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REVIEW

Omics-informed insights into biochar–*Trichoderma* interactions in plant–soil systems: mechanisms of defense and context-dependent responses

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Abstract

The combined application of biochar and *Trichoderma* spp. represents a promising strategy for enhancing plant resilience and soil health; however, the molecular mechanisms underlying their synergistic interactions remain poorly understood and inadequately integrated. This review critically synthesizes evidence from transcriptomic, proteomic, metabolomic, and microbiome analyses to elucidate how biochar-*Trichoderma* interactions modulate plant defense signaling pathways and stress adaptation responses. Transcriptomic analyses reveal context-dependent activation of the jasmonic acid (JA), salicylic acid (SA), and ethylene (ET) signaling pathways. Correspondingly, proteomic and metabolomic datasets demonstrate variable yet recurrent upregulation of pathogenesis-related (PR) proteins, reactive oxygen species (ROS)-scavenging enzymes, and phenylpropanoid-derived metabolites. Notably, accumulating evidence suggests that these molecular responses are highly context-dependent, varying substantially with soil type, biochar physicochemical characteristics, and *Trichoderma* strain specificity. We critically examine major methodological limitations in existing omics investigations, including inadequate reproducibility under field conditions and insufficient integration of molecular and ecological datasets. Finally, we propose a systems biology framework for designing functionally optimized biochar–microbe formulations and identify research priorities for translating insights into agronomically robust and field-deployable technologies.

Keywords Biochar · *Trichoderma* · Plant–microbe interactions · Multi-omics · Plant defense mechanisms · Rhizosphere microbiome · Induced systemic resistance · Sustainable agriculture

Introduction

Contemporary agriculture today faces the dual challenge of enhancing productivity while ensuring environmental sustainability. In this context, innovative solutions such as biochar and beneficial fungal inoculants such as *Trichoderma* spp. have emerged as promising tools for sustainability. These biologically based approaches address the growing demand for eco-friendly farming practices while providing viable alternatives to conventional synthetic fertilizers and pesticides.

Biochar, a carbon-rich product derived from the pyrolysis of organic biomass, has garnered attention for its multifaceted role in soil enhancement. It improves soil physical properties, such as porosity and water retention, and enhances nutrient availability while serving as a long-term carbon sequestration agent (Dai et al. 2020). Luo et al. (2023) estimated that 9.3% of crop residue carbon is retained in soil annually over three decades with biochar application. Biochar amendments can also mitigate global warming potential in various soil types by reducing greenhouse gas emissions, including CO_2, CH_4, and N_2O (Li et al. 2022). Biochar also provides a conducive habitat for beneficial microbes, further

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underscoring its potential in modern agriculture (Bolan et al. 2023). Additionally, biochar plays a vital role in soil remediation by reducing the bioavailability of heavy metal contamination (Mansoor et al. 2021).

Trichoderma spp., a genus of beneficial fungi, are well recognized for their plant growth-promoting and biocontrol capabilities. These fungi suppress plant pathogens through mechanisms such as mycoparasitism, competition, and the production of antimicrobial secondary metabolites (Contreras-Cornejo et al. 2016; Vinale and Sivasithamparam 2020). Moreover, they enhance plant resilience by triggering induced systemic resistance (ISR), a defense priming mechanism in plants (Abdelkhalek et al. 2022). Their role in improving nutrient uptake and promoting root growth solidifies their position as important agents of sustainable plant health management (Singh et al. 2019; Fazeli-Nasab et al., 2022).

The synergy between biochar and *Trichoderma* offers a promising avenue for sustainable agriculture by merging the structural and chemical benefits of biochar with the biological strengths of *Trichoderma*. Biochar provides a conducive habitat for *Trichoderma*, enhancing its proliferation and activity (Cao et al. 2022); Sani et al. (2020) demonstrated that the combined application not only promoted plant growth but also allowed for a 50% reduction in synthetic NPK fertilizer use without compromising yield. This interaction improves pathogen suppression and boosts plant defense mechanisms, nutrient cycling, and overall soil health.

Recent studies have demonstrated specific benefits of this combination. Paveen et al. (2025) showed that biochar and *Trichoderma* at optimized concentrations and particle sizes significantly enhanced root mass by 23% and provided effective biocontrol against *Sclerotina sclerotiorum*, lowering disease severity by 40% in chickpea. This shows that biochar not only acts as a soil amendment but also supports the proliferation of *Trichoderma*, which further enhances plant resilience against pathogens. The combination of biochar with *Trichoderma harzianum* has also been shown to enhance phytoremediation efficiency in cadmium- and arsenic-contaminated soils (Yao et al. 2023). Such integrations align with the global need for environmentally sustainable and economically viable farming practices, reducing reliance on chemical fertilizers and pesticides. Both biochar and *Trichoderma* have been shown to influence plant hormonal pathway and trigger specific gene expression (Jaiswal et al. 2020; Bitik et al. 2026). Biochar contributes to plant resilience through its interaction with key hormonal pathways such as JA, SA, and ET (Jaiswal et al. 2020). These phytohormones are central to the plant defense mechanisms, particularly in ISR. Similarly, *Trichoderma* spp. is renowned for their role in eliciting plant defense responses through their interaction with hormonal signaling pathways and activation of defense-related genes (Siddaiah et al. 2017; Xu et al. 2020).

Despite growing empirical evidence supporting the agronomic benefits of combined biochar and *Trichoderma* applications, the mechanistic basis of their interaction remains poorly resolved. Most existing studies focus on phenotypic outcomes such as growth promotion or disease suppression (Sani et al. 2020; Kumari et al. 2025), while treating molecular responses as secondary or isolated observations. Critically, there is a lack of integrative understanding of how biochar physicochemical properties intersect with *Trichoderma* strain-specific traits to modulate plant hormonal signaling, redox homeostasis, and defense gene networks. Current omics studies are often conducted in isolation, lack cross-validation under field-relevant conditions, and rarely connect transcriptional or metabolic responses to rhizosphere-level ecological processes (Zhang et al. 2023; Khan et al. 2025; Ullah et al. 2026). This fragmentation has limited reproducibility and slowed the translation of laboratory findings into reliable agricultural applications. This review critically examines the molecular and systems-level interactions between biochar and *Trichoderma* spp., with a focus on identifying reproducible mechanisms of plant defense priming and stress tolerance. Rather than cataloguing positive outcomes, this work evaluates the consistency, limitations, and translational relevance of transcriptomic, proteomic, metabolomic, and microbiome-based evidence. Emphasis is placed on understanding how biochar physicochemical properties and *Trichoderma* strain-specific traits shape hormonal cross-talk, redox balance, and defense gene regulation, with the aim of guiding the rational design of next-generation biological soil amendments.

