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ARTICLE

The emerging role of Fungi in sustainable farming and global food security

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Abstract

Fungi are essential components of ecosystems, serving not only as decomposers and pathogens but also as vital contributors to plant growth, soil health, and food security. With the growing global demand for sustainable and environmentally friendly agriculture, the role of fungi has become increasingly important. This review explores the diverse and expanding applications of fungi in modern green agriculture and assesses their ecological mechanisms, agronomic advantages, and potential implementation challenges. From ancient agriculture to the present, mycorrhizae play a central role in regenerative agriculture. These symbiotic relationships are essential for the survival of most plants, while in crops, they significantly improve productivity. This concept has been further expanded to utilise mycorrhizal symbiosis in soil rehabilitation. Recent advancements in fungi as plant growth promoters have shown significant effects in green agriculture. From simple volatile organic compounds to metabolites, fungi enhance and facilitate nutrient solubilization and availability. The application of fungi as biofertilizers, growth promoters, and biological control agents is not a single-directional process. Fungal antagonism involves not only pathogen suppression but also increased plant resistance coupled with growth promotion. For instance, application of *Trichoderma* species comes with a number of benefits. The use of entomopathogenic fungi has a long history and is now expanding towards the control of viruses and phytoplasma. Moving forward, the involvement of mushrooms in circular agriculture has been highly productive in many regions. In addition, fungi are gaining recognition in aquaculture and livestock production, waste recycling, fungal protein production, mycelium leather, and mulching. However, there are still many barriers to overcome, and the environmental adaptability and evolutionary dynamics of fungi pose ongoing challenges. Recent advancements in gene editing offer promising solutions, yet policy adoption and public acceptance remain hard barriers to overcome. In the era of artificial intelligence (AI), we believe that AI and machine learning will further enhance fungal applications, especially in disease epidemiology and crop management. Overall, this review serves as a comprehensive reference for researchers, farmers, and policymakers, providing insights and future directions while emphasising the urgent need for integrated, nature-based solutions. Fungi are poised to be key drivers in achieving regenerative, resilient, and decentralised food systems amid global climate and food security challenges.

Keywords – Bioremediation – Climate change –Entomopathogenic –Plant growth promotion – Soil degradation

INTRODUCTION

The global demand for agricultural products is escalating rapidly. This is mostly driven by continuous population growth as the global population is expected to reach 8.5 billion by 2030, 9.7 billion by

2050, and 10.4 billion by the end of the century (United Nations). To meet the food requirements of this expanding population, agricultural production must increase by approximately 60% by 2050 (FAO 2017). Despite the significant advancement in agricultural technology and intensification, global hunger and food insecurity continue to rise (Fig. 1). According to FAOSTAT (2025), nearly 30% of the global population experienced moderate or severe food insecurity in 2022, lacking reliable access to nutritious food (Fig. 2). Malnutrition remains a significant challenge among children in underdeveloped regions, while rising obesity rates are widespread elsewhere, reflecting unbalanced dietary norms. Moreover, healthy diets remain unaffordable for around three billion people, particularly in low-income regions (FAO, IFAD, UNICEF, WFP & WHO 2023). Under these circumstances, global food production faces a complex set of interconnected challenges that threaten both productivity and sustainability.

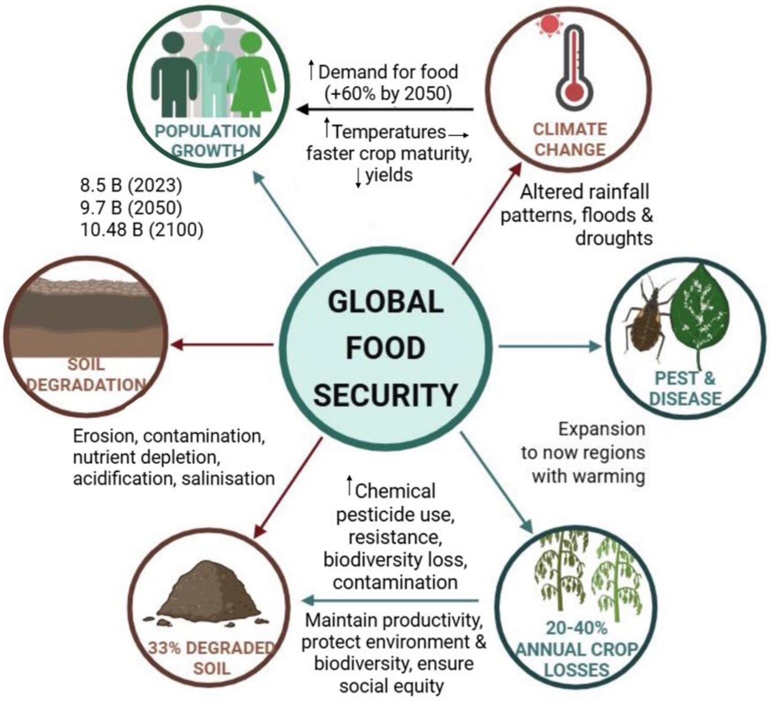

Figure 1 – An overview of challenges in global food production

Climate change is one of the most pervasive threats to agricultural productivity. The rising average temperatures (Fig. 2) accelerate crop development but reduce yields of staple crops such as wheat, maize, and rice (Zhao et al. 2017, Neupane et al. 2022). Precipitation patterns have shifted over the years, with both unprecedented flooding and prolonged droughts, simultaneously affecting global food production (Trenberth 2005, Zhang et al. 2015, Hou et al. 2024). Recent studies indicate that up to 70% of the crop yield reductions can be attributed to human-mediated climate change (Allan et al. 2023). In the tropics, the impact could be more severe (Parry et al. 2010, Tito et al. 2018). For instance, Muluneh (2021) reported that African agricultural yields could decline by over 30%, potentially pushing millions into food insecurity.

Apart from climate change, soil degradation and erosion are among the major limiting factors in agriculture (Lal et al. 2001). Over 33% of global soils are moderately to highly degraded (Smith et al. 2024) primarily due to erosion, contamination (Ahmad et al. 2015, Rashid et al. 2023), nutrient depletion (Tan et al. 2005, Holloway et al. 2008), acidification (Du et al. 2024b), and salinisation (Ondrasek et al. 2011). These processes have ultimately resulted in declining soil fertility and reduced land availability (Kopittke et al. 2024, Dixit et al. 2024). They are also strongly associated with the excessive use of synthetic chemicals such as fertilisers and pesticides, which influence soil biodiversity (Tripathi et al. 2020, Nath et al. 2023). Insect pests and pathogens are responsible for 20–40% of global crop losses annually (FAO 2021). Pest and disease incidences have increased over the years, which is a direct reflection of global warming, as these pests and pathogens are expanding into new geographical ranges, making the formerly temperate regions more vulnerable (Roos et al. 2011, Gu et al. 2018, Skendžić et al. 2021, Zhao et al. 2023c). Therefore, this latitudinal and altitudinal shift in agricultural pests and diseases (Bebber et al. 2013) represents one of the most urgent challenges. Moreover, the widespread occurrence of pests and diseases is associated with the intense use of chemical pesticides. The excessive use of synthetic chemicals leads to the development of resistance (Hahn 2014, Kole et al. 2019), affects non-target and beneficial insects (pollinators), contaminates soil and water resources, and results in residual accumulation in humans and animals (Hashimi et al. 2020, Elhamalawy et al. 2024). For instance, fungicides such as chlorothalonil and mancozeb have been detected in water bodies and shown to affect aquatic life and disrupt endocrine systems (Zubrod et al. 2019, Seshoka et al. 2021).

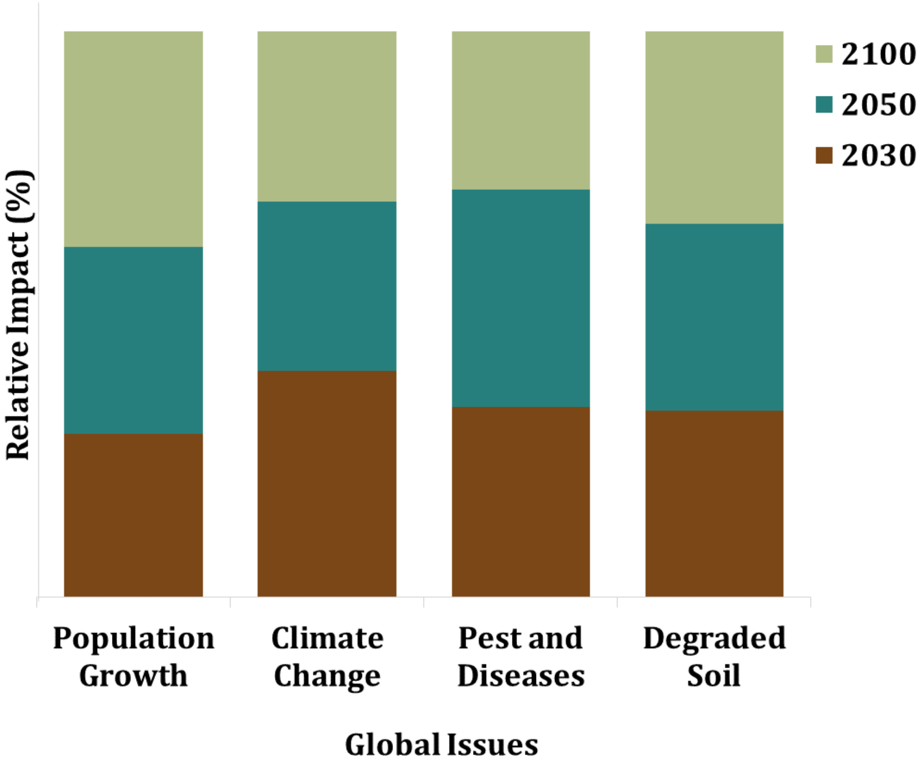

Figure 2 –Global food insecurity index based on regions. Mean temperature change of the meteorological year. Use of Agricultural Pesticides. Adaptation from FAO's State of Food Security and Nutrition report, available online at www.fao.org/interactive/state-of-food-security-nutrition/en/ and Adaptation from FAOSTAT available at www.fao.org.

