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REVIEW ARTICLE

Botrytis cinerea: The Cause of Tomatoes Gray Mold

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ABSTRACT

Tomato (*Solanum lycopersicum* L.) is an important and valuable fruit because of its unique economic, health, and nutritional benefits. Among the fungal diseases affecting tomato crops, gray mold caused by *Botrytis cinerea* Pers.: Fr., is considered one of the most devastating diseases leading to an accountable loss. This airborne pathogen has the ability to kill tomato cells and produce toxins, causing massive production losses at all development stages and even post-harvest. Annual economic yield losses due to gray mold have been estimated at more than 80%. Currently, cultural practices and fungicide applications are employed for the management of gray mold due to the lack of reliable resistant cultivars. 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 symptoms and signs, epidemiology, ecology, disease development, disease cycle, and disease management.

Keywords: Tomato, *Solanum lycopersicum*, *Botrytis cinerea*, gray mold

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INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is a widely cultivated vegetable crop that holds a paramount position in global agriculture and food consumption. Due to its exceptional popularity and demand, it ranks as one of the most consumed vegetables worldwide (Fu *et al.*, 2020).

The annual production of tomatoes has been estimated at around 189.1 million tons in 2021 (Solimene *et al.*, 2023). Tomato cultivation spans across diverse regions, including the tropics and subtropics, with countries like China and India being major producers (Laranjeira *et al.*, 2022).

However, despite its significance in agriculture and as a food source, tomatoes are highly susceptible to various plant pathogens, leading to poor yields and economic losses in many countries. Among the pathogens affecting tomatoes, the fungus *Botrytis cinerea* poses a significant challenge to tomato production (Sarven *et al.*, 2020).

Botrytis cinerea is one of the most destructive fungal pathogens that affects a large number of pre-and post-harvest crops. *B. cinerea* is responsible for gray mold diseases, resulting in significant economic losses worldwide. This fungus is primarily a necrotrophic pathogen, inducing host cell death to access nutrients. Unlike many *Botrytis* species, *B. cinerea* has a wide host range, affecting over 500 plant species (Williamson *et al.*, 2007). It is considered a generalist pathogen, infecting various crops such as fruits, vegetables, and ornamental flowers. However, the most severely affected crops include vegetables e.g., tomato, cucumber, zucchini and fruit-bearing plants e.g., grape, strawberry, raspberry (Rodríguez *et al.*, 2014). *B. cinerea* is known for its flexibility in infection modes, high reproductive output, and the ability to survive for extended periods. It spreads through asexual conidia, which are dispersed by wind or water. The pathogen can also survive as mycelia from sclerotia, infected tissues, or seeds, providing alternative sources of inoculum. In addition to its asexual cycle, *B. cinerea* can undergo a sexual cycle, forming apothecia that release ascospores. However, the sexual cycle is rarely observed in nature (Cheung *et al.,* 2020). The annual economic losses caused by *B. cinerea* on different crops can reach $100 billion worldwide, which reflects the importance of this pathogen (Hua *et al.,* 2018). Tomato crops are particularly susceptible to extensive damage caused by *B. cinerea*, resulting in significant pre- and post-harvest losses worldwide (Dik and Wubben, 2007).

Controlling *B. cinerea* is challenging due to its genetic variability and the presence of both asexual and sexual stages. Fungicides have been the primary means of control; however, their efficacy is limited, and the pathogen has developed resistance to several conventional fungicides (Alzohairy *et al.,* 2021). The reliance on fungicides raises concerns about human health and environmental safety. Understanding the host-pathogen interaction and the microenvironment in which *B. cinerea* operates is crucial for effective management strategies (Williamson *et al.,* 2007). Developing sustainable control measures that minimize environmental impact and reduce the risk of fungicide resistance is essential (Roca-Couso *et al.,* 2021). Given the significant economic losses caused by *B. cinerea*, ongoing research, and efforts to control this pathogen are of utmost importance in agricultural practices.

IDENTIFICATION OF *Botrytis cinerea* AND HISTORY

Botrytis cinerea was first described by Christiaan Hendrik Persoon in 1794 and is considered a major pathogen within the *Botrytis* genus (Persoon, 1794). Taxonomic confusion previously existed between *Botrytis* spp. and *Botryotinia* spp., as they induce similar symptoms as *Sclerotinia* spp. However, in 1949, it was confirmed that *Botryotinia fuckeliana* represents the sexual stage of *B. cinerea*, establishing them as anamorphs and teleomorphs of the same fungus. *B. cinerea* belongs to the *Sclerotiniaceae* family of the *Leotiomycetes* class (Gregory, 1949 and Amselem *et al.,* 2011).

