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Review

Cereal Health Regulation by Arbuscular Mycorrhizal Fungi (AMF): Insights from Tripartite Plant–AMF–Pathogen Systems Within the One Health Framework

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Abstract

Tripartite interaction among arbuscular mycorrhizal fungi (AMF), small grain cereals—including wheat, barley, oats, and rye—and pathogenic organisms constitute a highly complex ecological system with major implications for plant health, productivity and resilience. AMF colonization increases nutrient acquisition, particularly phosphorus and nitrogen, while concurrently priming host defense mechanisms that increase resistance to a broad spectrum of pathogens. These benefits, however, are strongly context-dependent and modulated by AMF species composition, host genotype, soil characteristics, and environmental conditions. AMF activate resistance pathways and modulate the rhizosphere microbiome, underscoring their central role in shaping plant–pathogen dynamics. Importantly, the relevance of these interactions extend beyond crop protection and yield stability to encompass food security and sustainability goals aligned with the One Health framework, which recognizes the interconnectedness of plant, environmental, and human health. Field implementation of AMF-based strategies has the potential to reduce reliance on chemical fertilizers and pesticides, thereby promoting sustainable cereal production, restoring soil biodiversity, and enhancing ecosystem services, with downstream benefits for human nutrition and environmental safety. This review integrates current knowledge on AMF–cereal–pathogen interactions, synthesizing mechanistic advances and applied perspectives while identifying critical knowledge gaps that must be addressed to effectively deploy AMF in resilient and sustainable agroecosystems within a One Health context.

Keywords: AMF; plant–microbe interactions; induced systemic resistance (ISR); priming; plant pathogen; rhizosphere microbiome; biocontrol; sustainable agriculture

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1. Introduction

AMF are ubiquitous soil symbionts forming mutualistic associations with the roots of approximately 80% of terrestrial plant species, including major cereal crops [1,2]. This ancient symbiosis, established as early as the Devonian period, is classically defined by

reciprocal resource exchange: AMF enhances host access to limiting soil resources, most notably phosphorus (P), but also nitrogen (N), water, and micronutrients, while receiving photosynthetically derived carbon in return [3]. Improved nutrient acquisition often translates into enhanced plant growth and vigor, indirectly increasing tolerance to both abiotic and biotic stresses [4,5]. In the broader context of the One Health framework, an integrated, unifying approach that emphasizes the interconnected and interdependent health of humans, animals, plants, and ecosystems, AMF represent a key ecological component supporting plant and ecosystem resilience. Within this background, AMF-driven improvements in soil structure, nutrient cycling, and plant health contribute not only to agricultural sustainability but also to ecosystem services that underpin food security and environmental quality.

Their ability to modulate plant immunity through mycorrhiza-induced resistance, a priming phenomenon that enables faster or more effective defense activation upon pathogen challenge, further reinforces their role as not only facilitators of plant nutrition but also active contributors to plant protection under stress conditions [2,6,7] (Figure 1).

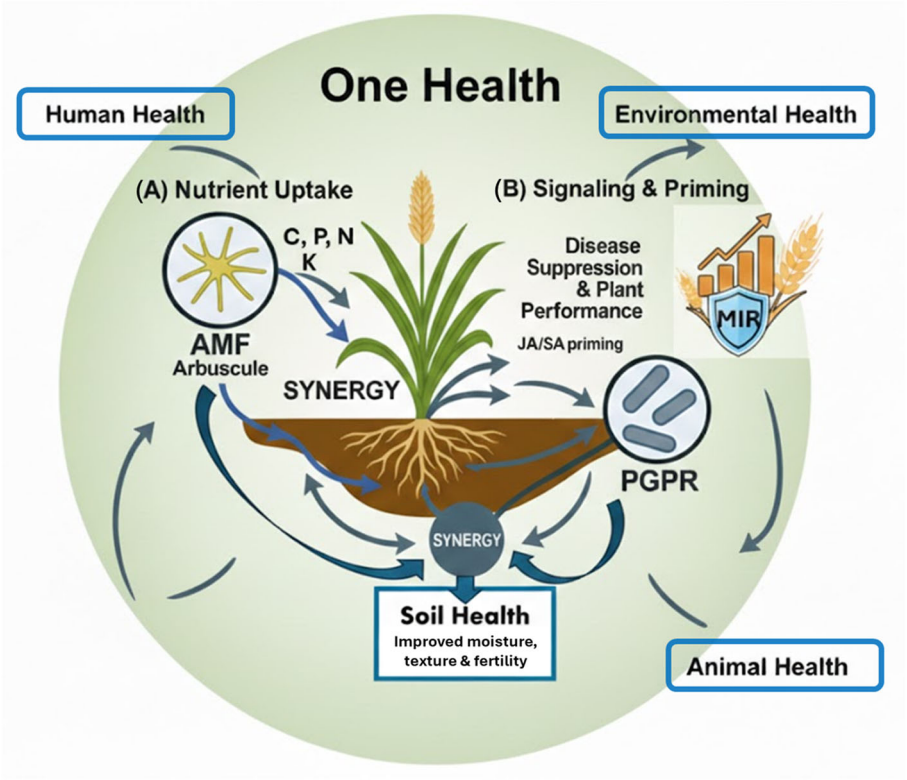

Figure 1. Multiple roles of Arbuscular Mycorrhiza Fungi (AMF) in the One Health framework. MIR = mycorrhiza-induced resistance.

This dual nutritional–defensive role is particularly relevant for small grain cereals such as wheat, barley, and oats, which represent cornerstones of global food security [8]. These crops supply a major fraction of human caloric intake and animal feed worldwide [9], yet their productivity is persistently constrained by a wide range of pathogens and pests including fungi, bacteria, viruses, and nematodes, which cause root rot, foliar blights, rusts, and systemic diseases. Under current climate change scenarios, pathogen and pests affect up to 20–40% of major cereal crops globally [10], posing escalating challenges to food security and agricultural sustainability. Although conventional disease control strategies, such as breeding for resistance and the use of synthetic fungicides, have historically reduced disease impacts, their long-term effectiveness is increasingly compromised by pathogen adapta-

tion, regulatory restrictions, and growing environmental and health concerns [11]. These limitations have driven a shift toward ecologically based disease management strategies, with particular emphasis on beneficial soil microorganisms [12]. Among them, AMF have attracted considerable interest as naturally occurring symbionts with the potential to simultaneously enhance crop performance and reduce disease pressure in an environmentally sustainable manner [13–15].

Mechanistically, AMF influence cereal–pathogen interactions through a combination of direct or indirect pathways. Improved nutritional and physiological status of mycorrhizal plants can increase host tolerance to infection, reducing disease severity even in the absence of direct pathogen suppression. In parallel, AMF can directly limit pathogen establishment by competing for root colonization sites and resources [16]. Mycorrhizal colonization also induces substantial changes in root exudation patterns and phytohormonal balance, reshaping the rhizosphere environment in ways that constrain pathogen proliferation [16]. Experimental evidence further demonstrates that AMF enhances host defense capacity by reinforcing cell walls, stimulating the synthesis of antimicrobial compounds and increasing the activity of defense-related enzymes [17].

Empirical support for these mechanisms is well documented in cereal systems. For example, wheat plants colonized by AMF exhibit reduced incidence of "take-all" disease caused by *Gaeumannomyces graminis*, alongside enhanced systemic resistance to foliar pathogens [18]. More broadly, AMF-associated cereals frequently display attenuated disease symptoms and improved growth or yield under pathogen pressure relative to non-mycorrhizal plants [19]. However, such outcomes are far from universal.

Indeed, tripartite interactions among AMF, cereals, and pathogens are intrinsically dynamic and highly context-dependent. The magnitude and even direction of AMF-mediated protection vary with fungal species or isolates, host genotype, soil fertility, resident microbiome composition, and climatic conditions [3]. A meta-analysis by Liu et al. [20] showed that AMF inoculation significantly reduced necrotrophic diseases but had no consistent effect on biotrophic pathogens. Chemical and transcriptomic analyses suggest that these contrasting responses are largely driven by AMF-mediated regulation of jasmonic acid (JA) and salicylic acid (SA) signaling pathways under glasshouse conditions, although changes in plant nutritional status and secondary metabolite profiles likely contribute to observed disease outcomes. In some cases, incompatibility between AMF and host genotype, or environmental conditions unfavorable to mycorrhizal functioning, may reduce or negate anticipated benefits [21]. Such variability underscores a critical gap in predictive understanding and highlights the need to identify the ecological and physiological drivers governing AMF–cereal–pathogen outcomes.

The scope of this review encompasses a comprehensive and integrative analysis of current knowledge regarding tripartite interactions among AMF, small grain cereals, and their pathogens. Our specific objectives include systematically synthesizing the literature on AMF-mediated disease resistance mechanisms in cereals, critically analyzing the sources of heterogeneity in experimental outcomes across different AMF species, cereal genotypes, pathogen types, and environmental contexts, identifying areas of consensus and divergence in the scientific literature regarding underlying mechanisms and practical efficacy, evaluating the molecular, physiological, and ecological processes that govern AMF–cereal–pathogen interactions, assessing the practical implications for sustainable agriculture within the broader One Health framework, and defining critical research gaps along with priority directions for future investigations.

2. Materials and Methods

To ensure the coverage and reproducibility of our analysis, we conducted a structured literature search following the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines adapted for narrative reviews, resulting in the selection of 150 articles. Our search strategy encompassed multiple major databases, including Web of Science, Scopus, PubMed, Google Scholar, and CAB Abstracts, covering publications from January 2000 through December 2025, with selective inclusion of earlier works that established foundational concepts. We employed a comprehensive Boolean search string combining terms related to arbuscular mycorrhizal fungi, small grain cereals, and plant pathogens or diseases, using Boolean combinations of keywords grouped into the following thematic categories:

(i) Arbuscular mycorrhizal fungi

("arbuscular mycorrhizal fungi", "AMF", "AMF species", "arbuscular mycorrhiza", "root-associated mycorrhizae", "mycorrhizal symbionts", "extraradical mycelium");

(ii) Small grain cereals

("small grain cereals", "wheat", "barley", "oats", "rye", "rice", "Triticum", "Hordeum", "Avena", "Secale", "Oryza");

(iii) Pathogenic fungi and plant diseases

("plant pathogenic fungi", "soil-borne pathogens", "foliar pathogens", "fungal diseases", "necrotrophic fungi", "biotrophic fungi", "Fusarium", "Blumeria", "Rhizoctonia", "disease severity", "pathogen suppression");

(iv) Tripartite and interaction-based frameworks

("tripartite interactions", "plant–microbe–pathogen interactions", "mycorrhiza-induced resistance", "systemic resistance", "immune priming", "pathogen tolerance", "host–symbiont compatibility");

(v) Environmental and agronomic context

("soil fertility", "phosphorus availability", "nutrient management", "climate stress", "drought", "salinity", "cropping systems", "tillage", "crop rotation", "sustainable agriculture").

