Review

Monosporascus root rot and vine decline disease of muskmelon (*Cucumis melo* L.): An overview

Dhuha Sulaiman Salim Al-Daghari, Abdullah Mohammed Al-Sadi and Rethinasamy Velazhahan*

Department of Plant Sciences, College of Agricultural and Marine Sciences, Sultan Qaboos University, Muscat 123, Sultanate of Oman

**Corresponding author email*: velazhahan@squ.edu.om

Muskmelon (*Cucumis melo* L.) is an important cucurbitaceous vegetable crop worldwide. This crop is affected by several fungal, bacterial and viral diseases, which have negative impacts on the production and productivity of the crop. Monosporascus root rot and vine decline (MRVD) caused by *Monosporascus cannonballus* is a destructive disease of muskmelon worldwide. It causes sudden wilt and collapse of melon plants at the fruiting stage, which results in total yield loss. The fungus also infects other cucurbits including pumpkin, cucumber, squashes and watermelon. Since the pathogen is soil-borne, control of MRVD is challenging. Management of MRVD disease through genetic resistance is not possible at present because no melon cultivars with a substantial level of resistance to *M. cannonballus* are commercially available. The disease can be controlled to some extent through grafting melon onto resistant rootstocks, pre-plant soil fumigation, soil solarization, crop rotation, application of fungicides and synthetic chemical inducers of plant resistance and biological control. In this review, we present a brief outline of the research conducted to date on MRVD of melon.

Keywords: *Cucumis melo*; cucurbits; soilborne disease; vine decline; wilt

Melons are popular and widely cultivated vegetable crops worldwide. According to FAO, the total area under cultivation of melons (including cantaloupes) in 2018 was 1.0 million ha globally with a total production of 27.3 million tonnes of fruits (FAO 2020). China ranks first in terms of production followed by Turkey, Iran and India. Melons are desired by consumers for their sweetness, flavour and texture (Lester 2008). In addition, melons are consumed as a health food as they are a rich source of carotene, folic acid, ascorbic acid, potassium and other compounds that are important human phytonutrients (Lester and Hodges 2008). Muskmelon (*Cucumis melo* L.; family: Cucurbitaceae) is affected by several diseases that limit production wherever the crop is cultivated. Monosporascus root rot and vine decline (MRVD) caused by *Monosporascus cannonballus* Pollack & Uecker (1974) (Ascomycota, Sordariomycetes, Diatrypaceae), is a serious disease of muskmelon in subtropical, hot and semi-arid to arid regions of the world (Martyn and Miller 1996; Aegerter et al. 2000; Armengol et al. 2011). The biology, pathology, epidemiology and management of MRVD of melon have been extensively reviewed (Martyn and Miller 1996; Cohen et al. 2000; Cohen et al. 2012). In this review, we present a brief overview of the current status of melon MRVD research and disease management strategies.

Disease distribution and economic importance

The occurrence of MRVD has been reported in several melon producing countries including China (Yan et al. 2016), Egypt (El-Desouky and El-Wakil 2003), Greece (Markakis et al. 2018), Guatemala (Bruton and Miller 1997b), Honduras (Bruton and Miller 1997a), India (Martyn and Miller 1996), Iran (Sarpeleh 2008), Israel (Reuveni et al. 1983), Italy (Aleandri et al. 2016), Japan (Uemastu et al.

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1985), Mexico (Chew-Madinaveitia et al. 2012), Oman (Al-Mawaali et al. 2013), Saudi Arabia (Karlatti et al. 1997), Taiwan (Tsay and Tung 1995), Tunisia (Martyn et al. 1994) and the USA (Martyn 2008). Al-Mawaali et al. (2013) conducted a survey in major muskmelon growing governorates of Oman during 2011-2012 and reported that the disease incidence ranged from 0 – 80%. Yield losses of up to 100% in muskmelon due to MRVD disease have been reported (Martyn and Miller 1996).

