Management of the soil-borne fungal pathogen – *Verticillium dahliae* Kleb. causing vascular wilt diseases

Beata Kowalska¹

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Abstract

Vascular wilt diseases caused by *Verticillium dahliae* Kleb. are difficult to control and lead to increasing losses of many crops worldwide. It can cause disease on not only horticultural crops but also many economically important crops such as vegetables, legumes, forest trees, woody and herbaceous plants. Reasons of this situation are various: (i) the specialization of crop production resulted in the accumulation of the pathogen in the soil, especially monoculture production; (ii) the lack of an efficient and safe soil fumigation method; (iii) the production in large amounts of survival structures—microsclerotia and melanized hyphae that are resistant to chemical and biological degradation.

Due to the lack of effective synthetic agents for eradication of *V. dahliae* from soil, considerable interest in this paper has been focused on biological control, especially the selection of microorganisms with mycoparasitic activity towards *V. dahliae* microsclerotia, that can decrease their number in soil. The main attention is paid on the *Trichoderma* fungi, non pathogenic *Fusarium* spp., *Talaromyces flavus* and bacteria *Bacillus* spp., *Pseudomonas* spp. and *Streptomyces* spp. that are discussed in this review. In this work the suppressive effect of organic amendments against this soil-borne pathogen is also mentioned. In addition biofumigation using toxic plant materials, which is an approach to the soil-borne pathogen management could be an effective method to control diseases caused by *V. dahliae*.

Keywords Antagonistic microorganisms · Biofumigation · Microsclerotia · Organic amendments · Verticilliosis

Introduction

The fungus *Verticillium dahliae* Kleb. is an economically important soil pathogen responsible for high yield losses of many crop species such as peppers, potatoes, strawberries, aubergines, lettuce, cauliflowers, cotton, sunflower and olive trees (Vallad et al. 2004; Jabnoun-Khiareddine et al. 2006; Meszka 2013; Bélair et al. 2018; Lio et al. 2019; Tükkán et al. 2020; Wang et al. 2021). Plant diseases caused by this pathogen are very common, which is associated with the wide range of host plants and the widespread occurrence of this pathogen in the soil environment. The microsclerotia of *Verticillium*, developing in the tissues of dead plants, can survive in the soil for several months or, under certain conditions, even several years. The fungus is also able to colonize non-host plants and form new microsclerotia, which are a

source of infection for host plants (Agrios 2005; Goicoechea 2006; Fradin and Thomma 2006; Klosterman et al. 2009).

V. dahliae can infect plants at any stage of the development. The fungus infects organs and tissues involved in the collection and transportation of water and nutrients. The pathogen survives the period without the host plant in the form of microsclerotia of 40–80 µm. The survival of microsclerotia in laboratory conditions during the year, at a temperature of about 25 °C, may be almost 100%. Vegetative mycelium and conidial spores are relatively unstable. The survival of the pathogen population in soil depends on many factors, including soil type, humidity, pH and temperature (Agrios 2005; Fradin and Thomma 2006). Most of the microsclerotia survive in the surface layer of the soil. Meszka (2013) found that 94–100% of *V. dahliae* microsclerotia in strawberry field were detected in the upper soil layer of 0–10 cm, and only single or no propagules were present at depth of 20 cm.

There are no sufficiently effective measures of protection against Verticillium wilt. The control of this disease is an urgent task. The most effective way to avoid the disease

✉ Beata Kowalska
beata.kowalska@inhort.pl

¹ The National Institute of Horticultural Research, Konstytucji
3 Maja 1/3, 96-100 Skierniewice, Poland

is to eliminate the pathogen from the soil, in particular its persistent forms—microsclerotia. To control the disease outbreaks, fungicides and fumigants should be applied at regular intervals throughout the growing season of the crop. However, it should be noted that there are evident issues with the use of synthetic fungicides, which include ecological disturbance, human health hazards and damage to aquatic ecosystems. Sterilants also lower populations of beneficial, non-target soil microorganisms. This decline in soil microbial diversity often leads to increased populations of pathogens due to reduced competition and antagonism. In many parts of the world, methyl bromide was extensively used to control soil borne pathogens, also *V. dahliae* before the implementation of the Montreal Protocol in 1986 to protect the ozone layer. Nowadays, environmentally friendly alternatives to broad-spectrum fungicides and fumigants are being developed and put into use (Panth et al. 2020).

