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

Abstract:

Plant-parasitic nematodes(PPN) are the major global menace to food production. Management methods based on synthetic chemicals is objectionable due to environmental and health risks. Therefore, use of biocontrol agents such as Arbuscular mycorrhizal fungi (AMF) is environmentally friendly options for management of plant-parasitic nematodes (PPN).Competition for nutrients and space,changing rhizosphere interactions, or increasing plant tolerance is themode of action of Arbuscular mycorrhizal fungi (AMF) against plant-parasitic nematodes (PPNs). Better knowledge of the mode of action of Arbuscular mycorrhizal fungi (AMF) will help to increase the efficacy of these biocontrol agents. This review presents a general idea of different mechanisms of Arbuscular mycorrhizal fungi (AMF)-mediated biocontrol, and their possible use in reducing plant-parasitic nematodes (PPN)population.

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 obligate parasites that can nourishfrom all plant parts,especially on roots. Though 4100 species of plant-parasitic nematodes has been described throughout the world, only a few genera is considered as major plant-pathogens, against many economically important crops”[1]. Worldwide plant-parasitic nematodes cause yield loss of 12.3% with USD$80 billion loss per annum. Due to change inclimate andcropping systems, it ispredictable to rise in yield loss [1].Market quality or visual imperfections also related with infection process which leads to additional losses.Plant-parasitic nematodes having different feeding pattern like ectoparasite, endoparasite, or semiendoparasite. During penetration inside the root by PPN they cause damage directly and the disease can be aggravated by other pathogens.Because of non-specific disease symptoms caused in the plant, and microscopic size, growers are often unaware of their presence and thereby nematode damage is likely to be ignored[2].However, the damages caused by PPN have been managed by reducing their population below threshold level byusing synthetic chemicals, both fumigant and non-fumigant nematicides. There are many disadvantages of usage of nematicides.Synthetic nematicides cause deterioration to the environment and human and domestic animal health besides high cost . Because of these, many nematicides are increasingly restricted.Therefore, other alternative methods to combat PPN are necessary. Microbial antagonists as biological control agents are one of the possible alternatives to chemical nematicides.Biocontrol agentsdepend on various environmental conditions for their efficacy. Therefore, special consideration should be given to its relationship to plant and environment.One of the projectedecofriendly options to manage PPNs is the use of biological control organisms, such as Arbuscular mycorrhizal fungi (AMF). These fungihave a symbiotic relationshipwith the host plant that can protect their host plant against biotic stress such as plant-parasitic nematodes (PPNs)[3].“AMF not only affects physio-biochemical pathways in the host plant but also reduced the penetration or invasion and colonization or reproduction of PPNs”[3].

2.Mycorrhizal Fungi

“Arbuscular mycorrhizal fungi (AMF) are having symbiotic relation with the host plantand are beneficial for the growth of host plants. AMF are found to becolonized in more than 80% of all land plant species”[4].These fungi are found in soil and act as bio-stimulators and bio-protectors [5,6]. Moreover, AMFcan increase the levels of N, P and Zn in the cropand thus act as natural biofertilizers[7].They nourish from the products of photosynthetic plants as well as lipids to grow and colonized [8].The common type of mycorrhizal association taking place in crops is the arbuscular type [9].AMF species are members of the phylum: Mucoromycota andsub-phylum:Glomeromycotina [10].SubphylumGlomeromycotina has 25 taxa and many orders, viz.,Glomerales, Archaeosporales, Paraglomerales, and Diversisporales.It has been observed that application of combination of different families are more efficient bioinoculant than mono-inoculant[6].

3.Interaction between Plant-parasitic Nematodes and AMF

Both the plant-parasitic nematodes (PPNs) and AMF requiresame resource from host plant roots. Interactive effects have been observed in those host plants[6,11].“The interactions between endoparasitic nematodes and AMF was observed to be stronger, i.e. more mutual effects of endoparasitic nematodes on AMF, than those between ectoparasites and AMF.AMF infected plants were damaged more by ectoparasites than by endoparasitic nematodes”[11].Migratory endoparasitic nematodes number was greater on AMF infected plants. Interactions appear to be very specific [11].“Among the sedentary endoparasites,based on closeness in root tissues, numbers of *Meloidogyne* sp. were reduced more by mycorrhizal infection than were those of

Heterodera sp. The AMF- nematode interactions arecomplexand depend onmany factors, viz., soil environment, AMF species, host plants, and nematodes species. Thereby the interaction is supposed to increase the resistance of plants to nematode infection”[12].