General symptoms

This disease has been referred to as melon collapse (Reuveni et al. 1983; Ucko et al. 1992; Garcia-Jimenez et al. 1994), sudden wilt (Cohen et al. 1996; Pivonia at al. 1997; Edelstein et al. 1999), vine decline (Bruton and Miller 1997a; Cohen et al. 1999), root rot and vine decline (Mertely et al. 1991; Martyn et al. 1994; Martyn and Miller 1996; Wolff and Miller 1998), Monosporascus wilt (Cohen et al. 2000) and sudden death and black pepper root rot (Martyn 2002). Affected plants show chlorosis and necrosis of the lower leaves and subsequent decline of the vine towards the fruiting stage (Martyn and Miller 1996; Cluck et al. 2009). Vines rapidly collapse just before harvest and the fruits are exposed to direct sunlight, which results in sunburn of fruits. Fruits obtained from the affected plants usually contain low levels of sugars and fall off from the pedicle before ripening (Martyn and Miller 1996). The above ground parts of the *M. cannonballus* infected plants show various symptoms including stunting, yellowing and death of crown leaves. The entire canopy may collapse approximately 10 – 14 days before harvest. Symptoms on the below ground parts of infected plants include lesions on the roots, absence of most of the feeder roots, root rot and death of the tap root under wet conditions. Numerous perithecia, the fruiting bodies of the fungus, appear on the infected roots towards the end of the season (Martyn and Miller 1996). The perithecia of *M. cannonballus* are embedded in the root cortex of infected plants. Under favourable conditions for disease development, more than 100 perithecia per cm length of necrotic root are produced (Martyn and Miller 1996). Development of symptoms usually begin with the commencement of fruiting, suggesting that stress during fruiting may be a factor in MRVD disease development (Al-Mawaali et al. 2013).

The pathogen

Monosporascus cannonballus is the primary pathogen of vine decline (Zitter et al. 1996; Martyn 2008) although other fungal pathogens such as *Pythium* spp., *Fusarium* spp., *Acremonium cucurbitacearum*, *Macrophomina phaseolina*, *Phytophthora drechsleri*, *Phoma* spp., *Verticillum dahliae* and *Rhizoctonia solani* have been implicated in the disease (Zitter et al. 1996; Pivonia et al. 1997; Aegerter et al. 2000; Al-Sadi et al. 2011; El-Kolaly and Abdel-Sattar 2013). In Oman, *M. cannonballus*, *P. aphanidermatum* and *R. solani* cause vine decline of muskmelon (Al-Mawaali et al. 2013). Aleandri et al. (2016) reported the involvement of *Olpidium virulentus, O. bornovanus* and *Melon necrotic spot virus* (MNSV) in addition to *M. cannonballus* in the development of root rot and vine decline of melon without any obvious synergistic effect among the pathogens. Two species of *Monosporascus* viz., *M. cannonballus* and *M. eutypoides* (Petrak) von Arx cause vine decline of melon (Pollack and Uecker 1974; Salem et al. 2013). The cultures of both species are morphologically similar. They produce perithecia containing smooth ascospores in the culture media. However, *M. cannonballus* produces one ascospore in each ascus, whereas *M. eutypoides* produces two or three ascospores in each ascus and rarely one. *M. cannonballus* produces large perithecia (289.1 – 626.5 μm diameter) that release ascospores of 32.5 – 50.0 μm in diameter (Hamza et al. 2007). The DNA sequence of the internal

transcribed spacer (ITS) regions 1 (ITS1) and 2 (ITS2) of *Monosporascus* spp. are highly conserved (Lovic et al. 1995). The PCR primers designed based on the ITS1 and ITS2 sequences specifically detect *Monosporascus* spp. isolated from infected cantaloupe, watermelon and honeydew melon plants (Lovic et al. 1995). Pico et al. (2008) standardized a real-time PCR assay based on ITS1 for specific and sensitive detection of *M. cannonballus*.

Survival of the pathogen

In the absence of suitable host plants the fungus is reported to survive in the soil for a long time in the form of ascospores (Krikun 1985; Martyn and Miller 1996; de Medeiros et al. 2008). The ascospores act as the primary inoculum of the pathogen to initiate infection on the roots (Stanghellini et al. 1996). Mertely et al. (1993b) studied the ascospore population density in commercial melon fields in Texas and reported that 3 – 15 ascospores were present per g of soil and the ascospore numbers were the highest at soil depths of 10 – 20 cm. An average density of 8.09 ascospores per g of soil cultivated with cantaloupe melons has been reported (de Medeiros et al. 2008).