Mechanistic basis of biochar–*Trichoderma* interactions in plant defense signaling

The beneficial effects observed following combined application of biochar and *Trichoderma* spp. are increasingly attributed to their capacity to modulate plant defense signaling across multiple biological scales. Rather than acting through a single dominant pathway, both agents independently influence plant hormone signaling networks (also termed phytohormonal networks), cellular redox balance (the equilibrium, between oxidants and antioxidants), and rhizosphere processes that collectively shaping induced systemic resistance (ISR) and abiotic stress tolerance (Mehari et al. 2015; Yuan et al. 2019; Jaiswal et al. 2020; Yao et al. 2023). Critically, their interaction is not merely additive; instead, synergistic effects emerge from convergence at shared signaling nodes, including JA, SA, and ET pathways, ROS signaling cascades, and mitogen-activated protein kinase (MAPK) networks (Yao et al. 2023).

This section synthesizes current evidence across three organizational levels: (1) biochar-driven modulation of signal transduction and hormone systems, (2) *Trichoderma*-mediated priming of plant defense networks through direct host interactions, and (3) integrative mechanisms arising from biochar- *Trichoderma* co-application (Fig. 1).

Biochar-driven modulation of signal transduction and plant hormone systems

Biochar influences plant defense signaling primarily through indirect modulation of the rhizosphere environment, the soil zone directly influenced by root secretions and microbial activity (Mushtaq et al. 2025). Specifically, biochar amendments alter soil physicochemical properties (e.g., pH, cation exchange capacity, porosity), microbial community structure, and redox potential (the soil's oxidation-reduction status) (Frenkel et al. 2017; Bolan et al. 2023). These rhizosphere-level changes translate into downstream effects on plant hormonal balance and stress responsive gene expression.

Multiple independent studies demonstrate that biochar application primes JA-dependent defenses against necrotrophic pathogens (microorganisms that kill host tissue prior to colonization) while simultaneously facilitating SA-associated systemic acquired resistance (SAR) through enrichment of beneficial microbial populations (Mehari et al. 2015; Rasool et al. 2021; Ahmad et al. 2024). However, the magnitude and directions of these effects vary substantially depending on biochar source material, pyrolysis conditions, and host plant species, a critical point often underemphasized in the literature (Prasad et al. 2018).

At the molecular level, biochar-induced ROS production functions as an early signaling molecule (also termed a secondary messenger), activating Ca^{2+}-dependent protein kinases and MAPK signaling cascades networks and subsequently regulate hormone-responsive transcription factors that control defense gene expression (Chen et al. 2019; Kong et al. 2022). Transcriptomic analyses (genome-wide gene expression profiling studies) consistently report upregulation of JA-responsive genes such as PDF1.2 (Plant Defensin 1.2), LOX (Lipoxygenase), and VSP (Vegetative Storage Protein), alongside context-dependent activation of SA-marker genes including PR1 (Pathogenesis-Related protein 1). For example, Mehari et al. (2015) demonstrated that hardwood-derived biochar significantly reduced *Botrytis cinerea* (a necrotrophic fungal pathogen, commonly known as gray mold) severity in tomato by enhancing JA-associated defense responses, including elevated expression of *PDF1.2* and *LOX*, while maintaining moderate activation of SA-responsive genes. Similarly, Rasool et al. (2021) reported suppression of *Fusarium oxysporum* (a soil-borne vascular wilt pathogen) in cucumber through biochar-mediated modulation of antioxidant enzymes and hormone signaling. However, these responses are highly variable and depend on biochar feedstock source (e.g., wood vs. manure), pyrolysis temperature (typically 300–700 °C), particle size, and application rate (Siddiqi and Husen 2019; Zhu et al. 2021). This context-dependency explains the substantial inconsistencies observed across experimental systems and limits generalizability (Meller Harel et al. 2012; Copley et al. 2017).

Beyond biotic stress responses, biochar also modulates ET-, ABA- (abscisic acid, a stress hormone regulating water balance), and MAPK-associated signaling under abiotic

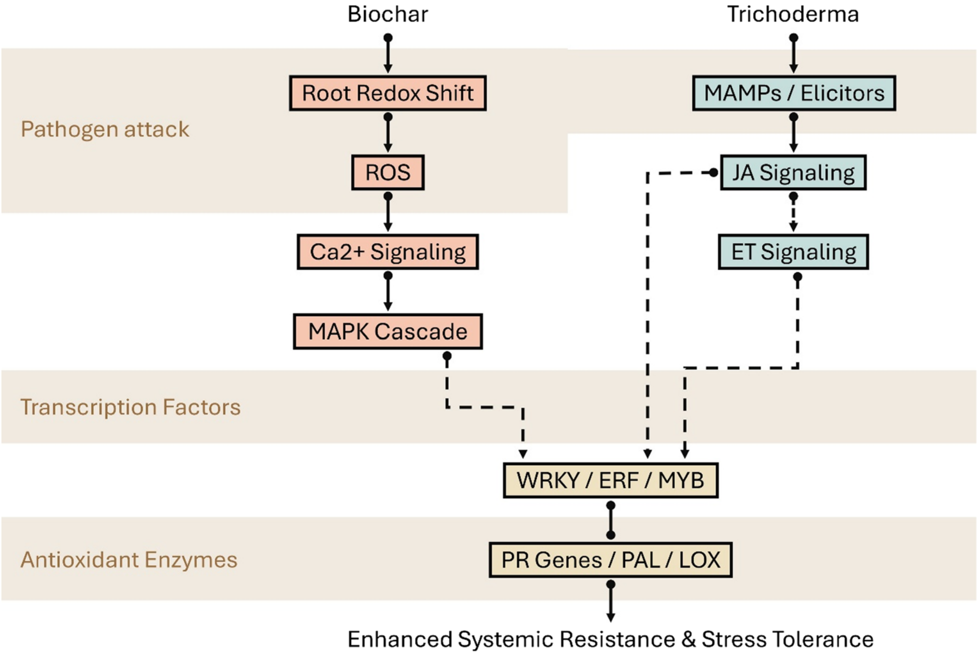

Fig. 1 Proposed KEGG-guided model illustrating the convergence of biochar-induced redox and MAPK signaling with *Trichoderma*-triggered JA/ET pathways. The model predicts signal integration at WRKY, ERF, and MYB transcriptional hubs, resulting in amplified defense gene expression, enhanced antioxidant capacity, and systemic stress tolerance