Botrytis species have traditionally been identified based on morphological features and the implementation of the *Botrytis* species recognition concept, with the characteristic "botryose" structure of conidiophores as a defining characteristic (Garfinkel, 2021). Morphological traits such as conidiophore dimensions, macroconidia size and shape, sclerotia morphology, and colony characteristics have historically been used to differentiate species (Coley-Smith *et al*., 1980 and Amselem *et al.,* 2011). However, the high intra-species variation and morphological plasticity within *Botrytis* species have posed challenges to traditional morphological identification methods. Variations in conidiophores, sclerotia, and conidial sizes among isolates have been observed, making it difficult to establish a standard phenotype for species identification (Paul, 1929 and Acosta Morel *et al.,* 2021). Additionally, some isolates fail to produce conidia or sporulate under specific cultural conditions, further complicating the identification process (Grant-Downton *et al.,* 2014). Consequently, the concept of "cryptic species" has emerged, referring to species that are morphologically indistinguishable but differ genetically, as exemplified by *B. pseudocinerea*. This species, initially considered a form of *B. cinerea*, was later recognized as distinct through molecular analysis and the inability to perform successful sexual crosses between the 2 species (Walker *et al.,* 2011).

The rise of molecular phylogenetics in *Botrytis* taxonomy has been a significant development in recent years. Staats *et al.,* (2007) and Acosta Morel *et al.,* (2021) played a crucial role in advancing molecular phylogenetics of *Botrytis*, establishing it as a widely used concept in *Botrytis* taxonomy. Recently, the implementation of molecular phylogenetics has rectified misidentified species, revived old ones, and discovered new species. Phylogenetic methods have become the primary approach for recognizing and describing *Botrytis* species, with morphology and other biological characteristics serving as complementary evidence (Garfinkel *et al.,* 2019). The combination of genetic sequencing, morphological analysis, pathogenicity tests, and sexual crosses has been used to provide comprehensive species descriptions. The integration of these approaches has facilitated a more complete understanding of *Botrytis* taxonomy. The taxonomy of the *Botrytis* genus, therefore, has undergone rapid restructuring, with the number of recognized species currently standing at 35 species (Garfinkel *et al.,* 2019).

SYMPTOMS AND SIGNS

B. cinerea is responsible for a very wide range of symptoms and these cannot easily be generalized across plant organs and tissues (Sarven *et al.,* 2020). Generally, the most common symptom on tomato leaves (mature to senescing leaves) and fruits is soft rot, accompanied by a breakdown of the parenchyma tissues and their soaking with water, followed by the rapid appearance of gray conidia masses (Burgess *et al.,* 1997 and Sarven *et al.,* 2020).

In greenhouse-grown tomatoes, the greatest damage occurs on stems at pruning wounds where the fungus can rot through the entire stem. A gray mold of mature tomato fruits occurs mainly post-harvest; an unusual 'ghost spot' symptom in unripe tomatoes is associated with successful host defense, but the symptom renders fruits unmarketable (Sarven *et al.,* 2020).

The pathogen extends also the node on the vegetative stems to give rise to a rapidly spreading pale brown visible lesion (Burgess *et al.,* 1997 and Williamson *et al.,* 2007). After dormancy, the tomato stem lesions turn white and show large black sclerotia. Asymptomatic infection of flower styles by this airborne pathogen results in premature fruit abscission associated with the generation of ethylene in a condition called 'runoff' (Santra and Banerjee, 2023).

ECONOMIC IMPORTANCE

Tomato gray mold, caused by the fungus *B. cinerea*, has significant economic importance in tomato cultivation. Here are some key aspects of its economic impact (Williamson *et al.,* 2007 and Sarven *et al.,* 2020):

Yield Losses:

Gray mold can lead to substantial yield losses in tomato crops. The disease affects various parts of the plant, including fruits, leaves, stems, and flowers. Infected fruits may experience rotting, softening, browning, and a decrease in marketable quality. The loss of marketable fruit reduces the overall yield and can significantly impact farmers' income.

Reduced Market Value:

Infected tomatoes often have compromised quality and appearance due to the presence of greyish-brown mold on the surface. Consumers tend to avoid purchasing or paying a lower price for such affected fruits. This reduction in market value directly affects the profitability of tomato producers.