Disease cycle

Infection of the roots can occur from the primary inoculum viz., ascospores that survive in the soil or plant debris (Waugh et al. 2003; Radewald et al. 2004). The fungus invades the fine feeder roots and causes mortality of the rootlets (Martyn 2002). The infection progresses to the adjacent roots through the root junction or from new infections. The lesions are formed predominantly on larger roots, whereas smaller roots die due to infection by the pathogen. The fungus colonizes the root tissues, invades the xylem and induces the plant to produce tyloses. Several perithecia are produced on the roots of infected plants. Each perithecium contains 200 or more asci, and when they rupture ascospores are released into soil. The root of a single plant can support the production of as many as 400,000 ascospores (Martyn 2002; Waugh et al. 2003).

Favourable conditions for disease development

M. cannonballus is a thermophilic fungus and is well adapted to arid and semi-arid climatic conditions. The optimum temperature range for mycelial growth under *in vitro* conditions is 25 – 35°C. The reproduction of *M. cannonballus* occurs at temperatures between 25 – 30°C with less reproduction at 35°C than at lower temperatures (Waugh et al. 2003). The optimum pH for growth ranges from 6 – 7 however; the fungus can grow at pH levels up to 9. Growth of the fungus is reduced at pH 5 and completely prevented at pH 4 (Martyn and Miller 1996). The fungus can tolerate high levels (8 – 10%) of sodium and calcium chlorides (Ferrin and Stanghellini 2006). Cohen et al. (1996) observed complete destruction of melon crop due to Monosporascus wilt in a commercial field in Israel in the autumn compared to winter, which has been attributed to the different soil temperatures between the cropping seasons (Kim et al. 1995). This conclusion was further supported by observations of enhanced MRVD disease incidence following artificial heating of the soil (Pivonia et al. 1999).

Host range

In addition to muskmelon, *M. cannonballus* can also infect watermelon, cucumber, squash and pumpkin (Mertely et al. 1993a). Stanghellini et al. (2010) found that germination of ascospores in the rhizosphere and subsequent attachment of germlings to roots of host plants occur only in cucurbitaceous crops, with the exception of *Cucurbita maxima*.

Toxin production by M. cannonballus

M. cannonballus produces various heat- and protease-labile proteins and low-molecular-weight compounds, which induce phytotoxicity in muskmelon leaves (Hosseini et al. 2018). The proteins produced by *M. cannonballus* have been identified as α-1,2-mannosidase and serine proteases and the low-molecular-weight compounds showed similarity to marasmines (Hosseini et al. 2018). Production by *M. cannonballus* of other low-molecular-weight compounds such as dehydroxyarthrinone, monosporascone, monosporascol A and demethylcerdarin has been reported (Piggott 2005). Al-Rawahi et al. (2018) reported that the culture filtrate of *M. cannonballus* induced necrotic symptoms and electrolyte leakage on cucumber leaves and reduced the vigour of cucumber seedlings. Al-Rawahi et al. (2018) further reported the production of thermostable and low-molecular-weight (< 14 kDa) toxic metabolites by *M. cannonballus*. Two metabolites viz., squalene and octocrylene have been identified in the toxin fraction.

Disease management

Several management strategies have been suggested to control MRVD such as cultivation of resistant cultivars (Crosby and Wolff 1998), soil fumigation (Stanghellini et al. 2003), fungicide application (Pivonia et al. 2010), destruction of plant residues after harvest (Radewald et al. 2004), application of plant-growth-promoting bacteria (Antonelli et al. 2013) and biocontrol agents (Zhang et al. 1999; Aleandri et al. 2015; Al-Daghari et al. 2020a) and grafting muskmelon onto resistant *Cucurbita* rootstocks (Beltran et al. 2008; Al-Mawaali et al. 2016; Edelstein et al. 2017).

