Monilia polystroma

Scientific Name

Monilia polystroma (anamorph) G.C.M. van Leeuwen, 2002

Synonyms:

Monilinia fructigena (Japanese isolates)

Common Name(s)

Asiatic brown rot, twig blight, twig canker

Type of Pest Fungal pathogen

Taxonomic Position Class: Leotiomycetes, Order: Helotiales, Family: Sclerotiniaceae

Reason for Inclusion in Manual

CAPS Target: AHP Prioritized Pest List - 2012 through 2014

Background

The genus *Monilinia* is in the family Sclerotiniaceae and is characterized by the production of conidial and stromatal anamorphs (asexual stage), apothecial ascomata, and ascospores (Byrde and Willetts, 1977). The genus *Monilia* is the anamorph.

Monilinia spp. are well-known pathogens causing brown rot of fruit trees in many fruit production regions of the world. Three species of *Monilinia*, *M. fructicola*, *M. fructigena*, and *M. laxa*, are particularly important with regard to fruit trees and ornamentals, because they cause serious blossom and twig blight and brown rot of fruits (Petróczy et al., 2012). In 2002, a new species (described based solely on the anamorph), *Monilia polystroma*, was distinguished from *M. fructigena* based on morphological and molecular characteristics of isolates from Japan (van Leeuwen et al., 2002). This work confirmed the earlier work of Fulton et al. (1999), which showed the isolates of *M. fructigena* from Japan, on the basis of ITS sequence data, were distinct from European isolates and could possibly be regarded as a separate species.

Monilinia laxa and M. fructigena are the main agents of brown rot in Europe and are widespread. *M. fructicola* is widespread in the United States, North America, South America, South Africa, and Australia, and it's also present in at least six countries in Europe (Bosshard et al., 2006; Petróczy and Palkovics, 2006; Duchoslavova et al., 2007; Pellegrino et al., 2009; De Cal et al., 2009; Hilber-Bodmer et al., 2010; Hinrichs-Berger and Muller, 2010). *M. laxa* is also known to occur in the United States, primarily in the Pacific Northwest. *M. fructicola* is particularly problematic in the United States due to fungicide resistance and increased adaptability and variability due to the frequent occurrence of the sexual stage (Fulton and Brown, 1997). *Monilia polystroma* is not

known to occur in the United States and to date has been reported from Japan, China, Czech Republic, Hungary, Poland, Serbia, and Switzerland (van Leeuwen et al., 2002; Petróczy and Palkovics, 2009; Zhu and Guo, 2010; EPPO Reporting Service, 2011; Hilber-Bodmer et al., 2010, 2012; Poniatowska et al., 2013; Vasic et al., 2013). The color of the pustules on infected plant tissue is buff for *Monilia polystroma* and *Monilinia fructigena* and grayish-brown for *M. fructicola* and *M. laxa* (Byrde and Willetts, 1977; van Leeuwen and van Kesteren, 1998).

Hu et al. (2011) discuss the existence of two additional *Monilinia* species in China. China is also known to have the four species discussed previously. *Monilia mumecola*, previously isolated in Japan from *Prunus mume* and causing brown rot of papaya in China, was found on peaches/nectarines in China. Yin et al. (2014) reported that *Prunus armeniaca* (apricot) is also a host of *M. mumecola*. A new species, *M. yunnanensis*, was also found on peaches/nectarines in China and recently described by Hu et al. (2011).

Pest Description

Colonies on potato dextrose agar (PDA) reach 50 to 60 mm in diameter after 6 days at 22°C under a 12 hr. light/12 hr. dark cycle. Colony margin even, sporogenous tissue slightly elevated above the colony surface (1 to 2 mm), color buff/pale luteous. Stromatal initials formed 10 to 12 days after inoculation at 22°C (71.6°F) under 12 hr. light/12 hr. dark cycle; mature, black stromatal plates first discrete, later coalescing. Macroconidia globose, ovoid or limoniform, smooth measuring 12 to 21 x 8 to 12 μ m, average 16.4 x 10.1 μ m (distilled water) when grown on cherry agar (CHA) at 22°C under NUV, and 11 to 20 x 8 to 11 μ m, average 14.9 x 9.1 μ m on pear fruit at 15°C (59°F). On fruit, a thick hyphal layer of stroma appearing after the fruit is colonized; conidial tufts buff to brownish gray. The authors were unable to induce the formation of apothecia and thus only describe the anamorphic stage (van Leeuwen et al., 2002).

