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# *Trichoderma* Beyond Biocontrol: Mechanisms and Agricultural Applications

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**ABSTRACT**

The agricultural value of *Trichoderma* extends beyond suppression of fungal pathogens. This review examines the mechanisms that support their multifunctionality, including mycoparasitism, competition, antibiosis, hydrolytic enzymes, volatile and non-volatile metabolites, root colonization, hormone-mediated signaling, nutrient mobilization, and microbiome remodeling. Evidence from primary studies shows that selected strains can promote root and shoot development, improve phosphorus acquisition, stimulate antioxidant defenses, alter rhizosphere nutrient availability, and increase crop performance under drought, salinity, heavy-metal stress, and disease pressure. Field studies demonstrate practical potential in seed dressing, soil inoculation, foliar treatment, and microbial consortia, but also show that efficacy is strain-, crop-, formulation-, and environment-dependent. The central challenge is therefore not to identify a universally superior *Trichoderma* strain, but to match defined traits and formulations to particular crop-soil-climate contexts. Future progress depends on reproducible field validation, mechanistic biomarkers, microbiome-aware formulation, ecological safety assessment, and integration with-not indiscriminate replacement of-other components of crop management.

**KEYWORDS**

*Trichoderma*, biological control, plant growth promotion, induced systemic resistance, nutrient mobilization, abiotic stress tolerance, mycoparasitism, rhizosphere microbiome, hydrolytic enzymes, secondary metabolites, sustainable agriculture, microbial inoculants

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## INTRODUCTION

The genus *Trichoderma* comprises ecologically versatile filamentous fungi that are widely distributed in soil, plant residues, rhizospheres, and plant-associated tissues. Their conventional agricultural identity has been primarily that of biological control agents, reflecting their well-documented ability to suppress a broad range of plant pathogens through direct and indirect mechanisms[1]. The agricultural importance of *Trichoderma* extends beyond disease suppression, however, as these fungi can influence plant growth, nutrient acquisition, stress tolerance, and the biological environment surrounding plant roots. Their ability to interact with both plants and soil microorganisms has therefore attracted increasing attention as a potential component of sustainable crop production.

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Recent reviews describe *Trichoderma* as plant-beneficial microorganisms capable of combining pathogen antagonism with root colonization, growth stimulation, improved nutrient acquisition, stress mitigation, and modification of the surrounding microbial community[2]. This broader understanding represents an important shift from the traditional pathogen-centered view of *Trichoderma* toward a more integrated plant-soil systems perspective. Rather than functioning solely through the direct inhibition of pathogens, *Trichoderma* species can establish associations with plant roots, compete with harmful microorganisms for nutrients and space, produce antimicrobial metabolites and hydrolytic enzymes, and stimulate plant defence responses. Through these interactions, they can influence both plant performance and the composition and activity of the rhizosphere microbial community.

At the plant level, successful root colonization by *Trichoderma* may promote growth and improve the plant's ability to tolerate biotic and abiotic stresses. At the pathogen level, mechanisms such as competition, mycoparasitism, antibiosis, and induced plant defence can contribute to disease suppression. At the soil and rhizosphere levels, *Trichoderma* can participate in nutrient cycling and interact with resident microbial communities, potentially altering the ecological conditions surrounding plant roots. Consequently, the agricultural phenotype of a *Trichoderma*-based inoculant is usually the outcome of several interacting mechanisms rather than the activity of a single antifungal compound[3].

This expanding understanding has transformed *Trichoderma* from a conventional biocontrol agent into a multifunctional component of plant health and sustainable agriculture. Nevertheless, the expression of these beneficial traits can vary among *Trichoderma* species and strains and can be influenced by plant genotype, soil properties, environmental conditions, and interactions with indigenous microorganisms. Understanding these interconnected mechanisms is therefore essential for translating the biological potential of *Trichoderma* into consistent and effective agricultural applications. This review examines the major mechanisms through which *Trichoderma* interacts with plants, pathogens, soil, and the rhizosphere, while highlighting its broader applications and the challenges that remain for reliable field-level implementation.

