Control Strategies of the Major Soilborne Fungal/Oomycete Diseases

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Globally, tomato is the second most cultivated vegetable crop next to potato, preferentially grown in temperate climates. Processing tomatoes are generally produced in field conditions, in which soilborne pathogens have serious impacts on tomato yield and quality by causing diseases of the tomato root system. Major processing tomato-producing countries have documented soilborne diseases caused by a variety of pathogens including bacteria, fungi, nematodes, and oomycetes, which are of economic importance and may threaten food security. Surveys in the Australian processing tomato industry showed that plant growth and yield were significantly affected by soilborne pathogens, especially *Fusarium oxysporum* and *Pythium* species. Globally, different management methods have been used to control diseases such as the use of resistant tomato cultivars, the application of fungicides, and biological control. Among these methods, biocontrol has received increasing attention due to its high efficiency, target-specificity, sustainability and public acceptance. The application of biocontrol is a mix of different strategies, such as applying antagonistic microorganisms to the field, and using the beneficial metabolites synthesized by these microorganisms.

Keywords: biocontrol ; fungus ; oomycete ; soilborne pathogen ; tomato

1. Tomato Corky Root Rot

1.1. Conventional Control Methods

Cultural Control

The disease development of corky rot is at optimum at 15.5–20 °C [1]. Thus, it is better to plant tomatoes in spring when the soils start to become warm.

Though effective against many other pathogens, crop rotation alone may not be effective in controlling corky root rot, for *P. lycopersici* has a wide host range including cucumber, eggplant, lettuce, melons, and pepper [2].

Physical Control

Soil solarization by covering the field with plastic film for a long period is a practical method for the control of corky root rot. In Italy, Vitale et al. [3] found that solarization performed with ethylene-vinyl-acetate film has an identical level of control effect on corky rot symptoms as compared with fumigation with methyl bromide, which was better than that of metham sodium and metham potassium fumigation. However, the level of success of solarization depends on the combination of high ambient temperatures, maximum solar radiation, and optimum soil moisture as well as the existing inoculum and disease levels [4][5]. Therefore, solarization usually has varying effectiveness, and is generally less effective in climates where high summer temperatures coincide with the rainy season due to the cooling effect of rainfall and extensive clouds blocking the solar radiation [4].

Chemical Control

In fields previously reported to have corky root rot, a preplant treatment with soil fumigation was shown to reduce disease in the subsequent tomato crop [3]. Methyl bromide (MBr) used to be a preferred chemical, but it was proved to be an ozone-depletion agent which is more destructive to stratospheric ozone than chlorine [6], thus its use has been phased out in developed countries by 2005 and in 2015 by the less developed countries as required by Montreal Protocol [7]. Potential alternative chemicals such as chloropicrin, metam sodium, metam potassium, and dazomet [3][8][9] can only provide a lower control level of corky root rot compared with MBr treatment. For example, Vitale et al. [3] found that metham sodium fumigation (MS, 353 litres a.i. ha^{-1}) and metham potassium fumigation (MK, 350 litres a.i. ha^{-1}) did not reduce the disease incidence of corky root rot in their trial. Therefore, with reduced efficiency of chemical controls, the management of corky root rot may require the addition of more effective methods such as the use of resistant cultivars and biocontrol.

Resistance Breeding

Though breeding for resistant cultivars is a common strategy for the control of crop disease, commercial variants of both processing and fresh consumption tomatoes are susceptible to corky root disease [10]. So far, only one single recessive gene (*pyl*) was shown to confer resistance to corky root rot and was introgressed into *Lycopersicon esculentum* from *L. peruvianum* [11]. The *pyl* gene is later found to possibly be a recessive allele of a susceptibility gene [12] and it has not been cloned yet.

1.2. Biological Control

Some fungivorous nematodes have been recorded as potential biocontrol agents for corky root rot. Hasna et al. [13] tested two fungivorous nematodes, *Aphelenchus avenae* and *Aphelenchoides* spp. against *P. lycopersici*, and concluded only *A. avenae* was able to significantly reduce the severity of tomato root rot in greenhouse trials with a population of 3 or 23 nematodes mL^{-1} soil. However, in a later on-farm trial covering two tomato seasons in Sweden, Hasna et al. [14] found even at a higher inoculation rate of 50 nematodes mL^{-1} soil, the application of *A. avanae* into infested soil did not reduce corky root disease severity. Thus, the potential of nematodes to control corky root rot may not be dismissed, but the application method may still need improvements.

In greenhouse trials, bacterial antagonists such as *Streptomyces* spp. have been found to effectively suppress corky root disease of tomatoes and enhance plant growth, resulting in higher yields. Bubici et al. [15] evaluated the antagonism of twenty-six *Streptomyces* spp. against corky root rot on tomatoes in both glasshouse and field conditions and found the most effective strain can reduce disease severity up to 64% in the glasshouse and 48% in the field.

Antagonistic fungi may also be used in the biocontrol against corky root rot. Fiume and Fiume [10] conducted glasshouse trials against corky root rot using *Trichoderma viride, Bacillus subtilis,* and *Streptomyces* spp., and concluded that the application of all three microorganisms significantly reduced the corky root symptoms in terms of disease index, with *T. viride* having the best results, followed by *Streptomyces* spp. Besoain et al. [16] performed UV on native *T. harzianum* to obtain mutants and found the mutants ThF1-2 and ThF4-4 inhibited the growth of *P. lycopersici* in vitro by 1.3 and 5 fold, respectively. Sánchez-Téllez et al. [17] further tested the mutant ThF1-2 in greenhouse tomato trials and found applying solid formulation ThF1-2 resulted in a significantly lower root damage caused by *P. lycopersici* compared with a previous trial using MBr. The control of *T. harzianum* against *P. lycopersici* seems to be correlated to the differential expression of extracellular fungal cell wall hydrolytic enzymes between isolates [18].

Organic amendments may also help in the control of corky root rot. Workneh et al. [19] found that the application of green manure and compost reduced the corky root rot severity in organic farm tomatoes by stimulating microbial activities in a field survey. However, *P. lycopersici* responds differently to different amendments. Hasna et al. [20] tested composts consisting of green manure, garden waste, and horse manure against corky root rot in greenhouse tomatoes and found that garden waste compost significantly reduced the disease, whereas horse manure compost significantly stimulated disease, while the green manure compost had no effect on the disease despite the increased microbial activity. It was concluded that the disease severity of corky root rot can be suppressed by composts with a low concentration of ammonium nitrogen and a high concentration of calcium, but further studies may be necessary to further prove this perspective.

2. Fusarium Crown and Root Rot (FCRR) of Tomato

2.1. Conventional Control Methods

Cultural Control

Hygiene and sanitation of the seeds and transplant seedlings are important for *Forl* management. For example, Muslim et al. [21] found that plants not challenged with the pathogen still become infected by FCRR, which is probably due to incomplete soil sterilization. It is also strongly recommended that all equipment coming in direct contact with soil is cleaned and disinfected [22]. The pathogen may also use colonized and infected plants as carrying vectors, thus the infected plants and their roots should be removed immediately.

Crop rotation with a non-host crop may also prevent FCRR. Crops susceptible to *Forl* such as eggplants and peppers should be avoided in the rotation [23], while non-hosts such as lettuce may be useful to reduce inoculum levels in the soil [24]. However, the efficiency of crop rotation may be limited for FCRR control, because the pathogen can survive as chlamydospores in the soil for a long time [25].

Physical Control

FCRR is favored by cooler temperatures, thus planting in warm periods and using warm water in irrigation is recommended to restrict the development of disease [26]. Soil solarization has also been demonstrated to control FCRR. In studies testing several solarization methods, soil solarization generally reduced populations of *Forl* down to a depth of 5 cm [22].

Chemical Control

Before the 2010s, the most effective method for FCRR control was soil disinfection using methyl bromide (MBr) [27][28]. However, MBr has been phased out globally since 2015. The ban on MBr prompted the study of alternative chemicals for the control of soilborne pests including *Forl*. So far, the tested alternatives include 1,3-dichloropropene, chloropicrin, dozamet, fosthiazate, and metam sodium, with similar effects on *Forl* compared with MBr [22][29][30]. For example, McGovern et al. [29] tested the application of metam sodium in field tomatoes and found that rotovation of metam sodium at 935 L/ha into preformed beds consistently reduced FCRR incidence equal to those achieved by methyl bromide-chloropicrin. Also, 1,3-dichloropropene+chloropicrin (60.5% and 33.3%, *w*/*w*) was tested on Italian field tomatoes [30] and was able to achieve a good tomato yield using drip application in sandy loam soils with slight *Forl* infections and severe infections of *Fol* and galling nematodes, which was similar to those of the plots treated with MBr.

