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Mechanisms and Efficacy of *Trichoderma* spp. Against Major Cashew (*Anacardium occidentale*) Pathogens

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How to Cite: Sokra, I., S. Somaly, H. Sarun, H. Meta, D. Wulandari. (2025). Mechanisms and Efficacy of *Trichoderma* spp. Against Major Cashew (*Anacardium occidentale*) pathogens. *Int. J. Agr. Syst.* 13(2): 162-175

ABSTRACT

Cashew (*Anacardium occidentale* L.) production in tropical and subtropical regions is under serious threat from fungal diseases, such as anthracnose (*Colletotrichum gloeosporioides*), powdery mildew (*Oidium anacardii*), vascular wilt (*Fusarium oxysporum*), and gummosis (*Lasiodyplodia theobromae*). For many years, disease management has relied heavily on synthetic fungicides, a practice that has raised environmental and public health concerns. Consequently, alternative and more sustainable disease control strategies have garnered considerable attention. Literature studies indicate that these fungi suppress diseases through several interacting mechanisms, including direct antagonism via mycoparasitism and antibiosis, as well as indirect effects associated with induced systemic resistance and plant growth promotion. Across various experimental systems, certain species, particularly *Trichoderma harzianum* and *T. asperellum*, have consistently demonstrated strong antagonistic activity against important cashew pathogens. Overall, the accumulated evidence supports the potential of *Trichoderma* spp. as effective, residue-free, and environmentally friendly biological control agents for improving disease management in cashew-based production systems.

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Keywords:

Anthracnose; cashew tree, gummosis; *Trichoderma* spp.; vascular wilt.

1. Introduction

Cashew (*Anacardium occidentale* L.) is an important tree crop both globally and regionally, contributing significantly to the economies of many tropical countries through the trade of its high-value nuts and fruits. It also serves as a major source of income and livelihood for millions of smallholder farmers, making the sustainable

production of this crop essential (Mc et al., 2024). However, cashew cultivation continues to face serious challenges from a complex range of biotic stresses, particularly those caused by fungal pathogens (Somaly & Sokra, 2024). Among the most destructive diseases are anthracnose (caused by *Colletotrichum gloeosporioides*), powdery mildew (caused by *Oidium anacardii*), gummosis (caused by *Lasiodiplodia* species), and the increasingly widespread vascular wilt associated with *Fusarium oxysporum*, all of which contribute substantially to disease incidence and tree mortality (Muntala et al., 2020; Sokra et al., 2024).

Historically, disease management strategies have relied heavily on synthetic fungicides (Mbasa et al., 2021). Although effective in the short term, this dependence has resulted in several major drawbacks, including the emergence of fungicide-resistant pathogen strains, accumulation of toxic chemical residues in the environment and agricultural products, and potential risks to human health (Ali et al., 2021). In response to these challenges, the agricultural sector is increasingly shifting toward ecologically sustainable alternatives (Pretty, 2018).

This review focuses on the potential of *Trichoderma* spp. as environmentally friendly biological control agents (Pretty, 2018). These ubiquitous soil fungi are well known for their strong plant growth-promoting and mycoparasitic capabilities, offering an effective and residue-free approach for the management of cashew diseases (Tedersoo et al., 2014). Therefore, this comprehensive review aims to synthesize the current knowledge regarding the multiple mechanisms of action employed by *Trichoderma* species against major cashew pathogens and critically evaluate the documented efficacy of *Trichoderma*-based formulations in controlling anthracnose, powdery mildew, vascular wilt, and gummosis in cashew trees.

2. Methodology

2.1 Research Location

This review was conducted at the University of Kratie in Kratie, Cambodia. This study compiled, analyzed, and synthesized published scientific evidence regarding the mechanisms and efficacy of *Trichoderma* spp. in controlling major fungal diseases of cashew (*Anacardium occidentale* L.).

2.2 Data Source, Tools, and Materials

Scientific literature was systematically collected from internationally recognized databases, including Google Scholar, Crossref.org, Scopus, and ScienceDirect. The search strategy included combinations of keywords such as *Trichoderma* spp., cashew diseases, anthracnose, powdery mildew, *Fusarium oxysporum*, *Lasiodiplodia theobromae*, biological control, and induced systemic resistance.

