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**REVIEW ARTICLE**

## Strawberry Grey Mould, a Devastating Disease Caused by the Airborne Fungal Pathogen *Botrytis cinerea*

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### ABSTRACT

Strawberry (*Fragaria ananassa* Duch.) is an important and valuable fruit because of its unique flavor and economic, nutritional and health benefits. It is one of the most consumed berries worldwide. Grey mould of strawberry fruits, caused by the necrotrophic ascomycete *Botrytis cinerea* Pers.: Fr., is one of the most important diseases. This airborne pathogen has the ability to kill strawberry cells through the production of reactive oxygen species and toxins causing massive production losses at all development stages and even post-harvest. The intensive production of strawberries has created a favorable environment for this disease. Strawberry grey mould management is typically very input-intensive, in particular with respect to chemical fungicides. As a result, the integrated pest management is required to control strawberry grey mould. A thorough understanding of *B. cinerea* epidemiology and infection processes is needed to guide future efforts in the development of innovative integrated management practices. This review summarizes the current knowledge of taxonomy and morphology, signs and symptoms, disease development, infection process, and control of *B. cinerea* using integrated disease management.

**Keywords:** Strawberry, *Fragaria ananassa*, *Botrytis cinerea*, grey mould disease, management practice.

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### INTRODUCTION

The strawberry (*Fragaria ananassa* Duch.; Family: *Rosaceae*) is one of the most important crops in the world economically, nutritionally and healthily. Nevertheless, strawberries are affected by many pathogens such as nematodes, fungi, viruses and bacteria (Petrasch *et al.*,

2019). Moreover, the pathogens with the greatest economic impact are fungi that cause serious damage or death (Fedele *et al.*, 2020 and Notte *et al.*, 2021). Among the fungal pathogens, we mention *Botrytis cinerea* which represents the major pathogen of strawberries worldwide (Breen *et al.*, 2022).

Strawberry grey mould, caused by the ascomycete *B. cinerea* Pers.: Fr. (teleomorph *Botryotinia fuckeliana* (de Bary) Whetzel), is one of the most important airborne diseases and can decrease fruit yield and quality both pre-harvest and post-harvest (Avenot *et al.*, 2020 and Kahramanoğlu *et al.*, 2022). *B. cinerea* infection causes heavy losses in strawberry crops in the field and in greenhouse at harvest, or even at the post-harvest. As a result, established management measures are required to manage grey mould in strawberries (Grabke, 2014 and Petrasch *et al.*, 2019).

It is difficult to manage *B. cinerea* because it has a wide variety of attack modes, various hosts as inoculum sources, and it can survive as conidia and/or mycelia or for long periods as sclerotia in crop debris (Alfonso *et al.*, 2000 and Feliziani and Romanazzi, 2016). Therefore, the most appropriate strategies used to reduce strawberry grey mould development were those able to integrate different approaches (De Angelis *et al.*, 2022). A detailed understanding of strawberry-*B. cinerea* interaction, the microenvironment and its antagonists on the host plant is essential for a good choice of a

control strategy against *B. cinerea* (Boff *et al.*, 2001; Blanco *et al.*, 2006 and Fedele *et al.*, 2020). Although chemical control (Ortuno *et al.*, 2014 and Feliziani and Romanazzi, 2016) and resistant cultivars (Evenhuis and Wanten, 2006 and Pelayo-Zaldívar *et al.*, 2007) is the mainstays of *B. cinerea* management, there are other types of management strategies, such as biological control (De Angelis *et al.*, 2022) and cultural activities (Fedele *et al.*, 2020; Li *et al.*, 2022 and Xiao *et al.*, 2022).

The aim of this paper is to briefly outline what is now known about *B. cinerea*, the pathogen that causes strawberry grey mould, including taxonomy, signs and symptoms, disease progression, epidemiology, control strategies, and management.

