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Management of tomato diseases caused by *Fusarium oxysporum*

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ABSTRACT

Fusarium wilt (FW) and Fusarium crown and root rot (FCRR) of tomato (*Solanum lycopersicum*) caused by *Fusarium oxysporum* f. sp. *lycopersici* and *F. oxysporum* f. sp. *radicis-lycopersici*, respectively, continue to present major challenges for production of this important crop world-wide. Intensive research has led to an increased understanding of these diseases and their management. Recent research on the management of FW and FCRR has focused on diverse individual strategies and their integration including host resistance, and chemical, biological and physical control.

1. Background

Fusarium oxysporum represents a species complex that includes many important plant and human pathogens and toxigenic microorganisms (Nelson et al., 1981; Laurence et al., 2014). Diseases caused by *Fusarium* spp., especially Fusarium wilt (FW) and Fusarium crown and root rot (FCRR) in tomato (*Solanum lycopersicum* L., formerly, *Lycopersicon esculentum* Mill.), have been, and continue to be, among the most intensively studied plant diseases. FW, caused by *F. oxysporum* f. sp. *lycopersici* Snyder and Hansen (*Fol*), was first described over 100 years ago in the UK (Massee, 1895), and FCRR, caused by *F. oxysporum* f. sp. *radicis-lycopersici* Jarvis and Shoemaker (*Forl*), was first observed in 1969 in Japan (Sato and Araki, 1974). Tomato is considered the second most important vegetable crop after potato; worldwide tomato production was estimated at about 162 million MT in 2012 (Anonymous, 2014). At present, both pathogens cause extensive losses to this important vegetable crop in the field and greenhouse, and remain major limiting factors for tomato production. Losses from FW can be very high given susceptible host-virulent pathogen combinations (Walker, 1971); yield losses of up to 45% were recently reported in India (Ramyabharathi et al., 2012). Losses from FCRR in greenhouse tomato have been estimated at up to 90% and 95% in Tunisia and Canada, respectively, and the disease has been observed at an incidence of 100% in the field in the USA (Hibar et al., 2007; Jarvis et al., 1983; McGovern et al., 1998).

2. Biology and epidemiology

2.1. Survival and dissemination

2.1.1. Conidia

Both *Fol and Forl* produce three types of asexual infectious spores: macroconidia, microconidia and chlamydospores; a sexual or anamorphic stage for *F. oxysporum* has not been described. *Fol* and *Forl* are indistinguishable morphologically but can be differentiated by host range, the symptoms that they cause in tomato, optimal disease environment, and by molecular techniques (refer to *Host range*, *Symptoms* and *Molecular techniques* below).

Macroconidia have been implicated in aerial dissemination of *Fol*, and both microconidia and macroconidia have been linked to

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the spread of *Forl* (Katan et al., 1997; Rekah et al., 2000; Rowe et al., 1977). Such aerial spread suggests the possibility of a polycylical phase for FW and FCRR, which is unusual for soilborne diseases. Mycelia of the pathogens can survive in association with plant debris as saprophytes and alternate hosts, and, most importantly, as thick-walled chlamydospores which enable long-term survival. Chlamydospores arise from modification (wall-thickening) of hyphal or conidial cells. Induction of chlamydospore formation in *F. oxysporum* is related to stress factors such as absence of the host (nutrient depletion) and unfavorable environmental conditions (Smith, 2007). As would be expected chlamydospores germinate when favorable conditions return including the presence of host root exudates (nutrient abundance) (Kommedahl, 1966). Chlamydospores of *F. oxysporum* f. sp. *niveum* were more heat-resistant and survived longer in the soil than conidia (Freeman and Katan, 1988). De Cal et al. (1997) reported that inoculation with chlamydospores of *Fol* caused more severe symptoms in tomato than with microconidia. A higher disease-producing potential of microchlamydospores compared to microconidia of *F. oxysporum* f. sp. *lini* was also observed in flax (Couteaudier and Alabouvette, 1990).

2.1.2. Host range

Fol and *Forl* can exist as necrotrophs by killing and consuming the nutrients contained in cells of their primary host, tomato, and, in some cases, as biotrophs in association with the root systems of unrelated plants. In addition to *S. lycopersicum*, Fol can infect and cause symptoms in *S. melogena*, *S. pimpinellifolium* and other *Solanum* spp. (Katan, 1971; Subramanian, 1970). *Amaranthus, Chenopodium, Digitaria, Malva* and *Oryzopsis* spp. were found to be symptomless carriers of *Fol* (Katan, 1971; Fassihiani, 2000).

The host range of *Forl* is considerably larger and includes both symptomatic and symptomless hosts in the Anacardiaceae (*Schinus terebinthifolius*); Cruciferae [*Brassica juncea* L., *B. oleracea* L. (five vars.), *Capsella bursa-pastoris* (L.) Medik.]; Cucurbitaeae [*Citrullus lanatus* var. *lanatus* (Thunb.) Matsum. & Nakai]; Leguminosae (*Arachis hypogaea* L., *Glycine max* L., *Melilotus alba* Medik., *Phaseolus vulgaris* L., *Pisum sativum* L., Trifolium *pretense* L., *Trifolium repens* L., *Vicia faba* L.); Molluginaceae (*Mullugo verticillata* L.); Plantaginaceae (*Plantago lanceolata* L., *Scoparia* sp.); Solanaceae (*Capsicum frutescens* L., *S. lycopersicum* L., *S. melongena* L.); and Umbelliferae [*Apium graveolens* L. var. *dulce* (Mill.) pers., *Daucus carota* L.,] (Jones et al., 1991; McGovern and Datnoff, 1992; Menzies et al., 1990; Rowe, 1980). According to these references certain leguminous plants are very susceptible to *Forl*, and the host range and virulence of the fungus varied by isolate.

2.1.3. Tomato seeds and transplants

Contamination/infection of tomato seeds by *Fol* has been documented (Elliott and Crawford, 1922; Elwakil et al., 1998). Contaminated seed was a suspected source of the movement of *Fol* race 3 in Brazil (Reis and Boiteux, 2007). Al-Askar et al. (2014) recovered isolates of *F. oxysporum* from tomato seeds at a high frequency that caused seed and root rot. Contamination of tomato seeds by *Forl* was detected at a low incidence (0.1–0.01 %) in fruit on stem-infected plants, and also occurred through transmission by the *Forl*-infested hands of workers (Menzies and Jarvis, 1994). Tomato transplants infected by *Forl* have been implicated in the long distance spread of the fungus (Hartman and Fletcher, 1991; McGovern and Datnoff, 1992). McGovern et al. (1993) determined that outbreaks of FCRR were linked to the infection of tomato transplants grown in reused Styrofoam and plastic transplant trays contaminated by *Forl*.

2.1.4. Soil and other media

Estimations of the survival of *Fol* in field soil range from more than 10 years (Katan, 1971) to indefinitely (Agrios, 2005). Presumably the survivability of *Forl* in the field is very similar; in addition, this fungus possesses the added ability of surviving in association with many unrelated alternate hosts. Although FCRR outbreaks have occurred in rock wool-based hydroponic systems, because extensive plant to plant spread was not observed, it was concluded that the primary factor in such outbreaks was the use of infected transplants (Mihuta-Grimm et al., 1990). Hartman and Fletcher (1991) also observed only limited spread of the pathogen in rock wool-grown tomato. Once contaminated, a growing medium can also be a source of pathogen inoculum and dissemination via wind, water, shoes, tools and equipment.

2.1.5. Irrigation water

Although there have been a number of reports of dissemination of other *formae speciales* of *F. oxysporum* in either surface water or closed hydroponic systems (Anderson and Nehl, 2006; Davis, 1980; Jenkins and Averre, 1983), there have been few reported cases of the spread of either *Fol* or *Forl* in this manner (Rattink, 1992; Xu et al., 2006). Increasing use of recycled irrigation in plant production, mandated by water conservation and reduction of environmental impacts from agriculture, would seem to make the movement of these and other plant pathogens in irrigation water more likely.

2.1.6. Structures/supports

Both *Fol* and *Forl* can infest and survive on and inside of wooden stakes used to support field-grown tomato (Jones and Woltz, 1968; McGovern and Datnoff, 1992). *Forl* could be recovered from stakes for at least 5 years (McGovern, unpublished data). In addition, *Forl* isolated from plastic stakes used to secure drip tubes in rock wool cubes was implicated in greenhouse outbreaks of FCRR (Toro et al., 2012). Shlevin et al. (2003) indicated that contaminated greenhouse structures (walls, poles) were a likely source of *Forl* inoculum.

