Review Article

Biocontrolmechanism of Arbuscular Mycorrhyzal fungi against plant-parasitic nematodes :A review

Abstract:

Plant- parasitic nematodes(PPN) are the major global threat to food production.Control strategies based on synthetic nematicides is undesirable due to environmental and health risks. Therefore, use of biocontrol agents such as Arbuscular mycorrhizal fungi (AMF) is environmentally friendly options for management of PPN. The antagonistic action of AMF against PPNs may be achieved by competition for nutrients and space, by increasing plant toleranceor by changing rhizosphere interactions by altering root exudations. An increased insight into their modes of action will therefore help to increase the efficacy of these biocontrol agents.This review presents an overview of different mechanisms of AMF-mediated biocontrol, and their potential involvement in reducing PPN infections.

Key words: Biocontrol, Plant-parasitic nematodes(PPN), Arbuscular mycorrhizal fungi (AMF), Mode of action, Root rhizosphere interactions.

1.Introduction

Plant-parasitic nematodes (PPNs) or phyto-nematodes are usually small soil-borne pathogens that can feed on all plant parts,although most species feed on roots. Over 4100 species of plant-parasitic nematodes were described to date, among which, a restricted group of genera is considered as major plant-pathogens, whereas others are specific to a more limited range of crops, both causing a high impact to economically important crops. Damage caused by plant nematodes has been estimated as a projected yield loss of 12.3% in excess of USD$80 billion per annum worldwide and are expected to rise in the near future as a result of climate change and cropping systems (Nicol et al., 2011). PPN consist of a wide range of species with different life styles that can cause major damage in many important crops worldwide. Additional losses could be related to food quality and visual imperfections associated with infection symptoms

.Thedirect damage caused by PPN can be aggravated by secondary infections of the wounded plant tissues by other pathogens. The full extent of worldwide nematode damage is likely to be underestimated, since growers are often unaware of their presence because the symptoms caused in the plant are often non-specific, making difficult to attribute crop losses to nematode damage (Siddique and Grundler,2018). However, the damages caused by PPN have been managed by chemical practices. This causes deterioration to the environment and public health in the long run, in addition to the high economic cost of nematicides. Therefore, it was necessary to search for alternative methods to combat PPN by looking at the interaction of PPN with the biological content of the soil.Microbial antagonists as biological control agents of nematodes are one of the potential alternatives to chemical nematicides; however, they are dependable under various environmental conditions. Therefore, attention should be paid to its relationship to plant in an unconventional form, to find or create an antagonistic relationship between PPN and some soil microorganisms to induce plants against nematodes.One of the proposed environmentally friendly options to manage PPN is the use of biological control organisms, such as arbuscular mycorrhizal fungi (AMF). AMF are obligate root symbionts that can protect their host plant against biotic stress factors such as plant-parasitic nematode (PPN) infection. Application of AM fungi not only modulates physio-biochemical pathways but also reduced the infestation, colonization, and invasion of plant-parasitic nematodes (Da Silva-Campos, 2024).

2.Mycorrhizal Fungi

Arbuscular mycorrhizal fungi are obligate root symbionts, estimated to colonize more than 80% of all land plant species and they are beneficial for the growth of host plants (Ferlian et al., 2018). AMF, which are found naturally in soil and behave as bio-stimulators and bio-protectors, may be extremely advantageous to sustainable agriculture by preserving plant productivity and alleviating soil-borne plant pathogens while causing no harm to the environment (da Silva Campos, 2020).AMF have been promoted as a natural tool to maintain and promote sustainable agriculture due to their role as natural biofertilizers; increasing the levels of nitrogen (N), P and Zn in the crop (Berruti et al., 2016). They also play a role as bio-protectants against fungal, bacterial, and nematode pathogens (Yang et al., 2014). To complete their life cycle, they consume lipids (Gianinazzi et al.2010)and products from photosynthetic plants. Though there are different kinds of mycorrhiza, the most common mycorrhizal association occurring in crops important in agriculture is the arbuscular type (van der Heijden et al.,2015).According to

Spatafora et al. (2016), most AMF species are members of the Mucoromycota phylum's Glomeromycotina sub-phylum. This subphylum has 25 taxa and many orders, including the Glomerales, Archaeosporales, Paraglomerales, and Diversisporales.Native mycorrhizal fungi strainsare used as biofertilizers and bioprotective agents to increase plant's yield and protect theplant from the pathogens, as an ecofriendly agent; however, the inoculation of plants withmany mycorrhizal species belonging to different families were found to be more efficientthan mono-inoculation.