#### Causal agent of strawberry grey mould:

|                   |                           |
|-------------------|---------------------------|
| <b>Domain:</b>    | •Eukaryota                |
| <b>Kingdom:</b>   | •Fungi                    |
| <b>Phylum:</b>    | •Ascomycota               |
| <b>Subphylum:</b> | •Pezizomycotina           |
| <b>Class:</b>     | •Leotiomycetes            |
| <b>Subclass:</b>  | •Leotiomycetidae          |
| <b>Order:</b>     | •Helotiales               |
| <b>Family:</b>    | •Sclerotiniaceae          |
| <b>Genus:</b>     | •Botrytis                 |
| <b>Species</b>    | • <i>Botrytis cinerea</i> |

*Botrytis cinerea* is classified as an anamorphic fungus with a necrotrophic lifestyle that causes serious losses on a wide range of dicotyledonous plants species (ornamental, vegetable and fruit plants) (Avenot *et al.*, 2020). It is a phytopathogenic fungus that causes grey mould disease in over 200 hosts species worldwide (Alfonso *et al.*, 2000 and Avenot *et al.*, 2020). Grey mould can develop fast and the disease can be devastating on the field, in greenhouses, and in post-harvest (Rui and Hahn, 2007 and Petrasch *et al.*, 2019). Losses can be severe throughout the production system, at harvest, during transportation, selling, and after final sale (Avenot *et al.*, 2020 and Notte *et al.*, 2021).

The name *Botrytis cinerea* is derived directly from the fungus' morphology: "*Botrytis*" is named after the Greek word for "bunch of grape berries", describing the grape-like morphology of conidiophores, and "*cinerea*" refers to the grey colour of sporulation (Williamson *et al.*, 2007 and Petrasch *et al.*, 2019). The genus *Botrytis* was created by Pier Antonio Micheli in 1729, who grouped it into the "Nova Plantarum Genera", and was later revised by Hennebert. *Botrytis cinerea* was first described by Persoon

and the name was accepted by the Swedish botanist Magnus Fries, who, together with Linnaeus, created the foundation of fungal systematics (Williamson *et al.*, 2007 and Petrasch *et al.*, 2019). The teleomorph or sexual form of *B. cinerea* is named *Botryotinia fuckeliana* (De Bary) Whetz. (Alfonso *et al.*, 2000 and Avenot *et al.*, 2020).

Primary identification of *B. cinerea* is from its atypical spore and macroconidiophore structure (Alfonso *et al.*, 2000 and Williamson *et al.*, 2007). This is a specialized structure comprising a terminal cluster of synchronously produced hydrophobic conidia, borne on a well-developed macroconidiogenous hypha, which resembles a bunch of grapes (Williamson *et al.*, 2007; Avenot *et al.*, 2020 and Notte *et al.*, 2021). These hyphae originate from a cushion-shaped stroma, which forms just beneath the host surface (Boff *et al.*, 2001; Williamson *et al.*, 2007; Feliziani and Romanazzi, 2016). Macroconidia are large, specialized blastoconidia measuring 8-14 × 6-9 μm (Williamson *et al.*, 2007 and Feliziani and Romanazzi, 2016). Macroconidia are oval, dry and hydrophobic, being produced singly on lateral branches for easy dispersal. When mature, conidia are easily detached from the ampullae by rain splash and/or air turbulence, which also serve to distribute them (Williamson *et al.*, 2007; Avenot *et al.*, 2020 and Notte *et al.*, 2021).

Primary cultures on potato dextrose agar appear fluffy grey, hyaline (light colored) at first, later becoming grey to greyish-brown with dark walled erect septate hyphae that grow in a creeping manner. The dark colored is attributed to the mature conidiophores, which branch alternately, frequently, in an irregular, erect, dendroid arrangement (Alfonso *et al.*, 2000; Williamson *et al.*, 2007; Latorre *et al.*, 2015 and Notte *et al.*, 2021).