Infection of plants

The secretions released from the roots of growing plants stimulate the germination of microsclerotia located in the soil or on fragments of dead plants. Infection is initiated at the top of the root or at the point of injury. The threshold number of microsclerotia that can cause verticilliosis depends, among other things, on the aggressiveness of the fungus isolate, the plant species and cultivar, the type of soil and the conditions in the soil, and ranges from several to several dozen of fungal propagules per gram of the soil (Short et al. 2015). For example, for the ornamental perennial plant *Aralia cordata* it was found that the degree of disease intensity on seedlings was directly proportional to the microsclerotia density in the soil. The first symptoms of the disease appeared on seedlings at 0.1 microsclerotia per gram of dry soil. At the density of 10 microsclerotia/g of dry soil, the infestation reached 40%, for 100 microsclerotia/g—about 50% and for 1000 microsclerotia/g—over 80% (Shiraishi et al. 2014).

After infection, the fungus penetrates the roots through the cortex crumb towards the conductive vessels. Then it spreads inside the plant producing shreds and spores, which are transported up the plant by means of transpiration. The mycelium that develops in the vessels, and formed gums hinder the water and mineral salts transportation. Conductive vessels are plugged and water transport is inhibited. The timing of the first appearance of the disease symptoms in the form of slight leaf withering, depends on the plant species and cultivar. At a later stage of the disease, changes in the conductive bundles appear. On the cross-section of the root and stem, they take on a light to dark brown colour, which can easily be observed when a section of the plant is cut lengthwise. Initially, these symptoms appear in the ground

part, then they are also visible in the upper part of the plant (Agrios 2005; Goicoechea 2006; Fradin and Thomma 2006).

The development of *Verticillium* wilt depends mainly to the ambient temperature. At temperatures below 20 °C, the fungus develops very quickly in the plant. If it is also cold during the day and the transpiration is not too intense, the disease can become apparent at the first higher temperatures. Periodic drying of the soil or the substrate encourages the development of the disease. *Verticillium* wilt can occur in all types of soil. However, it has been found that in areas with lower temperatures, the disease develops more rapidly in light soils, while in warmer areas—in heavy soils (Fradin and Thomma 2006; Goicoechea 2006).

V. dahliae can also occur in the complex with other pathogens and nematodes. One of examples of the complexed disease is co-occurrence of *V. dahliae* and *Colletotrichum coccodes* in pepper plants (Ślusarski and Spotti 2016; Tyvaert et al. 2019). A damaged root system, caused by *C. coccodes*, can become more problematic when the pepper plants are bearing fruits, in combination with vascular pathogens *V. dahliae*. Synergistic and additive responses between *V. dahliae* and several species of plant-parasitic nematodes have been also reported by many researchers (Lamberti et al. 2001; Daami-Remadi et al. 2009; Bélair et al. 2018). The majority of these interactions occur with the root-lesion nematodes, *Pratylenchus* spp., and potato cyst nematodes, *Globodera rostochiensis* and *G. pallida*, *Meloidogyne* spp.

Chemical and physical eradication of *V. dahliae* from soil

Chemical, pre-vegetational soil disinfection is the most effective method of combating the pathogen by destroying the microsclerotia and vegetative forms of *V. dahliae*. The following chemicals are permitted in some European countries, including Poland: propamocarb in the form of a complex with 530 g hydrogen chloride, III aluminium phosphate—310 g, dazomet 95% and sodium metam 51%. The application of disinfectants via drip irrigation, also known as chemigation, is an approach that could be a feasible practice against *verticillium* wilt (Gomez-Galvez et al. 2019, 2020). Experimental studies showed high effectiveness of chloropicrin applied by drip irrigation to protect peppers against *Verticillium* wilt. The highest efficacy of this compound was obtained when 40 g m⁻² was applied. Delayed occurrence of the first symptoms of the disease by 3–6 weeks was also observed. However, chloropicrin is not approved for the use in agriculture (Short et al. 2015; Ślusarski and Spotti 2016).