Studies were included if they were peer-reviewed journal articles, reviews, or meta-analyses investigating AMF–cereal–pathogen interactions and reporting mechanistic, physiological, molecular, or field-based data in English. We excluded conference abstracts without full data, works focusing exclusively on non-cereal crops unless they provided critical mechanistic insights, research examining only AMF–plant nutrition without pathogen context and with insufficient methodological detail for quality assessment.

Quality assessment of the included research evaluated experimental design rigor, adequacy of sample sizes, appropriateness of statistical analyses, reproducibility of methods, and clarity of conclusions. The 150 high-quality publications that form the primary basis of this review were selected through this rigorous process, with particular emphasis placed on recent molecular and omics-based investigations that have advanced our mechanistic understanding of AMF–pathogen–cereal interactions. This approach ensures that our synthesis rests on a solid foundation of reliable evidence while acknowledging areas of uncertainty and ongoing debate within the scientific community (Figure 2).

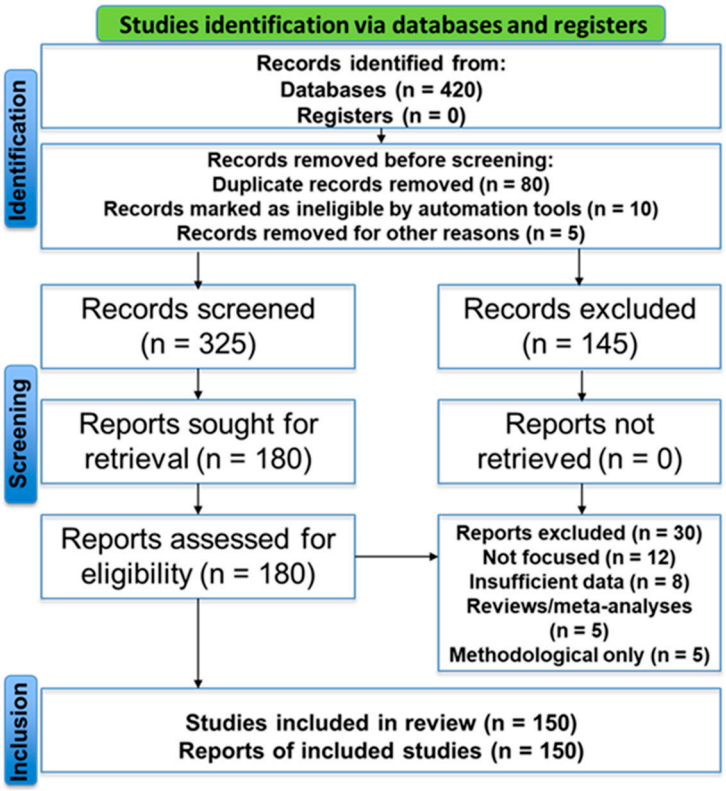

Figure 2. PRISMA 2020 flow diagram adapted for a narrative review, showing the identification, screening, eligibility assessment, and inclusion of studies from databases (Scopus, WoS, ScienceDirect, Google Scholar) in the narrative review "Arbuscular Mycorrhizal Fungi (AMF), Small Grain Cereals, and Pathogens: Tripartite Interactions for Plant Health and Sustainable Agriculture" within the One Health Framework.

3. AMF-Mediated Functions in Small Grain Cereals: Integrative Synthesis Across Mechanisms and Study Contexts

AMF consistently emerge as key functional partners of small grain cereals, acting as extensions of the root system and enhancing plant growth and vigor, particularly under nutrient-limited conditions [22–24]. Experimental field and meta-analysis-based studies converge on the conclusion that the extensive extraradical mycelium of AMF substantially expands the soil volume explored by the plant, increasing access to poorly mobile nutrients such as P and, to a lesser extent, nitrogen and micronutrients [25–29]. Quantitative syntheses confirm these trends, with meta-analyses reporting increases of approximately 95–122% in P availability and 64–90% in N availability, translating into higher biomass and yield formation in cereals [30]. However, these benefits are not uniform across systems. High-input fertilization regimes, particularly in maize-based systems, frequently suppress AMF colonization, whereas low-input or organically managed wheat systems maintain higher AMF diversity and functionality [31–36]. These contrasts underscore that AMF-mediated nutritional benefits are contingent on management intensity, crop phenology, soil depth, and the partitioning between root-associated and rhizosphere AMF communities.

Recent investigations reveal a methodological shift from descriptive colonization assessments toward molecular, metagenomic, and functional approaches aimed at elucidating microbial-mediated nutrient cycling and carbon–P trade-offs [37,38]. While these approaches have refined mechanistic understanding, comparative analysis shows that molecular insights often outpace field validation, reinforcing the need to critically assess the agronomic relevance of laboratory-derived mechanisms [39,40].

Beyond nutrition, AMF play a central role in regulating cereal water relations and drought tolerance. Evidence across controlled and semi-field experiments demonstrates that AMF hyphal networks enhance soil water retention by accessing micropores and stabilizing soil aggregates via fungal exudates [19,41]. At the plant level, AMF modulates stomatal conductance, root hydraulic conductivity, and aquaporin expression, leading to higher tissue water content under water deficit [42,43]. Table 1 documents consistent associations between AMF colonization, osmoprotectant accumulation, antioxidant activity, and improved photosynthetic performance under drought stress [44,45]. A critical integrative insight emerging from molecular studies is the central role of abscisic acid (ABA), which increases during mycorrhizal establishment and coordinates both fungal colonization and plant stress signaling through ABA-dependent and ABA-independent pathways [46–48]. Comparative transcriptomic and hormonal analyses further demonstrate extensive crosstalk between ABA, JA, SA, and cytokinins, forming a regulatory network that fine-tunes symbiosis and stress resilience [49–51]. Nevertheless, the available evidence, including the patterns summarized in Table 1, shows that the magnitude of drought-related benefits varies with AMF species, host genotype, and environmental severity, indicating that AMF-mediated drought tolerance is conditional rather than universal [52].

AMF also enhances cereal tolerance to other abiotic stresses, including soil salinity, heavy metal contamination, and acidity [5,53,54]. AMF-mediated stress alleviation is associated with improved ionic homeostasis (notably favorable K^+/Na^+ ratios), enhanced antioxidant enzyme activity, reduced uptake of toxic ions, and phytohormonal modulation [14,55–57]. In saline soils, AMF-colonized cereals consistently show superior osmotic adjustment and Na^+ exclusion [14,56], while under heavy metal stress, AMF sequester metals within fungal structures and improve plant nutritional and water status [58]. Yet, comparative analysis reveals that these protective effects depend strongly on contamination level, soil chemistry, and AMF identity, with some reports documenting diminished colonization under severe stress conditions [41].

In parallel with their role in abiotic stress mitigation, AMF also play multifaceted functions in plant defense against pathogens. Across wheat, barley, maize, and rice systems, AMF colonization frequently reduces disease severity through a combination of direct and indirect mechanisms [59–61]. Competitive exclusion of pathogens for colonization sites, nutrients, and plant-derived carbon has been repeatedly documented, limiting pathogen establishment in root tissues [16,62,63]. These effects are further translated into reduced incidence of diseases such as Fusarium crown rot, common root rot, and downy mildew [64–66]. This distinction is critical for interpreting AMF efficacy and its long-term implications for pathogen dynamics.

Structural and biochemical root modifications further contribute to AMF-mediated defense. The works summarized in Table 1 consistently report increased root branching, enhanced biomass, thickened epidermal and cortical cell walls, and localized lignin and callose deposition hallmarks of MIR [67–70]. These anatomical changes block pathogen penetration and are often accompanied by elevated phenolic content and reduced pathogen progression, particularly in wheat [65,71,72].

At the molecular level, AMF prime host immune responses, enabling faster and stronger activation of defense pathways upon pathogen attack. This primed state involves upregulation of defense-related genes, jasmonate-regulated signaling components, secondary metabolism enzymes, and enhanced accumulation of phytoalexins, antioxidants, and reactive oxygen species (ROS) [70,72–75]. Comparative evidence indicates that AMF-induced resistance is strongly modulated by environmental conditions such as soil moisture, planting density, and nutrient availability [13,76,77], reinforcing the concept of context-dependent immunity rather than constitutive protection.

A further integrative dimension of AMF function is their capacity to reshape rhizosphere microbial communities. AMF frequently enrich beneficial microbial taxa and suppress pathogens through shifts in microbial diversity and functional potential [78–80]. Indigenous AMF consortia often outperform commercial inocula in colonization efficiency and disease reduction, reflecting local adaptation and compatibility with native microbiomes [72,81–83]. Moreover, synergistic interactions between AMF and plant growth-promoting rhizobacteria (PGPR) consistently enhance plant growth and systemic immunity beyond the effects of single inoculations [79,84,85], although outcomes remain sensitive to microbial combinations and environmental context.

Regarding yield, some investigations report maintained productivity despite increased pathogen sporulation, pointing to tolerance rather than resistance as the dominant response [86].

In synthesis, AMF emerge as central integrators of nutrient acquisition, abiotic stress tolerance, and pathogen resistance in small grain cereals. Their effects arise from the interplay of physical soil exploration, biochemical and hormonal regulation, immune priming, and microbial community restructuring. At the same time, the comparative analysis underscores substantial variability driven by AMF taxa, host genotypes, soil properties, and management practices. While *omics*-based approaches have significantly advanced mechanistic understanding, a persistent gap remains between molecular insight and field-level predictability—an issue also evident in the patterns summarized in Table 1. Bridging this gap will require long-term, integrative, and standardized research that explicitly connects molecular mechanisms with ecological dynamics and agronomic decision-making, thereby enabling reliable deployment of AMF-based strategies in sustainable cereal production systems.

Table 1. Overview of the impact of arbuscular mychorizal fungi (AMF) and other microorganisms in cereal crops: a synthesis of methodologies, physiological responses, and stress mitigation. [1] = Research article; [2] = book chapter, [3] = review; [4] = PhD dissertation; [5] = communication in workshop; ↑ = increase; ↓ = decrease.