When conditions are unfavourable for growth, the fungus can form a secondary mycelial phase, a compact stone-like sclerotium, which comprises a dark mass of hyphae consisting of a medulla and a dark brown to black cortical layer of cells extremely variable in shape and size (Alfonso *et al.*, 2000; Williamson *et al.*, 2007; Latorre *et al.*, 2015 and Notte *et al.*, 2021).

#### Symptoms and signs:

Grey mould manifestation depends on the infected strawberry part and the physiological status of the tissue (Haile *et al.*, 2019). This disease can be prevalent at all stages of strawberry development (Bulger *et al.*, 1987).

Newly expanding young leaves may be infected by this pathogen but don't illustrate symptoms because the fungus remains dormant in these tissues (Liang *et al.*, 2018). When the leaves are mature and beginning to senesce and decline, *B. cinerea* can become active and construct the characteristic grey, velvety growth on the dead parts of the leaf (Williamson *et al.*, 2007). The fungus can contaminate flowers and cause the disease of blossom blight (Haile *et al.*, 2019). Symptomatic flowers revealed brown, discolored lesions on the petals, sepals and receptacle (Petrasch *et al.*, 2019). If the disease continues to expand through the flower, *B. cinerea* will kill the pedicel, causing the entire flower to wither and die (Breen *et al.*, 2022).

In many cases, the diseased flower shows no signs because this fungus can colonize the internal tissues of the flower but stay dormant (Bulger *et al.*, 1987). Once the fruits initiate to develop, *B. cinerea* becomes active and causes a light brown decay at the end of young fruit calyx (similar decay has been observed on fruits in different stages; white, pink, and red) (Pelayo-Zaldívar *et al.*, 2007 and Xiong *et al.*, 2018). Mature red fruits are particularly sensible to *B. cinerea* infection following physical damage, as the airborne pathogen can quickly colonize the damaged tissue and spread all through the fruit (Petrasch *et al.*, 2019). If environmental conditions support the *B. cinerea* development, all plant parts may be covered with grey and fuzzy growth of the fungus, and a grey carpet of the spores was observed (Haile *et al.*, 2019). This phytopathogen which develops on a contaminated fruit easily moves to other fruits which are in contact with the infected one resulting in the formation of diseased fruit clusters (Petrasch *et al.*, 2019). Completely rotten fruits become shriveled, dried, tough and mummified. Undeveloped fruits may become deformed and die before maturity (Petrasch *et al.*, 2019). On cold-stored post-harvest strawberry fruits, the growth of this disease may be whiter in color because the pathogen generally requires light to entirely develop the grey spores (Li *et al.*, 2013).

#### **Economic importance:**

*Botrytis cinerea* is a devastating airborne pathogen causing millions of dollars of damage to a wide range of crops worldwide. The pathogen provokes pre-harvest and post-harvest diseases resulting in significant economic losses (Elad, 1996; Alfonso *et al.*, 2000 and Grabke, 2014). The economically important host crops are strawberry, grape, lettuce and cabbage worldwide (Dianez *et al.*, 2002). In New

Zealand, the berry fruit (\$17 million) and floriculture (\$55 million) are primarily the most affected by *B. cinerea* disease (Grabke, 2014; Petrasch *et al.*, 2019 and Kahramanoğlu *et al.*, 2022). In 2000, annual losses attributable to this airborne pathogen were over \$20 million in kiwi fruit, either through direct crop loss or through the millions of dollars spent every year in controlling this pathogen (Grabke, 2014; Petrasch *et al.*, 2019 and Kahramanoğlu *et al.*, 2022). In the Far East and North America, the market value of fungicide against *Botrytis* spp. was approximately \$28.6 million. Yield losses claimed by strawberry grey mould were recorded to 50%, conversely under favorable conditions for the growth and development of this airborne pathogen (100%) (Grabke, 2014; Petrasch *et al.*, 2019 and Kahramanoğlu *et al.*, 2022).