The interest in hydrogen peroxide as an environmental disinfectant has increased due to the ease of treatment, the broad spectrum of activity and the lack of toxic by-products. A significant reduction of *V. dahliae* conidia and

microsclerotia in soil was reported in olive plants cultivation. Injection of peroxygen-based products into the irrigation system has shown to be an effective water disinfection technique to prevent the pathogen introduction, reduce its accumulation in soil, and decrease the systemic infection to levels that do not cause expression of *Verticillium* wilt symptoms on young olive plants (Gomez-Galvez et al. 2019, 2020).

Thermal and biological methods of *Verticillium* wilt control

Soil solarisation was first applied in Israel in 1976. It is an environment-friendly, pre-planting method of using solar energy to control pathogens in the soil. Its effectiveness depends on the possibility of obtaining a sufficiently high temperature to eliminate the pathogens (Alabouvette et al. 2006). It has been experimentally proven to be effective in destroying *V. dahliae* microsclerotia located 10 and 20 cm deep in the soil at 48°C. In southern countries, such as Spain or Italy, where average temperatures are much higher than in countries in the central Europe, soil solarization is a frequently used procedure. Therefore, in many countries, thermal soil disinfection is a relatively rare procedure due to technical difficulties and high costs. Thermal soil decontamination with steam is also possible. It was found that the treatment of soil with steam of 50 °C for 30 min can significantly reduce *V. dahliae* in soil.

In the face of environmental pollution by chemical plant protection products, numerous scientific research is being undertaken all over the world, leading to the development of an effective biological method of combating this pathogen. The following mechanisms may be responsible for the pathogen elimination process—production of volatile toxic compounds with antifungal effect; increase in the population of antagonistic microorganisms; degradation of microsclerotia by enzymes produced by soil microorganisms (Panth et al. 2020). Therefore, plant materials such as biofumigants and antagonistic microorganisms may be used to reduce the pathogen population.

Soil biofumigation with plant materials

Biofumigation can be used as an alternative to conventional soil fumigation to control soil-borne pathogens. Many plants contain substances which can be effectively used as biofumigants. Among the plants showing biofumigation activity, species belonging to Brassicaceae are a large group. In these plants glucosinolates—biologically active compounds—are found as secondary metabolites. They consist of glucose, sulfonic oxime and side chain with

aliphatic, aromatic or indole structure. Destruction of plant tissue, e.g. during decomposition in soil, causes hydrolysis of glucosinolates with the use of myrosinase enzyme and a number of biologically active compounds are formed, e.g. isothiocyanates, nitriles, thiocyanates, epitriles (Cartea et al. 2011; Szczygłowska et al. 2011; Neubauer et al. 2015). About 100 different types of glucosinolates are known. The profile and concentration of these compounds vary depending on the plant species, but also on the organ in which they occur (Laegdsmand et al. 2007; Cartea et al. 2011; Sikorska-Zimny and Beneduce 2020).

In biofumigation very effective is brassicaceous seed meal (BSM). BSM is the material remaining after extracting the oil from mustard, canola, or rapeseed seeds. BSM has been shown to alter the soil biology which then aids in the suppression of plant diseases (Mazzola et al. 2015). In Germany, the biofumigation potential of the meal obtained from the seeds of four different plant species Brassicaceae—*Brassica napus*, *Sinapis alba*, *B. juncea* and *B. carinata* was studied. The meal obtained from the seeds of these species was applied as a 0.4% addition to the soil artificially contaminated with *V. dahliae* microsclerotia. The highest effectiveness in elimination of microsclerotia was demonstrated by material from *B. juncea* and *B. carinata*. A correlation between the efficacy and content of 2-propenyl isothiocyanate was observed. Seeds of *B. juncea* and *B. carinata* contained 82.8–108.1 $\mu\text{mol g}^{-1}$ of this compound and their efficacy ranged from 62.5–100%. Under natural conditions, the effectiveness of *B. juncea* was lower than under laboratory conditions and depended largely on the soil type, organic carbon content and the degree of soil contamination. It was possible to eliminate microsclerotia from the naturally infected soil using milled seeds of *B. juncea* at a dose of 4.0 t/ha (Neubauer et al. 2015).

