

Taxonomy, distribution, epidemiology, disease cycle and management of brown rot disease of peach (*Monilinia* spp.)

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Abstract

Peach is a temperate fruit and is grown in various edaphoclimatic settings worldwide. Brown rot, caused primarily by *Monilinia* spp. is one of the most destructive peach diseases. The disease results in severe pre-harvest and post-harvest losses. More than half of the world's post-harvest losses of peach can be attributed to brown rot disease. Despite the widespread adoption of management strategies such as pruning, removing fruit mummies, eliminating wild plums, chemical control remains an effective strategy for managing brown rot disease. However, environmental and human health impacts of chemical control and fungicides resistance consequences, these management tactics tend to be re-evaluated. The aim of this review is to comprehensively sum up the available information on the taxonomy, distribution, epidemiology, symptomology, molecular and morphological characterization of brown rot disease, and to date management approaches. However, fast paced current research on brown rot disease of peach management should be carefully updated for the full-proof control of the fungi. Nevertheless, more research and review of the information regarding various aspects of diseases management exclusively biocontrol agents are needed to exploit their actual potential, which is the salient objective of this review. This review will open new avenues giving future prospects and research agenda to the scientists working on this serious pathosystem of peach.

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Introduction

Peach (*Rosaceae* family; subfamily *Prunoideae*) is the most popular tree fruit that belongs to the genus *Prunus* and subgenus *Amygdalus* (Hammerschlag, 2012). The peach species can be used in breeding as a source of resistance against pests and diseases in peach grafting (Byrne *et al.*, 2012). Among the peach species, *P. persica* ranked 3rd most valuable and commercially significant fruit crop, followed by apple (*Malus* spp.) and pear (*Pyrus* spp.). China is the main origin of peach trees and the primary producer of peach fruits worldwide (Li *et al.*, 2018), followed by Spain, Italy, and the United States. Numerous fungal pathogens threaten the quality and production of peach; however, brown rot caused by *Monilinia* spp. is considered the most destructive disease of peach (Luo, 2017).

The prevalence of brown rot (BRI) varies substantially throughout the fruit's development. Fruits are less susceptible to brown rot at early stages; however, they become resistant during pit hardening and more susceptible in later stages of development (Obi *et al.*, 2018). Besides, brown rot pathogens (*Monilinia* spp.) are polycyclic, and the pathogens are infecting numerous times during the host development. The pathogens overwinter in mummified fruits (Casals *et al.*, 2015), in the canopy or on the ground (Hrustić *et al.*, 2012), in fruit peduncles, in cankers on twigs, spurs, and branches (Villarino *et al.*, 2013; Kreidl *et al.*, 2015). Hence serve as sources of primary inoculum, thereby infecting blooms, buds, and young shoots (Obi *et al.*, 2018). The global annual worth of *Monilinia* spp. losses are 1.7 billion Euros; annual losses for peach, cherry, and plum yield only in the United States are approximately 170 million USD, and annual losses for peach and apricot crops in Australia are approximated to be 1 million AUD (Martini and Mari, 2014). In Spain, particularly, the disease has been associated with over 60% of fruit loss after harvest (Obi *et al.*, 2018). Besides, more than 50% of the global post-harvest loss has been ascribed to brown rot disease, especially in peach late-ripening varieties (Casagrande, 2021).

Various management strategies, including cultural, biological, chemical, physical, botanical, and host-resistance techniques, are used to manage brown rot disease. The previous review has addressed some management strategies (Obi *et al.*, 2018). Unfortunately, our understanding of the taxonomy, distribution, epidemiology, morphological and molecular characterization, and management strategies is limited. This review article provides an extensive update on general taxonomy, global distribution, disease cycle and epidemiology, symptomology, molecular and morphological characterizations of brown rot, and up-to-date management strategies.

Genus's description and taxonomic classification of *Monilinia* spp.

In 1796, Persoon identified a fungus observed on rotting pear, plum, and peach fruits in 1796, which was the first description of a brown rot fungus (Kumari *et al.*, 2018). Persoon, first named it *Torula fructigena*, but later he modified the generic name to *Monilia* [*Monilia fructigena*]. Several writers published descriptions of the anamorph of *Monilia* under several particular names during the nineteenth century. For example, Kunze & Schmidt (1817) called it *Oidium fructigenum*, a brown rot fungus that caused buff-colored pustules on fruits (Sigei, 2018). In Europe, Wallroth (1833) was the first to recognize two different brown rot fungi. *Oospora fructigena* produced 'ochraceis' pustules, whereas *Oospora laxa* produced 'griseis' pustules. In 1851 Bonorden modified the latter term to *Monilia cinerea*, which European workers still used until recently (Sigei, 2018; Mack *et al.*, 2021).

Many workers believed there was just one brown rot fungus in Europe, *Monilia fructigena* Pers., until the early 20th century. A brown rot fungus identified in North America was also given that name by Smith in 1889 (Biggs, 2019). Based on variations in the color of sporogenous tissue on culture medium and fruits, spore diameters, and findings from cross-inoculation studies, Woronin in 1900 offered solid evidence that two separate fungal forms existed in Europe. Although the teleomorph state had never been observed, Schroter in 1893 was sure that both species belonged to the genus *Sclerotinia* (Yildiz and Ozkilinc, 2020). *Sclerotinia cinerea* (Bon.) Schroter produced ash-grey pustules, while *Sclerotinia fructigena* (Pers.) Schroter produced buff-ochreous pustules (Landi *et al.*, 2018). The monilioid species, like many other divergent forms, were previously classified within the genus *Sclerotinia* due to the significant resemblance of the apothecia and the inability to identify the importance of the pseudosclerotium. Because no other initially proposed generic or subgeneric title or idea for this group was acceptable. Later, in 1928, Edwin Honey proposed *Monilinia* to encompass this new genus of *Sclerotinia* monilioid species (Dowling, 2015). The term *Monilinia* originated from the Latin word for Monile, which means Necklace, since the conidia have a structure like beads of a necklace (Honey, 1936).

Monilinia is a necrotrophic fungus (Ascomycota) belonging to the Helotiales (Leotiales) order, which includes both human and plant infections (Obi *et al.*, 2018). The *Monilinia* spp. causes brown rot disease, cankers, blossom, and wood blight of the flowers of some growing members of the family *Rosaceae*. Almost thirty-five species of *Monilinia* have been described. Among them, four *Monilinia* spp. i.e., *Monilinia fructigena*, *Monilinia fructicola*, *Monilinia laxa*, and *Monilia polystroma*, are causing severe brown rot of stone fruits, apples, pears, and quince. Further, *Monilinia* spp. was categorized Junctoriae and Disjuntoriae (Honey, 1928). Among the *Monilinia* spp., the *M. fructicola* is widely responsible for causing the brown rot disease of peach (Villarino *et al.*, 2013). *M. fructicola* has a sexual stage of reproduction, but in 2011, the botanical code was changed to allow only one name for each fungus. The name was chosen for both sexual and asexual stages of the fungus (Ondejková *et al.*, 2010). Later on, scientists proposed differentiating names, i.e., “American brown rot”, “fruit brown rot”, and “peach brown rot” are used for *M. fructicola*, and the “European brown rot” is referred to as *M. laxa* (Marcet-Houben *et al.*, 2021).

