one geographic region often require recalibration before being applied elsewhere because disease development depends on local climatic conditions and crop management practices [311]. Consequently, future research should prioritize robust multi-location validation, integration of disease forecasting with biological control scheduling, and development of affordable decision-support tools suitable for commercial strawberry production.

Looking forward, the convergence of artificial intelligence, Internet of Things (IoT) technologies, autonomous robotic systems, and real-time disease forecasting is expected to transform the management of *B. cinerea* [312]. Future precision agriculture platforms may continuously integrate environmental monitoring, pathogen detection, and automated application of biological control agents, enabling highly targeted interventions while minimizing pesticide inputs and environmental impact. However, interdisciplinary collaboration among plant pathologists, microbiologists, engineers, and data scientists will be essential to translate these promising technologies into economically viable tools for commercial strawberry production.

9 Field Constraints and Adoption Challenges

9.1 Environmental and Agronomic Conditions Affecting Efficacy

The efficacy of BCA in managing *B. cinerea* is highly affected by environmental heterogeneity and agricultural practices that impact microbial-mediated survival and colonization in the phyllosphere and rhizosphere ecosystems [313]. Microclimatic factors such as relative humidity, temperature variation, UV radiation, and pH values are critical to determining microbial survival and activity. For *Trichoderma harzianum* and *Clonostachys rosea*, optimal environmental conditions include above 85% relative humidity and 20–25°C; however, for *Bacillus* species, higher tolerance for water stress and pH changes is required, but they are sensitive to UV radiation [314–316].

Adverse conditions in the environment can weaken BCAs for the production of antifungal metabolites, surface colonization, and competition for ecological niches with the native flora [317]. For example, the rate of sporulation and the production of chitinase in *Trichoderma* spp. are significantly affected during drought conditions, thus weakening their ability to protect during critical stages of flowering and fruiting [318].

Agronomic factors also have a central role. Canopy architecture and irrigation practices directly affect leaf wetness duration, which again affects both *B. cinerea* infection dynamics and BCA survival. Overhead irrigation, for example, may favor spore dispersal of the pathogen while washing off the applied biocontrol

agents. On the other hand, drip irrigation and open canopy management do increase the persistence of BCAs and decrease gray mold incidence. Mulching and organic amendments further improve soil microbiome stability and help in the establishment of mutualistic microbes that cause indirect suppression of *B. cinerea* [319–321].

Therefore, site-specific integration of BCAs into precision agronomic frameworks is a prerequisite for consistent field performance. Recent modeling studies, in which environmental sensors couple with microbial activity indices, show predictive microclimate data can be used to optimize application timing, which can significantly improve the consistency of *B. cinerea* suppression across variable production systems [322,323].

9.2 Technical and Logistical Limitations

While BCAs are considered a green alternative to synthetic fungicides, technological and logistical issues still need to be resolved for their wide-scale implementation. One of the main drawbacks is the poor shelf life and storage stability of microbial preparations. This may be observed in a number of biocontrol products derived from live microorganisms, which show a high viability loss after 3–6 months, particularly under non-refrigeration conditions [324]. Loss of viability drastically reduces field efficacy. Although progressive drying techniques, such as freeze-drying, spray drying, and fluidized bed coating, give several months of extra stability to products, production costs are still high at the moment [325].

The quality of the formulation, besides, affects cell adherence, spore germination, and compatibility with adjuvants or carriers. For instance, inert fillers like kaolin or talc can enhance dispersal but may adversely affect microbial viability during storage. In addition, the absence of standardized protocols for quality control regarding microbial counts, genetic stability, and thresholds for contaminants continuously results in batch-to-batch variability [326].

On a regulatory front, the complicated registration procedure for microbial biocontrol agents is also an equally challenging issue. Variations in data requirements across the European Union, the United States, and emerging countries result in slow registration and hinder investment from the private sector [327,328].

To mitigate such bottlenecks, international harmonization is being developed in terms of common risk assessment tools, identity verification of microorganisms, and efficacy testing. Further, new methods such as “dry inoculum banks” and co-formulation designs have been proposed to improve the efficiency of the microbe production pipelines of BCA [329].