Study (Ref.)	Focus & Methodology	Host/Microorganism	Growth/Yield Impact	Stress Response (Biotic/Abiotic)	Key Strategic Insights
Vannini et al. [85] [1]	Proteomics; JA-defense	Wheat (AMF + PGPB)	↑ Growth ↑ Nutrient uptake	Microbe-dependent bioprotection	Synergistic effects are highly species-specific.
Mustafa et al. [71,72] [1]	Defense pathway; polyphenols	Wheat (*F. mosseae. R. irregularis*)	P-level-dependent growth	↑ Systemic resistance (−78% powdery mildew)	Strong focus on pathogen-specific wheat defense.
Gernns et al. [86] [1]	Photosynthesis & tolerance	Barley (Single AMF)	Yield maintained	↑ Pathogen sporulation	Tolerance does not always reduce pathogen load.
Fiorilli et al. [70] [1]	Transcriptomics & proteomics	Wheat (Single AMF)	↑ Biomass ↑ Yield ↑ Nutrients uptake	↑ Resistance to *X. translucens*	Molecular & metabolomic proof of AMF-induced resistance.
Sudheer et al. [87] [2]	Stress & defense	Land plants (AMF)	↑ Nutrition uptake	↑ Tolerance	Foundation for sustainable agriculture models.
Charakas and Khokhani [88] [3]	Tripartite molecular signaling	*Brachypodium*, oats, carrot (*R. irregularis* & bacteria)	↑ Nutrition uptake ↑ Yield	↑ Biotic tolerance ↓ Drought stress via hyphal water flow	Synergistic interaction improves field applicability.
Singh et al. [89] [3]	Induced systemic resistance	Crops (AMF & soil microorganisms)	↑ Growth	Multiple inhibitory mechanisms	Focus on multi-microorganism inhibitory networks.

Table 1. *Cont.*

Study (Ref.)	Focus & Methodology	Host/Microorganism	Growth/Yield Impact	Stress Response (Biotic/Abiotic)	Key Strategic Insights
Kumar et al. [90] [2]	Biochemical defenses	Crop (single AMF)	↑ Growth	↑ Biotic stress tolerance	Emphasis on enzymatic defense activations.
Maharshi et al. [91] [2]	JA/SA, PR proteins & callose	Crop (single AMF)	↑ Nutrient uptake	↑ Systemic resistance	Detailed mapping of hormone signaling pathways.
Pérez-de-Luque et al. [78] [1]; Savastano and Bais [92] [3]	Priming & synergies	Land plants (AMF & PGPR)	Microbial type-dependent growth	↑ Synergistic systemic resistance	Points out the need for deeper molecular research.
Song et al. [73] [1]; Martin et al. [29] [3]	Resistance and defense priming	Maize (*G. mosseae*); different host plants (AMF)	↑ Growth ↑ Nutrient uptake	↑ Tolerance ↑ Priming ↑ DIMBOA and defense genes ↓ Disease impact	AMF-mediated priming as key mechanism of bioprotection; DIMBOA identified as central phytoalexin in AMF-enhanced immunity.
Ullah et al. [93] [3]	Common mycorrhizal networks	Crops (AMF and microbial consortia)	Influence growth and sharing	↑ Tolerance	Networks are vital for ecosystem sustainability.
Magkourilou et al. [94] [1]; Davidson-Lowe et al. [95] [1]; Bernaola Alvarado [96] [1]; Bernaola and Stout [97] [1]	Herbivore interaction	Maize, rice, potato (AMF); potato (*Globodera pallida*)	Soil-dependent biomass ↑ P in uninfected plants Different impact on C and nutrient dynamics	↑ Pathogen resistance ↑ Susceptibility to nematodes *Armyworm larvae*.	Impact varies significantly based on herbivore type.
Guigard et al. [98] [1]; Li et al. [99] [1]; Campos-Soriano et al. [100] [1]	Symbiotic compatibility & systemic defense induced	Rice (*F. mosseae*, *R. intraradices*, *R. irregularis*, *G. intraradices*); wheat (*Piriformospora indica*)	Growth depends on AMF/plant combination	↓ *Xanthomonas oryzae*, *Rhizoctonia cerealis*, *F. graminearum* and *Magnaporthe oryzae* diseases ↑ Resistance-related genes and priming	Priming depends on specific AMF–plant combinations.
Deja-Sikora et al. [101] [1]	Virus interaction	Potato (*R. irregularis*, *F. mosseae*)	↑ Photosynthesis ↑ Tuber weight	↓ Growth losses, ↓ Oxidative stress & H_2O_2 ↓ Lipid peroxidation	AMF mitigates growth losses from viral (PVY) infection.
Duan et al. [76,77] [1]; Wilkes et al. [102] [1]; Torppa [103] [4]; Abdullah [104] [1]	Field management	Wheat (*F. mosseae*, indigenous AMF, *Bacillus* sp., earthworms)	↑ Biomass and yield (+28.5%) in drought and low densities	↑ Drought tolerance	Intensive agriculture reduces AMF colonization and soil biodiversity.
Yadav et al. [105] [1]; Singh and Prakash [106] [4]	Tripartite consortia	Wheat (AMF & *Bacillus* sp.)	↑ Nutrient content ↑ Yield	↑ Stress tolerance ↑ Antioxidants	Synergic benefits of the bacteria/AMF/host plant link.
Albqmi et al. [107] [1]; Gupta et al. [108] [1]; Gao et al. [109] [3]	Heavy metals remediation	Wheat & other cereals (AMF, *R. intraradices*)	↑ Growth ↑ Photosynthesis	↑ Antioxidants ↓ As and Cd toxicity	Critical for crop safety in contaminated soils.
Khan et al. [24] [3]	Plant physiology	Cereals (*Glomus* spp., *Rhizophagus* spp., *Funneliformis* spp.)	↑ Nutrient uptake, ↑ Biomass ↑ Photosynthesis	↑ Tolerance to drought, salinity, heavy metals, pathogens ↑ Antioxidant systems	Recent findings, mechanisms, and research gaps on AMF-cereals symbiosis.
Slimani et al. [54] [3]; Kuila and Ghosh [110] [1]	Sustainable agriculture	Cereals, oilseeds and other crops (*R. irregularis*, *F. mosseae*, *G. versiforme*)	↑ Growth/fitness ↑ Nutrient uptake ↑ Yield/quality	↑ Tolerance of drought, salinity, heavy metals ↑ Resistance to pathogens, nematodes, insects; ↑ Osmotic/ antioxidant/hormonal regulation	AMF as a key tool for climate-resilient agriculture.

Table 1. *Cont.*

Study (Ref.)	Focus & Methodology	Host/Microorganism	Growth/Yield Impact	Stress Response (Biotic/Abiotic)	Key Strategic Insights
Zhang et al. [22] [1]; Pellegrino et al. [111] [1]	Meta-analysis	Maize, wheat, rice, barley, sorghum, millet, oat (AMF)	↑ Yield (+16–20%) ↑ Nutrients uptakes	↑ Drought and pathogen tolerance	Large-scale evidence of yield benefits across soils (texture and organic content) under stress.
Liu et al. [112] [1]; Tu et al. [113] [1]; Kazan and Gardiner [114] [3]; Thapa et al. [115] [1]; Troth [116] [4]; Ding et al. [117] [1]; Kugler et al. [118] [1]; Chetouhi et al. [119] [1]	*Fusarium*—transcriptomics; susceptible wheat transcriptomic and effect on microbial network	Cereal (*Fusarium* and plant microbial networks)	↓ Yield (severe yield losses)	↑ Microbial networks in diseased plants ↑ Phytohormone production ↑ JA/ET/SA ↑ Stress pathway RLKs modulate FHB resistance.	Transcriptome networks and genome-wide gene expression. DON is not virulent factor in root infection.
Navarro-Borrell et al. [120] [5]	AMF + dark septate endophytes interactions	Wheat, pea, chickpea, lentil (AMF and dark septate endophytes)	Inconsistent yield effects	↑ Nutrient uptake ↑ Stress tolerance	Studied specifically in semi-arid prairie systems.
Brito et al. [121] [1]; Xavier and Boyetchko [122] [1]	Biostimulant systems	Crops (Indigenous AMF)	↑ Growth ↑ Microbial network	↓ Soil-borne disease	Tillage and rotation affect AMF effectiveness.

4. From Interaction to Ecosystem: Biotic and Abiotic Constraints Shaping Tripartite Relationships

Research on the tripartite interaction among AMF, small grain cereals, and pathogens has become increasingly central because it represents the intersection between productivity, input reduction, and durable crop protection, three pillars of sustainable agriculture. Within this framework, AMF symbioses are consistently seen as multifunctional partners that enhance nutrient acquisition (especially P) while also improving tolerance to biotic and abiotic stressors, thereby shifting the baseline "stress physiology" of cereal hosts [24,87]. Over the last two decades, the field has moved from relatively simplified bipartite viewpoints (plant–microbe or plant–pathogen) toward more ecologically realistic tripartite systems in which AMF, host plants, and pathogens (or additional microorganisms) are treated as simultaneously interacting players rather than isolated pairs [85,88]. This conceptual shift is particularly consequential for cereals—wheat, rice, and barley—given their global food-system centrality and the recurring yield instability caused by major pathogens such as *Fusarium graminearum* and *Blumeria graminis* [100,113]. The stakes are underscored by Fusarium head blight, which not only reduces yield but also introduces mycotoxin contamination, with direct food and feed safety implications [114,118].

A critical unresolved issue, however, is not whether AMF can influence cereal–pathogen outcomes, but instead when, how, and how reliably AMF can do so within real-world environmental and management gradients [71,112]. Although AMF-induced systemic resistance and enhanced defense responses are widely reported [72,91], the mechanistic basis of these effects, and their reproducibility across AMF taxa, cereal genotypes, and pathogen lifestyles, remains incompletely characterized [101,115]. Importantly, the literature contains conflicting findings: AMF colonization can be associated with protection in many systems, yet in some contexts it corresponds with unchanged outcomes or even elevated susceptibility to particular pathogens [86,97]. This "benefit–cost" ambiguity is not a minor inconsistency; it is a signature that the tripartite interaction is governed by contextual controls rather than a universal AMF-to-resistance pathway. In practical terms, this uncertainty constrains the deployment of AMF as a dependable biocontrol tool and limits its integration into sustainable cereal management at field scale [78,110]. Critically, the controversy also implies that mechanistic models focusing exclusively on immune

priming may be insufficient unless they explicitly incorporate resource trade-offs, microbial community shifts, and environment-dependent signaling thresholds as co-determinants of the outcome [92].

In this manuscript, the tripartite relationship is framed as a multitrophic interaction network in which AMF simultaneously mediates nutrient exchange and modulates host immune signaling, with cascading consequences for cereal growth and pathogen performance [106,122]. In comparative terms, this framing is more integrative than earlier "single mechanism" narratives because it treats disease outcomes as emergent properties of multiple coupled processes: (i) molecular signaling between host and symbiont, (ii) reallocation of host resources (C, N, P) among growth, symbiosis, and defense, and (iii) restructuring of rhizosphere microbial communities that may amplify or counteract AMF effects [88,120]. This network perspective is essential because it allows for the possibility that AMF may reduce disease via immune priming in one setting but shift resource allocation or microbial antagonism in another—producing the appearance of inconsistent "AMF effects" when the underlying drivers actually differ.