In conclusion, the usual criteria for identifying *Monilinia* spp. are spore color, conidial pustules produced on infected fruits, mode of branching of germ tubes arising from conidia, cultural characteristics, and host and tissue specificities (Willetts and Suzanne, 2019). When using these criteria to identify an isolate, comparing unknown with known cultures is often necessary. This may be inconvenient and dangerous, as exotic cultures must be collected, and new pathogens may be introduced. Furthermore, the characters vary even within species and are not always satisfactory for accurate identification. Hence *Monilinia* spp. have had multiple scientific names allocated to them over the years because the asexual and sexual stages of the organism were discovered at different dates or points in time. This pleomorphic fungal nomenclatural system has undoubtedly become a subject of dispute among mycologists as new molecular data have begun to expose the inadequacies of using morphological characteristics to assign scientific names.

Global distribution

Throughout the past 20th century, the pathogen of brown rot in China was reported as *M. laxa* and *M. fructigena* (Yin *et al.*, 2017). However, in the year 2005 *M. fructicola*, was first reported from China and later, it was widely found in the United States, Australia, Canada, and New Zealand (Yin *et al.*, 2017; Tran *et al.*, 2020). The researcher found that *M. fructicola*, is the leading species already present in China for a long period (Yin *et al.*, 2015). In Europe, *M. fructigena* is the most common pathogen and is thought to be known as an unidentified pathogen in Canada, Australia, America, and New Zealand (Papavasileiou *et al.*, 2016). The anamorph species *M. polystroma*, found as in close relative species to *M. fructigena*, was reported in Japan (Van Leeuwen *et al.*, 2002), Hungary (Petróczy and Palkovics, 2009), Italy (Abate *et al.*, 2018) and Poland (Poniatowska *et al.*, 2013). The global distributions of *Monilinia* spp. are shown in Figure 1.

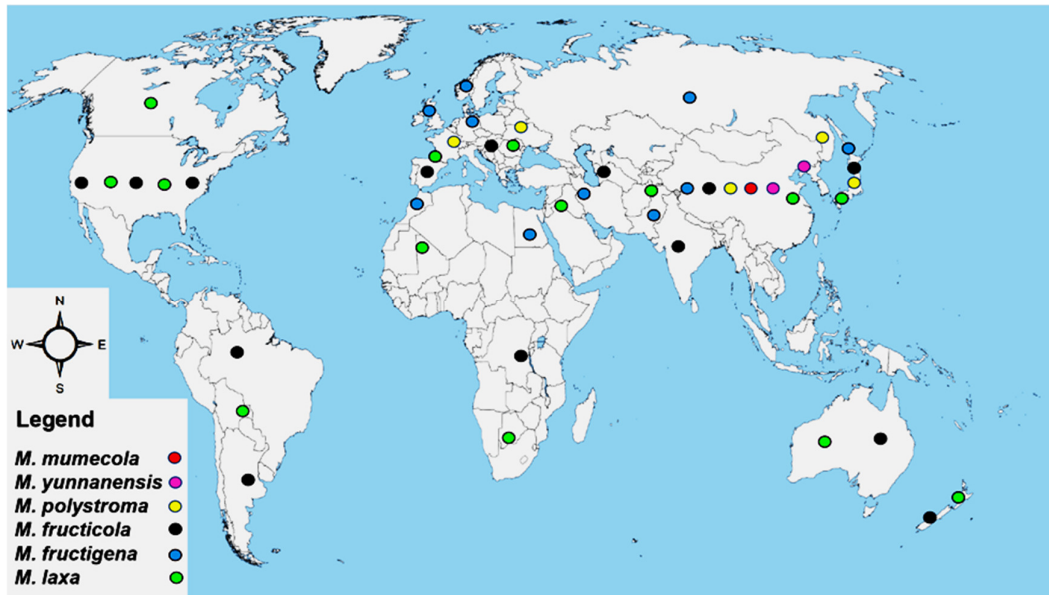


Figure 1. Geographic distribution of brown rot causing *Monilinia/Monilia* spp.

Characterization

Morphological characterization

The colony color of most of the brown rot pathogens is greyish/greenish brown/grey however, there are variations in the margins. For example, margins of the *M. laxa* are serulated, whereas margins of *M. fructicola* colony are not serulated. Also, there are variations in the conidia sizes. For example, *M. laxa* conidia range from 11-13×8-9.5 μm and one short, twisted germ tube in each conidium. Similarly, the Colony color of *M. fructicola* is greenish-brown. Dimensions of conidia range from 12.5-14.5 ×8-10 μm; however, in contrast to *M. laxa* there is one long and straight germ tube per conidia (Obi *et al.*, 2018).

Similarly, colony color of *M. mumecola* is similar to *M. laxa*. However, margins of *M. mumecola* are lobbed in contrast to *M. laxa*. However, both colony colors are gray-green compared. Also, there are differences in conidia size. For example, the conidia of *M. mumecola* are the largest on average, and those of the *M. laxa* are the smallest.

Similarly, the conidia of *M. yunnanensis* are smaller on average compared with the *M. fructigena* and *M. fructicola* (Hu *et al.*, 2011). Table 1 provides an overview of the brown rot fungi's distinctive characteristics. Comparison between *Monilinia* spp. is based on differences in colony growth rate, sporulation intensity, colony morphology is given in Table 1.