However, there are still several factors that may reduce the efficiency of *Forl* chemical control. For example, *Forl* chlamydospores were found to survive in the soil at a depth beyond 50 cm, which is unreachable by soil fumigation [26]. Also, *Forl* can efficiently colonize sterilized soil [31]. Therefore, soil fumigation may instead create favorable soil conditions for *Forl* colonization by reducing microbial competition.

Resistance Breeding

Resistant tomato varieties can also be used to control FCRR. The resistance of tomatoes to FCRR is found to be controlled by a single dominant locus (*Frl*) on chromosome 9 [32][33]. This gene has been successfully crossed into commercial tomato lines, with many *Forl*-resistant cultivars currently available. However, no additional resistant genes have been identified.

2.2. Biocontrol

Forl is believed to have poor competitive fitness against other microorganisms [26], thus biocontrol via organic amendments or biocontrol agents may be effective for the management of *Forl*.

Several antagonistic microorganisms have been tested for their properties to control FCRR. Sivan et al. [34] applied *Trichoderma harzianum* as seed coating or wheat-bran/peat in tomatoes grown in FCRR-infested field and recorded a 26.2% increase in yield of treated plots compared with the control, with the control of *Forl* at the highest effect on root tips. Datnoff et al. [35] also applied *T. harzianum* and *Glomus intraradices* into tomato fields with FCRR history and recorded a significant reduction in disease severity and disease incidence of FCRR by applying the fungi both combined and separately. Several hypervirulent binucleate *Rhizoctonia* strains were also found to reduce the vascular discoloration caused by FCRR on tomatoes up to 100% in greenhouse conditions and up to 70% in the field [21]. Moreover, a non-pathogenic endophytic *F. solani* strain was reported to reduce disease incidence of *Forl* when applied alone in glasshouse tomato by 47%, the effects of which improved when combined with certain fungicides [36]. *Pythium oligandurm* was also found to trigger the host defence of greenhouse tomatoes when challenged by *Forl* in the form of deposition of newly formed barriers beyond the infection sites [37].

Several bacteria species may also control FCRR. *Pseudomonas fluorescens* was found to synthesize the antibiotic 2,4-diacetylphloroglucinol, which suppressed the growth of *Forl* in vitro [38]. A further study found that *P. fluorescens* WCS365 used chemotaxis towards *Forl* hyphae, enabling it to efficiently colonize *Forl* and achieve control effects [39]. In a later screening by Kamilova et al. [40], strong competitive biocontrol strains *P. fluorescens* PCL1751 and *P. putida* PCL1760 were found to successfully suppress FCRR under the soil and hydroponic conditions. In addition, Baysal et al. [41] assessed in a greenhouse trial the effect of two *Bacillus subtilis* bacteria strains QST713 and EU07, and concluded that EU07 had a better disease inhibitory effect (disease incidence reduced by 75%) compared with QST713 (disease incidence reduced by 52%), and the inhibition may be achieved by YrvN protein coded in the genome of EU07 as a subunit of protease enzyme. Lytic enzymes, cellulases, proteases, 1,4-b-glucanase, and hydrolases from the secreted proteins from *B. subtilis* EU07 and FZB24 and concluded these essential proteins of *Bacillus* bacteria play an important role in the control of *Forl* [42].

Organic amendments promoting microbial activity may also be used in FCRR management, but they do not have consistent effects in field conditions. Straw was incorporated into the soil to manage FCRR by Jarvis [26], but the *Forl* soil population increased around and inside the straw, which only started to fall when the straw decomposed. However, Kavroulakis et al. [43] concluded that a compost mix made from grape marc wastes and extracted olive press cake can enhance tomato defensive capacity under *Forl* stress by making the pathogen unable to penetrate and colonize the host root, resulting in a 40% reduction in the disease incidence compared to the control. However, the plants in this trial were grown completely in the compost, making large-size commercial applications likely unrealistic.

3. Fusarium wilt Disease of Tomato

3.1. Conventional Control Methods

Cultural Control

Crop rotation can be used to manage *Fusarium* wilt, and it is recommended not to plant the same or related type of crop for at least four years if one crop is severely infected by *Fusarium* wilt [44]. The recommended crops for rotation are grasses and cereals [45].

Hygiene should also be practiced for *Fol* control. Disease-affected plants should be removed immediately. Used farming tools should be disinfected and cleaned before reuse. The use of sanitized footwear and clothes on the farm may help prevent the transportation of infected soils between paddocks [44]. Fallowing is another strategy for *Fol* control. Briefly, the land is left uncultivated for a period, and for *Fol*, it is recommended to practice fallowing during the summer months to let the high temperature and excessive drying reduce soil levels of *Fol* [46].

Physical Control

Soil solarization can also be used to control *Fol* residing in soil, preferably performed in the summertimes. However, since the development of *Fusarium* wilt favors warm temperatures (27–28 °C) [47], this strategy may not work in zones with cool climates.

Chemical Control

Soil fumigation with MBr was an effective method for *Fol* management however, with the phase-out of MBr the value of chemical control on *Fol* has drastically reduced. Though alternative chemicals such as chloropicrin, dimethyl disulfide, metam sodium, and 1,3-dichloropropene are available, they all lack the broad-spectrum volatile characteristics of MBr, which made it highly effective [48]. Systemic fungicides such as benomyl, thiabendazole, and thiophanate have also been used to control tomato *Fusarium* wilt [46], but it was believed that there are no fungicides especially effective for the control of this disease [44].

Resistance Breeding

The application of tomato cultivars resistant to *Fusarium* wilt is currently the most feasible management method.

The resistance to *Fol* was first identified by Bohn and Tucker in 1939 [49], who identified one single, dominant resistance locus later named *I* gene from one wild tomato accession of *S. pimpinellifolium*, Missouri accession 160 [50]. This gene was crossed into the first commercial *Fol*-resistant tomato cultivar and was located at tomato chromosome 11 [51].

Later, the second race of *Fol*, named *Fol2* was reported to spread widely in Florida in the 1960s [52], which led to another screening for the corresponding resistant gene. The resistant gene was again found in wild tomato relatives- a natural hybrid PI126915, which was name *I-2* and mapped to chromosome 11 [53].

In 1979, the third race of *Fol–Fol3* was reported in Australia in fresh tomato production [54]. McGrath et al. [55] were the first to identify resistance to *Fol3* in the *S. pennellii* accession PI414773 in 1987, and Scott and Jones [56] later identified a dominant *Fol3* resistance locus in the *S. pennellii* accession LA716. This newly discovered gene was later named *I-3* and used as the primary source of *Fol3* resistance in commercial varieties. Gene *I-3* was mapped to chromosome 7 [57], and McGrath et al. located another gene *I-7* gene in chromosome 8 [58].

Three additional genes with partial resistance to *Fol2* were also found by Sela-Buurlage et al. [51]. These researchers studied 53 introgression lines with chromosomes from LA716 and identified alleles *I-4* and locus *I-5* on chromosome 2, with locus *I-6* on chromosome 10 of *S. pennellii*. However, none of these genes have their effects validated nor used for commercial purposes so far.

3.2. Biological Control

Potential biocontrol agents against *Fol* on tomatoes have been actively tested in a large number of studies. The most commonly used biocontrol agents belonged to various microbial genera including fungi (*Aspergillus* spp., *Chaetomium* spp., *Glomus* spp., non-pathogenic *Fusarium* spp., *Trichoderma* spp. and *Penicillium* spp.) and bacteria (*Bacillus* spp., *Pseudomonas* spp., *Streptomyces* spp., and *Serratia* spp.) [59].

Among the different genera of biocontrol microorganisms, non-pathogenic *Fusarium* strains are of high interest. In 1993, Alabouvette et al. [60] concluded that among the many groups of microorganisms tested for biocontrol activity, only non-pathogenic *Fusarium* species and fluorescent *Pseudomonads* showed consistent responses. In a later review by Ajilogba et al., these strains were found to be involved in most research conducted on plant biological enhancement using fungal endophytes [44]. One representative strain, *F. oxysporum* Fo47, was successfully tested against *Fol* [61][62][63], with the major mode of function being the induction of systemic resistance and priming of the plant defence reaction.

Another review by Raza et al. [59] analyzed biocontrol trials conducted between 2000 and 2014 and concluded that non-pathogenic *Fusarium* species and *Pseudomonas* species were supported by most research to be more effective in controlling *Fusarium* wilt in natural soil, while *Penicillium*, *Streptomyces*, and *Aspergillus* strains were more effective in growth media. However, the authors also found that 79% of the tests on tomatoes were conducted in greenhouse conditions, with 12% conducted in the field condition. Thus, for processing tomatoes grown predominately in field conditions, further field tests on the efficiency of different biocontrol agents are necessary.