9.3 Grower Perception and Technology Transfer

The long-term success of biological control technologies also depends on both the scientific merits of these innovations and other human or socio-economic factors. As a demonstration, for farmers to embrace BCAs, the key factor rests largely in their confidence in the technology, cost-benefit ratio, and ease of integration into existing agro-technologies [330,331]. Several factors contribute to this gap, including inconsistent performance under varying environmental conditions, higher initial costs compared with conventional fungicides, limited commercial availability of some biological products, and uncertainty regarding their economic return [161]. Furthermore, growers may be reluctant to replace well-established chemical control programs unless alternative strategies provide consistent disease suppression and are supported by clear technical recommendations [332]. Effective technology transfer is therefore essential to bridge the gap between scientific research and commercial implementation. Extension services, demonstration trials, farmer field schools and collaboration among researchers, industry partners, and growers play a crucial role in increasing confidence in sustainable disease management practices [333,334]. Providing

practical guidelines on product selection, application timing, compatibility with existing IPM programs, and cost-benefit analyses may substantially facilitate the adoption of biological control agents and natural products [335]. In addition to online decision aid systems are useful in timing and dosage standardization of biocontrol efficacy in regional conditions [336].

On the policy front, the development of incentive programs and certification frameworks for ecologically sound methods of biological control may help fast-track the adoption of biological control. Subsidies on listed bio-control agents, training of farm technicians, and public-private partnerships have worked well in increasing their adoption rate in high-value horticultural crops. Overall, what is most critical in this case is developing a culture of innovation through collaboration and conversion of scientists, growers, and policymakers [326,337,338]. Future efforts should also focus on simplifying the implementation of eco-friendly technologies through user-friendly decision-support tools, standardized application protocols, and improved commercial formulations.

10 Current Challenges and Future Perspectives

10.1 Variability of Field Performance (Environmental and Contextual Dependence)

Molding caused by the fungus *B. cinerea* is a common epidemic affecting strawberry, not only in open fields and orchards, but also in greenhouse protected cultivations. Despite the multiple management strategies that can be employed. However, limited research has evaluated how environmental conditions influence the performance of different disease management strategies at different points in time and space, making research extremely difficult. Biological and Chemical control methods also introduce additional variables that affect the environment. Many documented cases exist concerning the variability associated with the use of BCAs, and the natural and synthetic diseased management systems and other services to manage pests [13,339,340]. While many BCAs show promising antagonist activity against *B. cinerea* in laboratory settings, their effectiveness is often significantly diminished and, in some cases, completely unpredictable in commercial strawberry production systems [13,341]. Soil characteristics, microclimate, phenology of the plants, agronomic management, and other microorganisms can interact to affect the establishment, persistence, and activity of some antagonistic organisms [342].

In natural agricultural systems, the ecological niche of BCAs is determined by the combined influence of abiotic conditions, including temperature, humidity, UV radiation, nutrient availability, and pH, together with interactions within resident microbial communities for BCAs, and these factors affect their ability to colonize the plant surfaces and their persistence in the canopy, rhizosphere, and therefore the activity of enzymes and overall antagonistic potential of the BCA. As an illustration of this, the ability to produce antifungal peptides and enzymes, including lipopeptides, hydrolytic enzymes, and VOCs of *Trichoderma* spp. and *Bacillus* spp., is affected by microclimate factors (temperature and leaf wetness duration) [343,344]. Environmental conditions can also directly influence the pathogen itself; for instance, conidial germination of *Botrytis* spp. can be completely inhibited after exposure to high temperatures such as 44°C for 30 min or 48°C for only 5 min. The field application of bioactive compounds such as essential oils and phenolic extracts may be hampered by the same issues encountered with conventional pesticides. Combining the effects of UV radiation and the instability of these compounds in the field may limit their use as plant protection products [345,346].

The impact of abiotic factors is only one portion of the farming system's complexity on the efficacy of biological control interventions. Introduced biological control agents (BCAs) may either be positively or negatively impacted by their competition with indigenous microorganisms, uneven distribution of soil nutrients, and plant-Microbiome interactions. This further emphasizes the need to take a mechanistic

approach to functionally integrate BCAs with traits and variables in the environment to enhance the predictability of their efficacy in the field. Consequently, recent ecological models have provided a framework to appreciate the contrast of significant or negligible contextual dependence in biological control, providing more guidance to articulate a precise contextualized implementation framework to enhance the efficacy of BCAs [342,347,348]. In strawberry cultivation, a number of research works advocate the building of microclimate data-integrating decision support systems, considering aspects like plant developmental stage (Fig. 6) and microbial community structure [349].