Table 1. Comparisons of the morphological differences among *Monilinia* spp

Species	Colony diameter (24h)	Colony Shape	Colony margins	Colony Color	Colony growth rate	Spore shape	Sporulation	Germ tube	References
<i>M. fructicola</i>	9-20 mm	Margin entire	Not serulated	Greenish brown	High/continuous radial growth	Lemon shaped	All over the surface of colony	Long and branching far from spore	(Martini & Mari, 2014)

<i>M. laxa</i>	2-11 mm	Lobed margin	Serulated	Grayish brown or hazel	Low/radial growth periodically stops	Ellipsoid, ovoid or limoniform	In older cultures, tufts of aerial mycelium developed where sporulation occurs	Short and branching near spore	(Lahlali <i>et al.</i> , 2020)
<i>M. fructigena</i>	0-12 mm	Margin entire	Not lobbed but entire	Creamy/buff-yellowish	Low-moderate growth rate	Cylindrical or lemon shaped	Aerial mycelium formed in concentric rings in which sporulation occur	Long and branching far from spore	(Vasić <i>et al.</i> , 2016)
<i>M. polystroma</i>	4-9 mm	Margin entire	Not lobbed but entire	Creamy/buff-yellowish	Moderate growth rate	Cylindrical or lemon shaped	Apparent mycelium tufts sporulation	Long and branching generally developed pointy sides of conidia	(Yin <i>et al.</i> , 2015)

Molecular characterization

To determine the difference between *Monilinia* spp. there are several molecular methods for its molecular characterization (Oliveira Lino *et al.*, 2016). Polymerase chain reaction (PCR) is an important technique for characterizing and detecting any DNA sequence. Till now, various PCR procedures such as cooperative PCR (Co-PCR), nested PCR (nPCR), real-time PCR (RT-PCR), multiplex PCR (MPCR), fluorescence in-situ hybridization (FISH) and DNA fingerprinting have been used to identify *Monilinia* spp. (Balodi *et al.*, 2017).

Förster and Adaskaveg (2000) used *Monilinia*-specific DNA primers for the first time to identify *Monilinia* spp. Ioos and Frey (2000) studied genetic diversity between *M. laxa*, *M. fructigena*, and *M. fructicola*, using endpoint PCR and synthesized primers to achieve rightly and directly on contaminated fruit (Obi, 2018). Later this procedure was known as the standard test, as described previously (Riccioni and Valente, 2015). By using PCR, the brown rot disease was detected in the stone fruits and flowers using a species-specific primer (Martini, 2013). Moreover, multiplex-PCR was used to identify and characterize *M. fructigena*, *M. fructicola*, *M. laxa*, and *M. polystroma*. To detect *Monilinia* spp. and brown rot disease universal diagnosis from stone fruits, employ two PCR procedures for brown rot disease along with detection of *Monilinia* spp. (Poniatowska *et al.*, 2013). In combination with universal primers and an internal control method for detecting brown rot were produced due to three chief species. All four *Monilinia* spp. (*M. laxa*, *M. fructicola*, *M. fructigena* and *M. polystroma*) can be identified using RT-PCR (Papavasileiou *et al.*, 2016). Similarly, a multiplex-PCR procedure was developed to identify three Chinese *Monilia* spp. *M. fructicola*, *M. mumecola*, *M. yunnanensis*, *M. laxa* and *M. fructigena* (Hu *et al.*, 2011). Three *Monilinia* spp. (*M. laxa*, *M. prunus* and *M. malus*) were detected and differentiated with the help of multiplex RT-PCR (Guinet *et al.*, 2016). Another researcher used high-resolution melting (HRM) techniques to differentiate between six *Monilinia* spp. from peach fruit (*M. laxa*,

M. fructicola, *M. fructigena*, *M. mumecola*, *M. lithartiana* and *M. yunnanensis*), and they examined melting curves of amplicons of two universal pairs of primers (Papavasileiou *et al.*, 2020). RT-PCR/quantitative polymerase chain reaction (qPCR) based techniques that are altered for detection of brown rot latent infection and to separate *Monilinia* spp. from flowers of peach fruit was compared with overnight freezing incubation technique (ONFIT) as described previously (Garcia-Benitez *et al.*, 2017). Other important techniques include the fast multiplex quantitative/real-time polymerase chain reaction (qPCR/RT-PCR method) described previously (Van Brouwershaven *et al.*, 2010). Subsequently, (Garcia-Benitez *et al.*, 2017) evaluated the methodology in terms of (i) test performance accuracy, (ii) repeatability, (iii) analytical specificity, (iv) sensitivity and (v) its reproducibility, as described by standard PM7/98 of the European Plant Protection Organization (EPPO) for *Monilinia* spp. i.e., for identification of brown rot latent infection. It is much sensitive, dependable, and fast as compared to ONFIT. An important point to manage and hinder the transmission of *Monilinia* spp. from infected to disease-free regions (Fazinić *et al.*, 2017) is to detect latent infection in plants rapidly and accurately in its early stages (Papavasileiou *et al.*, 2016). One of the successful methods to identify latent infection of brown rot is the overnight freezing-incubation technique (ONFIT) and it takes 7-9 days of test time-cost (Bernat *et al.*, 2017). qPCR-based techniques detect the latent infection however high cost of consumables and reagents as compared to ONFIT and an indication of false-positive results due to non-viable fungal DNA detection (Garcia-Benitez *et al.*, 2017). Identification methods based on DNA have many advantages like dependability, high sensitivity, time-saving, and more specific than artificial cultivation, traditional and serological assay methods (Guinet *et al.*, 2016). For instance, the multiplex RT-PCR assay method is a one-step process and was used by (Guinet *et al.*, 2016). It is a successful and rapid method to identify three main brown rot causing *Monilinia* spp. (*M. laxa*, *M. fructicola* and *M. fructigena*). Researchers concluded, in the sense of phytosanitary laws and regulations, the excellent dependability of their findings is of utmost importance, considering that test data was produced and the assay is completely checked in coordination with the EPPO guideline (Petter *et al.*, 2011). In brief, procedures regarding molecular biology are increasingly giving ways for well-timed detection of quarantined phytopathogen along with *Monilinia* spp. This approach speeds up the identification of *Monilinia* spp. compared to quantitative characteristic-based approaches because it does not require pathogen isolation. Eventually, these approaches can be energized to directly and especially detect species attacking the peach fruit. Its significance, no wonder, is also linked with overlapping classical screening methods.

Reproduction

Thin-walled primary hyphae, often 250 μm in length and 7-10 μm in width, with one may be more branches formed before the 1st septum. The secondary and corresponding branched division is normally narrower (Poniatowska *et al.*, 2021). The sclerotium is a hard, sterile, dark, or brightly colored structure and typically doesn't form. The apothecia are produced haphazardly on mummified fallen fruits in the spring season.