In the lifecycle of *Monilia polystroma*, like *M. fructigena*, the teleomorph (sexual stage) hardly plays a role. Apothecia are seldom found in the field (Willetts and Harada, 1984; Batra and Harada, 1986). Harada (1977) managed to obtain apothecia *in vitro* with *M. polystroma* isolates (referred to at that time as *Monilinia fructigena*).

Biology and Ecology

Due to the recent species description of *Monilia polystroma*, very little is known about the biology and ecology of the pathogen. It is expected, however, that the biology and ecology will be similar to other brown rot fungi, particularly *Monilinia fructigena*. Casals et al. (2010) evaluated the effect of temperature (0 to 38°C; 32 to 100.4°F) and water activity (a_w: 0.87 to 0.99) on the percentage of conidial germination over time for *Monilinia laxa*, *M. fructicola*, and *M. fructigena*. The three species of *Monilinia* studied were able to germinate over a wide temperature range (0 to 35°C; 32 to 95°F) at 0.99 a_w, but no germination occurred at 38°C (100.4°F) for any of the tested isolates. The optimum temperature for germination occurred after four hours of incubation and was in the range 15 to 30°C (59 to 86°F) for the studied species. Isolates of *M. fructicola* and

M. fructigena reached 85 to 99% germination after two hours of incubation at 25°C (77°F) at 0.99 a_w ; while *M. laxa* needed four hours.

Conidia of brown rot fungi, in general, overwinter in fruit mummies or cankerous lesions. These conidia serve as a primary inoculum source in the spring. Under unfavorable climatic conditions, infections can remain latent in immature fruit until conditions become favorable for disease development later in the season (Gell et al., 2008).



Figure 1. Apples naturally infected with *Monilinia fructigena* at; a) 5 days incubation and b) 14 days incubation. Photo courtesy of DAFF (Department of Agriculture, Fisheries, and Forestry-Australia).

Infection of *Monilinia fructigena* takes place via cracks and wounds in the fruit skin (Xu and Robinson, 2000) and also via fruit-to-fruit contact (Michailides and Morgan, 1997). Wind, water, insects, birds, and man are responsible for the dispersal of *Monilinia*

conidia in pome and stone fruit orchards (Byrde and Willetts, 1977; Bannon et al., 2009). Splash dispersal is important for short range spread within a tree (Bannon et al., 2009). Lack (1989) reported spread by insects. Kable (1965) discovered that airborne conidia ensured a wide dispersal of conidia within an orchard. Van Leeuwen et al. (2002b) observed that late infected fruits in one season can contribute to primary inoculum of M. fructigena in the next spring, and in early summer dropped fruit (such as fruit on the ground from very late thinning) can contribute to infection on the tree. Disease incidence can be controlled by avoiding fruit wounds caused by biotic



Figure 2. Apples infected with *Monilinia fructigena*. Photo courtesy Radek Sotalar – Czech. Republic.

(insects, birds, man) and abiotic (frost, hail) agents.

Monilia polystroma may colonize infected fruit of some cultivars slightly faster than *Monilinia fructigena* (van Leeuwen et al., 2002). In addition, van Leeuwen et al. (2002) speculate that the abundant stroma formed by *Monilia polystroma* may enhance the survival of the species by inhibiting decomposition of infected fruits, possibly increasing the amount of primary inoculums produced in the next season compared with *Monilinia fructigena*.

Symptoms/Signs

Damage will be similar to those caused by *Monilinia fructigena* (van Leeuwen et al., 2002). Symptoms include twig and leaf blights, stem cankers, and brown fruit rots (Fig. 1 to 3).



Figure 3. Peaches inoculated with a) *Monilinia fructigena*; b) *M. fructicola*; and c) *M. laxa*. **Note:** *Monilia polystroma* will be similar to *Monilinia fructigena* shown in panel A. Photo courtesy of DAFF (Department of Agriculture, Fisheries, and Forestry-Australia).