Organic amendments are another group of biocontrol agents. For example, Borrego-Benjumea et al. [64] tested poultry manure, olive residue compost, and pelletised poultry manure for tomatoes grown in natural sandy soil and concluded that the combination of pelletized poultry manure with heating or solarization achieved the greatest reduction in *Fusarium* wilt severity. In a later study by Zhao et al. [65] testing chicken manure, rice straw, and vermicompost in a long-term tomato monocultural soil, vermicompost addition significantly increased soil pH, ammonium nitrogen, soil organic matter, and dissolved organic carbon, which promoted beneficial bacteria suppressing *Fol.* Organic amendments are often applied in combination with biocontrol microorganisms for better effects in different studies [59][66][67]. It was also suggested that the combined application of biocontrol organisms and amendments can increase the biocontrol efficiency of various genera of fungi and bacteria, with the exceptions of *Pseudomonas* and *Penicillium* [59].

4. Phytophthora Root Rot of Tomato

4.1. Conventional Control Methods

Cultural Control

Crop rotation is often used to manage *P. capsici* along with many other soilborne pathogens, but its effectiveness is limited by the long survival of oomycetes in the soil and the wide host range of *P. capsici*. The host range of *P. capsici* was reported to cover at least 45 species of cultivated plants and weeds from 14 families of flowering plants [68], thus the selection of rotation crops for *P. capsici* is very narrow. Also, Lamour and Hausbeck [69] found *P. capsici* can survive as oospores for a 30-month nonhost period during crop rotation. Therefore, long rotations are required even if non-host crops are available, which may make crop rotations economically unfeasible.

It is very difficult to control *P. capsici* once the pathogen becomes established in the field. Thus, most control strategies are aimed at limiting free water to minimize inoculum spread and crop loss, which includes planting at well-drained sites or on a raised bed with controlled irrigation [70].

Physical Control

Soil solarization was found to be effective against *Phytophthora* root rot on tomatoes. From a trial in Florida a soil solarization treatment that heated the soil to a maximum of 47 °C at 10-cm depth had similar effects to MBr treatment at the same site in reducing the *P. capsici* population [4].

Chemical Control

The application of chemicals has been another approach to managing *P. capsici*. However, the phasing out of MBr has reduced the cost-efficiency of chemical control [71]. Other chemicals frequently applied include cyazofamid, dimethomorph, fluopicolide, fosetyl-Al, mandipropamid and mefenoxam (metalaxyl) [72][73][74][75]. Despite the various choices of chemicals, extensive use of fungicide has led to the emergence of resistant *P. capsici* strains, which makes it very hard to protect crops from *P. capsici*. For example, Lamour and Hausbeck [69] collected 141 isolates of *P. capsici* in Michigan and found

around 60% to be intermediately sensitive or insensitive to mefenoxam. Even more recent groups of chemicals such as fluopicolide and cyazofamid have resulted in the fast emergence of pathogen resistance. Jackson et al. [73] concluded that among the 40 *P. capsici* isolates tested, all were either intermediately sensitive or resistant to cyazofamid at 100 µg/mL application rate. More recently, Siegenthaler and Hansen [75] found that out of 184 *P. capsici* isolates collected in Tennessee, 84 were resistant to fluopicolide.

Resistance Breeding

Until the 2010s, only several tomato strains moderately resistant to *P. capsici* were commercially available. Quesada-Ocampo and Hausbeck [71] screened 42 tomato cultivars and wild relatives for their resistance against *P. capsici*, and found *Solanum habrochaites* accession LA407, was resistant to all *P. capsici* isolates tested, with four additional cultivars having moderate resistance. However, the authors analyzed the genes of these cultivars and found a lack of correlation between genetic clusters and susceptibility to *P. capsici*, indicating that resistance was distributed in several tomato lineages. In a subsequent study, Quesada-Ocampo et al. [76] generated 62 backcross lines using LA407, and tested their resistance against different *P. capsici* strains and used annotated markers to locate genes related to the resistance. Though the researchers found that the resistance had a good inheritability among the population, they failed to find any annotated markers strongly associated with *P. capsici* resistance, with genes with annotation linked to disease resistance responses mapped to all chromosomes segregated among the population with the exceptions for 8, 9, 11, and 12. Therefore, the resistance of tomatos to *P. capsici* has not been related to specific gene/loci so far, and further studies are required.

4.2. Biocontrol

With insufficient levels of conventional control measures against *Phytophthora* root rot of tomatoes, antagonistic microbes and organic amendments have been tested to find feasible biocontrol approaches. Bacteria species are frequently studied for their biocontrol properties against *Phytophthora* root rot. Moataza [77] tested five *Pseudomonas fluorescences* strains against *Rhizoctonia solani* and *P. capsici* in tomato pot trials, and concluded that two strains, NRC1 and NRC3 had strong lytic activities leading to the destruction of the pathogen, Sharma et al. [78] tested 20 *Bacillus* strains against *P. capsici* on tomatoes grown in net house, and found one species, *B. subtilis* showed the best efficiency in terms of decreased disease severity. Furthermore, Syed-Ab-Rahman et al. [79] tested three bacteria- *B. amyloliquefaciens*, *B. velezensis* and *Acinetobacter* sp. on tomato, and concluded all three bacteria promoted tomato growth while significantly reducing the *P. capsici* load in their roots. An oomycete, *Pythium oligandrum* was also tested, and was believed to synthesize two Necrosis- and ethylene-inducing peptide 1 (Nep1)-like proteins PyolNLP5 and PyolNLP7, which induced the expression of antimicrobial tomato defensin genes against *P. capsici* [80].

The application of organic amendments is another approach to biocontrol. For *P. capsici* management, Nicol and Burlakoti [81] aerated compost and water and produced four aerobic compost teas. When tested in the glasshouse, the researchers concluded that if these products were drenched in potting mix before and after *P. capsici* inoculation, the disease progression was reduced by over 70%, with improved plant growth. Other efforts of using composts against *P. capsici* have generally been attempted on pepper [82][83][84], so the effects of these composts on tomatoes are unknown.

5. Pythium Root Rot and Damping-Off

5.1. Conventional Control Methods

Cultural Control

The application of pathogen-free seedlings and the control of irrigation are found to be effective forms for tomato *Pythium* disease management [85][86].

For *Pythium* species, crop rotation is generally not considered to be effective in the control of tomato infections because most *Pythium* species have a wide host range [87]. However, one study on wheat found that 3–4-year rotation cycles using wheat, canola and legume resulted in a significantly smaller disease incidence compared with less diverse rotations such as two-year wheat-canola [88]. The reason behind this finding may be that different crops have significantly different susceptibilities to *Pythium* infection, which may restrict the soilborne pathogen inoculum build-up after each crop, and eventually reducing the disease incidence in the next crop.

Physical Control

Soil solarization is an effective method for *Pythium* control with a long-period (six weeks to 60 days) of solarization during the summertime having been shown to significantly reduce the soilborne population of *P. aphanidermatum* in tropic zones [89][90]. In a field trial on tomatoes infected by *Pythium* spp., solarized soil showed a significantly lower mean damping-off incidence compared with un-solarized soil (2.15% compared with 68%) [91].

Chemical Control

Several chemicals have been used to manage *Pythium* species, including hymexazol, mefenoxam (metalaxyl), phosphonate, thiram and 8-Hydroxyquinoline [92][93][94][95][96]. The chemicals can be applied as seed treatment [97][98] or soil drenching [99] for seedlings of tomato.

In addition to the common economic and environmental concerns of chemical control, several major *Pythium* species collected from the production of various crops have developed resistance against several chemicals, especially mefenoxam. For example, Porter et al. [100] reported over 50% of the *Pythium* soil population consisted of mefenoxam-resistant isolates in ten of 64 potato fields from Oregon and Washington. Del Castillo Munera and Hausbeck [101] tested a total of 202 *Pythium* spp. isolates collected from Michigan, and found 39% of these, mostly *P. ultimum* and *P. cylindrosporum* isolates were intermediate to highly resistant to mefenoxam. For another major species *P. irregulare*, Aegerter et al. [102] tested four *P. irregulare* isolates from a greenhouse extensively applying mefenoxam and found no inhibition of growth of any isolate occurred at mefenoxam concentrations of 10 µg/mL or less. For other *Pythium* species such as *P. aphanidermatum*, resistance to mefenoxam was also reported [103][104]. In a rare case, Garzón et al. [95] even reported that the disease severity of a mefenoxam-resistant *P. aphanidermatum* on geranium can be stimulated by sublethal doses of mefenoxam.

Resistance Breeding

Though the deployment of resistant cultivars is a common and effective strategy for crop disease management, currently there is no *Pythium*-resistant tomato. The only potentially useful genetic resource against *Pythium* is the genes encoding pathogenesis-related (PR) proteins, with PR-1 protein showing antifungal activity against oomycetes [105]. Tomato has two related genes, *PR1b1* and *PR1a2*, each encoding a basic and an acidic PR-1 protein [106], but the resistance of PR proteins is not pathogen-specific, with only limited effects against *Pythium* species.