In response to these interconnected challenges, sustainable agriculture emerged as a vital framework. It emphasises maintaining productivity while preserving the environment and biodiversity and promoting social equality (Kamakaula 2024, Yadav & Singh 2024). Over the years, sustainable agricultural practices have continued to evolve to address the ecological, economic, and social dimensions of the modern food system.

In sustainable agriculture, the use of beneficial microorganisms has emerged as one of the most promising tools (Higa et al. 1994, Javaid 2010, Ray et al. 2020). Among these microorganisms, fungi play a key role in delivering essential ecosystem services and provide a wide range of agronomic benefits (Hyde et al. 2019). They provide vital components in improving soil health, and as mycorrhizal symbionts, in improving phosphorus, nitrogen, and water uptake (Martínez-García et al. 2017, Wahab et al. 2023, Yasanthika et al. 2025), while saprobic fungi decompose organic matter, releasing nutrients back into the soil (Tennakoon et al. 2022, Niego et al. 2023b). Over the years, these ecological benefits of fungi have been elucidated, and numerous beneficial fungal groups have been identified. For instance, *Trichoderma* species are widely recognised as effective plant growth promoters and biocontrol agents exhibiting several promising agricultural traits (Rao et al. 2022, Joo et al. 2022). Entomopathogenic fungi such as *Beauveria bassiana* and *Metarhizium anisopliae* act as natural insecticides, while many other fungi are used as antagonists to plant pathogens (Meyling & Eilenberg 2007, Chen et al. 2019). Moreover, certain fungi can degrade pesticides, heavy metals, and other environmental pollutants, thereby contributing to cleaner, more sustainable agroecosystems (Hyde et al. 2019).

Hyde et al. (2019) have outlined 50 diverse applications of fungi across industries, emphasising their vast biotechnological potential. Fungi produce a broad spectrum of enzymes, antibiotics, secondary metabolites, pigments, and bioactive compounds (Hyde et al. 2019, Niego et al. 2023a), many of which can be harnessed as biopesticides, growth promoters and fertilisers. Interestingly, these applications offer low-toxicity, biodegradable, and cost-effective alternatives to synthetic agrochemicals, aligning with global efforts to reduce greenhouse gas emissions and environmental pollution.

This review explores the potential of fungi to advance sustainable agriculture. It presents and discusses current and emerging applications of fungi, evaluates the associated challenges and knowledge gaps, and proposes future directions for research and implementation. By highlighting fungal solutions, this review contributes to the broader discourse on creating resilient, low-impact, and future-ready farming systems.

The paper begins with the oldest fungal plant association, the mycorrhizae association and its crucial role in green agriculture. We then explore various applications, including plant growth promotion, biofertilizers, and biocontrol, followed by emerging insights into their roles in circular farming systems and agroforestry. Subsequently, we investigate the applications of fungi in livestock and aquaculture, as well as other innovative uses, such as myco-filters and bio-fumigation. Given the limitations of fungi as biological control agents, we examine the potential of genetically modified fungal organisms using gene-editing technologies, particularly the CRISPR system. In the context of the modern AI era, we also discuss how artificial intelligence can be integrated to support and optimise sustainable agricultural practices. Examples and illustrations support each section to enhance understanding, while critically evaluating both the positive and negative implications. Furthermore, we emphasise that green does not always mean safe, noting potential drawbacks of fungal inoculations. Finally, our concluding remarks offer predictions on how fungi may be employed in the next decade to further advance sustainable agricultural practices.

1. Role of mycorrhizae for green agriculture

The relationship between plants and arbuscular mycorrhizal fungi (AMF) is one of the most important factors in the evolution of terrestrial plants (Helgason & Fitter 2005, Guo et al. 2024). Arbuscular mycorrhizal symbiosis predates the evolution of plant roots (Kuyper & Jansa 2023). The earliest fossil evidence of arbuscular mycorrhizal fungi is of isolated spores from the Ordivician of Wisconsin, dated 460 million years ago (Mya), in early Devonian Rhynie Chert, where features similar to extant *Glomus* species (Redecker et al. 2000). Hyphal and arbuscular structures were found in the protostele roots of *Rhynia* and *Asteroxylon*, the earliest vascular plant species (Remy et al. 1994). One of the most important of these partnerships is the interaction between plant roots and arbuscular mycorrhizae. Many crops species partner with them, though crops in the Brassicaceae and Chenopodiaceae are exceptions and generally do not form mycorrhizal associations (Newman & Reddell 1987). The arbuscular mycorrhizae can provide up to 80% of the nutrients and water a plant needs to grow, and the plants in return provide up to 30% of the photosynthates; the food substance made through photosynthesis, that the fungi utilise (Averill et al. 2019).

Symbiosis

Mycorrhizae are divided into two main categories: ecto- and endo-mycorrhizae. Ectomycorrhizal fungi do not penetrate plant cell walls; instead, they form a net-like structure around the plant root, popularly known as the 'Hartig net' (Kariman et al. 2018). Endo-mycorrhizal fungi penetrate the cortical cells of a plant. The majority of endophytic mycorrhizae are of the arbuscular mycorrhizal type; monophyletic, belonging to the Glomeromycota, and are capable of increasing plant nutrient concentrations in plant leaves, roots, and litter (Brundrett 2009). It has been elucidated that the type of root-associated fungi present has a more influence on a plant's nutrient levels than its associations with nitrogen-fixing bacteria or support from plant leaf traits (Hestrin et al. 2019). Arbuscular mycorrhizal fungal associations that live below ground have proven capable of making one of the largest influences on plant tissue nutrient status, a symbiosis referred to as the mother of all plant root symbioses and surpassing the contributions of ectomycorrhizal fungi (Kuyper & Jansa 2023). More than 70% of higher plants establish associations with these fungi (Chandwani et al. 2023). Mutualistic associations enable the plant to absorb nutrients better, particularly phosphorus. Plants sometimes get up to 90% of their phosphorus through these soil fungi (Averill et al. 2019). Those plants in symbiosis with mycorrhizal fungi are more tolerant of biotic and abiotic stresses, such as insect attacks, pathogens, and drought.

Leaf detections

It has been known for a while that blumenol C (plant hormone) derivatives are produced exclusively in roots after colonisation by mutualistic fungi (Maier et al. 1999, Wang et al. 2018, Walther 2021). Plants like wild tobacco *Nicotiana attenuata* produce blumenol C derivatives in their roots when they have established a functional symbiosis with arbuscular mycorrhizal fungi (Wang et al. 2018a). Blumenols are most likely produced in the roots and then transported to other parts of the plants (Walther 2021). When this substance is transported into leaves, it can serve as a foliar marker for the detection of fungal associations (Wang et al. 2018). Most ecological interactions are highly species-specific. Scientists have shown blumenol accumulation in leaf tissues of other plant species, including important crop varieties and vegetables (Walther 2021). The ubiquity of markers in the shoot across distant plant families is likely due to the long common history of mycorrhizal fungi and plants (You et al. 2023), suggesting that these markers play an essential role for plants colonised with arbuscular mycorrhizal fungi.

Roles of AMF

The primary function of AMF is their contribution to plant nutrition, particularly phosphorus (P) (Arachchige et al. 2021), often a limiting resource, and, similarly, to quite a few other micronutrients (Clark & Zeto 2000), especially in nutrient-deficient and constrained soils. Among the number of micronutrients that have gone in records as being supported by AMF are; sodium (Na), zinc (Zn), selenium (Se), rubidium (Rb) and strontium (Sr) (Suzuki et al. 2001); iron (Fe) (Caris et al. 1998); copper (Cu) (Marschner & Dell 2006); calcium (Ca) and magnesium (Mg) (Li et al. 2006); sulphur (S) (Allen & Shachar-Hill 2009), in situations delimited by certain environmental conditions.

Reduction of root invasion by soil-borne microbial plant pathogens (Filho 2022) plays an inimitable secondary role, as attributed to arbuscular mycorrhizal fungi. Reduction in plant uptake of phytotoxic heavy metals (Gohre & Paszkowski 2006), improved host plant water balance in periods of both, too much water and drought (Auge 2001), soil particle aggregation through the cohesive action of a water-stable glycoprotein (Glomalean) (Rillig & Mummey 2006), reduction in insect herbivory by induced plant response (Bennett et al. 2009), increase in insect pollination (Gange & Smith 2005), percentage increase in F_1 generation seed germination (Srivastava & Mukerji 1995), are some of the other notable observations to date. There is also sufficient evidence to suggest that AM fungi play a significant role in soil N and C cycles (Govindarajulu et al. 2005, Jones et al. 2009) and make a considerable contribution to terrestrial ecosystem C sinks (Wright & Upadhyaya 1998).

AMF in plant breeding

Knowing which genes control root colonisation could help breeders to develop certain crop cultivars with a higher affinity for mycorrhizal fungi, to ensure improved nutrient uptake, drought tolerance, and disease resistance (De Vita et al. 2018). Pawlowski et al. (2020) have already identified trait loci associated with mycorrhizal colonisation through whole genome sequencing, using soybeans. The novel diagnostic marker (blumenol C) for the colonisation of AM fungi can be very useful in the study of mycorrhizal associations (Mindt et al. 2019), not only for breeding purposes, which rely on high-throughput screenings, but also for basic research into the fundamental questions about the information transferred from plant to plant through fungal networks (You et al. 2023).

AMF in weed suppression

Weeds pose one of the most serious problems in crop production, with potential crop losses of up to 34% each year (Oerke, 2006). In conventional farming systems, actual losses to losses have been kept at low levels, mainly through intensive tillage and herbicide application. With the increasing restrictions on chemical use (e.g., EU 91/414/EEC), the emergence of ecologically more sound farming systems (e.g., organic farming) and the recognition of the importance of weeds to maintain and/or enhance on farm biodiversity (Arachchige et al. 2021, Grundy et al. 2010), focus has shifted to sustainable alternative approaches to chemical weed management. The use and manipulation of organisms that selectively damage weeds have long been recognised as one such alternative, but little attention has been paid to soil biota despite its known influence on weed biology and ecology (Boyetchko 1996). Common weeds that support Arbuscular mycorrhizal colonisation in each respective locality can be utilised to maintain threshold AMF populations during fallow periods between successive crops (Fig. 3) (Arachchige et al. 2021).

