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REVIEW

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Mitigation of replant disease by mycorrhization in horticultural plants: A review

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ABSTRACT

Replant disease refers to the result of monoculture-continuous repetitive planting of congeneric crops or coordinal crops in the same soil for many years. Such disease is recognized as one of the main limiting factors affecting plant growth and production of horticultural plants in many countries. As a result, replant disease in horticultural plants has become a world problem in agriculture and also a bottleneck restricting the sustainable development of agriculture. In general, replant disease results in unfavorable growth of horticultural plants, which is due to allelopathy, autotoxicity, and the imbalance of both soil physical-biochemical traits and soil microflora. An environmentally friendly contribution to this could be bio-controlled by beneficial microorganisms. Arbuscular mycorrhizal fungi, one of soil-inhabiting fungi, can form a symbiotic association in roots to mitigate the negative effects of replant disease in many horticultural plants. Moreover, arbuscular mycorrhizal fungi do not produce any environmental pollution in soils and are a potential biological control. The soil fungi could regulate better morphological, physiological and molecular levels in plants to respond to the disease. This review mainly outlined the current knowledge in mycorrhizal mitigation of replant disease in horticultural plants, which appears to be a promising strategy to improve growth of horticultural plants in replant soils.

Keywords: arbuscular mycorrhizal fungi, glomalin, replant disease, root exudates, soil microflora

INTRODUCTION

Replant disease is a complex and compound disease that often occurs in horticultural crops. In general, replant disease refers to the monoculture-continuous repetitive planting of congeneric crops or coordinal crops in the same soil for many years (Utkhede, 2006; Bent et al., 2009), directly resulting in restraining plant development, decreasing resistance to diseases, decreasing yields of fruit, and ultimately worsening the soil environment (Rutto and Mizutani, 2006). Replant disease decreases plant growth as a result of heavily reduced photosynthesis by means of hindering chlorophyll synthesis, which results in leaf chlorina (yellowing) (Tewoldemedhin et al., 2011). Additionally, the degree of replant disease depends on the activity and extension of roots. Under monoculture conditions, plant root activity is decreased and thus absorption of nutrients is reduced. This is followed by the morphological symptoms such as less lateral roots, the entire root system becoming dark brown with the apex becoming black and root decay (Wang et al., 2007). The increase in pathogenic nematodes, soil-borne fungi (e.g.,

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Fusarium and *Venturia*), bacteria, actinobacteria and oomycetes variously triggers soil replant disease (Benizri et al., 2005; Rumberger et al., 2007). Hence, replant disease in horticultural plants has become a world problem in agriculture, which strongly affects crop production (Yang et al., 2012).

Arbuscular mycorrhizal fungi (AMF) can form a symbiotic association with most terrestrial plants (Wu et al., 2013). Almost 3-20% of plant carbohydrates can be absorbed by AMF for the growth and development of mycorrhizas. In return, AMF provide inorganic substances for the host plant (Ortas, 2012). Compared with non-AMF plants, mycorrhizal plants absorb more mineral nutrients by the mycorrhizal hyphal network into the roots (Baslam et al., 2011). Earlier studies showed that AMF play a key role in improving resistance to biotic and abiotic stresses, including replant disease. AMF effects on replant disease were found in peach, cucumber, grape, apple, tomato, pepper, strawberry and watermelon (Huang et al., 2003, Tab. 1). For example, Rutto and Mizutani (2005) revealed that the growth performance of peach (*Prunus persica* L. 'Ohatsumomo Batsch') under mycorrhization was better than under non-mycorrhization, providing a view in mitigation of replant disease. Wang et al. (2012) also observed that out of *Glomus mosseae*, *G. intraradices* and *G. versiforme*, cucumber (*Cucumis sativus* L. 'Jinyou No. 3') plants inoculated only with *G. mosseae* had greater biomass production under replanted conditions which implies that AMF-mitigated replant disease is strongly dependent on the AMF species used. This review outlines the occurrence, reasons and mitigation paths of replant disease, and focuses on mycorrhizal functioning on the reduction of replant disease in horticultural plants.

OCCURRENCE OF REPLANT DISEASE IN HORTICULTURAL PLANTS

Replant disease is a worldwide problem, especially with the development of a large-scale intensive horticultural industry. In the pursuit of economic efficiency, there has been an increasing obstacle to continuous succession in horticultural production. In developed countries with large cultivated area, modern agricultural science and technology further intensified replant intensity. As a result, replant disease has become a bottleneck restricting the sustainable development of agriculture (Yu, 2011). The occurrence of replant disease involves many biological and non-biological factors inside the plant-soil-microbe complex and its environment (Ogweno and Yu, 2006).

Soil physical-chemical imbalances

Soil nutrient imbalance may be the primary dimension for the replant problem in horticultural cultivation and management (Wilson et al., 2004; Xie and Li, 2008). In general, enhanced application of chemical fertilizers results in soil secondary salinization, nitrate accumulation, acidification, and soil sealing which are manifestations of nutrient imbalance (Gąstoł and Domagała-Świątkiewicz, 2015). Nitrate accumulation originates from long-term unreasonable fertilization, as well as irrational irrigation and cultivation that raises the underground water, and further increases soil secondary salinization (Yang et al., 2015). Also, acidic fertilizers containing nitrogen have a considerable negative effect on the soil porosity, volume density, relative water content and water retention capacity and thereby they accelerate the process of soil acidification (Ortas, 2012).