This review evaluates *Trichoderma* beyond direct biocontrol across eight linked dimensions: Antagonistic mechanisms; plant recognition and induced resistance; growth and root-system regulation; nutrient mobilization and soil fertility; abiotic-stress tolerance; secondary metabolites and volatile organic compounds; molecular and microbiome-level processes; and agricultural deployment. It then compares representative studies, identifies unresolved gaps, and proposes a systems-level framework for reliable use.

## DIRECT AND INDIRECT MECHANISMS OF BIOCONTROL

**Mycoparasitism, competition, and lytic enzymes:** Direct antagonism begins with ecological occupation and resource capture. *Trichoderma* can colonize root-associated substrates rapidly, compete with pathogens for nutrients and space, and confront pathogen hyphae through recognition, attachment, coiling, penetration, and degradation. Reviews consistently identify mycoparasitism, competition, antibiosis, hydrolytic enzymes, and plant-defense induction as complementary rather than mutually exclusive mechanisms[4]. The distinction matters because a strain may suppress a pathogen *in vitro* through direct contact but fail in soil if it cannot establish, obtain nutrients, or maintain activity under the local temperature and moisture regime.

Hydrolytic enzymes provide a biochemical basis for pathogen degradation. Chitinases, β-1,3-glucanases, proteases, cellulases, and related enzymes can attack structural polymers in fungal cell walls or other biological substrates[5]. In a primary study of *T. hamatum* FB10, cell-free extracts showed protease, amylase, cellulase, chitinase, and glucanase activity, while the strain inhibited several fungal pathogens and

improved soil urease, phosphatase, catalase, and saccharase activities in green gram-associated soil[3]. These results connect pathogen antagonism to broader substrate transformation, although enzyme activity measured in culture or pot systems should not be treated as a direct estimate of field disease suppression.

Competition also operates through iron and other limiting resources. Siderophore production can reduce the availability of iron to competing microorganisms, while nutrient scavenging and rhizosphere occupation can alter the balance between introduced and resident populations. A recent synthesis of plant-growth-promoting traits emphasizes that these functions are not universal across the genus: some strains are stronger phosphate solubilizers, whereas others contribute more through auxin production or siderophore activity[6]. This functional unevenness is a central reason to characterize isolates by traits rather than by species name alone.

**Antibiosis and context-dependent metabolites:** *Trichoderma* produces chemically diverse secondary metabolites, including peptaibols, polyketides, terpenoids, pyrones, siderophores, and other non-ribosomal products. These compounds can inhibit pathogens directly, influence plant growth, or act as signals in inter-organism communication[7]. The biological outcome depends on concentration, exposure route, pathogen identity, plant genotype, and the nutritional and physical environment in which the fungus grows.

Primary experiments illustrate this context dependence. *T. hamatum* FB10 produced 6-pentyl-α-pyrone as a major volatile compound and its metabolites inhibited bacterial, fungal, and nematode targets while also promoting green-gram growth[7]. In a tomato study, challenging *T. harzianum* with *Fusarium chlamydosporum* altered the metabolite profile: The induced extract contained approximately 64 detected compounds, with methyl dihydrojasmonate representing about 21% of the extract, and increased antimicrobial and plant-biostimulant activity relative to an extract from *Trichoderma* grown alone[8]. The finding supports a cue-dependent model of metabolite production rather than the assumption that a strain has a fixed chemical phenotype.

Genetic regulation reinforces that interpretation. Deletion of the histone deacetylase gene *hda1* in *T. atroviride* altered secondary-metabolite profiles, volatile emissions, oxidative and osmotic stress responses, and mycoparasitic activity against *Botrytis cinerea* and *Rhizoctonia solani*[9]. Chromatin state is therefore part of the applied phenotype: A strain's genome may encode useful biosynthetic capacity, but environmental cues and regulatory networks determine which products are expressed.

## PLANT-*TRICHODERMA* COMMUNICATION AND INDUCED RESISTANCE

**Root recognition and colonization:** Beneficial interaction requires compatibility. The plant supplies chemical signals and a colonization niche, while the fungus must distinguish host-derived cues from competitive or hostile signals. In *T. harzianum* B97, plant recognition induced a previously uncharacterized Plant Communication Associated gene cluster; experimental disruption of this cluster impaired plant colonization[10]. This result identifies early chemical communication as a functional determinant of establishment, not merely a descriptive feature of the interaction.