In the research carried out by Smolińska et al. (2010) a positive effect was obtained by adding rapeseed cake and mustard seed meal to the contaminated *V. dahliae* soil in which pepper was grown. The addition of this material in the amount of 0.5% (w/v) positively influenced the development of plants and increased the yield of pepper compared to the infected control. Moreover, it reduced the number of fungal colony-forming units isolated from soil.

Smolińska and Kowalska (2008) studied the effectiveness of plant material from Brassicaceae and Solanaceae plants and antagonistic microorganisms, on survival of microsclerotia and development of *Verticillium* wilt of eggplant. The authors observed that the addition of rapeseed meal, or water extracts from rapeseed meal, significantly reduced the number of *V. dahliae* microsclerotia in the soil. The population of *V. dahliae* could be decreased through toxic activity of compounds released during decomposition of plant material, as well as by simple compounds such ammonium or by degradation products

of glucosinolates such isothiocyanates, nitriles or thiocyanates. After addition of the plant material microorganisms, mainly *Pseudomonas*, *Bacillus* and yeast, developed intensively. They could act either directly on microsclerotia and mycelium or on plants, stimulating their growth (Smolińska and Kowalska 2008). Lazarovits et al. (2000) also observed that the application of high N-containing organic amendments to soil reduced the occurrence of Verticillium wilt of tomato.

The efficacy of soil fumigation using broccoli crop residues for the control of *V. dahliae* and *Rhizoctonia solani* was evaluated by Guerrero et al. (2019). Biosolarization treatments reduced levels of both fungal pathogens and resulted in significant lower percentages of affected plants. Moreover, the treatments improved marketable yield. Similarly, the study conducted by Ikeda et al. (2015) showed that crop rotation with broccoli decreased Verticillium wilt of eggplants. The effects of broccoli in reducing microsclerotia and suppressing disease could be influenced by following mechanisms: production of volatile antifungal substances such as allyl-isothiocyanate by broccoli residue; increase in antagonistic microorganisms; degradation of microsclerotia melanin by enzymes produced by soil microorganisms in the presence of broccoli lignin (Ikeda et al. 2015). Rotation with broccoli can therefore be a novel means of controlling Verticillium wilt and might serve as a commercial alternative to soil fumigation.

The herbs have been known for centuries as plants with antimicrobial effects. In field condition negative effect of lavender (*Lavandula angustifolia*) and lavandin (*Lavandula x intermedia*) on the fungus *V. dahliae* was shown. The addition of plant materials (stems, leaves, flowers) to the soil caused a decrease in microsclerotia survival and reduced withering of strawberry plants (Yohalem and Passey 2011). The monoterpenoids associated with the *Lavandula* spp. are of lower volatility than the isothiocyanates associated with Brassicaceae decomposition and were detected one week after material incorporation into soil. This suggests both differences in mode of action and the possibility of combining either the chemicals or the materials that produce them in order to further enhance efficacy.

The eradication effect of organic amendments from herbs: *Diplotaxis virgata*, *Lavandula stoechas* and *Thymus mastichina* on *V. dahliae* microsclerotia was confirmed by study of López-Escudero et al. (2007). The organic debris reduced also the disease incidence and severity of cotton plants.

Biosolarization with different organic amendments can be recommended as an effective management strategy for the control of Verticillium wilt especially in repeated monocultures which are cultivated intensively.