stress conditions. Under salinity stress, biochar reduced Na^+ (sodium ion) accumulation in plant tissues while modulating ABA, JA, and ET levels, resulting in improved growth and enhanced oxidative stress tolerance (Farhangi-Abriz and Torabian 2018). Similar protective effects have been documented under drought, heavy metal toxicity, and heat stress, where biochar elevated activities of antioxidant enzyme (e.g., superoxide dismutase, catalase, peroxidase) and stabilized photosynthetic efficiency (Kumar et al. 2021; Awad et al. 2022; Cheng et al. 2023). However, biochar effects are not universally beneficial. Excessive application rates or biochar with inappropriate physicochemical properties can disrupt hormonal equilibrium or inadvertently enhance pathogen fitness, as demonstrated in *Rhizoctonia solani* (a soil-borne fungal pathogen causing damping-off disease) patho-systems where certain biochar types increased disease incidence (Copley et al. 2017). These contrasting outcomes underscore the critical need for mechanistic understanding and context-specific optimization rather than blanket recommendations based on empirical observations alone.

Trichoderma-mediated priming of hormonal and defense networks

In contrast to biochar's indirect, rhizosphere-mediated effects, *Trichoderma* spp. exerts their influence through direct molecular interactions with host plants. These fungi actively manipulate plant immune signaling via three primary mechanisms: (1) physical root colonization, (2) secretion of protein elicitors and other immunogenic molecules and (3) emission of volatile organic compounds (VOCs), small airborne signaling molecules (Contreras-Cornejo et al. 2016; Vinale and Sivasithamparam 2020). Unlike biochar, which primarily modulates the soil environment, *Trichoderma* directly engages pattern recognition receptors on plant cell membranes, initiating signal transduction cascades analogous to those triggered by pathogen-associated molecular patterns (PAMPs).

Root colonization by *Trichoderma* triggers rapid cellular responses, including transient ROS bursts (controlled production of reactive oxygen molecules serving as danger signals) and cytosolic Ca^{2+} fluxes (rapid increases in calcium ion concentration within the cell cytoplasm). This early signaling activates MAPK cascades and initiate JA/ET-dependent ISR pathways (Brotman et al. 2013; Martínez-Medina et al. 2017). Multiple studies demonstrate preferential activation of JA-dominant defense against necrotrophic fungi and plant parasitic nematodes, while SA signaling is selectively modulated depending on pathogen lifestyle (biotrophic vs. necrotrophic), For instance, in *Arabidopsis* (a model plant species), colonization by *Trichoderma harzianum* T22 activated JA/ET-dependent ISR, conferring enhanced resistance against necrotrophic pathogens such as *Alternaria brassicicola (*a fungal leaf pathogen*)*, while exhibiting minimal dependence on SA signaling (Martínez-Medina et al. 2017). Comparable JA-biased priming has been documented in economically important crops including tomato and maize, where *Trichoderma* inoculation upregulated defense-related transcription factors and genes encoding phenylpropanoid pathway enzymes– enzymes that synthesize antimicrobial compounds and cell wall fortification materials (Martínez-Medina et al. 2017; Yuan et al. 2019; Ji et al. 2021). These defense responses are orchestrated by transcription factors including WRKY (protein recognizing W-box DNA motifs), ERF (ethylene response factors), and MYB (myeloblastosis family proteins) and are accompanied by coordinate upregulation of defense-related genes including PR1, PDF1.2, PAL, and LOX (Aamir et al. 2023; Kabir and Bennetzen 2024).

Complementary proteomic (protein level) and transcriptomic (gene expression) analyses further reveal broad metabolic reprogramming following *Trichoderma* colonization, including secondary metabolism pathways, phenylpropanoid pathways, and antioxidant enzyme systems (Brotman et al. 2013; Yuan et al. 2019; Zhang et al. 2022). Importantly, *Trichoderma*-induced defense priming is dynamic and flexible rather than constitutively activated, enabling plants to modulate defense intensity based on actual threat perception and thereby optimize growth–defense trade-offs under varying biotic and abiotic pressures (Leonetti et al. 2017; Kumhar et al. 2022). This conditional defense activation minimizes fitness costs associated with maintaining high constitutive defense levels in the absence of stress.

Combining biochar and *Trichoderma* signaling into a unified defence framework

The functional integration of biochar and *Trichoderma* emerges from convergence at shared signaling hubs rather than parallel, independent actions. Biochar establishes a permissive rhizosphere environment, one that promotes microbial survival and activity, that enhances *Trichoderma* survival, colonization, and metabolic output, while *Trichoderma* translates this ecological advantage into molecular defense activation within the host plant (Fig. 2). Empirical support for this integration comes from studies demonstrating that biochar-amended soils significantly enhance *Trichoderma* root colonization and persistence, ultimately leading to stronger ISR outcomes compared to either treatment applied alone. For instance, Sani et al. (2020) reported improved suppression of soil-borne pathogens when *Trichoderma* was applied in biochar-enriched substrates, an effect linked to enhanced microbial activity, stabilized redox conditions, and amplified JA-related defense gene expression in the host plant (Sani et al. 2020; Da Silva et al. 2022; Rehaman 2023).