Proteomic evidence also shows bidirectional molecular adjustment. During interaction between *Arabidopsis thaliana* and *T. atroviride*, shotgun secretome analysis identified 126 plant proteins and 1,027 fungal proteins, with hundreds differentially modulated. Fungal glycosidases, endopeptidases, dehydrogenases, and other enzymes changed in response to the plant, while the plant altered peroxidases, proteases, secondary-metabolite catabolism, and defense-associated proteins. The plant enzyme glutamate: glyoxylate aminotransferase GGAT1 was partially required for growth stimulation and systemic resistance in that system[11]. These data support a negotiated interaction in which both partners remodel their secreted machinery.

**Hormonal signaling and ISR:** Root colonization can prime systemic defense without requiring the fungus to be present at the site of later pathogen attack. The best-supported signaling model involves dynamic interactions among jasmonic acid (JA), ethylene (ET), salicylic acid (SA), auxin, and, under abiotic stress, abscisic acid (ABA). In cucumber, root inoculation with *T. longibrachiatum* H9 increased growth, reduced gray-mold disease, and induced transcriptomic, proteomic, and hormonal changes involving JA, ET, and SA; JA and SA contents were higher after inoculation[12]. In oilseed rape, *T. harzianum* TH12 and its culture filtrate induced temporally distinct JA/ET- and SA-associated marker genes, and activation of these pathways was associated with reduced symptoms of *Sclerotinia sclerotiorum*[13].

An ISR should not be treated as a uniform switch. A primary study of *T. asperellum* 152-42 in alfalfa linked disease reduction to JA signaling, defense enzymes, defense-gene expression, sucrose metabolism, MAPK signaling, and rhizosphere restructuring; the strain also increased hay yield by 10-13% in field trials[14]. By contrast, a greenhouse study of arbuscular mycorrhizal fungi and *T. harzianum* in tomato found that beneficial inoculation redirected a *Fusarium*-challenged plant from a JA-dominated state toward an SA-associated state, but co-inoculation did not improve pathogen suppression beyond single inoculations[15]. Thus, "hormone modulation" describes a context-sensitive rebalancing process, not a single universal pathway.

Host genotype is another source of variation. In tomato, one genotype responded to *T. harzianum* with lower *Botrytis* lesion area, greater plant height, and more root biomass, whereas another genotype did not show the same benefit. The responsive genotype showed distinctive enrichment of BR, phenylpropanoid, and JA/ET-related programs alongside reduced SA-associated expression[16]. Selection of a compatible crop genotype may therefore be as important as selection of the fungal strain.

## PLANT GROWTH PROMOTION AND ROOT-SYSTEM ARCHITECTURE

**Auxin-like activity and volatile signaling:** Growth promotion can occur through physical colonization or through diffusible and volatile signals. A synthesis of *Trichoderma* growth mechanisms reports indolic compounds, including indole-3-acetic acid (IAA), and volatile compounds such as 6-pentyl-2H-pyran-2-one and sesquiterpenes as contributors to root and shoot responses[17]. These compounds may modify endogenous hormone signaling, carbohydrate metabolism, root branching, and photosynthetic performance.

The primary evidence also warns against generalization. In a comparative study of several strains, IAA production and plant responses were strain-dependent; some strains inhibited primary-root growth *in vitro*, whereas physical separation from the plant allowed selected strains to increase shoot and root biomass, root production, and chlorophyll content. *Trichoderma asperellum* LU1370 promoted growth in plate assays but reduced growth in soil[18]. This contrast shows why growth-promotion assays must include the intended substrate and application route rather than relying on a single axenic plate test.

Root architecture is an important intermediate phenotype because it links signaling to resource acquisition. In pea grown under phosphorus limitation, native *T. asperellum* G3 solubilized phosphate in broth and increased root growth, shoot growth, biomass, total dry weight, chlorophyll, and carotenoids after inoculation[19]. The study was conducted in pots, so it supports a biological mechanism and host response but does not establish yield benefits under field conditions.