#### **Disease cycle and epidemiology:**

*Botrytis cinerea* overwinters as sclerotia or dormant mycelium predominantly in dead strawberry debris, but also in straw mulch, mummified berries, and weeds (Stromeng *et al.*, 2009 and Feliziani and Romanazzi, 2016). In the spring (under appropriate conditions), the fungus develops mycelium and produces large quantities of conidia (primary source of inoculum) (Blanco *et al.*, 2006). Infected senescent petals, calyxes and stamens can facilitate primary infections in the strawberry fruits (Hua *et al.*, 2018). *B. cinerea* secretes an arsenal of secondary metabolites, toxins and enzymes to facilitate the penetration into strawberry. *B. cinerea* is able to penetrate strawberry tissues directly using cutinases, pectinases and proteases, or by taking advantage of natural openings (such as via open stomata) or wounds (Boff *et al.*, 2001). Conidia are released from conidiophores in response to vibrations or a rapid decline in relative humidity and are disseminated by air currents and water splashes (Petrasch *et al.*, 2019). Wounds and flowers are the main entrance of *B. cinerea* infections (Gourgues *et al.*, 2004). The germ tubes of the conidia easily penetrate the strawberry epidermis on petals, pistils and stamens (Govrin and Levine, 2000). Once *B. cinerea* is established in the parts of flower, the fungus invades the developing fruit, usually remaining quiescent until the fruit is ripped or damaged (Breen *et al.*, 2022). The mycelia growth in infected flower receptacles causes a characteristic rot at the end of the calyx (Rui and Hahn, 2007). The production of spore begins rapidly as the berries ripen and continues throughout the fruiting season (Hua *et al.*,

2018). This serves as the inoculum secondary source (Boff *et al.*, 2001 and Xiong *et al.*, 2018). It then colonizes senescent tissues and produces conidia during the periods of high humidity or leaf wetness, which serves as another source of inoculum (Li *et al.*, 2013). During the secondary infections, *B. cinerea* starts the necrotrophic phase without quiescence (Stromeng *et al.*, 2009; AbuQamar *et al.*, 2017).

*Botrytis cinerea* prefers moderate temperatures ranged between 15°C and 25°C but is able to grow at low 0°C, which makes it one of the most dangerous pathogens for stored crops (Bulger *et al.*, 1987 and Boff *et al.*, 2001). In addition to moderate temperatures, surface wetness or prolonged periods of high relative humidity are necessary for the development of strawberry grey mould (Boff *et al.*, 2001 and Blanco *et al.*, 2006). These conditions favor conidial germination, spore production and host penetration (Blanco *et al.*, 2006). Thus, overhead irrigation and frequent rains amplify the incidence of grey mould (Blanco *et al.*, 2006 and Hua *et al.*, 2018). Disease dissemination and infection is augmented by mechanical, hail, bird and insect damage, and by intensive planting, where infected strawberry can easily come into contact with healthy tissue (Stromeng *et al.*, 2009; Li *et al.*, 2013 and Hua *et al.*, 2018).

#### **Disease Management:**

Control of strawberry grey mould is difficult due to the genetic diversity, *Botrytis cinerea* variety of infection and survival as sclerotia mycelia and conidia (Alfonso *et al.*, 2000). The best approach to manage this disease is to integrate cultural practices with the application of fungicides or/and biological agents (AbuQamar *et al.*, 2017).

The elimination of infected berries and debris and drip irrigation decrease the inoculum source and the surface wetness; these practices diminish the disease incidence (Legard *et al.*, 2000). Thus, tunnels and greenhouses decrease the excessive rainfall problems (Evenhuis and Wanten, 2006). Wider strawberry spacing allocates adequate aeration and decreases disease incidence but may cause a reduction in overall yield (Blanco *et al.*, 2006). Any technique that decreases relative humidity and surface wetness of leaves and fruits, and that increases light penetration and air circulation should be applied. Fertilization of strawberries with nitrogen should be limited, because N promotes vegetative growth and augments the disease incidence (more than 60%) when climatic conditions are favorable. Controlling insect pests that damage strawberries or carry *B.*

