

## Decoding plant immunity through mutualistic coordinated functions of Arbuscular Mycorrhizal Fungi and *Trichoderma* spp.

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### ABSTRACT

Arbuscular mycorrhizal fungi (AMF) and *Trichoderma* spp. are pivotal, yet distinct, architects of rhizosphere health whose combined activities offer a powerful, sustainable route to crop protection. This review synthesizes current knowledge on the molecular, biochemical, and ecological facets of AMF–*Trichoderma* interactions that underpin coordinated plant immunity. AMF initiate symbiosis through strigolactone-mediated signaling and Myc-factor perception via the common symbiosis signaling pathway, leading to arbuscule formation, enhanced nutrient exchange and systemic priming. Complementarily, *Trichoderma* spp. exerts direct antagonism against pathogens through mycoparasitism, hydrolytic enzymes and secondary metabolites, while also eliciting host defenses and inducing pathogenesis-related proteins. Co-inoculation studies reveal synergistic outcomes improved root colonization, amplified antioxidant and defense enzyme activities, modulation of SA/JA/ET signaling, and reshaping of the rhizosphere microbiome toward disease-suppressive states. We evaluate evidence from pot and field experiments, highlight mechanistic overlaps between mycorrhiza-induced resistance and *Trichoderma*-mediated ISR, and discuss how common mycorrhizal networks may amplify interplant defense signaling. Critical gaps are identified, including the molecular basis of compatibility, strain-specific effects, formulation challenges, and long-term ecosystem impacts. We advocate integrative approaches combining multi-omics, controlled ecological trials, and formulation science to translate laboratory insights into robust bioinoculant strategies. By decoding this underground cross-talk, the review frames AMF–*Trichoderma* consortia as a promising, ecologically grounded component of next-generation crop health management, preferable in climate resilient agroecosystems.

**Keywords:** AMF; *Trichoderma*; ISR; MIR; Plant development; Rhizosphere; Biocontrol

### INTRODUCTION

Arbuscular Mycorrhizal Fungi (AMF), the hidden treasure chest beneath the soil constitutes an indispensable component of the subterranean “wood-wide web.” Representing one of the most ancient fungal lineages, AMF have fossil records extending over 400 million years, signifying their primordial role in the terrestrial colonization of plants and establishment of root symbioses (Nadeem *et al.*, 2017 ;). Their ecological ubiquity and functional diversity make them vital to plant health and soil ecosystem stability. Nearly 80–90% of vascular plants, including approximately 90% of cultivated crops, establish symbiotic associations with AMF (Diagne *et al.*, 2020). The ecological significance of AMF and other beneficial microbes extends beyond nutrient acquisition (Srivastava and Bora, 2023). These fungi in association with other microbes facilitate improved uptake of phosphorus, nitrogen, and trace minerals while enhancing water relations and plant resilience

under abiotic stresses such as drought, salinity, and heavy metal toxicity (Bora and Bora, 2008a; 2020; Chen *et al.*, 2020), thereby paving the way for bioprospecting soil-plant health (Srivastava *et al.*, 2022), by exploiting the microbial diversity of rhizosphere to rhizosphere hybridization (Srivastava *et al.*, 2025). Moreover, as the most widespread and biomass-dominant group among mycorrhizal fungi, AMF play a pivotal role in the suppression of soil-borne pathogens through a repertoire of antagonistic and inhibitory interactions (Berg, 2009). Mycorrhizal colonization not only enhances plant growth and nutrient dynamics but also contributes to root disease mitigation by fortifying cell walls through lignification and callose deposition, competing with pathogens for infection sites, and altering the rhizospheric microbiome to favour beneficial antagonists (Sikes *et al.*, 2009).

Complementing the beneficial effects of AMF, *Trichoderma* species have emerged as potent biocontrol agents (BCAs) with broad-