The primary and most frequent symptom is fruit rot (Fig. 1 to 3). Initial fruit lesions are brown, circular, and firm (Fig. 2). Eventually, the whole fruit decays and turns brown. Tufts of mycelium and conidia (cream-white to buff colored) sprout from the skin of the infected fruit (Fig. 1, 3), often arranged in concentric rings (Fig. 2) (Byrde and Willetts, 1977). When the relative humidity is low and/or when the fruits are not ripe, no mycelium and very few or no conidial tufts develop. Rotted fruits may either fall to the ground or dry out on the tree, leaving a hard, shriveled 'mummy'. Mummified fruit hang on branches of trees until spring or fall to the ground where they remain throughout the winter months, partly or completely buried beneath the soil or leaf litter (Byrde and Willetts, 1977). Infection of fruit can take place at any time during fruit development, but the disease is only severe in ripe or ripening fruit.

Specific symptoms of *Monilia polystroma* in apple from Hungary (Fig. 4) include brownish dieback on the leaf petioles and laminas and on small fruits and fruit pedicels. Infected areas are covered with yellowish exogenous stromata (a compact mass of

mycelium (with or without host tissue) that supports fruiting bodies or in which fruiting bodies are embedded) (Petróczy and Palkovics, 2009).



Figure 4. Brownish dieback symptoms and yellowish stromata on apple cv. 'Ashton Bitter' from Hungary. Photo courtesy of Tibor Szabo.

Pest Importance

Brown rot of stone fruits is an extremely destructive disease. The pathogens that cause brown rot of stone fruit also occur on apple and pear fruit trees. The disease may destroy or seriously reduce a crop by rotting mature fruit, either on the tree or after harvest.

Monilia polystroma causes severe fruit rot of fruit trees and is closely related to *Monilinia fructigena*, a regulated pest in the United States. Impacts of *Monilia polystroma* are likely to be similar to the impacts of *Monilinia fructigena*, which causes losses of apple and stone fruits, both before and after harvest. Twigs and shoots can also be infected, albeit less frequently. Crops may be severely reduced or destroyed due to the infection.

In general, *M. fructigena* is less damaging than *M. fructicola* or *M. laxa*. The severity of the disease varies from year to year depending upon environmental and storage conditions. *M. fructigena* is highly infectious and is reported to cause considerable losses in Europe during summer when warm temperatures are favorable to disease development (Scopes and Ledieu, 1983). The greatest losses are often observed in apple and plum fruits. Losses of between 7 and 36% have been reported in European apple orchards and between 0.2 and 1.5% in stored fruits (Jones and Aldwinckle, 1990; van Leeuwen et al., 2000). Latent infections can also occur, with symptoms developing after fruit ripening.

Monilinia polystroma (a synonym for *Monilia polystroma*) is listed as a harmful organism in Canada (USDA-PCIT, 2013). There would be trade implications with Canada if this pest were found in the United States.

Known Hosts

Cerasus avium (bird cherry), *C. vulgaris* (morello cherry), *Cydonia* spp. (quince), *Malus domestica* (apple), *M. pumila* (apple), *Prunus armeniaca* (apricot) *P. avium* (sweet cherry), *P. cerasus* (sour cherry), *P. domestica* (plum), *P. persica* (peach), *Prunus* spp. (stone fruit), and *Pyrus* spp. (pear).

(van Leeuwen et al., 2002; Hilber-Bodmer et al., 2012; Poniatowska et al., 2016)

Reports of damage caused by *M. polystroma* are often mixed infections with other pathogens, and specific reports of economic damage attributed to this pathogen are currently unavailable. Therefore, the extent of damage exclusively attributed to *M. polystroma* in specific hosts is unclear.

Known Vectors (or associated insects)

Monilia polystroma is not known to be a vector, is not known to be vectored by another organism, and does not have any associated organisms. Insects may play a role in the dispersal of conidia, like in *Monilinia fructigena* (Lack, 1989), but this has not been studied specifically for *Monilia polystroma*.

Known Distribution

Asia: China and Japan. **Europe:** Croatia, Czech Republic, France, Hungary, Italy, Poland, Serbia, Slovenia, and Switzerland (van Leeuwen et al., 2002; Petróczy and Palkovics, 2009; Zhu and Guo, 2010; Hilber-Bodmer et al., 2010, 2012; EPPO Reporting Service, 2011; Poniatowska et al., 2013, 2016; Vasic et al., 2013; Martini et al., 2014; Di Francesco et al., 2015; Munda, 2015).

Isolates of *Monilinia fructigena* from other areas of east Asia should be examined to determine whether some isolates actually belong to *Monilia polystroma* (van Leeuwen et al., 2002).