2.1.7. Insects

Transmission of both *Fol* and *Forl* to tomato by shore flies (*Scatella stagnalis* Fall. Diptera) has been reported (Corbaz and Fischer, 1994; Matsuda et al., 2009). In addition, transmission of *Forl* by fungus gnats (*Bradysia* spp. Diptera) from diseased plants to healthy tomato transplants has been demonstrated (Gillespie and Menzies, 1993). These vectors may be controlled through cultural, chemical and biological tactics (Jandricic et al., 2006; Price et al., 1991; Van Eppenhuijsen et al., 2001).

2.1.8. Root-knot nematodes

Although plant-parasitic nematodes including *Meloidogyne* spp. have been reported to predispose plants to a number of soilborne pathogens (Powell, 1979), there have been contrasting opinions on the ability of root-knot nematodes to cause loss of resistance to *Fol*. *Meloidogyne incognita* was reported to cause loss of resistance in tomato to race 1 of *Fol* (Jenkins and Courson, 1957; Sidhu and Webster, 1977). However, other researchers found that simultaneous, or prior infection of tomato plants by *M. incognita* did not affect resistance to either race 1 or 2 of the pathogen (Jones et al., 1976). Abawi and Barker (1984) also found that resistance to *Fol* race 1 was unaffected by root-knot nematode populations, but observed additive damage by the two pathogens in non-*Fol*-resistant cvs. Prior infestation of greenhouse soil with *M. incognita* did not appear to predispose tomato plants to *Forl* infection (Jarvis et al., 1977). Despite uncertainty as to the resistance-breaking ability of root-knot nematodes, the importance of their control in their own right is certain.

2.2. Symptoms

Both *Fol* and *Forl* can cause damping off of tomato seedlings typified by yellowing, stunting and wilting and, in the case of *Forl*, premature loss of cotyledons and developing leaves, and basal stem necrosis. Wilt symptoms caused by *Fol* in mature tomato plants include yellowing and wilting of foliage which is usually most noticeable after flowering and fruit set and during the hottest time of the day. Fusarium wilt symptoms can have a one-sided appearance because of invasion and blockage of discrete sectors of vascular tissue, and vascular discoloration that can extend up the entire stem length even into the vascular tissue of petioles. Symptoms of FW are exacerbated by warm temperatures (~28 °C), low soil pH and use of ammonium-based fertilizers.

Fusarium crown and root rot symptoms also include yellowing and wilting which generally occur around the time of first harvest and especially during the hottest time of the day. However, the vascular discoloration caused by *Forl* in tomato is generally limited to 20–30 cm above the soil line. The crown rot fungus also causes substantial cortical discoloration in the lower stem in contrast to that occurring with FW which is typified by vascular tissue discoloration only. Other characteristic symptoms of FCRR include total rot of the tap or main root and brown stem lesions at the soil line; proliferation of adventitious roots above the necrotic area may also occur. Masses of white mycelium and yellow to orange conidia may appear in the necrotic stem tissue of dead and dying plants. Lateral spread of *Forl* within field rows has been observed and may occur through root contact and movement in irrigation water (McGovern and Datnoff, 1992). Symptoms of FCRR are enhanced by cool temperatures (10–20 °C), water-logged soil, irrigation with saline water (Triky-Dotan et al., 2005) and, as with FW, by low soil pH and ammoniacal nitrogen.

2.3. Genetic analysis

Currently three races of *Fol*, R 1, 2, 3 (also known as races 0, 1, 2) have been identified, and three corresponding loci, *I-1, I-2* and *I-3*, in tomato have been identified which confer resistance to the pathogen through several major dominant genes (Panthee and Chen, 2010; Scott et al., 2004). Three avirulence genes (*avr*1, *avr*2 and *avr*3) carried in various combinations in different *Fol* races, are recognized by tomato cvs. possessing the corresponding resistance genes triggering defense responses against the pathogen (Andolfo et al., 2014). Inami et al. (2012) suggested the following explanation for the appearance of new races of *Fol*: race 2 emerged from race 1 through loss of the *avr*1 gene or through loss of gene function through transposon-insertion; race 3 emerged when a point mutation occurred in the *avr*2 gene. *Fol* has been further characterized by vegetative compatibility group (VCG) analysis which determines parasexual mating compatibility in the fungus; VCGs 0030 to 0032 contain races 1 and 2, and race 3 is assigned to VCGs 0030 and 0033 (Elias and Schneider, 1991; Marlatt et al., 1996).

Thus far no races of *Forl* have been identified. However, seven VCGs (0090-0096) were identified for *Forl* isolates from Israel, Belgium, Canada, Greece, France, Italy, Japan, and the United States; two of these VCGs (0090, 0091) could be further divided into two subgroups each (Katan et al., 1991). VCG group 0097 was identified in Belgium (Katan and Katan, 1999). Two new VCGs (0098, 0099) were described from Florida, USA, and it was suggested that VCG 0094 originated in that state and was disseminated to Europe (Rosewich et al., 1999). Huang et al. (2013) determined that up to 69.8% of *Forl* isolates from Florida could be grouped into one of three VCGs: 0094, 0098 or 0099, with frequencies of 38.6, 24.4, and 6.8%, respectively. Isolates of *Forl* are not vegetatively compatible with those of *Fol* and the two special forms appear to exist as genetically isolated populations. Further genetic differentiation between *Fol* and *Forl* is possible (see *Molecular techniques* Section 2.4.3).

2.4. Pathogen detection and monitoring

An essential prelude to developing effective plant disease management strategies is accurate pathogen detection, identification and population density monitoring. In the case of *Fol*, identification to the level of race is critical for deployment of resistance.

2.4.1. Isolation

A number of techniques have been used to estimate population densities of *Fusarium* spp. in the field by plating on to selective or semi-selective media. This process generally takes a number of weeks to complete and requires microscopy to identify species of the fungus. McMullen and Stack (1983) compared soil dilution, sieved debris and root piece plating on Komada's, Martin's rose Bengal, and the Nash-Smith medium, and found that population estimates of *Fusarium* spp. was highly dependent on the isolation technique but not on the medium used. Isolation procedures for *Fusarium* were reviewed by Windels (1992). Differentiation of *Fol* and *Forl* from non-pathogenic *F. oxysporum* requires the additional use of a bioassay and/or molecular techniques as indicated below.

2.4.2. Bioassays

A tomato seedling assay to determine pathogenicity and to differentiate *Fol* and *Forl* based on symptom expression was developed by Sanchez et al. (1975), and closely mimics the symptoms observed in mature tomato plants. After 5–7 d, seedlings infected by *Fol* exhibit extensive vascular discoloration and little external discoloration, while those infected by *Forl* exhibit a distinctive hypocotyl rot and little vascular discoloration. A similar seedling assay was used by Apodaca-Sánchez et al. (2001) to study *Forl*. A tomato seedling assay using root wounding and dipping in fungal inoculum was developed by Jones et al. (1992) to identify resistance to *Forl* in tomato.

2.4.3. Molecular techniques

A number of molecular techniques show great promise in increasing the effectiveness of FW and FCRR management. Hirano and Arie (2006) developed a useful PCR assay to differentiate between *Fol* and *Forl*, and the three races of *FOL* based on sequence polymorphisms in the *endo* polygalacturonase (*pg1*) and *exo* polygalacturonase (*pgx4*) genes of the fungi. Lievens et al. (2003) developed a rapid (24 h) DNA array procedure for the simultaneous detection of *Fol* and *Verticillium dahlia* from multiple substrates including tomato tissue, a greenhouse potting mix and water. *F. oxysporum* f. sp. *lycopersici* produces a number of unique virulence-related proteins which are secreted in the xylem (SIX) of tomato (Houterman et al., 2007; Rep et al., 2005). The SIX genes can be used to differentiate between races of *Fol*, and between *Fol* and other *formae speciales* of *F. oxysporum* (Lievens et al., 2009). Such emerging technologies as next-generation sequencing and metagenomics should provide even more powerful diagnostic tools for plant pathogens. While promising, molecular techniques for plant pathogen detection and identification have limitations, as is the case with all diagnostic techniques. False positives and negatives are possible with PCR-based assays; such tests may not distinguish between DNA from live or dead cells, and substrate components may interfere with signal detection.

3. Management

To be successful a plant disease management program must examine the sum total of interactions occurring between plant and

pathogen and either eliminate those interactions or tip the balance in favor of the plant. Reduction of pathogen inoculum viability (population densities) and/or functionality (ability to successfully infect the host) are the keys.