spectrum efficacy against phytopathogens of annual (Sharma *et al.*, 2020;2021 ; Bora *et al.*, 2023) as well as perennial crops( Saikia *et al.*, 2021; Bora *et al.*, 2021a ; 2021b; Bora and Bora, 2022) . These fungi colonize plant roots and the rhizosphere, where they enhance plant vigour and immunity through multiple mechanisms, including the secretion of hydrolytic enzymes (chitinases, glucanases, and proteases) and the production of secondary metabolites such as antibiotics and volatile organic compounds (VOCs) (Harman *et al.*, 2004; Mukherjee *et al.*, 2011). Economically important species, including *T. harzianum*, *T. asperellum*, *T. viride*, *T. atroviride*, *T. virens*, and *T. reesei*, are widely exploited for their multifaceted roles in promoting plant growth and suppressing soil-borne pathogens (Sharma *et al.*, 2014 ;Bora *et al.*, 2020a,b ;2022). These facts underline the importance of microbes in plant health solutions. The compatibility between AMF and *Trichoderma* species presents a promising synergistic strategy in the biological management of soil-inhabiting pathogens. Studies indicate that co-inoculation of these beneficial microbes can amplify plant growth responses, nutrient uptake, and systemic resistance (Bharat, 2016). Notably, *Trichoderma* spp. has been identified as one of the most effective BCAs against many soil and foliar pathogens significantly reducing disease incidence and enhancing plant biomass under various application regimes (Asad *et al.*, 2014; Bora *et al.* 2023; Tabing *et al.*, 2025) , besides its compatibility with agrochemicals (Bharadwaz *et al.*, 2023) and non-target pests (Bharadwaz *et al.*, 2024) for engineering plant biometrics ( Bora *et al.*, 2025).While, AMF primarily function through mutualistic nutrient exchange and systemic defensepriming, *T. asperellum* exerts its influence via antagonistic biocontrol mechanisms. Their combined application thus represents a holistic and complementary approach to crop management integrating symbiotic enhancement with pathogen suppression. Harnessing this dual functionality could revolutionize sustainable agriculture by reducing chemical dependencies and fortifying plants against biotic and abiotic stresses.

## AMF–PLANT ASSOCIATION FOR MULTIPLE BENEFITS

The establishment of arbuscular mycorrhizal symbiosis represents one of the most sophisticated examples of interkingdom communication, underpinned by a finely tuned molecular dialogue between plants and fungi. Akiyama *et al.* (2005) demonstrated that the initiation of AMF–plant interaction begins when plant roots exude strigolactones into the rhizosphere, serving as signaling molecules that stimulate hyphal branching and metabolic activation in arbuscular mycorrhizal fungi. In response, AMF release lipochitooligosaccharide-based Myc factors, which are perceived by the plant through LysM-type receptor kinases. This recognition event activates the common symbiosis signaling pathway, a conserved signaling cascade also employed during rhizobial nodulation (Parniske, 2008; Maillet *et al.*, 2011).The early stages of colonization involve the formation of hyphopodia on the root epidermis, specialized structures that mediate fungal adhesion and penetration into the outer cell layers (Genre *et al.*, 2005). Following successful entry, fungal hyphae proliferate both interand intracellularly through the cortical tissue, culminating in the differentiation of highly branched arbuscules. These arbuscules act as the primary sites of nutrient exchange, facilitating bidirectional transfer primarily of phosphorus from the fungus to the plant, and photosynthetically derived carbon from the host to the fungus (Smith and Read, 2010).

The establishment and maintenance of functional arbuscules are tightly regulated by plant-derived transcriptional networks. Key transcription factors such as RAM1 and MYB1 orchestrate the activation of symbiosis-specific genes essential for arbuscule development and turnover (Luginbuehlet *et al.*, 2017). Additionally, phytohormones including abscisic acid, gibberellins, and ethylene exert modulatory effects on the extent and intensity of AMF colonization, reflecting a complex hormonal crosstalk that fine-tunes symbiotic compatibility (Mukherjee and Ané, 2011).Collectively, the colonization strategy of AMF embodies a highly conserved yet remarkably adaptable process that has co-evolved with terrestrial plants. This intricate molecular synergy underscores the central role of AMF as pivotal mediators of

nutrient exchange, signaling integration, and ecosystem stability across both natural and agricultural systems.

### AMF FOR PLANT GROWTH PROMOTION AND NUTRIENT ACQUISITION

AMF represent an integral component of plant health and soil fertility, profoundly influencing plant growth, nutrient uptake, and overall physiological performance (Srivastava and Bora, 2023 ; Bora *et al.*, 2024 ). The symbiotic association between AMF and plant roots significantly enhances nutrient acquisition efficiency, particularly under nutrient-limited or stress-prone conditions (Begum *et al.*, 2019). By extending an extensive extraradical hyphal network beyond the rhizosphere, AMF effectively expand the absorptive surface area of roots, facilitating the uptake of key macronutrients such as nitrogen (N), phosphorus (P), and potassium (K), as well as essential micronutrients including zinc (Zn) and iron (Fe) (Smith and Smith, 2011; Lehmann *et al.*, 2014 ; Srivastava *et al.*, 2023).