Pathway

There have been 69 shipments of *Pyrus* sp. propagative material from known host countries since January, 2003 (AQAS, queried July 30, 2013). During the same timeframe, there have been 51 shipments of *Malus* sp., 47 shipments of *Prunus* sp., and 1 shipment of *Cydonia* sp. (all propagative material) from known host countries. Shipment sizes ranged from 1 gram to 9110 plant units. These shipments are likely comprised of a mixture of seed, plants, and cuttings based on the units of measure used.

Recently, the import of potential host plant material (with the exception of seeds), including all known host genera of *M. polystroma*, has been more tightly controlled to prevent the spread of the Citrus Longhorned Beetle (CLB) and Asian Longhorned Beetle (ALB). Import of *Malus* sp. plants for planting is allowed from several countries in Europe (Belgium, France, Germany, Netherlands), which are geographically close to the known host countries. Import of *Prunus* sp. plants for planting material are allowed from Netherlands. Import of *Pyrus* sp. propagules is prohibited from all countries except Canada. Effective May 11, 2011, import of *Cydonia* sp. plants for planting is prohibited from shipment of host plant material is lowered (USDA, 2013).

Transport of *Monilia polystroma* host plant material from known host countries into the United States is common and creates a large potential pathway for this pest. For example, there have been 363 interceptions of *Pyrus* sp. plant material destined for propagation or consumption from known host countries since 2003. A significant portion of these interceptions was fruit intended for consumption. Interceptions were made in shipping cargo, airline baggage, and mail. There were also interceptions of *Cydonia* sp. (3), *Malus* sp. (311), and *Prunus* sp. (90) plant material since 2003. (AQAS, 2013).

Potential Distribution within the United States

Susceptible hosts are present in the United States. According to a recent host analysis developed by USDA-APHIS-PPQ-CPHST, the eastern half of the continental United States has a moderate to high level of risk of *Monilia polystroma* establishment based solely on the presence of susceptible hosts. Most areas of the western United States have a low risk; while portions of California, Washington, and Oregon have a moderate risk.

Survey

<u>CAPS-Approved Method*</u>: Visual survey is the approved survey method for *M. polystroma*. For visual survey, collect symptomatic plant material.

*For the most up-to-date methods for survey and identification, see Approved Methods on the CAPS Resource and Collaboration Site, at <u>http://caps.ceris.purdue.edu/</u>.

<u>Literature-Based Methods</u>: Survey for *Monilia polystroma* consists of visual inspection for symptoms, tissue sampling, and pathogen isolation.

Key Diagnostics/Identification

<u>CAPS-Approved Method*</u>: Morphological. Identification of brown rot fungi is commonly based on morphology and colony characteristics. This is the CAPS-Approved method until molecular methods can be validated for regulatory use.

Identification of the three main *Monilinia* species (*fructicola*, *laxa*, and *fructigena*) is commonly based on morphology and colony characteristics. Identification is possible by combining cultural characteristics, such as growth rate, growth pattern and color, with

morphological data, such as conidial dimensions and the length of the germ tube (van Leeuwen and van Kesteren, 1998; De Cal and Melgarejo, 1999). Most of these characters are quantitative and overlap, so the identification has to be conducted under standardized conditions and starting from pure cultures. Lane (2003) also provides information for distinguishing the three main *Monilinia* spp. based on cultural characteristics (*M. fructigena*, *M. fructicola*, and *M. laxa*). *Monilia polystroma* can be distinguished from *M. fructigena* based on morphological and molecular characteristics of isolates (van Leeuwen et al., 2002).

Hu et al. (2011) discuss two additional *Monilinia* spp. in China: *Monilia mumecola* and *Monilinia yunnanensis*.