The scope of this review does not allow a comprehensive inclusion of the very extensive number of research papers dealing with the management of FW and FCRR. Therefore, preference for inclusion was generally given to the most recent papers that deal with management of *Fol* and *Forl* under commercial conditions or approximating that environment, especially research that includes a yield/biomass component. In a few cases, where there was little or no data on a specific management practice, information was drawn from other *F. oxysporum* pathosystems.

3.1. Resistance

3.1.1. Traditional breeding

Plant resistance to pathogens is viewed as the most economically sound and ecologically benign method of disease management. However, host–pathogen interactions involving resistance are far from simple. The analogy of an arms race has been used to explain the co-evolution of plants and their pathogens; plants develop resistance mechanisms, pathogens develop strategies to overcome the plant resistance, plants, in turn, develop new defensive measures which select for further changes in the pathogen (Stahl and Bishop, 2000). Two types of plant resistance have been described. The first is termed polygenic, horizontal or minor-gene resistance, does not recognize specific races of the pathogen, and confers a low level of resistance generally based on multiple genes which act to create physical and/or chemical barriers that impair the invasion of the pathogen (Agrios, 2005). Polygenic resistance is generally thought of as being more long-lasting than resistance resulting from single genes. Although polygenic resistance to *Fol* has been recognized in a number of tomato cvs. such as Homestead and Marglobe (Crill et al., 1973; Gao et al., 1995), it does not appear to be a primary focus of commercial tomato breeding programs.

The second type of plant resistance, known as monogenic, vertical or major-gene resistance, is generally based on individual resistance (*R*) genes in the host that enable recognition of specific pathogen races, and imparts a high level of resistance (Agrios, 2005). Monogenic resistance in tomato to *Fol* is mainly expressed as callose deposition, phenolic accumulation and the formation of outgrowths (tyloses) in xylem parenchyma cells adjacent to vessel elements (Beckman, 2000; Takken and Rep, 2010). These responses, if timely, limit further infection of water-conducting tissue by *Fol*. Tomato cvs. resistant to *Fol* races 1 to 3 have been bred through introgression of genes from the wild tomato relatives *Solanum pennellii* (syn *Lycopersicon pinnellii*) and *S. pimpinellifolium* (formerly *Lycopersicon pimpinellifolium*) (Takken and Rep, 2010). Resistance to *Forl* currently used in breeding programs deploys a single dominant gene derived from *S. peruvianum* L. [formerly *Lycopersicon peruvianum* (L.) Mill] (Fazio et al., 1999). Many hundreds of conventionally-bred tomato cvs. have resistance to *Fol* races 1 and 2. Many also possess combined resistance to *Fol* races 1 and 2 and *Forl*. Fewer possess resistance to all races of *Fol*. A combination of complete resistance to *Fol* and *Forl* resistance is the rarest type. Table 1 lists tomato cvs. reported to be highly resistant to *Forl*, all races of *Fol*, and various combined resistances to both pathogens. Molecular techniques such as Quantitative Trait Locus (QTL) analysis and functional genomics may help to elucidate the complex resistance genome of tomato and lead to additional, and possibly more durable, disease management strategies.

3.1.2. Genetic modification

Genetic modification of plants using molecular techniques has resulted in a number of disease-resistant crops, but this approach remains controversial; for some individuals the advantage of a shorter developmental period for resistance through genetically modified (GM) crops vs. traditional breeding does not outweigh their presumed negative ecological effects. After the demise of the genetically engineered tomato cv. Flavr Savr (Bruening and Lyons, 2000), no new GM tomatoes have been marketed; but this trend could be changing. A research group in the UK has developed a genetically modified tomato plant which produces purple fruit containing much higher anthocyanin levels than normal, is resistant to the fruit rot pathogen *Botrytis cinerea*, and has a longer shelf life (Butelli et al., 2008; Zhang et al., 2013); regulatory approval and consumer acceptance is pending.

Be that as it may, progress has been made in engineering tomato for resistance to *Fol* especially through transformation with genes

Table 1
Tomato cvs. reported to be highly resistant to *Fusarium oxysporum* f. sp. *lycopersici* (*Fol*) and *F. oxysporum* f. sp. *radicis-lycopersici* (*Forl*).

Tomato cultivar	Fruit type	Application/ Adaptability[a]	Source[b]
Resistant to Fol races 1, 2, 3			
Tymoty	Cherry	GH	Hazera
Samurai	Plum		Harris–Moran
Katya, Sheena, Olivia	Plum	F	Hazera
Charger, Supremo	Plum	F, E. USA – Central America	Sakata
Afrodita, Meteoro, Mixteco	Plum	Mexico, USA	US Agriseeds
BHN 602, 685	Round	F, Worldwide	BHN Seed
Fiorentino	Round	Protected culture	Enza Zaden
Amelia VR, Halcon, Red Mountain, Solar Fire	Round		Harris–Moran
SunGuard	Round	USA	Seminis
Finishline, Redline, Rocky Top, Seventy III	Round	F, S.E. USA	Syngenta
Fabiola, Julieta, USATX 012, 0128, 0250	Round	Mexico, USA	US Agriseeds
Resistant to Fol races 1, 2 and Forl			
Trebus	Cherry	Protected culture	Enza Zaden
Komeett, Merlice	Cluster	GH	De Ruiter
Avalantino, Brired, Diamantino, Dirk	Cluster		Enza Zaden
Antonella, Ladylee	Cluster		Hazera
Clermon, Clinchy, Classy, Idoia, T47100, etc.	Cluster	GH	Syngenta
Prunus	Plum	GH	De Ruiter
Atavico, Savantas, Susanti	Plum	GH	Enza Zaden
Sabroso (resistant to *Fol* races 1, 3 and *Forl*)	Plum		Hazera
Hybrid 46	Plum	USA	Seminis
Celine, T35206	Plum	GH	Syngenta
Bolzano, Beorange, DRW 7749, Foronti, Torero, etc.	Round	GH	De Ruiter
Floyd, Fizuma, Kanavaro	Round	GH	Enza Zaden
Afamia, Amaneta, Elpida, Ingar. etc.	Round	Worldwide	Enza Zaden
HM 1823, HM 8829, Sophya (green fruit)	Round		Harris–Moran
Verdone (green fruit)	Round		Hazera
Raceway, Rally	Round	F, S.E. USA	Sakata
Crown Jewel	Round	USA	Seminis
Bigdena, Euforia, Evolution, Franco, Growdena, Jimbo, etc.	Round	GH	Syngenta
Tomato Tex 2721	Round	GH	Takii
Resistant to Fol races 1, 2, 3 and Forl			
Barbarian	Plum		Harris–Moran
Juan Pablo	Plum	Mexico, USA	US Agriseed
Hechihero	Round	Subtropical areas	Enza Zaden
Sebring, Soraya, Sunkeeper	Round	F, S.E. USA	Syngenta

[a] GH = greenhouse, F = field.
[b] More information on these and other tomato cvs. may be obtained from the seed sources.

derived from other plant species. Transgenic tomato plants expressing pathogenesis-related defense protein (defensin) genes from *Medicago sativa*, and *Wasabia japonica* were more resistant to *Fol* than non-transformants (Abdallah et al., 2010; Khan et al., 2011). Transgenic tomato lines expressing a high level of another pathogen related protein, chitinase, from wheat were found to be highly resistant to *Fol* and the trait was inheritable by the T_1 and T_2 generations (Girhepuje and Shinde, 2011). Transformation of tomato with a rice-derived chitinase also significantly reduced the incidence of *Fol* (Abbas et al., 2008). On the other hand, transgenic tomato plants that over-expressed a tobacco anionic peroxidase gene were as susceptible to *Forl* as the controls (Lagrimini et al., 1993). Increasing awareness of global issues such food shortages and human nutrition, and climate change may lead to greater acceptance of GM crops and expand the range of strategies rapidly available for management of disease and other plant stressors.

3.1.3. Induced resistance

Plants have latent defensive systems that can be activated upon pathogen attack. Induced resistance in plants refers to a state of heightened defensive capacity created by a prior stimulus (Kuc, 1995). Two different types of induced resistance have been extensively studied: systemic acquired resistance (SAR) and induced systemic resistance (ISR). SAR is induced by the exposure of a plant to abiotic (chemicals) or biotic (pathogenic and nonpathogenic microorganisms) elicitors, is dependent on salicylate (salicylic acid) production, and is associated with the accumulation of pathogenesis-related (PR) proteins; on the other hand, ISR is triggered by exposure of roots to specific strains of plant growth-promoting rhizobacteria (PGPR), particularly *Bacillus* and *Pseudomonas* spp., is dependent on ethylene and jasmonate (jasmonic acid), independent of salicylate, and is not associated with the accumulation of PR proteins (Vallad and Goodman, 2004). Over the last 20 years, there has been much research done to elucidate the mechanisms underlying the effects of induced resistance on a number of pathogens including *Fol* and *Forl*. However, few field trials have evaluated induced resistance for management of FW and FCRR; the majority of such research has utilized tomato seedlings and potted plants. The effectiveness of recently tested chemical inducers of resistance to *Fol* and *Forl* is shown in Table 2. The management of *Fol* and *Forl* through ISR by PGPR is discussed in Section 3.3.