Phosphorus acquisition is one of the most widely documented benefits of AMF symbiosis due to its low solubility and mobility in soil. Through their hyphal extensions, AMF can access phosphate ions from soil regions beyond the depletion zone surrounding roots, thereby increasing phosphorus availability to host plants. AMF colonization has been shown to enhance plant phosphorus uptake by 20–80%, depending on soil conditions and fungal species involved (Heijden *et al.*, 2015). Nitrogen, though less extensively studied in AMF systems, is also acquired through fungal networks, with AMF facilitating the uptake of both inorganic (ammonium and nitrate) and organic nitrogen forms (Hodge and Fitter, 2010). Furthermore, interactions between AMF and nitrogen-fixing or mineralizing soil microbes can indirectly augment nitrogen availability to plants (Govindarajulu *et al.*, 2005; Leigh *et al.*, 2009). Potassium uptake, though more mobile in soil, is similarly enhanced by AMF associations, as colonization improves root morphology and alters rhizosphere chemistry, thereby promoting solubilization and efficient translocation of K (George *et al.*, 1995; Garcia and Zimmermann, 2014). Beyond their role in nutrient uptake, AMF profoundly influence plant physiology and stress resilience. The symbiosis enhances water

uptake and retention, improving relative water content and water-use efficiency under drought stress (Ruiz-Lozano *et al.*, 2016). Plants colonized by AMF exhibit improved photosynthetic performance through enhanced stomatal regulation, elevated chlorophyll content, and greater photosystem II efficiency. The presence of AMF also upregulates antioxidant enzymes such as peroxidase (POD), catalase (CAT), and superoxide dismutase (SOD), which mitigate oxidative damage under environmental stress (Dey and Ghosh, 2022). Additionally, AMF promote the accumulation of osmoprotectants like proline, contributing to salinity and drought tolerance (Evelin *et al.*, 2009). The influence of AMF extends to the modulation of plant hormonal balance, stimulating the synthesis of growth-regulating phytohormones such as auxins, cytokinins, and gibberellins, which collectively promote enhanced root and shoot development (Ludwig-Müller, 2010; Bucher *et al.*, 2009). At the ecosystem level, AMF contribute to soil aggregation and structural stability through the secretion of glomalin-related soil proteins, which improve aeration, water retention, and microbial habitat quality (Rillig, 2004; Miransari, 2011). Altogether, the AMF–plant symbiosis represents a cornerstone of sustainable crop production systems, providing a natural and multifaceted mechanism for improving plant nutrition, productivity, and resilience while reducing dependence on chemical fertilizers.

### AMF-MEDIATED PLANT DEFENSE AGAINST PHYTOPATHOGENS

AMF play a dual role in modulating plant immunity initially suppressing host defenses to facilitate symbiotic establishment, and subsequently enhancing systemic resistance against diverse pathogens. Fiorilli *et al.* (2024) demonstrated that AMF alter plant immunity through a finely tuned regulatory process, beginning with transient suppression of the basal immune response to allow fungal colonization. During early symbiotic signaling, plant roots secrete strigolactones that activate AMF hyphae, which in turn release lipochitoooligosaccharide-based Myc factors. These are recognized by LysM-type receptor kinases such as OsCERK1 and OsMYR1, triggering the Common Symbiosis Signaling Pathway characterized by nuclear

calcium spiking rather than cytosolic  $\text{Ca}^{2+}$  influx, thereby enabling colonization without eliciting immune rejection (Carotenuto *et al.*, 2017).

To maintain compatibility, AMF secrete effector proteins that modulate plant immune responses. Notably, SP7 and RiSLM, two well-characterized effectors, interact with plant transcription factors such as ERF19 and bind to chitin fragments, thereby masking fungal cell wall components from host chitinases and preventing defense gene activation (Kloppholz *et al.*, 2011; Zeng *et al.*, 2020). Once symbiosis is established, AMF-mediated signaling contributes to the activation of a broad spectrum of defense mechanisms, including enhanced nutrient uptake, competitive exclusion of pathogens, induction of systemic resistance, and modulation of host immune networks (Smith and Read, 2011).