Soil enzymatic activity reflects the relative intensity of biochemical processes as well as the transformation of the substances in the soil (Wang et al., 2015; Sun et al., 2015a). Zhao et al. (2010) observed that the activity of soil proteinase, polyphenoloxidase, urease, and saccharase was substantially decreased in the rhizosphere with an increase of continuous cropping time. However, Zhang et al. (2015b) indicated that the activity of catalase and peroxidase in the soil was simultaneously increased with a decrease of soil polyphenoloxidase activity. Hence, replant disease of the same crop or even different crops brings about diverse effects in soil enzymes. There are also positive interactions between replant disease and soil enzymes. This is possibly due to the changes of the root micro-environment (Utkhede, 2006).

Soil aggregates are characterized by porosity and water stability in the soil and they coordinate the balance of solid, liquid and gas phases (Rillig et al., 2015). Huang et al. (2015) reported that long-term continuous monoculture decreased the soil aggregate percentage in 0-60 cm layer which is connected with a decrease of both soil organic carbon and glomalin-related soil protein (GRSP) (Wang et al., 2015). As a result, replant soil is characterized by a destroyed structure which strongly inhibits crop growth (Zou et al., 2014).

Soil microflora imbalance

Continuous monoculture conditions provide parasitic and breeding sites of pathogens in roots because the

Table 1. Effects of arbuscular mycorrhizal fungi on mycorrhizal status and physiological traits in horticultural plants grown in replant soils – part 1

Host species	Fungal species	Variables	References
Apple	*Acaulospora laevis*	col%$^{\uparrow}$, vesicles$^{\uparrow}$, biomass$^{\uparrow}$	Ridgway et al. (2008)
	Scutellospora calospora	col%$^{\uparrow}$, vesicles$^{\uparrow}$, biomass$^{\uparrow}$	
	Glomus mosseae	col%$^{\uparrow}$, vesicles$^{\downarrow}$, biomass$^{\uparrow}$	
	G. fasciculatum	col%$^{\uparrow}$, vesicles$^{\uparrow}$	Mehta and Bharat (2013)
	G. mosseae	biomass$^{\uparrow}$	Čatská (1994)
	G. fasciculatum	biomass^{ns}	
	G. intraradices	col%$^{\uparrow}$, biomass$^{\uparrow}$	Gastol and Domagala-Swiatkiewicz (2015)
	G. mosseae	col%$^{\uparrow}$, biomass$^{\uparrow}$	
	G. agregatum	col%$^{\uparrow}$, biomass$^{\uparrow}$	
Cucumber	*Glomus caledonium*	col%$^{\uparrow}$, biomass^{ns}	Hu et al. (2010)
	G. mosseae	col%$^{\uparrow}$, biomass$^{\uparrow}$	Wang et al. (2012)
	G. intraradices	col%^{ns}, biomass$^{\downarrow}$	
	G. versiformis	col%$^{\downarrow}$, biomass$^{\downarrow}$	
Ginkgo	*G. mosseae*	col%$^{\uparrow}$, biomass$^{\uparrow}$, root activity$^{\uparrow}$, chl%$^{\uparrow}$, leaf blight$^{\downarrow}$	Qi et al. (2002)
	G. intraradices	col%$^{\uparrow}$, biomass$^{\uparrow}$, root activity$^{\uparrow}$, chl%$^{\uparrow}$, leaf blight$^{\downarrow}$	
	G. versiformis	col%$^{\uparrow}$, biomass$^{\uparrow}$, root activity$^{\uparrow}$, chl%$^{\uparrow}$, leaf blight$^{\downarrow}$	
Grape	*Glomus mosseae*	col%$^{\uparrow}$, leaf SOD$^{\uparrow}$, leaf MDA$^{\downarrow}$, biomass$^{\uparrow}$	Guo et al. (2009)
	G. etunicatum	col%$^{\uparrow}$, leaf SOD$^{\uparrow}$, leaf MDA$^{\downarrow}$, biomass^{ns}	
	G. versiformis	col%$^{\uparrow}$, leaf SOD$^{\uparrow}$, leaf MDA$^{\downarrow}$, biomass$^{\uparrow}$	
	G. mosseae	col%$^{\downarrow}$, vesicles$^{\downarrow}$, biomass$^{\uparrow}$	Waschkies et al. (1994)
Peach	*Gigaspora margarita*	col%^{ns}, vesicles$^{\downarrow}$, biomass$^{\downarrow}$	Rutto and Mizutani (2006)
	Funneliformis mosseae (formerly *G. mosseae*)	col%$^{\uparrow}$, vesicles$^{\uparrow}$, soil POD$^{\uparrow}$, soil CAT$^{\uparrow}$, soil PPO$^{\downarrow}$, GRSP$^{\uparrow}$	Zhang et al. (2014, 2015b)
	Glomus mosseae	col%$^{\uparrow}$, vesicles$^{\uparrow}$, biomass^{ns}	Yang (2014)
	G. etunicatum	col%$^{\uparrow}$, vesicles$^{\uparrow}$, biomass^{ns}	
	G. deserticola	col%$^{\uparrow}$, vesicles$^{\uparrow}$, biomass^{ns}	
	G. geosporum	col%$^{\uparrow}$, vesicles$^{\uparrow}$, biomass^{ns}	
	G. intraradices	col%$^{\uparrow\downarrow}$, vesicles$^{\uparrow}$, nematodes$^{\downarrow}$	Calvet et al. (2001)
	G. mosseae	col%$^{\uparrow\downarrow}$, vesicles$^{\uparrow}$, nematodes$^{\downarrow}$	
	G. etunicatum	col%$^{\uparrow\downarrow}$, vesicles$^{\uparrow}$, nematodes$^{\downarrow}$	