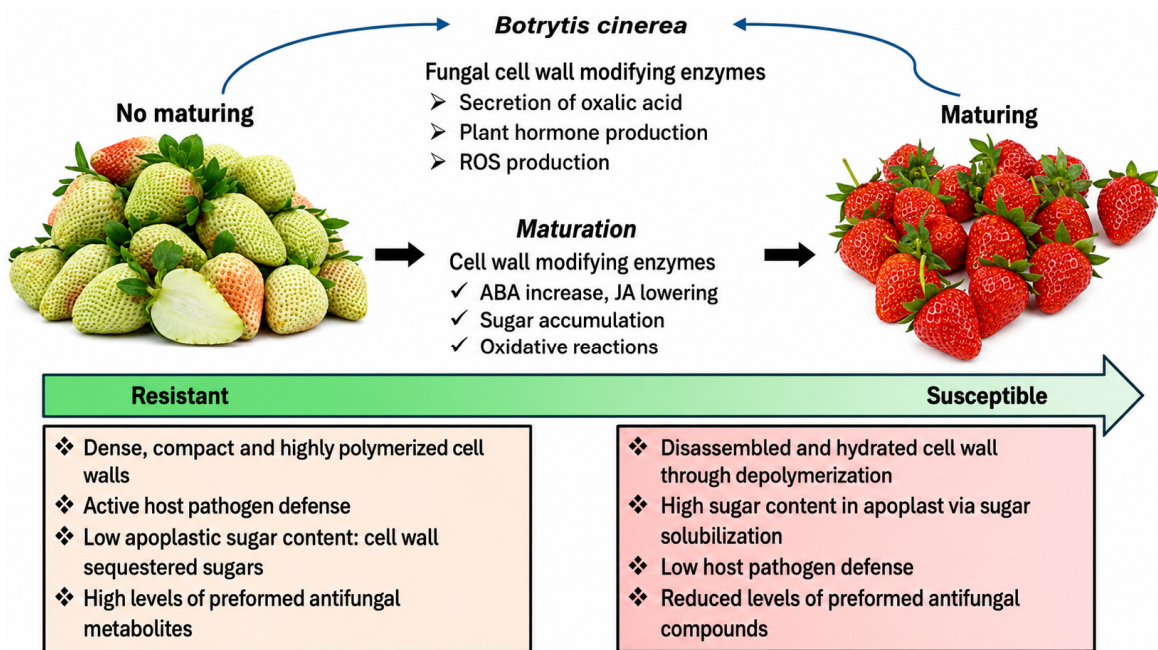


Figure 6: Physiological and biochemical changes during ripening drive differential susceptibility of strawberry to *Botrytis cinerea*.

10.2 Formulation and Regulatory Limitations

The formulation method influences the efficiency of BCA and bio-based biological control agents (BoBCA) in controlling *B. cinerea* gray mold in strawberry production. Many of the antagonists we studied in the laboratory were effective against *B. cinerea*, but most were ineffective in the field. Field organisms, such as of *B. cinerea* antagonists, fail due to various environmental stresses. Including desiccation of field organisms, changes in ambient temperature, exposure to UV radiation, and changes in field humidity during active flourishing periods are just a few of the factors that affect *B. cinerea* antagonists. This is a critical limitation for mass strawberry production. The combination of high field humidity, dense canopies, and frequent high-volume micro irrigation of strawberry production makes the mature strawberry flowers and new fruit particularly susceptible to infection by *B. cinerea* [117,350]. To improve the reliability of BCAs under these conditions, recent research has focused on advanced formulation strategies to protect microbial propagules and enhance their persistence in the phyllosphere [351]. Some studies focus on protective biopolymers, alginate matrices, resin chips, and nano-emulsions that induce the controlled release of microbial propagules and increase their adhesion to plant surfaces while exerting protective stress to the microorganisms [352]. Similarly, protective additives such as osmoprotectants, UV-protectants, and nutrient carriers can improve microbial survival, enable rapid colonization of pathogen infection sites,

and enhance the consistency of gray mold suppression [350,353]. Aside from safeguarding the environment, enhancing the storage stability of biological formulations is essential for their commercialization and utilization. Most microbial biocontrol agents have poor stability. Cell viability may decrease significantly prior to field application, resulting in a loss of activity [354]. As a result, the development and application of new formulation technologies that improve the stability of microbial BCAs is critical for commercial strawberry production systems to achieve control of *B. cinerea* [355].

10.3 Strawberry Microbiome Engineering

The strawberry microbiome represents a rich reservoir of plant-associated microbial consortia inhabiting different compartments, including the rhizosphere, endosphere, phyllosphere, and carposphere, where resident endophytes are directly adapted to their natural ecological niche. These communities commonly include genera such as *Bacillus*, *Pseudomonas*, *Aureobasidium*, and *Trichoderma*, which often exhibit enhanced colonization ability and stronger natural antagonistic activity against *B. cinerea* compared to exogenous strains. In addition to their direct antagonism, there is increasing data that native microbiota interact highly with the host plant and establish three-way interactions between the plant, beneficial microbes, and the pathogen [117,356,357]. Investigating microbial diversity associated with strawberry by applying culture-dependent and culture-independent approaches can detect new biocontrol agents with traits and features to the strawberry habitat, also enhanced biofilm capacity, nutrient competition, siderophore production, or activation of host defense mechanisms [358]. Furthermore, the strawberry microbiome can be intentionally manipulated to enhance populations of beneficial microorganisms that naturally suppress *B. cinerea*. This can be achieved through the application of prebiotics, which selectively stimulate indigenous beneficial microbes, or through microbiome engineering, an approach that modifies the microbial community by introducing beneficial microbial consortia or by adopting cultivation practices that favor naturally occurring antagonistic microorganisms [359].