At the molecular level, cereals colonized by AMF and subsequently exposed to pathogens frequently show induction of defense-related genes, proteins, and metabolites. Evidence synthesized across roughly 30 scientific contributions supports activation of canonical defense pathways, including JA- and SA-associated signaling, alongside increased accumulation of pathogenesis-related (PR) proteins and phenolic compounds—responses compatible with enhanced resistance phenotypes in multiple cereal–pathogen combinations [72,85,91]. A particularly revealing pattern is that systemic defense gene induction has been reported even without pathogen challenge, implying that AMF can establish a primed immune state that lowers the activation threshold for rapid and strong responses upon infection [73,100]. Critically, a comparative reading of these observations suggests two non-mutually exclusive interpretations: (1) AMF generate a "preparation" state beneficial under high disease pressure, or (2) AMF drive a constitutive defense posture that could carry energetic costs, potentially becoming disadvantageous when pathogen pressure is low or when carbon/nutrient limitations make defense investment expensive—an important hypothesis for explaining context-dependent trade-offs reported elsewhere [86,97]. High-throughput transcriptomic and proteomic investigations deepen this picture by showing that AMF symbiosis does not simply "turn defenses on," but instead remodels host immune networks while also intersecting with pathogen virulence strategies [70,113,118]. This connection is crucial: if AMF-induced changes in host physiology alter the pathogen's perceived environment (e.g., nutrient availability, oxidative status, or signaling landscape), pathogen gene expression and infection strategies may shift accordingly, sometimes in ways that are not captured by measuring only disease severity endpoints. However, the degree and specificity of defense activation vary strongly by AMF species, cereal genotype, and pathogen type, indicating that the tripartite system is governed by selective compatibility and signaling specificity rather than a uniform response [71,98,101]. A comparative implication here is that "AMF-mediated resistance" is better treated as a family of outcomes (with multiple mechanistic routes) than as a single conserved phenomenon, which aligns with observed variability and helps reconcile apparently contradictory reports [86,97].

A parallel source of heterogeneity arises from experimental design choices, particularly inoculum composition. Work ranges from single AMF isolates to complex microbial consortia including PGPB and other beneficial microorganisms, complicating cross-study comparability. The relative merits of native AMF consortia versus commercial formulations remain debated, with several reports emphasizing the superior adaptability and performance of native consortia under local soil and climate conditions [85,92,105]. Criti-

cally, this is not just a practical observation but a mechanistic one: colonization efficiency and downstream effects on growth and immunity depend on AMF diversity, functional complementarity, and compatibility with the host genotype [71,98,101]. Reviews of the mycorrhizosphere further reinforce that AMF effects can propagate via microbial network restructuring and common mycorrhizal networks that facilitate nutrient exchange and may suppress pathogens indirectly [88,93,106]. In comparative terms, dual inoculations with AMF and PGPB often produce more pronounced improvements in growth and immune priming than AMF alone, suggesting either additive functional partitioning (e.g., nutrient mobilization plus signaling priming) or true synergism in which one partner increases the effectiveness of the other [78,92]. However, the inoculation efficiency is context-dependent: the direction and magnitude of these benefits vary with host genotype and inoculation timing, implying that microbial "stacking" is not automatically beneficial and may require agronomically calibrated deployment [78,92].

Improvements in cereal growth and yield metrics represent one of the most consistent outcomes of AMF colonization. Enhanced biomass, grain yield, and grain nutrient content are commonly attributed to improved P and N uptake coupled with better stress tolerance [70,76,105]. Although meta-analyses support overall positive yield responses under field conditions, they also show that effect sizes vary across crops, cultivars, and environments, indicating that AMF are not a universal yield "booster" but rather a conditional yield stabilizer in many situations [22,111]. This distinction matters: if AMF benefits are strongest under stress or low-input conditions, then the agronomic value proposition may lie more in resilience and input substitution than in maximum yield under high-input management. Consistent with this, conditional effects are frequently observed, with soil moisture, planting density, and nutrient availability acting as major determinants of realized benefits [76,77]. Moreover, there are cases where AMF colonization is linked to increased pathogen load or susceptibility, yet yield is maintained due to tolerance mechanisms that buffer disease impacts [86,97]. This is a particularly important comparative insight: AMF may shift the balance between resistance (reducing pathogen success) and tolerance (reducing yield penalty per unit disease), and these two strategies have different ecological and management implications, including potential effects on pathogen population dynamics over time [86,97].

Pathogen control itself remains a key target outcome, and evidence indicates that AMF inoculation can reduce disease severity, pathogen biomass, and infection structure development in cereals [110]. MIR is frequently described as a systemic mechanism of defense in which mycorrhizal colonization initiates local immune modulation at the root interface and generates mobile signals that systemically prime defense pathways, leading to enhanced activation of immune-regulatory genes and the accumulation of antimicrobial metabolites across the plant [71–73,91,100]. However, the interaction is not always linear: some research reports altered pathogen dynamics without direct suppression, including increased sporulation with minimal yield impact—again, consistent with the tolerance-versus-resistance distinction and with the possibility that AMF-driven physiological changes may inadvertently favor certain pathogen life-history traits while still protecting host productivity [86]. In contrast, combinations of AMF with PGPB repeatedly induce stronger suppression and resistance outcomes than single inoculations, suggesting that multi-microbe strategies may better buffer variability by engaging multiple defensive routes simultaneously [78,85]. The critical requirement is that such strategies also introduce additional layers of specificity and environmental dependency, which must be explicitly managed rather than assumed away.

Environmental and agronomic constraints ultimately determine whether AMF-mediated benefits are expressed. Soil type, P status, and moisture conditions directly control AMF colonization and, by extension, plant benefit realization [71,97,102]. At the system

level, tillage and crop rotation shape AMF propagule availability, community composition, and functional capacity, acting as macro-drivers of whether inoculation or indigenous AMF communities can persist and deliver consistent outcomes [54,76,87]. Accordingly, field trials and meta-analyses repeatedly emphasized that AMF performance varies across sites, supporting the conclusion that AMF-based interventions require locally tailored strategies rather than one-size-fits-all recommendations [22,111]. Finally, contamination by heavy metals and metalloids (e.g., cadmium, arsenic) introduces additional complexity: such stressors can reduce colonization in some cases, yet under certain conditions AMF may still enhance plant stress tolerance, particularly when combined with organic amendments—demonstrating that "constraint" and "benefit" can co-occur depending on how soil physicochemical properties and management are considered together [107,109].

Overall, the tripartite AMF–cereal–pathogen system is best understood as an environmentally contingent network in which outcomes are jointly shaped by symbiont identity, host genotype, pathogen strategy, microbial community context, and agronomic management [71,92,112]. A critical comparative reading of the evidence suggests that future progress depends less on demonstrating that AMF can help—which is already well supported—and more on resolving the boundary conditions that determine whether AMF promote resistance, tolerance, or, in some cases, susceptibility, and on translating those boundary conditions into operational decision rules for sustainable cereal production [22,78,110,111].

5. Microbial Community Alteration as a Mechanistic Bridge Between AMF Symbiosis and Disease Outcomes

AMF exert system-level effects on small grain cereal health by reshaping rhizosphere microbial communities, thereby mediating indirect but often decisive influences on plant growth, stress tolerance, and disease outcomes. As summarized in Table 2, evidence across wheat and barley systems consistently shows that AMF inoculation alters both microbial community composition and functional attributes, frequently enriching beneficial taxa while suppressing or displacing pathogenic groups [70,78–80]. Importantly, these effects are not uniform but emerge from interactions among AMF identity, host genotype, soil conditions, and management legacy, reinforcing the view that AMF act as context-dependent ecosystem engineers rather than deterministic drivers of a fixed "beneficial microbiome". Comparative analysis of the scientific works reported in Table 2 reveals pronounced species-specific differences among AMF. *Funneliformis mosseae* repeatedly shows a stronger capacity than *Rhizophagus irregularis* to restructure rhizosphere microbial communities and enhance pathogen resistance in cereals, including improved resistance to *Xanthomonas translucens* and powdery mildew in wheat [70,72], as well as improved productivity and microbial biomass under drought [76]. In contrast, *R. irregularis* displays more variable outcomes, with positive effects on microbial catabolic diversity and growth under certain conditions [78], but reduced performance under soil disturbance or suboptimal host–soil compatibility [123]. These contrasts suggest that AMF-driven microbial alteration depends not only on colonization success, but also on functional traits such as extraradical mycelium integrity, carbon demand, and signaling capacity—traits that differ substantially among AMF taxa. Table 2 further underscores the superiority of indigenous AMF consortia over commercial inocula in many contexts. Research on wheat and barley indicates that native AMF, often enhanced through compost or organic management, promote higher arbuscule formation, increased glomalin production, and more favorable microbial networks than commercial formulations, which in some cases even reduce native AMF colonization [82,83]. This pattern critically challenges the assumption of inoculum transferability and emphasizes ecological filtering as a dominant constraint.

From a review perspective, this raises concerns about extrapolating results from controlled inoculation trials to field-scale applications without accounting for local microbial legacies and soil structure.

Mechanistically, AMF-mediated microbial alteration operates through intertwined plant-driven and microbe-driven pathways. As documented in Table 2, AMF colonization triggers host transcriptional and biochemical responses—including polyphenolic accumulation, reactive oxygen species production, callose deposition, and modulation of antioxidant enzymes—that directly influence microbial recruitment and pathogen establishment [70–72,78,124]. Concurrently, transcriptomic and meta-transcriptomic analyses reveal that AMF and associated microbiota jointly reprogram pathways involved in nutrient mobilization, organic acid metabolism, siderophore production, and antifungal compound biosynthesis [125–130]. Critically, these functional shifts often correlate more strongly with disease outcomes than taxonomic diversity alone, reinforcing the need to interpret AMF effects through a functional microbiome lens rather than relying solely on diversity metrics. Environmental and host-genotypic modulation emerges as a dominant feature the body of research considered. Soil P availability, moisture regime, planting density, and disturbance intensity consistently determine whether AMF-induced microbial restructuring translates into disease control or merely neutral shifts [76,77,123,130]. At the same time, host genotype exerts strong control over microbial recruitment, with specific genetic loci (e.g., QRMC-3HS in barley) governing bacterial community assembly independently of root morphology [111,131]. This genotypic control provides a mechanistic explanation for why identical AMF inocula can yield divergent microbial and disease outcomes across cultivars, and it highlights plant breeding as a complementary lever for stabilizing AMF benefits [132–134].