Symbols ↑, ↓ and ^{ns} mean significant increase, significant decrease and no significant difference by mycorrhizal inoculation, respectively. Abbreviation: Root colonization, col%; Chlorophyll contents, chl%; Soil nutrient contents, sn%; glomalin-related soil protein, GRSP; catalase, CAT; polyphenol oxidase, PPO; peroxidase, POD; superoxide dismutase, SOD

Table 1. Effects of arbuscular mycorrhizal fungi on mycorrhizal status and physiological traits in horticultural plants grown in replant soils – part 2

Host species	Fungal species	Variables	References
Pepper	unknown	soil CAT$^{\uparrow}$, sn%$^{\uparrow}$	Ren et al. (2016)
Strawberry	*Glomus intraradices*	col%$^{\uparrow}$, biomass$^{\uparrow}$	Qi et al.(2001)
	G. versiformis	col%$^{\uparrow}$, biomass$^{\uparrow}$	
	G. mosseae	col%$^{\uparrow}$, biomass$^{\uparrow}$	
	G. mosseae	leaf POD$^{\uparrow}$, leaf CAT$^{\uparrow}$, leaf SOD$^{\uparrow}$, chl%$^{\uparrow}$	Hu (2016)
Tomato	*Glomus intraradices*	col%$^{\uparrow}$, vesicles$^{\uparrow}$	Akköprü and Demir (2005)
Watermelon	*Glomus mosseae*	col%$^{\uparrow}$, biomass$^{\uparrow}$	Ren et al. (2015)
	G. etunicatum	col%$^{\uparrow}$, biomass$^{\uparrow}$, pathogen$^{\downarrow}$	Zhao (2011)
	G. versiformis	col%$^{\uparrow}$, soil PPO$^{\uparrow}$, soil protease$^{\uparrow}$, soil urease^{ns}, saccharase^{ns}	Zhao et al. (2010)

Symbols ↑, ↓ and ^{ns} mean significant increase, significant decrease and no significant difference by mycorrhizal inoculation, respectively. Abbreviation: Root colonization, col%; Chlorophyll contents, chl%; Soil nutrient contents, sn%; glomalin-related soil protein, GRSP; catalase, CAT; polyphenol oxidase, PPO; peroxidase, POD; superoxide dismutase, SOD

presence of the rhizosphere can produce hydrocyanic acid (HCN) bacteria and actinomycetes resistance to cyanide and thus induces higher number of pathogens in roots and soil (Benizri et al., 2005). As reported by Li et al. (2016), nematode communities changed soil conditions in replanted strawberry (*Fragaria ananassa* Duch. 'Confidant'), and there was a competitive relationship between nematodes and plants for nutrient elements (Calvet et al., 2001). Replant soil accumulates more root exudates, which can promote faster reproduction of pathogenic nematodes (Wang et al., 1998).

In replant soils, the growth and fecundity of soil microflora are seriously disturbed and the dynamic balance of the microbial population density is negatively affected (Allison et al., 2007; Rumberger et al., 2007). In apple tree cultivation, soil micro-organisms biodiversity particularly bacteria, fungi and nematodes were richer prominently in non-replant soil than in replant soil (Utkhede, 2006). It was noted that long-term continuous monoculture results in both a decrease of soil microflora diversity and an increase of harmful microflora (Yao et al., 2006). Although AMF is present in replant soils, it has shown thin mycorrhizal formations in the root cortex and penetration into the central cylinder (Aldea, 1998). As stated by Sun et al. (2015b) soil microflora generally changed from "bacterial" high fertility in non-replant soil to "fungal" low fertility in replant soil.

Allelopathy and autotoxicity

Allelopathy is a kind of complex compounds that directly or indirectly impacts plant growth and development. These compounds are derived from root exudates or plant stubble (the remaining stumps of former crops), and microbial metabolism (Zhao et al., 2009). The effect of allelopathy in plants themselves is known as autotoxicity (Cheng and Cheng, 2016). Yu and Matsui (1994) isolated 11 phenolic substances from the root exudates of cucumber (*Cucumis sativus* L. 'Jinyan No. 4') and found that phenolic substances released by the roots could be accumulated to a certain extent in replanted cucumber and inhibit the growth of the next crop. In addition, alfalfa (*Medicago sativa* L. 'Vernal') plants secrete saponins and phenolic substances into the rhizosphere which seriously affect growth of latter crops (Hoagland et al., 2001; Chon, 2006).