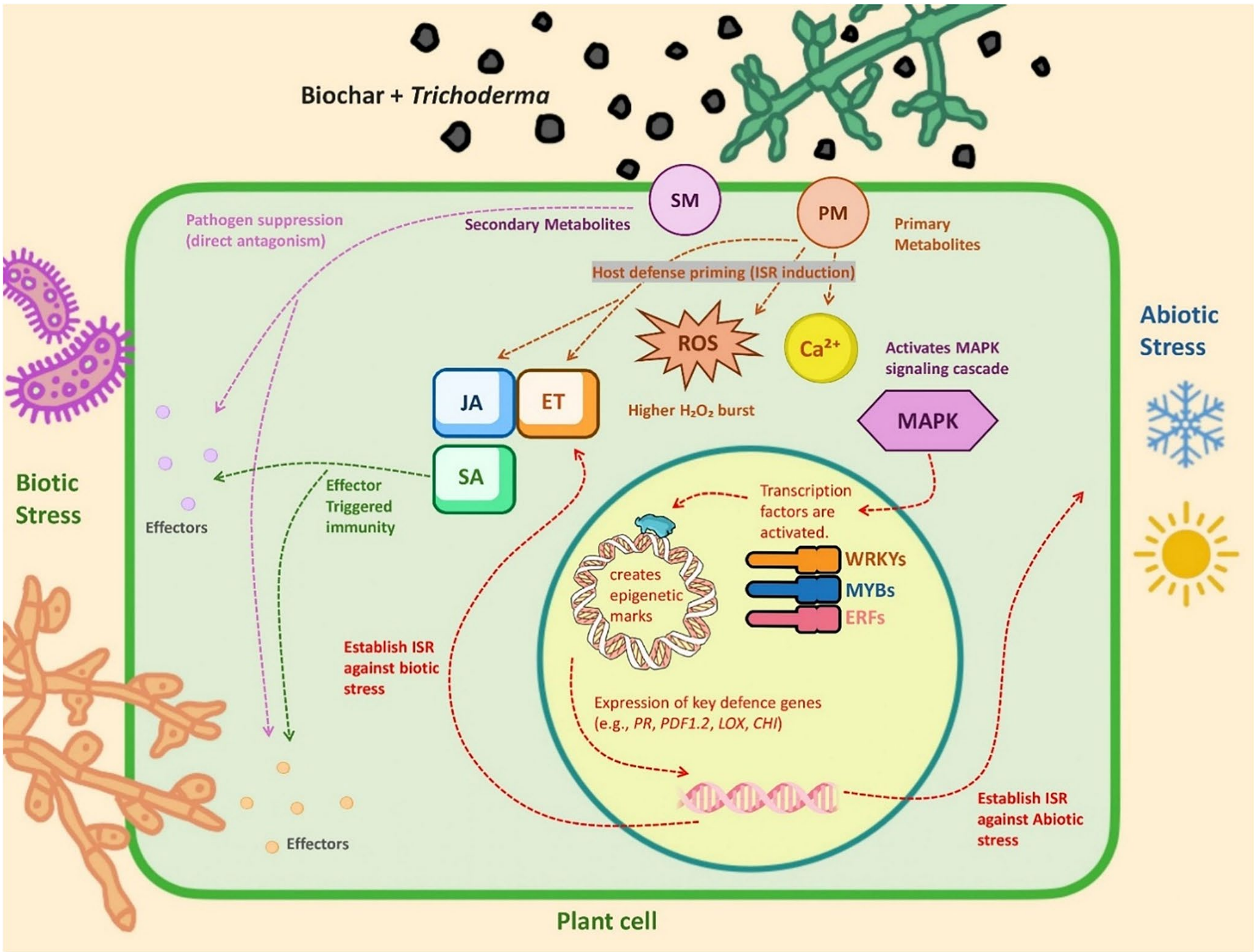

Fig. 2 Integrated mechanistic model of hormonal and redox signaling underlying biochar–*Trichoderma*-induced systemic resistance: The integrated pathway explains how plants simultaneously establish ISR against pathogens and enhance tolerance to abiotic stress. This synthesis highlights a unified redox–hormonal architecture

As illustrated in Fig. 1, biochar-induced redox modulation and MAPK activation intersect with *Trichoderma*-derived JA and ET signaling at transcriptional control points governed by WRKY, ERF, and MYB regulators (Mehari et al. 2015; Ji et al. 2021; Kong et al. 2022). This signaling convergence amplifies defense gene expression, stabilizes antioxidant capacity, and reinforces systemic resistance under biotic and abiotic stress contexts (Yuan et al. 2019; Yao et al. 2023).

Crucially, this integrated signaling framework explains why combined biochar–*Trichoderma* applications often outperform either component alone, while also accounting for context-dependent failures observed under field conditions (Liu et al. 2024). Without compatibility between biochar physicochemical properties and *Trichoderma* strain-specific traits, signaling coherence breaks down, resulting in inconsistent or antagonistic outcomes. Thus, the biochar–*Trichoderma* system should be conceptualized as a coupled signaling network rather than a simple additive input, highlighting the necessity of systems-level optimization for successful agronomic translation.

Omics approaches to decipher plant-microbe-soil interactions

Transcriptomics and gene expression related in ISR

Recent transcriptomic investigations have highlighted that combined application of biochar and *Trichoderma* application can activate multiple defense-related signaling pathways, thereby enhancing ISR in plants (Yu et al. 2023). Biochar amendment stimulates the JA and SA pathways, resulting in the upregulation of JA-responsive genes such as PDF1.2 and LOX, both critical for plant defense under pathogen challenge (Copley et al. 2017; Zhu et al. 2021). In addition, biochar can activate the phenylpropanoid pathway (a metabolic route that produces antimicrobial and antioxidant compounds), contributing to abiotic stress tolerance by modulating antioxidant metabolism and enhancing expression of stress-responsive genes under oxidative and heavy-metal stress conditions (Cheng et al. 2023).

Trichoderma spp. can further amplify these transcriptomic responses through the secretion of elicitors that prime expression of defense-related genes such as PR1 and ERF (ethylene response factors). Beyond these, *Trichoderma* induces activation of a broad range of disease-resistance genes, including NAC (NAM, ATAF, and CUC), Basic Helix-Loop-Helix (bHLH), and Serine/Threonine Protein Kinase (STK), as well as genes associated with cellular protection such as ATP-Binding Cassette (ABC) transporters and heat shock proteins (HSPs). These genes play pivotal roles in plant immunity and are regulated through interconnected JA and SA signaling cascades that together enhance plant resistance to diverse stresses (Ji et al. 2021; Kabir et al. 2024).