The use of antagonistic microorganisms

Application of beneficial microorganisms for the management of plant diseases have gained the attention of scientists and farmers in recent years (Alabouvette et al. 2006; Copping and Duke 2007; Angelopoulou et al. 2014; Ghorbanpour et al. 2018; Millan et al. 2021). The inhibitory effects of several bacterial and fungal antagonistic isolates in controlling and reducing Verticillium wilt have been documented in many studies (Berg et al. 2006; Gizi et al. 2011; Jorjani et al. 2011; Eljounaidi et al. 2016; Antoniou et al. 2017; Deketelaere et al. 2017; Abada et al. 2018; López-Moral et al. 2021). The search for biological methods for the destruction of propagation forms of *V. dahliae*, mainly microsclerotia, is aimed at inhibiting the development of these forms, reducing their survival rate, preventing them from germinating, protecting the roots from infection by sprouting microsclerotia. Requirements for the development of a successful biological control agents (BCA) are an understanding of the modes of action of the antagonist, its ecological fitness and an efficient and economically feasible delivery system.

Bacteria

The use of bacterial strains to control soil borne diseases has been extensively studied, and several examples of successful disease control have been reported. The antagonistic mechanisms of action of these bacterial strains include production of antibiotics, siderophore production, enzyme secretion, hormone production, and inducing systemic resistance in host plants (Alabouvette et al. 2006; Fira et al. 2018; Le et al. 2018). Due to these modes of action, they have been recognized as strong potential candidates for biological control of plant pathogens, particularly soil-borne ones, among them *V. dahliae*. Most of the biological control bacteria belong to *Pseudomonas* and *Bacillus* genera, capable to colonize the root system. Bacteria of the *Bacillus* group produce a wide array of antagonistic compounds of different structures, e.g. enzymes such as proteases, amylases, glucanases, cellulases, and chitinases which take part in fungal cell wall degradation. They possess a broad spectrum of antagonistic activity against plant pathogens (Bharathi et al. 2004; Fira et al. 2018; Zhao et al. 2021).

Pseudomonas bacteria are capable of limiting the growth of many phytopathogens through direct antagonistic mechanisms, e.g. by releasing antibiotics such as pyolutecherine and pyrrolnitrin into the soil environment. *Pseudomonas* are able to produce siderophores chelating compounds (e.g. pyoverdine, pyochelone and its precursor

salicylic acid) in iron-poor conditions. As a consequence, they cause a deficiency of this element for pathogens. They also produce numerous exoenzymes that break down cell walls of other microorganisms (Jorjani et al. 2011; Angelopoulou et al. 2014).

The possibility of managing cotton *Verticillium* wilt disease efficiently by seed treatment with antagonistic bacteria was presented by Mansoori et al. (2013). According to the results, most of the bacterial isolates, especially *Pseudomonas fluorescens* showed effectiveness in controlling and reducing *Verticillium* wilt disease. Also *Pseudomonas* spp. strains isolated from healthy nursery-produced olive plants had antagonistic activity against *V. dahliae* in olive cultivation (Gómez-Lama Cabanás et al. 2018).

Two biological control agents—*Paenibacillus alvei* or the nonpathogenic *Fusarium oxysporum* and two inoculation strategies (seed coating or amendment of the transplant soil plug) were assessed against *Verticillium* wilt of eggplant. Mixing the transplant soil plug with the two microbial agents reduced *Verticillium* wilt symptom development. Furthermore, a positive correlation was revealed between the release strategy and the BCA rhizosphere population. Correlation analysis also showed that disease severity was negatively correlated to the rhizosphere size of the BCA population (Mansoori et al. 2013; Angelopoulou et al. 2014).

The in vitro and in vivo researches conducted by Elshafie et al. (2017) indicate that the application of *Burkholderia gladioli* pv. *agaricola* strain ICMP 12,322 can enhance disease protection and improve the consistency of biological control against tomato wilt disease caused by *V. dahliae*. The activity was correlated with its ability to produce extracellular hydrolytic enzymes.

Streptomyces spp. are gram-positive bacteria that are ubiquitous in soil. Their prolific antibiotic production has made them the subject of numerous studies on the biocontrol of plant pathogenic bacteria, fungi and nematodes. *Streptomyces* spp. reduced disease in potatoes caused by *V. dahliae* (Wiggins and Kinkel 2004). The antifungal activity was connected with production of antifungal substances such as amphotericin and nystatin. Moreover, *Streptomyces* spp. produce chitinases which penetrate hyphae (mycelium) of pathogenic fungi (Kisiel and Jęckowska 2019). Additionally, another biocontrol mechanism of antagonistic *Streptomyces* spp. against *Verticillium* wilt may be involved. The microorganisms induce systemic disease resistance, enhance defense-related responses and reduce the pathogenic effect of *V. dahliae* (Xue et al. 2016).