Most of the *Monilinia* spp. conidia are blastic and produced in chains with the earliest spore at the remote end, sometimes with truncate ends, ellipsoid or ovoid, and hyaline (greyish-buff in mass). Conidia germinate on water agar and produce un-branched germ tubes (18 h at 25 °C). Even so, for conidia directly taken from the fruit, it may be more different. A phialides spermatia (microconidia) situation is somehow present and frequently is noticeable in old colonies (Vasić *et al.*, 2016). They are formed from the sporodochia before a hyphal tip expands and a septation forms between the hypha and the newly shaped conidium; another conidium grows out of the first until a chain of conidia forms. From a single parent, two of the conidia may grow to form in a chain shape (Jenkinson *et al.*, 2017). On both ends, conidia are ellipsoid, tapering from ends with papillae and lemon-like shape. Usually, the shape of spores is blastic, forming a chain at the tip of hyphae; when mycelia breakdown they can also be arthric (Levatić *et al.*, 2020). In conidia, *M. fructicola* does not contain any disjunctors or spacers. When conidia size increases, pressure builds up between them until they

start separating from each other (Byrde and Willetts, 2013). Dry climatic conditions and disturbances such as wind tolerate them to completely detach and disseminate (Bardetti *et al.*, 2019). Conidia are multinucleate, and conidial size determines by the number of nuclei. Due to the number of nuclei decreasing and increasing temperature, size varies, mostly ranging from 12-16×8-11µm (Everhart, 2012). Nuclei pass from the first conidia into that later go through septal spores during conidia forming in chains. Commonly conidia have four to eight nuclei, and the last one has a typical form, having the fewest nuclei and those first hold the most. Conidia normally shape a single germ tube character; this may differ between strains. Later dispersal and formation of germ tube of conidia, nuclei go into the germ tube; on the other hand, the number of nuclei in conidium remains constant because of the mitotic division of nuclei (Everhart, 2012).

Disease cycle and epidemiology

Monilinia spp. are a polycyclic fungus and completes more than one cycle per season (Larena *et al.*, 2021). The fungi pass through different cycles of the secondary phase in the early development of the host. These pathogens survive in multiple mummified fruit structures during the winter season, throughout the year (Casals *et al.*, 2015), or maybe in plant canopy or above soil (Hrustić *et al.*, 2018) fruit stalk, twigs, branches and spurs (Kreidl *et al.*, 2015). It has been reported that it serves as a source of initial inoculum on the infected residues and becomes secondary inoculum when climate favours for appropriate spore conditions, contaminating buds, blossoms, and newly grown shoots of peach. Throughout the (Martini and Mari, 2014) fruit ripening period, propagules of brown rot are almost everywhere.

Additionally, suppose the weather is damp and moist for a longer duration. In that case, the disease is almost likely to occur (Obi *et al.*, 2018) if bruises are on the fruit's peel. Water, wind, birds, humans, and insects transmit fungi. It can also be transmitted by rain or overhead splashes of irrigation (Obi *et al.*, 2018).

Moreover, the insects and storms cause injuries; as a result, fruits are cracked, limbs rub, twig becomes wounded, and handling is important points that influence the ultimate crop loss because of rot disorder (Everhart *et al.*, 2013). Therefore, proper sanitization of the orchard is required to minimize the disease throughout the growing seasons, particularly at the beginning of spring (Martini and Mari, 2014). If the fruit is young and is safe from wounds, it will remain uninfected. During harvesting and packaging, caution needs to be taken to avoid ripped fruit from injuries. Additionally, wild and abundant stone fruit trees should be eliminated as they become collateral sources for new diseases (Rungjindamai *et al.*, 2013). The contamination of flowers will start to wilt quickly; around the shuck of flower, a tan-gray colored bunch of threads and asexual spore (conidia) masses will develop (Villarino *et al.*, 2010). The fungus soon spreads via pedicel to twig and induce canker formation. During the early developmental stages of fruit, if the weather is moist, conidial masses will be formed quickly on the newly cankered surface of the twig. Spores are airborne and will be separated like ascospores with the onset of the summer season. The disease cycle of brown rot disease is shown in Figure 2. Nevertheless, the disease will remain latent if environmental conditions are not suitable (Rungjindamai *et al.*, 2013) until the fruit is mature, the optimum time for disease progress (Thomidis, 2017; Obi *et al.*, 2018).

In the USA, ascospores constitute the major primary inoculum of brown rot disease (Keske *et al.*, 2013). Fruit mummies on the orchard floor typically develop apothecia when the host begins to blossom (Villarino *et al.*, 2010). In a previous study, apothecia appeared four days after the first buds began to open. Apothecia formation is expedited when mummies are partially covered with moist soil and shaded by weeds, though filtered light is necessary for hymenium development (Martini and Mari, 2014). Exposure to direct sunlight, high temperatures, or low humidity causes shrivelling and disintegration of apothecia, though they may revive during cooler night temperatures and release ascospores (Rungjindamai *et al.*, 2014). Apothecia deteriorate several weeks after their formation, generally releasing all spores within one week. *Monilinia* spp., overwinters in sclerotized mummies, peduncles, blighted blossoms, and cankers (Lowe *et al.*, 2016). Sporodochia form on these plant structures and bear greyish-brown conidial masses that become the primary inoculum (Martini and Mari, 2014). However, the conidia are rarely the primary inoculum (Villarino *et al.*, 2012). Secondary inoculum

sources are conidia forming new cankers, blighted blossoms, and rotten fruit. Fruit infections are formed when the fungus enters through wounds, trichome sockets, and stomata (Oliveira Lino *et al.*, 2016). *Monilinia* spp. conidia may also form latent infections in unripe fruit (Hu *et al.*, 2011). Wind storms, rain splashes, and insects are the reasons to spread conidia and may survive for months if they are not scorched by the sun (Oliveira Lino *et al.*, 2016).