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Literature-Based Methods:

<u>Culture/Isolation:</u> For isolation, the standard procedure is to place pieces of infected material (with or without surface sterilization) on slightly acidic agar medium (pH 4-4.5) (EPPO, 2009). Isolation of *Monilinia* spp. from stone fruit and pome fruit surfaces is difficult, however, due to the presence of several fast-growing fungal species such as *Rhizopus, Alternaria*, and *Penicillium* spp. It is also possible to have mixed *Monilinia* infections. Phillips and Harvey (1975) tested a medium containing pentachloronitrobenzene (PCNB), canned strained peaches, neomycin, streptomycin, agar, and distilled water and found that though it was not totally selective that it could be used to estimate spore density of *Monilinia* spp. on the surface of fruit. Amiri et al. (2009) developed a selective medium for recovery and enumeration of *Monilinia* species that may be useful for *Monilia polystroma*. This selective medium, referred to as APDA-F500, is composed of acidified potato dextrose agar (pH 3.6) amended with fosetyl aluminum (fosetyl-AL) at 500 µg/ml. Holb and Chauhan (2005) showed that the best carbohydrate sources for mycelia growth of *Monilia polystroma* were glucose, fructose, and saccharose; while the best nitrogen source was peptone.

<u>Molecular:</u> Several molecular methods have been developed to distinguish *Monilinia* species. Fulton and Brown (1997) and Snyder and Jones (1999) established a PCR-based method of targeting to distinguish *M. fructigena* from *M. fructicola* and *M. laxa* based on the group I intron in the gene for the ribosomal subunit. Subsequent studies, however, showed that these methods were not reliable because some isolates of *M. fructicola* lack a group I intron in their nuclear rDNA small subunit (Förster and Adaskaveg, 2000; Fulton et al., 1999; Hughes et al., 2000; Cote et al., 2004b). Other PCR primers and protocols for *M. fructicola* were published by Förster and Adaskaveg (2000), Boehm et al. (2001), and Ma et al. (2003). However these methods discriminate *M. fructicola* from *M. laxa* but have not been validated for distinguishing *M. fructicola* from *M. fructigena*. Fluorescent AFLP fingerprinting and inter-simple sequence repeat analysis has been used to examine the genetic diversity of *M. fructicola* (Fan et al., 2010; Gril et al., 2010).

Ma et al. (2005) developed a pair of PCR primers specific to *M. laxa* on the basis of the differences in the DNA sequence of the intron 6 of β -tubulin gene from *M. laxa*, *M. fructicola* and other fungal species.

loos and Frey (2000) designed species-specific primer pairs for Monilinia fructigena, M. fructicola, and *M. laxa* based on the ribosomal internal transcribed spacer (ITS) region. This method, while testing for all three Monilinia species, produces PCR amplicons of the same size (356 bp), so three separate PCR reactions have to be performed in order to identify the species. Hughes et al. (2000) also developed species-specific primers for Monilinia fructigena, M. fructicola, and M. laxa. An internal control based universal PCR protocol was developed for Monilinia spp., and species-specific primers were designed by using SCAR makers (Gell et al., 2007). Miessner and Stamler (2010) and Hily et al. (2010) developed a primer/primers based on difference in the intron-exon of the cytochrome b gene to distinguish Monilinia fructigena, M. fructicola, and M. laxa. Cote et al. (2004) developed a multiplex PCR that can distinguish Monilinia fructigena, M. fructicola, M. laxa, and Monilia polystroma on inoculated and naturally infected apple and stone fruit. This PCR method uses a common reverse primer (MO 368-5) and three species specific forward primers (MO 368-8R, MO 368-10R, and Laxa - R2) to differentiate the three Monilinia species. In this assay, a 402-bp PCR product for M. fructigena, a 535-bp product for M. fructicola, and a 351-bp product for M. laxa are produced. Furthermore, another specific 425-bp PCR product was amplified, enabling the identification of isolates of Monilia polystroma. Malvarez et al. (2001) were able to use the Cote et al. (2004) primers (prior to their publication) to identify species of Monilinia in Uruguay. Upon comparing the *M. fructigena* and *M. polystroma* sequences with the genomic sequence of unknown function previously described by Cote et al. (2004). Petroczy et al. (2012) revealed insertions and substitutions in the M. polystroma sequences. Repetitive sequence motifs were identified, which can be used for differentiation between *M. fructigena* and *M. polystroma*.

According to EPPO (2009), the PCR method of Hughes et al. (2000), loos and Frey (2000), and Cote et al. (2004) have been shown not to give cross-reaction with *Monilia polystroma*.