Recent transcriptomic data further demonstrate co-expression of genes involved in secondary metabolite biosynthesis and antioxidant pathways, both critical components of plant resilience (Tu et al. 2023). For example, both nanoscale biochar and *Trichoderma* have been shown to upregulate WRKY transcription factors under stress conditions, highlighting their central role in defense gene regulation during ISR (Brotman et al. 2013; Cheng et al. 2023) (Fig. 3). In muskmelon, a 5% biochar amendment significantly alleviated cadmium stress, with transcriptomic analyses identifying cytochrome P450, WRKY transcription factors, and annexin genes as key mediators of this tolerance (Cheng et al. 2023). Similarly, *Trichoderma asperelloides* T203 colonization in *Arabidopsis thaliana* roots modulated defense responses under saline stress, upregulating WRKY18 and WRKY40 and suppressing JAZ (Jasmonate ZIM-domain) repressors (Fig. 3). Suppression of JAZ genes consequently released the inhibition of JA-regulated defense genes such as FMO1 (Flavin-Containing Monooxygenase 1), PAD3 (Phytoalexin Deficient 3), and CYP71A13 (Cytochrome P450 71A13), thereby reinforcing JA-mediated defense and promoting long-term stress tolerance (Brotman et al. 2013).

Collectively, transcriptomic studies suggest that biochar and *Trichoderma* can modulate systemic defense signaling; however, reproducibility across plant species and environmental conditions remains limited. A major limitation of current datasets is the lack of temporal resolution (most studies capture single time points rather than dynamic gene expression changes over time) and poor standardization of biochar physicochemical properties, which complicates cross-study comparison. Future work should prioritize time-resolved transcriptomics under field-mimicking conditions, alongside standardized characterization of soil physicochemical variables.

Metabolomics in biochar-*Trichoderma* synergy

Metabolomic analyses provide valuable insights into the biochemical pathways modulated through biochar–*Trichoderma* interactions, particularly those governing production

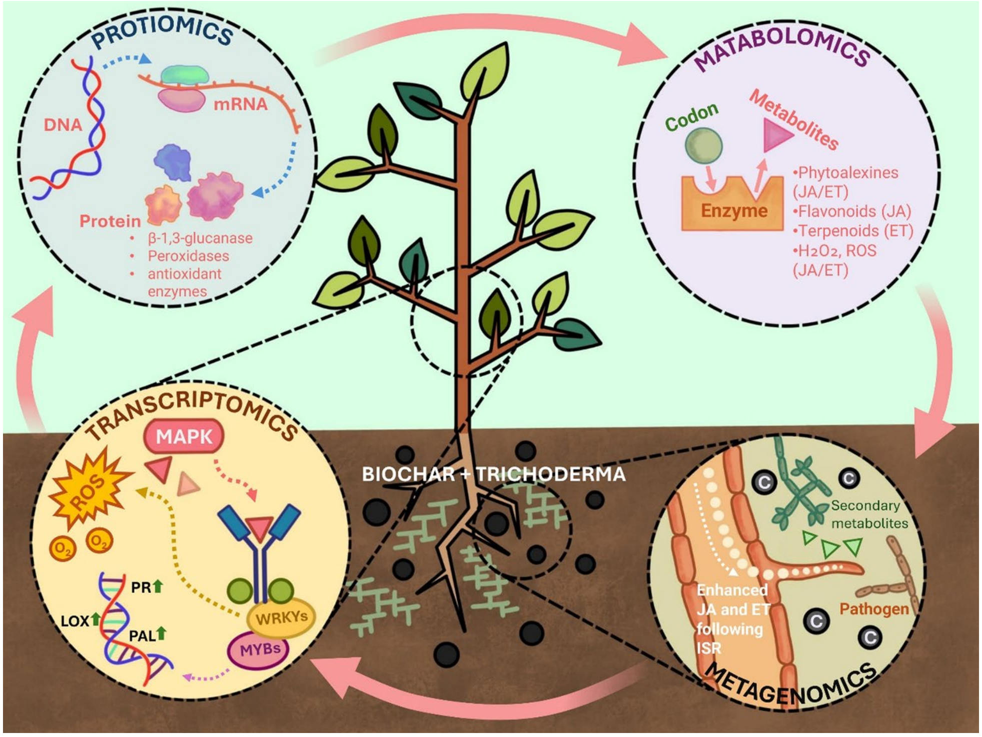

Fig. 3 A integrative multi-omics framework illustrating how biochar and *Trichoderma* co-regulate plant defense and rhizosphere function: The diagram highlights how biochar–*Trichoderma* synergy drives a coordinated ISR network, enhances JA/ET-mediated defense, and suppresses soil-borne pathogens through multi-scale molecular and ecological feedbacks. This integrated perspective provides a mechanistic foundation for understanding biochar–microbe-induced resilience in plant–soil systems

of secondary metabolites that underpin stress mitigation and plant defense. Comparative metabolite profiling indicates that their synergy enhances the accumulation of defense-related compounds such as phytoalexins, phenolic acids, and flavonoids, which are critical for pathogen suppression and oxidative stress reduction (Isah 2019; Tu et al. 2023; Paveen et al. 2025).

For instance, biochar-mediated enhancement of drought tolerance has been reported in *Leptochloa fusca* (Kallar grass) (Saleem et al. 2023), where physiological and metabolite changes revealed reduced oxidative damage following biochar amendment. Under drought stress, biochar-treated plants exhibited decreased levels of ROS such as hydrogen peroxide (H_2O_2), superoxide radicals, and hydroxyl ions, along with reduced levels of malondialdehyde (MDA) concentrations (Saleem et al. 2023). MDA is a lipid peroxidation marker (a compound released during oxidative damage to cell membranes) indicative of oxidative injury; its decline therefore has been linked to biochar's role in enhancing redox homeostasis (Saleem et al. 2022). Similarly, *Trichoderma* asperelloides T203 treatment in *Arabidopsis thaliana* roots upregulated antioxidant genes including MDAR (Monodehydroascorbate Reductase), APX1 (Ascorbate Peroxidase 1), and GST (Glutathione S-Transferase), which collectively increased ascorbate content and improved salt stress tolerance (Brotman et al. 2013). Each gene contributes to oxidative stress alleviation via distinct mechanisms: MDAR scavenges ROS, APX1 rapidly neutralizes H_2O_2, and GST catalyzes detoxification of reactive metabolites.