4.Biocontrol mechanism of AMF

Various mechanisms have been projected to play a role in the biocontrol efficacy of AMF against PPN.Competition for space or nutrients arisesbetween AMF and PPNs as they require same resource. Another mechanism is through plant-mediated effects which is anindirect effect.Indirect effectof AMF on plant is through the plant tolerance or plant defense induction and also through altered plant exudation results in altered rhizosphere interactions. Cameron et al.[13]stated that biocontrol of PPNs results from a combination of these different mechanisms.However, the comparative importance of a specific mechanism can vary depending on the AMF-nematode-plant interaction.

4.1.Protective effectsof AMF

Both abiotic as well as biotic stress (PPNs)can be alleviated by AMF. *In vitro*, green house and field experiments showedprotecting effects against PPNs by AMF in banana, coffee and tomato [14].Most of the phytopathogenic nematodes penetrateand damage the roots of their host plants [15].However, the overall effects vary with thenematode species and their mode of parasitism,surrounding environment,plant genotype. Some reports showed that AMF inoculation reduces thereproduction and infestationof phytopathogenic nematodesin plant roots[16,17].AMF inoculation in the nursery plant canenhanced tolerance to phytopathogenic nematodes and increases their growth [16].Veresoglou and Rillig[18]describedthrough meta-analyses,the suppressive effect of AMF on nematodes belonging to different genera of plant parasitic nematodes according to their feeding habit (sedentary or migratory).Usually, AMF have shown a significant reduction in nematodes population when healthy mycorrhizal diversity (different genera or species) present in the rhizosphere [19,20].The sedentary endoparasitism makes them more susceptible to changes in plant composition by AMF than are the migratory endoparasites. AMF reduced the numbers of the sedentary endoparasiticnematodes (*Meloidogyne, Heterodera*, and *Globodera*)and thesenematodes rarely infect regions colonized by VA fungi. Similarly,Ectoparasitic nematodes are more likely to be affected indirectly by AMF-induced changes in plant functioning(increased free amino acids in leaves,especially arginine,higher chitinase activity in roots,an increase in soluble sugars and phenols in roots) and thus reduced the numbers,e,g.*Tylenchorhynchus* spp.[19].Hol and Cook[21] observed an increase in migratoryendoparasitic nematode (*Pratylenchus* spp.,*Radopholus* spp.,*Hirschmanniella* spp.) numbers on inoculation with AMF. Due to penetration and movement of migratory nematodes, AMF can change root morphology of host plant and helps infungal colonization.Mycorrhizal *Phaseolus vulgaris*showed an initial increase followed by decrease in*Ditylenchus dipsaci*populationthan on non-mycorrhyzal controls; similarlyon tobacco,*Aphelenchoides ritzemabosi* populations decreased on mycorrhyzal compared to non mycocrhyzal plants [22].Some studies have shown that *Rhizophagus intraradices* and *Funneliformis mosseae* reduce tomato root penetration by false root-knot nematode *Nacobbus aberrans*[23]. Similarly,*Glomus intraradices, G. mosseae,* and *G. etunicatum*reduce*M. javanica*infection in peach trees [24].depending on the host genotypes, both positive and negative results have been observed, for example,the addition in root colonization by *Rhizophagus clarus, Claroideoglomus* etunicatum,*Gigaspora rosea, G. margarita, Scutellospora calospora*, and *S. heterogama* caused an increase in the population of *Pratylenchus brachyurus* in maize [25]but reduces population in cotton [12].

4.2.Higher NutrientUptake of host plant

“AMF normally act on the hostplant, helps in uptake of plant nutrient and water. AMF also can change root morphology by increasing root growth and branching, or can change the rhizosphere interactions”[26].“By receiving resources such asphotosynthetic carbon from their host, they improve plant growth and development and help plants to cope with various abiotic and biotic stresses”[27,28].“AMFareknowntobeabletoincrease theuptakeofwaterandmineralnutrients such as phosphate, zinc and nitrogen fortheirhostplant”[29,30].Bodker et al.,[31]proposed that“AMF-mediated biocontrol mechanism is due to the higheruptakeofphosphate”.Pettigrew et al.,[32]stated that “cotton fields with a better nutrient statusare able to tolerate higher population densitiesof sedentary semi-endoparasite,*Rotylenchulus reniformis*. AMF-mediated nutrient status of the host plant can increase or decrease the PPN population densities”.“Apositive correlation was observed between migratory ectoparasite(*Helicotylenchus* spp.)population densities and mineral content (Mg) in rice. A negativecorrelationwasobservedbetweenthemigratoryendoparisite (*Pratylenchuszeae*) andZnorFe,and between *M. incognita* andMgandCa” [31].