Figure 3 – Some common weed/crop plants were observed to harbour ample colonisation of AMF in the dry zone of Sri Lanka. **a.** *Euphorbia heterophylla* (dicot weed) - showing vesicles, arbuscules and hyphae, **b.** *Eleusine indica* (monocot weed) – showing arbuscules and hyphae, **c.** *Sesamum indicum* (dicot dry zone crop) – showing vesicles, arbuscules and hyphae. (Magnifications x 400) [photo credit: Arachchige LID].

Arbuscular mycorrhizal fungi can also negatively influence the growth of some weespecies, indicating that they have the potential to determine weed community structure (Rinaudo et al. 2010). It has been recognised that mycorrhizal weed growth reductions can be amplified in the presence of a crop (Rinaudo et al. 2010, Veiga et al. 2011). Rinaudo et al. (2010) showed that arbuscular mycorrhizal fungi suppressed weeds grown in the community and that this effect was even stronger in the presence of a crop plant like sunflower, a reaction similar to phytoremediation in action (above) how the individual weed species respond to arbuscular mycorrhizal fungi and how such the presence or absence of a crop lie in the hands of enthusiastic future agriculturists influences individual responses.

AMF in farming

Many crops are mycorrhizal, and there is widespread evidence that crop plants benefit from the arbuscular mycorrhizal associations in the same way as any other plant (Weber 2014, Chen et al. 2018). However, many agricultural practices, including the use of fertilisers and biocides, tillage, and monocultures affect the arbuscular mycorrhizal formation and reduce it over time (Mohamed et al. 2023, Li et al. 2024). Furthermore, growing non-mycorrhizal crops, for instance, some members of the Brassicaceae family, such as cabbage, broccoli, and cauliflower, are detrimental to arbuscular mycorrhizal fungi and have reduced them over the decades, only to assist in polluting the environment (Trautwig et al. 2023). There is an increasing interest in finding sustainable ways to reap agricultural produce without depending much on agricultural chemicals.

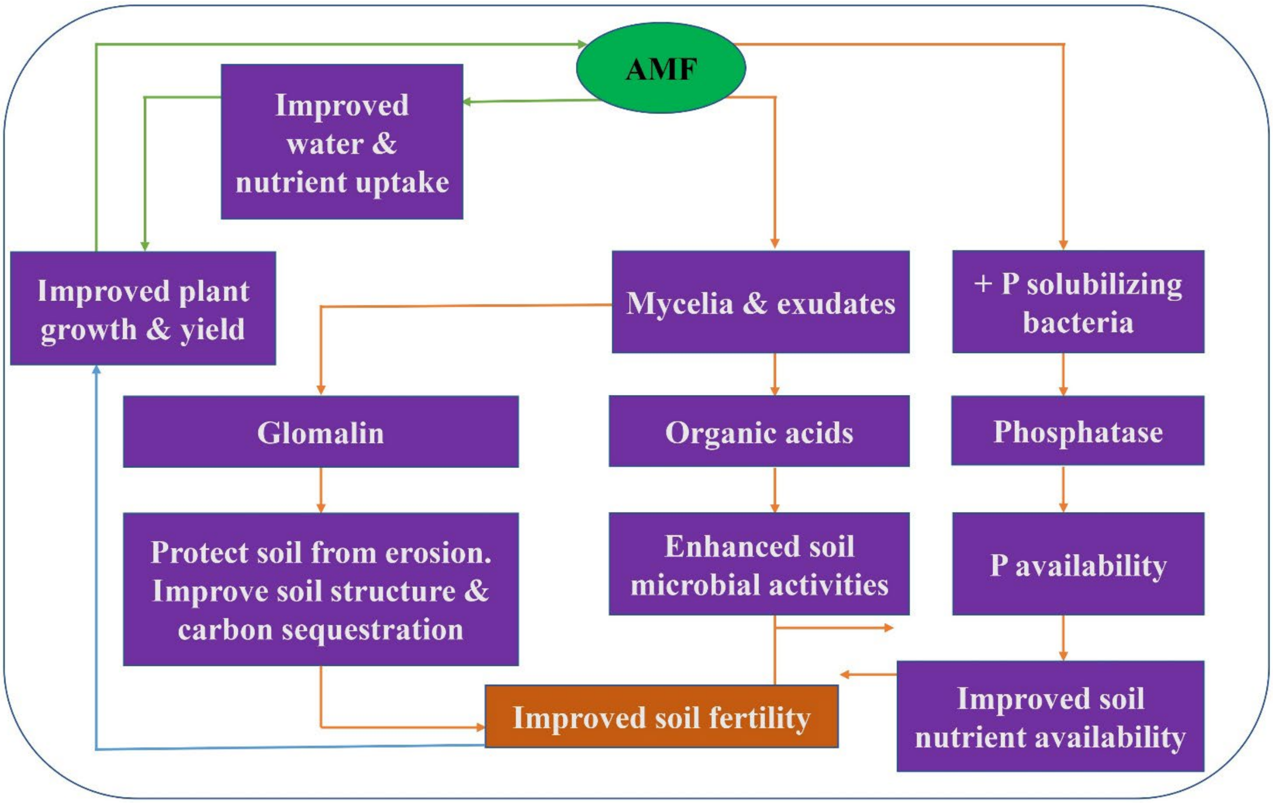

Figure 4 –How Mycorrhizae Improve Soil Fertility and Plant Growth (as adapted from Fall et al. 2022).

Arbuscular mycorrhizal fungi provide one potential example of alternative biologicals, with a range of associated advantages. There is no doubt that farmlands often harbour a multitude of pathogens which are ready to infect plants, just adding to the losses. It has proven positive to inoculate soils with mycorrhizal fungi to help maintain and, more often, to improve yields without relying on additional fertilisers or pesticides. The latest in a series, a Zurich research team in a large-scale field trial, has shown this possibility with an increased plant yield of up to 40% (Lutz et al. 2023). In addition, it was further disclosed that the inoculation of AMF functioned best when there were many fungal pathogens already present in the soil. What else can be more promising? In other words, mycorrhizal fungi had only a minor influence on fields that were not contaminated with pathogens. With just a few soil indicators (mainly soil fungi), the team was able to predict the success of inoculation in nine out of 10 fields, and so was the prediction of crop yields ahead of the harvesting season. This no doubt underpins that for the optimum plant nutrition, plant growth, and sustainable crop yields; one needs to harness the best of mycorrhizal associations by effectively incorporating them into the agricultural and management frameworks.

There is a point to ponder though; several crops including alfalfa, bitter gourd, cotton, corn, rice, sorghum, sesame, soybeans, and wheat are already known to form associations with endomycorrhizal fungi, while there is a group (sugar beet, mustard, canola, buckwheat, cabbage, cauliflower, Brussels sprout, and broccoli) who do not associate with mycorrhizal fungi.

AMF in Organic Farming

It is evident that arbuscular mycorrhizal fungi provide several beneficial ecosystem services. Organic farming systems could understandably be less detrimental to AMF because they exclude the use of water-soluble synthetic fertilisers and most biocides, along with diverse crop rotations. The evidence available suggests that this can lead to increased AMF inoculum in soils, greater crop colonisation and enhanced nutrient uptake (Gosling et al. 2006). Arbuscular mycorrhizal fungi might therefore be able to supplement organic systems for the absence of fertiliser and biocide inputs. Evidence on increased yields is scant, likely due to direct, high rates of AMF presence, especially in the short run. Arbuscular mycorrhizal associations cannot be regarded in absolute isolation as a mere input; they are a part of the agro ecosystem, very much, and the success rate depends on how farm management practices are diverted in the management of this naturally available but extremely valuable asset, particularly in the long-term sustenance of agriculture.

2. Fungi in plant growth promotion

Associations between plants and plant growth-promoting fungi greatly benefit plant health and development. These fungi promote seed germination, shoot and root growth, photosynthetic efficiency, biomass production, flowering, and yield, while contributing to plant protection by inducing systemic resistance against phytopathogens (Hossain et al. 2017). The modes of action of these plant growth-promoting fungi include the mineralisation of essential macro- and micronutrients, the production of volatile organic compounds needed for plant growth, and the amelioration of abiotic stresses. They also produce phytohormones and defence-related enzymes that help inhibit attacks by pathogenic microbes (Hossain et al. 2017, Hossain & Sultana 2020, Thambugala et al. 2020, Adedayo & Babalola 2023). Among the fungi that promote plant growth, mycorrhizal and endophytic fungi play a significant role (Baron & Rigobelo 2022, Adedayo & Babalola 2023).

Rhizosphere, the narrow zone of soil surrounding plant roots, is a natural habitat for numerous beneficial microorganisms, including fungi. Some rhizosphere-resident fungi act as plant growth-promoting fungi. This group of fungi is one of the main sources of biotic inducers, known to confer many advantages to their host plants, and they play a significant role in sustainable agriculture (Hossain et al. 2017, Murali et al. 2021). As given in the previous section, mycorrhizae are one of the main groups associated with plant growth-promoting fungi (Chauhan et al. 2023). Plant growth-promoting rhizobacteria (PGPR) also interact with arbuscular mycorrhizal fungi to enhance plant growth (Chauhan et al. 2023). Other rhizosphere-inhabiting fungi, *Trichoderma*, *Fusarium*, *Penicillium* and fungi-like species such as *Phytophthora* tend to have a positive effect on the plant growth of various crop plants by enhancing their innate immunity (Murali et al. 2021, Thambugala et al. 2022, Adedayo & Babalola 2023, Chauhan et al. 2023).