Host plant resistance

Growing resistant cultivars is the best method for the management of MRVD. A few cultivars such as 'Doublon' belonging to *Cucumis melo* ssp. *melo* (cultivar group Cantalupensis), 'Deltex' belonging to *C. melo* ssp. *melo* (cultivar group Ameri) have been reported as tolerant to *M. cannonballus* (Wolff and Miller 1998; Crosby et al. 2000; Iglesias et al. 2000a). The wild accession of *Cucumis melo* ssp. *agrestis* namely 'Pat 81' was shown to be highly resistant to *M. cannonballus* (Fita et al. 2007; Castro et al. 2020). Park et al. (2013) identified 11 melon cultivars including, K133069, K134068, PI 414723 and 'Wondae' showing resistance to *M. cannonballus.* Al-Mawaali et al. (2013), while screening muskmelon cultivars for MRVD resistance under field conditions, reported that the cultivar 'Shahd F1' had resistance to vine decline. Iranian melon cultivars 'Sfidak bekhat' and 'Sfidak khatdar' were found to be moderately resistant (Salari et al. 2012). The size and structure of the root system were attributed in part to the resistance response of melon plants to MRVD (Cohen et al. 2000). The cultivars of melon that showed tolerance to MRVD exhibited localized browning and mild root rot symptoms upon infection and a well-developed root system (increased root length and more lateral roots) which penetrates deeply into the soil (Iglesias et al. 2000b; Dias et al. 2004). Crosby and Wolff (1998) reported that the melon cultivar 'Deltex' was more tolerant to MRVD than 'Caravelle' because of its vigorous root system. Fita et al. (2008) when comparing the *M. cannonballus* tolerant and susceptible melon cultivars to identify the tolerance features, observed significant reduction in the root:vine ratio in susceptible cultivars after inoculation with *M. cannonballus*. The root biomass was also reduced in susceptible cultivars compared to resistant cultivars. Fita et al. (2008) suggested that the severity of root lesions, root architecture and root:vine ratio are important indicators of MRVD resistance in breeding programmes. Roig et al. (2012) while investigating the gene expression responses of *M. cannonballus* resistant ('Pat 81') and

susceptible ('Piel de Sapo') cultivars using melon oligo-based microarray analysis suggested the association of jasmonic acid signalling in the MRVD resistance response of plants.

Grafting muskmelon onto resistant rootstocks

Grafting susceptible vegetable crops onto resistant rootstocks is one of the strategies commonly used to manage soil-borne diseases such as damping-off, Fusarium wilt, Verticillium wilt, Phomopsis root rot, bacterial wilt, MRVD and nematodes (Edelstein et al. 1999; Cohen et al. 2005; Cohen et al. 2007; Bletsos and Olympios 2008; King et al. 2008; Al-Mawaali et al. 2012). The increased resistance of the grafted plants has been attributed to vigorous growth of roots and quick replacement of infected and/or dead roots of grafted plants (Lee and Oda 2003; Martyn 2008). Grafting susceptible melons onto resistant and/or tolerant *Cucurbita* spp. rootstocks has been suggested as one of the important methods for control of MRVD of melon (Lee and Oda 2003; Cohen et al. 2005; 2007; Beltran et al. 2008; Martyn 2008). Several reports suggest the use of rootstocks such as *C. maxima*, *C. maxima* × *C. moschata* and *C. moschata* × *C. moschata* for the management of MRVD (Edelstein et al. 1999; Cohen et al. 2007). Al-Mawaali et al. (2016) when studying the effect, on vine decline disease, of grafting muskmelon cultivars 'Samit', 'Shahd', 'Caramel' and 'Tamara' onto rootstocks viz., 'Tetsukabuto' (hybrid squash), 'Mubyeongjangsoo' (hybrid squash) and 'Strong Tosa' (*C. maxima* x *C. moschata* intraspecific hybrid) reported that 'Shahd' grafted onto 'Tetsukabuto' and 'Strong Tosa' rootstocks and 'Caramel' grafted onto 'Mubyeongjangsoo' significantly reduced the disease incidence compared with non-grafted control plants.

Agronomic practices

Modification of irrigation regime

Through alterations in the irrigation regime, the size and structure of the plant root system can be modified. Reuveni et al. (1983) reported that daily irrigation at the fruiting stage of the crop reduced the MRVD incidence compared with irrigation given every 3 days. Frequent irrigation of soil brings the soil moisture level to saturation, so the diseased plants get enough water and thereby resist wilting compared to the plants grown in drier soil with less frequent irrigation. However, Pivonia et al. (2004) reported that reduced and less frequent irrigation of melon plants delayed the commencement of plant collapse and reduced the level of MRVD incidence, but the fruits obtained from such treatments were of low quality due to lack of moisture. The delay in collapse of melon plants under reduced irrigation was attributed to the development of deeper root system and reduced fruit load.