4.3.AlteredRootMorphology of host plant

AMF helps in better root growth and branching,often show increased root biomass production. Gutjahr and Paszkowski [33]observed that better AMF colonizationincreased secondary and tertiary root formation and improve the root morphology of rice.However, it has been observed thattap roots seems to profit more from AMF colonization than fibrous roots in terms of gained biomass and nutrient gaining [6]. Inhibition of root growth caused by PPNScan be corrected by anincreaseinrootvigor,byhighernutrient uptakecapacity.Elsen et al.[16]observed that "decreasedroot branchingdue to *Radopholussimilis* and *P.coffeae* in bananawasimproved bytheincreasedbranchingtheAMF,*Funneliformismosseae"* .

4.4.Competition for nutrients and space in host root

"PPNscompetefornutrientsorforspaceininfectionsiteswith AMF.In the ecological position both the organisms have thesamefood requirementsespecially carbon.Four to 20% carbonfrom of the total assimilated carbontransfer from the host plant to the AMF"[34]."Due to the difference in carbon sink strength in different AMF species mediate different levels of biocontrol. For example, the AMF,*R.irregularis* could not showbioefficacyagainst*R.similis* and *P.coffeae* in banana nor on *M. incognita* in tomato regardless of its higher carbon sink strength compared to *F.mosseae"*[28]."In AMF-PPN interactions,both of them compete for space alsoas they reside in the sam roots"[35]."In general, mycorrhizal arbuscules entirely form in the root cortex,migratory endoparasitic nematodes also found on the root cortex,forming anegative effects. However,competition for spacebetweenAMFandsedentaryendoparasiticnematodescan be observedincasethefeedingcellsextendintothecortex.The feeding cells form within the vascular cylinder due to root-knot nematode and cyst nematodes feeding may break the endodermis and spreadinto the cortex and competition for space occurs.The feeding cells of *Heterodera avenae* are restricted to cells within the endodermis and thus may not be affected by direct competition with AMF"[35]. DosAnjos et al.[36]showed bioefficacy of well established AMFsymbiosis on*M. incognita*invasion as well asreproductionwhereas co-inoculation of both organism had no effect.Alban etal.[17] found that pre-inoculation of *M. exigua* led to a significant increase in the subsequent colonization of AMF compared to un-inoculated mycorrhizal plants.Holand Cook[21] observed that AMFcolonizationwasreducedbyectoparasitic, migratoryendoparasiticandsedentaryendoparasiticnematodes. Ingreenhouseexperiments, *R.similis* and *P.coffeae* in banana affectedtheoccurrenceof *F.mosseae* colonization,butnotthe intensity[16].However in another experiment, it was observed that rootcolonization by

R.irregularis in *invitro* bananaplantletswasnotaffectedeither by *R.similis*[14] orby *P.coffeae* in transformed carrotroots[16].DosAnjosetal.[36]observed that *M. incognita* couldnegativelyaffectthesporulationoftheAMF,*Scutellospora heterogama* in sweetpassionfruit.The composition of the AMF community was different between infected and uninfected roots.delMarAlguaciletal.[37] reported thatthehighestAMFdiversitywasfoundinuninfectedroots comparedto *M. incognita* infectedroots. TheirresultsindicatethatAMF colonizationmightalsobesuppressedbyPPNs.However, AMF colonization dependonthe AMF speciesassomeAMFspecieswerenotaffectedbythePPNs.

4.5.Effects through induced systemic resistance in host plants

"AMFcan activate plant mediated resistance mechanisms to nematode infection. PPNinvasion orfurther development to adulthood is impared in such a resistant host plant. Phenylpropanoid pathway is the important host resistant mechanism involved in AMF colonized plant.Resistant mechanism involved in activation 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"[38]."The jasmonic acids (JA) dependent pathwayaffects the phenolic content in many crops and is able to mediate resistance to PPN" [39]."AMF colonized cells causes the activation of a JA-mediated resistancetermed as mycorrhizal induced resistance (MIR)"[40]. "The plant recognizes MAMPs (microbe-associated molecular patterns) which triggers a defensive response. Later on, the recognition of effectors released by the fungus in response to plant defenses activates a more specific defensive response"[41]."Inmaize,thepresenceofthe9- LOXgene(ZmLox3) provedtobenecessaryforresistanceagainst *M. incognita"*[42]."Several other plant genes wereupregulatedwhen AMF andnematodewerebothpresentintheroot,indicating a primingofthesedefensegenes.Such type of genes were reported in *R.irregularis* colonized grapevine after infection by the ectoparasite,*X. index*[43]andbanana against *R.similis* and *P.coffeae"*[16].Theproductsofthesegenes includechitinase1bwhich involved in a protective mechanism against the PPN. Li et al.[44] reported a class III chitinase gene in *Glomus versiforme* colonized grapevine roots after infection by *M. incognita*. Further expression of this gene in transgenic tobacco plants enhanced the resistance against the root-knot nematode, but did not affect the AMF. This gene affected the viability of the eggs and also reduced the amount of egg-masses and thus productivity of the females [45].APR10proteinisolatedfrom