In metabolomic studies, plants treated with biochar or *Trichoderma* exhibited elevated levels of jasmonates, salicylic acid (SA) derivatives, and terpenoids (Roychowdhury et al. 2025). These compounds serve both as signaling molecules and antimicrobial metabolites, collectively strengthening plant immune responses to multiple phytopathogens (Sood 2023). For example, biochar amendment significantly reduced bacterial wilt disease caused by *Ralstonia solanacearum* in tomato, accompanied by higher activities of defense enzymes and increased accumulation of phenolic and lignin-like polymers that restricted pathogen colonization and scavenged ROS (Yao et al. 2023). However, excessive biochar application can produce antagonistic effects. High concentrations of maple bark biochar increased the severity of damping-off disease in tomato caused by *Rhizoctonia solani*. Gas chromatography–mass spectrometry (GC-MS) analyses revealed that this biochar influenced the mannitol cycle (a metabolic pathway used by certain fungi for osmotic regulation and energy storage), thereby enhancing the pathogen's stress tolerance and competitive fitness (Copley et al. 2015). Since mannitol serves as a carbon reserve and osmoprotectant in fungi, inclusion of *Trichoderma* could counteract such effects by suppressing soilborne pathogens and rebalancing microbial interactions in the rhizosphere.

Additionally, biochar and *Trichoderma* both promote the biosynthesis of osmolytes such as proline and soluble sugars, which are essential for osmotic adjustment under abiotic stress conditions (Nahar et al. 2016). Studies have demonstrated that *T. harzianum* and biochar alleviate salinity stress by enhancing osmolyte accumulation, boosting antioxidant defense, and improving nutrient uptake (Rawal et al. 2022). In wheat, biochar reduced salinity-induced oxidative damage by increasing proline content, lowering ROS levels (H_2O_2 and MDA), and stimulating antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and peroxidase (POD) (Wu et al. 2023; Shahzadi et al. 2024). Similarly, *Trichoderma* inoculation in Indian mustard enhanced growth and salt tolerance through elevated proline levels, higher antioxidant enzyme activities (SOD, POD, APX, glutathione reductase—GR), reduced Na^+ accumulation, and improved K^+ uptake (Ahmad et al. 2015).

This suggests that biochar primarily modifies soil physicochemical properties and *Trichoderma* enhances plant-microbe signaling, both ultimately contribute to reduced ROS accumulation and improved nutrient homeostasis. Their combined application may therefore offer synergistic benefits: biochar provides a conducive microenvironment for *Trichoderma* colonization, while *Trichoderma* enhances root physiology and nutrient acquisition. Still, many of these responses remain correlative, and further validation is required to establish causal mechanisms. This integrative interaction, revealed through metabolomic profiling, underscores the biochemical basis of ISR activation and stress mitigation, holding significant promise for sustainable crop production in stress-prone agroecosystems (Sharma et al. 2024).

Proteomics in pathogen suppression and induced systemic resistance

Proteomic analyses provide critical insights into the molecular mechanisms underlying the synergistic effects of biochar and *Trichoderma* on plant defense. By identifying differentially expressed proteins and enzymes, these approaches reveal how biochar- *Trichoderma* interaction modulates ISR and strengthens host immunity against both biotic and abiotic stressors (Khan et al. 2025; Ullah et al. 2026). Recent studies employing LC–MS/MS (liquid chromatography tandem mass spectrometry, a technique for identifying and quantifying proteins) and quantitative proteomic profiling have reported the upregulation of key defense proteins, signaling molecules, and enzymes that collectively contribute to pathogen inhibition and stress tolerance (Jaiswal et al. 2020).

Pathogenesis-related (PR) proteins are pivotal components of the plant defense arsenal, directly contributing to antifungal activity and immune signaling (La Spada et al. 2020; Wang et al. 202). Individual studies have reported significant upregulation of PR proteins, including chitinases and β−1,3-glucanases, enzymes that degrade fungal cell walls and thereby restrict pathogen colonization. For instance, synergistic action between chitinase (~2.0 U/mg) and β−1,3-glucanase (~80–82 U/mg) was observed in resistant mango cultivars (Bhadauran and Elaichi), leading to enhanced resistance against *Fusarium mangiferae*—a phenomenon absent in susceptible cultivars (Ebrahim et al. 2011). Their combined expression is more effective than either enzyme alone, a pattern consistent across other plant systems such as tobacco and tomato. These enzymes therefore serve as reliable biochemical markers for disease resistance and proteomic indicators of systemic defense activation.

Interestingly, the dual functionality of PR proteins in both plant immunity and pathogen virulence represents a notable proteomic paradox. PR-2 (β−1,3-glucanases), PR-3/PR-8/PR-11 (chitinases), PR-9 (peroxidases), and PR-10 (ribonucleases) are known to be enzymatically active defense proteins regulated by genes such as Gns6 in *Oryza sativa* and Chi2/Chi14 in *Cucumis sativus* (dos Santos et al., 2023; Chouhan et al., 2023). However, pathogens themselves have evolved PR1-like effectors that mimic host proteins. Proteomic and genomic evidence shows that *Fusarium oxysporum* (Fpr1), *F. graminearum* (FgPR1L-4), *Cytospora chrysosperma* (CcCAP1), and *Phytophthora sojae* (PsCAP1) produce PR1-like members of the CAP superfamily to suppress pattern-triggered (PTI) and effector-triggered immunity (ETI) (Han and Schneiter 2024). These findings highlight the complexity of host–pathogen protein interplay that biochar-*Trichoderma* systems may help rebalance toward host resistance.

Hormonal and antioxidant defense pathways

Proteomic studies have also shown that biochar and *Trichoderma* modulate the abundance of antioxidant enzymes such as superoxide dismutase (SOD) and peroxidases to mitigate oxidative stress during pathogen attack or environmental adversity (Zhu and Gao 2025). Key enzymes involved in hormone signaling pathways, including LOX and PAL, are frequently upregulated under biochar-*Trichoderma*-induced ISR (Jaiswal et al. 2020), suggesting integrated regulation of JA and SA signaling.

In cucumber, *Trichoderma* longibrachiatum H9 was shown to prime the plant proteome by upregulating proteins involved in multihormonal signaling (JA, SA, and ET), stress response, and secondary metabolism (Yuan et al. 2019). These included enzymes associated with α-linolenic acid metabolism (involved in JA biosynthesis), phenylalanine metabolism (involved in SA biosynthesis), and cysteine and methionine metabolism (involved ET biosynthesis). Moreover, phenylpropanoid and flavonoid biosynthetic enzymes were enriched, indicating enhanced antimicrobial compound formation and cell-wall reinforcement. Enrichment of MAPK cascade proteins and phosphorylation-related proteins further confirmed robust systemic signaling characteristic of ISR (Yuan et al. 2019) (Fig. 3).