Fungi

Talaromyces flavus (Klöcker) Stolk & Samson has been described as an antagonist against *V. dahliae* and as a potential biological control agent. Its antagonistic

abilities against *V. dahliae* were evaluated in several experiments (Naraghi et al. 2010a, b, 2012). As an example an alginate formulation of *T. flavus* reduced the population of *V. dahliae* in soil by above 90%. The antagonist also reduced colonisation by *V. dahliae* of roots and infection of eggplants. In other field experiments with potato cultivation *T. flavus* was tested for efficacy to control wilt diseases. After application of a *T. flavus* preparation, stems were less densely colonised by *V. dahliae* and moreover higher yields of potato tubers were observed (Nagtzaam 1998). Moreover, *T. flavus* was applied with other antagonists *Bacillus subtilis*, *Fusarium oxysporum* or *Gliocadium roseum*. In the experiments root colonisation and stem infection by *V. dahliae* were similar as application of the single microorganism. The results suggest that *T. flavus* is compatible with these antagonists. A cheap mass production of the fungus and an appropriate formulation were developed. A solid state cultivation process has been developed for the mass production of these ascospores (Kersten 2000).

Among biological control agents there are microscopic fungi of the *Trichoderma* species, to which a lot of attention has been paid for several decades (Hermosa et al. 2012; Nawrocka and Małolepsza 2013; Błaszczuk et al. 2014; Waghunde et al. 2016; Oskiera et al. 2017; Szczech et al. 2017; Nawrocka et al. 2018). *Trichoderma* species form diverse, filamentous fungi group, common in the ecosphere. These fungi are characterized by rapid growth and intensive production of spores. Some are able to effectively colonize roots and shoots and efficiently communicate with plants by chemical signals. *Trichoderma* strains are known mainly to suppress diseases caused by pathogens or alleviate abiotic stress. *Trichoderma* may exhibit mycoparasitic properties or be a pathogen antagonist (Hermosa et al. 2012; Błaszczuk et al. 2014; Waghunde et al. 2016). In the literature there are numerous reports presenting antagonistic activity of *Trichoderma* strains towards *V. dahliae* pathogen (Ślusarski and Pietr 2009; Meszka and Bielenin 2009; Fotoohiyan et al. 2017; Carrero-Carron et al. 2018). According to the study conducted by Fotoohiyan (2017), twenty out of 72 isolates of *T. harzianum* showed in vitro antagonistic activity towards *V. dahliae*. All 20 isolates were capable of inhibiting the mycelial growth through production of volatile or non-volatile metabolites. Results of the greenhouse experiments were positive and indicated that the occurrence of wilt disease in pistachio plants treated with the antagonists alone or in combination with pathogenic fungus was lower than in plants inoculated with the pathogen only. *Trichoderma* GFP22 isolate was effective in biocontrol of *Verticillium* wilt of olive plants (Carrero-Carron et al. 2018). Treatment with the fungus reduced the extent of pathogen growth and root colonization by the strain reduced the percentage of pathogen colonies recovered from stems of olive plants.

The other fungi used for *V. dahliae* control are non-pathogenic *Fusarium* strains. Gizi et al. (2011) evaluated the biocontrol efficacy of non-pathogenic *Fusarium oxysporum* eggplant stem injection application method against *V. dahliae*. It was revealed that stem injection seven days before transplanting the seedlings to the soil infested by *V. dahliae* microsclerotia resulted in reduced Verticillium wilt severity of eggplants. Moreover, the qPCR analysis showed that the application of *F. oxysporum* reduced significantly the amount of *V. dahliae* DNA in the stem tissues compared to the control treatment (Gizi et al. 2011).