5.2. Biocontrol

For biocontrol of *Pythium* disease on tomatoes, several bacteria strains have been studied. Postma et al. [107] tested four bacteria strains against *P. aphanidermatum* and found three strains, *Pseudomonas chlororaphis*, *Peanibacillus polymyxa* and *Streptomyces pseudovenezuelae*, significantly controlled *P. aphanidermatum* in under greenhouse conditions. The effect of *Streptomyces* bacteria was also supported by the study of Hassanisaadi et al. [87], who found two root-symbiont *Streptomyces* species significantly decreased disease incidence and improved performance of greenhouse tomato under *P. aphanidermatum* in stress out of the 116 tested species. For *Bacillus* bacteria, Martinez et al. [108] tested one *B. subtilis* strain MBI600 in a peat-based potting mix and concluded the addition of this strain significantly reduce tomato and sweet pepper damping-off and root rot while promoting root growth. Samaras et al. [96] also tested MBI600 on greenhouse tomatoes and concluded that the application of this strain achieved satisfactory control efficacy compared to chemical treatment with 8-Hydroxyquinoline.

For the application of fungal antagonists, the current focus seems to be on the *Trichoderma* species. Caron et al. [109] tested one local *T. harzianum* strain MAUL-20 on greenhouse tomatoes and found that it significantly reduced *P. ultimum* disease incidence, with a better effect compared with Rootshield™, a biofungicide based on *T. harzianum* KRL-AG2. Cuevas et al. [94] also tested *T. parceramosum*, *T. pseudokoningii* and *T. harzianum* respectively, and found the application of the *Trichoderma* pellets into the field before seeding can minimize the activity of *Pythium* spp., with a higher seed germination rate compared with the treatment using chemical fungicide mancozeb. Elshahawy and El-Mohamedy [110] tested the effects of five *Trichoderma* strains on *P. aphanidermatum* damping-off of tomatoes and concluded that under field conditions the combined application of the five isolates reduced by half the root rot severity while almost doubling the survival of tomato. This was thought to be through activating tomato defence enzymes and increasing leaf chlorophyll content, with an increased yield.

Interestingly, even arbuscular mycorrhizal fungi suppressing plant growth may also be used to control *Pythium* species. Larsen et al. [111] pre-treated greenhouse tomato seedlings with *Glomus intraradices*, *G. mosseae*, *G. claroideum*, and then challenged the seedlings with *P. aphanidermatum*, with the hypothesis that the application of growth-suppressive fungi may trigger plant defence response in terms of *PR-1* expression to prepare the plants for *Pythium* infection.

However, the application of arbuscular mycorrhizal fungi did not affect *PR-1* gene expression, with only *G. intraradices* reducing the pathogen root infection level of *P. aphanidermatum*, thus the hypothesis was not confirmed.

Several organic amendments have also been tested against *Pythium*, such as canola residues and composts (animal bone charcoal, compost tea, solid green wastes, or green waste +manure) [107][112][113][114]. Also, Jayaraj et al. [115] found that formulating amendments such as lignite with biocontrol agents such as *B. subtilis* can greatly increase their shelf life, with good effects on *Pythium* suppression and plant growth promotion.

6. Tomato Verticillium Wilt

6.1. Conventional Control Methods

Cultural Control

Crop rotation with non-host crops is an effective strategy for *Verticillium* wilt management. The known non-host crops include small grain crops such as wheat and corn [116], and long rotations lasting over four years are recommended [117].

Hygiene is also important for *Verticillium* wilt control. pathogen-free seed and disease-free transplants should be used [117], with infected crop debris removed and destroyed away from the field. Equipment and foot ware should be washed to prevent the movement of infested soil between fields. *Verticillium* also prefers humid soil, thus maintaining well-drained soil, and eliminating excessive soil moisture may also limit the development of the pathogen [118].

Physical Control

Verticillium prefers cool temperatures for survival and developing symptoms, thus heating the soil through solarization could be an effective control method. Currently, solarization against *Verticillium* wilt is practiced generally in Mediterranean, desert, and tropical climates, because these climates allow the accumulation of adequate heat to neutralize the pathogen [119]. However, the data on solarization alone showed poorer performance compared with the MBr application, which can be improved when combined with the fumigation using MBr alternatives [120].

Chemical Control

Soil fumigation is also used to control *Verticillium* wilt. MBr alternatives such as chloropicrin (CP) (trichloronitromethane) are traditionally used as in formulations together with MBr to achieve a broader spectrum of activity [120]. In a trial by Gullino et al. [121], CP applied by shank injection at rates ≥30 g/m^2 induced a satisfactory and consistent control of tomato *Verticillium* wilt, with no phytotoxicity, but the efficiency was slightly lower than standard MBr application and may have been influenced by soil type and organic matter content. Metam-sodium and 1,3-dichloropropene are other alternative soil fumigants, which have been applied in combination or with metam-sodium alone in the United States to reduce soil populations of *V. dahliae* [122]. Several other chemicals such as fungicides including azoxystrobin, benomyl, captan, thiram, and trifloxystrobin, and a plant defense activator, acibenzolar-S-methyl were also recommended [15][120][123].

Resistance Breeding

By far, the most feasible and economic control for *Verticillium* wilt is the application of resistant cultivars. The resistance gene in tomato to *V. dahliae* was first identified as a single dominant factor in the reciprocal crosses between the wilt-resistant variety W6 (Peru Wild × Century) and Moscow, a susceptible variety, and named as *Ve* in 1951 [124]. *Ve* was found to be a locus, which contains two genes, *Ve1* and *Ve2*, with only *Ve1* found to mediate resistance in tomato [125]. The strains of *V. dahliae* resistant to *Ve1* and *V. albo-atrum* were assigned to race 2 [125]. The *Ve1* gene has been incorporated into many commercial cultivars. However, all the current verticillium-resistant gene resources are against *V. dahliae* race 1, thus all race 2 strains of *V. dahliae* and *V. albo-atrum* can still infect the resistant cultivars.

6.2. Biocontrol

Biological control may be a promising method to control *Verticillium* wilt, given that most current management methods have limited efficiency. Various microorganisms have been tested against *V. dahliae*, such as bacteria *Bacillus subtilis* and *B. velezensis* [126], and fungi including *Burkholderia gladioli* [127], *Gliocladium* spp., *Penicillium* sp. [128][129], *Trichoderma* spp. [130], *Talaromyces flavus* [131], and even *V. klebahnii* and *V. isaacii* with low pathogenicity [132]. Though most of the microorganisms are found to be effective in trials, most of the trials were carried out in greenhouses or with sterilized soil, with only a few verified in field conditions. Larena et al. [129] conducted a field assay using *P. oxalicum* and concluded that seedlings needed to be treated with 10^6–10^7 CFU/g of the biocontrol agent around a week before transplanting to achieve

a sufficient level of control, but only in a certain soil type (loam soil, pH = 7.0), and the formulation may not be feasible for tomato mass production due to the high CFU density requirement.

The application of organic amendments is known as another approach for crop disease biocontrol. It has long been known that bloodmeal and fishmeal can eliminate the incidence of *Verticillium* wilt in tomato [120]. Compared to animal-based amendments (manure), plant-based amendments not only support beneficial microbial activities but also have greater efficiency on pathogens due to deleterious chemicals produced by the plants, in addition to supporting beneficial microbial activities [133]. Giotis et al. [134] concluded that fresh Brassica tissue, household waste compost, and composted cow manure significantly reduced soilborne disease severity of tomato *Verticillium* wilt, with enhanced plant growth. Similar results were also achieved by Kadoglidou et al. [135], who applied soil incorporated spearmint and oregano-dried plant material, which caused disease suppression resulting in increased fruit yields of tomatoes inoculated with *V. dahliae*. Moreover, Ait Rahou et al. [136] used compost based on green waste (quackgrass) to greenhouse tomatoes inoculated with *Verticillium* and concluded that growth regulators directly produced by the microorganisms in the compost improved plant growth significantly. However, when Lazarovits et al. [137] applied compost made from sewage sludge to suppress *V. dahliae* in tomato plants, phytotoxicity was detected over one month, which may have been due to the excessive accumulation of plant-toxic heavy metals in soils. To conclude, though organic amendments may be useful for *Verticillium* wilt management, they may also carry toxic compounds which may lead to undesired effects.