Experimental evidence supports the protective role of AMF against multiple pathogens. For instance, *Rhizophagus irregularis* suppressed *Plasmopara viticola* infection in grapevine by modulating the biosynthesis of stilbenoids and inhibiting pathogen effector activity (Cruz-Silva *et al.*, 2021). Similarly, *Funneliformis mosseae* colonization in tomato upregulated genes associated with flavonoid and chlorogenic acid biosynthesis, conferring resistance to Tomato Mosaic Virus (Aseel *et al.*, 2019). Such mycorrhiza-induced metabolic reprogramming primes the plant for rapid and amplified defense upon pathogen challenge. However, similar reprogramming in microbial diversity of rhizosphere as well as endosphere of host plant either with invasion of pathogen (Bora *et al.*, 2019; Das *et al.*, 2023; Kumari *et al.*, 2023) or inoculation with microbial antagonist are widely reported (Bora *et al.*, 2016a; 2016b; 2020a) through the release of wide ranging secondary metabolites as plant defense molecules (Bora *et al.*, 2023). Plants associated with AMF often exhibit primed immunity, a physiological state characterized by faster and stronger activation of defense responses upon infection. Primed plants show elevated reactive oxygen species (ROS) accumulation, callose deposition, and increased pathogenesis-related (PR) protein levels (Mauch-Mani *et al.*, 2017). Recognition of microbial signals occurs via pattern-recognition

receptors (PRRs) and resistance (R) proteins, initiating pattern-triggered immunity (PTI) and effector-triggered immunity (ETI), respectively (Couto and Zipfel, 2016; Bigeard *et al.*, 2015). AMF-mediated immunity (MIR) shares mechanistic similarities with both induced systemic resistance (ISR) and systemic acquired resistance (SAR), leading to broad-spectrum, long-lasting protection against biotic stresses (Fiorilli *et al.*, 2024).

Phytohormones play a pivotal role in orchestrating AMF-induced defense. Liao *et al.* (2018) reported that nearly all major plant hormones participate in regulating AMF symbiosis, with dynamic shifts in their levels across colonization stages. Salicylic acid (SA) exhibits a biphasic response initially accumulating to mediate early recognition and subsequently acting to prevent over-colonization (Jung *et al.*, 2012). Conversely, jasmonic acid (JA) and its active form JA-Ile remain consistently upregulated, enhancing resistance through MYC2-dependent pathways (Fiorilli *et al.*, 2024). Ethylene (ET) and abscisic acid (ABA) function as fine-tuning regulators, particularly under nutrient limitations or during callose deposition (Martínez-Medina *et al.*, 2016).

Mycorrhiza-induced resistance (MIR) predominantly operates through JA and ET signaling networks, activating genes such as AOS1, AOC1, and OPR3 (JA biosynthesis), NCED (ABA biosynthesis), and PAL, a key enzyme in the phenylpropanoid pathway (Pozo and Aguilar, 2007; López *et al.*, 2010; Pieterse *et al.*, 2014). Remarkably, AMF can transmit defense-related signals through common mycorrhizal networks (CMNs), enabling interplant communication. This facilitates systemic immunity across neighbouring plants via mobile signals, including JA and SA (Song *et al.*, 2010). Collectively, AMF-mediated plant defense integrates transcriptional, biochemical, and physiological mechanisms, reinforcing both local and systemic immunity. The capacity of AMF to modulate complex immune signaling while maintaining mutualistic harmony underscores their immense potential as natural allies in sustainable biocontrol strategies and resilient crop production systems. The biocontrol efficacy of AMF against a variety of pathogens has further been summarised (Table 1).

Table1: Biocontrol efficacy of different AMF species against various phytopathogens