3.1.4. Grafting

The use of disease-resistant vegetable rootstocks, including the deployment of grafted tomato, is a common practice in Asia and parts of Europe and its use has accelerated due to the prohibition of methyl bromide (MB); however, adoption of the practice for tomato production in the US has been slow presumably due to its perceived high cost vs. MB, and because of the critical use exemptions from the MB phase-out granted to tomato growers (King et al., 2008). Rivard and Louws (2008) indicated that the technique would be a very useful component in organic production especially with heirloom varieties which lack resistance to *Fol* and other soilborne pathogens. They conducted field studies in the USA and observed 0% and 29% FW incidences in heirloom tomato plants grafted on 'Maxifort' and 'Robusta' rootstocks, respectively, compared to 100% incidence in the self-grafted controls. However, the impact of the rootstocks on yield was not consistent. 'Maxifort' also reduced FW symptom expression to 0% in shade house experiments conducted in Mexico, and produced either significant or non-significant yield increases in four of five grafted tomato cvs. compared to the non-grafted controls. Three other rootstocks, 'Vigostar', 'Aloha' and 'RT-160961' also completely inhibited symptom expression of *Fol* until 5 months after planting, at which time FW severity reductions of 90, 92, and 94%, respectively, were observed. Grafting with 'Vigostar' and 'Aloha' resulted in non-significant yield increases in all combinations compared to non-grafted plants, while use of the rootstock 'RT-160961' caused non-significant yield decreases in all cvs. (Báez-Valdez et al., 2010). The mechanisms of resistance conferred by rootstocks against *Fol* appear to be similar to those seen in resistant cvs.: impairment of pathogen movement through vascular tissue due to accumulation of phenolic compounds, and the development of tyloses (Báez-Valdez et al., 2010). The severity of FCRR was significantly lower in tomato plants grafted on the *Forl*-tolerant rootstock 'Natalia' than in plants grafted on *Forl*-sensitive 'Cuore di Bue'; proteomics detected a difference in the representation of proteins in the tolerant rootstock that could be indicative of the defense response (Vitale et al., 2014). Kleinhenz (2013) created a list of tomato rootstocks and their resistances to soilborne pathogens including *Fol* and *Forl* which may be accessed online.

3.2. Chemical

3.2.1. Disinfestants (disinfectants)

Given their tenacious survival on and in all types of horticultural surfaces including tomato seeds, irrigation water, containers, supports, and structures, elimination of *Fol* and *Forl* propagules through disinfestation is an essential component of their management. Disinfestants (sensu Agrios, 2005) commonly used in agriculture such as sodium hypochlorite (NaOCl), hydrogen peroxide (H_2O_2), and ozone (O_3) are strong oxidizers that inactivate pathogens through protein and nucleic acid disruption and/or function impairment; other common disinfestants, alcohols (ethanol, isopropyl alcohol) and quaternary ammonium salts, cause denaturation of proteins and membrane disruption (McDonnell and Russell, 1999).

Treatment of tomato seed with NaOCl and HCl greatly reduced but did not completely eliminate *Forl* (Menzies and Jarvis, 1994). After soaking seed of China aster (*Callistephus chinesis* L. Nees) highly contaminated with *F. oxysporum* f. sp. *callistephi* (12% incidence) in NaOCl, the pathogen could not be detected (Elmer and McGovern, 2013). A phenolic compound, hydroquinone, was highly effective in disinfesting peanut seed contaminated with *F. oxysporum* (Elwakil and El-Metwally, 2000).

Spray application of NaOCl and another oxidizer, peroxyacetic acid, reduced microconidial densities of *F. oxysporum* f. sp. *callistephi* on Styrofoam to an undetectable level; hydrogen peroxide, ethanol, Lysol®, and a quaternary ammonium salt significantly reduced microconidial numbers but the pathogen could still be detected (Gilbert et al., 2007). Mixing a NaOCl (Clorox®) solution with soil contaminated with *F. oxysporum* f. sp. *vasinfectum* reduced the number of chlamydospores to an undetectable level (Bennett et al., 2011). Formaldehyde killed dry macroconidia of *Fol* deposited on glasshouse structures, but gaseous methyl bromide plus chloropicrin, and sprays of benzimidazole fungicides did not (Weststeijn, 1973). Spraying a quaternary ammonium salt solution was ineffective in sanitizing reused Styrofoam transplant trays contaminated with *Forl* (McGovern et al., 1993). Toro et al. (2012) demonstrated that soaking plastic irrigation stakes in NaOCl or a quaternary ammonium salt solution reduced *Forl* to an undetectable level. Personnel disinfestation (hands and shoes) should be routinely practiced especially in tomato transplant production; dispensers of alcohol-based antimicrobials for hand cleansing, and foot baths containing hydrogen peroxide or quaternary ammonium salts can be used (Woodske and Sabaratnam, 2012).

Feliciano Cayanan et al. (2009) found that the free chlorine threshold and critical contact time to inactivate conidia of *F. oxysporum* in water was 14 mg/L for 6 min. NaOCl (Clorox®) was superior to a number of household detergents in reducing *F. oxysporum* f. sp. *vasinfectum* conidial numbers in water;

Table 2
Effectiveness of chemically induced resistance in managing Fusarium wilt and Fusarium crown and root rot in tomato.

Elicitor	Production site and country[a]	Disease reduction (%)[b]	Yield increase (%)[c]	Induction products	Comments	References
Acibenzolar-S-methyl (Bion®)	Laboratory, Greece	FCRR 10% (S)*	N.D.	N. D.		Myresiotis et al., 2012
Acibenzolar-S-methyl (Actigard®)	F, USA	FW, N.S.	N.S.	N.D.	Foliar spray or by drip irrigation	Vallad and Huang, 2010
Benzothiadiazole	Canada, (tomato seedlings)	FCRR 70% Root lesion reduction	N.D.	Accumulation of phenolics and β-1,3-glucans in plant cells	Foliar spray	Benhamou and Belanger, 1998
Chitosan	Canada, (tomato seedlings)	FCRR Increased seedling survival, reduced number of root lesions	N.D.	Accumulation of phenolics and β-1,3-glucans in plant cells	Seed coating and soil treatment	Benhamou et al., 1994
	GH, Egypt (tomato seedlings)	FCRR 40% (I) 16% (S)	N.D.	Accumulation of phenolics, chitinases, glucanases	Applied as a root dip at the highest rate	El-Mohamedy et al., 2014
Composts (wheat, broad bean, cowpea straw)	GH, Egypt (tomato seedlings)	FW 53–73% (I)*[d] 47–78% (S)*	53–71% (Biomass)*	Alkaline phosphatase, peroxidases (POX), polyphenol oxidase (PPO). tyrosine ammonia lyase	*Compost treatments were generally more effective than the fungicide Topsin M	Abdel-Fattah and Al-Amri, 2012
Jasmonic acid	GH, Brazil (52-day-old plants)	FW 48% (AUFWIPC)[e]	N.D.	Chitinases (CHI), glucanases (GLU), lipoxygenase (LIP), phenylalanine ammonia lyase (PAL), PPO, POX	Foliar spray	Ferraz et al., 2014
Salicylic acid	GH, India (hydroponically grown plants)	~50% (S) – foliar spray ~40% (S) – root feeding	N.D.	Salicylic acid (SA), peroxidase (POD), PAL		Mandal et al., 2009
Validamycin A	GH, Japan (tomato seedlings)	FW 36–100% (S)	N.D.	SA, PR proteins	Sprayed on 56-day-old plants of six tomato cvs.	Ishikawa et al., 2005
Validoxylamine A	"	FW 61–100% (S)	N.D.	"	"	

[a] GH = greenhouse and F = field.
[b] FW = Fusarium wilt, FCRR = Fusarium crown and root rot, I = disease incidence and S = disease severity.
[c] N.D. = not done, N. S. = not significantly different than the control.
[d] Asterisks (*) refer to comments in the same row.
[e] AUFWIPC = area under the Fusarium wilt index progress curve.

chlamydopores of the fungus were found to be more resistant than conidia (Bennett et al., 2011). (Physical disinfestation techniques are presented in Section 3.4.)