Real-time PCR methods have been developed by Luo et al. (2007) and van Brouwershaven et al. (2010). The Luo et al. (2007) method, which is based on the Ma et al. (2003) primer for *M. fructicola*, is a SYBR Green assay and has been tested only against *M. fructicola*, *M. laxa*, *Botrytis cinerea*, *Botryosphaeria dothidea*, and *Alternaria alternata*. The van Brouwershaven (2010) method is a Taq man assay and has been validated against *Monilinia fructigena*, *M. laxa*, *M. fructicola*, and *Monilia polystroma*; a FAM-labeled probe will detect *M. fructicola* while a VIC-labeled probe will detect *M. fructigena*, *M. laxa*, and *Monilia polystroma* as a group. Since the United States currently has both *M. fructicola* and *M. laxa*, at present these real-time methods may be of limited utility for the detection of exotic *Monilinia* or *Monilia* species.

Seven different PCR methods were tested by Hu et al. (2011) to differentiate *Monilinia* spp. None of the six molecular tools alone were able to distinguish all five *Monilinia*

species (*M. fructigena, M. fructicola, M. laxa, M. yunnaensis, and M. mumecola*) (loos and Frey 2000; Ma et al. 2003, 2005; Cote et al., 2004; Gell et al., 2007; Miessner and Stammler, 2010; Hily et al., 2010). Note: The authors didn't test *Monilia polystroma*.

M. fructigena, M. fructicola, and *M. laxa* were reliably differentiated by the methods of loos and Frey (2000), Miessner and Stammler (2010), and Hily et al. (2010). However, neither of these methods was able to distinguish *M. fructigena* from *M. yannanensis*. Likewise, the methods developed by loos and Frey (2010), Ma et al. (2003, 2005) did not distinguish between *M. mumecola* and *M. laxa*. The method developed by Hily et al. (2010) did not distinguish *M. mumecola* from *M. fructicola*. Additionally, the methods of Miessner and Stammler (2010) and Hily et al. (2010) did not distinguish between *M. mumecola* from *M. fructicola*. Additionally, the methods of Miessner and Stammler (2010) and Hily et al. (2010) did not distinguish between *M. yunnanensis* and *M. laxa*.

Hu et al. recently (2011) developed an additional multiplex PCR to distinguish *M. fructicola* from *M. mumecola*, *M. yunnanensis* in China. Additional work needed to see if these primers distinguish *M. fructigena, Monilinia laxa*, and *Monilia polystroma*, because the authors did not find these species in China and did not present any specific data for these species.

Easily Confused Pests

Monilia polystroma could easily be confused with other brown rot fungi, particularly *Monilinia fructicola, fructigena,* and *laxa. Monilia mumecola* is another brown rot fungi of stone fruit that could be confused with *M. polystroma. Monilia polystroma* was first classified as a *Monilinia fructigena. Monilinia laxa* is considered to be more a pathogen of blossoms and twigs than of fruit and primarily occurs on *Prunus* spp. *M. fructigena* is mainly a fruit pathogen and primarily occurs on apple, pear, and other pome fruit trees, although it is also found on *Prunus* spp. (USDA ARS, 2011). *M. fructicola* is a pathogen of blossoms, twigs, and fruits and mainly affects stone fruits but can occur on apples, pears, and other pome fruits (USDA ARS, 2011). The color of the pustules on infected plant tissue is buff for *M. fructigena* and grayish-brown for *M. fructicola* and *M. laxa* (van Leeuwen and van Kesteren, 1998).

Monilia polystroma is quite similar to *Monilinia fructigena* but differences do exist. *Monilia polystroma* forms a large number of dark/black stromata in agar culture (van Leeuwen et al., 2002). *Monilinia fructigena* has the largest macroconidia where the conidia of *Monilia polystroma* are slightly smaller. Colonies of *Monilia polystroma* are similar to those of *M. fructigena*, but black stromatal plates occur on the colonies after incubation for 10 to 13 days, and *Monilia polystroma* isolates grow faster than *M. fructigena* isolates under the same conditions (van Leeuwen et al., 2002).

Other fungi can cause rots with similar symptoms to *Monilia polystroma* (*Penicillium* spp., *Mucor* spp.). Avoid collecting fruits with blue, green, or yellow colored molds or fruit that are 'leaking' fluid.

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Reviewer(s): Dr. Laszlo Palkovics, Corvinus University of Budapest, Department of Plant Pathology, Budapest, Hungary

Draft Log

June 2014: Added information about apricot as a new host for *M. mumecola*.

August, 2014: Added Italy to distribution.

July, 2016: Updated host, distribution, and mapping information.