**Growth, yield, and product quality:** Field evidence demonstrates that growth promotion can persist beyond seedlings. In grape, greenhouse applications of *T. harzianum* M10, *T. atroviride* P1, or their major metabolites suppressed powdery mildew, while field application of *T. harzianum* T22 or 6-pentyl-α-pyrone increased yield, grape polyphenols, and antioxidant activity; the isolated compound produced effects

comparable to the living fungus in that experiment[20]. In saline soil, field inoculation with *T. harzianum* ST02 increased sweet-sorghum stem yield, height, stem diameter, and stem sugar content by 35.52%, 32.68%, 32.09%, and 36.82%, respectively, while also increasing available N, P, and K and altering bacterial community structure and nitrogen-cycling genes. These are encouraging results, but they belong to defined crop-strain-site combinations and should not be extrapolated to all formulations or agroecosystems.

## NUTRIENT MOBILIZATION, SOIL FERTILITY, AND BIOREMEDIATION

*Trichoderma* can contribute to nutrient-use efficiency through organic-acid production, phosphatases, phytases, siderophores, and changes in root development and microbial decomposition. Phosphate mobilization is especially relevant because fixed phosphorus is poorly available to plants. A primary study of *T. asperellum* G3 documented phosphate solubilization accompanied by reduced medium pH and improved pea growth under phosphorus-deficit conditions[19]. A separate chickpea study identified alkaline phosphatase as a major predictor of gradual phosphate release by two interacting *Trichoderma* isolates; the co-culture also produced IAA, siderophores, gibberellic acid, organic acids, and growth-promoting metabolites, and improved chickpea growth and soil alkaline-phosphatase activity in net-house trials[21].

Nutrient effects can emerge indirectly through microbial community change. In saline sweet-sorghum soil, *T. harzianum* increased nutrient availability and organic matter while changing bacterial community structure and increasing the relative abundance of Actinobacteria and nitrogen-cycling genes[22]. In rice seedlings under saline-alkaline stress, co-inoculation of *T. longibrachiatum* and *Bacillus aryabhattai* increased available N, P, and K more than either strain alone and altered the abundance of several bacterial and fungal groups[23]. Because these studies combine inoculation with complex soil processes, they support rhizosphere-level nutrient cycling rather than a simple claim that *Trichoderma* directly supplies all nutrients to the plant.

The same metabolic versatility creates possible bioremediation applications. A 2026 maize pot study found that *T. harzianum* Zag-1 tolerated lead *in vitro* and reduced lead-associated losses in biomass, chlorophyll, water status, and oxidative stability while increasing antioxidant activities and osmolyte-related metabolites in inoculated plants[24]. Such findings justify further work on contaminated soils, but food-chain transfer, metal speciation, persistence, and long-term ecological effects require field-scale assessment before agronomic recommendations.

## ABIOTIC-STRESS TOLERANCE

**Drought, salinity, and oxidative stress:** Drought and salinity affect water status, ion balance, photosynthesis, root growth, and redox homeostasis. A 2025 meta-analysis found that *Trichoderma* inoculation generally increased shoot and root biomass and chlorophyll-related or photosynthetic traits under drought, salinity, and heavy-metal stress. It also reported stress-specific changes in stomatal conductance, relative water content, antioxidant enzymes, reactive oxygen species, malondialdehyde, phenolics, and proline[25]. Because this is synthesis-level evidence, it supports a recurring pattern across studies but does not imply that every strain improves every response variable.

Primary experiments clarify the mechanisms and their limits. In wheat, *T. simmonsii* T137 altered 1,913 differentially expressed genes under water stress; genes related to carbohydrate metabolism and photosynthesis were upregulated, while ABA, proline, trehalose, and some non-enzymatic antioxidant pathways were downregulated relative to stressed controls. The treated plants maintained a healthier phenotype with lower hydrogen peroxide, proline, and malondialdehyde, suggesting that protection may reduce the need for a strong canonical stress response rather than simply intensify it[26]. In maize exposed to salinity, drought, or their combination, *T. harzianum* with arbuscular mycorrhizal fungi increased root dry weight, root volume, biomass, and SOD and APX activity; combined inoculation also altered secondary metabolites[27].