2.3 Data collection

Relevant studies were selected based on their direct relevance to *Trichoderma* in the control of cashew pathogens. Information was extracted on *Trichoderma* species or strains, target pathogens, antagonistic mechanisms (mycoparasitism, antibiosis, competition, induced systematic resistance, and plant growth promotion), experimental conditions (in vitro, greenhouse, and field studies), and efficacy parameters. Efficacy parameters included the percentage of mycelial growth inhibition, reduction in disease severity or incidence, and qualitative or quantitative descriptions of plant defense responses. The

collected data were organized and synthesized to facilitate a comparative evaluation of *Trichoderma* spp. against major cashew pathogens and to identify existing knowledge gaps and future research needs.

3. Results and Discussion

3.1 Overview of *Trichoderma* spp.

3.1.1 Taxonomy and Species Diversity Relevant to Agriculture

The genus *Trichoderma* belongs to the family Hypocreaceae of the phylum Ascomycota (Kubicek et al., 2008; Rashad et al., 2025). Many species have teleomorphs (sexual stages) that are classified under the genus *Hypocrea*, which is largely defined and employed based on the asexual or anamorphic state of *Trichoderma* (Overton et al., 2006). For nearly two centuries after its first description in 1794, the classification of *Trichoderma* has remained challenging because of the significant morphological variability among genera. However, modern taxonomy has moved from relying solely on macroscopic and microscopic features (such as conidiophore structure and spore color) to more robust molecular approaches, particularly the sequencing of the translation elongation factor 1- α (*tef1*) gene and the internal transcribed spacer (ITS) region of the DNA (Singh et al., 2020).

3.1.2 General Biology: Growth, Reproduction, and Colonization

Trichoderma species are fast-growing fungi commonly isolated from diverse environments, particularly natural soils, decaying wood, and the rhizosphere of plants (Waghunde et al., 2016). These conidia allow widespread dispersal and constitute a major source of inoculum in the form of fungicides (Martinez et al., 2023). Furthermore, under adverse environmental conditions, many *Trichoderma* species may form thick-walled spores, known as chlamydospores, which enable them to survive and persist in the soil for extended periods (Lewis & Papavizas, 1984). Ecologically, *Trichoderma* spp. are considered opportunistic, avirulent plant symbionts with elevated rhizosphere capacity, meaning they may colonize and grow along the root surfaces of developing plants over long distances, establishing stable and beneficial relationships with host plants (Konappa et al., 2020).

3.1.3 Historical and Current Use as a Biocontrol Agent

The potential of *Trichoderma* species as biological control agents (BCAs) was first recognized in the 1930s. Since then, extensive research has demonstrated their usefulness in combating a wide spectrum of soil-borne and foliar pathogens, including critical threats such as *Rhizoctonia*, *Pythium*, and *Fusarium* spp. (Ibrahim et al., 2022). The commercial use of *Trichoderma*-based products has accelerated significantly in recent decades, driven by the global demand for sustainable agricultural practices (Sheridan et al., 2014). Today, *Trichoderma* species have been developed into a wide range of commercial products employed worldwide as fungicides (for disease prevention), bioprotectants (for induced systemic resistance), biostimulants (to enhance nutrient uptake and root growth), and biofertilizers (for nutrient leaching) (Khakimov et al., 2020).

3.2 Major Cashew Pathogens

3.2.1 Anthracnose (*C. gloeosporioides*)

Anthrachnose represents a ubiquitous hemibiotrophic pathogen that causes blight on inflorescences, leaves, and nuts, resulting in the greatest yield loss (Figure 1). Anthrachnose, caused by the fungal pathogen *Colletotrichum gloeosporioides* (Penz.), is one of the most significant and economically widespread diseases affecting cashew (*A. occidentale* L.) cultivation in tropical and subtropical regions worldwide (Dos Santos et al., 2019). This disease poses a major threat to cashew production, leading to substantial yield losses that may exceed 30–70% in severe cases (Hsieh et al., 2023).