A particularly integrative insight from Table 2 concerns microbial network effects and synergistic interactions. Co-inoculation of AMF with PGPR, such as *Bacillus* spp., repeatedly enhances pathogen containment and immune priming beyond the effects of AMF alone [78,79,84]. Similarly, microbiome transplantation and enrichment with taxa such as *Stenotrophomonas rhizophila* demonstrated that AMF benefits propagate through broader microbial networks rather than acting as isolated drivers [135,136]. Evidence from disease-suppressive soils further showed that pathogen pressure itself reshapes microbial community structure and functional gene clusters, enriching antagonistic microorganisms and reinforcing suppression mechanisms [137–140]. These findings collectively argue for a network-based interpretation of AMF function, where outcomes emerge from multipartner interactions rather than single symbiotic links. Field-scale evidence strengthens this argument. The study by Lutz et al. [141], demonstrates that AMF inoculation success across 54 maize fields was better predicted by soil microbiome indicators—particularly pathogen abundance—than by conventional soil chemical parameters. This result has broad implications for cereal systems, suggesting that AMF effectiveness depends on preexisting microbial context and that microbiome diagnostics may be essential for rational deployment of AMF-based strategies.

AMF-driven microbial community alteration is a central but highly conditional mechanism linking symbiosis to disease resistance and stress tolerance in small grain cereals. AMF can reshape rhizosphere communities, activate host defenses, and interact synergistically with other beneficial microorganisms, yet these effects are filtered by AMF identity, host genotype, soil environment, and management practices. While *omics* approaches have greatly advanced mechanistic resolution, Table 2 collectively illustrates that predictability remains limited without ecological and agronomic contextualization. Future progress will depend on explicitly coupling molecular insights with microbiome-aware field experimentation and standardized reporting frameworks, thereby enabling AMF to be positioned not

as universal solutions, but as strategically deployable components of sustainable cereal production systems.

Table 2. Evidence for arbuscular mycorrhizal fungi-driven microbial community shifts and functional outcomes in cereal cropping systems. [1] = Research article; [2] = review; [3] = book chapter.

Study (Ref.)	AMF Species & Effects	Mechanism of Action	Environmental & Genotypic Factors	Microbial Synergy
Fiorilli et al. [70] [1]	*F. mosseae* improves wheat yield and resistance to *Xanthomonas translucens*	Transcriptomic/proteomic changes in nutrient transport and defense	Wheat genotype affects AMF responsiveness	n.d.
Pérez-de-Luque et al. [78] [1]; Ikan et al. [84] [1]	AMF and PGPR improve growth and drought tolerance in wheat *R. irregularis* increased rhizobacterial colonization	Immune priming (callose) and signaling; proline synthesis and photosynthetic activity under drought	Wheat genotype and water regime influence AMF/PGPR colonization and priming	AMF + PGPR work together in drought responses
Marrassini et al. [83] [1]; Duan et al. [76] [1]; Garmendia et al. [132] [1]	AMF consortia, *F. mosseae* *R. intraradices* improve barley and stressed wheat productivity	Arbuscular formation linked to yield, and soil organic C; Photosynthesis/proline metabolism modulation	Genotype, soil moisture/planting density and elevated CO_2/drought influenced AMF and plant response	n.d.
Ji et al. [79] [1]; George and Ray [127] [1]; Talaat and Shawky [129] [1]; Ghabous et al. [133] [1]	*F. mossea* and consortia enhance soil health, microbial community and nutrient uptake under stressed wheat and barley	Reduced oxidative damage via enzyme activity (catalase/peroxidase). Increased K/Na ratio and growth traits under salinity	Salinity levels and soil chemical modulate AMF and influence microbial shifts	AMF mitigated salinity effects by improving osmotic adjustment
Mustafa et al. [71,72] [1]; Bziuk et al. [135] [1]	*F. mosseae*, *R. irregularis*, commercial inoculum and microbiome transplant increase powdery mildew resistance in wheat and barley	Polyphenols accumulation and defense genes induction	P supply, cultivar type and pathogen presence influenced AMF colonization and modulated defense responses	Microbiome transplant increased beneficial microorganism diversity
Liu et al. [136] [2]; Tracanna et al. [138] [1]	*Stenotrophomonas rhizophila* increases in response to *Fusarium*, and suppressive soils enrich *Fusarium*-antagonistic genes	Upregulation JA/SA signaling and antifungal pathways	Soil suppressiveness, microbiome composition and pathogen presence activate bacterial defense	Tripartite interaction among plant–pathogen–microbiome
Liu et al. [124] [1]	*R. intraradices* and *F. mosseae* + Se alter bacterial communities and alleviate Cd stress in wheat	Increased microbial network complexity; reduced Cd availability	Outcomes depend on the soil contamination level	AMF + Se influenced microbial communities
Wilkes [82] [1]	Indigenous AMF enhanced by compost; commercial inoculum reduced AMF colonization in wheat	Increased AMF arbuscules and soil glomalin linked to growth	Soil tillage/texture influence AMF-host interactions	Compost promoted beneficial microbial interactions

Table 2. *Cont.*

Study (Ref.)	AMF Species & Effects	Mechanism of Action	Environmental & Genotypic Factors	Microbial Synergy
Pellegrino et al. [111] [1]; Wahbi et al. [126] [1]; Thirkell et al. [134] [1]	Multiple AMF and *R. irregularis* improved growth, yield and nutrient uptake in wheat and barley, and soil microbial diversity	Organic acid metabolism/P mobilization pathways enhanced; positive correlation between AMF colonization and yield; enhanced fertilizer N uptake and utilization efficiency	Soil organic matter, pH, climate and cultivar and field conditions influenced AMF effects	AMF influenced soil microbial community and is a biofertilizer
Duan et al. [77] [1]; Campos et al. [130] [1]; Gdanetz and Trail [137] [1]	*F. mosseae*, *R. irregularis* and microbial community benefits depend on management and water regime in wheat	Enhanced soil organic C and N absorption mechanism; gene expression linked to stress tolerance and growth	Environmental stress/planting density and management strategy (soil disturbance) influenced AMF benefits	Intact extraradical mycelium is critical for AMF function
Seguel et al. [40] [1]; Conceição et al. [123] [1]; Alotaibi et al. [128] [1]; Faria et al. [142] [1];	Native AMF consortia and *R. irregularis* protect against heavy metal (Mn and Al) toxicity in wheat and barley	Antioxidant enzyme activities/nutrient partitioning modulated; upregulation of proline pathway; root colonization correlated with P and Al uptake efficiency	Soil disturbance/AMF composition influenced protection; acidic soil conditions influenced AMF performance; barley genotype and soil Al saturation levels affect outcomes	AMF consortia shaped associated microbiomes affecting plant defense
Iqbal [143] [1]	*F. mosseae*, *G. eaticatium*, *R. irregularis*, *G. claroideum* improve growth, nutrient content, and soil C storage in wheat	Increased P accumulation and C storage	Soil physiochemical changes linked to AMF inoculation	n.d.
Li et al. [144] [1]	Resistant wheat varieties have higher bacterial diversity and altered fungal abundance	Microbial community structure linked to disease resistance	Wheat genotype influenced rhizosphere microbiota	Potential for microbial biocontrol agents
Liu et al. [112] [1]	Microbial community composition shifted with pathogen	Functional genes involved in metabolism and signaling altered by infection in wheat	Wheat defense pathways correlated with microbiome changes	Pathogen infection disrupted microbial community networks
Yin et al. [140] [1]	Fungal diversity decreased with planting cycles and pathogen pressure in wheat	Pathogen infection enhanced separation of fungal community clusters	Monocropping and pathogen presence influenced fungal dynamics	n.d.
Singh et al. [89] [2]; Delaeter et al. [145] [2]; Jeffries and Barea [146] [3]	AMF activated plant defense and product metabolites inhibiting pathogens	Molecular and physiological mechanisms of AMF-induced defense; mycorrhizal diversity supports plant health	Soil and environmental conditions affect AMF function	Synergistic microbial interactions in pathogen suppression
Azcón-Aguilar and Barea [147] [2]; Elliott et al. [148] [1]	AMF induce root morphological changes and alter rhizosphere microorganisms and community structure in wheat	Local elicitation of plant defense compounds by AMF. P uptake increased, but not directly via AMF	Pathogen type and soil conditions influence AMF protective effects Wheat cultivar differences affect C-nutrient exchange	Cooperation with other rhizosphere antagonists enhances control

Table 2. *Cont.*

Study (Ref.)	AMF Species & Effects	Mechanism of Action	Environmental & Genotypic Factors	Microbial Synergy
Borowicz [149] [1]	AMF reduced fungal pathogen growth but variable effects on nematodes	AMF–pathogen interactions depend on pathogen type and feeding mode	Low-P soils and controlled conditions	Need for broader environmental and species range research
Escudero-Martinez et al. [131] [1]	(No AMF involved) QRMC-3HS locus shapes bacterial rhizosphere composition	Differential expression of NLR and cell wall-modifying genes	Genotypic variation influences microbiota without altering root traits	Locus influences bacterial network structure; no fungal/AMF synergy
Hazzoumi et al. [150] [1]	*Glomus*, *Gigaspora*, and *Acaulospora* genera enhanced chlorophyll and phenolics, improved growth and nutrient assimilation in wheat	AMF increased root density and P uptake with phosphate fertilization	Soil origin of AMF influenced inoculum effectiveness	AMF improved physiological and biochemical plant parameters
Hayden et al. [125] [1]	(No AMF involved) Suppressive soils reduce *Rhizoctonia solani* disease via active rhizosphere microbiome	Non-suppressive soils showed higher expression of antibiotic and ROS detox pathway	Soil suppressiveness linked to microbial functional profiles	Functional microbial networks modulate pathogen control

6. Critical Analysis and Synthesis: Strengths, Limitations, and Unresolved Dimensions of Tripartite AMF–Cereal–Pathogen Research

Current research exploring tripartite interactions among AMF, small grain cereals, and pathogens has expanded substantially, yielding important advances in the understanding of molecular, physiological, and ecological processes underlying plant nutrition, stress tolerance, and disease resistance. As synthesized in Table 3, a major strength of this research lies in the consistent demonstration that AMF can enhance plant growth, nutrient acquisition, and resistance to pathogens through systemic defense activation, immune priming, and synergistic interactions with other beneficial microorganisms [72,78,85,91,100]. These findings collectively support the conceptualization of AMF as multifunctional symbionts capable of integrating nutritional and defensive functions within cereal cropping systems.

Table 3. Strengths and weaknesses of current research on arbuscular mycorrhizal fungi-cereal-pathogen interactions.