3.Interaction between Plant-parasitic Nematodes and AMF

Plant parasitic nematodes and AMF share plant roots as resource for food and space.The coexistence of AMF and nematodes in the phytobiome has prompted a number of investigations into their interactive effects on plants (Yang et al., 2014 Zhang et al.,2020).Based on proximity in tissue, the interactions between endoparasites and AMF would be stronger, i.e. more reciprocal effects of endoparasitic nematodes on AMF, than those between ectoparasites and AMF. However, relative to AMF-free plants, AMF infected plants were damaged more by ectoparasites than by endoparasites. Of the sedentary endoparasites, numbers of root-knot nematodes were reduced more by mycorrhizal infection than were those of cyst nematodes. Migratory endoparasitic nematodes number was greater on AMF infected plants. Interactions appear to be very specific. The outcomes of AMF nematode interactions are determined by many factors during the interactions between organisms and their physical, physiological and temporal environments. The interactions between mycorrhizal fungi and nematodes are complicated and depend on the soil conditions, fungal species, host plants, and nematodes. Mycorrhizal-nematode interaction is prospected to increase the resistance of plants to nematode infection(Ferreira et al.,2018).

4.Biocontrol mechanism of AMF

Various mechanisms have been proposed to play a role in the biocontrol effect of AMF against PPN. The different mechanisms cannot be considered as completely independent from each other and biocontrol probably results from a combination of different mechanisms (Cameronetal., 2013). AM fungi are model organisms, besides potential role in nutrient cycling; they modulate biochemical pathways directly or indirectly which lead to better plant growth under biotic and abiotic stress conditions. The relative importance of a specific mechanism can vary depending on the specific AMF-pathogen-plant interaction. Several mechanisms can be involved in the AMF-mediated biocontrol; direct effects of AMF on the pathogen, involving competition for space or nutrients, or indirect, plant-mediated, effects. The latter can further be divided into the effects of AMF on plant tolerance, plant defense induction and altered plant exudation leading to altered rhizosphere interactions.