Endophytic fungi are a fascinating group of host-associated fungal communities that colonise the intercellular or intracellular spaces of host tissues, offering benefits to their hosts while simultaneously deriving advantages for themselves (Alam et al. 2021, Liao et al. 2025). Among the mechanisms of growth promotion by plant growth-promoting endophytic fungi, the most important are the acquisition of nutrients and the production of phytohormones, tolerance to biotic and abiotic stresses, and combat against phytopathogens (Baron & Rigobelo 2022). These fungi enhance nutrient acquisition by plants through various mechanisms, including solubilising phosphate, promoting nitrogen fixation, and increasing the root system surface area (Hossain & Sultana 2020). These fungi promote plant growth by producing and providing phytohormones, including auxins, cytokines, and gibberellins, suggesting that they can regulate host signalling to influence physiological and metabolic activities (Fite et al. 2023). The common genera of plant growth-promoting endophytic fungi include *Aspergillus*, *Chaetomium*, *Cladosporium*, *Fusarium*, *Penicillium*, *Sarocladium*, and *Trichoderma* (Alam et al. 2021, Răut et al. 2021, García-Latorre et al. 2023). In this section, we have provided two case studies: one on volatile organic compounds produced by *Trichoderma* and *Cladosporium,* and the other on seed growth promotion by orchid mycorrhizal fungi.

2.1 Volatile organic compounds from *Trichoderma* and *Cladosporium* for plant growth promotion

Trichoderma is one of the most widely researched genera of filamentous fungi with numerous applications in agriculture, environment, and industry (Tyśkiewicz et al. 2022, Guzmán-Guzmán et al. 2023, Woo et al. 2023). *Trichoderma* species produce and emit volatile organic compounds (VOCs) of agricultural significance (Vinale et al. 2008, Lee et al. 2015, 2016, Nieto-Jacobo et al. 2017, Salwan et al. 2019, Phoka et al. 2020). The VOCs, commonly referred to as volatile metabolites, are characterised by their low molecular mass, high vapour pressure (>0.01 kPa), low boiling point, and low polarity (Insam & Seewald 2010). These compounds constitute various groups of chemicals, including hydrocarbons, alcohols, ketones, aldehydes, alkanes, alkenes, esters, aromatic compounds, which are capable of promoting plant growth and inducing defence mechanisms (Table 1) (Lee et al. 2016, Fincheira & Quiroz 2018, Salwan et al. 2019, da Silva et al. 2021). *Trichoderma aggressivum*, *T. asperellum*, *T. asperelloides*, *T. atroviride*, *T. azevedoi*, *T. brevicompactum*, *T. harzianum*, *T. inhamantum*, *T. koningiopsis*, *T. longibrachiatum*, *T. pseudokoningii*, *T. stromaticum*, *T. virens*, and *T. viride* have been reported to produce VOCs (Lee et al. 2016, Nieto-Jacobo et al. 2017, Phoka et al. 2020, Wonglom et al. 2020, da Silva et al. 2021, Dini et al. 2021, Kong et al. 2022). Previous studies have shown the effectiveness of VOC mixtures produced by *Trichoderma* species in improving the growth of various plants (Table 1). For instance, *Arabidopsis* plants exposed to VOCs produced by *T. asperelloides* PSU-P1, *T. asperellum* GJS 02-65, *T. atroviride* IMI206040 and GJS 01-209, *T. harzianum* CECT 2413, and *T. koningiopsis* T-51 resulted in higher plant growth than unexposed plants (Lee et al. 2015, 2016, Nieto-Jacobo et al. 2017, Phoka et al. 2020, You et al. 2022, Rubio et al. 2023). VOCs produced from *T. asperellum* T1 and *T. azevedoi* CEN1241 can promote lettuce growth (Wonglom et al. 2020, da Silva et al. 2021). Early seed germination and plant biomass of radish were improved by exposure to VOCs produced by *T. harzianum* KNU1 (Joo & Hussein 2022). Tomato seedlings exposed to VOCs produced by *T. atroviride* LZ42 exhibited longer primary roots and a greater total dry weight of roots compared to unexposed plants (Rao et al. 2022). The 6-pentyl-2H-pyran-2-one, in VOC mixtures produced by *Trichoderma* species, is a key element in growth promotion (Vinale et al. 2008, Garnica-Vergara et al. 2015, Lee et al. 2015, Nieto-Jacobo et al. 2017, Rao et al. 2022). Although not all *Trichoderma* species produce 6-pentyl-2H-pyran-2-one, this suggests that 6-pentyl-2H-pyran-2-one is not the only factor in plant growth promotion (Kottb et al. 2015, Lee et al. 2016, Nieto-Jacobo et al. 2017, Joo & Hussein 2022).

Cladosporium species are a common occurrence and ubiquitous (Dugan et al. 2004, Bensch et al. 2012, Ogórek et al. 2012). In plant associations, *Cladosporium* species can be found as endophytes, phylloplane fungi, saprobes, and pathogens (Tibpromma et al. 2018, Bensch et al. 2012, Baron & Rigobelo 2021, Costa et al. 2022, Yang et al. 2023). Some *Cladosporium* species have been reported to produce VOCs with agricultural significance, benefiting plants by promoting plant growth. Li et al. (2019) found that VOCs produced by *C. sphaerospermum* TC09, *C. cladosporioides* CL-1, and *C. halotolerans* NGPF1 enhanced the growth of tobacco seedlings and increased productivity in peppers, resulting in early flowering and increased fruit yield (Paul & Park 2013, Jiang et al. 2021b). Tomato seedlings exposed to VOCs produced by *Cladosporium* sp. T1, T2, and T3 exhibited higher total weight, plant height, and root length, as well as larger leaf size than those unexposed plants (Răut et al. 2021). Moreover, tomato, kimchi cabbage, bok choy, and broccoli seedlings exposed to VOCs produced by *C. halotolerans* NGPF1 had higher shoot length, root biomass, and chlorophyll content than unexposed seedlings (Jiang et al. 2021b). β-caryophyllene, 2-methyl-butanal and 3-methyl-butanal in VOC mixtures produced from *Cladosporium* species have been reported to play an important role in promoting plant growth (Naznin et al. 2013, Lee et al. 2015, Jiang et al. 2021b, Walther et al. 2021).

The production of VOCs in *Trichoderma* and *Cladosporium* is directly influenced by both the species and the strain, as well as by growth conditions, developmental stage, and the abiotic or biotic cues received from the environment (Lee et al. 2015, 2016, Dini et al. 2021, Rubio et al. 2023). Depending upon the above, VOCs from the same *Trichoderma* and *Cladosporium* species and strain can either stimulate plant growth or induce toxicity (Lee et al. 2016, Salwan et al. 2019). Furthermore, key considerations for the utilisation of fungal volatiles in promoting plant growth include their efficacy, specificity, potential ecological impacts, practical application methods, and safety in terms of human health.

Table 1. Examples of the use of VOCs produced from *Trichoderma* and *Cladosporium* for plant growth promotion.

***Trichoderma* strains**	**Major volatile organic compounds**	**Treated plant**	**Result**	**Reference**
T. asperellum strain T1	6-Pentyl-2H-pyran-2-one Succinic acid, 2-(2-chlorophenoxy) ethyl ester	Lettuce (*Lactuca sativa*)	Enhanced plant growth (biomass, number of shoots and roots, fresh and dry weight), chlorophyll content and induced defence response	Wonglom et al. (2020)
T. asperellum strain GJS 02-65	6-Pentyl-2H-pyran-2-one Ethyl 2-methylbutyrate Octadecane	Arabidopsis (*Arabidopsis thaliana*)	Enhanced plant growth and chlorophyll content	Lee et al. (2016)
T. harzianum strain KNU1	γ-Cadinene 2-Methyl-6-methylene-1,7-ctadiene Allo-aromadendren	Radish (*Raphanus sativus*)	Enhanced the early seed germination and increased plant biomass	Joo & Hussein (2022)
T. azevedoi strain CEN1241	1-Octen-3-ol γ-Muurolene 1-Isopropyl-4,8-dimethylspiro [4,5] dec8-en-7-o	Lettuce (*Lactuca sativa*)	Enhanced plant growth and biomass	da Silva et al. (2021)
T. atroviride strain IMI206040	1-Octen-3-ol 3-Octanone 6-Pentyl-2H-pyran-2-one	Arabidopsis (*Arabidopsis thaliana*)	Increased shoot height, root length and total biomass	Nieto-Jacobo et al. (2017)
T. atroviride strain LZ42	6-Pentyl-2H-pyran-2-one 2-pentylfuran	Tomato (*Solanum lycopersicum*)	Enhanced length of the primary roots and total root dry weight	Rao et al. (2022)
T. asperelloides strain PSU-P1	2-Methyl-1-butanol 6-Pentyl-2H-pyran-2-one	Arabidopsis (*Arabidopsis thaliana*)	Enchanted fresh weight, root length, and total chlorophyll content and induced defense responses	Phoka et al. (2020)
T. atroviride strain GJS 01-209	6-Pentyl-pyran-2-one	Arabidopsis (*Arabidopsis thaliana*)	Enhanced plant growth	Lee et al. (2015)
T. harzianum strain CECT 2413	6-Pentyl-2H-pyran-2-one	Arabidopsis (*Arabidopsis thaliana*)	Induced plant development, jasmonic acid- and salicylic acid-dependent defences	Rubio et al. (2023)
T. harzianum strain M10, T22, and TH1, *T. asperellum* strain KV906, and *T. virens* strain GV41	Harzianic acid 6-Pentyl-α-pyrone	Olive trees (*Olea europaea*)	Enhanced VOCs production and affected methylerythritol	Dini et al. (2021)

Trichoderma strains	Major volatile organic compounds	Treated plant	Result	Reference
			1-phosphate, lipid-signalling, and shikimate pathways	
T. koningiopsis strain T-51	β-Phellandrene 1,3,6,10-cyclotetradecatetraene,3,7,11-trimethyl-14-(1-methylethyl)-, [S- (E, Z, E, E)]-	Arabidopsis (*Arabidopsis thaliana*)	Enchanted rosette diameter, root length, and fresh weight.	You et al. (2022)
T. viride	Isobutyl alcohol Isopentyl alcohol 3-methylbutanal	Arabidopsis (*Arabidopsis thaliana*)	Increase plant fresh weight, lateral root growth, and total chlorophyll concentration	Hung et al. (2013)
C. cladosporioides strain CL-1	α-Pinene β-Caryophyllene	Tobacco (*Nicotiana tabacum*)	Improved the growth of seedlings, root development, and biomass	Paul & Park (2013)
C. halotolerans strain NGPF1	2-Methyl-butanal 3-Methyl-butanal	Tobacco (*Nicotiana benthamiana*), tomato (*Solanum lycopersicum*), kimchi cabbage (*Brassica rapa*), bok choy (*Brassica chinensis*), and broccoli (*Brassica oleracea*)	Increased shoot, root biomass and chlorophyll content	Jiang et al. (2021b)

It is obvious that VOCs, particularly those produced by *Trichoderma* and *Cladosporium* species, have emerged as powerful bioactive agents in sustainable agriculture. They offer significant promise for promoting plant growth and enhancing stress resistance. However, several knowledge gaps remain that limit further applications and potential use of these compounds. Given the priority, to date, there is limited understanding of VOCs biosynthetic pathways, plant recognition mechanisms, and the strain-specific variability in VOCs profiles. Identification of these pathways will help in the mass production and industrialisation of these compounds. Integrating knowledge on genomics, metabolomics, and synthetic biology will help to enhance VOCs yield and consistency and field-compatible formulations.