Crotalariapallida showsnematostaticandnematicidaleffects mostly targeting a digestive proteinase of the nematode,*M. incognita*[46]. The shikimate pathway has been concerned in AMF-mediated resistance in different plant species against many nematodes [47]. Genes of 5-enolpyruvyl shikimate-3-phosphatesynthase (ESPS) and a heat shock protein70-interacting protein (HIP) were also found[43].“They are helpful in regulation of the auxin synthesis which is of importance for nematode feeding site formation and their location [48].Theshikimatepathwayproduces precursorsforvariousaromaticsecondarymetabolitese.g.,flavonolsynthaseagainst *M. incognita*, *R.similis*, and *P. penetrans*”[47].Mitogen-activated protein (MAP) kinase (MAPK)signaling pathways play a vital role in hypersensitive response (HR) , immune responses, and oxidative burst to pathogen attack byrestricting the penetration, invasion and reproduction of root-knot nematode[49].Hao et al.[43] showed that glutathione S-transferase which is 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.Similarly, Beneventietal.[50] suggestedanimportantroleforROSgenerationintheresistance ofsoybeanto *M. javanica* astheyfoundanover-representationofgenescontainingvariousoxidaseand peroxidasedomainsupregulatedintheincompatibleinteraction.Similar results were reported on the MAPKmediateddefense-priming in soybean in responseto *Heterodera glycines* infection [51] and in rice against *M. graminicola*[15]. AMF may induce host tolerance against potato cyst nematode (PCN). However, host tolerance depends of PCN density[52].Similar results were observed using AMF against the migratory nematodes *R. similis* and *P. coffeae*in banana [16];*P. penetrans* in apple seedlings [53] and *M. arenaria* in red ginger by *Gigaspora albida*, *Claroideoglomus etunicatum*, and *Acaulospora longula*[54] or migratory endoparasite, *Scutellonema bradys* in yam by *F. mosseae* and *Glomus dussii*[55].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 mechanism as well as antioxidation in the susceptible and resistant inbred lines of rice infected by *M. graminicola*[56].Similarly, colonization of pines (*Pinus thunbergii*) promoted a lasting resistance against the pine wilt nematode *Bursaphelenchus xylophilus*, which is transmitted by *Monochamus* and feeds by colonizing the vascular bundles [57]. 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

Naturally plant roots have a close relationship with rhizosphere microorganisms.Plant root exude a wide range of both primary metabolites and secondary metabolites, viz., sugars and organic acids , amino acids, phenolic compounds, flavonoids, or strigo-lactone. These metabolites varies in quantity and quality [58]. Auto regulation of the symbiosis of AMFdepends on kinds of root exudate[59].An altered root exudation results in modifications in rhizosphere interactions [60].These exudates can affect microbial attachment to nematode surfaces.Rootexudate, theircompositionandleveldue to AMF-PPN interaction effecthatching,motility,andhost locationof nematodes [61].Tomato roots colonized by *F. mosseae*makes temporal paralysis of the second-stage infective juveniles (J2) and reduced the penetration and infection rates of *M. incognita* and *P. penetrans*[62].Similarly, mycorrhizalroot exudatesimpared hostlocationandpenetrationby *R.similis* comparedtonon-mycorrhizalbananaroot[63].After being exuded from the root,the plant hormone, strigolactones, activate hyphal branching and enhanced growth and energy metabolism of AMF. However, the strigolactones play a role in host attraction and subsequent invasion of*H.schachtii*. In rice also, signaling mediated by strigolactones suppresses jasmonate accumulation and promotes root-knot nematode infection [64]..Wu et al.,[64]observed that strigolactones help in nematode defense in tomato.Moreover, rootexudatescanalsocauseachangeinmicrobial diversitylikefacultative anaerobic bacteria,*Pseudomonas fluorescens*, *Streptomyces* species and chitinase-producing actinomycetes, and fungi (*Trichoderma* spp.) intherhizosphere andthereforeaffectplant-pathogen interactions[29;65].

5.Conclusion and future perspectives

AMF 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.Application of AMF may be enormously advantageous to sustainable agriculture by preserving plant productivity and alleviating soil-borne plant pathogens especially plant-parasitic nematodes. Mycorrhizal amendments in the field are an ecofriendlyplanand act as a valuable alternative to nematicides.The integration ofexperimental data knowledge in the fieldin a particular crop after the treatmentwith a particular strain or formulation of AMF, together withdetailed analysis of the plant responses could help to a profound understanding ofthose complex interactions.It is beneficial to utilize native species rather than introducing exotic strains to the area. Isolation and identification of new strains, their mode of actionwill help will eventually lead toward future field applications of AMF against PPN.

Disclaimer (artificial intelligence)

Authorhereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of this manuscript.

Competing interests

Author has declared that no competing interests exist.

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