4.1.Protective effectsof AMF

AMF can alleviate plant stress caused by abiotic as well as biotic factors, including PPN (Singh et al., 2011). *In vitro*, green house as well as field experiments indicated protective effects against PPN by AMF in plants such as banana, coffee and tomato (Koffi et al., 2013). These protective effects ranged from a reduction in infection and reproduction to an enhanced tolerance. Typically found in the rhizosphere, phytopathogenic nematodes including RKN colonize the roots of their host plants and have opposing effects on the health of those plants (Zhou et al., 2020). However, few reports indicated that AMF inoculation reduces the infestation of plant roots by phytopathogenic nematodes (Elsen et al.,2008). Growing plants with AMF inoculation in the nursery can increase their growth and safeguard them from infection caused by soil-borne phytopathogens including phytopathogenic nematodes (Elsen et al., 2008).Published meta-analyses describe the generallysuppressive effect that AMF have on nematodes (Veresoglouand Rillig, 2012). These analyses includednematodes belonging to different genera and they grouped plantparasiticnematodes into their feeding modes (sedentary ormigratory). AMF reduced the numbers of the sedentary endoparasiticnematodes (*Meloidogyne*, *Heterodera*, and *Globodera*spp.) and the ectoparasitic nematodes (*Tylenchorhynchus* spp.).However, some analyses showed an increase in migratoryendo-parasitic nematode numbers on inoculation with AMF(Hol and Cook, 2005). Grouping the nematodesinto their broad feeding modes has the effect of obscuring thedata on interactions of AMF with *Pratylenchus* spp. and thosewith other migratory endo-parasites including *Radopholus*spp.and *Hirschmanniella* spp. Usually, AMF exhibit an antagonistic effect on plant-parasitic nematodes, and several studies have shown a significant reduction in nematodes when healthy mycorrhizal diversity present in the rhizosphere (Gough et al., 2020; Poveda et al., 2020). In recent years, many investigations have been reported where AMF showed protective effects against plant parasitic nematodes (PPN)in various crop plants (Alban et al., 2013). The feeding cells induced within the vascular cylinder by root-knot and cyst nematodes may breach the endodermis, spreading into the cortex where they may be direct competition for space with AMF.The feeding cells of *Heteroderaavenae* are confined to cells within the endodermis and thus may not be affected by direct competition with AMF. The sedentary endoparasitism make them more sensitive to changes in plant physiology by AMF than are the migratory endoparasites.VAFdonot colonize regions infected by endoparaasitic nematodes, and nematodes rarely infect regions colonized by VA fungi. AMF can change root morphology with consequences for penetration and movement of migratory nematodes. They move within the cortex,benefit from AMF so may be feeding on cells suitable for AMF colonisation.*Ditylenchus dipsaci* numbers first increased and then decreased on mycorrhizal *Phaseolus vulgaris* compared to non-mycorrhyzal controls; similarly*Aphelenchoidesritzemabosi* populations decreased on mycorrhyzal compared to non mycocrhyzaltobacco(Sikora and Dehne,1979). Enhancing host resistance and/or tolerance by AMF could be a promising alternative.AMF may enhance host tolerance and increase resistance by slowing down nematode development. The net effects vary with the environment,plant genotype, nematode species and fungal isolate. Mode of parasitism of nematode affects the nature and outcome of interactions with AMF. Ectoparasitic nematodes are unaffected by direct competition with AMF and are more likely to be affected indirectly by AMF-induced changes in plant physiology(increased free amino acids in leaves,especiallyarginine,higher chitinase activity in roots,an increase in soluble sugars and phenols in roots. Strictly direct mechanisms of mycorrhizal fungi against nematodes are not yet described as they normally act through the plant host, either providing the plant with higher nutrient and water uptake, altering root morphology by increasing root growth and branching, or making the plants more competitive for nutrients and space with other plants, or altered rhizosphere interactions (Wani et al., 2017). Recent studies have confirmed these mechanisms, for example, mycorrhizas (*Rhizophagusintraradices*and *Funneliformismosseae*) reduce tomato root penetration by false root-knot nematode *Nacobbus aberrans* (Marro et al., 2018), in the same way as the application of *Glomus intraradices, G. mosseae,* and *G. etunicatum* against *M. javanica* in peach trees (Calvetet al., 2001). In contrast, the increment in root colonization by mycorrhizae (*Rhizophagusclarus*, *Claroideoglomus*etunicatum,*Gigaspora rosea*, *G. margarita*, *Scutellosporacalospora*, and *S. heterogama*) caused an increase in the population of nematodes *Pratylenchusbrachyurus* in maize crop (Brito et al., 2018) which is opposite to the effect in cotton (Ferreira et al., 2018). All these mechanisms and their effectiveness on the populations and the capacity of infection of the phytoparasitic nematodes will depend closely on the local environmental conditions.

4.2.Higher NutrientUptake

Application of AMF to agricultural soils might help to enhance uptake of soil nutrients in crops in a more sustainable manner, thereby reducing reliance on chemical fertilisers.In exchange for photosynthetic carbon from their host, they boost plant growth and development by enhancing nutrient uptake (Bender et al.,2015) and also help plants to cope with various stresses imposed by abiotic and biotic elements, including parasitic nematodes on plants (Schouteden et al., 2015). Arbuscularmycorrhizalfungiareknowntobeabletoincrease theuptakeofwaterandmineralnutrientsfortheirhostplant, suchasphosphateandnitrogen(Baumetal., 2015) butprobablyalsomicro-elementssuchaszinc(Smithand Smith, 2011). Higheruptakeofphosphatehasbeenproposedasamechanism fortheAMF-mediatedbiocontrol (Bodkeretal., 1998). Fritzetal. (2006) showedthattomatoplantscolonizedby *Rhizophagusirregularis* showedsignificantlylesssymptomscausedby *A. solani* than non-mycorrhizalplants,whilenoincreaseinphosphateuptake wasobserved.Plantswithabetternutrientstatusareabletotoleratehigher PPNpopulationdensitiesintheirroots,asobservedincotton fieldsinfestedwiththesedentarysemi-endoparasiticnematode *Rotylenchulusreniformis* (Pettigrewetal., 2005). Regressionanalysisofnematodepopulationdensitiesagainstthemineral contentinricealsorevealedapositivecorrelationbetween migratoryectoparasitic *Helicotylenchus* spp.andMg,however, a negativecorrelationwasobservedbetweenthemigratoryendoparisiticnematode *Pratylenchuszeae* andZnorFe,and between *M. incognita* andMgandCa.These observationsindicatethatthenutrientstatusofthehostplantcan affectPPNpopulationdensitiesinbothapositiveandnegative way.