References

1. Shankar, R.; Harsha, S.; Bhandary, R. A Practical Guide to Identification and Control of Tomato Diseases. Available online: https://www.researchgate.net/file.PostFileLoader.html?id=589eb904615e2793034a4db2&assetKey=AS%3A460474400677895%401486797060834 (accessed on 30 November 2022).
2. Ekengren, S.K. Cutting the Gordian knot: Taking a stab at corky root rot of tomato. Plant Biotechnol. 2008, 25, 265–269.
3. Vitale, A.; Castello, I.; Cascone, G.; D'Emilio, A.; Mazzarella, R.; Polizzi, G. Reduction of corky root infections on greenhouse tomato crops by soil solarization in South Italy. Plant Dis. 2011, 95, 195–201.
4. Coelho, L.; Chellemi, D.O.; Mitchell, D.J. Efficacy of solarization and cabbage amendment for the control of Phytophthora spp. in North Florida. Plant Dis. 1999, 83, 293–299.
5. Yücel, S.; Özarslandan, A.; Colak, A.; Ay, T.; Can, C. Effect of solarization and fumigant applications on soilborne pathogens and root-knot nematodes in greenhouse-grown tomato in Turkey. Phytoparasitica 2007, 35, 450–456.
6. Manö, S.; Andreae, M.O. Emission of methyl bromide from biomass burning. Science 1994, 263, 1255–1257.
7. Gareau, B.J. Lessons from the Montreal Protocol delay in phasing out methyl bromide. J. Environ. Stud. Sci. 2015, 5, 163–168.
8. Rosskopf, E.N.; Chellemi, D.O.; Kokalis-Burelle, N.; Church, G.T. Alternatives to methyl bromide: A Florida perspective. Plant Health Prog. 2005, 6, 19.
9. Locascio, S.J.; Gilreath, J.P.; Dickson, D.W.; Kucharek, T.A.; Jones, J.P.; Noling, J.W. Fumigant alternatives to methyl bromide for polyethylene-mulched. HortScience 1997, 32, 1208–1211.
10. Fiume, G.; Fiume, F. Biological control of corky root in tomato. Commun. Agric. Appl. Biol. Sci. 2008, 73, 233–248.
11. Doganlar, S.; Dodson, J.; Gabor, B.; Beck-Bunn, T.; Crossman, C.; Tanksley, S.D. Molecular mapping of the py-1 gene for resistance to corky root rot (Pyrenochaeta lycopersici) in tomato. Theor. Appl. Genet. 1998, 97, 784–788.
12. Milc, J.; Bagnaresi, P.; Aragona, M.; Valente, M.T.; Biselli, C.; Infantino, A.; Pecchioni, N. Comparative transcriptome profiling of the response to Pyrenochaeta lycopersici in resistant tomato cultivar Mogeor and its background genotype—Susceptible Moneymaker. Funct. Integr. Genom. 2019, 19, 811–826.
13. Hasna, M.K.; Lagerlöf, J.; Rämert, B. Effects of fungivorous nematodes on corky root disease of tomato grown in compost-amended soil. Acta Agric. Scand. Sect. B-Soil Plant Sci. 2008, 58, 145–153.
14. Hasna, M.K.; Ögren, E.; Persson, P.; Mårtensson, A.; Rämert, B. Management of corky root disease of tomato in participation with organic tomato growers. Crop Prot. 2009, 28, 155–161.
15. Bubici, G.; Marsico, A.D.; D'Amico, M.; Amenduni, M.; Cirulli, M. Evaluation of Streptomyces spp. for the biological control of corky root of tomato and Verticillium wilt of eggplant. Appl. Soil Ecol. 2013, 72, 128–134.
16. Besoain, X.A.; Pérez, L.M.; Araya, A.; Lefever, L.; Montealegre, J.R. New strains obtained after UV treatment and protoplast fusion of native Trichoderma harzianum: Their biocontrol activity on Pyrenochaeta lycopersici. Electron. J. Biotech

nol. 2007, 10, 604–617.

17. Sánchez-Téllez, S.; Herrera-Cid, R.A.; Besoain-Canales, X.A.; Pérez-Roepke, L.M.; Montealegre-Andrade, J.R. In vitro and in vivo inhibitory effect of solid and liquid Trichoderma harzianum formulations on biocontrol of Pyrenochaeta lycop ersici. Interciencia 2013, 38, 425–429.
18. Pérez, L.; Besoaín, X.; Reyes, M.; Pardo, G.; Montealegre, J. The expression of extracellular fungal cell wall hydrolytic enzymes in different Trichoderma harzianum isolates correlates with their ability to control Pyrenochaeta Lycopersici. Bi ol. Res. 2002, 35, 401–410.
19. Workneh, F.; Van Bruggen AH, C.; Drinkwater, L.E.; Shennan, C. Variables associated with corky root and Phytophthor a root rot of tomatoes in organic and conventional farms. Phytopathology 1993, 83, 581–589.
20. Hasna, M.K.; Mårtensson, A.; Persson, P.; Rämert, B. Use of composts to manage corky root disease in organic tomato production. Ann. Appl. Biol. 2007, 151, 381–390.
21. Muslim, A.; Horinouchi, H.; Hyakumachi, M. Control of Fusarium crown and root rot of tomato with hypovirulent binucle ate Rhizoctonia in soil and rock wool systems. Plant Dis. 2003, 87, 739–747.
22. Ozbay, N.; Newman, S.E. Fusarium crown and root rot of tomato and control methods. Plant Pathol. J. 2004, 3, 9–18.
23. Altinok, H.H.; Yüksel, G.; Altinok, M.A. Pathogenicity and phylogenetic analysis of Fusarium oxysporum f. sp. capsici is olates from pepper in Turkey. Can. J. Plant Pathol. 2020, 42, 279–291.
24. Zhang, S.; Roberts, P.D.; McGovern, R.J.; Datnoff, L.E. Fusarium Crown and Root Rot of Tomato in Florida. Institute of Food and Agricultural Sciences (IFAS), Publication PP52. Available online: https://edis.ifas.ufl.edu/publication/PG082 (a ccessed on 30 November 2022).
25. McGovern, R.J. Management of tomato diseases caused by Fusarium oxysporum. Crop. Prot. 2015, 73, 78–92.
26. Jarvis, W.R. Epidemiology of Fusarium oxysporum f. sp. radicis-lycopersici. In Vascular Wilt Diseases of Plants, 1st e d.; Tjamos, E.C., Beckman, C.H., Eds.; Springer: Berlin, Germany, 1989; pp. 397–411.
27. Cao, X.; Guan, Z.; Vallad, G.E.; Wu, F. Economics of fumigation in tomato production: The impact of methyl bromide ph ase-out on the Florida tomato industry. Int. Food Agribus. Manag. Rev. 2019, 22, 589–600.
28. Horinouchi, H.; Katsuyama, N.; Taguchi, Y.; Hyakumachi, M. Control of Fusarium crown and root rot of tomato in a soil system by combination of a plant growth-promoting fungus, Fusarium equiseti, and biodegradable pots. Crop. Prot. 200 8, 27, 859–864.
29. McGovern, R.J.; Vavrina, C.S.; Noling, J.W.; Datnoff, L.A.; Yonce, H.D. Evaluation of application methods of metam sod ium for management of Fusarium crown and root rot in tomato in southwest Florida. Plant Dis. 1998, 82, 919–923.
30. Minuto, A.; Gullino, M.L.; Lamberti, F.; D'addabbo, T.; Tescari, E.; Ajwa, H.; Garibaldi, A. Application of an emulsifiable mixture of 1, 3-dichloropropene and chloropicrin against root knot nematodes and soilborne fungi for greenhouse tomat oes in Italy. Crop Prot. 2006, 25, 1244–1252.
31. Benhamou, N.; Charest, P.M.; Jarvis, W.R. Biology and Host-Parasite Relations of Fusarium oxysporum f. sp. radicis-ly copersici. In Vascular Wilt Diseases of Plants, 1st ed.; Tjamos, E.C., Beckman, C.H., Eds.; Springer: Berlin, Germany, 1986; pp. 95–105.
32. Mutlu, N.; Demirelli, A.; Ilbi, H.; Ikten, C. Development of co-dominant SCAR markers linked to resistant gene against th e Fusarium oxysporum f. sp. radicis-lycopersici. Theor. Appl. Genet. 2015, 128, 1791–1798.
33. Fazio, G.; Stevens, M.R.; Scott, J.W. Identification of RAPD markers linked to fusarium crown and root rot resistance (F rl) in tomato. Euphytica 1999, 105, 205–210.
34. Sivan, A.; Ucko, O.; Chet, I. Biological control of Fusarium crown rot of tomato by Trichoderma harzianum under field c onditions. Plant Dis. 1987, 71, 587–592.
35. Datnoff, L.E.; Nemec, S.; Pernezny, K. Biological control of Fusarium crown and root rot of tomato in Florida using Trich oderma harzianum and Glomus intraradices. Biol. Control 1995, 5, 427–431.
36. Malandrakis, A.; Daskalaki, E.R.; Skiada, V.; Papadopoulou, K.K.; Kavroulakis, N. A Fusarium solani endophyte vs. fun gicides: Compatibility in a Fusarium oxysporum f. sp. radicis-lycopersici–tomato pathosystem. Fungal Biol. 2018, 122, 1 215–1221.
37. Benhamou, N.; Rey, P.; Chérif, M.; Hockenhull, J.; Tirilly, Y. Treatment with the mycoparasite Pythium oligandrum trigge rs induction of defense-related reactions in tomato roots when challenged with Fusarium oxysporum f. sp. radicis-lycop ersici. Phytopathology 1997, 87, 108–122.
38. Duffy, B.K.; Défago, G. Zinc improves biocontrol of Fusarium crown and root rot of tomato by Pseudomonas fluorescen s and represses the production of pathogen metabolites inhibitory to bacterial antibiotic biosynthesis. Phytopathology 1 997, 87, 1250–1257.