*cinerea* spores can help in controlling secondary infection. Disease forecasting systems, which use leaf wetness and local temperature to predict outbreaks, have been successful in reducing severe crop damage and minimizing the number of fungicides applied per season (Rui and Hahn, 2007). Soil sterilization at 55°C for 15 min proved lethal to *Botrytis* spp. It is clear that greenhouse conditions are easier to handle with field-grown strawberries, however some other techniques can be applied to both field and greenhouse crops; good soil drainage, putting straw mulches or polythene cover to reduce the plant and soil-surface contact (Legard *et al.*, 2000 and Fedele *et al.*, 2020), choosing the correct time and rate of fertilizer applications, weeds management (weeds increase the infection of *Botrytis* spp., impede air circulation, and can be a source of inoculum), eliminating of rotten strawberries frequently and remove them away (Legard *et al.*, 2000 and Williamson *et al.*, 2007), planting in raised beds and effective pruning (Legard *et al.*, 2000; Li *et al.*, 2022 and Xiao *et al.*, 2022).

Biological control strategies have been developed for the management of strawberry grey mould as an alternative to chemical control. Biological agents used in formulations against *B. cinerea* comprise acibenzolar, filamentous fungi (*Trichoderma harzianum* and *Gliocladium roseum*), yeasts (*Rhodotorula glutinis*, *Aureobasidium pullulans* and *Candida oleophila*) or/and bacteria (*Pseudomonas syringae* and *Bacillus subtilis*). Biological control agents act as mycoparasites, as inhibitors of sporulation and germination, as competition for nutrients, as secretors of fungicidal mycotoxins, as inducers of strawberry plant defense mechanisms (Eccleston *et al.*, 2010; Feliziani and Romanazzi, 2016; De Angelis *et al.*, 2022 and Kahramanoğlu *et al.*, 2022).

Some strawberry cultivars are less susceptible to grey mould disease than others, but no cultivar is resistant. Due to the lack of strawberry cultivars resistant to *B. cinerea* and of stable and reliable biological agents, the main means of controlling this disease in commercial strawberry greenhouses and fields has been through the fungicides application to from or before flowering (Evenhuis and Wanten, 2006; Pelayo-Zaldívar *et al.*, 2007 and Rhouma *et al.*, 2022).

Chemical control represents the most successful strategy for management strawberry grey mould. It has been estimated that fungicides used against *B. cinerea* cost around €540 million per year (10% of the world

fungicide market) (Legard *et al.*, 2000). Fungicides are presently used to manage *B. cinerea* with different modes of action such as Hydroxylanilides (Fenhexamid), Phenylpyrroles (Fludioxonil), Succinate Dehydrogenase inhibitors (Boscalid), DeMethylation inhibitors (Tebuconazole), methionine biosynthesis inhibitors (Pyrimethanil) and Dicarboxamides (Iprodione) (Mertely *et al.*, 2000; Creemers *et al.*, 2006 and Feliziani and Romanazzi, 2016). Factors affecting the choice of fungicide are fungicide resistance risk, action mode (protectant, curative or both), efficacy, fungicide treatment interval, cost, presence of other diseases or pests (Dianez *et al.*, 2002; Mertely *et al.*, 2002; Fernandez-Ortuno *et al.*, 2014 and Rhouma *et al.*, 2022).

The fruits of strawberry are extremely susceptible to infection. Therefore, physical handling should be reduced to decrease fruit damage throughout packing and harvesting. Rapid cooling of harvested strawberry fruit to 0-3°C is necessary. A delay of one hour highlighted the amplification of post-harvest losses due to grey mould. Storage at these low temperatures is essential to retard grey mould and slow fruit respiration (Droby *et al.*, 2009; Feliziani and Romanazzi, 2016 and Li *et al.*, 2022).

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## CONFLICTS OF INTEREST

The author(s) declare no conflict of interest

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