Autotoxicity acts as a special form of allelopathy. Root exudates can stimulate the occurrence of pathogenic fungi, bacteria and nematodes in the rhizosphere or they can affect the germination of dormant spores of pathogens, to produce invasive structures for further infestation (Bais et al., 2006; Yin et al., 2016). On the basis of the root exudates of strawberry (*Fragaria ananassa* Duch. 'All Star'), it was concluded that root secretions triggered an increase in the electrolyte percentage and lipid peroxidation in root cells, resulting in more extensive accumulations of reactive oxygen species in roots (Zhen et al., 2004). Hence, replant management often inhibits plant growth and decreases the resistance to soil-borne diseases.

MITIGATED PATHS OF REPLANT DISEASE

Soil amelioration and field management

The reasonable use of fertilizers can effectively alleviate the occurrence of continuous cropping obstacles (Gąstoł and Domagała-Świątkiewicz, 2015). It was found that applying organic fertilizers such as pig manure and chicken manure into soil could improve the crop resistance to replant disease (Maskina, 1988; Wu et al., 2009). This is due to a more balanced nutrient ratio in organic fertilizer than in chemical fertilizer. In addition, introducing invertebrates such as earthworms (Feng, 2017) is efficient for mitigation of replanting problems.

Drip irrigation can dramatically increase the absorption of both water and nutrients and better soil aggregate structure, in comparison with traditional irrigation (Marouelli et al., 2013). Results of Wei et al. (2009) showed that drip irrigation under continuous cropping conditions markedly improved the soil ecological environment and enhanced resistance to replant disease. Currently, the technique of returning straw to farmland also improves the soil environment under continuous cropping conditions because straw can weaken the nitrification and denitrification reactions, reduce the accumulation of nitrates and nitrites and supply nutrients in the process of straw decomposition (Zhou et al., 2004).

Optimization of cropping systems

To mitigate continuous replant disease, reasonable crop rotations, intercropping and interplanting are often used in the field to increase the total amount of soil microbes as well as the bacterial/fungal ratio to alleviate continuous cropping disease (Mamolos and Kalburtji, 2001). Khan et al. (2014) intercropped maize (*Zea mays* L. 'Baiding No. 1') with peanut (*Arachis hypogaea* L. 'Yueyou No. 92'), and observed that intercropping significantly reduced the population of fungi, elevated the population of bacteria in maize rhizospheric soil, and increased soil enzymatic activity and carbon utilization with a decrease of nitrogen. Nanjappa et al. (2008) showed that in the system of peanut (*Arachis hypogaea* L.) and pepper (*Capsicum annum* L.) rotation, sunshine intensities produced different effects, and stronger light intensity was accompanied with greater yields of peanut and pepper. Earlier studies showed that the rotations of plant genotypes, distant relatives, soil water status, and "allelopathic crops" with the corresponding crops could reduce the hazard of replant disease (Alvey et al., 2003; Zhu and Fox, 2003). Furthermore, a similar conclusion was found in the rotation and intercropping of cassava (*Manihot esculenta* Crantz 'M. Col 113 Crantz') with legumes, such as cowpea (*Vigna unguiculata* L. 'Blackeye Walp'), peanut (*Arachis hypogaea* L. 'VA 98R') and mung bean (*Vigna radiata* L. 'Partov') (Sieverding and Leihner, 1984).

Breeding of resistant varieties

With the development of the molecular techniques in horticultural plants, genetic engineering and crop genetics and breeding technology have become important fields that enhance the tolerance to replant disease (Moose and Mumm, 2008). Lin (2010) analyzed the changes of proteomics in continuous cropping of heterophylla (*Pseudostellaria heterophylla* Miq. 'Zheshen No. 2 Pax') in replant versus non-replant soil. They found that the expression level of several proteins of leaves related to cell division and protein synthesis under replant soil was decreased which resulted in a decrease in the number of soil bacteria and bacterial species diversity. These results showed that breeding for high expression of relevant proteins (e.g., pathogenesis-related proteins) in plants is a major pathway for alleviation of replant disease. Duan et al. (2011) proposed that varieties resistant to replant disease should have characteristics of no self-toxicity, little autotoxicity, production of beneficial allelochemicals and root exudates. Wild horticultural plant species generally show better resistance than corresponding cultivars, because rhizospheric allelochemicals and effective microorganisms cause degeneration of pathogens as a result of antagonistic reactions. Thereby, under continuous cropping conditions, inclusion of wild ancestors into breeding programs is a possible pathway to enhance crop resistance to replant disease.

Application of chemical and biological preparations

Pesticides are used to control fungal diseases, including carbendazim, chlorothalonil and mancozeb by seed dressing irrigation, foliar spraying and other ways (Guo et al., 2010). However, pesticides have lots of underlying problems in endurance, residues, and thus their application must be limited. Moreover, long-term use of soil disinfectants results in the accumulation of toxic substances, such as methyl bromide, pentachloro-nitrobenzene, and formalin (Yao et al., 2006). These soil disinfectants can also include chloropicrin and quintozene (Eayre et al., 2000; Sewell et al., 2010). In addition to disinfectants, high temperature, sunlight and steam are often used to eliminate soil pathogens in replant soils (Guo et al., 2010). In addition, fungicides often have detrimental effects on non-target beneficial microorganisms, including AMF (Comby et al., 2017).