The magnitude and direction of response depend on the stress combination and delivery system. Recent synthesis warns that evidence for broad heat- and cold-stress protection remains limited, that microbiome co-occurrence does not prove causal network repair, and that biochar should not be described as a validated *Trichoderma* carrier without direct evidence[28]. Climate-smart use therefore requires multi-stress and multi-location trials, not only single-stressor experiments in sterile or highly controlled substrates.

## SECONDARY METABOLITES AND VOLATILE ORGANIC COMPOUNDS

Secondary metabolites provide a bridge between direct antagonism, plant signaling, and ecosystem interactions. Non-volatile products can act at the site of contact or in the rhizosphere, whereas VOCs can influence organisms without physical contact. In *T. atroviride*, targeted disruption of NADPH oxidase genes changed VOC profiles, fungistatic activity, and plant-growth promotion. The effects of mutants on Arabidopsis biomass and fungal inhibition differed according to the oxidase affected, and changes in compounds including 6-pentyl-pyrone were associated with contrasting growth-promoting and fungistatic outcomes[29]. This is evidence for regulatory coupling between fungal redox biology, chemical emission, and ecological function.

Metabolite identity alone is insufficient to predict agricultural performance. In a tomato study, metabolites produced by *T. afroharzianum* TRI07 inhibited *Alternaria alternata*, reduced disease incidence and severity in greenhouse plants, increased antioxidant enzymes, and altered phenolic and flavonoid profiles[30]. In grapes, living *Trichoderma* and purified metabolites both improved disease control and fruit biochemical quality[20]. Yet metabolite mixtures can change with growth conditions, extraction method, pathogen contact, and formulation. Product development must therefore define the active chemical or biological fraction under realistic production and application conditions rather than assuming that an *in vitro* extract represents the field product.

## MOLECULAR, GENOMIC, AND EPIGENOMIC PERSPECTIVES

Genome-scale approaches are expanding the ability to connect strain identity with function. Comparative genomics of *T. asperellum* and the closely related *T. asperelloides* identified differences in gene numbers and in genes associated with chitinases, cellulases, xylanases, secreted proteases, peptaibols, siderophores, and other plant- or soil-health traits; the authors emphasized that additional transcriptomic, proteomic, and efficacy studies are necessary before assigning functional consequences to the genomic differences[31]. This caution is appropriate: gene presence is a capacity indicator, not proof of expression or agronomic effect.

Transcriptomics and metabolomics can instead reveal condition-specific activity. In tomato colonized by *T. harzianum* T34, host analysis identified 156 consistently significant genes and broader changes involving transcription factors, carbohydrate metabolism, secondary-metabolite biosynthesis, nitrogen metabolism, and defense-related processes[32]. In melon treated with a commercial formulation containing *T. asperellum* ICC012 and *T. gamsii* ICC080, RNA sequencing and co-expression analysis associated disease mitigation with hub genes involved in dehydration response, lignin biosynthesis, phenylpropanoid metabolism, MAPK signaling, plant-pathogen interaction, and transporter activity[33]. These studies provide mechanistic hypotheses and candidate markers, but their predictive value for field performance remains to be tested.

Epigenetic regulation adds a further layer. In *Arabidopsis*, mutations in RNA-directed DNA methylation components altered the balance between JA/ET and SA signaling, impaired full expression of *T. atroviride*-mediated systemic resistance, and affected root colonization and growth-defense trade-offs[34]. In the fungus itself, histone deacetylase Hda1 regulated secondary metabolism, mycoparasitism, and stress tolerance[9]. The combined evidence suggests that successful inoculation depends on dynamic regulation in both partners, not simply on constitutive expression of defense or antifungal genes.

## *TRICHODERMA* AND THE PLANT MICROBIOME

A plant-associated *Trichoderma* strain enters an existing microbial network. Its effects can include direct suppression of pathogens, recruitment of beneficial taxa, modification of root exudates, changes in soil enzyme activity, and altered ecological competition. In red kidney bean, *T. harzianum* reduced root-rot incidence and severity, increased plant growth and antioxidant enzymes, decreased *Fusarium* abundance, enriched potentially beneficial bacteria, and produced a more stable rhizosphere network in a pot experiment[1]. In Masson pine, *T. koningiopsis* changed root exudates, particularly organic acids, which promoted beneficial *Trichoderma*, *Penicillium*, and *Bacillus* strains and inhibited *Fusarium*; a defined organic-acid mixture reduced damping-off incidence by 73.33% in seedlings[35]. These studies move beyond simple inoculant recovery by linking fungal treatment to host exudation and community assembly.