3.2.2. Fungicides

Although a wide array of fungicides show activity against *Fol* and *Forl*, they are generally used less frequently than fumigants and other disease management strategies, except in a greenhouse context in certain countries. An interesting study by Amini and Sidovich (2010) determined that bromuconazole and prochloraz when applied as soil drenches at 10 μg ai/ml were more effective in reducing the severity of FW than azoxystrobin, benomyl, carbendazim, and fludioxonil at the same rate; however, all fungicides tested significantly reduced FW compared to the control. Benomyl was also effective against FCRR in greenhouse rock wool systems (Mihuta-Grimm et al., 1990). Another benzimidazole, carbendazim, generally reduced FW and increased yield/biomass in multiple experiments. The efficacy of fungicides in managing FW and FCRR is shown in Table 3.

3.2.3. Fumigants

After resistance, pre-plant fumigation has been the most common management strategy for FW and FCRR, especially in North America and Europe. Bromomethane (methyl bromide) in various combinations with trichloronitromethane (chloropicrin) has been the standard treatment for these and other soilborne diseases, nematodes and weeds; however, methyl bromide is being phased out in compliance with the Montreal Protocol because it is considered an ozone-depleting substance (Watson et al., 1992). Therefore, the primary motivation in agricultural fumigation research for the last two decades has been the identification of methyl bromide alternatives. A number of fumigants including 1,3-dichloropropene + chloropicrin, chloropicrin, methyl isothiocyanate, propylene oxide and sodium azide have been tested in multiple trials, mainly in Florida, USA, in comparison to methyl bromide + chloropicrin against *Fol* and *Forl*. All fumigants produced consistent reductions in FW or FCRR equivalent to methyl bromide + chloropicrin except propylene oxide; 1,3-dichloropropene + chloropicrin also consistently produced yields equivalent to methyl bromide + chloropicrin. Table 4 lists soil fumigants and their equivalencies to methyl bromide + chloropicrin in reducing FW and FCRR and increasing yield. Adoption of alternative fumigants will be based not only on efficacy but also on safety, environmental impact, and cost.

3.2.4. Anaerobic soil disinfestation (biological soil disinfestation)

Anaerobic soil disinfestation (ASD), also known as biological soil disinfestation, consists of application of organic matter and other labile carbon, followed by irrigation, and covering the soil surface with polyethylene mulch, to create microbial-driven anaerobic soil conditions which suppress soilborne pests including fungi, bacteria, nematodes, and weeds (Momma et al., 2013). The development of ASD was based on observations that the irrigated paddy rice-upland crop rotation system used in Japan was suppressive to soilborne plant pathogens. Reduction in the population densities of fungal pathogens by ASD has been attributed to anaerobic conditions, high temperatures, organic acid generation (acetic acid, *n*-butyric acid), volatile compound accumulation, and release of

Table 3
Effectiveness of fungicides in managing Fusarium wilt and Fusarium crown and root rot in tomato.

Fungicide and formulation	Production site and country[a]	Rate and application method	Disease reduction (%)[b]	Yield increase (%)[c]	Chemical group	References
Azoxystrobin, (Quadris 25 SC)	GH, Iran	10 μg ai/ml, soil drench	FW (S) Pr 69% Cr 52%	N.D.	Methoxy-acrylate	Amini and Sidovich, 2010
Benomyl	GH (hydroponic, plants grown in rock wool, contaminated with infested soil), USA	0.11 g ai/L, three different soil drench regimes	FCRR (S) ~50–90%	N.S.	Benzimidazole	Mihuta-Grimm et al., 1990
Benomyl (Fundazol 50 WP)	GH, Iran	10 μg ai/ml, soil drench	FW (S) Pr 94% Cr 87%	N.D.	Benzimidazole	Amini and Sidovich, 2010
Bromuconazole (Vectra SC)	GH, Iran	10 μg ai/ml, soil drench	FW (S) Pr 100% Cr 100%	N.D.	Triazole	Amini and Sidovich, 2010
Carbendazim	GH, India	2 g/kg seeds	FW (S) 19%	N.S.	Benzimidazole	Anitha and Rabeeth, 2009
	GH, India	2 g/kg seeds + 0.2% soil drench	FW (S) 58%	130% (biomass)	"	Shanmugam and Kanoujia, 2011
	F, India	0.1%, soil drench	FW (S) N.S.	24%	"	Khan and Khan, 2002
	GH, India	0.1%, seedling dip and soil drenches	FW (I) 82%	95%	"	Sundaramoorthy and Balabaskar, 2013
Carbendazim (Kolfugo Super SC)	GH, Iran	10 μg ai/ml, soil drench	FW (S) Pr 91% Cr 84%	N.D.	"	Amini and Sidovich, 2010
Fludioxonil (Maxim SC)	GH, Iran	10 μg ai/ml, soil drench	FW (S) Pr 69% Cr 67%	N.D.	Phenylpyrrole	Amini and Sidovich, 2010
Hymexazol (Tachigaren 36 SL)	Laboratory, Greece	0.8 μg/ml, soil drench	FCRR (S) 45%	N.D.	Isoxazole	Myresiotis et al., 2012
Prochloraz (Sportak EC)	GH, Iran	10 μg ai/ml, soil drench	FW (S) Pr 100% Cr 100%	N.D.	Imidazole	Amini and Sidovich, 2010
Prochloraz 50% WP	GH, Thailand	1 mg/ml, soil spray	FW (S) 22%	42%	Imidazole	Charoenporn et al., 2010

[a] GH = greenhouse, F = field.
[b] FW = Fusarium wilt, FCRR = Fusarium crown and root rot; I = disease incidence, S = disease severity, Pr = preventative, Cr = curative.
[c] N.D. = not done, N. S. = not significantly different than the control.

metal ions (Fe^{2+}) (Momma, 2008; Momma and Kobara, 2012; Momma et al., 2013). In field trials in Japan, *Fol* was strongly suppressed by ASD when 1% ethanol was used as the carbon source (Momma et al., 2010). Population densities of *Fol* were reduced by ASD using a variety of cover crops as the carbon source in one of two greenhouse experiments in the USA (Butler et al., 2012).

3.2.5. Plant nutrition and soil chemistry

The nutrition of plants can influence their susceptibility to disease (Datnoff et al., 2007; Engelhard, 1989). In addition, soil pH and form of nitrogen in fertilizers have long been thought to affect a plant's susceptibility to diseases including wilts caused by *F. oxysporum* (Engelhard and Woltz, 1973; Huber and Watson, 1974). In the USA, Jones and Woltz (1968) found that application of calcium hydroxide reduced the incidence and rate of development of FW in tomato, and attributed this reduction to an increase in the soil pH (7.5 or 8.0), and not to increased calcium accumulation. (Calcium content in tomato tissue was not significantly affected by soil amendment type.) They further theorized that increasing soil pH decreases the availability of micronutrients (iron, manganese, zinc) essential to *Fol* (Jones and Woltz, 1970). They were, thus, able to create conditions favorable and unfavorable to wilt by manipulating soil pH and nutrients; wilt was increased by low pH, high NH_4–N, high P, high Mg and all supplied micronutrients, and decreased by high pH, high NO_3–N, low P, low Mg and omission of iron, manganese and zinc (Woltz and Jones, 1973). Not surprisingly, FCRR is also reduced by a soil pH above 6.0 and by NO_3–N (Jones et al., 1991). It has been suggested that *F. oxysporum* is more sensitive to lower nutrient availability than plants, and that this is the basis of its management through nutrition (Woltz and Jones, 1981). Based primarily on this body of research, standard recommendations for management of FW and FCRR and similar Fusarial diseases in other crops include maintaining the soil pH between 6.5 and 7.0 and avoidance of NH_4–N.

Other researchers found that FCRR severity was significantly increased by ammonium–nitrogen [NH_4Cl, $(NH_4)_6Mo_7O_{24}$, and $(NH_4)_2SO_4$], $NaH_2PO_4 \cdot H_2O$, Fe-EDDHA, $MnSO_4$, and MoO_3, and $ZnSO_4 \cdot 7H_2O$, and decreased by low rates of nitrate–nitrogen (NH_4N0_3) in a non-circulating hydroponic system (Duffy and Défago, 1999). Soil application of fly ash, a residue of coal combustion that contains significant amounts of silicon dioxide and calcium dioxide, decreased FW and *Fol* population densities and increased yield in tomato grown in microplots in India (Khan and Singh, 2001). Soil application of silicon as sodium metasilicate nonahydrate ($Na_2SiO_3 \cdot 9H_2O$) significantly reduced symptoms of FCRR in tomato plants maintained in growth chambers, and the increased Si content of roots was significantly correlated with symptom reduction (Huang et al., 2011).