In study conducted by Mulero-Aparicio et al. (2020), the non-pathogenic strain of *Fusarium oxysporum* was the most effective treatment, achieving a total reduction of the inoculum density of *V. dahliae* in the naturally infested soil two months after planting. Application of *F. oxysporum* and the grape marc compost reduced significantly the Verticillium wilt incidence in 1-year and/or 30 year-old olive plants in comparison with the untreated control plants.

The other fungal group which can control *V. dahliae* are arbuscular mycorrhizal fungi (AMF). Arbuscular mycorrhizal symbioses play a key role in nutrient cycling in the ecosystem and also protect plants against environmental biotic and abiotic (e.g. drought, cold, heavy metal toxicity) stress. It is well known that AMF affect the water balance of both over-watered and drought-stressed plants. Several mechanisms can be involved in bioprotection by arbuscular mycorrhizal fungi against soil-borne pathogens. AMF are able to increase the uptake of water and mineral nutrients for their host plant, such as phosphate and nitrogen but also microelements such as zinc. Moreover, they enhance plant tolerance, induce systemic resistance (ISR) and alter rhizosphere interactions (Pringle et al. 2009; Baum et al. 2015).

AMF were found to reduce the detrimental effects of *V. dahliae* on growth and yield of pepper (Idoia et al. 2004) and strawberry (Sowik et al. 2016). Bioprotection against Verticillium wilt was determined by plant at the time of pathogen attack. The highest efficacy of AMF occurred when *V. dahliae* was inoculated during the vegetative stage of plants. AMF allowed leaf relative water content to be maintained for longer and delayed both the appearance of disease symptoms and the decrease of photosynthesis in *Verticillium*-inoculated plants. These benefits on plant physiology increased pepper yield (Idoia et al. 2004). Inhibition of disease development in strawberry plants was accompanied by increased stomatal conductance, transpiration rate and as result, leaf water potential (Sowik et al. 2016).

Agrotechnical methods

Addition of organic amendments

Applying organic fertilization has a very beneficial effect on the content of soil organic matter, which improves soil properties and provides a buffer against the adverse effects of many stress factors, including stress caused by pathogens. Increased soil organic matter content results in increased microbial activity, as well as increased soil suppressiveness. Active management of soil microbial communities could be an effective method to develop natural suppression of soilborne plant pathogens, including *V. dahliae*.

At the present time, European regulations require the recycling of wastes. The use of biodegradable waste for fertilizer purposes is an important part of the currently recommended circular economy system, in which plant materials left over from production should be reused. For organic wastes, composting is an important process since it transforms organic waste which can then be used in agriculture. Composts contain nutrients, especially microelements, which improve soil fertility, and most of them possess some capacity to increase soil suppressiveness to diseases of crops (Noble and Coventry 2005; Alabouvette et al. 2006). The disease suppressive effects of composts are lost after sterilization or pasteurization indicating the microbial population of the compost as the main factor responsible for suppressiveness (Bonanomi et al. 2010, 2017; De Corato et al. 2016, 2018; Antoniou et al. 2017; Singh et al. 2019). Compost suppressiveness has been attributed to biotic and/or abiotic factors. As an example the studies conducted by Avilés and Borrero (2017) show that olive mill composts demonstrated to be suppressive to Verticillium wilt. High oligotrophic actinomycete populations were associated with the disease reduction. Similar observations were conducted by Varo-Suárez et al. (2018) who showed significant reduction in the severity of the symptoms of *V. dahliae* in olive cultivation after using grape marc compost and solid olive-waste combined with other organic amendments. Kanaan et al. (2018) observed that tomato waste compost suppressed *V. dahliae* in eggplant cultivation. Reduced levels of symptoms and lower fungal colonization were detected in xylem of eggplants planted in tomato waste compost (Kanaan et al. 2018).

In the course of studies aimed at limiting the use of chemicals, it was found that soil enrichment with organic material containing large amounts of organic nitrogen ($N > 8\%$), e.g. bone meal, fish meal, reduces the development of verticilliosis. This phenomenon may be caused by HNO_2 , ammonia or volatile fatty acids released during

decomposition. These compounds, acting toxic to the pathogen, reduce its number. As a result of the decomposition of organic substances, changes in the populations of soil microorganisms may also be beneficial from the point of view of plant development (Noble and Coventry 2005; Alabouvette et al. 2006).