Host Plant	Disease / Pathogen	AMF Strain	Responses related to AMF Inoculation	References
Multiple crops	<i>Phytophthora</i> spp., <i>Rhizoctonia solani</i> , <i>Thielaviopsis basicola</i> , <i>Fusarium oxysporum</i>	<i>Glomus mosseae</i> , <i>G. intraradices</i> , <i>G. etunicatum</i>	Demonstrated broad-spectrum suppression of soil-borne phytopathogens through mycorrhizal colonization and improved plant vigour.	Schönbeckand Dehne (1977); Steinkellner <i>et al.</i> (2012)
<i>Solanum lycopersicum</i> L.	<i>Meloidogyne javanica</i>	<i>Funneliformismosseae</i>	Caused reduction in galling, nematode reproduction, and morphometric parameters of females in tomato plants inoculated.	Siddiqui <i>et al.</i> (1998)
<i>Solanum lycopersicum</i>	Wilt ( <i>Fusarium oxysporum</i> )	<i>Funneliformismosseae</i>	Reduced pathogen population and wilt incidence; enhanced plant growth and phosphorus uptake.	Khallalet <i>et al.</i> (2007)
<i>Zea mays</i> L.	<i>Striga hermonthica</i> Del Benth (1836)	<i>Glomus etunicatum</i> , <i>Scutellospora fulgida</i> , <i>G. margarita</i>	Reduced <i>Striga</i> plant incidence, increased plant biomass and phosphate content.	Othiraet <i>et al.</i> (2012)
<i>Solanum tuberosum</i>	Bacterial wilt ( <i>Ralstonia solanacearum</i> )	<i>Glomus intraradices</i> , <i>G. etunicatum</i>	Combination treatments resulted in zero disease severity and highest root colonization (36–50%), indicating strong suppression of bacterial wilt and enhanced plant health.	Tahatet <i>et al.</i> (2012)
Multiple crops	<i>Meloidogyne incognita</i> , <i>Heterodera glycines</i>	<i>Glomus mosseae</i> , <i>G. fasciculatum</i>	Reduced nematode infection via defensive gene activation and competitive root colonization.	Vos <i>et al.</i> (2013); De Sá and Campos (2020)
<i>Solanum tuberosum</i>	Potato virus Y (PVY)	<i>Rhizophagus irregularis</i>	Milder symptoms and significant stimulation of shoot growth observed in PVY-infected plants inoculated with AMF.	Thiem <i>et al.</i> (2014)
<i>Morus</i> spp.	<i>Pseudomonas syringae</i> pv. <i>syringae</i>	<i>Glomus fasciculatum</i> + phosphate	Co-inoculation reduced disease incidence and improved plant health parameters.	Kamble and Agre (2014)
<i>Solanum lycopersicum</i>	Leaf spot ( <i>Alternaria alternata</i> )	<i>Glomus fasciculatum</i>	Successful prevention of <i>A. alternata</i> -induced infection; improved physiological performance.	Nair <i>et al.</i> (2015)
<i>Glycine max</i>	<i>Pseudomonas syringae</i> pv. <i>glycinea</i> (Psg)	<i>Entrophospora infrequens</i>	Only <i>E. infrequens</i> significantly reduced pathogen colonization; enhanced leaf biomass and stem mass, highlighting species-specific bioprotection.	Malik <i>et al.</i> (2016)
<i>Cucumis melo</i> L.	Fusarium wilt	<i>Funneliformis mosseae</i>	Showed the greatest capacity for reduction of disease incidence.	Martínez-edina <i>et al.</i> (2011)
<i>Saccharum officinarum</i> L.	<i>Striga hermonthica</i> Del Benth (1836)	<i>Glomus etunicatum</i> , <i>Scutellospora fulgida</i> , <i>G. margarita</i>	Stimulated plant growth, biomass, and physiological parameters in presence of <i>Striga</i> .	Manjunatha <i>et al.</i> (2018)
<i>Solanum lycopersicum</i>	Bacterial wilt ( <i>Ralstonia solanacearum</i> )	<i>Glomus mosseae</i>	Complete suppression of disease; increased shoot/root biomass, spore count, and nutrient uptake.	Aguk <i>et al.</i> (2018)
<i>Glycine max</i>	Root pathogens (unspecified) under N fertilization	<i>Rhizophagus irregularis</i>	Co-inoculation improved biomass and chlorophyll content, demonstrating enhanced disease resistance and nutrient-use efficiency.	Spagnoletti <i>et al.</i> (2020)
<i>Vitis vinifera</i>	Downy mildew ( <i>Plasmopara viticola</i> )	<i>Rhizophagus irregularis</i>	Altered expression of effector genes linked to pathogen virulence; disrupted infection mechanism and improved host resistance.	Cruz-Silva <i>et al.</i> (2021)
<i>Solanum lycopersicum</i>	<i>Botrytis cinerea</i> ; <i>Pseudomonas syringae</i> pv. <i>tomato</i> (Pst) and pv. <i>oryzae</i>	<i>Gigaspora margarita</i>	Induced systemic resistance; JA-mediated signalling enhanced, offering broad-spectrum protection against fungal and bacterial pathogens.	Fujita <i>et al.</i> (2022)