39. de Weert, S.; Kuiper, I.; Lagendijk, E.L.; Lamers, G.E.; Lugtenberg, B.J. Role of chemotaxis toward fusaric acid in colon ization of hyphae of Fusarium oxysporum f. sp. radicis-lycopersici by Pseudomonas fluorescens WCS365. Mol. Plant-M icrobe Interact. 2004, 17, 1185–1191.

40. Kamilova, F.; Validov, S.; Lugtenberg, B. Biological control of tomato foot and root rot caused by Fusarium oxysporum f. sp. radicis-lycopersici by Pseudomonas bacteria. In Proceedings of the II International Symposium on Tomato Disease s, Kusadasi, Turkey, 8–12 October 2007; Volume 808, pp. 317–320.

41. Baysal, Ö.; Çalışkan, M.; Yeşilova, Ö. An inhibitory effect of a new Bacillus subtilis strain (EU07) against Fusarium oxys porum f. sp. radicis-lycopersici. Physiol. Mol. Plant Pathol. 2008, 73, 25–32.

42. Baysal, Ö.; Lai, D.; Xu, H.H.; Siragusa, M.; Çalışkan, M.; Carimi, F.; Tör, M. A proteomic approach provides new insight s into the control of soil-borne plant pathogens by Bacillus species. PLoS ONE 2013, 8, e53182.

43. Kavroulakis, N.; Ehaliotis, C.; Ntougias, S.; Zervakis, G.I.; Papadopoulou, K.K. Local and systemic resistance against f ungal pathogens of tomato plants elicited by a compost derived from agricultural residues. Physiol. Mol. Plant Pathol. 2 005, 66, 163–174.

44. Ajilogba, C.F.; Babalola, O.O. Integrated management strategies for tomato Fusarium wilt. Biocontrol Sci. 2013, 18, 11 7–127.

45. Miller, S.A.; Rowe, R.C.; Riedel, R.M. Fusarium and Verticillium Wilts of Tomato, Potato, Pepper, and Eggplant. The Oh io State University Extension. Available online: https://www.cabdirect.org/cabdirect/abstract/20127800677 (accessed on 30 November 2022).

46. Bawa, I. Management strategies of Fusarium wilt disease of tomato incited by Fusarium oxysporum f. sp. lycopersici(S acc.) A Review. Int. J. Adv. Acad. Res. 2016, 2, 32–42.

47. Larkin, R.P.; Fravel, D.R. Effects of varying environmental conditions on biological control of Fusarium wilt of tomato by nonpathogenic Fusarium spp. Phytopathology 2002, 92, 1160–1166.

48. Yu, J.; Land, C.J.; Vallad, G.E.; Boyd, N.S. Tomato tolerance and pest control following fumigation with different ratios o f dimethyl disulfide and chloropicrin. Pest Manag. Sci. 2019, 75, 1416–1424.

49. Bohn, G.W.; Tucker, C.M. Immunity to Fusarium wilt in the tomato. Science 1939, 89, 603–604.

50. Takken, F.; Rep, M. The arms race between tomato and Fusarium oxysporum. Mol. Plant Pathol. 2010, 11, 309–314.

51. Sela-Buurlage, M.; Budai-Hadrian, O.; Pan, Q.; Carmel-Goren, L.; Vunsch, R.; Zamir, D.; Fluhr, R. Genome-wide disse ction of Fusarium resistance in tomato reveals multiple complex loci. Mol. Genet. Genom. 2001, 265, 1104–1111.

52. Katan, T.; Shlevin, E.; Katan, J. Sporulation of Fusarium oxysporum f. sp. lycopersici on stem surfaces of tomato plants and aerial dissemination of inoculum. Phytopathology 1997, 87, 712–719.

53. Sarfatti, M.; Katan, J.; Fluhr, R.; Zamir, D. An RFLP marker in tomato linked to the Fusarium oxysporum resistance gen e I2. Theor. Appl. Genet. 1989, 78, 755–759.

54. Grattidge, R.; O'Brien, R.G. Occurrence of a third race of Fusarium wilt of tomatoes in Queensland. Plant Dis. 1982, 6 6, 165–166.

55. McGrath, D.J.; Gillespie, D.; Vawdrey, L. Inheritance of resistance to Fusarium oxysporum f. sp. lycopersici races 2 and 3 in Lycopersicon pennellii. Aust. J. Agric. Res. 1987, 38, 729–733.

56. Scott, J.W.; Jones, J.P. Monogenic resistance in tomato to Fusarium oxysporum f. sp. lycopersici race 3. Euphytica 198 9, 40, 49–53.

57. Catanzariti, A.M.; Lim, G.T.; Jones, D.A. The tomato I-3 gene: A novel gene for resistance to Fusarium wilt disease. Ne w Phytol. 2015, 207, 106–118.

58. Chitwood-Brown, J.; Vallad, G.E.; Lee, T.G.; Hutton, S.F. Breeding for resistance to Fusarium wilt of tomato: A review. G enes 2021, 12, 1673.

59. Raza, W.; Ling, N.; Zhang, R.; Huang, Q.; Xu, Y.; Shen, Q. Success evaluation of the biological control of Fusarium wilt s of cucumber, banana, and tomato since 2000 and future research strategies. Crit. Rev. Biotechnol. 2017, 37, 202–21 2.

60. Alabouvette, C.; Lemanceau, P.; Steinberg, C. Recent advances in the biological control of Fusarium wilts. Pestic. Sci. 1993, 37, 365–373.

61. Aimé, S.; Cordier, C.; Alabouvette, C.; Olivain, C. Comparative analysis of PR gene expression in tomato inoculated wit h virulent Fusarium oxysporum f. sp. lycopersici and the biocontrol strain F. oxysporum Fo47. Physiol. Mol. Plant Patho l. 2008, 73, 9–15.

62. de Lamo, F.J.; Spijkers, S.B.; Takken, F.L. Protection to tomato wilt disease conferred by the nonpathogen Fusarium oxysporum Fo47 is more effective than that conferred by avirulent strains. Phytopathology 2021, 111, 253–257.

63. Duijff, B.J.; Pouhair, D.; Olivain, C.; Alabouvette, C.; Lemanceau, P. Implication of systemic induced resistance in the suppression of fusarium wilt of tomato by Pseudomonas fluorescens WCS417r and by nonpathogenic Fusarium oxysporum Fo47. Eur. J. Plant Pathol. 1998, 104, 903–910.

64. Borrego-Benjumea, A.; Basallote-Ureba, M.J.; Abbasi, P.A.; Lazarovits, G.; Melero-Vara, J.M. Effects of incubation temperature on the organic amendment-mediated control of Fusarium wilt of tomato. Ann. Appl. Biol. 2014, 164, 453–463.

65. Zhao, F.; Zhang, Y.; Dong, W.; Zhang, Y.; Zhang, G.; Sun, Z.; Yang, L. Vermicompost can suppress Fusarium oxysporum f. sp. lycopersici via generation of beneficial bacteria in a long-term tomato monoculture soil. Plant Soil 2019, 440, 491–505.

66. Barakat, R.M.; Al-Masri, M.I. Trichoderma harzianum in combination with sheep manure amendment enhances soil suppressiveness of Fusarium wilt of tomato. Phytopathol. Mediterr. 2009, 48, 385–395.

67. Mwangi, M.W.; Muiru, W.M.; Narla, R.D.; Kimenju, J.W.; Kariuki, G.M. Effect of soil sterilisation on biological control of Fusarium oxysporum f. sp. lycopersici and Meloidogyne javanica by antagonistic fungi and organic amendment in tomato crop. Acta Agric. Scand. Sect. B—Soil Plant Sci. 2018, 68, 656–661.

68. Hausbeck, M.K.; Lamour, K.H. Phytophthora capsici on vegetable crops: Research progress and management challenges. Plant Dis. 2004, 88, 1292–1303.

69. Lamour, K.H.; Hausbeck, M.K. Effect of crop rotation on the survival of Phytophthora capsici in Michigan. Plant Dis. 2003, 87, 841–845.

70. Lamour, K.H.; Stam, R.; Jupe, J.; Huitema, E. The oomycete broad-host-range pathogen Phytophthora capsici. Mol. Plant Pathol. 2012, 13, 329–337.

71. Quesada-Ocampo, L.M.; Hausbeck, M.K. Resistance in tomato and wild relatives to crown and root rot caused by Phytophthora capsici. Phytopathology 2010, 100, 619–627.

72. Bower, L.A.; Coffey, M.D. Development of laboratory tolerance to phosphorous acid, fosetyl-Al, and metalaxyl in Phytophthora capsici. Can. J. Plant Pathol. 1985, 7, 1–6.