The VOCs production is highly sensitive to environmental conditions, and it is also strain-specific, with inconsistent efficacy under field scenarios. Concerns surrounding ecological impacts, non-target effects, and human health safety further highlight the need for comprehensive ecotoxicological assessments. Establishing regulatory frameworks and conducting multi-site field trials will be crucial to translating these microbial metabolites into commercially viable, environmentally friendly crop enhancement tools.

2.2 Seed germination and seedling growth promotion of *Gastrodia elata* Blume by symbiotic fungi *Mycena* and *Armillaria* species

Symbiotic fungi, particularly orchid mycorrhizal fungi (OMF), play a crucial role in promoting seed germination for many orchid species through nutrient supplementation, degradation of the seed coat, and promotion of protocorm formation (Jin et al. 2024). These fungi provide essential nutrients that are vital for the early development of orchid seedlings. Most orchid mycorrhizal fungi form pelotons inside the cells of adult roots or protocorms and seedlings (Liu et al. 2024). Most orchid species that are mycoheterotrophic during seed germination and seedling development maintain distinct associations with members of a restricted group of fungal partners throughout their lifetimes. In contrast, others switch symbionts while transitioning from the protocorm to the seedling adult stage (Desjardin et al. 2008, 2010, Dearnaley et al. 2016, Naranjo-Ortiz & Gabaldón 2019, Li et al. 2024).

Gastrodia elata Blume is a rootless and leafless heterotrophic orchid, unable to perform photosynthesis to produce nutrients (Shan et al. 2021). It relies on symbiotic interactions with fungi to obtain nutrients necessary for its complex life cycle (Liu et al. 2024). The seeds of *G. elata* are dust-like, structurally simple, and lack nutritional reserves, making seed germination under natural conditions entirely dependent on fungi such as *Mycena* (Park et al. 2012). The poor germination of *G. elata* seeds is primarily due to the hydrophobic barrier formed by the seed coat, which restricts water uptake, and the accumulation of germination inhibitors such as phenolics and abscisic acid (ABA) (Miyoshi & Mii 1988; Yamazaki & Miyoshi 2006). The seed coat of *G. elata* is primarily composed of lignin. Therefore, degrading the lignin layer is crucial for promoting seed germination (Li et al. 2016).

The germination of orchid seeds is highly dependent on their symbiotic association with specific orchid mycorrhizal fungi (OMFs), as well as on environmental conditions. Due to their extremely small size, lack of endosperm, absence of internal nutrient reserves, and a hydrophobic seed coat, most orchid seeds have limited ability to absorb water and nutrients, which suppresses seed germination. Consequently, both seed germination and subsequent seedling development rely on exogenous nutrients supplied by OMFs (Dearnaley et al. 2016). Studies have shown that more than 99% of orchids in nature are myco-heterotrophic during at least part of their life cycle, and over 200 species have been found unable to photosynthesise and completely dependent on nutrients from their fungal symbionts throughout their whole life histories (Li et al. 2024). Therefore, orchid seed germination and subsequent growth rely on exogenous nutrients such as carbon, nitrogen, phosphorus, minerals, and vitamins provided by symbiotic mycorrhizal fungi (Naranjo-Ortiz & Gabaldón 2019).

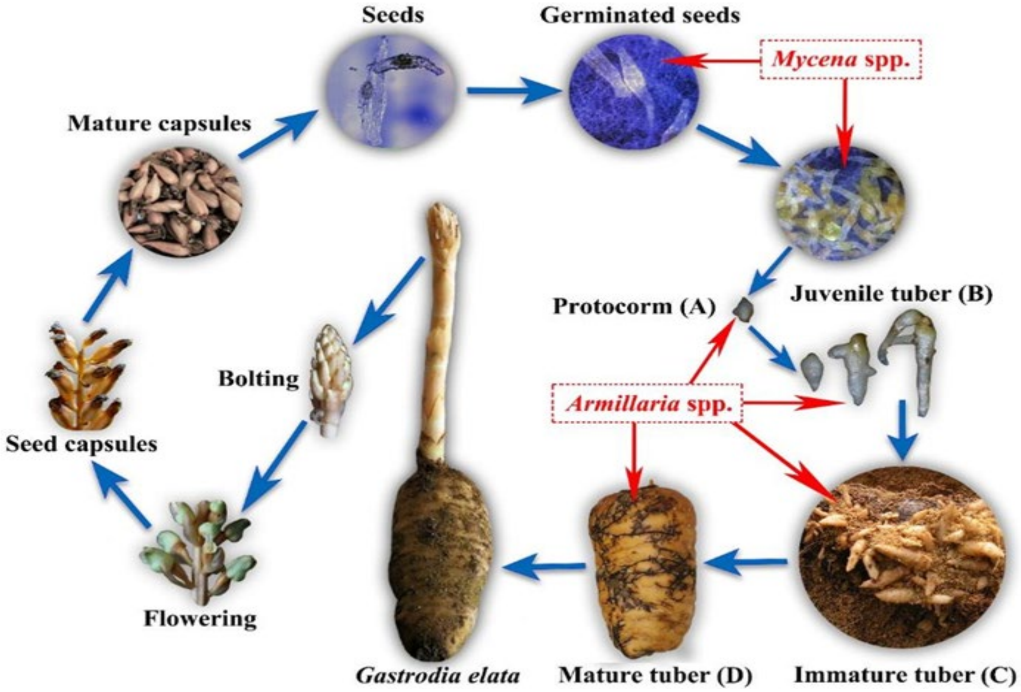

Figure 5 -The life cycle of *Gastrodia elata* with *Mycena* species and *Armillaria* species

Mycena (Pers.) Roussel is a genus in Mycenaceae (Agaricales) with *Mycena galericulata* (Scop.) Gray., which serves as the type species with about 600 species (He et al. 2024). Members of this genus are distributed worldwide and include both saprotrophic and pathogenic fungi (Liu et al.

2022a). The fruiting bodies of *Mycena* are rarely more than a few centimetres in width and are characterised by a small conical or bell-shaped cap and a thin, fragile stem (Liu et al. 2022a). Most species are grey or brown, and many *Mycena* species are bioluminescent, with 52 bioluminescent species currently identified. Several bioluminescent *Mycena* species have shown the ability to enhance seed germination in Orchidaceae, particularly by promoting the germination of *G. elata* seeds (Desjardin et al. 2010). *Gastrodia elata* seeds are small and lack endosperm; therefore, they have limited nutrition for germination. *Mycena* species provide essential nutrients to the seeds, facilitating their germination and early development.

Mycena species produce lignin-degrading enzymes such as manganese peroxidase and laccase, which facilitate hyphal invasion into the seeds (Ren et al. 2021) and break down this barrier, enabling the seeds to absorb water and nutrients more effectively. In addition, *Mycena* species also promote the formation of protocorms, which are the initial growth stage of orchid seedlings (Desjardin et al. 2010). This is a critical step in the orchid life cycle. Different *Mycena* species can vary in their effectiveness at promoting orchid seed germination. For example, *Mycena osmundicola*, *M. orchidicola*, *M. anoectochila*, and *M. dendrobii* have all been identified as effective in promoting the germination of *G. elata* seeds.

Mycena species occupy orchid seeds by penetrating the seed coat first, then moving through the suspensor remnant, stipe cell, peloton cells, and digestive cells (Fan et al. 1999). Within the embryonic cells, *Mycena* hyphae form a highly branched network that eventually develops into specialised peloton structures (Zhao et al. 2024). These pelotons, as key structures for nutrient exchange, either transfer organic carbon, water, and inorganic nutrients absorbed by the fungi to the seed or are digested to provide the essential nutrients for seed growth (Yeh et al. 2019). After receiving nutrients from *Mycena* hyphae, orchid seeds undergo vigorous cell division, causing the embryo to expand, break through the seed coat, germinate, and form protocorms (Fig. 5). In the early developmental stages of *G. elata*, *Mycena* species supply essential nutrients required for seed germination, protocorm growth, and differentiation (Yuan et al. 2025). As protocorms develop into vegetative propagation corms, *Armillaria* species gradually become the dominant symbiotic partners, supporting tubular enlargement, flowering, and fruit development (Tsai et al. 2016).

Armillaria (Fr.) Staude (Basidiomycota, Physalacriaceae) is widely distributed worldwide and impacts more than 500 host species. Throughout the growth of *G. elata*, symbiotic *Armillaria* functions as the sole nutrient source, and its growth characteristics directly influence the quality and yield of the plant. Its hyphae absorb nutrients, whereas rhizomorphs formed under stress or during later stages facilitate the transport of water, nutrients, and oxygen, as well as the exploration of new nutrient sources (Wong et al. 2019).

Before invading *G. elata*, *Armillaria* species form rhizomorphs that attach to the plant's epidermis. Hyphae within these rhizomorphs mechanically penetrate the epidermal cells and directly reach a layer of cortical cells located outside the endodermis, where internal colonisation is established (Xu 2001). The vegetatively propagated corms of *G. elata* then derive nutrients and energy from *Armillaria* to develop into mature tubers. Research has shown that *G. elata* induces *Armillaria* colonisation by secreting specific compounds such as strigolactones, and subsequently produces enzymes including glycoside hydrolases, carbohydrate-binding modules, and glycosyl-transferases that degrade fungal tissue to obtain energy (Hua et al. 2024). These enzymes contribute to cell wall degradation and the biosynthesis of secondary metabolites, both essential for the establishment and maintenance of the symbiotic relationship. Alternatively, *Armillaria* may directly invade immature tubers and subsequently colonise new tubers along the vascular bundles (Irwin et al. 2007).