It has been shown that liquid pig manure can limit under certain conditions the occurrence of potato disease caused by *V. dahliae*. Volatile fatty acids are responsible for this effect. The effectiveness of this fertilizer was higher in acidic soil, which had high buffer properties, such that the addition of the fertilizer did not rapidly increase its pH. Fatty acids were more easily released from the fertilizer when applied to dry and heated soil (Conn et al. 2004). Cole et al. (2020) demonstrated that poultry manure could be a promising amendment to control potato early die complex which induces premature vine senescence and dramatically reduces yield in potatoes. The disease is caused by complex of *V. dahliae* and nematode *Pratylenchus penetrans*. In the field, plots treated with poultry manure at two different rates (high—11.2 t/ha or low—2.8 t/ha) had significantly higher potato yields and also significantly fewer nematodes and *V. dahliae* microsclerotia than control plots.

Cropping system

Mixed cropping, intercropping and crop rotation are important practices that are widely emphasized around the world to avoid the inoculum buildup of soilborne pathogens. When the same crop is grown in a field year after year, development and persistence of soilborne pathogens is almost certain (Alabouvette et al. 2006). This problem is particularly serious in the cultivation of peppers, eggplant or olives, which are grown for many years on the same sites. A high concentration of soil pathogens such as *V. dahliae* is common (Ślusarski and Pietr 2009). Pepper or eggplant should be rotated with legume, cole crops, or lettuce but not within the Solanaceae family (chili, potato etc.) to reduce Verticillium wilt. Some of the leguminous crops like clover, vetch, pea should be used in crop rotation, what can add the biomass in the field, thus increasing beneficial microbial population, and also adding nitrogen to the soil (Panth et al. 2020).

Effects of crop rotation between rice paddyfields and strawberry nurseries on the control of Verticillium wilt of strawberry were studied by Ebihara et al. (2010). Verticillium wilt of strawberry was controlled completely with one paddy rice cultivation in infested fields. The number of microsclerotia of *V. dahliae* decreased under the flooding conditions for paddy rice cultivation.

Promising results were obtained using broccoli as a trapping plant for *V. dahliae* (Shetty et al. 2000; Zhao et al. 2021). It was found that rotation with the use of broccoli reduced the risk of verticilliosis in the eggplants. The

pathogen infected broccoli plants with a high frequency (37–94% depending on the sample tested), but at the same time did not cause disease symptoms—the degree of plant infection was low, below 1 on the 0–4 scale. Disease changes in the form of brown conductive bundles were visible only in the roots, while stalks remained uninfected. Microsclerotia were not formed. When growing eggplants as a follow-up plant in this field, a significantly lower frequency of verticilliosis was observed, 53% lower than in the control sample, grown without rotation with broccoli. Similar observations were made in the United States, where cultivation of broccoli, cauliflower or lettuce before pepper reduced the occurrence of verticilliosis on this plant (Shetty et al. 2000). However, it should be mentioned that this method can not be suggested for areas that both *V. dahliae* and *V. longisporum* are present since these hosts (broccoli, cauliflower, etc.) are very suitable for *V. longisporum*, another pathogenic species of *Verticillium* (Depotter et al. 2016).

Appropriate crop rotation may be one of the methods to reduce the number of the pathogen in the soil. It should be noted that this method reduces the population of *V. dahliae* in the soil only to a small extent and may be of practical importance in soils where the pathogen count is low.

Conclusion

Currently, there is no fully effective, single applied method for control Verticillium wilt, so the best strategy relies on the integrated implementation of different measures, taking into account the specific circumstances of each field, area or region. The application of biological methods to control soilborne fungus *V. dahliae* should be implemented in plant protection. In the absence or declining of chemical plant protection products, biological agents are the perspective and safer for the environment than the use of synthetic fungicides. However, the efficiency is much lower. Therefore, complex, multiple methods of protection against this pathogen should be applied at once.

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Declarations

Ethical approval This article does not contain any studies with human participants or animals performed by the author.

Conflict of interest The authors declare no conflict of interest.

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