Aspect	Strengths	Weaknesses
Molecular and Physiological Mechanisms of AMF-Mediated Resistance	- Induction of systemic resistance in cereals - Activation of defense-related genes - Activation of JA and SA signaling pathways [72,91,100]. - Proteomic and transcriptomic analyses clarify pathways and proteins involved in tripartite interactions and AMF' role in priming plant immunity [75,85].	- Controlled conditions, not reflecting field reality [71]. - Gene expression varies across cultivars and AMF species [98]. - Distinction between direct activation and priming remains unclear [72].
AMF Species Diversity and Plant Genotype	- Different AMF species vary in colonization and protection, with *F. mosseae* often very effective in disease control and growth promotion [71,101]. - Plant genotype influences colonization and defense activation → importance of host-symbiont compatibility [98,101].	- Only single species or cultivars studied → limited ecological validity [71,101]. - Mechanisms behind genotype-specific responses are poorly understood. - Environmental interactions not well explored [98].

Table 3. *Cont.*

Aspect	Strengths	Weaknesses
Synergistic Effects AMF/PGPR	- Synergistic effects AMF/PGPR improving growth and defense beyond single inoculations [78,85,92,102]. - Combined inoculations activate specific proteomic and immune responses → Microbial consortia hold great potential in sustainable agriculture.	- Molecular bases of synergisms still unclear. - Results inconsistent due to dependence on microbial combinations, genotype, and environment [85,95]. - Timing and inoculation methods rarely standardized [92].
Methodological Approaches and Experimental Design	- Multi-omics and isotope tracing improve understanding of nutrient exchange and defense signaling [70,85,88,94]. - Field trials and meta-analyses offer realistic data on AMF effects on yield and resistance [22,105,111].	- Limited replication, short experiments, lack of environmental variability [71,97]. - Complexity often oversimplified, ignoring microbial community dynamics and soil heterogeneity [88,112]. - In vitro and field results frequently diverge [88].
Ecological and Agronomic Factors Affecting AMF	- Soil nutrients, moisture, planting density, and tillage strongly affect colonization and protection [71,76,77,103]. - Low P enhances colonization and disease resistance [71,97] → Integrated management is required to optimize AMF advantages.	- Combined effects of agronomic factors remain poorly quantified. - Key variables often not reported, reducing reproducibility [71,97]. - Context-dependent benefits make broad recommendations difficult.
Pathogen Dynamics and Host Defense	- complex AMF–host–pathogen molecular signals influence disease and resistance [113–115]. - AMF can reduce pathogen development and modulate host susceptibility [72,100]. - AMF alter pathogen distribution and virulence within host tissues [101].	- Pathogen diversity and co-infections often poorly understood [116]. - AMF effects on pathogen population dynamics remain unclear [86,96].
Tripartite Interactions into Sustainable Agriculture	- AMF and microbial consortia can enhance cereal crop resilience, yield, and soil health [54,87,93,105]. - Managing microbial communities and mycorrhizal networks enhances nutrient uptake and pathogen control [93,94].	- Practical use is limited by inconsistent field performance, economic constraints, and incomplete understanding of microbial ecology [110,121] - Need for long-term, interdisciplinary research for real-world implementation [54,110].

At the molecular and physiological level, scientific research has achieved particularly strong mechanistic resolution. Transcriptomic and proteomic works have repeatedly documented the activation of JA-and SA-dependent signaling pathways, induction of defense-related genes, and modulation of proteins involved in nutrient transport and stress responses following AMF colonization [72,75,85,91,100]. As reported in Table 3, these approaches have clarified key components of AMF-mediated resistance and priming, offering detailed insight into how symbiosis reshapes host immune networks. However, a critical limitation is that most of this evidence derives from controlled or semi-controlled experimental systems that only partially reflect field complexity [71]. Moreover, gene expression patterns vary substantially across cereal cultivars and AMF species, and the distinction between constitutive defense activation and true priming often remains unresolved [72,98]. This ambiguity complicates functional interpretation and limits the predictive value of molecular markers across diverse agroecosystems.

Variation in AMF species identity and host genotype represents another central axis of both strength and uncertainty. Comparative evidence consistently shows that AMF species differ markedly in colonization efficiency and protective capacity, with *Funneliformis mosseae* often emerging as particularly effective in promoting growth and suppressing disease in cereals [71,101]. In parallel, host genotype strongly influences colonization success and defense activation, underscoring the importance of host–symbiont compatibility [98,101].

Yet, as presented in Table 3, much of the available evidence is based on single AMF species or a limited number of cultivars, constraining ecological validity and obscuring the mechanisms underlying genotype-specific responses. Environmental interactions with genotypes are also insufficiently explored, leaving a major gap in understanding how genetic and ecological filters jointly shape tripartite outcomes.

Synergistic interactions between AMF and PGPR represent one of the most promising but least resolved areas of research. Combined inoculations often enhance plant growth and defense more effectively than single-microbe applications, with evidence of amplified immune and proteomic responses [78,85,92,102]. Table 3 highlights the potential of microbial consortia as tools for sustainable agriculture yet also emphasizes critical weaknesses: the molecular bases of these synergisms remain poorly characterized, results are highly inconsistent across microbial combinations and environments, and key variables such as inoculation, timing and delivery methods are rarely standardized [85,92,95]. As a result, while synergistic AMF–PGPR interactions are conceptually attractive, their reproducibility and scalability remain uncertain.

Methodological advances constitute another major strength of the field. The integration of multi-*omics* approaches, isotope tracing, and increasingly sophisticated field trials has improved understanding of nutrient exchange, defense signaling, and yield responses [22,70,85,88,94,105,111]. Meta-analyses and long-term field evidence provide valuable realism, demonstrating that AMF can enhance yield and resistance under certain conditions. Nonetheless, Table 3 clearly indicates persistent methodological shortcomings, including limited replication, short experimental durations, and inadequate representation of environmental variability [71,97]. Furthermore, a large body of work simplifies system complexity by neglecting microbial community dynamics and soil heterogeneity, contributing to frequent discrepancies between in vitro and field results [88,112]. These limitations bring into focus a structural tension between mechanistic depth and ecological realism that remains largely unresolved.

Ecological and agronomic factors further complicate interpretation and application of AMF research. Strong evidence shows that soil nutrient status, moisture, planting density, and tillage practices exert major control over AMF colonization and disease suppression [71,76,77,103]. Low P availability in particular often enhances both colonization and resistance responses, pointing to the necessity of integrated nutrient management [71,97]. However, as Table 3 emphasizes, combined effects of agronomic variables are rarely quantified, key contextual parameters are often underreported, and context-dependent outcomes limit the formulation of broad management recommendations. This lack of standardization reduces reproducibility and hampers cross-study comparison.

Pathogen dynamics introduce an additional layer of uncertainty. While accumulating evidence demonstrates that AMF can reduce pathogen development, alter tissue colonization patterns, and modulate host susceptibility [72,100,101], pathogen diversity, co-infection scenarios, and population-level effects are poorly understood [86,96,116]. The molecular dialogue among AMF, host plants, and pathogens is increasingly recognized as complex and bidirectional [113–115], yet few investigations explicitly address how AMF influence pathogen evolution, virulence strategies, or long-term epidemiological dynamics.

When considered within a sustainable agriculture framework, current findings indicate both substantial opportunities and significant limitations. As summarized in Table 3, AMF and microbial consortia clearly have the potential to enhance cereal resilience, yield stability, and soil health, particularly when microbial communities and mycorrhizal networks are actively managed [54,87,93,105]. At the same time, practical implementation is limited by inconsistent field performance, economic considerations, and incomplete understanding of soil microbial ecology [110,121]. Therefore, the synthesis of current evidence points to

a critical need for long-term, interdisciplinary research that integrates molecular biology, microbial ecology, agronomy, and socio-economic analysis [54,110].

In conclusion, the tripartite AMF–cereal–pathogen research landscape has reached a level of mechanistic sophistication that clearly demonstrates potential, but not yet predictability. Table 3 makes clear that future progress will depend less on further proof-of-concept studies and more on resolving context dependence, improving methodological standardization, and explicitly linking molecular mechanisms to field-scale ecological processes. Only through such integrative efforts can AMF-based strategies transition from promising experimental tools to reliable components of sustainable cereal production systems.

7. Agreement and Divergence: Convergent Patterns, Context Dependence, and Sources of Inconsistency

There is broad consensus that AMF positively influence small grain cereals by enhancing plant growth, nutrient uptake, and defense capacity against pathogens. As summarized in Table 4, numerous lines of research converge on the observation that AMF colonization frequently activates systemic host defense responses, including the induction of pathogenesis-related proteins, peroxidases, chitinases, and JA- and SA-regulated pathways, resulting in increased resistance to a range of cereal pathogens [72,73,91,100]. This agreement provides a robust mechanistic foundation for viewing AMF as active modulators of plant immunity rather than passive nutrient symbionts.

Table 4. Comparative synthesis of consistent and contrasting outcomes in arbuscular mycorrhizal fungi–cereal–pathogen interaction.

Comparison Criterion	Studies in Agreement	Studies in Divergence	Potential Explanations
Molecular defense activation	- AMF often triggers systemic defense responses (PR proteins, peroxidase, chitinases) and pathways (JA/SA), increasing resistance in cereals [72,73,91,100].	- AMF induce tolerance instead of resistance (e.g., higher pathogen sporulation but stable yield) [86]. - Defense activation varies with AMF species and host genotype [98,101].	Differences in host–AMF combinations, pathogen type (biotroph vs. necrotroph), tissue-specific responses, and timing/measurements.
Microbial inoculum composition	- AMF species influence colonization and pathogen containment; *F. mosseae* often performs best [71,72,76]. - Dual inoculation AMF + PGPR can synergistically enhance plant growth and immune priming [78,85,92,102].	- Protection depends on inoculum type, not just colonization level [71]. - Dual inoculation effects vary on microbe combination and host genotype and can be antagonistic [92,102]. - Some AMF species may increase susceptibility [86,101].	Variation in microbial strains, inoculum sources, interactions with native microbiomes, timing, and host genotype.
Plant growth and yield parameters	- AMF generally increases biomass, yield, and nutrient uptake (Mg, Zn, P) in cereals [22,24,70,76,77,111]. - Positive effects occur in both stress and non-stress conditions [54,87].	- Growth benefits depend on plant density, water availability, and soil type [76,77]. - AMF may increase pest susceptibility under specific conditions [96,97].	Environmental conditions, agronomic practices, plant genotype, AMF compatibility, and differences between field vs. greenhouse experiments.