Post-Harvest Losses:

Gray mold can continue to develop and spread during the storage and transportation of harvested tomatoes. Infected fruits may rot further, leading to post-harvest losses. These losses can occur both in field-grown tomatoes and in tomatoes produced in greenhouses or storage facilities.

Increased Production Costs:

Managing and controlling gray mold requires additional resources and costs. Farmers may need to invest in preventive measures, such as improving air circulation, implementing pruning techniques, and applying fungicides. These expenses, along with potential yield losses, contribute to increased production costs for tomato growers.

Impact on Export Market:

Grey mold can have implications for tomato exports. Importing countries often have strict quality standards, and the presence of gray mold can lead to rejected shipments or reduced market access. This can have a detrimental impact on the export-oriented tomato industry and limit economic opportunities.

Dependence on Fungicides:

To manage grey mold, farmers often rely on fungicide applications. However, this increases the use of chemicals, which can have environmental consequences and additional costs. Additionally, over time, the fungus may develop resistance to certain fungicides, requiring the use of alternative products or strategies.

Overall, the economic importance of tomato grey mold lies in its ability to cause yield losses, reduce market value, increase production costs, contribute to post-harvest losses, and affect export opportunities. Implementing effective disease management practices and investing in resistant tomato varieties can help mitigate these economic impacts and sustain tomato production.

LIFE CYCLE AND EPIDEMIOLOGY

The life cycle and epidemiology of *B. cinerea* the cause of tomato gray mold involves several stages and factors that contribute to the disease's development and spread. Here's an overview of the life cycle and epidemiology (Williamson *et al.,* 2007; Orozco-Mosqueda *et al.,* 2023 and Santra and Banerjee, 2023):

Survival and Overwintering:

Botrytis cinerea survives between growing seasons through various survival structures. These include mycelium and sclerotia present in infected plant debris, soil, or on host plants. These structures can persist in the environment and serve as sources of inoculum for subsequent infections.

Primary Infection:

In spring or under favorable environmental conditions, the fungus starts its life cycle by producing asexual spores called conidia. These conidia are produced on infected plant debris or directly on infected plant tissues. They are easily dispersed by wind, water, or human activities.

Dispersal and Infection:

Conidia are dispersed over short distances and can land on healthy plant tissues. They can enter the plant through wounds, natural openings, or directly penetrate the plant surface. High humidity and moisture facilitate conidial germination and subsequent infection.

Infection and Colonization:

Once the conidia germinate, the fungus grows and penetrates the plant tissues. It secretes enzymes and toxins that break down the plant cell walls, facilitating its invasion and colonization. The infected tissues show characteristic symptoms of gray mold, including water-soaked lesions, fluffy greyish-brown mold, and rotting.

Spore Production and Secondary Infection:

As the fungus colonizes the infected tissues, it produces abundant conidia on the surface of infected plant parts. These conidia are then released into the surrounding environment. Secondary infections occur when these conidia land on healthy tissues, initiating new infection cycles.

Disease Spread:

The gray mold disease can spread rapidly within a field or greenhouse under conducive conditions. Factors such as high humidity, moderate temperatures (around 20-25°C), and poor air circulation promote the development and spread of the disease. The movement of infected plant material, tools, equipment, and workers between infected and healthy plants can also contribute to disease spread.

Sexual Reproduction:

In some cases, under specific conditions, *B. cinerea* can undergo sexual reproduction. This involves the formation of sexual structures called ascocarps, which produce sexual spores called ascospores. Ascospores can contribute to the genetic diversity and survival of the fungus over long periods.

Understanding the life cycle and epidemiology of this disease is crucial for implementing effective disease management strategies. These may include cultural practices, proper sanitation, pruning, fungicide applications, and the use of resistant varieties to minimize disease impact and reduce crop losses.

DISEASE MANAGEMENT

Management of tomato gray mold is difficult due to the genetic diversity of *Botrytis cinerea*, survival as mycelia of sclerotia and conidia, and the wide range of host plants. The best approach to control this disease is the application of integrated plant disease management (cultural control, chemical control, host resistance, biological control, etc.) (Rhouma *et al.*, 2022 and Santra and Banerjee, 2023).