## TRICHODERMA: THE MULTIFUNCTIONAL FUNGUS

The genus *Trichoderma* is an ubiquitous Deuteromycotina fungus widely found in the soil, rhizosphere, plant endosphere, air, phylloplane, tree barks etc. have long been explored in agriculture and industry (Saikia *et al.*, 2022a; Handique *et al.*, 2024). The genus includes around 370 species including the commercially used species viz., *T. viride*, *T. asperellum*, *T. harzianum*, *T. hamatum*, *T. Koningii*. In agriculture it is used as bioagent against phytopathogens, growth and germination enhancer, as well as for biodegradation of organic pollutants (Rahman *et al.*, 2021; Bora *et al.*, 2024). As a bioagent against plant pathogens *Trichoderma* has been widely used in organic and conventional crop management system against many soil borne pathogens such as *Ralsonia solanacearum* in solanaceous crops (Bora and Bora, 2008b; 2010) as well as foliar pathogens such as *Pestalotiopsis* in tea (Bora *et al.*, 2022), *Colletotrichum* spp. in chilli (Saikia *et al.*, 2022 b), *Xanthomonas oryzae* pv *oryzae* in rice (Saikia *et al.*, 2020; Bora *et al.*, 2025) etc. The bioagent showed its efficacy through in vitro and in planta studies against *Fusarium oxysporum* f.sp. *cubense* causing wilt disease (Damodaran *et al.*, 2023; Baruah *et al.*, 2024), the most devastating pathogen with wide genetic variability (Baruah *et al.*, 2025). Efficacy of *Trichoderma* as entomopathogen is also being reported by many workers (Saha *et al.*, 2025) adding more value to the bioagent. The biocontrol potential of *Trichoderma* is attributed to its direct antagonism as well as its ability to modulate host defense through ISR as indirect mechanism. *Trichoderma* produce many volatile and non volatile pesticidal secondary metabolites which directly target the pathogens. Further its aggressive colonization, hyperparasitism and growth promoting traits makes it a more suitable microbial candidate in agroecosystem (Bora and Rahman, 2022.). However, instead of using *Trichoderma* alone, microbial consortia is found more superior and hence, efforts are being made to explore developing synthetic microbial communities (Sharma and Bora, 2025). Inclusion of *Trichoderma* with entomopathogens such as *Beauveria bassiana*, *Bacillus thuringiensis* (Erla

*et al.*, 2022; Yein *et al.*, 2024) besides AMF can take care of multiple issues in one go.

## SYNERGISTIC INTERPLAY BETWEEN AMF AND TRICHODERMA SPP

The synergistic association between AMF and *Trichoderma* species has emerged as an ecologically sound and sustainable strategy for enhancing plant growth, nutrient acquisition, and resistance against soil-borne pathogens. AMF form mutualistic associations with the roots of most terrestrial plants, improving mineral nutrient uptake particularly phosphorus and conferring tolerance to biotic and abiotic stresses (Rahman *et al.*, 2023). Likewise, *Trichoderma* spp. are well-recognized rhizosphere-competent fungi exhibiting multiple mechanisms of biocontrol, including mycoparasitism, antibiosis, and induced systemic resistance. When these beneficial microorganisms are co-inoculated, they often exhibit synergistic effects that exceed the benefits conferred by either organism alone (Saha *et al.*, 2025). Early investigations demonstrated that the combined inoculation of AMF with other beneficial microbes such as *Bacillus subtilis*, *Pseudomonas fluorescens*, and *Trichoderma harzianum* significantly enhanced the suppression of soil-borne pathogens including *Fusarium oxysporum*, *Verticillium dahliae*, and *Sclerotium rolfsii* (Srivastava *et al.*, 2010; Tanwar *et al.*, 2013). The synergism between AMF and *Trichoderma* spp. is largely attributed to their complementary functional roles like strengthening the plant's physical and nutritional defense systems, while *Trichoderma* actively suppresses pathogens through enzymatic degradation, antibiotic secretion, and competitive exclusion (Martínez-Medina *et al.*, 2016).