Microbiome remodeling can also be causal at the community level, but the evidence is still developing. *T. asperellum* FJ035 altered cucumber rhizosphere communities, and microbiome-transfer experiments supported a role for the remodeled community in Fusarium-wilt suppression. A simplified consortium containing the fungal strain and six associated bacterial strains reduced disease by 71.43% and increased plant weight by 54.69%[36]. In wheat, a minimal consortium of *T. harzianum* T19 and *Bacillus rugosus* PM16 suppressed crown rot, improved growth traits, enriched beneficial taxa, reduced pathogen-associated fungi, and altered metabolites and rhizosphere enzyme activities[37].

Consortia are not automatically superior. In tomato, *T. harzianum* and *Streptomyces microflavus* showed cross-antagonism *in vitro* and the combined treatment initially produced smaller roots than single inoculants, even though it induced stronger resistance responses in planta[38]. Likewise, AM fungi plus *T. harzianum* did not provide additive Fusarium suppression in tomato[15]. Consortium design should therefore be based on compatibility, resource partitioning, host response, and field persistence, with in planta testing given greater weight than agar co-culture alone.

## AGRICULTURAL APPLICATIONS AND DELIVERY SYSTEMS

**Application routes and crop contexts:** Agricultural deployment includes seed coating or dressing, soil incorporation, root dipping, nursery treatment, drenching, foliar application, and integration into organic amendments or biofertilizer formulations. The appropriate route depends on the target niche: Seed treatment can protect germinating roots, soil application can support rhizosphere establishment, and foliar treatment can deliver metabolites or induce above-ground defense. A review of application strategies emphasizes the importance of preventive timing, application frequency, delivery method, native strains, formulation, and combination with other antagonists[39].

Field studies show that formulation and strain selection can determine whether laboratory traits become agronomic benefits. A gamma-ray-improved *T. virens* mutant produced more secondary metabolites and was developed into a talc-based seed dressing using tamarind seeds for mass multiplication. Across replicated microplots, on-farm demonstrations, and larger farmer-field trials, the formulation improved germination and growth, reduced seedling mortality, improved yield and pod bearing, and advanced flowering in chickpea and lentil; toxicological testing reported no toxicity to the tested mammals, birds, or fish[40]. In coffee, 175 isolates were screened, and wettable-powder and water-dispersible-granule formulations of selected strains were evaluated in greenhouse and multi-location field trials over three years. The study found strong *in vitro* and greenhouse performance for selected isolates and supported their field potential against coffee wilt, while also demonstrating the need for location-specific evaluation[41].

Applications are most defensible within integrated disease and crop management. In sugarcane, combining *T. harzianum* and *T. viride* produced lower red-rot incidence than either strain alone in greenhouse and field experiments[42]. In maize affected by late wilt, field application of *T. viride* with

*Azospirillum brasilense* reduced disease incidence and severity and increased growth and yield parameters[43]. These results support combination strategies, but compatibility and dose must be empirically established for each crop and product.

**Sustainable and climate-smart agriculture:** The sustainability argument for *Trichoderma* is strongest when its multifunctionality reduces several constraints simultaneously: Pathogen pressure, nutrient limitation, water stress, or poor establishment. Field-scale maize inoculation with a consortium containing *T. harzianum* OMG16, *Pseudomonas* sp. RU47, and *Bacillus atrophaeus* ABi03 increased plant growth and fitness across intensive and extensive farming systems, with effects linked to iron uptake, hormonal balance, reactive-oxygen detoxification, iron-chelating root exudates, and rhizosphere community shifts[44]. In saline sweet sorghum, the fungal inoculant improved both plant performance and rhizosphere nutrient status[22]. Such examples suggest that the most valuable products may be multifunctional inoculants integrated with reduced or targeted chemical inputs rather than universal replacements.

Sustainability also requires ecological restraint. A recent biosafety-focused review notes that repeated or prolonged application could alter microbial biodiversity, reduce beneficial resident microbiota, and expose non-target organisms to bioactive metabolites; it recommends site-specific strategies, monitoring, and ecotoxicological assessment[45]. The ecological benefits of a product must therefore be evaluated over the time horizon of repeated use, not inferred from one season of disease suppression.