Isolation of rhizospheric bacteria from relative wild species is superior in achieving anticipative effects in mitigating replant disease (Duan et al., 2011). To some extent, the introduction and activation of antagonistic bacteria against harmful fungi and nematodes is a good way to relieve replant disease. Both antagonistic bacteria and pathogens have similar adaptability in the same ecosystem. Antagonistic bacteria secrete antibiotic active substances to inhibit pathogenic microorganisms, and also promote the growth and reproduction of beneficial bacteria, which play an important role in the prevention of replant disease (Bryk and Mikicinski, 2009).

Additionally, grafting is often used to mitigate replant disease, because disease-resistant rootstocks in horticultural production possess better root development and greater capacity in both endogenous hormone production and antioxidant protected systems, collectively, leading to enhanced soil-borne disease resistance and alleviation of autotoxicity (Huang et al., 2016).

UNDERLYING MECHANISMS OF AM FUNGI MITIGATING REPLANT DISEASE

Mycorrhiza is a reciprocal symbiosis structure established between plant roots and AMF in the soil (Wu et al., 2008). In general, AMF can promote the absorption and utilization of water and mineral nutrient, improve plant growth, enhance the tolerance of abiotic stresses including drought, salinity, temperature stress, waterlogging and heavy metal pollution, together with biotic stresses e.g. fungal and bacterial disease, insects and nematodes (Nedeem et al., 2017). AMF can also efficiently ameliorate soil relevant parameters which improves water-stability aggregates (WSAs), soil organic carbon (SOC) and soil enzyme activities (Mehta and Bharat, 2013). AMF inoculation directly or indirectly affects the composition and content of root exudates, the soil microbes population and the growth and development of plants. As stated by Ortas et al. (2017), mycorrhizal application has been introduced into vegetables (e.g., onion, pepper, tomato, cucumber, and eggplant) and fruit trees (citrus, apple, grapevine and plum). Large-scale production of mycorrhizal fungi and their coating on seeds can provide a convenient approach to apply mycorrhiza into fields. Roy-Bolduc and Hijri (2012) proposed two approaches of using AMF in fields: native mycorrhizal inoculums selection and adopting cultural practices to enhance the indigenous AMF population.

Earlier study conducted by Čatská (1994) found that AMF application could replace soil chemical treatments in mitigating apple (*Malus domestica* Borkh 'Kids Orange Red') replant disease. Such effects were confirmed in many horticultural plants, as shown in Tab. 1. Although AMF can increase nutrition of the host plant, replant disease is not associated with mineral nutrition (Čatská, 1994). AMF-mitigated replant disease is a complex issue. Based on the analysis of previous studies, the underlying mechanisms regarding AMF mitigation of replant disease in horticultural plants are discussed as follows.

Regulating the root and soil microflora balance

In general, the root and soil microflora composition is different in replant versus non-replant soil (Čatská, 1994). Proliferation and numbers of fluorescent pseudomonades and total aerobic bacteria are much higher on roots in replant than in non-replant soil (Sheng and Wu, 2007). Although replant soil strongly negatively affects root mycorrhizal colonization, such colonization still causes resistance of roots to pathogens in replant soil, because mycorrhizal fungi have shown resistance to soil pathogenic fungi, including *Phytophtora parasitica*, *Fusarium oxysporum*, *Pythium ultimum*, and to soil pathogenic bacteria, including *Preudomonas syringae* and *P. solanacearum* (Waschkies et al., 1994). As a result, mycorrhizal plants grown in replant soil possess a lower amount of phytotoxic micromycetes and a higher amount of diazotroph bacteria than in non-replant soil (Čatská, 1994), thereby optimizing the root and soil microflora diversity (Bharadwaj et al., 2008; Arturssonet et al., 2005). Moreover, diazotroph bacteria can produce more than antibiotics and phytohormones to resist replant disease. In addition, AM watermelon (*Citrullus lanatus* Thunb. 'Jingxin') plants enhanced the abundance of bacteria and actinomycetes and inhibit fungi under replant soil conditions (Zhao et al., 2010). Similar conclusions have been reached for apple under the condition of replant disease where mycorrhizal apple (*Malus domestica* Borkh 'Starking Delicious') seedlings increased the number of fungi, bacteria and actinomycetes in soils, resulting in better characteristics in the pH and nutrient levels of parasitic sites (Mehta and Bharat, 2013). Such AMF effects possibly provide the equilibrium between favorable and harmful microorganisms, and restore the original dynamic balance. AM-regulated soil and root microflora may be ascribed to alterations in root exudation of the host plant, competition for host resources and direct effects of mycorrhizal fungal exudates, individually or interactively (Vierheilig et al., 2003).