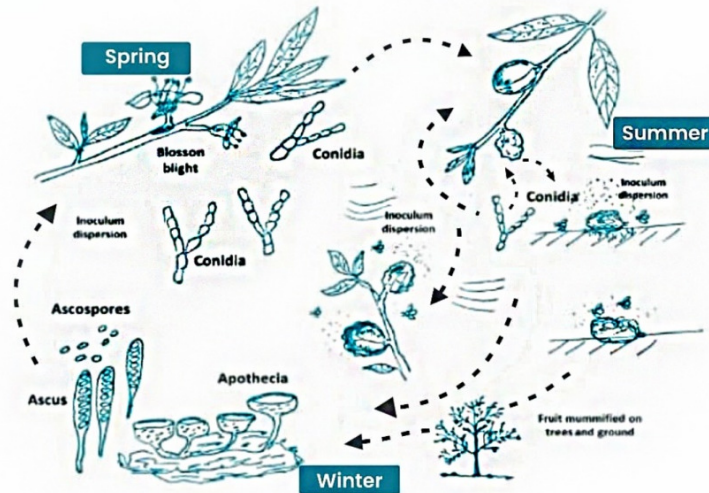


Figure 2. Disease cycle of brown rot of peach

Note: Original figure

Symptoms and signs

The major symptoms of brown rot disease are the blight of blossoms, twig cankers, and fruit rots (Figure 3). Blossom blight is initiated by conidia or ascospores that can infect any flower part: petals, stamens, pistils, and sepals (Martini and Mari, 2014). Browning anthers or necrotic lesions indicate the presence of blossom blight three to six days after infection (Rungjindamai *et al.*, 2013). As mycelia grow and spread throughout the flower tissue, they form a meshwork of stroma that encompasses the entire flower and eventually can grow through the pedicel into the branch. Sporodochia burst through the blossom surface in rainy weather and produce conidia (Pereira *et al.*, 2020). In wet weather, blossoms become rotten and soft, while they become fragile and brittle in dry weather. Chemicals released by the fungus prevent the blossom from dropping from the branch, and often the blossom becomes attached to the surface of the branch with a gummy exudate (Papavasileiou *et al.*, 2020). Twig cankers form when the fungus enters a twig through the petiole of a blighted blossom or a fruit spur. The primary phloem of the branch becomes obstructed with *Monilinia* conidia and a gummy exudate that is often released onto the surface of the branch (Martini and Mari, 2014; Lichtemberg *et al.*, 2017). If the cankers form in large branches, they can cause severe stress to the tree, resulting in secondary infection and tree death (Rivera *et al.*, 2018). However, cankers are more commonly found on small twigs that can become girdled at the location of the canker and die from the canker location to the tip of the branch (Oliveira Lino *et al.*, 2016). Cankers can be as long as 90 cm. They are generally more severe when they form from fruit infection than blossom infections (Dowling, 2015). Cankers are generally reddish-brown colours and are often sunken into the branch (Rungjindamai *et al.*, 2013). As shown in Figure 4, fruit rots typically occur in mature fruit, and lesions begin as small brown spots that rapidly grow and become softer as the infection progresses (Angeli *et al.*, 2017). Sometimes the rot does not appear until 48 hours after infection, depending on weather conditions. Conidia are formed in the lesion as soon as 24 hours after the infection begins to show, and generally, the whole fruit becomes covered with conidia and rot (Angeli *et al.*, 2017). Eventually, this fruit will turn into a mummy. As in blossom blight, chemicals released by *Monilinia* anchor the

fruit onto the tree and prevent fruit drop. Mummies may remain attached to the tree for several years, providing a continuous source of inoculum. Latent infections can occur in immature fruit and eventually cause post-harvest rots (Dowling, 2015).

Epidemiology

The awareness of favorable environmental conditions of *Monilinia* spp. is necessary for creating a predictive model to understand brown rot epidemiology and to provide a disease management plan (Larena *et al.*, 2021). Significant abiotic elements that determine the capacity of conidia to germinate and the development of *Monilinia* conidia outside of the host are temperatures, duration of wetting, and water activity (Obi, 2018). For species of *M. fructicola*, the effects of these factors on the pathogenicity of *Monilinia* spp. combine with those of spore humidity, spore age, and concentration of the inoculum. Almost 80% fertilization of conidia will start at 25 °C and 0.99 water activity in 2 h, but time varies up to 4h in the case of *M. laxa*. Pathologists notice that *Monilinia* species will grow at a temperature of 0-35 °C with 0.99-0.95 water activity, but the typical optimum temperature for species *M. fructicola* and *M. laxa* is described as ranges between 24.5 °C and 19.8 °C, respectively (Angeli *et al.*, 2017). The predicted high temperature for the growth of the lesion is more for *M. fructicola* (30 °C) than *M. laxa* (10 °C); resulting from the fact that *M. fructicola* is not favoured by the cold environment like *M. laxa*. According to a previous study, *M. fructicola* favors for hot climates in contrast to *M. laxa*. Besides, under typical favorable situations *M. laxa* is as hostile as *M. fructicola* on fruits (Bernat *et al.*, 2017). When free water is not available in the host plant, *M. laxa* in contrast to others (*M. fructicola* and *M. fructigena*) could grow properly because the host is too sensitive. The lowest temperature at which both *M. fructicola* and *M. laxa* can grow was thought to be 4.7 °C and 0 °C, respectively (Obi *et al.*, 2018). But some reports also show conidial growth at -4 °C (Larena *et al.*, 2021). Generally, conidia can germinate on a wide temperature range from 0-35 °C, if there is the availability of 0.99-0.90 water activity and relative humidity in equilibrium, with two h exposure in-vitro and stone fruits, are usually stored at 0 °C. So, it is concluded that pathogen can grow on the skin of peach under 0-40°C at 100-80% relative humidity (Villarino *et al.*, 2012). Hence, a typical optimum temperature of germination and development of brown rot in fruit peach at the seedling stage is reported as 22.5-25 °C, with above 79% of total fruits can get the disease during a moist period of minimum of 12 h (Obi, 2018).

Host range of brown rot disease

Under suitable environmental conditions, brown rot disease will infect all the peach species and many other members of the *Rosaceae* family. The extensive cultivation of fruit trees in temperate regions and their long lifespan ensures that hosts are readily available. The main commercial crops that are hosts are apples [*Malus domestica*], pears [*Pyrus communis*], quinces [*Cydonia oblonga*], plum [*Prunus domestica*], and sweet cherries [*Prunus avium*]. Sour cherry [*Prunus pseudocerasus*] is a less important host than nectarine, apricot, and peach. Many records of the brown rot fungi attacking other plants (Maresi *et al.*, 2013). If located near orchards, wild hosts may be inoculum sources (Johnson *et al.*, 2021). In recent years, new hosts, e.g., hawthorn [*Crataegus monogyna*], common flowering quince [*Chaenomeles lagenaria*], loquat [*Eriobotrya japonica*] were also reported to be infected by *Monilia* spp. in China (Luo, 2017; Zhou *et al.*, 2021).

Management of brown rot disease

Chemical control

Different fungicides are used against brown rot disease in stone fruit (Table 2). In commercial areas of stone fruit production, considerable use of synthetic fungicides like dicarboximides (DCFs), methyl benzimidazoles carbamates (MBCs), demethylation inhibitors (DMIs), quinone outside inhibitors (QoIs) and succinate dehydrogenase inhibitors (SDHIs) results in the induction of resistance in *Monilinia* spp. For example, isolates of *M. fructicola* showing resistance against MBC fungicide benomyl (Chen *et al.*, 2014) and