## METHODOLOGICAL COMPARISON

Previous research has demonstrated the potential of *Trichoderma* under controlled laboratory and greenhouse conditions; however, the strength and applicability of evidence can vary considerably across experimental settings. Laboratory studies provide controlled conditions for investigating mechanisms and interactions, while greenhouse experiments provide a more complex environment. Field trials offer greater practical relevance but are influenced by environmental variability and other factors (Table 1). This variation in experimental evidence highlights an important knowledge gap: findings demonstrated under controlled conditions do not always translate consistently into field-level effectiveness.

Across these designs, the most persuasive evidence comes from convergence: A strain or consortium should show a reproducible agronomic phenotype, establish or persist in the intended niche, alter a plausible mechanism, and retain efficacy under realistic field variation. A high enzyme activity, a differential-expression list, or an *in vitro* inhibition zone is useful for screening but is not sufficient as a product-performance endpoint.

## LIMITATIONS AND FUTURE PERSPECTIVES

**From strain identity to predictive function:** Species-level labels remain too coarse for application. Comparative genomic work shows that even closely related species differ in gene inventories associated with enzymes and secondary metabolites[31], while primary growth assays show that strains of the same broad group can produce opposite plant responses under different environments[18] . Research should therefore combine multilocus or genome-scale identification with standardized trait panels, colonization measurements, metabolite profiles, and host-response biomarkers. The goal is a predictive strain-by-context model, not a longer catalogue of species.

**Field reproducibility and formulation science:** Field efficacy remains less predictable than laboratory or greenhouse performance. Coffee trials, seed-dressing studies, and field inoculation experiments demonstrate that delivery technology, application timing, site, and formulation are part of the biological intervention[40,41]. Future trials should report viable propagule dose at application and at harvest, shelf-life and storage conditions, carrier chemistry, compatibility with common agrochemicals, colonization kinetics, weather and soil covariates, and yield responses across locations and seasons. Formulations should be compared on a common basis rather than treating "*Trichoderma* application" as a single intervention.

Table 1: Changes in strength between different experimental designs

| Study | Design and system | Main measurements | Key finding and evidentiary contribution |
|---|---|---|---|
| Environmental growth conditions of *Trichoderma* spp.[25] | Comparative *in vitro*, plate, and soil assays with multiple *Trichoderma* strains and *Arabidopsis* | IAA-related responses, VOC effects, root and shoot biomass, chlorophyll | Growth promotion and IAA/VOC effects were strain- and environment-dependent; one strain promoted growth in plates but reduced it in soil. This is strong evidence against single-assay generalization |
| *T. longibrachiatum* H9 in cucumber[12] | Root inoculation with pathogen challenge; transcriptome, proteome, and hormone analysis | Growth, gray-mold disease, DEGs/DEPs, JA and SA | Root colonization promoted growth and reduced foliar disease while activating JA/ET- and SA-associated responses. The multi-omics design links phenotype to candidate signaling pathways but remains crop- and strain-specific |
| Native *T. asperellum* G3 in pea[19] | Phosphate-solubilization assay plus phosphorus-deficit pot experiment | Solubilized phosphate, pH, root and shoot traits, biomass, pigments | Phosphate mobilization coincided with improved pea growth under P limitation. The study supports a nutrient-mediated mechanism but does not establish field-scale fertilizer replacement |
| Mutant *T. virens* seed dressing[40] | Mutant development, transcriptomics, greenhouse disease pressure, replicated and farmer-field trials | Secondary metabolites, mycoparasitism-related genes, germination, mortality, growth, yield, toxicology | The formulated mutant produced repeated field benefits in chickpea and lentil. Its multi-stage design provides stronger translational evidence than *in vitro* antagonism alone |
| *T. harzianum* ST02 in sweet sorghum[22] | Field trial in saline soil with rhizosphere analysis | Yield components, sugar content, soil nutrients, organic matter, bacterial community, N-cycling genes | Inoculation improved crop performance and rhizosphere nutrient status while restructuring bacterial communities. The field design supports agronomic relevance, but site and season dependence remain important |
| *T. asperellum* 152-42 in alfalfa[14] | Strain screening, pot experiments, transcriptomics, microbiome sequencing, and field trials | *in vitro* inhibition, disease index, JA signaling, defense genes, microbiome, hay yield and protein | The study integrated direct antagonism, immune priming, metabolic reprogramming, microbiome change, and field productivity. It is a strong model for trait-to-field translation, although independent multi-location replication is still needed |
| Microbial consortium in maize[44] | Long-term field trial across intensive and extensive systems with an early drought episode | Growth and fitness, iron uptake, hormones, ROS detoxification, root exudates, rhizosphere sequencing and metagenomics | The consortium improved plant fitness across farming systems and linked the response to iron acquisition and community change. This is among the more ecologically realistic designs, but consortium-specific effects cannot be assigned to *Trichoderma* alone |