4.3.AlteredRootMorphology

Mycorrhizal plants often show increased root growth and branching, enhanced AMF colonizationincreased lateral root formation (secondary and tertiary rooting)and modulates the root morphology of rice which is beneficialfor plant growth and development(Gutjahr and Paszkowski, 2013).TherootmorphologyresponsesresultingfromAMFcolonization seemtodependonplantcharacteristics,withtaprootsforexample appearingtoprofitmorefromAMFthanfibrousrootsintermsof gainedbiomassandnutrientacquisition(Yangetal., 2014). Positiveeffectscould resultfromanincreaseinrootvigor,duetoahighernutrient uptakecapacity.Itmightevencounterbalancethesuppressed rootgrowthcausedbyPPN.Forexample,decreasedroot branchingcausedbythemigratoryendoparasiticnematodes *Radopholussimilis*and *P.coffeae* in bananawascounterbalanced bytheincreasedbranchingduetocolonizationbytheAMF *Funneliformismosseae* (Elsen et al., 2003).

4.4.Direct competition for nutrients and space

Competitionfornutrientsorforspaceandinfectionsitesdo occurbetweenmicro-organismswiththesamephysiological requirementsinanecologicalniche,especiallywhereresources suchascarbonmightbelimited.The carbon transfer from the host plant to the AMF is estimated to range from 4 to 20% of the total assimilated carbon (Hammer et al., 2011). As there is a difference in carbon sink strength between different AMF species, different AMF species mediate different levels of biocontrol . For example, the AMF *R.irregularis* could not exert a stronger biocontrol effect on *R.similis* and *P.coffeae* in banana nor on *M. incognita* in tomato despite its higher carbon sink strength compared to *F.mosseae* (Schouteden et al.,2015).Competition for space could also be involved in AMF-PPN interactions since they both reside in roots and higher AMF colonization degree of the root leads to a higher level of AMF-mediated biocontrol (Jung et al., 2012).Negative effects duetospaceconstrictioncanbeexertedonPPN asmycorrhizalarbusculesexclusivelyforminthecortex,where alsomigratoryendoparasiticnematodesfeed.Spacecompetition betweenAMFandsedentaryendoparasiticnematodescouldbe broughtintoplayincasethefeedingcellsextendintothecortex. Cystnematodefeedingcells,theso-calledsyncytia, areconfinedwithintheendodermisandshouldthereforebeless affectedbyAMF. DosAnjos et al. (2010) concluded that when the symbiosis was well established prior to *M. incognita* inoculation, *M. incognita* reproduction was reduced, whereas co-inoculation had no effect.Alban etal. (2013) found that pre-inoculation of *M. exigua* led to a significant increase in the subsequent colonization of AMF compared to uninoculated mycorrhizal plants.Holand Cook (2005) observed that AMFcolonizationwasreducedbyectoparasitic, migratoryendoparasiticandsedentaryendoparasiticnematodes. Ingreenhouseexperiments, *R.similis* and *P.coffeae* in banana affectedthefrequencyof *F.mosseae* colonization,butnotthe intensity(Elsenetal., 2003). Contrastingly,rootcolonization by *R.irregularis* in *invitro* bananaplantletswasnotaffectedeither by *R.similis* (Koffietal., 2013) orby *P.coffeae* in transformed carrotroots(Elsenet al., 2003). DosAnjosetal. (2010) showedthat *M. incognita* couldnegativelyaffectthesporulationoftheAMF *Scutellosporaheterogama* in sweetpassionfruit,while delMarAlguaciletal. (2011) alsoreported thatthehighestAMFdiversitywasfoundinuninfectedroots comparedto *M. incognita* infectedrootsandgalls,andthat thecompositionoftheAMFcommunitywasdifferentbetween infectedanduninfectedroots.TheirresultsindicatethatAMF colonizationmightalsobesuppressedbyPPN,dependingonthe AMF speciesassomeAMFspecieswerenotaffectedbythePPN.

4.5.Effects through induced systemic resistance

Several authors reported that mycorrhizal fungi could activate plant mediated resistance mechanisms to nematode invasion. Phenylpropanoid pathway is the firstline of plant defense imparting host resistance by reprogramming the downstream signaling involving activation and accumulation of antioxidant enzymes (PAL, TAL, Pox, APx, etc.) and various defense-related biomolecules such as phytoalexins, callose, pectin, lignin derivatives and other metabolites toxic to the pathogens (Weng et al.,2022).