Table 4. *Cont.*

Comparison Criterion	Studies in Agreement	Studies in Divergence	Potential Explanations
Pathogen suppression capacity	- AMF usually reduces pathogen severity via enhanced defense, phenolics, and H_2O_2 accumulation [71–73,100]. - AMF induces MIR and priming [70,72,91].	- AMF increases susceptibility or pathogen reproduction, though plants may maintain yield via tolerance [86]. - Type of AMF or inoculation conditions can increase pathogen growth or alter virus distribution [96,97,101].	Pathogen type, AMF strain, host resistance level, environment, and whether protection occurs through resistance or tolerance.
Environmental and agronomic context	- Low P, reduced tillage, and crop rotation support AMF colonization and disease suppression [71,76,77]. - Reduced tillage and crop rotation promote native AMF and enhance colonization and crop performance [103,121]. - Microbial effects vary with soil type, moisture, and management [87,97,105,107].	- AMF benefits decline under high P, irrigation, dense planting [76,77,97]. - AMF effect on pest susceptibility varies with soil [96,97]. - Stressors like heavy metals or arsenic alter AMF functionality [107,108].	Differences in soils, climate, farming practices, native microbiomes, and abiotic stresses lead to variable results.

At the same time, Table 4 brings to light important divergences that complicate generalized conclusions. Several investigations report that AMF do not always reduce pathogen pressure directly but instead promote host tolerance, characterized by stable yield despite elevated pathogen sporulation or colonization [86]. This distinction between resistance and tolerance is often underappreciated, yet it has major implications for interpreting disease outcomes and long-term pathogen dynamics. Comparative analysis suggests that whether AMF-mediated protection is displayed as resistance or tolerance depends on AMF species identity, host genotype, pathogen lifestyle (e.g., biotrophic versus necrotrophic), and the timing and tissue specificity of defense activation [98,101]. Divergent findings therefore do not necessarily contradict one another but may reflect different ecological and physiological endpoints being measured.

A second major area of both agreement and divergence concerns microbial inoculum composition. It is consistently reported that AMF species differ in colonization efficiency and protective capacity, with *F. mosseae* often outperforming other taxa in promoting growth and suppressing disease in cereals [71,72,76]. Moreover, dual inoculation strategies combining AMF with PGPR frequently show synergistic effects on growth and immune priming [78,85,92,102]. However, Table 4 also documents substantial variability in these outcomes: protection is not solely determined by colonization level, synergistic effects can be inconsistent or even antagonistic depending on microbial combinations and host genotype, and certain AMF species have been associated with increased susceptibility to specific pathogens [86,101]. These divergences point to complex interactions among introduced microorganisms and native microbiomes, as well as strong dependence on inoculum source, strain-level variation, and inoculation timing.

With respect to plant growth and yield, there is strong agreement that AMF generally enhances biomass production, grain yield, and nutrient uptake—including P, Mg, and zinc—in small grain cereals [22,24,70,76,77,111]. Positive effects have been observed under both stress and non-stress conditions, reinforcing the multifunctional role of AMF in cereal systems [54,87]. Nonetheless, Table 4 shows that growth benefits are highly conditional: plant density, water availability, soil type, and management intensity strongly

modulate outcomes, and in some cases, AMF colonization has been linked to increased pest or pathogen susceptibility under specific conditions [96,97]. These contrasting results emphasize that growth promotion and disease resistance are not always tightly coupled and may respond differently to environmental and agronomic drivers.

Pathogen-reducing capacity is also represented by agreement and divergence studies. Many findings report reduced disease severity following AMF colonization, associated with enhanced defense responses, increased phenolic content, and accumulation of reactive oxygen species such as H_2O_2 [71–73,100]. The induction of MIR and immune priming is widely documented [70,72,91]. Conversely, Table 4 identifies multiple reports in which AMF increased pathogen reproduction or altered pathogen distribution within host tissues, again without necessarily reducing yield due to compensatory tolerance mechanisms [86,96,97,101]. These results suggest that AMF-mediated effects on pathogens are not uniformly suppressive and may instead reconfigure host–pathogen interactions in ways that decouple disease metrics from productivity outcomes.

Environmental and agronomic context emerges as one of the most consistent explanatory factors underlying both agreement and divergence. There is broad consensus that low P availability, reduced tillage, and crop rotation favor AMF colonization and enhance beneficial outcomes, including disease mitigation and improved crop performance [71,76,77,103,121]. Conversely, high P inputs, intensive irrigation, and dense planting often diminish AMF benefits or alter their effects on pest and pathogen susceptibility [76,77,97]. Additional stressors, such as heavy metal contamination or arsenic, further modify AMF functionality and can either constrain or redirect their protective capacity [107,108]. As Table 4 illustrates, differences in soil properties, climate, farming practices, and native microbial communities collectively generate substantial variability, limiting the transferability of results across systems.

In synthesis, Table 4 demonstrates that the strongest points of agreement concern the existence of AMF effects on cereal growth, nutrition, and defense, whereas divergence primarily concerns the direction, magnitude, and mechanism of these effects. Much of the apparent inconsistency can be attributed to differences in experimental design, host–AMF–pathogen combinations, environmental context, and the metrics used to assess protection (resistance versus tolerance). Hence, a critical reading may suggest that future research should move beyond binary assessments of "beneficial" versus "non-beneficial" AMF effects and instead explicitly define the ecological and physiological conditions under which specific outcomes are expected. Only through such a framework can agreement and divergence be reconciled into a predictive understanding of tripartite AMF–cereal–pathogen interactions suitable for sustainable agricultural application.

8. Gaps and Future Research Directions: Resolving Context Dependence and Advancing Translational Relevance

Despite many studies demonstrating that arbuscular mycorrhizal fungi (AMF) can enhance nutrient acquisition, modulate plant immunity, and influence pathogen dynamics in small grain cereals, major conceptual and methodological gaps continue to limit predictive understanding and practical application. As synthesized in Table 5, the most pervasive challenge across the literature is the strong context dependency of AMF effects, which vary with fungal species, cereal genotype, pathogen type, and interacting environmental factors such as soil fertility, moisture, and temperature [71,76,77,97]. This context dependence complicates extrapolation from controlled experiments to field-scale agroecosystems, where multiple stressors and biotic interactions operate simultaneously and non-linearly.

Table 5. Critical knowledge gaps and future research directions for arbuscular mycorrhizal fungi within sustainable and One Health-oriented cereal production.

Gap Area	Knowledge Gap Description	Future Research Directions	Justification	Research Priority
Molecular specificity of AMF-induced defense pathways	Variation in defense gene activation across AMF species, cereal genotypes, and pathogen types.	- Comparative molecular approaches across diverse AMF species and cereal genotypes - Multi-omics and gene editing to dissect signaling and gene network specificity.	Clarifying molecular specificity is essential to predict and optimize AMF-mediated defense responses.	High
Synergistic mechanisms in AMF–PGPR–cereal interactions	Molecular basis of AMF–PGPR synergism on cereal immunity and growth.	- Integrated transcriptomic, proteomic, and metabolomic analyses of co-inoculation - Standardized timing and microbial consortia.	Synergistic effects can boost resistance and growth, but inconsistent results hinder application; mechanistic insights would enable optimized microbial designs [78,85,92].	High
Environmental and agronomic influences on AMF	Effects of soil type, moisture, nutrients, tillage, and planting density on AMF colonization and pathogen suppression.	- Multifactorial field trials modeling combined agronomic influences - predictive frameworks for site-specific AMF use.	Environmental context strongly shapes AMF performance; quantitative gaps limit reliable field deployment [71,76,77,97].	High
Long-term and transgenerational impacts of AMF	Persistence of AMF induced benefits across plant generations and long-term field conditions.	Longitudinal field trials tracking AMF effects on progeny traits, yield stability, and disease resistance over multiple seasons.	Evidence suggests inherited benefits, but long-term sustainability and inheritance remain unverified [70].	Medium
AMF effects on pathogen dynamics and co-infections	AMF influence on pathogen communities, virulence, and co-infection dynamics in cereals.	- Combined AMF colonization and pathogen population analyses in controlled and field settings - Multi-pathogen inoculation and metagenomic approaches.	Pathogen interactions shape disease severity; conflicting reports of increased susceptibility reveal major knowledge gaps [86,116].	Medium
Functional roles of bacterial partners in AMF tripartite associations	Roles and mechanisms of bacteria associated with AMF in mycorrhizosphere and their influence on cereal-pathogen interactions.	- Metagenomics to characterize AMF-associated bacterial communities - functional assays to assess their roles in nutrient exchange and pathogen suppression.	Bacterial partners may enhance or modulate AMF effects, but their identities and functions remain largely unknown [88,106].	Medium
Standardization and ecological relevance of methodologies	Heterogeneity in replication levels, experimental design, and ecological realism across AMF studies.	- Develop standardized protocols for AMF inoculation, pathogen challenge, and environmental simulation - Increase replication and incorporate field-relevant complexity.	Methodological inconsistency constrains reproducibility and translation to agricultural systems [71,88,97].	High

Table 5. *Cont.*

Gap Area	Knowledge Gap Description	Future Research Directions	Justification	Research Priority
Impact of soil contaminants and amendments	Impacts of heavy metals and organic amendments on AMF colonization, cereal performance, and pathogen resistance.	- Analyze AMF–plant interactions under contamination - Monitor AMF community shifts under contamination and amendments.	Contaminants strongly affect AMF and plant health; amendments may mitigate toxicity, but mechanisms and field applicability need clarification [107,108].	Medium
Role of common mycorrhizal networks (CMNs) in pathogen management	CMN contributions to nutrient sharing and pathogen defense among cereal plants, especially during pathogen stress.	Isotope tracing and network analysis to quantify nutrient and defense signal flows in multi-plant systems under pathogen challenge.	CMNs may redistribute resources and influence disease dynamics, but ecological complexity and practical relevance require deeper study [93,94].	Medium
Genetic basis of AMF compatibility and induced resistance	Genetic determinants regulating AMF colonization efficiency and mycorrhiza-induced resistance in cereals.	GWAS and functional genomics to identify host genes controlling AMF compatibility and defense priming, validated via gene editing.	Host genotype strongly modulates AMF benefits; identifying key genes enables breeding for enhanced symbiosis and resistance [98,115].	High

At the molecular level, a critical gap concerns the specificity of AMF-induced defense pathways. While transcriptomic and proteomic approaches consistently show activation of defense-related genes and signaling pathways, the magnitude, timing, and functional relevance of these responses differ markedly among AMF species, host genotypes, and pathogen lifestyles [98,115]. Table 5 underscores the need for comparative molecular approaches that explicitly span this diversity and for integrated multi-*omics* studies—potentially combined with gene editing—to disentangle signaling specificity from general stress responses. Without such resolution, molecular markers of AMF-mediated resistance remain difficult to generalize or deploy in breeding and management programs.