73. Jackson, K.L.; Yin, J.; Ji, P. Sensitivity of Phytophthora capsici on vegetable crops in Georgia to mandipropamid, dimethomorph, and cyazofamid. Plant Dis. 2012, 96, 1337–1342.

74. Kousik, C.S.; Keinath, A.P. First report of insensitivity to cyazofamid among isolates of Phytophthora capsici from the southeastern United States. Plant Dis. 2008, 92, 979.

75. Siegenthaler, T.B.; Hansen, Z.R. Sensitivity of Phytophthora capsici from Tennessee to mefenoxam, fluopicolide, oxathiapiprolin, dimethomorph, mandipropamid, and cyazofamid. Plant Dis. 2021, 105, 3000–3007.

76. Quesada-Ocampo, L.M.; Vargas, A.M.; Naegele, R.P.; Francis, D.M.; Hausbeck, M.K. Resistance to crown and root rot caused by Phytophthora capsici in a tomato advanced backcross of Solanum habrochaites and Solanum lycopersicum. Plant Dis. 2016, 100, 829–835.

77. Moataza, M.S. Destruction of Rhizoctonia solani and Phytophthora capsici causing tomato root-rot by Pseudomonas fluorescences lytic enzymes. Res. J. Agric. Biol. Sci. 2006, 2, 274–281.

78. Sharma, R.; Chauhan, A.; Shirkot, C.K. Characterization of plant growth promoting Bacillus strains and their potential as crop protectants against Phytophthora capsici in tomato. Biol. Agric. Hortic. 2015, 31, 230–244.

79. Syed-Ab-Rahman, S.F.; Xiao, Y.; Carvalhais, L.C.; Ferguson, B.J.; Schenk, P.M. Suppression of Phytophthora apsica infection and promotion of tomato growth by soil bacteria. Rhizosphere 2019, 9, 72–75.

80. Yang, K.; Dong, X.; Li, J.; Wang, Y.; Cheng, Y.; Zhai, Y.; Dou, D. Type 2 Nep1-like proteins from the biocontrol oomycete Pythium oligandrum suppress Phytophthora capsici infection in solanaceous plants. J. Fungi 2021, 7, 496.

81. Nicol, R.W.; Burlakoti, P. Effect of aerobic compost tea inputs and application methods on protecting tomato from Phytophthora capsici. In Proceedings of the IV International Symposium on Tomato Diseases, Orlando, FL, USA, 24–27 June 2013; Volume 1069, pp. 229–233.

82. González-Hernández, A.I.; Suárez-Fernández, M.B.; Pérez-Sánchez, R.; Gómez-Sánchez M, Á.; Morales-Corts, M.R. Compost tea induces growth and resistance against Rhizoctonia solani and Phytophthora capsici in pepper. Agronomy 2021, 11, 781.

83. Jiang, Z.Q.; Guo, Y.H.; Li, S.M.; Qi, H.Y.; Guo, J.H. Evaluation of biocontrol efficiency of different Bacillus preparations and field application methods against Phytophthora blight of bell pepper. Biol. Control 2006, 36, 216–223.

84. Kim, K.D.; Nemec, S.; Musson, G. Control of Phytophthora root and crown rot of bell pepper with composts and soil amendments in the greenhouse. Appl. Soil Ecol. 1997, 5, 169–179.

85. Male, M.F.; Vawdrey, L.L. Efficacy of fungicides against damping-off in papaya seedlings caused by Pythium Aphanider matum. Australas. Plant Dis. Notes 2010, 5, 103–104.
86. Paulitz, T.C.; Zhou, T.; Rankin, L. Selection of rhizosphere bacteria for biological control of Pythium aphanidermatum on hydroponically grown cucumber. Biol. Control 1992, 2, 226–237.
87. Hassanisaadi, M.; Shahidi Bonjar, G.H.; Hosseinipour, A.; Abdolshahi, R.; Ait Barka, E.; Saadoun, I. Biological control of Pythium aphanidermatum, the causal agent of tomato root rot by two Streptomyces root symbionts. Agronomy 2021, 1 1, 846.
88. Harvey, P.; Lawrence, L. Managing Pythium root disease complexes to improve productivity of crop rotations. Outlooks Pest Manag. 2008, 19, 127.
89. Triki, M.A.; Priou, S.; El Mahjoub, M. Effects of soil solarization on soil-borne populations of Pythium aphanidermatum a nd Fusarium solani and on the potato crop in Tunisia. Potato Res. 2001, 44, 271–279.
90. Reddy, G.S.; Rao, V.K.; Sitaramaiah, K.; Chalam, T.V. Soil Solarization for Control of Soil-borne Pathogen Complex due to Meloidogyne incognita and Pythium aphanidermatum. Indian J. Nematol. 2001, 31, 136–138.
91. Jayaraj, J.; Radhakrishnan, N.V. Enhanced activity of introduced biocontrol agents in solarized soils and its implications on the integrated control of tomato damping-off caused by Pythium spp. Plant Soil 2008, 304, 189–197.
92. Abbasi, P.A.; Lazarovits, G. Seed treatment with phosphonate (AG3) suppresses Pythium damping-off of cucumber se edlings. Plant Dis. 2006, 90, 459–464.
93. Al-Balushi, Z.M.; Agrama, H.; Al-Mahmooli, I.H.; Maharachchikumbura, S.S.; Al-Sadi, A.M. Development of resistance t o hymexazol among Pythium species in cucumber greenhouses in Oman. Plant Dis. 2018, 102, 202–208.
94. Cuevas, V.C.; Sinohin, A.M. Performance of selected Philippine species of Trichoderma as biocontrol agents of dampin g off pathogens and as growth enhancer of vegetables in farmers' field. Philipp. Agric. Sci. 2005, 88, 63–71.
95. Garzón, C.D.; Molineros, J.E.; Yánez, J.M.; Flores, F.J.; del Mar Jiménez-Gasco, M.; Moorman, G.W. Sublethal doses of mefenoxam enhance Pythium damping-off of geranium. Plant Dis. 2011, 95, 1233–1238.
96. Samaras, A.; Roumeliotis, E.; Ntasiou, P.; Karaoglanidis, G. Bacillus subtilis MBI600 promotes growth of tomato plants and induces systemic resistance contributing to the control of soilborne pathogens. Plants 2021, 10, 1113.
97. Rajendraprasad, M.; Vidyasagar, B.; Devi, G.U.; Rao, S.K. Biological control of tomato damping off caused by Pythium debaryanum. Int. J. Chem. Stud. 2017, 5, 447–452.
98. Salman, M.; Abuamsha, R. Potential for integrated biological and chemical control of damping-off disease caused by P ythium ultimum in tomato. BioControl 2012, 57, 711–718.
99. Dukare, A.S.; Prasanna, R.; Dubey, S.C.; Nain, L.; Chaudhary, V.; Singh, R.; Saxena, A.K. Evaluating novel microbe a mended composts as biocontrol agents in tomato. Crop. Prot. 2011, 30, 436–442.
100. Porter, L.D.; Hamm, P.B.; David, N.L.; Gieck, S.L.; Miller, J.S.; Gundersen, B.; Inglis, D.A. Metalaxyl-M-resistant Pythiu m species in potato production areas of the Pacific Northwest of the USA. Am. J. Potato Res. 2009, 86, 315–326.
101. Del Castillo Múnera, J.; Hausbeck, M.K. Characterization of Pythium species associated with greenhouse floriculture cr ops in Michigan. Plant Dis. 2016, 100, 569–576.
102. Aegerter, B.J.; Greathead, A.S.; Pierce, L.E.; Davis, R.M. Mefenoxam-resistant isolates of Pythium irregulare in an orna mental greenhouse in California. Plant Dis. 2002, 86, 692.
103. Lee, S.; Garzón, C.D.; Moorman, G.W. Genetic structure and distribution of Pythium aphanidermatum populations in P ennsylvania greenhouses based on analysis of AFLP and SSR markers. Mycologia 2010, 102, 774–784.
104. Lookabaugh, E.C.; Kerns, J.P.; Shew, B.B. Evaluating Fungicide Selections to Manage Pythium Root Rot on Poinsettia Cultivars with Varying Levels of Partial Resistance. Plant Dis. 2021, 105, 1640–1647.
105. Niderman, T.; Genetet, I.; Bruyere, T.; Gees, R.; Stintzi, A.; Legrand, M.; Mosinger, E. Pathogenesis-related PR-1 protei ns are antifungal (isolation and characterization of three 14-kilodalton proteins of tomato and of a basic PR-1 of tobacc o with inhibitory activity against Phytophthora infestans). Plant Physiol. 1995, 108, 17–27.
106. Tornero, P.; Gadea, J.; Conejero, V.; Vera, P. Two PR-1 genes from tomato are differentially regulated and reveal a nov el mode of expression for a pathogenesis-related gene during the hypersensitive response and development. Mol. Plan t-Microbe Interact. 1997, 10, 624–634.
107. Postma, J.; Clematis, F.; Nijhuis, E.H.; Someus, E. Efficacy of four phosphate-mobilizing bacteria applied with an anima l bone charcoal formulation in controlling Pythium aphanidermatum and Fusarium oxysporum f. sp. radicis lycopersici in tomato. Biol. Control 2013, 67, 284–291.