**Causal microbiome mechanisms:** Amplicon sequencing frequently identifies taxa that co-vary with inoculation or disease suppression, but co-occurrence is not proof of causation. Stronger designs include microbiome transfer, synthetic-community reconstruction, targeted removal or addition of candidate taxa, isotope tracing, root-exudate measurements, and time-resolved sampling. The FJ035 cucumber study and the Masson-pine root-exudate study illustrate the value of linking community changes to transfer experiments or defined metabolites[33]. Similar causal validation is needed in field soils.

**Combined stresses, crop genotype, and ecological safety:** Most mechanistic experiments isolate one stress, one pathogen, or one host genotype. Yet field crops experience combinations of drought, salinity, heat, nutrient limitation, pathogens, and agrochemical exposure. Evidence for broad heat and cold protection remains limited, and host genotype can determine whether ISR occurs[12]. Multi-stress experiments should be paired with genotype-by-strain trials. At the same time, repeated-use studies should examine native microbial diversity, non-target organisms, metabolite persistence, horizontal gene transfer, and possible trade-offs between disease resistance and growth. Safety should be evaluated as an ecological property, not only as acute toxicity.

**Translational omics and responsible engineering:** Transcriptomics, proteomics, metabolomics, genome mining, and epigenomics can identify candidate genes and pathways, but their applied value depends on validation. The next step is to test whether candidate markers predict colonization, metabolite production, stress protection, or yield across independent strains and environments. Gene editing and synthetic biology may help dissect mechanisms or improve traits, but engineered strains require especially careful assessment of ecological persistence, gene flow, non-target effects, and regulatory status. A rational pipeline should move from discovery to knockout or complementation, then to controlled plant tests, formulation stability, multi-location field trials, and post-release monitoring.

## CONCLUSION

*Trichoderma* is best understood as a context-dependent biological platform rather than as a single-purpose fungicide. Its agricultural effects arise from the interaction of direct antagonism, resource competition, lytic enzymes, secondary metabolites, volatile signals, root colonization, hormone rebalancing, nutrient mobilization, stress physiology, and microbiome assembly.

The genus has genuine multifunctional potential: Selected strains improve growth, nutrient acquisition, stress responses, disease resistance, and field performance. These benefits are not universal. Strain identity, plant genotype, soil properties, microbial community, formulation, application route, and environmental conditions determine whether a mechanism becomes an agronomic outcome. Reliability will come from systems-level matching rather than from searching for one universally superior strain.

The practical future of *Trichoderma* lies in validated strain-crop-soil combinations, stable and compatible formulations, microbiome-aware consortia, and integration with cultural, genetic, nutrient, and chemical practices. Such a strategy preserves the strengths of biological inoculants while recognizing their ecological limits. Moving beyond biocontrol therefore means moving beyond single-function claims toward measurable, mechanistically informed, and field-tested plant-soil technologies.

## SIGNIFICANCE STATEMENT

*Trichoderma* has important agricultural functions that extend beyond conventional biological control of plant pathogens. This review integrates evidence on its roles in plant growth promotion, nutrient mobilization, stress tolerance, secondary metabolism, and rhizosphere microbiome interactions. It also highlights the variability of responses among strains, crops, formulations, and environmental conditions. The review emphasizes the need for field-validated, context-specific strategies for the reliable application of *Trichoderma* in sustainable agriculture.

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