to DMI fungicides are reported from the USA (Chen *et al.*, 2013) and by other regions such as Brazil (May-De Mio *et al.*, 2011; Lichtemberg *et al.*, 2019), Greece (Malandrakis *et al.*, 2012), Spain (Egüen *et al.*, 2015), and Serbia (Hrustić *et al.*, 2018). Overexpression or mutations of the 14 α -demethylase gene (*MfCYP51*) is responsible for resistance against DMI fungicides. The mutation was reported from the Brazilian isolates of *M. fructicola*, producing a glycine to serine substitution at codon 461 (Lichtemberg *et al.*, 2017). The second example is the production of DMI fungicide resistance of *M. fructicola* isolates was highly linked with the Mona element in the promoter of the *MfCYP51* gene, which produces the over-expression of *MfCYP51* gene (Pan *et al.*, 2020). Resistance against DCF fungicide iprodione was reported from New Zealand (Egüen *et al.*, 2015; Tran *et al.*, 2019) and Western Australia (Tran *et al.*, 2019). In the Eastern United States, there is a report of resistance against MBC and DMI fungicides in *M. fructicola* in stone fruits (Chen *et al.*, 2013). Another report from South Carolina shows resistance in *M. fructicola* against MBC (Zhu *et al.*, 2016). The resistance mechanism against MBC fungicides was explained as a typical example (Lesniak *et al.*, 2021). Some researchers sequenced β -tubulin gene (*TUB2*) isolated from different isolates of *M. fructicola* that show low resistance and high resistance; results revealed a single mutation difference of codon 6 and 198 in different isolates. Another famous and commonly used DMI fungicide, propiconazole, from Australia is losing its efficiency against *Monilinia* spp. (Kreidl *et al.*, 2015), and results in a serious threat to its sustainability (Kreidl *et al.*, 2015). There is a proper schedule to apply fungicides. For example, weekly application during the flowering phase will protect blossom blights and ripped fruits in the maturity phase. The monthly application will protect immature fruits. But, in exceptional cases, this schedule is not always efficient, especially due to humid conditions during the stage of flowering along with the harvesting phase (Holmes *et al.*, 2011). The phenomenon of the development of resistance in fungi against fungicide due to continuous application urges more research to develop alternative techniques to manage the brown rot of stone fruits. In China, the resistance to MBC fungicides was also reported from some provinces such as Shandong, Hebei, Beijing and Yunnan based on the point mutation of *E198A* of the *TUB2* gene (Luo, 2017). Fortunately, the resistance to other classes of fungicides such as DCFs, DMIs, QoIs and SDHIs is still not detected.

Table 2. Different fungicides used against *Monilinia* spp

Species	Active ingredient (a.i)	Chemical name	Green house/Fields	References
<i>M. fructicola</i>	Tebuconazole	Alpha-[2-(4-chlorophenyl)ethyl]-alpha-(1,1-dimethylethyl)-1H-1,2,4-triazole-1-ethanol	Green house	(Martini & Mari, 2014)
<i>M. fructicola</i>	Thiophanate Methyl	(dimethyl[1,2-phenylene]-bis(iminocarbonothioyl))bis[carbamate]	Both	(Martini, 2013)
<i>M. fructicola</i>	Azoxystrobin	Methyl (2E)-2-(2-[[6-(2-cyanophenoxy)pyrimidin-4-yl]oxy]phenyl)-3-methoxyprop-2-enoate	Both, but mostly in green house	(Madeline E Dowling <i>et al.</i> , 2016)
<i>M. fructicola</i>	Propiconazole	1-[[2-(2,4-dichlorophenyl)-4-propyl-1,3-dioxolan-2-yl]methyl]-1,2,4-triazole	Both, but mostly in green house	(Madeline E Dowling <i>et al.</i> , 2016)
<i>M. fructicola</i>	Iprodione	3-(3,5-dichlorophenyl)-N-(1-methylethyl)2,4-dioxo-1-imidazoline-carboxamide	Green house, frequent use in field	(Madeline Elizabeth Dowling 2015)
<i>M. fructicola</i>	Cyprodinil	(4-cyclopropyl-6-methyl-pyrimidin-2-yl)-phenyl-amine	Green house	(Madeline Elizabeth Dowling, 2015)
<i>M. laxa</i>	Propiconazole	1-[[2-(2,4-dichlorophenyl)-4-propyl-1,3-dioxolan-2-yl]methyl]-1,2,4-triazole	Green house	(Wan, Kahramanoğlu, & Okatan, 2021).
<i>M. laxa</i>	Thiophanate Methyl	(dimethyl[1,2-phenylene]-bis(iminocarbonothioyl))bis[carbamate]	Green house	(Martini, 2013)
<i>M. laxa</i>	Benomyl	methyl-1-[(butylamino)carbonyl]-H-benzimidazol-2-ylcarbamate	Both	(Wan <i>et al.</i> , 2021)
<i>M. laxa</i>	Tebuconazole	Alpha-[2-(4-chlorophenyl)ethyl]-alpha-(1,1-dimethylethyl)-1H-1,2,4-triazole-1-ethanol	Green house	(Martini, 2013)
<i>M. fructigena</i>	Thiophanate Methyl	(dimethyl[1,2-phenylene]-bis(iminocarbonothioyl))bis[carbamate]	Both, but mostly in green house	(Martini, 2013)

<i>M. fructigena</i>	Tebuconazole	Alpha-[2-(4-chlorophenyl)ethyl]-alpha-(1,1-dimethylethyl)-1H-1,2,4-triazole-1-ethanol	Both	(Martini, 2013)
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Biological control

Phytochemicals such as lemon myrtle oil show antifungal properties to control *M. fructicola* (Lazar-Baker *et al.*, 2011). In study 22, post-harvest diseases, including brown rot caused by *Monilinia* spp. were managed using methyl jasmonate (*MeJA*) sole or combined with yeast *Cryptococcus laurentii*, combined effect of these products can control *M. fructicola* (Narayanasamy, 2013). Chitosan (CS) and oligochitosan (OCS) can also manage *M. fructicola* (Yang *et al.*, 2012). Another successful fungicide is berberine, reported in previous studies (Fu *et al.*, 2017); after experimental confirmation based on sixteen sub-cultures in vitro, they concluded that it does not induce resistance in *M. fructicola* and do not produce any harm to leaves of the plant even after two years of continuous use.

Various fungal and bacterial biocontrol agents have been used against brown rot disease as shown in Table 3. *Bacillus amyloliquefaciens* CPA-8, which has been examined in the laboratory and under field conditions, is another biological agent regarded as an important possible or supplementary way to control brown rot disease (Gotor-Vila *et al.*, 2017). This is effective against diseased fruit and its nectar produced due to *M. laxa* and *M. fructicola* under both laboratories and field conditions. Few attempts have been made in the biological control of *M. fructigena*; some of them are described by Batra in 1977 (Hrustić *et al.*, 2012), including experiments with *Trichoderma viride* has not been prepared for commercial application. Some practical applications of the bacteria *Bacillus subtilis* and *Pseudomonas cepacia* in strawberries [*Fragaria ananassa*] and sweet cherries [*P. avium*] have been made. It was also shown that isolates of *Aureobasidium pullulans*, *Epicoccum purpurascens*, *Sordaria fimicola*, and *Trichoderma polysporum*, applied individually or in mixtures to wounded apples, gave good protection from infection of *M. fructigena* (Lahlali *et al.*, 2020). Some experiments have been undertaken in commercial orchards involving control of twig blight and fruit rot of peaches and plums [*P. domestica*] due to *M. laxa* by the application of fungal antagonists such as *E. nigrum*, *Penicillium frequentans*, or *Penicillium purpurogenum* (Martini and Mari, 2014; Ortega *et al.*, 2019), or the control of fruit rot of peaches induced by *M. fructicola* using *B. subtilis* (Casals *et al.*, 2021). These antagonists may also be effective against *M. fructigena*. Formulations of *P. frequentans* were found more effective than a fungicide in reducing conidial numbers of *Monilinia* spp. (primarily *M. laxa*) on peaches in the orchard in Spain (Guijarro *et al.*, 2019). Four applications of *E. nigrum* conidia in the season significantly reduced post-harvest brown rot in most of a set of trials controlled in Italy, France and Spain (May-De Mio *et al.*, 2014), but the greatest effect for stone fruit was found at the time of pit hardening and in the month before harvest (Mustafa *et al.*, 2021).