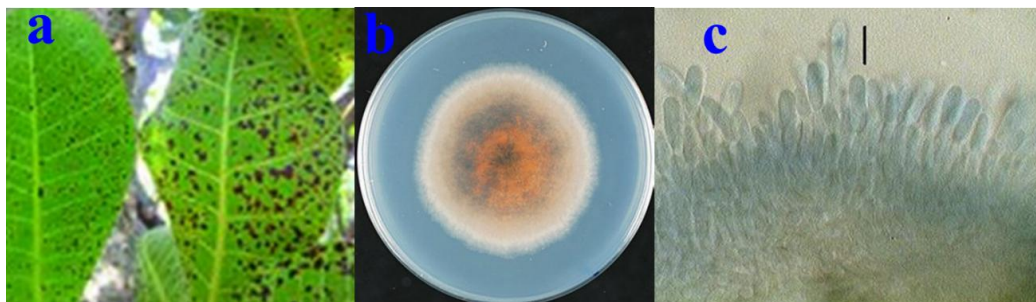


Figure 1. *C. gloeosporioides*. (a) symptom of *C. gloeosporioides* on cashew nut leaves, (b) *C. gloeosporioides* culture on PDA for 10 days growth, (c) Conidiophores bearing conidia of *C. gloeosporioides*.

3.2.2 Powdery Mildew (*O. anacardii* / *Erysiphe quercicola*)

Powdery mildew is universally recognized as the most critical fungal disease affecting cashew (*A. occidentale* L.), often causing severe yield losses that may range from 70% to total (100%) of the crop in severely affected areas (Swart, 2004). The disease is primarily caused by a fungus traditionally known as *O. anacardii* Noack, although recent molecular studies have reclassified the causative agent in cashew as *Erysiphe quercicola*, the perfective (sexual) stage of the fungus (Zakaria, 2022). This obligate parasite is highly specialized and attacks the most succulent parts of the cashew tree, especially during the flowering and main fruiting stages (Zakaria, 2022).

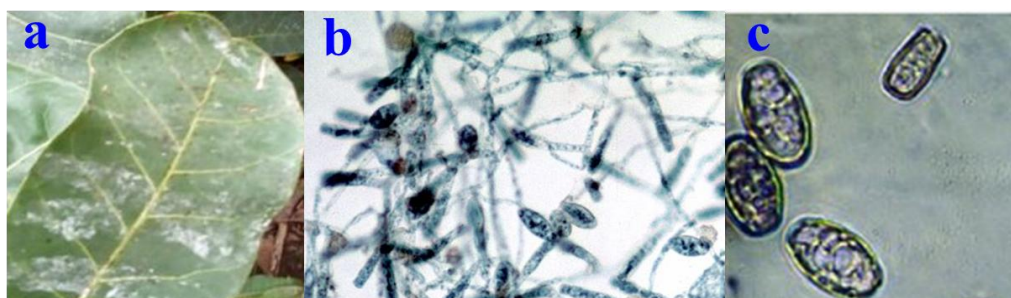


Figure 2. Powdery mildew. (a) powdery mildew on cashew nut, (b) Conidia and conidiophores of *O. anacardii*, (c) Conidia of *Erysiphe quercicola*.

3.2.3 Vascular Wilt (*F. oxysporum*)

Cashew disease, caused by the soil-borne fungus *F. oxysporum*, is a devastating vascular disease of cashew trees (*A. occidentale*) that may cause total crop loss, especially in young plants (Mbaso et al., 2021). The disease is characterized by the fungus invading and colonizing the xylem vessels (water-carrying tissue) of the tree, which is favored by warm soil temperatures and elevated humidity (Monteiro et al., 2022).

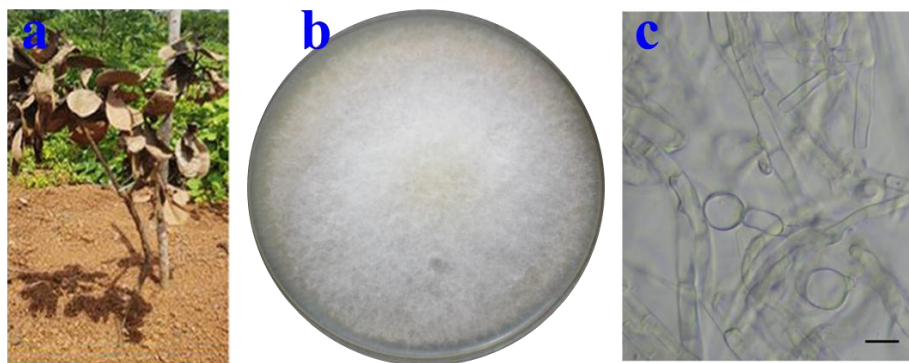


Figure 3. Vascular Wilt (*F. oxysporum*). (a) *F. oxysporum* on cashew nut tree, (b) *F. oxysporum* on PDA, (c) thick-walled chlamydospores.