Jasmonate biosynthesis and accumulation of jasmonic acids (JA) significantly affect the phenolics content in many crops.The continuous recognition of the AMF within the colonized cells causes the activation of a JA-mediated SAR through the plant termed as mycorrhizal induced resistance (MIR)(Pozo and Azcón-Aguilar, 2007).The plant recognizes MAMPs (microbe-associated molecular patterns) type molecular patterns which triggers a generalist defensive response of the MAMP-triggered immunity type. Subsequently, the recognition of effectors released by the fungus in response to plant defenses activates a more specific defensive response (Nishad et al., 2020). Inmaize,theexpressionorpresenceofthe9- LOXgene(ZmLox3) provedtobeessentialforresistanceagainst *M. incognita* (Gao etal., 2008). The JA- dependent pathway is able to mediate resistance to PPN (Fan et al., 2015). However,the MIR defense response against PPN is probably not solely linked to the JA-dependent pathway. Several plant genes wereupregulatedwhen AMF andnematodewerebothpresentintheroot,indicating a primingofthesedefensegenes. The primed activation of several other plant defense- related genes was recently also reported in *R.irregularis* colonized grapevine after infection by the ectoparasitic *X. index* (Hao et al., 2012)andbanana against *R.similis* and *P.coffeae*. (Elsen etal., 2008).Theproductsofthesegenes includechitinase1b. Li et al. (2006) reported the primed transcriptional activation of a class III chitinase gene in *Glomus versiforme* colonized grapevine roots upon infection by *M. incognita*. Constitutive expression of this gene in transgenic tobacco plants enhanced the resistance against the RKN, but did not affect the AMF. This strongly suggests that the class III chitinase gene is involved in a protective mechanism against the PPN. Though this mostly affected the viability of the eggs and also reduced the amount of egg-masses and thus productivity of the females (Chan et al., 2015).APR10proteinpurifiedfrom *Crotalariapallida* showsnematostaticandnematicidaleffects against *M. incognita*, targetingadigestiveproteinaseofthe nematode(Andradeetal., 2010). The shikimate pathway has been implicated in AMF-mediated biocontrol in different plant species against many nematodes (Vos et al., 2013). Genes of 5-enolpyruvyl shikimate-3-phosphatesynthase (ESPS) and a heat shock protein70-interacting protein (HIP) were also primed (Hao et al., 2012). They are related to the regulation of the auxin balance which is of importance for nematode feeding site formation and possibly location (Gheysen and Mitchum, 2011). Moreover, theshikimatepathwayproduces precursorsforvariousaromaticsecondarymetaboliteswhichare producedthroughthephenylpropanoidpathwayamongwhich flavonolsynthaseagainst *M. incognita*, *R.similis*, and *P. penetrans*hasbeenreportedtobeprimed(Vosetal., 2013). Mitogen-activated protein (MAP) kinase (MAPK)signaling pathways play a crucial role in plant defense, hypersensitive response (HR) reaction, immune responses, and oxidative burst to pathogen attack. HR reaction and programmed cell death by modulating the generation of reactive oxygen species(ROS) at the infection site and thereby restricting the penetration, invasion and further colonization of RKN (Kyndt et al., 2012). Hao et al. (2012) showed that glutathione S-transferase which is probably involved in the detoxification of reactive oxygen species (ROS) that can be imposed by the stress of the cell's hypertrophy and necrosis following root-knot nematode infection in mycorrhizal tomato roots infection. (Vosetal., 2013). Similarly, Beneventietal. (2013) suggestedanimportantroleforROSgenerationintheresistance ofsoybeanto *M. javanica* astheyfoundthroughpyrosequencing anover–representationofgenescontainingvariousoxidaseand peroxidasedomainsupregulatedintheincompatibleinteraction.Similar results were reported on the MAPKmediateddefense-priming in soybean in responseto *Heteroderaglycines* infection (McNeece et al., 2019) and in rice against *M. graminicola*(Zhou et al., 2020).Arbuscular mycorrhizal fungi (AMF) may induce host tolerance against potato cyst nematode (PCN). Greater PCN densities reduce the increased tolerance that AMF may confer on their hosts. This may be due to reduced mycorrhizal colonisation of hosts under higher PCN infection and potentially a threshold at which the presence of PCN severely impacts fungal growth (Bell *et al.*,2022).Similar results were observed in banana using AMF Glomusintra radices against the migratory nematodes *Radopholussimilis* and *Pratylenchuscoffeae* (Elsen et al., 2008); reduction of *P. penetrans* infestation in apple seedlings by AMF (Ceustermans et al., 2018), and of *Meloidogyne arenaria* in red ginger by *Gigaspora albida*, *Claroideoglomusetunicatum*, and *Acaulosporalongula* (Da Silva-Campos et al., 2017), or the control of the migratory endoparasitic nematode *Scutellonemabradys* in yam by *F. mosseae* and *Glomus dussii* (Tchabiet al., 2016). The combined application of *F. mosseae, R. fasciculatus,* and *R. intraradices*was found to enhance the accumulation and activities of biomolecules and enzymes related to defense priming as well as antioxidation in the susceptible and resistant inbred lines of rice pre-challenged with *M. graminicola* (Malviya et al.,2023). Similarly, colonization of pines (*Pinus thunbergii*) promoted a lasting SAR against the pine wilt nematode *Bursaphelenchusxylophilus*, which is transmitted by beetles of the genus *Monochamus* and feeds by colonizing the vascular bundles (Nakashima et al., 2016). Interestingly, those fungi do not only act systemically controlling nematodes-infection but enhance plant defenses against pathogens transmitted by the nematodes.