Enhancement of enzyme activities in the soil and plants

Soil enzyme activities can reflect the status of soil fertility and soil biological activity (Allison et al. 2007). Liu et al. (2011) found that AMF could secrete multiple soil enzymes, such as urease and phosphatase, eventually balancing the nutrients, pH and flora structure of replant soil. Zhang et al. (2015b) observed that inoculation with *Funneliformis mosseae* significantly increased the activity of catalase (CAT) and peroxidase (POD) in replant soils of peach (*Prunus persica* L. Batsch 'Great White') and decreased the activity of soil polyphenol oxidase (PPO), as compared with non-AMF inoculation. Among these enzymes, CAT is involved in soil detoxification of H_2O_2 accumulation (Huang et al., 2017; Liu et al., 2008). POD can eliminate soil allelochemicals and is associated with the synthesis of soil humus (Kong, 2007). PPO can oxidize soil substances, including amines and heterocyclic compounds (Wang et al., 2010). As a result, mycorrhizas strongly provide a greater soil microbial environment and soil fertility within the replant soil rhizosphere through better soil antioxidant enzyme activities in order to alleviate replant disease (Zhang et al., 2015b).

AM symbiosis can regulate activities of some hydrolytic enzymes in the soil to maintain balanced nutrient levels in the plant-soil system (Yang, 2014). As stated by Rutto and Mizutani (2006), the N content in leaves of peach (*Prunus persica* L. Batsch 'Ohatsumomo Batsch') was higher after inoculation with *Gigaspora margarita* and was due to the enhanced urease level under mycorrhization, resulting in intensive N decomposition and thus a decrease of N in the mycorrhizosphere. Similarly, Hu (2016) found that inoculation with *Glomus mosseae* significantly increased urease, acid phosphatase and sucrase activities under different levels of p-hydroxybenzoic acid, leading to a better nutrient status in the host plant.

In addition to soil enzyme activities, AMF inoculation strongly stimulates plant antioxidant protective systems to enhance tolerance to replant disease in horticultural plants (Tab. 1). In grape (*V. vulpina* × *V. labrusca* 'Beta') inoculation with *Glomus mosseae*, *G. etunicatum* and *G. versiformis* significantly enhanced leaf SOD activity under replant soil conditions, thereby inducing a lower membrane lipid peroxidation (lower MDA level) (Guo et al., 2009). Similarly, *G. mosseae* mycorrhizal strawberry (*Fragaria* × *ananassa* 'Sweet Charlie') exhibited greater activity of SOD, POD and CAT in leaves, as compared with non-mycorrhizal plants under replant soil conditions (Hu, 2016). Hence, AM plants grown in replant soil have higher antioxidant protective systems allowing them to tolerate replant disease.

Changes in root exudates

Studies found that AM plants excreted more isoflavones, glyceollin and coumestrol into the rhizosphere, with resistance to nematodes and pathogenic fungi under replant soil conditions (Tewoldemedhin et al., 2011). In the early stages of alfalfa (*Medicago sativa* L. 'Vernal') inoculated by mycorrhizal fungi, the concentration of several isoflavones in roots increased faster, including antitoxin and its prednisone and formononetin (Chon, 2006). This definitely reveals that the resistant products of plant secondary metabolism can to a certain degree be induced by mycorrhization to inhibit the infection, occurrence and development of pathogens. Root exudates, especially phenolic acids, terpenes and phytoalexins are closely related to disease resistance of plants (Yin et al., 2016). Also, the contents of secondary metabolites and the activities of antioxidant enzymes in roots are increased by mycorrhization (Wu et al., 2010) which is positively correlated with resistance to replant disease (Zhou et al., 2011). Furthermore, Hu (2016) analyzed the changes in allelochemicals of strawberry (*Fragaria × ananassa* 'Sweet Charlie'), and found that inoculation with *Glomus mosseae* could change the contents of root exudates, especially phenolic acid allelochemicals. Also, the allelopathic composition of strawberry rhizosphere soil identified by high performance liquid chromatography technology showed p-hydroxybenzoic acid, pilocarpine, vanillin, p-coumaric acid, ferulic acid and benzoic acid. A study by Guo et al. (2009) showed that *Glomus versiforme*–inoculated mycorrhizal grape (*V. vulpina × V. labrusca* 'Beta') released nerolidols in root exudates, but the non-AM control did not show nerolidol synthesis. On the other hand, root exudates also indirectly stimulate mycorrhizal associations impacting soil enzyme activities and the soil microbe population to change rhizospheric micro-environments (Paterson et al., 2007). As a result, changes in root exudates by mycorrhization can indirectly relieve replant disease in horticultural plants.

Greater soil aggregate stability by glomalin-related soil proteins

Glomalin that is released by spores and hyphae of AMF is defined in the soil as the glomalin-related soil protein (GRSP). GRSP is a major carbon source in the soil and can reflect the ecological status of the soil which is an indicator of soil fertility. GPRS can fix and disturb organic carbon in the soil, which provides a rich total carbon to increase plants biomass. Lovelock et al. (2004) demonstrated a significant positive correlation between organic carbon and GRSP contents. GPRS can be accumulated in the soil to improve its structure to be more suitable for plant growth (Rillig et al., 2002) because GPRS in many conditions, e.g., soil, sand, clay particles and organic matter, glues soil aggregates for better soil aggregate stability, in terms of the glycoprotein trait.