108. Martinez, C.; Bourassa, A.; Roy, G.; Desbiens, M.C.; Bussières, P. Efficacy of PRO-MIX® with Biofungicide against Root Diseases caused by Pythium spp. and Rhizoctonia spp. In Proceedings of the XXVII International Horticultural Congress-IHC2006: International Symposium on Sustainability through Integrated and Organic, Seoul, Republic of Korea, 13–19 August 2006; Volume 767, pp. 185–192.

109. Caron, J.; Laverdière, L.; Thibodeau, P.O.; Bélanger, R.R. Utilisation d'une souche indigène de Trichoderma harzianum contre cinq agents pathogènes chez le concombre et la tomate de serre au Québec. Phytoprotection 2002, 83, 73–87.

110. Elshahawy, I.E.; El-Mohamedy, R.S. Biological control of Pythium damping-off and root-rot diseases of tomato using Trichoderma isolates employed alone or in combination. J. Plant Pathol. 2019, 101, 597–608.

111. Larsen, J.; Graham, J.H.; Cubero, J.; Ravnskov, S. Biocontrol traits of plant growth suppressive arbuscular mycorrhizal fungi against root rot in tomato caused by Pythium aphanidermatum. Eur. J. Plant Pathol. 2012, 133, 361–369.

112. St Martin, C.C.G.; Dorinvil, W.; Brathwaite, R.A.I.; Ramsubhag, A. Effects and relationships of compost type, aeration and brewing time on compost tea properties, efficacy against Pythium ultimum, phytotoxicity and potential as a nutrient amendment for seedling production. Biol. Agric. Hortic. 2012, 28, 185–205.

113. Jenana RK, B.; Haouala, R.; Triki, M.A.; Godon, J.J.; Hibar, K.; Khedher, M.B.; Henchi, B. Composts, compost extracts and bacterial suppressive action on Pythium aphanidermatum in tomato. Pak. J. Bot. 2009, 41, 315–327.

114. Postma, J.; Nijhuis, E.H. Pseudomonas chlororaphis and organic amendments controlling Pythium infection in tomato. Eur. J. Plant Pathol. 2019, 154, 91–107.

115. Jayaraj, J.; Radhakrishnan, N.V.; Kannan, R.; Sakthivel, K.; Suganya, D.; Venkatesan, S.; Velazhahan, R. Development of new formulations of Bacillus subtilis for management of tomato damping-off caused by Pythium aphanidermatum. Biocontrol Sci. Technol. 2005, 15, 55–65.

116. Butterfield, E.J.; DeVay, J.E.; Garber, R.H. The influence of several crop sequences on the incidence of Verticillium wilt of cotton and on the populations of Verticillium dahliae in field soil. Phytopathology 1978, 68, 1217–1220.

117. Babadoost, M. Important fungal diseases of tomato in the United States of America. In Proceedings of the III International Symposium on Tomato Diseases, Ischia, Italy, 25–30 July 2010; Volume 914, pp. 85–92.

118. Iott, M.C. Utility of Grafting and Evaluation of Rootstocks for the Management of Verticillium Wilt in Tomato Production in Western North Carolina. Master's Thesis, North Carolina State University, Raleigh, NC, USA, 2013.

119. Stapleton, J.J. Soil solarization in various agricultural production systems. Crop. Prot. 2000, 19, 837–841.

120. Goicoechea, N. To what extent are soil amendments useful to control Verticillium wilt. Pest Manag. Sci. Former. Pestic. Sci. 2009, 65, 831–839.

121. Gullino, M.L.; Minuto, A.; Gilardi, G.; Garibaldi, A.; Ajwa, H.; Duafala, T. Efficacy of preplant soil fumigation with chloropicrin for tomato production in Italy. Crop Prot. 2002, 21, 741–749.

122. Rowe, R.C.; Powelson, M.L. Potato early dying: Management challenges in a changing production environment. Plant Dis. 2002, 86, 1184–1193.

123. Ordentlich, A.; Nachmias, A.; Chet, I. Integrated control of Verticillium dahliae in potato by Trichoderma harzianum and captan. Crop. Prot. 1990, 9, 363–366.

124. Baergen, K.D.; Hewitt, J.D.; Clair, D.S. Resistance of tomato genotypes to four isolates of Verticillium dahliae race 2. HortScience 1993, 28, 833–836.

125. Fradin, E.F.; Zhang, Z.; Juarez Ayala, J.C.; Castroverde, C.D.; Nazar, R.N.; Robb, J.; Thomma, B.P. Genetic dissection of Verticillium wilt resistance mediated by tomato Ve1. Plant Physiol. 2009, 150, 320–332.

126. Dhouib, H.; Zouari, I.; Abdallah, D.B.; Belbahri, L.; Taktak, W.; Triki, M.A.; Tounsi, S. Potential of a novel endophytic Bacillus velezensis in tomato growth promotion and protection against Verticillium wilt disease. Biol. Control 2019, 139, 104092.

127. Elshafie, H.S.; Sakr, S.; Bufo, S.A.; Camele, I. An attempt of biocontrol the tomato-wilt disease caused by Verticillium dahliae using Burkholderia gladioli pv. agaricicola and its bioactive secondary metabolites. Int. J. Plant Biol. 2017, 8, 7263.

128. Jabnoun-Khiareddine, H.; Daami-Remadi, M.; Ayed, F.; El Mahjoub, M. Biocontrol of tomato Verticillium wilt by using indigenous Gliocladium spp. and Penicillium sp. isolates. Dyn. Soil Dyn. Plant 2009, 3, 70–79.

129. Larena, I.; Sabuquillo, P.; Melgarejo, P.; De Cal, A. Biocontrol of Fusarium and Verticillium wilt of tomato by Penicillium oxalicum under greenhouse and field conditions. J. Phytopathol. 2003, 151, 507–512.

130. Jabnoun-Khiareddine, H.; Daami-Remadi, M.; Ayed, F.; El Mahjoub, M. Biological control of tomato Verticillium wilt by using indigenous Trichoderma spp. Afr. J. Plant Sci. Biotechnol. 2009, 3, 26–36.

131. Naraghi, L.; Heydari, A.; Rezaee, S.; Razavi, M.; Jahanifar, H.; Khaledi, E. Biological control of tomato Verticillium wilt disease by Talaromyces flavus. J. Plant Prot. Res. 2010, 50, 360–365.
132. Puri, K.D.; Hu, X.; Gurung, S.; Short, D.P.; Sandoya, G.V.; Schild, M.; Subbarao, K.V. Verticillium klebahnii and V. isaacii Isolates Exhibit Host-dependent Biological Control of Verticillium Wilt Caused by V. dahliae. PhytoFrontiers 2021, 1, 276–290.
133. Acharya, B.; Ingram, T.W.; Oh, Y.; Adhikari, T.B.; Dean, R.A.; Louws, F.J. Opportunities and challenges in studies of host-pathogen interactions and management of Verticillium dahliae in tomatoes. Plants 2020, 9, 1622.
134. Giotis, C.; Markelou, E.; Theodoropoulou, A.; Toufexi, E.; Hodson, R.; Shotton, P.; Leifert, C. Effect of soil amendments and biological control agents (BCAs) on soil-borne root diseases caused by Pyrenochaeta lycopersici and Verticillium albo-atrum in organic greenhouse tomato production systems. Eur. J. Plant Pathol. 2009, 123, 387–400.
135. Kadoglidou, K.; Chatzopoulou, P.; Maloupa, E.; Kalaitzidis, A.; Ghoghoberidze, S.; Katsantonis, D. Mentha and oregano soil amendment induces enhancement of tomato tolerance against soilborne diseases, yield and quality. Agronomy 2020, 10, 406.
136. Ait Rahou, Y.; Ait-El-Mokhtar, M.; Anli, M.; Boutasknit, A.; Ben-Laouane, R.; Douira, A.; Meddich, A. Use of mycorrhizal fungi and compost for improving the growth and yield of tomato and its resistance to Verticillium dahliae. Arch. Phytopathol. Plant Prot. 2021, 54, 665–690.
137. Lazarovits, G.; Conn, K.; Tenuta, M. Control of Verticillium dahliae with soil amendments: Efficacy and mode of action. In Advances in Verticillium Research and Disease Management, 1st ed.; Tjamos, E.C., Rowe, R.C., Heale, J.B., Fravel, D.R., Eds.; APS Press: St Paul, MN, USA, 2000; pp. 274–291.