A closely related gap lies in the mechanistic basis of synergistic interactions between AMF and PGPR. Although co-inoculation frequently enhances growth and immune priming beyond single-microbe applications, results are inconsistent and highly dependent on microbial combinations, host genotype, and inoculation timing [78,85,92]. As emphasized in Table 5, integrated transcriptomic, proteomic, and metabolomic analyses under standardized co-inoculation regimes are required to determine whether observed synergisms reflect additive effects, true functional complementarity, or indirect shifts in microbial community structure. Clarifying these mechanisms is essential to move from empirical microbial mixtures toward rationally designed consortia.

Environmental and agronomic modulation of AMF performance represents another high-priority gap. Strong evidence indicates that soil type, nutrient status, moisture regime, tillage, and planting density collectively shape AMF colonization and reduction of pathogen pressure [71,76,77,97]. However, most investigations address these factors in isolation, leaving their combined effects poorly quantified. Table 5 underscores the need for multifactorial field experiments and predictive frameworks capable of integrating agronomic variables into site-specific AMF deployment strategies. Without such quantitative models, AMF applications will remain opportunistic rather than reliably optimized.

Temporal scale constitutes an additional underexplored dimension. While short-term experiments demonstrate clear benefits of AMF colonization, the long-term and transgenerational stability of these effects remains uncertain. Evidence suggests that AMF-induced changes in plant performance and microbial communities may persist beyond a

single growing season, yet rigorous longitudinal field trials tracking yield stability, disease resistance, and progeny traits are scarce [70]. As noted in Table 5, addressing this gap is essential for evaluating the sustainability of AMF-based interventions over multiple cropping cycles.

Pathogen ecology itself remains insufficiently integrated into AMF research. Although AMF can alter pathogen development and host susceptibility, their influence on pathogen population dynamics, virulence evolution, and co-infection scenarios is poorly understood [86,116]. Table 5 identifies a clear need to combine AMF colonization with direct pathogen population analyses, multi-pathogen inoculations, and metagenomic approaches. Such work is necessary to resolve conflicting reports of AMF-induced resistance versus susceptibility and to understand whether AMF favor resistance, tolerance, or epidemiological trade-offs under field conditions.

Another emerging gap concerns the functional roles of bacterial partners within AMF-associated microbial networks. Bacteria inhabiting the mycorrhizosphere may enhance nutrient exchange, modulate immune responses, or suppress pathogens, yet their identities and functions remain largely unresolved [88,106]. As shown in Table 5, metagenomic characterization and functional assays are required to determine whether these bacteria act as consistent co-drivers of AMF effects or as context-dependent modifiers. This knowledge is crucial for integrating AMF into broader microbiome-based management strategies.

Methodological inconsistency represents a structural limitation across the field. Heterogeneity in experimental design, replication, and ecological realism undermines reproducibility and cross-study comparison [71,88,97]. Table 5 emphasizes the urgency of developing standardized protocols for AMF inoculation, pathogen challenge, and environmental simulation, alongside increased replication and incorporation of field-relevant complexity. Without such standardization, mechanistic advances will continue to outpace translational reliability.

Environmental contamination adds further complexity. Heavy metals and metalloids can strongly affect AMF colonization and function, sometimes reducing effectiveness but in other cases enhancing stress tolerance when combined with organic amendments [107,108]. As summarized in Table 5, targeted research is needed to clarify how contaminants and amendments reshape AMF communities and plant responses, particularly under realistic field conditions.

Finally, the roles of common mycorrhizal networks (CMNs) and host genetic determinants remain insufficiently explored. CMNs may redistribute nutrients and defense signals among cereal plants, influencing disease dynamics at the stand level, yet their ecological relevance and management implications remain largely speculative [93,94]. Similarly, host genetic loci regulating AMF compatibility and mycorrhiza-induced resistance are only beginning to be identified [98,115]. As Table 5 indicates, genome-wide association studies and functional genomics could enable breeding strategies that enhance beneficial symbiosis while minimizing undesirable trade-offs.

From a broader perspective, these gaps also intersect with One Health considerations, including grain nutritional quality, food safety, environmental sustainability, and risks associated with non-native inoculum introduction. Addressing summarized challenges (Table 5) will therefore require long-term, multidisciplinary research integrating molecular biology, microbial ecology, agronomy andbreeding,. Only through such integrative efforts can AMF-based strategies evolve from promising experimental tools into robust, context-specific, and sustainable solutions for cereal production systems.

9. Theoretical and Practical Implications

Current research consistently displays AMF as central yet highly context-dependent regulators of plant defense, nutrient acquisition, and growth in small grain cereals. Across wheat and barley systems, AMF function as mutualistic symbionts that enhance host resilience to pathogens through the induction of systemic resistance and the priming of plant defense pathways, particularly in response to soil-borne fungal challenges [72,91,100]. Molecular investigations, notably transcriptomic and proteomic analysis, have substantially advanced mechanistic understanding by identifying signaling pathways activated during AMF colonization and pathogen exposure. These include stimulation of JA biosynthesis, accumulation of defense-related proteins, and activation of mitogen-activated protein kinase (MAPK) cascades, reinforcing classical models of induced systemic resistance while also revealing a higher degree of specificity and regulatory complexity in plant–fungus–pathogen interactions than previously recognized [85,91,100]. Importantly, comparative evidence demonstrates that AMF-mediated protection is not uniform but strongly shaped by fungal species identity and host genotype. Comparisons between *F. mosseae* and *R. irregularis*, as well as among different cereal cultivars, reveal pronounced differences in pathogen-reducing efficiency and growth promotion [71,98,101]. This variability underscores the central role of host–symbiont compatibility and challenges assumptions of broadly transferable AMF benefits, indicating that genotype-specific frameworks are necessary for both experimental interpretation and practical application.

Beyond simplified plant–fungus pairings, increasing attention has been directed toward tripartite and multipartite interactions involving AMF, PGPR, and cereal hosts. Dual-inoculation experiments reveal that microbial consortia can generate synergistic effects on nutrient acquisition and immune priming, but also display occasional antagonism, depending on microbial composition and host context [85,92,102]. These findings place the mycorrhizosphere as a dynamic interaction network rather than a collection of additive symbioses, integrating nutrient exchange, immune modulation, and pathogen suppression in ways that more closely resemble field conditions than single-inoculant systems.

Meta-analytical evidence further supports the overall positive contribution of AMF to cereal performance, demonstrating increased grain yield and nutrient uptake across multiple crops and environments [22,76,111]. At the same time, these quantitative syntheses demonstrate strong modulation by environmental variables, including soil P availability, water status, and planting density. Such patterns align with ecological theory, emphasizing that symbiotic outcomes are governed by resource availability and stress gradients rather than intrinsic symbiont effects alone.

Crucially, AMF influences not only host physiology but also pathogen behavior. Work centered on *F. graminearum* illustrates that AMF colonization can alter pathogen dynamics and host defense activation, thereby integrating pathogen biology into emerging models of tripartite plant–fungus–pathogen systems [112,113,115]. This perspective advances the field beyond host-centric resistance models and underscores the need to consider pathogen life-history traits when evaluating AMF-mediated outcomes.

From a practical point of view, the capacity of AMF to enhance nutrient uptake while inducing systemic resistance positions them as promising components of strategies aimed at reducing chemical fertilizer and pesticide inputs in cereal production [24,72,105]. However, their variable performance across AMF taxa, cereal genotypes, and environments necessitates site-specific and system-adapted inoculation strategies rather than generalized applications [71,76,98]. Emerging evidence further indicates that combining AMF with PGPR can improve both growth and immune priming relative to single-microbe inoculants, offering new opportunities for the development of more robust and multifunctional biofertilizers [78,85,92].

In addition to biotic stress mitigation, AMF contribute to cereal tolerance under abiotic constraints, including drought and heavy metal contamination, extending their relevance to degraded soils and climate-stressed agroecosystems [107–109]. Insights from molecular and ecological approaches to AMF–host–pathogen interactions also carry implications for breeding, suggesting that selection for genotypes with enhanced mycorrhizal compatibility and defense responsiveness could improve yield stability and sustainability in small grain cereals [98,115,118]. Finally, agronomic practices that conserve and promote native AMF communities—such as reduced tillage, crop rotation, and organic amendments—can be synergistically combined with inoculation strategies to strengthen soil health, enhance cereal productivity, and support long-term agroecosystem resilience [103,110,121].

10. Conclusions

Current evidence identifies AMF as key regulators of tripartite interactions among small grain cereals and pathogens, with effects spanning molecular, physiological, and ecological scales. AMF enhance plant growth, nutrient acquisition, and disease resilience through systemic defense activation and immune priming, involving JA- and SA-mediated signaling, phenolic accumulation, and structural barriers. These responses are highly dependent on AMF species identity and host genotype, underscoring the specificity of effective symbioses.

AMF performance is further shaped by microbial inoculum composition, with co-inoculation with plant growth-promoting rhizobacteria often enhancing nutrient uptake and resistance through synergistic interactions. While such consortia align with sustainable and One Health-oriented agriculture by reducing chemical inputs, their effectiveness remains strongly context-dependent.

Environmental and agronomic factors, including soil properties, nutrient availability, moisture, and management practices, critically modulate AMF colonization and outcomes, explaining variability between controlled and field experiments. Pathogen responses are similarly complex, ranging from direct suppression to tolerance-based mitigation, with implications for disease dynamics and food safety.

Overall, AMF represent multifunctional tools for improving cereal productivity, ecosystem resilience, and food-system sustainability. However, realizing their full potential requires interdisciplinary, site-specific strategies that integrate molecular mechanisms, microbial ecology, host genetics, agronomic management, and One Health principles.

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Abbreviations

The following abbreviations are used in this manuscript:

AMF	Arbuscular mycorrhizal fungi
MIR	Mycorrhiza-induced resistance
PGPB	Plant growth-promoting bacteria
PGPR	Plant growth-promoting rhizobacteria
ABA	Abscisic acid
CMN(s)	Common mycorrhizal network(s)
JA	Jasmonic acid
MAPK	Mitogen-activated protein kinase
C	Carbon
N	Nitrogen
P	Phosphorus
H_2O_2	Hydrogen Peroxide
PR (proteins)	Pathogenesis-related proteins
PRISMA	Preferred Reporting Items for Systematic Reviews and Meta-Analyses
ROS	Reactive oxygen species
SA	Salicylic acid
DON	Deoxynivalenol
DIM-BOA	2,4-dihydroxy-7-methoxy-2 H-1, 4-benzoxazin-3(4 H)-one
QTL(s)	Quantitative Trait Locus
GWAS	Genome-wide association study
QRMC-3HS	QTL–Rhizosphere Microbiota Composition on the short arm of chromosome 3H
Cd	Cadmium
NLR	Nucleotide-binding oligomerization domain-like receptors

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