3.3. Biological

During the past three decades, there has been much research conducted on management of *Fol* and *Forl* through biological control, and a large number of commercial biocontrol products have been developed (McSpadden Gardener and Fravel, 2002). The beneficial microorganisms identified include both bacteria and fungi; various combinations of each have also been examined. The interactions occurring between biocontrol agents and plant pathogens including *Fol* and *Forl* are complex, as are the interactions between soil microflora in general, and may involve individual or combined mechanisms including: antibiosis, competition for nutrients (especially Fe through bacterial siderophore production)

Table 4
Effectiveness of fumigants in managing Fusarium wilt and Fusarium crown and root rot in tomato relative to methyl bromide + chloropicrin (MeBr + Cp).

Fumigant	Production site and country[a]	Rate, and application method	MeBr:Cp ratio, rate (soil injection)	Disease reduction relative to MeBr (+, =, -)[b]	Yield/biomass increase relative to MeBr (+, =, -)	References
1,3-dichloropropene + trichloronitromethane (chloropicrin) (81:17)	F, USA F, USA	200 and 327 L/ha, soil injection 392 kg/ha, soil injection	67:33, 336 kg/ha 98:2, 400 kg/ha	[c]FCRR (I, S) (=) FW (I) (=)	(=) (=)	McGovern and Vavrina, 2004 Gilreath and Santos, 2004
1,3-dichloropropene + chloropicrin (63:34)	GH, Italy	900–1200 mg/L drip irrigation	98:2, 40 g/m^2 (hot gas application)	FW, FCRR (I) (=)	(=)	Minuto et al., 2006b
	F, USA	330 L/ha	67:33, 400 kg/ha	FW (I) (=)	(=)	Santos et al., 2006
Chloropicrin (Cp)	F, USA	350 kg/ha, soil injection	98:2, 400 kg/ha	FW (I) (=)	(–)	Gilreath and Santos, 2004
Chloropicrin followed by methyl isothiocyanate (MITC)	F, USA	Cp, 170 kg/ha, soil injection, MS, 710 L/ha, drip irrigation	67:33, 400 kg/ha	FW (I) (=)	(=)	Santos et al., 2006
MITC	F, USA	935 L/ha, soil spray and incorporation	67:33, 392 kg/ha and 403 kg/ha	FCRR (I, S) (=)	(=)	McGovern et al., 1998
	F, USA	320 kg/ha, soil spray and incorporation	98:2, 400 kg/ha	FW (I) (=)	(–)	Gilreath and Santos, 2004
	F, USA	400 kg/ha, granular dispersal and soil incorporation	98:2, 400 kg/ha	FW (I) (=)	(–)	Gilreath and Santos, 2004
Propylene oxide	F, USA	425 L/ha, soil injection	67:33, 400 kg/ha	FW (I) (=/–)	(=/–)	Santos et al., 2006
Sodium azide	F, USA	112 kg ai/ha, drip irrigation	336 kg/ha	FCRR (I) (+)	(=)	Rodriguez-Kabana et al., 2003
Sodium azide	F, USA	85 kg/ha	67:33, 400 kg/ha	FW (I) (=)	(=/–)	Santos et al., 2006

[a] GH = greenhouse, F = field.
[b] +, =, – indicate that the fumigant surpassed, equaled or underperformed, respectively, methyl bromide + chloropicrin in disease management and yield.
[c] FW = Fusarium wilt, FCRR = Fusarium crown and root rot; I = disease incidence, S = disease severity.

and colonization sites, induced resistance and hyperparasitism/predation (Pal and McSpadden Gardener, 2006).

The management of FW and FCRR using biological control has encompassed a wide range of microorganisms alone and in combination. Combinations of biocontrols evaluated against *Fol* and *Forl* include different isolates of the same bacterial species, different bacterial genera, different fungal genera, and mixtures of bacteria and fungi. A number of biocontrols directly reduced spore production, germination and/or survival through antibiosis; competition and induced resistance were other modes of action documented in recent studies. In general, biocontrols significantly reduced FW and FCRR symptoms and increased yields, and in some cases were superior to conventional fungicides. In the majority of cases, combinations of biocontrol agents were more effective than their individual components. This result suggests that increasing microbial diversity is beneficial in plant disease management. Szczech (2008) has made a similar observation. The effectiveness of biocontrol agents against *Fol* and *Forl*, and their modes action, if determined in the research cited, are summarized in Table 5.

The suppression of plant disease through the use of mature composts has mainly been attributed to biological factors – the increase of microorganisms that suppress plant pathogens, including actinomycetes and *Bacillus* spp. (Hoitink and Fahy, 1986). Borrero et al. (2004) in Spain found that grape marc (solid remains of grape pressing) and cork composts were highly and moderately suppressive, respectively, to FW, and indicated that elevation of soil pH and microbial β-glucosidase production were major factors in reduction of the disease. Composts utilizing banana leaves, mushroom or sugarcane waste (2%, w/w) were the most effective against FW among those tested in pot studies in India; they reduced *Fol* population densities by 78–80%, disease index by 67–74%, and disease incidence by 44–96%, and increased total fungal and bacterial population in the soil by 62% and 49%, respectively (Raj and Kapoor, 1997). Vermicompost (earthworm waste compost) added to a number of different container media significantly reduced FW, and increased plant biomass and populations of antagonistic bacteria, actinomycetes and fungi (Szczech, 1999).

A number of studies have also examined the ability of composts to suppress FCRR. Composts utilizing orange peels, wheat straw or grape marc reduced FCRR incidence and *Forl* population densities in greenhouse trials in Israel (Raviv et al., 2005). Significant FCRR suppression and increased yield resulted from the use of a yellow cedar sawdust-plant waste compost mixture (2:1, v/v) in greenhouse research conducted in Canada (Cheuk et al., 2005). A compost of vegetable waste and *Posidonia oceanica* (a common Mediterranean seaweed) (70:30%, v/v) decreased the incidence of FCRR in greenhouse research in Tunisia (Kouki et al., 2012). These researchers showed that species of *Bacillus*, *Burkholderia*, and *Pseudomonas* isolated from the compost exhibited strong antimicrobial activity against *Forl*. Suppression of FCRR by coffee compost combined with a chemical fertilizer was attributed to the fungistatic activity of non-pathogenic *F. oxysporum* isolates (Ikeda et al., 2006).

3.4. Physical

3.4.1. Heat

Techniques that use heat to inactivate or weaken pathogens include steam, solarization and composting (McGovern and McSorley, 1997). The latter two techniques also manage pathogens through the buildup of beneficial and antagonistic microorganisms and increase of nutrients available for plant growth (Katan, 1981; McGovern and McSorley, 1997). Lethal temperatures for *Forl* in roots in soil have been reported to be 57.5–60 °C for 30 min (Baker and Roistacher, 1957; Bollen, 1985).

Table 5
Effectiveness of biological control agents in managing Fusarium wilt and Fusarium crown and root rot in tomato.