4.6.Altered rhizosphere interactions

Plant roots typically have a close association with mutualistic rhizosphere microorganisms.Together, they exude a wide range of both primary metabolites and secondary metabolites.Such metabolites can modify the surface properties of nematodes and affect microbial attachment to nematode surfaces.An altered root exudation results in modifications in rhizosphere interactions (Kuila and Ghosh, 2022).Root exudates,viz., sugars and organic acids , amino acids, phenolic compounds,flavonoids, strigo-lactone varies in quantity and quality in mycorrhizal and non-mycorrhizal plants and even the plant or AMF species involved (Lioussanne et al., 2008). Differential root exudation is an important parameter used by the host plant for auto regulation of the symbiosis (Schaarschmidt et al., 2013).TheAMFsymbiosisleadstoan alteredrootexudationcompositionandlevelwhichcaninturnimpactthePPNinthe rhizosphereintermsofhatching,motility,chemotaxis,andhost location(Jones et al., 2004).Tomato roots with *F. mosseae* reduced the penetration and infection rates of *M. incognita* and *Pratylenchus penetrans* through altered root exudation ; alsoa temporalparalysisofthesecond-stageinfectivejuveniles(J2)in thepresenceofmycorrhizaltomatorootexudateswasobserved in *invitro* assays(Vos et al.,2012).Mycorrhizalroot exudatesreducedhostlocationandpenetrationby *R.similis* comparedtonon-mycorrhizalcontrolbananaplants(Vosetal., 2012). The plant hormone, strigolactones, after being exuded from the root, activate hyphal branching and enhanced growth and energy metabolism of symbiotic AMF, and once the symbiosis is established, its production by the plant roots decreases (Wu et al., (2022). However, the strigolactones do not contribute to cyst nematode (*Heteroderaschachtii*) hatching;instead they do play a role in host attraction and subsequent invasion. In rice, signaling mediated by strigo-lactones suppresses jasmonate accumulation and promotes RKN infection .Wu et al., (2022) stated that strigolactones play a positive role in nematode defense in tomato.Moreover, alteredrootexudationcanalsocauseachangeinmicrobial diversityintherhizosphere,andthereforeaffectplant-pathogen interactions(Lioussanne, 2010). Somereports showanincreaseinfacultativeanaerobicbacteria,fluorescent pseudomonads, *Streptomyces* speciesandchitinase-producing actinomycetes, and fungi (*Trichoderma*spp)afterAMFcolonization(Philippot et al., 2013).

5.Conclusion and future perspectives

Application of mycorrhizal amendments in the field is an attractive proposition for crop protection strategies as a valuable alternative to heavy reliance on pesticides that are increasingly restricted for environmental reasons .The integration ofempirical data knowledge in the field after the treatmentwith a particular strain or formulation of AMF, together withdetailed analysis of the plant responses at the molecular levelin a particular crop could help to a deep understanding ofthose complex interactions.Though AMF are not yet widely used in conventional agriculture, recent data help to develop a better insight into the modes of action, which will eventually lead toward future field applications of AMF against PPN.Rather than introducing AMF species that are foreignto the area, it may be beneficial to utilise native species in agriculturalsystems as they have evolved *in situ,* acclimating and adapting to thespecific environment and are therefore likely to have a higher chanceof success and persistence .

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