Biochar-induced proteomic modulation

Biochar amendment has also been associated with proteomic reprogramming that supports structural fortification and defense activation (Gao et al. 2023). In tomato roots, biochar treatment enhanced resistance to *Ralstonia solanacearum* by upregulating proteins involved in lignin biosynthesis, sulfur compound metabolism, and anion transport (Jaiswal et al. 2020; Yao et al. 2023). qRT-PCR (Quantitative reverse transcription polymerase chain reaction a method for measuring gene expression levels) validation confirmed consistency between transcript and protein levels, particularly for ubiquitin and cinnamoyl-CoA reductase—key proteins that prevent excessive tissue damage and promote lignin deposition, thereby creating physical barriers against pathogen invasion.

Similarly, certain reports indicate concentration-dependent or context-specific proteomic responses. Dissolved biochar, for example, can impair the biocontrol potential of *Steinernema feltiae* by inducing oxidative stress, suppressing SOD and CAT activity, and disrupting antioxidant defense pathways (Wang et al. 2025a, b). Such findings highlight the need to optimize biochar formulation and concentration to ensure compatibility with beneficial microorganisms.

Stress adaptation and cross-protection mechanisms

Proteomic evidence also suggests that *Trichoderma* primes plants for SAR against nematodes and salinity stress. In tomato, *T. harzianum* activated SA-dependent defense genes and ethylene biosynthesis, upregulating PR-1, PR-5, and ACO (1-aminocyclopropane-1-carboxylic acid oxidase)—a key enzyme converting ACC into ethylene, which mediates defense responses (Leonetti et al. 2017). Under salt stress, expression of PR-1, PR-2, and PR-5 was enhanced, accompanied by upregulation of Isochorismate synthase (ICS) and PAL, enzymes essential for SA biosynthesis (Boamah et al. 2023). Similarly, biochar treatment increased the activities of PPO, POD, LOX, and PAL—enzymes frequently quantified in proteomic assays as markers of immune activation (Fig. 3).

Integrated proteomic perspective

Collectively, proteomic studies reveal that biochar and *Trichoderma* activate overlapping but complementary defense networks involving PR proteins, antioxidant enzymes, and hormone-mediated signaling. Biochar enhances the rhizosphere environment and nutrient availability, creating optimal conditions for Trichoderma colonization, while *Trichoderma* modulates plant proteomes toward ISR and SAR activation (Jaiswal et al. 2020; Yao et al. 2023). Upregulation of proteins associated with secondary metabolism, oxidative stress mitigation, and structural reinforcement underscores a synergistic defense mechanism at the protein level. These proteomic signatures reinforce the concept that biochar-*Trichoderma* synergy primes plants for robust, multilayered resistance to both biotic and abiotic stresses. However, many of these responses remain correlative, and further functional validation is required to establish causal mechanisms.

Toward integrated multi-omics frameworks

Despite advances across individual omics layers, true multi-omics integration remains limited. Most Sstudies mentioned previously generate parallel datasets without resolving causal links between transcriptional, proteomic, and metabolomic responses (Ji et al. 2021; Yu et al. 2023; Cheng et al. 2023; Saleem et al. 2023; Sood et al. 2023). Future research should adopt integrative frameworks such as network-based modeling, multi-layer correlation analysis, and isotope-assisted fluxomics to connect gene expression with protein activity and metabolite dynamics. Such approaches are essential to move from associative patterns to mechanistic causality in biochar–*Trichoderma* systems. A comparative summary of major omics approaches, including their strengths and limitations, is provided in Table 1. Despite these advances, the majority of studies rely on correlative omics data, and direct causal links between molecular changes and phenotypic outcomes remain limited. Emerging evidence also suggests that plant molecular responses can influence rhizosphere microbial dynamics through alterations in root exudation patterns (Zhalnina et al. 2018; Iannucci et al. 2021). For instance, transcriptional reprogramming of pathways involved in secondary metabolite biosynthesis may lead to the release of compounds that selectively recruit beneficial microbes, including *Trichoderma* spp. and other plant growth-promoting organisms (Xie et al. 2025). However, direct experimental linkages between plant omics data and microbial community restructuring remain limited, highlighting a key gap in current research.

Table 1 Comparative overview of omics approaches in biochar–*Trichoderma* mediated plant–soil interactions: their key insights, strengths, and limitations

Omics approach	Key Insights	Strengths	Limitations	Relevance to biochar–*Trichoderma*
Transcriptomics	Gene expression (JA, SA, PR genes)	High sensitivity, pathway mapping	Poor correlation with protein levels	Identifies ISR activation
Proteomics	Protein abundance & enzymes	Functional insight	Low coverage, complex extraction	contribute to defense proteins
Metabolomics	Secondary metabolites, ROS	Direct phenotype link	Context-dependent variability	Reveals biochemical outputs
Microbiomics	Community shifts	Ecological relevance	Limited functional resolution	Shows rhizosphere dynamics

Future prospects

Despite the growing body of evidence supporting the synergistic benefits of biochar and *Trichoderma* spp. in enhancing plant resilience and soil health, future research must transition from descriptive outcomes to mechanistic and translational insights. Descriptive studies typically report phenotypic or expression-level changes without resolving causality (e.g., upregulation of PR genes under biochar treatment mentioned previously) (Jaiswal et al. 2020; Yao et al. 2023). Mechanistic studies, in contrast, identify causal pathways, such as JA-dependent signaling validated through mutant analysis or pathway inhibition. Translational insights extend these findings into field-applicable strategies, including optimized biochar formulations or strain-specific *Trichoderma* inoculants tested under agronomic conditions. Bridging these levels remains a critical gap in current research. A promising direction lies in the integration of multi-omics platforms including transcriptomics, proteomics, metabolomics, and microbiomics to construct a systems-level understanding of biochar-*Trichoderma*-plant-soil interactions. These approaches can help unravel the temporal dynamics of hormonal signaling, identify keystone microbial taxa, and decode metabolite fluxes that underpin ISR and abiotic stress tolerance. An emerging frontier in this context is the exploration of bio-activated hormonal signaling, wherein SA, JA, and ET pathways are naturally triggered by microbial elicitors and soil amendments. Unlike exogenous hormone applications, bio-activation represents a biologically integrated defense strategy, often mediated by root colonization, VOCs, and ROS signaling (Bhatt et al. 2024; Castejón-del Pino et al. 2025). Investigating how biochar-*Trichoderma* synergy influences bio-activation of these pathways particularly through the upregulation of key defense genes such as PR1, PDF1.2, LOX, and ERF could reveal novel regulatory nodes and priming mechanisms (Sofy et al. 2022; da Mota et al. 2025). This knowledge would be instrumental in designing next-generation bio-stimulants and functional soil amendments that promote sustainable and climate-resilient agriculture.