Biological control agent	Production site and country[a]	Disease reduction (%)[b]	Fruit weight increase (%)[c]	Mode of action vs. *Fol*/*Forl*	Comments	References
Individual biocontrols						
Achromobacter xylosoxidans	GH, Italy	FW[b] 50% (I)	122% (biomass)	Nutrient competition (siderophores)		Moretti et al., 2008
Aspergillis awamori	F, India	FW 37% (S)	36%	Not determined (reduced rhizosphere population density of *Fol*)	*More effective than the fungicide carbendazim	Khan and Khan, 2002
Bacillus amyloliquefaciens	F, India	FW 44–46% (I)	32–40%*,[d]	Induced systemic resistance	*More effective than the fungicide carbendazim	Loganathan et al., 2014
B. subtilis	F, India	FW 53–64% (I)*	53–78%*	Induced systemic resistance		
Chaetomium globsum	GH, Thailand	FW 44% (S)*	88%*	Antibiosis (reduced growth and conidial production)	*More effective than the fungicide prochloraz	Charoenporn et al., 2010
C. lucknowense	GH, Thailand	FW 36% (S)*	84%*	Antibiosis (reduced growth and conidial production)		
Emericella nidulans	GH, Lao PDR	FW 63% (S)	160%	Antibiosis (reduced growth and conidial production)	Palm oil-based formulation	Sibounnavong, 2012
Fusarium oxysporum (non-pathogenic)	F, USA	FW 57–78% (I)	38%	Induced resistance	Isolate CS-20 Biodac formulation	Larkin and Fravel, 1998
	GH, Brazil	FW 38–58% (S)	8–72% (height)	Not determined		Silva and Bettiol, 2005
Fusarium oxysporum (non-pathogenic)	GH, Greece	FCRR 78% (I)	N.D.	Induced resistance	Biocontrol at highest concentration applied prior to *Forl*	Kavroulakis et al., 2007
Penicillium digitatum	F, India	FW 21% (S)	33%	Not determined (reduced rhizosphere population density of *Fol*)		Khan and Khan, 2002
Pseudomonas chlororaphis	GH, The Netherlands	FCRR ~44–60% (I)	N.D.	Antibiosis (phenazine-1-carboximide)		Chin-A-Woeng et al., 1998
P. fluorescens	GH, F, India	FW GH: 53% (I) F: 65–85% (I)	GH: 33–140% F: 28–55%	Antibiosis and nutrient competition (siderophores)	Liquid and talc seed formulations	Manikandan et al., 2010
	GH, F, India	FW GH: 72% (I) F: 6.9–74% (I)	GH: 100% (vigor increase)	Induced systemic resistance		Ramamoorthy et al., 2002
P. putida (FC-8B)	GH, Italy	FW 41–94% (I)	18–129% (biomass)	Nutrient competition and/or antibiosis (reduced chlamydospore germination)		Srinivasan et al., 2009
Rhizophagus intraradices (formerly *Glomus intraradices*)	F, India	FW 30% (I)	10%	Not determined		Srivastava et al., 2010
	GH, Mexico	FW 72% (S)	N.S.	Not determined		Fierro-Coronado et al., 2013
	F, USA	FCRR 18–71% (I)* 16–53% (S)*	N.S.	Not determined	*Disease decrease not consistently significant	Datnoff et al., 1995
Streptomyces griseus	GH, India	FW 57% (S)	N.S.	Antibiosis (chitinase)	Seed treatment. More effective than the fungicide carbendazim.	Anitha and Rabeeth, 2009
Trichoderma harzianum	GH, Thailand	FW 41% (S)	87%	Antibiosis (reduced growth and conidial production)		Charoenporn et al., 2010
	F, Israel	FCRR 30–80% (I)	6–18%*	Not determined	*Yield increase not consistently significant	Sivan et al., 1987
	GH, Egypt	FCRR 40% (I) 24% (S)	N.D.	Accumulation of phenolics, chitinases, glucanases	Applied as a root dip at the highest rate	El-Mohamedy et al., 2014
	F, USA	FCRR 33–55% (I)* 25–44% (S)*	N.S.	Not determined	*Disease decrease not consistently significant	Datnoff et al., 1995
Biocontrol combinations						
Bacillus amyloliquefaciens, B. subtilis (Companion®)	Laboratory, Greece	FCRR 60% (S)*	N.D.	Induced systemic resistance	*More effective than individual biocontrols	Myresiotis et al., 2012
B. subtilis (two isolates)	GH, India	FW 55% (S)	183% (Biomass)	Antibiosis, induced systemic resistance		Shanmugam and Kanoujia, 2011
B. subtilis, P. fluorescens (two strains)	GH, India	FW (I) 78%*	139%*	Not determined	*More effective than individual biocontrols. Disease reduction	Sundaramoorthy and Balabaskar, 2013

Table 5 (*continued*)

Biological control agent	Production site and country[a]	Disease reduction (%)[b]	Fruit weight increase (%)[c]	Mode of action vs. *Fol*/*Forl*	Comments	References
					lower and yield higher than carbendazim.	
B. subtilis, Beauveria bassiana	GH. F, India	FW GH: 81% (I)* F: 82–84% (I)*	GH: 11%* F: 41–56%*	Induced systemic resistance	*More effective than individual biocontrols	Prabhukarthikeyan et al., 2013
Acaulospora spp., *Glomus* spp., *Gigaspora* spp., *T. harzianum*	GH, Kenya	FW – N.S.	56%*	Not determined	*More effective than individual biocontrols	Mwangi et al., 2011
Pseudomonas sp., *R. intraradices*, *T. harzianum*	F, India	FW 74% (I)*	33%	Not determined	*More effective than individual biocontrols	Srivastava et al., 2010
R. intraradices, *T. harzianum*	F, USA	FCRR 68–74% (I)* 38–56% (S)	N.S.	Not determined	*More consistent than individual biocontrols	Datnoff et al., 1995
T. harzianum, *Aspergillus ochraceus*, *Penicillium funiculosum*	F, USA	FCRR 68% (I)*	N.S.	Not determined	*Individual biocontrols not tested	Marois and Mitchell, 1981

[a] GH = greenhouse and F = field.
[b] FW = Fusarium wilt and FCRR = Fusarium crown and root rot, I = disease incidence, S = disease severity.
[c] N.D. = not done, N.S. = not significantly different from the control.
[d] Asterisks (*) refer to comments in the same row.

3.4.2. Steam

In the past, steam was a commonly used soil disinfestant for high value horticultural crops grown in greenhouses, such as ornamentals and vegetables. However, high fuel costs led growers to switch to the less expensive soil fumigation. Concern over the ecological impacts of fumigants, especially methyl bromide, has led to a reevaluation of soil disinfestation alternatives including steam. Disinfestation of soil using aerated steam is preferable because it reduces pathogen densities at lower temperatures (60–70 °C/30 min) than non-aerated steam (at or near 100 °C), and avoids total elimination of beneficial microorganisms that may help to prevent a resurgence of soilborne pathogens (Bollen, 1974). The soil should be of good tilth, and free of clods, plant debris, and excessive moisture for the technique to be effective. Steaming (80 °C/12 h) under tarps in a greenhouse in the Netherlands was as effective as chloropicrin and methyl bromide in reducing FW (Weststeijn, 1973). On the other hand, Rowe et al. (1977) reported that Ohio greenhouse growers failed to manage FCRR with steam (80–85 °C/4-6 h) and theorized that the failure was due to recontamination of soil by airborne microconidia. It is probable that the growers' steaming practice made the soil more conducive to reinfestation by eliminating beneficial microorganisms. Treating wooden tomato stakes under a tarp with steam (93.3 °C/30 min) reduced *Fol* to an undetectable level (Jones and Woltz, 1968). Steam disinfestation of Styrofoam transplant trays at 71 °C for 45 min reduced *Forl* population densities to an undetectable level (McGovern et al., 1993).

3.4.3. Solarization

Soil solarization uses clear mulch of various compositions to trap solar energy and heat the soil. Solarization of the interior surfaces of closed greenhouses is also possible through this same phenomenon. Solarization can reduce pathogen densities through thermal inactivation, the increase in thermophilic/thermotolerant antagonistic microorganisms, accumulation of volatiles, and changes in the soil gas composition, and by weakening pathogens through sublethal heating (Katan and DeVay, 1991; Freeman and Katan, 1988). Challenges to solarization include the limitation of its greatest effect to the upper 10–30 cm of soil, and the hindrance posed by cloud cover in warm humid climates (McGovern and McSorley, 2012).

Soil solarization conducted for 40 d reduced densities of *Fol* at soil depths of 10, 20, and 30 cm in greenhouse research in Chile, and equaled the effectiveness of methyl bromide (Montealegre et al., 1997). Soil solarization conducted for 8 wk in a greenhouse in Cyprus reduced the population density of *Fusarium* spp., by 91–98% and also equaled methyl bromide in FW reduction and yield increase (Ioannou, 2000). Double-layered polyethylene (PE) mulch, single PE and virtually impermeable film (VIF) raised the soil temperature at 15 cm to 45–50 °C for 220, 17, and 5 h, respectively, during 6 wk field experiments in Palestine (Barakat and Al-Masri, 2012). Double PE also reduced *Fol* population densities by 83% and FW by 43%, and increased fresh weight by 94%. Multiple field experiments conducted in the USA evaluating solarization of raised beds for 40–55 d found no differences in the incidence of Fusarium wilt and yield compared with methyl bromide plus chloropicrin (Chellemi et al., 1997).

A field experiment conducted in the USA using raised beds indicated that solarization for 7 d with clear VIF was superior to clear low density (PE) mulch in reducing soil population densities of *Forl* (Chellemi and Mirusso, 2006). Solarization for 26 d using 40-μm-thick, low density PE managed FCRR and FW in a series of experiments conducted in greenhouses in Italy (Minuto et al., 2006a). Solarization conducted in greenhouses in southern Italy provided a better level of control over *Fol* and *Forl* and had higher yields than chloropicrin + 1,3-dichloropropene fumigation (Lombardo et al., 2012.). However, solarization in the field and greenhouse trials in Israel was generally found to be ineffective against *Forl*, but did provide an acceptable reduction of FCRR when combined with biological control agents or reduced rates of fumigants (Gamliel et al., 2009; Sivan and Chet, 1993) (Refer to Integrative strategies section 3.6).