In peach (*Prunus persica* L. Batsch 'Great White'), inoculation with *Funneliformis mosseae* more significantly increased easily extractable GRSP and total GRSP concentration in the replant soil than non-AMF inoculation, irrespectively of whether the replant soil was autoclaved or not (Zhang et al., 2014, 2015b). Such increase of GRSP in replant soils heavily improved the soil aggregate stability in the size of 2-4 mm and 1-2 mm in autoclaved replant soil, but not in un-autoclaved replant soil (Fig. 1, Zhang et al., 2014, 2015b). Possibly replant soil generally exhibits negative effects on AMF colonization and subsequent GRSP production, thereby strongly altering the GRSP role in the aggregate stability of replant soil.

In addition to greater soil aggregate stability, GRSP can glue some toxic substances, including heavy metals, gallotannic acids, cyanogentic glycosides and hydrocyanic acids (Wu et al., 2014). GRSP can chelate some toxic substances in replant soil, thereby partly mitigating the degree of replant disease.

Balanced nutrient levels in plants

AMF can improve nutrient absorption in host plants, thereby alleviating the adverse effects of replant disease caused by the imbalance of mineral nutrients (Liu et al., 2011). AMF connects the root cells of host plants and enlarge the rhizospheric soil by hyphae, thereby, increasing the root surface area of absorption and indirectly easing the impact of growth disorders caused by replant disease through an infertile nutrient area within the root absorption range. Studies showed that the mycorrhizal apple (*Malus domestica* Borkh 'Topaz') possessed greater ability to uptake nutrients such as P, S, Ca, Mg and K from soil (Gąstoł and Domagała-Świątkiewicz, 2015). Moreover, mycorrhizal roots also absorb more N and improve N utilization (Ren et al., 2016; Rutto and Mizutani, 2006). Mehta and Bharat (2013) demonstrated that mycorrhizal apple (*Malus domestica* Borkh 'Starking Delicious') seedlings had a higher level of P concentration in comparison with non-mycorrhizal plants which allowed mycorrhizal plants to tolerate soil-borne pathogens in replanted apple. The studies of Bharat and Bhardwaj (2001) and Raj and Sharma (2009) on apple (*Malus domestica* Borkh 'Red Delicious') in India found that apple seedlings infected by indigenous AMF enhanced immunity to pathogenic bacteria, resulting in a lower incidence of root rot. In addition, common mycorrhizal networks can transfer mineral nutrients and carbohydrates between neighboring plants, with the purpose of comprehensively improving the growth environment of the host plants (Zhang et al., 2015a).

Apart from plant nutrients, in replant soils, application of mycorrhizal fertilizer also significantly increases soil fertility for horticultural plants. For example, AMF application induced significantly higher available K, P and N contents in 10-year replant soil of pepper (*Capsicum annuum* L. 'Chinese Red') plants (Ren et al., 2016) which

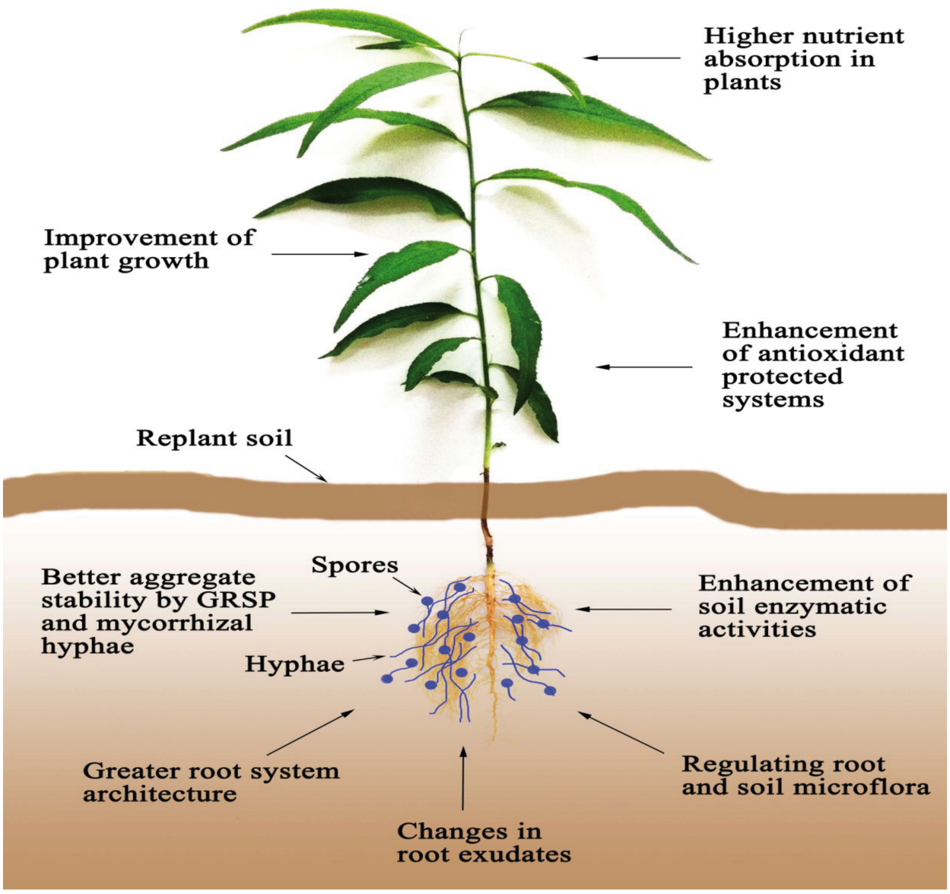

Figure 1. Underlying mechanisms of AMF on mitigating replant disease in horticultural plants

benefited the nutrient absorption of the host plants. However, a high P supply often reduces mycorrhizal colonization on host plants, resulting in an enhanced susceptibility of plants to pathogens (Mustafa et al., 2016). So, mycorrhizal application should be carefully considered in orchards.