3.2.4 Gummosis/Dieback (*Lasiodiplodia theobromae*)

Gummosis/Dieback in cashew, caused by the fungus *L. theobromae* (a member of the Botryosphaeriaceae family), represents a serious disease in tropical and subtropical regions, often emerging as an opportunistic pathogen when the cashew tree is under stress (e.g., drought or heat) (de Souza et al., 2024). The disease is characterized by a distinctive set of symptoms on the cashew tree (*A. occidentale*), the most notable of which include the extensive exudation of gum (gummosis) from the trunk and woody branches, the formation of dark, depressed cankers on the bark, and the dieback (wilting and necrosis) of young twigs and branches, which may progress to the death of the entire tree (Cardoso et al., 2004).

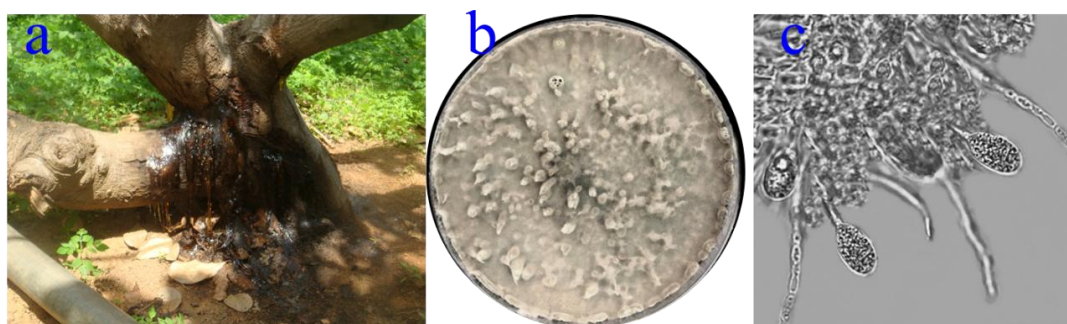


Figure 4. Gummosis/Dieback (*L. theobromae*). (a) gummosis on cashew tree, (b) *L. theobromae* on PDA, (c) Conidiogenous cells and paraphyses.

3.3 General Antagonistic Mechanisms of *Trichoderma*

3.3.1 Mycoparasitism

Mycoparasitism is one of the primary antagonistic mechanisms employed by *Trichoderma* species, in which they directly attack, penetrate, and digest other fungi, including plant pathogens, to acquire nutrients. This complex process begins with chemotaxis, in which *Trichoderma* senses and grows directionally toward the host pathogen, likely in response to small molecules and cell wall fragments released by the host (García-Sánchez et al., 2024). The critical stage represents hydrolytic attack, in which the mycoparasite secretes a potent cocktail of cell wall-degrading enzymes (CWDEs), predominantly chitinases, β -1,3-glucanases, and proteases (Karlsson et al., 2017). The process involves a sequence of well-defined stages, beginning with chemotaxis and recognition of the host pathogen, followed by attachment and subsequent hyphal

coiling. Subsequently, *Trichoderma* secretes cell wall-degrading enzymes, including chitinases, β -1,3-glucanases, and proteases, which facilitate the penetration of the host hyphae. This enzymatic degradation results in the lysis of the pathogen and subsequent nutrient acquisition, leading to a reduction in pathogen inoculum (Figure 5).