Structural solarization of enclosed greenhouses in Israel conducted for 20 d produced temperatures exceeding 60 °C and inactivated 69–95% of *Forl* chlamydospores; however, the technique was not completely effective because the low relative humidity encountered made the pathogen less active and more resistant to heat (Shlevin et al., 2003).

3.4.4. Composting

Composting involves the controlled microbial degradation of organic material, and is most commonly conducted aerobically. Besides heat, aerobic composting produces ammonia, carbon dioxide, and water, while anaerobic decomposition produces CH_4, CO_2 and many intermediate organic compounds (Golueke, 1972). Unless controlled through deliberate heat release through ventilation, the temperature of composting masses typically peaks at 80 °C. However, optimal microbial activity for substrate decomposition requires that the temperatures of compost piles be maintained below 60 °C (Finstein and Miller, 1985). Careful temperature control also allows for the survival and increase of pathogen antagonists in compost such as actinomycetes and *Bacillus* spp. (Hoitink and Fahy, 1986). Therefore, while not inherently a soil disinfestation procedure, composting may lead to pathogen reduction through physical (heat buildup), chemical (generation of toxicants) and biological (increase of pathogen antagonists) processes. However, pathogens may survive in the cooler edges of non-rotated compost piles, and if sufficiently high temperatures are not consistently maintained.

Composting for 14 d at 40 °C, 7 d at 45 °C, 3 d at 50 °C, and 1 d at 55 °C, or longer at each of these temperatures reduced chlamydospore densities of *Forl* in talc to undetectable levels (Noble et al., 2011). On the other hand, *Fol* in wheat kernels survived a compost temperature of at least 65 °C (possibly as high as 74 °C) and a composting duration of up to 21 d (Christensen et al., 2001).

3.4.5. Water treatment

Physical techniques for disinfestation of recirculated irrigation water/nutrient solutions include filtration, heat, and UV radiation. Filtration for pathogen removal may involve slow percolation through course material such as fine sand, rock wool, etc. or more rapid movement through membranes (ultrafiltration). Slow filtration also has a biological component – a microbial biofilm which forms on the surface of the filtration material; therefore, it is not compatible with chemical water disinfestation. If the water contains large amounts of clay and solids both systems will require a pre-filtration step. Slow filtration is less costly to install and maintain but is less effective in managing *Fusarium* than membrane filtration which can completely eliminate the pathogen if a pore size of 0.05 μm is used (Incrocci and Leonardi, 2004). Slow filters consisting of carbon nanoparticles or pozzolanic particles greatly reduced (93–99%) but did not completely eliminate *F. oxysporum* propagules in soilless culture of tomato (Amooaghaie, 2011; Déniel et al., 2006).

Disinfestation of recycled irrigation water by pasteurization has been practiced for some time in Europe, especially in the Netherlands, and generally requires that the water or nutrient solution be heated to 95 °C/30 min to eliminate bacterial, fungal and viral pathogens (Newman, 2004). Runia and Amsing (2001) determined that most plant pathogens in water, including conidia of *F. oxysporum*, could be killed at 54 °C/15 s. Therefore, in an effort to reduce energy costs, they recommended heating irrigation water to 60 °C for 2 min to eliminate bacteria and fungi and 85 °C/3 min if viruses were an issue.

Ultraviolet radiation in the UV-C spectrum (240–280 nm) is used for inactivation of fungi, bacteria and viruses through nucleic acid disruption; a wavelength of 254 nm is most commonly used to disinfest irrigation water (Zheng et al., 2012). High clarity water is critical for UV disinfestation; prefiltration may be a necessary to reduce water opacity to an acceptable level. UV-doses from a high-pressure lamp of 28 mJ/cm^2 and 84 mJ/cm^2 reduced the population density of *Fol* conidia by 90% and 99%, respectively. A low-pressure lamp totally eliminated conidia of the pathogen at a UV-dose of 70 mJ/cm^2 (Runia, 1994). In research with a commercial UV production unit, UV radiation at a dose of 150 mJ/cm^2 eliminated conidia of *Forl* from water (Jamart et al., 1994).

3.5. Crop rotation/intercropping

As mentioned previously, a major challenge in managing both *Fol* and *Forl* is their extreme longevity in soil even in the absence of hosts. In a 5-year field study conducted in the USA, Chellemi et al. (2012) evaluated the effect of five land management practices on FW in tomato grown on PE mulch-covered, raised beds: organic (broiler litter and urban plant debris incorporation, cover crop), bahiagrass-strip tillage (herbicides, synthetic fertilizer), conventional (fumigation, herbicides, synthetic fertilizer), weed fallow (herbicides, synthetic fertilizer), and disk fallow (herbicides, synthetic fertilizer). Weed fallow and disk fallow resulted in FW incidences >14%. Disease incidence was >4% after a 3- or 4-year bahiagrass rotation or organic production practices. Conventional production practices resulted in a 2–15% FW incidence. Repeated tomato culture resulted in a FW incidence of ≥20% except in the organic treatment where it was ≤3%. Yields exceeded 35 t/ha following all land management practices except the bahiagrass-tillage program, and declined by 11, 14, and 19% when tomato followed bahiagrass-tillage, weed fallow, and disk rotations, respectively.

It has been suggested that growing tomato after paddy rice can reduce FW (Cerkauskas, 2005). Although a 4-month submergence in a paddy rice field did not reduce the population density of *Fol*, it did prevent increase of the pathogen during subsequent tomato culture (Komada et al., 1970). Intercropping watermelon with aerobic rice reduced the incidence and severity of Fusarium wilt and increased soil populations of bacteria and actinomycetes (Ren et al., 2008). However, intercropping tomato with leek, cucumber or basil had no effect on FW incidence or severity, indicating the absence of allelopathic activity (Hage-Ahmed et al., 2013).

3.6. Integrative strategies

The combined effect of a number of different management strategies on FW and FCRR has been examined including integration of biological with chemical, and physical with biological or chemical practices.

3.6.1. Biological + chemical

In field trials in Egypt, application of PGPR strains (*Azotobacter* sp., *Bacillus cereus*, *B. megaterium*) in combination with humic acid was more effective in increasing yield/plant in two experiments, and in reducing FW (AUDPC) in one of the two experiments than the individual treatments (Abdel-Monaim et al., 2012). *Pseudomonas fluorescens* combined with a reduced rate of the fungicide benomyl was more effective in decreasing FW incidence in greenhouse-grown tomato in Japan (Someya et al., 2006) than either treatment alone. Omar et al. (2006) similarly reported FCRR reduction from a combination of *Burkholderia cepacia* with a reduced rate of the fungicide carbendazim in the UK. The integration of *Bacillus subtillis* (Companion®) with either the fungicide hymexazol or the resistance elicitor acibenzolar-s-methyl produced greater reductions in the FCRR disease index than any of the treatments alone (Myresiotis et al., 2012). Integration of *Trichoderma harzianum* with the resistance elicitor chitosan resulted in enhanced management of FCRR in a greenhouse trial in Tunisia (El-Mohamedy et al., 2014).

3.6.2. Physical + biological or chemical

Inconsistent effects on plant yield and FCRR reduction were observed when *Streptomyces griseus* (Mycostop®) was integrated

with soil solarization in greenhouse experiments conducted in Italy (Minuto et al., 2006a). Neither the effectiveness of soil solarization in management of FCRR nor yield was increased through combination with *T. harzianum* or *Paenebacillus lentimorbus* in greenhouse experiments in Chile (Montealegre et al., 2005).

A number of greenhouse and field experiments in Israel evaluated integration of soil solarization with biological and/or chemical practices for management of FCRR. The combination of *T. harzianum* with a sub-lethal dose of methyl bromide or with soil solarization was effective (Sivan and Chet, 1993). Soil solarization combined with a reduced rate of metam sodium, or with metam sodium plus formalin using an improved solarization film was as effective as methyl bromide in reducing the disease and increasing yields (Gamliel et al., 2000, 2009).

The effectivess of soil solarization against FCRR in greenhouse-grown tomato in Turkey was improved by application of hydrogen peroxide + benzoic acid applied through drip irrigation during the solarization process (Yuce et al., 2011). Soil solarization for 3 wk coupled with application of a half rate of the fumigant dazomet was very effective in reducing FCRR symptoms in greenhouse experiments in northern Italy (Minuto et al., 2000). Rowe and Farley (1981) demonstrated that integration of the use of healthy tomato transplants with application of the fungicide captafol following steam disinfestation gave excellent control of FCRR in greenhouses in the USA.

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