The symbiotic relationship among *G. elata*, *Mycena*, and *Armillaria* offers a promising model for fungal-based crop production, where plants rely entirely on fungal nutrient provision rather than soil fertilisation. While this system holds great potential for sustainable agriculture and industrial applications, several key research gaps must be addressed. First, the host specificity and fungal diversity of *Mycena* species remain poorly understood, with most studies limited *to M. osmundicola*. Broader sampling and identification of new *Mycena* species with enhanced enzymatic activity and symbiotic efficiency are essential. Furthermore, there has been no exploration of how these symbioses develop at the level of functional genomics. Transcriptomic, proteomic, and metabolomic studies are needed to investigate fungal-host signalling, peloton formation, and metabolite exchange. Such knowledge could expand the application of *Mycena* and related species to other economically important crops beyond orchids. To date, no cross-species trials have been conducted to evaluate broader agricultural potential. Additionally, *Mycena* species produce industrially valuable enzymes such as peroxidase and laccase, which, through appropriate fermentation and industrial protocols, could be harnessed for bioremediation and eco-friendly bleaching. There is also scope for developing commercial *Mycena* based seed germination enhancers, especially for high-value medicinal, horticultural, and endangered plants.

The *Gastrodia–Mycena–Armillaria* is a unique system that showcases fungal symbioses to support nutrient self-sufficiency, overcome germination barriers, and sustain long-term plant growth without photosynthesis. Industrialising such fungal associations for seed germination, enzyme production, and regenerative agriculture could revolutionise soilless farming, land rehabilitation, and low-input agriculture. However, this requires a deeper functional understanding alongside ecological and environmental monitoring to ensure safety, sustainability, and scalability.

3. Biofertilizer

Biofertilizers are living microorganisms that enhance both soil fertility and plant growth. They improve soil fertility by nitrogen fixation, phosphorus solubilisation, or stimulating nutrient uptake (Itelima et al. 2018, Gulshan et al 2022). In this process, beneficial microbes improve soil health. In contrast, these introduced organisms are involved in the recycling of organic matter (Ortiz & Sansinenea 2022), in which fungi, as a source of biofertilizers, are mainly utilised as decomposers to release N, P, K, and trace elements (Panda 2022, Kumar et al. 2023a). Nutrient exchange, on the other hand, is a mutual nutrient trade between fungi and plants (Behie & Bidochka, 2014). Most of the mycorrhizal associations are categorised here (Miller & Allen 1992, Fabiańska et al. 2019). Fungi secrete enzymes to break down lignin and cellulose, which are major components of plant litter, proteins into amino acids and then to nitrogen and phosphate and organic phosphorus into inorganic phosphate (Kjøller & Struwe 2002, Pritsch & Garbaye 2011). Fungi are actively involved in enzymatic activities by secreting laccase, cellulase, xylanase, protease, and phytase (El-Gendi et al 2021, McKelvey & Murphy 2011). Ecologically, biofertilizers reduce dependency on synthetic fertilisers and thus minimise pollution and soil degradation. Economically, they lower farming costs, enhance crop yields sustainably and support long-term agricultural resilience.

In the following section, we discuss the application of fungi as biofertilizers to enhance soil, improve nutrition, and facilitate recycling and exchange. We have provided case studies on *Aspergillus* and *Penicillium* as mineral solubilisers, the potential of fungal-bacterial biofilm bio-fertilisers, and, finally, the challenges and future directions.

3.1 Application of mineral-solubilising *Aspergillus* and *Penicillium* as biofertilizer in agriculture

Soil minerals play a crucial role in plant development, growth, and productivity. Typically, around 95–99% of soil minerals are present in insoluble forms, including carbonates, phosphates, oxides, and complex forms (Lian et al. 2008, Gadd 2010). Thus, only 1 to 5% of the soil samples contained minerals readily available for plant uptake. Mineral-solubilising fungi are commonly found in soil and often associated with plant rhizospheres (Shrivastava et al. 2018, Khuna et al. 2021). Their presence has a significant impact on providing the essential soluble minerals required for plant uptake (Gyaneshwar et al. 2002, Sharma et al. 2013). Previous studies have demonstrated that mineral-solubilising fungi constitute approximately 0.1% to 0.5% of the total fungal populations present in soil (Kucey 1983, Sharma et al. 2013). These fungi possess the capability to solubilise a range of insoluble minerals including calcium, copper, cobalt, iron, manganese, magnesium, phosphorus, potassium, and zinc. This comes from their ability to reduce pH levels by secreting organic acids (e.g., citric, gluconic, 2-ketogluconic, malic, oxalic, succinic, and tartaric acids), as well as through mechanisms such as chelation, exchange reactions, and mineralisation (Jain et al. 2014, Mendes et al. 2014, Pawar & Thaker 2009, Singh & Reddy 2011, Khuna et al. 2023, Mayadunna et al. 2023).

Typically, the fungal genera *Aspergillus* and *Penicillium* are the predominant mineral-solubilising fungi found in soil (Wakelin et al. 2004, Sharma et al. 2013, Kumar et al. 2018, Islam et al. 2019). *Aspergillus aculeatus*, *A. amstelodami*, *A. awamori*, *A. brasiliensis*, *A. brunneoviolaceus*, *A. candidus*, *A. clavatus*, *A. fischeri*, *A. flavus*, *A. foetidus*, *A. fumigatus*, *A. hydei*, *A. nidulans*, *A. niger*, *A. sclerotiorum*, *A. sydowii*, *A. tamarii*, *A. terreus*, *A. terricola*, *A. tubingensis*, and *A. versicolor* have been reported as mineral-solubilizing fungi (Gupta et al. 1994, Jain et al. 2012, Singh & Reddy 2012, Saxena et al. 2013, Mendes et al. 2014, Baron et al. 2018, Doilom et al. 2020, Khalil et al. 2021, Li et al. 2021, Balogun et al. 2022, Bhatnagar & Yadav 2023). In addition, *P. albidum*, *P. arenicola*, *P. aurantiogriseum*, *P. brevicompactum*, *P. canescens*, *P. chrysogenum*, *P. claviformis*, *P. crustosum*, *P. decumbens*, *P. expansum*, *P. frequentans*, *P. funiculosum*, *P. glabrum*, *P. guaibinense*, *P. islandicum*, *P. italicum*, *P. janthinellum*, *P. jensenii*, *P. lividum*, *P. melinii*, *P. miczynskii*, *P. olsonii*, *P. pinophilum*, *P. purpurogenum*, *P. restrictum*, *P. rugulosum*, *P. soli*, *P. solitum*, *P. thomii*, *P. variable*, *P. verruculosum*, and *P. waksmanii* were also were also reported to have mineral solubilizing properties (El-Azouni 2008, Morales et al. 2011, Saxena et al. 2013, Mendes et al. 2014, Doilom et al. 2020, Khalil et al. 2021, Arias et al. 2023; Bhatnagar & Yadav 2023). Numerous studies have demonstrated the efficacy of mineral-solubilising *Aspergillus* and *Penicillium* fungi in enhancing the growth, yield, and quality of many crops, as evidenced by experiments conducted either in controlled greenhouse conditions or through field trials (Table 2). Inoculation with these fungi has been shown to improve soil nutrient availability and plant uptake.

Mineral-solubilising fungi as biofertilizer

Mineral-solubilising *Aspergillus* and *Penicillium* species are being increasingly recognised for their potential as biofertilizers in agriculture (David et al. 2023, Mayadunna et al. 2023). Application of these fungi as biofertilizers offers several advantages in agricultural systems. Firstly, these fungi contribute to the sustainable management of soil fertility by releasing bound minerals, thereby reducing dependence on chemical fertilisers (Iqbal et al. 2023). This approach corresponds to organic farming principles and helps alleviate the negative environmental effects associated with chemical fertilisers, including soil degradation and water pollution. Secondly, these biofertilizers contribute to the development of resilient cropping systems by enhancing plant tolerance to abiotic stresses such as drought, salinity, and temperature extremes (Pang et al. 2024).

Examples of commercially available phosphate-solubilising biofertilizer products for liquid applications include Agright^{TM} (*Aspergillus* sp.), BIOFERT (*Aspergillus* sp.), Green Awamori (*Aspergillus awamori*), JumpStart$^{®}$ (*Penicillium bilaiae*), Shayona (*Aspergillus* spp.), and Rootnet (*Aspergillus* spp.). Additionally, Mn Sol B$^{®}$ (*Penicillium citrinum*) is a commercially available product of powdered and liquid manganese solubilising biofertilizer. Several previous investigations have reported that the utilisation of JumpStart$^{®}$ has the potential to enhance the growth and yield of various crops such as Indian mustard (Sheoran & Chander 2013), maize (Leggett et al. 2015, Gómez-Muñoz 2018), rice (Geethalakshmi & Sangameshwari 2021), switchgrass (Simpson et al. 2020), and wheat (Sánchez-Esteva et al. 2016), while also improving phosphorus uptake.