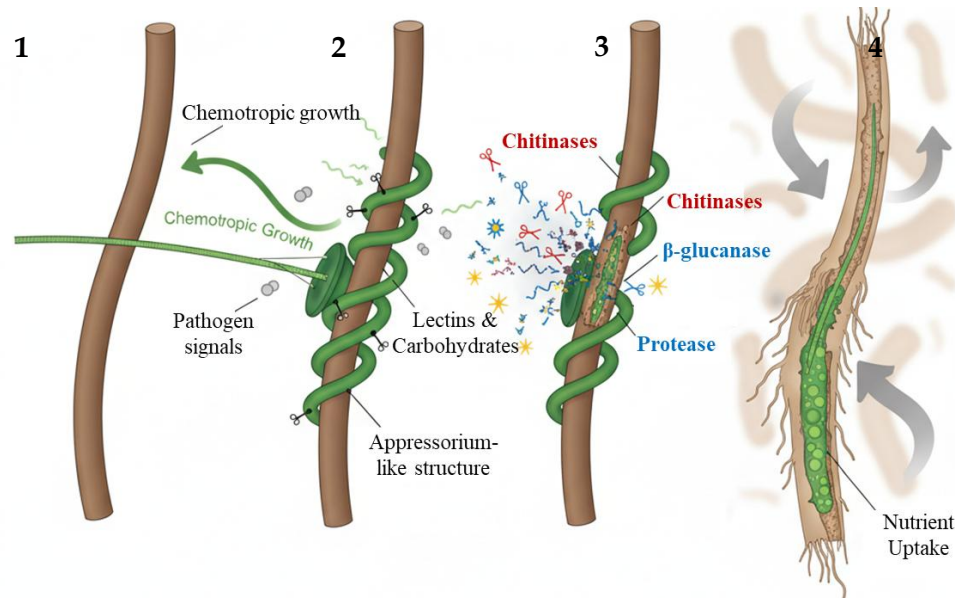


Figure 5. Sequential Stages of Mycoparasitism by *Trichoderma* Species.

3.3.2 Antibiosis

Antibiosis represents a pivotal antagonistic mechanism utilized by *Trichoderma* species, in which they secrete a diverse arsenal of low-molecular-weight secondary metabolites that are toxic to or inhibit the growth and function of pathogenic fungi and bacteria. This form of chemical warfare is highly effective against a broad spectrum of plant pathogens and often works synergistically with mycoparasitism (Nehra et al., 2022).

3.3.3 Induced Systemic Resistance (ISR)

Induced systemic resistance (ISR) represents a sophisticated indirect mechanism in which *Trichoderma* species, upon colonizing plant roots, trigger a whole-plant defense response without the plant experiencing an actual disease outbreak. This process begins with the release of elicitor molecules by the fungus, such as hydrophobins and specific cell wall fragments, which are recognized by the plant immune system (Gruber & Seidl-Seiboth, 2012).

3.3.4 Competition for Nutrients and Space

Trichoderma species are highly effective competitors for nutrients and space in the soil and on plant roots, which is crucial for their function as biocontrol agents. This competition is fierce because *Trichoderma* is a fast-growing fungus that rapidly colonizes available substrates, physically occupying space and quickly utilizing resources before slower-growing plant pathogens can establish themselves (Waghunde et al., 2016).

3.4 Efficacy of *Trichoderma* Against Cashew Pathogen Species

3.4.1 Efficacy Against Anthracnose (*C. gloeosporioides*)

Table 1 illustrates that the *Trichoderma* genus comprises highly effective biocontrol agents that utilize a sophisticated and multi-modal strategy to suppress

phytopathogens, such as *C. gloeosporioides*, the causal agent of anthracnose (Peralta-Ruiz et al., 2023). Their primary mechanisms include mycoparasitism, where they directly attack pathogen hyphae using cell wall-degrading enzymes such as β -1,3-glucanase and chitinase, and antibiosis, involving the secretion of powerful volatile and non-volatile antifungal compounds such as peptaibols and pyrones (Waghunde et al., 2016).

Table 1. Mechanisms of action and efficacy of different *Trichoderma* species against *C. gloeosporioides* on cashew plant.