Table 3. Target pathogens used in biological control (BA) against *Monilinia* spp.

Pathogens	Biocontrol agent	Formulations	Disease and host	References
<i>Monilinia</i> spp.	<i>Penicillium frequentans</i>	FOR1, FOR2,7,8 & 16 others	Brown rot, Stone fruits (Peach, apricot, cherry)	(Gotor-Vila <i>et al.</i> , 2017)
<i>Monilinia</i> spp.	<i>Epicoccum nigrum</i>	Fresh conidia	Brown rot, Stone fruits (Peach, apricot, cherry)	(Case, 2018)
<i>M. laxa</i>	<i>Penicillium purpurogenum</i>	Strain 828	Brown rot Pome and stone fruits	(Rungjindamai, Jeffries, & Xu, 2014)
<i>M. laxa</i>	<i>Penicillium agglomerans</i>	EPS125	Brown rot Peach, pear	(Montesinos, Francés, Badosa, & Bonaterra, 2015)

<i>M. laxa</i> , <i>M. fructicola</i>	<i>Trichoderma viridae</i>	NA	Brown rot Peach, plum	(Di Francesco, Cameldi, & Mari, 2016)
<i>M. fructicola</i> , <i>M. fructicola</i>	<i>Bacillus subtilis</i>	CPA-8	Brown rot, Stone fruits (Peach, apricot, cherry)	(Montesinos <i>et al.</i> , 2015)

Physical control

Many physical control methods are used to manage brown rot disease, as shown in Table 4). These methods involve wet heat treatment, dry heat treatment (Liu *et al.*, 2012), hot water incubation (Jemric *et al.*, 2011), control by chitosan sole or with the association of *Bacillus* CPA-8 (Casals *et al.*, 2012) with the help of radio frequencies, air exposure or water immersion (Sisquella *et al.*, 2013) and hydro cooling methods (Bernat *et al.*, 2017). Some researchers have controlled post harvested brown rot disease by dipping contaminated fruit of a plant in hot water of temperature 48 °C for 12 minutes and nectar at temperature 48 °C for 6 minutes (Jemric *et al.*, 2011; Fallik, 2019). This method is named a hot water dipping technique. This method is verified for not damaging fruit or nectar quality. The time of fruit exposure to hot water varies in different cultivars because more exposure to high temperatures will ultimately damage the plant. Other experiments to manage disease reveal that if infected part of the plant is placed in hot water of temperature 60 °C for 20 sec (Spadoni *et al.*, 2014), 40 sec (Casals *et al.*, 2010a), or 60 sec (Karabulut *et al.*, 2010), they will inhibit the development of *M. laxa*. In replacement of water, hot air can also control the disease. This management procedure was reported by (Casals *et al.*, 2010b), who exposed the contaminated fruit and nectar to the hot air of a temperature of 50 °C for 2h; as a result, both *M. fructicola* and *M. laxa* was controlled completely. Some other useful management techniques, including radiofrequency heating, were also described (Casals *et al.*, 2010a). Direct pathogen elimination, reduction and inducing host defence in peach plants led to the substantial reduction of fungi in the plant. This is done using wet or dry heat treatment (Liu *et al.*, 2012). The researchers linked the control influence for managing *M. fructicola* development, ROS accumulation in the cells, deterioration of mitochondria resulting in low levels of ATP and activating host defence by producing enzymes in the host (Casals *et al.*, 2012). Casal *et al.* (2012) used a high temperature of 50 °C for 2 h, 95-99% relative humidity (RH), chitosan for 1 minute, and 20°C or biological antagonist, *B. subtilis* strain CPA-8. This combination results in the elimination of pre-existing *Monilinia* spp. (Spadoni *et al.*, 2014) exposed a self-contaminated fruit with *M. laxa*, too hot water having 60 °C for 20 seconds (15 min/48 h post-inoculation) to study the influence of heat on disease and response of fruit for high temperature. Based on its positive result, this method was used to control disease (Sisquella *et al.*, 2013) exhibited an experiment to improve management's Radio Frequency method (RF). He immersed the fruit in water for 9 minutes and then exposed it to the air for up to 18 minutes (RF of 27.12 MHz) at 20 °C. He concluded that this immersed fruit technique could be used as a successful post-harvest alternative method to manage brown rot disease of nectar and peach. Later, researchers concluded that for controlling post-harvest disease, RF technique, especially with immersions at 40 °C for 4.5 minutes, would be more encouraging and appealing at commercial use for both fruit and nectar (Sisquella *et al.*, 2014). Besides, they recorder a substantial reduction in brown rot incidence of contaminated fruit; normal brown rot incidence is thought to be 92%, but in diseased fruit treated with this technique, it reduced up to 26%; also, they were succeeded for 100% disease control (Sisquella *et al.*, 2014). Furthermore, researchers suggested that "a particular water tool must be designed to measure the financial cost methodology" before using this method commercially. Bernat *et al.* (2017), treated contaminated fruits that were infected for like 2-24 hours ago with hydro-cooling and water dump methods. This was a successful management method compared to directly stored fruit at 0 °C without any treatment, but it failed to manage old infection (≥ 48 hours).