10.4 Multi-Omics and Predictive Modeling

New technologies across multiple domains, including predictive modeling, give us the opportunity to better understand the biological management of gray mold caused by *B. cinerea* in strawberry production systems. Integrated multi-omics approaches, including metagenomics, transcriptomics, proteomics, and metabolomics, provide powerful tools to characterize the strawberry agroecosystem by elucidating interactions among the plant host, microbial antagonists, and the pathogen [360]. More precisely, metagenomic evaluations analyze BCAs employed and identify keystone taxa and functionally relevant microbial groups in the strawberry phyllosphere and rhizosphere community. Furthermore, proteomic and transcriptomic approaches examine host plant responses to BCAs [361]. These changes can involve defense mechanisms, such as the phenylpropanoid defense response and the activity of defense response (DR) proteins, the production of ROS signaling, and the plant's response to jasmonic acid defense signaling pathways. Metabolomic analyses, in conjunction with the BCAs, can also demonstrate the presence of antifungal secondary metabolites and volatile organic compounds [362–364].

In addition to mechanistic understanding, multi-omics approaches combined with machine learning and ecological network modeling provide powerful tools to develop predictive frameworks for biological control [365]. For instance, supervised machine learning algorithms such as random forests and support vector machines have been used to identify key microbial taxa associated with disease suppression and to predict the efficacy of BCAs under varying environmental conditions [366]. With similar approaches, co-occurrence-based ecological network analyses can reveal not just keystone species, but also microbial

consortia that occupy the central role in pathogen suppression [367]. These kinds of analyses enable modeling of microbial interactions and the assessment of BCA efficacy under different scenarios of humidity, temperature, and plant developmental stages. Thus, these models can indicate the operational zones of ecological frameworks in which the integration of biological control strategies can yield the most significant advantages. This can enhance the management frameworks for reducing the impact of *B. cinerea* in strawberry production systems, while also integrating reliable and sustainable control methods.

11 Conclusion

B. cinerea remains one of the most challenging pathogens affecting strawberry production worldwide due to its broad host range, high genetic variability, efficient dispersal capacity, and ability to establish latent infections. These biological characteristics, combined with favorable environmental conditions and intensive production systems, contribute to the persistent prevalence of gray mold and the significant economic losses associated with the disease.

Although chemical fungicides have long been the cornerstone of gray mold management, the increasing occurrence of fungicide-resistant populations, along with environmental and regulatory concerns, highlights the limitations of relying exclusively on chemical control. Consequently, the development of sustainable and integrated management strategies has become a major priority for both researchers and growers.

This review highlights the importance of combining multiple approaches for effective disease suppression. Cultural practices help reduce inoculum pressure and create less favorable conditions for pathogen development, whereas biological control agents, including antagonistic bacteria, fungi, and yeasts, provide effective suppression through diverse mechanisms such as competition, antibiosis, mycoparasitism, and induction of host resistance. In parallel, natural compounds derived from plants have emerged as valuable alternatives or complements to conventional fungicides due to their broad-spectrum antifungal activity and environmental compatibility.

Recent advances in microbial ecology, microbiome research, formulation technologies, multi-omics approaches, and nanotechnology are significantly improving our understanding of plant–microbe–pathogen interactions and creating new opportunities to enhance the efficacy and reliability of biological control strategies. Nevertheless, challenges related to field performance, formulation stability, commercialization, and regulatory approval still need to be addressed before large-scale adoption can be fully achieved.

Overall, the future of gray mold management in strawberry production will likely depend on the integration of biological control agents, natural compounds, cultural practices, and innovative technologies within holistic disease management programs. Such an integrated approach offers the greatest potential to reduce fungicide dependency, improve disease control, preserve fruit quality, and promote the long-term sustainability of the strawberry production system.

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Mohammed Radi, Mohammed Taoussi, Ikram Legrifi, Mohammed Khadiri, Hakima Achetoui and Sohaib Khatib; visualization, Sohaib Khatib, Essaid Ait Barka and Jamal Ibijbjen; supervision, Rachid Lahlali. All authors reviewed and approved the final version of the manuscript.

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