Additionally, the development of 'designer biochar' tailored to selectively enrich *Trichoderma* spp. and beneficial microbial consortia represents a novel avenue for functional soil microbiome engineering. These biochars could be optimized for specific soil types, crops, and stress conditions using predictive modeling and machine learning algorithms (Fig. 4). Coupling this approach with CRISPR-based functional genomics in *Trichoderma* spp. may allow for the fine-tuning of elicitor production, root colonization traits, and stress-responsive gene activation, thereby enhancing biocontrol efficacy and plant growth promotion (Frenkel et al. 2017; Zygourakis 2017; Wang et al. 2025a, b).

Future research should prioritize mechanistic validation under agronomically realistic conditions. Multi-omics integration must progress beyond parallel data generation toward establishing functional causality, particularly through isotope labeling, microbial knock-out systems, and time-resolved field-scale trials. New biochar designs should be guided by physicochemical–microbial compatibility metrics rather than generalized assumptions of microbial stimulation. Without rigorous field validation, the biochar-*Trichoderma* concept will remain a laboratory-scale phenomenon with limited agricultural impact. Given the substantial heterogeneity in biochar physicochemical properties arising from differences in feedstock composition and pyrolysis conditions, mechanistic interpretations should be considered context-dependent rather than universally applicable. While certain trends—such as enhanced microbial colonization or modulation of plant defense pathways—are frequently observed, their magnitude and direction may vary significantly across systems.

Conclusion

The synergy between biochar and *Trichoderma* represents an emerging paradigm in sustainable agriculture, coupling soil physicochemical enhancement with biologically driven plant defense. Evidence from transcriptomic, metabolomic, and proteomic studies suggests that their combined application activates multilayered defense networks involving JA, SA, and ET signaling, driving upregulation of defense genes, antioxidant enzymes, and secondary metabolites, thereby strengthening ISR and SAR. Biochar improves soil structure and nutrient dynamics, creating favorable conditions for *Trichoderma* colonization, while *Trichoderma* primes plants through release of elicitors and regulation of defense-related proteins. Omics-driven insights now enable a systems-level

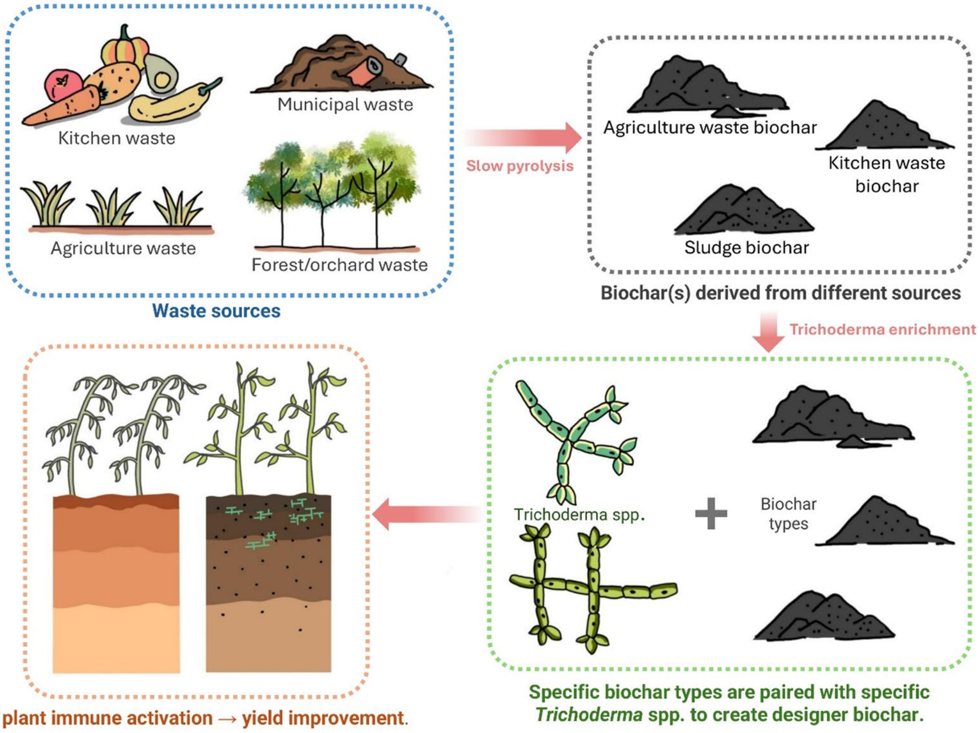

Fig. 4 Conceptual workflow for developing designer biochar through targeted pairing of feedstock-derived biochars with specific *Trichoderma* strains

understanding of this biochar-*Trichoderma* relationship, revealing its potential to reprogram plant–microbe–soil interactions beyond conventional biofertilization or pathogen suppression. Such integration offers a mechanistic basis for designing tailored bioformulations that enhance crop productivity and resilience under climate stress.

Future research should prioritize mechanistic validation under agronomically realistic conditions. Multi-omics integration must progress beyond parallel data generation toward establishing functional causality, particularly through isotope labeling, microbial knock-out systems, and time-resolved field-scale trials. New biochar designs should be guided by physicochemical–microbial compatibility metrics rather than generalized assumptions of microbial stimulation. Without rigorous field validation, the biochar-*Trichoderma* concept will remain a laboratory-scale phenomenon with limited agricultural impact. Given the substantial heterogeneity in biochar physicochemical properties arising from differences in feedstock composition and pyrolysis conditions, mechanistic interpretations should be considered context-dependent rather than universally applicable. While certain trends—such as enhanced microbial colonization or modulation of plant defense pathways—are frequently observed, their magnitude and direction may vary significantly across systems.

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Declarations

Competing interests The authors declare no competing interests.

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