Table 4. Physical treatment to control brown rot in peach, conditions, periods and effects

Treatment	Temperature	Period of exposure	Effects	References
Hot water dipping (HWD)	48 °C	6/12 min	Reduced brown rot incidence (BRI) and no significant loss of fruit quality	(Jemric <i>et al.</i> , 2011)
Heat treatment (HT)	40 °C	5/10 min	Significant reduction in peach BR	(Liu <i>et al.</i> , 2012)
Heat treatment (HT) 95% RH	50 °C	2 h	Proposed as a potential strategy to control brown rot on peaches and nectarines	(Casals <i>et al.</i> , 2012)
Radio frequency (RF) of dipping in hot water (HT)	60 °C	20 s	A 100% BRI reduction at 6 to 12 h after inoculation and 85.7% BRI reduction at 0 to 48 h after inoculations compared to untreated fruit	(Spadoni <i>et al.</i> , 2014)
Radio frequency (RF) at 27.12MHz of water immersion	20 °C	9 min	Controlled brown rot without adverse external and internal damage in both peaches and nectarines	(Sisquella <i>et al.</i> , 2013)
Radio frequency (RF) at 27.12MHz of exposition in air	20 °C	18 min	Brown rot incidence significantly reduced in both peaches and nectarines of different fruit size	(Sisquella <i>et al.</i> , 2013)
Radio frequency (RF) at 27.12MHz of water immersion	40 °C	4.5 min	Reduced BRI in stone fruits inoculated (0-48 h) before treatment and at all maturity levels evaluated in both peaches and nectarines without impaired fruit quality	(Sisquella <i>et al.</i> , 2014)
Hydro cooling (HC) and water dump (WD)	4 °C	30s /10 min	Reduced BRI by 50-77% when treated at 2/24 h of fruit harvest	(Bernat <i>et al.</i> , 2017)

Cultural control

Some varieties of peaches show dominant genetic tolerance against certain diseases (Byrne *et al.*, 2012). As diseased parts of plants serve as reservoirs of infection, they should be eliminated from the field to control the spread of disease in spring and summer. This method is an important and efficient sanitary control technique (Mustafa *et al.*, 2021). The intelligent location of orchards can reduce the likelihood of severe disease outbreaks. A limited benefit may also follow from measures designed to alter the environment in established orchards in the host's favor, e.g., pruning for increased air circulation (Connor *et al.*, 2014). Cultural practices such as removing mummified fruit and pruning of infected twigs, with subsequent burning or deep-burying, and removing wild host plants near orchards reduce the inoculum level, but these procedures alone are not sufficient to control the disease (Yoder *et al.*, 2016).

Nevertheless, Holb and Schem (2007), found that fallen or thinned immature fruit infected with *M. fructigena* on the ground provided a significant source of inoculum in Hungarian apple orchards. Labour-intensive removal of such fruit could be economically feasible for organic management operations where chemicals used for disease control were less effective. In 1954 Wormald emphasized that hygiene is equally necessary during and after seasons of light infection (Kumari *et al.*, 2018). Good hygiene can also reduce the population of insects that serve as spore vectors. Manuring can influence disease incidence, and applications of potassium have brought about a reduction in disease incidence on apricots [*P. armeniaca*] (Yin *et al.*, 2017). High doses of nitrogen fertilizer are positively correlated with infection by *M. fructigena* (Obi *et al.*, 2020). Injuries to the plant may result from weather conditions. Hail can readily damage fruit, and it is useful to apply a protectant fungicide without delay when such injury occurs (Wells and McManus, 2013). Care during

picking and handling is essential, and fruit should be picked with its stalk intact (Zhu *et al.*, 2016). Particular care is needed in packing and storing fruit because the fungus can grow from one fruit to others in contact with it. Damaged fruit should not be stored (Xu *et al.*, 2021). Mechanical harvesting of peaches [*P. persica*] can also cause injuries that may lead to severe rotting.

Vectors control

Control of insects that serve as vectors and/or provide wounds for infection is essential for effective control of *M. fructigena*. Fungicides do not control infection if applied after mechanical injuries have become inoculated. Bird feeding may be reduced in orchards remote from houses using explosive scares; wasp nests can be sought out and destroyed. Direct control of other vectors often attracted to rotten and damaged fruit seems difficult to achieve (Sigei, 2018). However, Holb in 2008 attributed a lower level of brown rot in orchards under integrated management in part to control wound-creating insects through insecticides (Bellamy *et al.*, 2021). Inorganic management, forecasting for insect control, particularly of codling moth (*Cydia pomonella*), is needed to prevent injuries that are major infection courts for *M. fructigena* (Obi *et al.*, 2018).

Conclusions

Many questions relating to the taxonomy of the brown rot pathogens are still unanswered. Therefore, more detailed studies and research are required about the taxonomic relationship among *Monilinia* spp. Besides, brown rot disease is widely spreading and almost present in all peach-producing countries. Moreover, there has been little progress in developing BR-resistant varieties of peach because of a lack of cooperation between growers, breeders, and phytopathologists, despite brown rot's importance. Also, brown rot research is restricted in many countries because of the low price and limited profit for farmers and the lack of national projects for breeding and general peach management (cultivation, marketing, innovations).

Moreover, crop breeders and pathologists should focus on joint ventures regarding this diseases management, besides this, consumer demand for healthy fruit and environmental concerns about pesticide use necessitates a sustainable solution such as incorporating biological control agents to battle brown rot in peaches. New insights about this disease have shown a clear association between brown rot tolerance in current peach genotypes and fruit quality attributes. Hence, brown rot management has been described in this research as a preventative technique rather than a chemotherapeutic one. Integrated Disease Management (IDM) and biological control tactics may lead towards sustainable peach fruit cultivation in future if host resistance is used properly and successfully. New tools, such as cultivar selection that are less tolerant of *Monilinia* spp. if not resistant, or the development and validation of mathematical models that can be used to predict the incidence of visible brown rot and latent infection at harvest and the subsequent development during the postharvest phase, could be very useful in the reduction of disease. Postharvest biocontrol and biological products in general will most likely continue to grow slowly in the future, but they will complement or be paired with low-risk chemical fungicides, natural antimicrobial chemicals, and other physical measures for an integrated brown rot control strategy. It is necessary to apply a fully customised strategy for each situation (species: cherry, peach, apricot, nectarine, plum; meteorological and seasonal conditions; conventional or organic production; destination market, etc.). Because stone fruits have a short postharvest life, the destination of the fruits after harvest (period between harvest and sale, distance between the point of production and the point of sale, etc.) must drive the implementation of brown rot management programmes. Molecular studies exclusively omics techniques viz., next generation sequencing and transcriptomics may help to elucidate the mechanism governing the interactions between *Monilinia* spp. and peach plants and may facilitate the development of new methods to increase the resistance level of peach against the fungus including the over expression of defense-related genes. Besides, the hybrid and hierarchical assembly strategy, using NGS such as Illumina and PacBio

sequencing technologies, can be used to produce new genomic draft of *Monilinia* spp. that improve the understanding of the genome of the brown rot fungi.

Authors' Contributions

Conceptualization, SI and AA; methodology, SI and AA; software, SI, IM, MS, and ZR; validation, MM, MK, MH and MAAA; formal analysis, SI; investigation, SI; resources, SI, data curation and collection, SI and AA, and SI, and AA; writing-original draft preparation, SI, AA, SAS and SAHN; writing-review and editing, SI, and AA; supervision, AA; and project administration, AA.

All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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