<i>Trichoderma</i> spp.	Mechanism of Action	Observed Efficacy	References
<i>T. harzianum</i> & <i>T. pseudokoningii</i>	Mycoparasitism (coiling, enzyme secretion), Antibiosis (volatile and non-volatile compounds), Competition (nutrients, space)	Inhibited <i>C. gloeosporioides</i> growth by 64–71%; reduced anthracnose incidence by 92–96% in vivo	Peralta-Ruiz et al. (2023)
<i>T. viride</i>	Mycoparasitism, Antibiosis, Competition	Maximum inhibition of <i>C. gloeosporioides</i> at 84.9%	Peralta-Ruiz et al. (2023)
<i>T. atroviride</i>	Mycoparasitism, Antibiosis (peptaibols, pyrones), Competition (siderophores), ISR	70–80% mycelial inhibition; reduced disease in beans and lettuce	El-Benawy et al. (2020)

3.4.2 Efficacy Against Powdery Mildew (*O. anacardii* / *Erysiphe quercicola*)

The effectiveness of various *Trichoderma* species in suppressing plant pathogens has been widely reported through multiple antagonistic mechanisms. A summary of studies describing target pathogens, modes of action, and levels of efficacy is presented in Table 2.

Table 2. Mechanisms of action and efficacy of different *Trichoderma* species against powdery mildew on cashew plant.

<i>Trichoderma</i> spp.	Mechanism of Action	Observed Efficacy	References
<i>T. atroviride</i>	ISR and Environmental Conditioning	Reduce white and increased fruit set.	Swaminathan et al. (2016)
<i>T. harzianum</i> T39	Mycoparasitism, ISR, and Competition	Reduce powdery mildew severity by up to 97%	Elad et al. (1998)
<i>T. afroharzianum</i>	Antibiosis/ Antifungal Metabolites	Inhibit the growth and spore germination of <i>Oidium</i>	Konappa et al. (2020)

Table 2 summarizes the effectiveness of various *Trichoderma* species as biocontrol agents against major plant pathogens through complex and multi-modal mechanisms. *T. harzianum* and *T. pseudokoningii* effectively suppressed *C. gloeosporioides*, the causal agent of anthracnose, through synergistic actions involving mycoparasitism (hyphal coiling and lytic enzyme secretion), antibiosis (production of volatile and non-volatile metabolites), and competition for nutrients and space. These mechanisms resulted in 64–71% inhibition of pathogen growth and a substantial reduction in disease incidence of 92–96% under in vivo conditions (Swaminathan et al., 2016).

3.4.3 Efficacy Against Vascular Wilt (*F. oxysporum*)

Table 3 presents the biocontrol mechanisms and documented efficacy of various *Trichoderma* species against soil-borne pathogens, particularly *Fusarium* wilt in cashew. *T. reesei* achieves disease control primarily via root colonization and competition, effectively excluding *Fusarium* from the rhizosphere and notably reducing the incidence and severity of wilt symptoms in cashew nurseries (Lilai et al., 2025). In contrast, *T. longibrachiatum* employs antibiosis, producing specific antifungal metabolites, DIBP and MEHP, which directly inhibit *Fusarium* growth and prevent the pathogen from reaching the vascular cylinder of the cashew tree, thus protecting the seedlings (Adeniyi et al., 2023).

Table 3. Mechanisms of action and efficacy of different *Trichoderma* species against *F. oxysporum* on cashew plant.

<i>Trichoderma</i> spp.	Mechanism of Action	Observed Efficacy	References
<i>T. reesei</i>	Root Colonization and Competition	Reduce the incidence and severity of wilt symptoms in cashew nurseries.	Lilai et al. (2025)
<i>T. longibrachiatum</i>	Antibiosis: 1, 2-Benzenedicarboxylic acid, bis (2-methylpropyl) ester (DIBP) and mono (2-ethylhexyl) ester (MEHP)	Inhibit the growth of <i>Fusarium</i>	Adeniyi et al. (2023)

3.4.4 Efficacy Against Gummosis/Dieback (*L. theobromae*)

Table 4 shows that the biocontrol activity of *Trichoderma* species against major cashew pathogens involves multiple and often complementary mechanisms. *T. hamatum* primarily exhibits mycoparasitic activity and the production of lytic enzymes, enabling direct degradation of the mycelium and cellular structures of *Lasiodiplodia* spp., particularly when applied as a paste or slurry to pruning wounds or early canker lesions on trunks and branches (Li et al., 2022). This mode of action not only suppresses pathogen colonization but also limits the further spread of infection within affected tissues. *T. asperellum* demonstrates a broader spectrum of antagonistic activity, combining mycoparasitism, antibiosis through the production of secondary metabolites such as 6-pentyl- α -pyrone, and the induction of systemic resistance (ISR) in host plants. These mechanisms effectively inhibit the growth and development of pathogens belonging to the Botryosphaeriaceae family, including *Lasiodiplodia* spp., while simultaneously promoting plant growth and enhancing the plant's defensive capacity

against subsequent infections (Yang, 2017). In addition to direct pathogen suppression, the ability of *Trichoderma* spp. to stimulate plant defense responses and improve plant vigor contributes significantly to their effectiveness as sustainable biological control agents. Such multifunctional activities highlight the potential of *Trichoderma*-based biocontrol strategies as environmentally friendly alternatives to synthetic fungicides for managing economically important diseases in cashew plantations.