Cultural control combines a lot of elements that must be put into practice: avoid unnecessary late watering and keep bed surfaces dry when the fruit is present to help reduce the chance of infection (Krasnow and Ziv, 2022); maintain low leaf humidity by rolling the sides of high tunnels, increasing aeration and avoiding overhead watering (Orozco-Mosqueda *et al.*, 2023); remove infected plants, stems, leaves and fruits by placing them in a plastic bag (Rhouma *et al.*, 2022); prune plants in the afternoon when the morning dew has dried (Orozco-Mosqueda *et al.*, 2023); remove all plant residues at the end of the season; make sure the soil contains enough calcium for growing plants to produce healthy tissues; provide good ventilation for the greenhouse. Keeping dry plants and low air humidity by opening vents in the greenhouse when temperatures rise. To improve air circulation: use fans to move the air inside the greenhouse (Krasnow and Ziv, 2022); choose a plant density that allows good air movement between plants; prune plants regularly to remove old, bushy sides and leaves to aid air movement; remove all plant debris from the previous and current crop - this material carries gray rot spores that can infect the next crop (Rhouma *et al*, 2021).

Fungicides may be required in fields and greenhouse-grown tomatoes if gray mold infections are occurring. Generally, fungicides will not suppress an established infection and are applied to protect against infection (Dal Bello *et al.,* 2008 and Rhouma *et al.,* 2023). Fungicides cannot prevent disease development in fruit touching infested soil or plant debris, so treatments are not recommended for processing tomatoes. But you shouldn't rely on chemicals alone to control gray mold (Koike *et al.,* 2007 and Rhouma *et al.,* 2023). Infection of bush tomatoes is more likely when vines grow into furrows, allowing fruit to contact irrigation water (Arteta *et al.,* 2009 and Santra and Banerjee, 2023). Factors affecting the fungicide choice are the presence of other diseases or pests, cost, fungicide treatment interval, efficacy, action mode, and fungicide resistance risk (Staples and Mayer, 1995 and El-Saadony*et al.,* 2022).

Biological control is undoubtedly a good option. Generally, microbial bioagents can effectively manage plant diseases through antibiosis, competition for places and nutrients, volatile compounds, parasitism, production of syringotoxins, syringomycins, and killer toxins (Abbey *et al.,* 2019), secretion of cell wall degrading enzymes (Köhl *et al.,* 2019 and Sarven *et al.,* 2020), and initiation of plant defense (Aqueveque *et al.,* 2017 and Mhlongo *et al.,* 2018). For that reason, developed and developing countries are taking a set of precautions. The foremost of these precautions is to increase the yield per unit and prevent the losses resulting from biotic/abiotic factors. In plant production, the annual loss rate is 36.5-100% (Mhlongo *et al.,* 2018). Contamination with pathogens can occur during storage, marketing and after the purchase of the consumer as it is during and after the harvest as well (Romanazzia *et al.,* 2016).

Biological control agents against *B. cinerea* act through a direct antagonistic effect on the pathogen, encompassing **(i)** antibiosis, **(ii)** competition, and **(iii)** mycoparasitism (Kasfi *et al.,* 2018 and Chen *et al.,* 2019). Indirect mechanisms include the induction of resistance by stimulating plant defense reactions and stimulating plant growth and soil fertilization (Köhl *et al.,* 2019 and Tian *et al.,* 2023).

Biocontrol experiments against *B. cinerea* have been attempted by the biological control agents which are most commonly filamentous fungi from the genera *Trichoderma* (Herrera-Téllez *et al.,* 2019 and Nawrocka *et al.,* 2023), *Ulocladium* and *Gliocladium* (Sarven *et al.,* 2020), bacteria from the genera *Bacillus* (Zhou *et al.,* 2021) and *Pseudomonas* (Hajji-Hedfi *et al.,* 2023) and yeasts from the genera *Pichia* and *Candida* (Kasfi*et al.,* 2018) under laboratory, fields and greenhouse conditions (Herrera-Téllez *et al.,* 2019 and Nawrocka *et al.,* 2023). Hajji-Hedfi *et al.,* (2023) found that disease severity in tomato seedlings and fruits was significantly reduced when treated with *Trichoderma* sp. and *Pseudomonas* sp. Furthermore, the combined treatment with *Trichoderma* sp., *Pseudomonas* sp., and salicylic acid-induced significant biochemical and physiological changes in fruit and seedlings (Hajji-Hedfi *et al.,* 2023).

To achieve successful disease management by biological control it is necessary to use a microbe that is adapted to both the crop and environmental niche where it must perform and to understand its environmental requirements and action mode (Hajji-Hedfi *et al.,* 2023 and Nawrocka *et al.,* 2023).

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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