Tillage, cover cropping and crop rotation

El-Moslemany et al. (2016) assessed the potential of cover crops to control MRVD and reported that, when compared with various other cover crops, the use of fodder beet (*Beta vulgaris* var. *crassa*) resulted in the lowest disease severity index and highest level of cantaloupe plant resistance to infection by *M. cannonballus*.

Nascimento et al. (2018) reported that the occurrence of *M. cannonballus* was lower in the no-tillage treatment compared to the conventional tillage system. Junior et al. (2018), when evaluating the response of different crops to infection by *M. cannonballus*, suggested that non-host crops such as cowpea, cotton and sesame plants could be used as alternative crops for cultivation, or in rotation with cucurbits in soil infested with *M. cannonballus*.

Soil fumigation

Fumigation of soil with methyl bromide used to be a common practice for MRVD control (Cohen et al. 2000). Methyl bromide at a dose of 50 g/m^2 effectively controls *M. cannonballus* (Reuveni et al. 1983; Martyn and Miller 1996). However, the use of methyl bromide is restricted in many countries because of environmental and biosafety issues. Mixtures of 1, 3-dichloropropene with chloropicrin or methyl bromide and chloropicrin have been shown to control MRVD and increase yield of muskmelon (Martyn and Miller 1996). Stanghellini et al. (2003) showed that fumigation with methyl iodide (448.4 kg/ha) or chloropicrin (249.0 kg/ha) effectively reduced *M. cannonballus* root infections.

Soil solarization

Disinfesting the soil by solarization is a safe method that can control diseases. It has been largely used in places with high air temperatures (Stapleton 2000). Soil solarization in the U.S. and Israel has been found to be ineffective in controlling MRVD, probably because of the heat tolerance of *M. cannonballus* (Cohen et al. 2000). However, a modified method of solarization involving a combination of solarization and reduced rates of fumigation has been shown to be more effective in controlling MRVD (Cohen et al. 2000). Solarization of the top layer (< 6 cm) of growth medium was highly effective in MRVD management and yield improvement compared to solarization of containers with a 9 – 10 cm layer of medium (Pivonia et al. 2002). The addition of biocontrol agents to soil has been suggested in order to obtain persistent efficacy (Stapleton and DeVay 1995; Stapleton 2000). The combined application of low doses of methyl-isothiocyanate-based fumigants such as metham-sodium and dazomet and soil solarization proved efficacious in controlling the disease. A mixture of 1,3-dichloropropene (65%) and chloropicrin (35%) was also reported to be effective when combined with solarization (Gamliel et al. 1996).

Biological control with antagonistic bacteria

Biological control using microbial antagonists is regarded as a cost-effective, environmentally friendly and effective component of integrated management of MRVD. El-Moslemany et al. (2010) reported that *Trichoderma album* suppressed *M. cannonballus* growth *in vitro*. Antonelli et al. (2013) reported that *Bacillus subtilis*/*amyloliquefaciens* (BsCR) and *Pseudomonas putida* (PpF4) isolated from solarized soil possess plant growth promoting traits and antagonistic activity towards *M. cannonballus*. Antonelli et al. (2013) further reported that, under greenhouse conditions, application of BsCR alone and in combination with PpF4 decreased the disease symptoms and significantly increased the root biomass. Recently, Al-Daghari et al. (2020a) reported that isolates of *Bacillus amyloliquefaciens*, *B. endophyticus*, *Pseudomonas resinovorans*, *P. aeruginosa* and *P. mendocina* from the rhizosphere of cucumber/ muskmelon restricted the mycelial growth of *M. cannonballus* under *in vitro* conditions and induced morphological abnormalities such as shrinkage, pit formation and deformation. Al-Daghari et al. (2020a) further reported that application of *P. resinovorans* B11 to seed and soil reduced the MRVD incidence by 93.1% under greenhouse conditions. *P. resinovorans* strain B11 has been shown to produce antifungal compounds viz., 4-hydroxy-4-methyl-2-pentanone and 5-hydroxy-2-pentanone (Al-Daghari et al. 2020b).

Biological control with mycorrhizal fungi

Arbuscular mycorrhizal fungi (AMF) are widely used in nursery crops because of their benefits to plant growth and protection. Aleandri et al. (2015) studied the effect of inoculation of AMF viz., *Rhizophagus irregularis* in a nursery medium on the control of MRVD and reported that mycorrhization provided complete protection against *M. cannonballus* and significantly increased the plant growth; they further reported that pre-transplanting inoculation with *R.*

irregularis reduced the disease severity and increased the fruit weight of melon.