Table 2 Examples of mineral-solubilising *Aspergillus* and *Penicillium* on plant growth promotion

Fungal species	Treated plant	Effect on the plant	References
A. brunneoviolaceus (HZ23 and HZ10) and *Penicillium oxalicum* (HZ06)	Eggplant (*Solanum melongena* L.)	Increased leaf size, length and biomass of seedlings and roots, and affected early flowering	Li et al. (2021)
A. chiangmaiensis (SDBR-CMUI4), *A. pseudopiperis* (SDBR-CMUI1), and *A. pseudotubingensis* (SDBR-CMUO2)	Arabidopsis (*Arabidopsis thaliana*), cassava (*Manihot esculenta* Crantz), onion (*Allium cepa* L.), and	- Increased dried biomass of shoot and root, chlorophyll content, and cellular inorganic phosphate content in all plants - Increased leaf number and leaf length in both Arabidopsis and onion plants	Khuna et al. (2021, 2023)

Fungal species	Treated plant	Effect on the plant	References
	sugarcane (*Saccharum officinarum* L.)	and improved the yield and quercetin content of onion bulbs - Increased root lengths of cassava and sugarcane	
A. flavus	Maize (*Zea mays* L.)	Increased seed germination percentage, shoot length, plant height, leaf number, cob length, 100 grain weight, grain yield, and mineral contents	Omomowo et al. (2020)
A. niger (PM-4)	Maize (*Zea mays* L.)	Enhanced plant height, cob length, biological yield, grain yield, and phosphorus content	Naeem et al. (2021)
A. niger (K7)	Soybean (*Glycine max* L.)	Increased seed germination percentage, shoot and root length, shoot and root biomass, leaf number, root nodulation, yield, and phosphorus uptake in plants	Saxena et al. (2016)
A. niger (S36) and *A. tubingensis* (S33)	Mung bean (*Vigna radiata* cv. RMG 492)	Increased shoot and root length, leaf number, dried biomass, yield, and phosphorus content	Jain et al. (2014)
A. niger (AY028) and *P. chrysogenum* (AY005)	Rice (*Oryza sativa* L.)	Increased plant height	David et al. (2023)
A. niger (AUMC 14260) and *P. chrysogenum* (AUMC 14100)	Wheat (*Triticum aestivum* cv. Gemmiza 9)	Increased growth, biochemical status, nutrient contents, and yield	Dawood et al. (2022)
P. brevicompactum	Coffee (*Coffea arabica* var. Costa Rica)	Increased coffee bean weight	Arias et al. (2023)
P. chrysogenum (T8)	Tomato (*Solanum lycopersicum* L.)	Increased shoot and root length, and total chlorophyll content of seedlings	Javed et al. (2019)
P. commune (MCC 1720)	Black gram (*Vigna mungo* (L.) Hepper)	Increased seed germination percentage, seedling vigour index, root and shoot length, biomass, and chlorophyll content	Banerjee & Dutta (2019)
P. expansum (NAUG-B1)	Brinjal (*Solanum melongena* L.)	Increased germination percentage, shoot and root length, dried biomass, chlorophyll and phosphorus content	Panchal et al. (2015)
P. guanacastense (JP-NJ2)	Masson pine (*Pinus massoniana* Lamb.)	Increased shoot length and root crown diameter of seedlings	Qiao et al. (2019)
P. menonorum (KNU-3)	Cucumber (*Cucumis sativus* L.)	Increased dry biomass of roots and shoots, chlorophyll content, total starch, protein content, and phosphorus content	Babu et al. (2015)
P. oxalicum (I1)	Maize (*Zea mays* L.)	Increased yield	Gong et al. (2014)
P. oxalicum (y2)	Rape (*Brassica napus* L.)	Improved fresh and dry weight, root length, and root dry weight	Wang et al. (2021b)

Genetic and Biochemical Basis of Mineral-solubilising Fungi

The mineral-solubilising capabilities of *Aspergillu*s and *Penicillium* species are linked to their genetic makeup and biochemical mechanisms that enable them to obtain essential nutrients from insoluble mineral forms. Among these main components is the biosynthesis of organic acids such as citric, oxalic, and gluconic acids. For instance, *A. niger* produces citric, gluconic, oxalic, and malic acids, which were regulated by glucose oxidase, gdh (gluconate dehydrogenase), and oahA (oxaloacetate hydrolase). In *Penicillium,* particularly *P. bilaiae,* citric and oxalic acids are involved, and those are mediated by genes regulating the TCA cycle, oxalate biosynthesis, and acid transporters. These acids are secreted into the rhizosphere, where they dissolve insoluble phosphates and metal oxides. Furthermore, it has been shown that, under nitrogen-limited conditions, citric acid production is enhanced, while oxalic acid is favoured under carbon-limited conditions. This further emphasises the importance of these genera in regenerative agriculture.

Additionally, these mineral-solubilising fungi possess secondary metabolite biosynthetic gene clusters such as polyketide synthases and non-ribosomal peptide synthetases. *Aspergillus niger* has been reported to produce over 20 cryptic biosynthetic gene clusters, which regulate the synthesis of bioactive compounds that may aid in mineral solubilization and microbial competition. Furthermore, these genes contribute to microbial competitiveness and mineral transformation. Proton-translocating ATPases further support acid secretion through electrochemical gradients, while siderophore-producing genes like sidA, sidC, and sidD enhance iron solubilization.

Genomic studies reveal that *A. niger* and *P. bilaiae* exhibit mitochondrial genome plasticity and harbour genes for phosphate transporters and acid tolerance. These abilities reinforce their adaptability and efficacy as biofertilizers. These integrated pathways collectively enable mineral-solubilising fungi to play a pivotal role in sustainable nutrient cycling and plant nutrition.

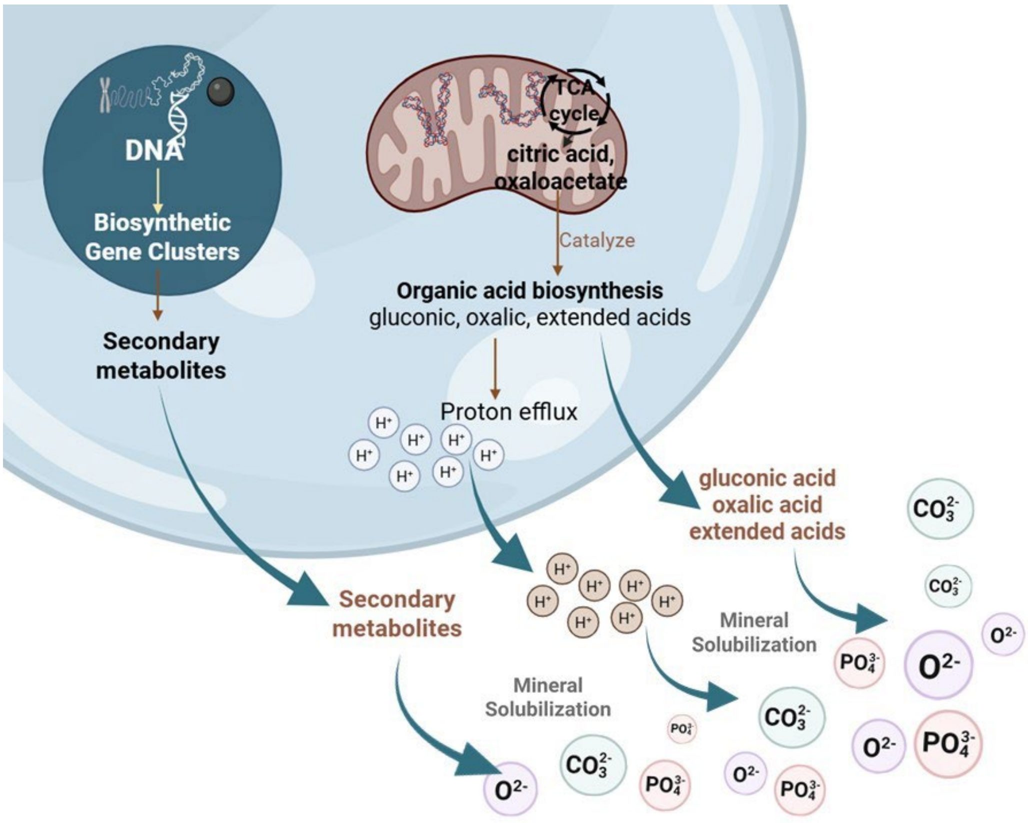

Figure 6 – Mechanisms of mineral solubilization in *Aspergillus* and *Penicillium* fungi. The diagram highlights the mobilisation of nutrients through organic acid secretion, proton efflux, and secondary metabolite production. Genes involved in acid biosynthesis, siderophore formation, and phosphate transport support mineral dissolution. Genomic adaptability and biosynthetic gene clusters further enhance their effectiveness as biofertilizers.

However, challenges remain in scaling up the production and application of mineral-solubilising *Aspergillus* and *Penicillium* for widespread agricultural use. Issues such as formulation optimisation, shelf-life stability, and compatibility with existing farming practices need to be addressed to ensure the successful application of these biofertilizers on a larger scale. Moreover, further research is needed to better understand the long-term effects of fungal inoculation on soil health, interactions between plants and microbes, and the dynamics of ecosystems.

3.2 Fungal-bacterial biofilm biofertilizers and commercial aspects in Sri Lanka

Introduction to biofilm biofertilizers (BFBFs)

Fungal-bacterial biofilm-based biofertilizers, known as biofilm biofertilizers (BFBFs), represent a novel concept in biofertilizer technology introduced to global agriculture (Seneviratne 2003, Seneviratne et al. 2007). Numerous studies have demonstrated that BFBFs exhibit superior efficacy compared to conventional biofertilizers, particularly for non-leguminous crops (Triveni et al. 2012; Hassani et al. 2013, Korniichuk & Zayarnyuk 2013, Swarnalakshmi et al. 2013, Santos et al. 2017, Velmourougane et al. 2017, Sudadi et al. 2018, Ricci et al. 2019, Singhalage et al. 2021). This enhanced effectiveness is attributed to the greater biochemical diversity secreted by biofilms compared to mono- or mixed-culture microbial inoculants, which helps restore the function and sustainability of degraded agroecosystems by breaking the dormancy of the soil microbial seed bank (Meepegamage et al. 2021, Buddhika et al. 2013, Herath et al. 2017).

Fungal-bacterial biofilms are structured microbial communities formed through the attachment of bacterial cells to fungal hyphae, embedded within a protective extracellular polymeric substance (EPS) matrix. This biofilm architecture facilitates enhanced metabolic cooperation, nutrient exchange, and stress resilience for both organisms. Fungi provide a stable biotic surface and carbon-rich exudates, while bacteria contribute nitrogen compounds and protective EPS. The synergistic interaction leads to upregulated gene expression, improved colonisation efficiency, and greater biochemical diversity compared to monocultures. These traits underpin the superior performance of biofilm biofertilizers (BFBFs) in restoring degraded soils and boosting crop productivity.