Table 4. Mechanisms of action and efficacy of different *Trichoderma* species against *L. theobromae* on cashew plant.

<i>Trichoderma</i> spp.	Mechanism of Action	Observed Efficacy	References
<i>T. hamatum</i>	Mycoparasitism and Lytic Enzymes	Direct breakdown of <i>Lasiodiplodia</i> mycelium	Li et al. (2022)
<i>T. asperellum</i>	Mycoparasitism, Antibiosis (producing 6-pentyl- α -pyrone), and ISR	Inhibit pathogenic growth (e.g., against <i>Botryosphaeriaceae</i> and <i>Lasiodiplodia</i>)	Yang (2017)
General <i>Trichoderma</i> spp.	Induced Systemic Resistance (ISR) & PGP	Enhance plant vigor and wound healing.	Somaly & Sokra (2024)

3.4.5 Comparison of *Trichoderma* spp. Against Pathogen Species

The diversity of antagonistic mechanisms exhibited by *Trichoderma* species contributes to variations in their effectiveness against plant pathogens. To evaluate these differences among the major pathogens of cashew, the percentages of mycelial growth inhibition achieved by various *Trichoderma* species were summarized and visualized in the heatmap presented in Figure 6.



Figure 6. Comparative antagonistic efficacy of *Trichoderma* species against major plant pathogens.

The values indicate the percentage of mycelial growth inhibition (MGI) observed in *in vitro* assays, with 0 representing no available data for the species-pathogen combination. The heatmap revealed significant species-specific differences in efficacy. For example, *T. atroviride* and *T. longibrachiatum* completely inhibited (100%) anthracnose, whereas *T. harzianum* demonstrated the highest control (98%) against powdery mildew. Conversely, certain combinations exhibited 0 values, highlighting gaps in the recorded data, particularly for gummosis and vascular wilt, suggesting that further evaluation of these species is necessary.

3.4.6 Application of *Trichoderma* spp. in Cashew Disease Management

The effectiveness of *Trichoderma* spp. in cashew disease control largely depends on the method and timing of application. Different approaches have been reported to target specific diseases and infection sites (Lilai et al., 2025). Soil application has been widely used to manage vascular wilt disease caused by *Fusarium oxysporum*. When applied as a soil drench or mixed with nursery substrates, *Trichoderma* colonizes the rhizosphere, competes with soil-borne pathogens, and enhances plant resistance to diseases (Kowalska, 2021). Several studies have shown a reduction in wilt incidence and improved seedling establishment following early soil treatment. Foliar applications are commonly used to control anthracnose and powdery mildew (Khaskheli et al., 2025). Spraying *Trichoderma*-based formulations on leaves, inflorescences, and young fruits allows for direct interaction with foliar pathogens and contributes to lower disease severity, particularly during flowering and early fruit development (Andrzejak & Janowska, 2022).

4 Conclusion

This review demonstrates that *Trichoderma* spp. are effective and sustainable biological control agents for managing major fungal diseases of cashew, including anthracnose, powdery mildew, vascular wilt, and gummosis. Evidence from previous studies has consistently shown that several *Trichoderma* species provide high levels of disease suppression through complementary mechanisms, such as mycoparasitism, antibiosis, induced systemic resistance, and plant growth promotion. Together, these actions enable both direct pathogen inhibition and enhancement of host defense responses. These results highlight the practical importance of *Trichoderma*-based strategies as environmentally compatible substitutes for synthetic fungicides. Within cashew production systems, their application has shown clear potential to enhance disease control while reducing the dependence on chemical inputs. Moreover, the ability to apply *Trichoderma* through multiple delivery methods strengthens its suitability for integration into comprehensive disease management programs in the field.

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