Biological control with hypovirulent isolates of M. cannonballus

The existence of double-stranded RNA (dsRNA) in several isolates of *M. cannonballus* isolated from infected muskmelon plants has been reported (Park et al. 1996; Cluck et al. 2009; Batten et al. 2000). Park et al. (1996) reported that dsRNA is responsible for cultural aberrations and reduction in virulence (hypovirulence) in *M. cannonballus*. Cluck et al. (2009) observed decreased perithecia production in a few spanish isolates of *M. cannonballus* containing 2, 3, and 3.5 kb dsRNA. It has been postulated that the dsRNA in *M. cannonballus* may be cleaved into small interfering RNAs (siRNAs) that match mRNA specific sequences, thereby interrupting pigmentation and production of perithecia (Cluck et al. 2009). The horizontal transfer of dsRNA in fungi has been well documented (Dalzoto et al. 2006; MacDonald and Fulbright 1991). For instance, horizontal transfer of dsRNA resulted in hypovirulence in *Cryphonectria parasitica*, the chestnut blight pathogen (MacDonald and Fulbright 1991). Batten et al. (2000) explored the possibility of controlling MRVD by using naturally occurring *M. cannonballus* isolates containing dsRNA; they stated that muskmelon plants co-inoculated with a hypovirulent, dsRNA+ isolate (Tx93-449^{+}) and a virulent, dsRNA− isolate (Az90-33^{-}) at an inoculum ratio of 10:1 (hypovirulent: virulent) did not show the symptoms of MRVD and were indistinguishable from the uninoculated plants. The authors concluded that hypovirulent dsRNA+ isolates of *M. cannonballus* have potential for development as biological control agents to MRVD.

Disease management with fungicides

Cohen et al. (1999) reported that fluazinam and kresoxim-methyl (10 µg a.i./ml) were the most effective in inhibiting the growth of *M. cannonballus*. However, the efficacy of fluazinam in the field was variable (Cohen et al. 1999). The differences in the level of inoculum in soil, prevailing temperatures during the cropping season, growing conditions and method of application of fungicide have been suggested as the causes for variations in control. El-Moslemany et al. (2010) reported that application of Topsin M 70 (Thiophanate-methyl) and Bio Zied (*Trichoderma album*), 2 days after the application of the chemical fungicides was highly effective in controlling MRVD.

Induction of systemic resistance

In recent years synthetic chemical inducers of plant defense mechanisms are used as an alternative to conventional chemical pesticides (Zhou and Wang 2018). These chemical inducers in general do not kill the pathogens directly. Disease resistance in plants can be induced by treatment with plant growth-promoting rhizobacteria (PGPR), plant extracts, chemical inducers, etc. (Walters et al. 2013). Aleandri et al. (2010) reported that seed treatment followed by foliar applications with methyl jasmonate (MeJA) (45.0 µM in 0.1% (v:v) ethanol/distilled water) significantly decreased the severity of the disease in soil naturally infected with *M. cannonballus*. Foliar application of acibenzolar-S-methyl (BTH) (a synthetic analogue of salicylic acid) (50 µg ml^{-1}) also significantly reduced the incidence of MRVD (Aleandri et al. 2010).

Conclusion and future perspectives

MRVD is one of the major problems in muskmelon cultivation worldwide. The soil-borne nature, broad host range and long-term persistence of ascospores of the pathogen in the soil make the control of MRVD very difficult. Though various strategies have been adopted for the management of MRVD, each method has its own shortcomings. Currently, muskmelon cultivars with resistance to MRVD

are not commercially available. There is a need for concerted efforts on identification of sources of resistance and their exploitation in breeding programmes. The factors involved in MRVD resistance need to be identified using omics approaches. Grafting muskmelon onto resistant rootstocks is an effective method of MRVD control. More MRVD resistant rootstocks have to be identified. The inheritance of dsRNA in hypovirulent isolates of *M. cannonballus* needs to be studied. Biological control using antagonistic microorganisms may be the best option for control of the disease. Habitat-specific antagonistic microorganisms have to be explored for biological control of MRVD. Mixtures of compatible biocontrol agents with varying modes of action need to be developed for the management of MRVD.

Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

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