The co-inoculation of AMF and *T. asperellum* has been shown to markedly improve root colonization, nutrient assimilation, and activation of host defense mechanisms compared to single inoculations (Basu *et al.*, 2021). This combined inoculation also induces significant shifts in the rhizosphere microbiome, fostering beneficial microbial communities that are suppressive to phytopathogens (Verma *et al.*, 2020). Martínez *et al.* (2011) reported that in melon (*Cucumis melo*) challenged with *Fusarium oxysporum* f. sp. *melonis*, the co-application of four AMF species with *T. harzianum* enhanced

AM root colonization particularly with *Glomus constrictum* and *G. intraradices* and resulted in improved shoot biomass, nutrient status, and reduced wilt severity compared with AMF alone. Similarly, Yuan *et al.* (2016) observed that the combined application of *Glomus mosseae* (Gm) and *T. harzianum* (BOF) achieved 68.2% control efficacy against tobacco bacterial wilt caused by *Ralstonia solanacearum*, which was substantially higher than that achieved by either Gm or BOF alone. Co-inoculated plants also exhibited increased height and biomass accumulation, demonstrating the synergistic potential of this dual bioinoculant approach. At the biochemical and molecular levels, both AMF and *T. asperellum* are capable of activating systemic plant defenses. Jung *et al.* (2012) demonstrated that AMF colonization enhanced the activities of peroxidase (POD), polyphenol oxidase (PPO), and phenylalanine ammonia-lyase (PAL), enzymes closely associated with lignification and the biosynthesis of antimicrobial phenolic compounds. Concurrently, *T. asperellum* stimulates the expression of pathogenesis-related (PR) proteins, including PR-1, PR-3, and PR-5, which play essential roles in defense against fungal pathogens (Shoresh *et al.*, 2010). Both organisms are known to modulate key phytohormonal signaling pathways, particularly those mediated by salicylic acid (SA), jasmonic acid (JA), and ethylene (ET), thereby generating an integrated and durable defense response (Basu *et al.*, 2021). Beyond their influence on plant physiology, the synergistic interaction between AMF and *T. asperellum* also exerts beneficial effects on soil ecological functions. Rilliget *et al.* (2015) reported that their co-inoculation enhances microbial diversity and nutrient cycling within the rhizosphere. AMF hyphal networks promote soil aggregation and carbon sequestration, while *T. asperellum* enhances enzymatic activities such as dehydrogenase and phosphatase, contributing to improved nutrient mineralization and soil fertility. Collectively, these findings underscore the multifaceted advantages of integrating AMF and *Trichoderma* spp. in crop management systems. Their synergistic interplay not only enhances plant growth and disease resistance but also contributes to soil health restoration and ecological sustainability. Thus, the combined use of AMF and *Trichoderma* represents a promising biotechnological approach for the development

of resilient and environmentally sustainable agroecosystems.

## CONCLUSION AND FUTURE PROSPECTS

The accumulated evidence positions arbuscular mycorrhizal fungi and *Trichoderma* spp. as complementary and potent allies for sustainable crop health. Their combined actions enhanced nutrient acquisition and water relations via AMF, together with direct pathogen suppression and defense elicitation by *Trichoderma* create a multifaceted barrier against biotic and abiotic stresses while improving soil structure and ecosystem functioning. Co-inoculation frequently yields synergistic gains in root colonization, defense enzyme activation, hormonal coordination (SA/JA/ET), and the assembly of disease-suppressive rhizosphere communities, indicating clear potential for integration into next-generation IPM strategies. However, realizing this potential at scale requires overcoming important constraints: pronounced strain- and host-specific responses, variable field performance under heterogeneous agronomic conditions, and challenges in formulation, delivery, and regulatory acceptance. Addressing these gaps demands standardized compatibility screening, multi-omics and ecological trials across diverse environments, durable formulation technologies, and long-term monitoring of ecosystem impacts.

Future studies should focus on overcoming the limitations of morphological identification of AMF, which is often hindered by spore plasticity and interspecific similarities. Incorporating molecular tools such as DNA barcoding and metagenomics will allow accurate species-level identification and selection of efficient strains (Sharam and Bora, 2025). Multi-omics approaches, including transcriptomics and proteomics, are essential to unravel the molecular basis of AMF–*Trichoderma asperellum* interactions and their impact on host plant defense and physiology. Furthermore, standardizing application methods, dosage, and co-inoculation protocols, followed by extensive field validation across diverse agro-ecological zones, is necessary for large-scale adoption. Developing stable and effective bioformulations combining AMF and *T. asperellum* will be pivotal to translate this synergistic technology into practical, sustainable agricultural applications.

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