Greater root system architecture

Root system architecture (RSA) refers as the spatial organization and arrangement of plant root systems in the soil, and plays a key role in controlling water and nutrient acquisition (Gérard et al., 2017). As reported by Zhang et al. (2014), replant soil heavily inhibited root development and the number of lateral roots in peach (*Prunus persica* L. 'Great White') seedlings. However, inoculation with *Funneliformis mosseae* strongly increased the root biomass and number of lateral roots in peach seedlings grown in unsterilized replant soil. In addition, significantly greater root length, root projected area, root surface area and root volume and thinner root diameter were also found in AMF peach seedlings than in non-AMF seedlings exposed to unsterilized replant soil (Tab. 2). Guo et al. (2009) also observed the greater root activity in AM grape (*V. vulpina* × *V. labrusca* 'Beta') plants than non-AM control grown in replant

Table 2. Effects of an arbuscular mycorrhizal fungus (*Funneliformis mosseae*) on root morphological traits in peach seedlings grown in unsterilized replant soils

Replant treatments	AMF treatments	Root length (cm)	Root projected area (cm^2)	Root surface area (cm^2)	Root diameter (mm)	Root volume (cm^3)
NRP	+AMF	738 ± 137 a	40.0 ± 4.9 a	125.6 ± 15.3 a	5.48 ± 0.16 a	1.72 ± 0.05 a
	-AMF	554 ± 106 b	27.8 ± 3.3 b	87.4 ± 8.8 b	5.01 ± 0.32 ab	1.10 ± 0.14 b
RP	+AMF	587 ± 67 ab	26.0 ± 3.6 b	81.8 ± 11.3 b	4.47 ± 0.79 b	1.03 ± 0.07 b
	-AMF	342 ± 108 c	19.6 ± 4.4 c	61.7 ± 10.7 c	5.73 ± 0.63 c	0.84 ± 0.10 c

Data (means ± SD, n = 4) followed by different letters indicate significant differences between treatments at $p < 0.05$. Abbreviation: +AMF, inoculation with *Funneliformis mosseae*; -AMF, inoculation without *Funneliformis mosseae*; NRP, non-replant; RP, replant soil. Such RSA changes by mycorrhization may be due to the allocation of glucose/sucrose to roots, the phytohormone modification and the regulation of endogenous polyamines, especially putrescine (Berta et al., 1993; Wu et al., 2011, 2012). As a result, greater RSA traits (e.g., length, area, volume, and activity) in replanted plants under mycorrhization will confer greater capacity to absorb water and nutrients from the soil and thus enhance stress tolerance, including the replant problem.

FUTURE PERSPECTIVES

The replant problem is a complex issue in horticultural plant production. Utilizing AMF as a microorganism agent has shown the potential value in mitigating soil replant disease. But, the mechanisms have been poorly studied, although glomalin, nutrients, root system architecture, antioxidant enzymes, root exudates and microflora balance were highlighted. There are still many issues that need to be clarified:

1. AMF can regulate the dynamic balance of the soil microflora to introduce or activate antagonistic bacteria for inhibition of pathogenic microorganisms. Thus, changes in soil microflora under mycorrhization need be further analyzed.
2. The changes in the components and concentrations of root exudates under mycorrhization need to be analyzed, and the potential components applied to test whether replant disease in horticultural plants can be mitigated.
3. Close attention should be paid to some metabolic pathways, such as salicylic acid and jasmonic acid (two key disease-resistant substances) which have not been studied. In addition, the processes of mycorrhiza-induced resistance in themselves remain elusive.
4. The RNA-seq technique should be used to screen high-efficiency up-regulated genes and metabolic pathways in plants and mycorrhizal fungi to understand the resistance to replant disease at molecular levels which is vital for the breeding of varieties resistant to replant disease.
5. More farmland studies for AMF application should be conducted to solve replant disease, because horticultural plants such as watermelon, pepper, eggplant, peach, apple and citrus are more mycorrhizal-dependent plants. Most earlier studies were conducted under controlled conditions and field experiments were scarce. More work needs to be moved from the lab to the field to confirm mycorrhizal roles in alleviating replant disease.
6. The potential capacity of various AMF species in mitigating replant diseas should be evaluated to screen highly efficient AM fungal strains in corresponding plants. In fact, the response of mycorrhizal inoculation in horticultural plants heavily depends on soil physical and chemical properties, plant species, inoculums, inoculation methods and other factors. As reported by Ridgway et al. (2008), a new species record in replant apple orchard in New Zealand, *Scutellospora pellucida*, was found. It provides the opportunity to determine whether the AMF strain is an effector in mitigating apple replant disease.

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AUTHOR CONTRIBUTIONS

L.H.L. – wrote the first manuscript (50%); Q.S.W. – critically revised the manuscript for important intellectual content (50%)

CONFLICT OF INTEREST

Authors declare no conflict of interest.

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