Agronomic and soil benefits of BFBFs

Application of BFBFs, combined with reduced chemical fertiliser (CF) rates, has been shown to increase soil nutrient content and enhance microbial community diversity (Meepegamage et al. 2021; Premarathna et al. 2021, Rathnathilaka et al. 2022). This reinstates complex interactions among soil, plant, and microbial parameters, ultimately resulting in ca. 20-30% higher rice grain yields than CF-only practices (Premarathna et al. 2021, Rathnathilaka et al. 2022). A significant correlation between a developed soil quality index and grain yield was observed exclusively in the BFBF treatments, highlighting the critical role of soil quality in eco-friendly rice cultivation supported by biofertilizers (Rathnathilaka et al. 2022). Conversely, CF alone appears insufficient to overcome the rice yield barrier in degraded soils, emphasising the necessity of BFBF-induced microbial activity. Furthermore, it has also been reported to improve rice grain quality by reducing toxic heavy metal content, lowering estimated daily intake and hazard quotients (Warnakulasooriya et al. 2025), enhancing antioxidant composition and capacity (Rathnathilaka et al. 2024), and modulating primary metabolite profiles (Pathirana et al. 2023).

Carbon sequestration and environmental impact

The gross carbon pool in soil, which partly emits CO_2 during tillage, plays a vital role in increasing preserved soil carbon stocks over time; a phenomenon observed only under BFBF treatment (Premarathna et al. 2021). Remarkably, the BFBF application sequestered ca. 30% more carbon in just 1.5 years with only 2.5 L/ha, whereas conventional farming practices require bulky organic matter inputs (~10 t/ha) to achieve comparable carbon sequestration (Jayasekara et al. 2022). This increase is primarily due to enhanced root growth and depth, promoting microbial carbon assimilation in the root zone. Furthermore, BFBF-treated plants exhibit higher photosynthetic rates, leading to greater rhizodeposition of fresh carbon into the soil than CF-only practices (Premarathna et al. 2023). These factors contribute to increased soil microbial biomass, mineral-reactive metabolites, organo-mineral complexes, and aromatic carbon availability, collectively stabilising soil carbon, reducing priming effects, and lowering soil respiration rates (Premarathna et al. 2023).

Table 3. Comparison between conventional biofertilizers and BFBF

Feature	Biofilm Biofertilizers (BFBFs)	Conventional Biofertilizers
Microbial Composition	Multi-species biofilm (fungi + bacteria)	Single or mixed microbial cultures

Feature	Biofilm Biofertilizers (BFBFs)	Conventional Biofertilizers
Structure	Embedded in the extracellular polymeric matrix (EPS)	Free-living or loosely associated microbes
Stability & Survival	High resilience to environmental stress	Lower survival under adverse conditions
Nutrient Exchange	Synergistic interactions enhance nutrient cycling	Limited interspecies cooperation
Colonization Efficiency	Strong root colonisation via biofilm adhesion	Variable colonisation depending on strain
Biochemical Diversity	Rich metabolite profile from cooperative metabolism	Narrower range of metabolites
Impact on Soil Microbiome	Reactivates dormant microbial seed bank	Minimal effect on native microbial diversity
Carbon Sequestration	Promotes deep root growth and microbial carbon assimilation	Limited impact on soil carbon dynamics
Crop Yield & Quality	20–30% higher yields; improved grain quality	Moderate yield improvement; limited quality effects
Environmental Benefits	Reduces chemical input, improves soil health, and mitigates runoff	Reduces fertiliser use, but has less impact on soil restoration
Adoption Challenges	Requires formulation consistency and farmer training	Easier to produce and apply, but less effective long-term

The journey of BFBF in Sri Lanka

The development of Biofilm Biofertilizers (BFBFs) in Sri Lanka represents a significant step toward reducing reliance on chemical fertilisers and promoting sustainable agriculture. Initially introduced as a natural alternative to synthetic fertilisers, BFBFs underwent extensive research, particularly in paddy cultivation. This research demonstrated that BFBF application could reduce chemical fertiliser use by up to 50% while boosting yields by 20–30% (Premarathna et al. 2021, Rathnathilaka et al. 2022). Notably, over 16% of Sri Lanka's total rice cultivation area has adopted the BFBF practices (Ekanayake et al. 2023).

From an economic perspective, local production of the BFBFs has empowered smallholder farmers by providing affordable, eco-friendly inputs. However, the initial adoption phase posed challenges, highlighting the need for farmer training and ongoing technical support. Environmentally, the BFBFs promote soil microbial diversity, mitigate the harmful effects of chemical overuse, and improve nutrient cycling and soil structure, factors essential for maintaining long-term soil fertility. Additionally, the BFBFs reduce nutrient runoff and water contamination, enhance carbon sequestration, and contribute to climate resilience in agriculture. In addition, the BFBF practice aligns well with the Colombo Declaration of 2019, which aims to halve nitrogen waste in agriculture by 2030 (Ekanayake et al. 2024). Overall, the BFBFs present a scientifically and environmentally valuable, eco-friendly, and economically viable alternative to excessive nitrogen fertiliser use, compromising rice yields. Despite these benefits, challenges remain in formulation consistency and quality control, underscoring the importance of regulatory oversight and ongoing scientific refinement.

3.3 Use of *Pisolithu*s and *Scleroderma* as biofertilizer in forestry

Globally, the area used for commercial forestry output is rapidly growing. It is estimated that the area of commercial forests worldwide would have grown by 20% to 50% by 2030 (FAO 2010). However, one of the biggest issues facing forest nurseries is the continued supply of high-quality seedlings for commercial forestry applications. Thus, the growth and development of seedlings at an early stage in nurseries is essential to the commercial propagation processes. To propagate seedlings, it is necessary to address and advance nutrient management, a fundamental practice for ensuring their quality. In this context, ectomycorrhizal fungi are a valuable tool for seedling propagation, as they contribute to the success and sustainability of nutrient availability for plant seedlings (Smith & Read 2010, Mello & Balestrini 2018, Policelli et al. 2020).

The ectomycorrhizal (ECM) symbiosis is a significant component of forest ecosystems in the boreal, temperate, subtropical, and tropical climatic zones (Brundrett 2004, 2009, Tedersoo et al. 2010, 2012, Brundrett & Tedersoo 2018). It is a type of mycorrhizal symbiosis which is characterised by a lack of intracellular hyphae, the development of a hyphal sheath (called the mantle) surrounding the root surface, and the presence of an intercellular hyphal network (called the Hartig net) (Brundrett 2004, 2009, Smith and Read 2010, Montesinos-Navarro et al. 2018). Of the estimated 20,000 fungal species identified, over 250 genera have been listed as ECM fungi, most belonging to Basidiomycota (within families *Amanitaceae*, *Boletaceae*, *Cantharellaceae*, *Cortinariaceae*, *Hydnaceae*, *Inocybaceae*, *Paxillaceae*, *Russulaceae*, *Suillaceae*, and *Tricholomataceae*) and some to Ascomycota (orders Pezizales and Tuberales) (Tedersoo et al. 2010, Tedersoo & Smith 2013, Clasen et al. 2018). The ECM fungi typically produce fruiting bodies in the Rhizosphere soil of the host plant, some of which are known to be edible and valuable for their medicinal properties on humans (Hall et al. 2007, Zambonelli & Bonito 2012).

Various species of ECM fungi in the genera *Pisolithus* and *Scleroderma,* which form ECM associations with a wide range of hosts, have been used as biofertilizers to promote plant growth, especially in the seedling stage of forestry plants, including plant genera *Acacia, Quercus, Eucalyptus*, *Nothofagus, Pinus*, and *Shorea*, as they produce a large number of spores (Brundrett 2004, 2009, Chen et al. 2006, Aggangan et al. 2010, Sebastiana et al. 2018, Zuo et al. 2022). These spores have been mostly used for seedling inoculation at concentrations ranging from 10^5–10^7 spores/ml (Chen et al. 2006, Bruns et al. 2009, Aggangan et al. 2010). Numerous studies have concluded that inoculating spores of *Pisolithus* and *Scleroderma* improves the growth of various seedling plants (Table 4 and Fig. 7).

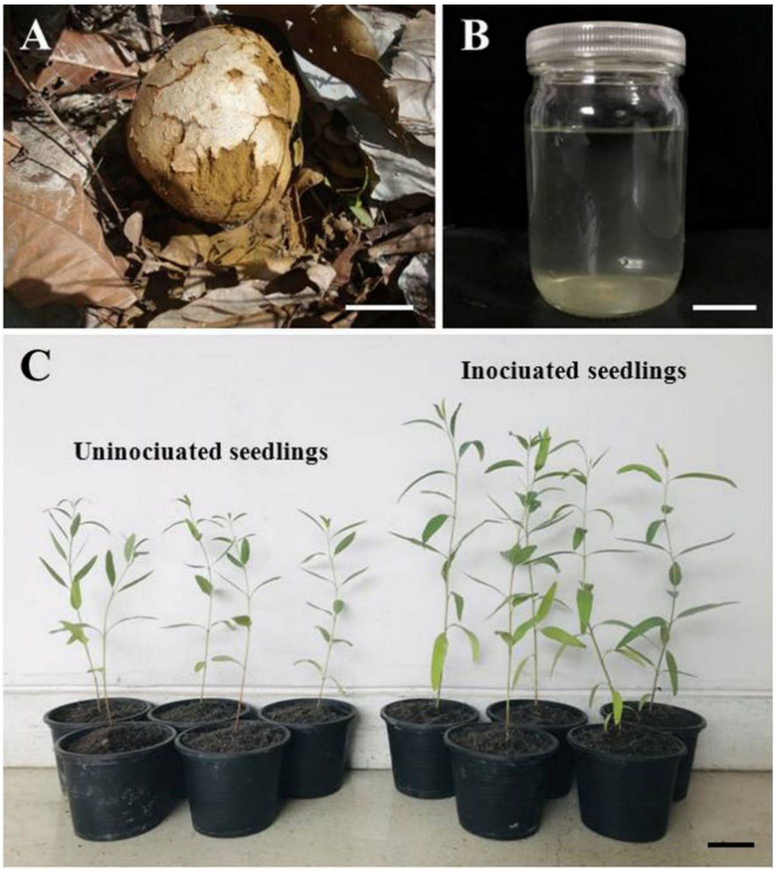

Figure 7 – Fruiting body of *Pisolithus albus* in a plantation of *Eucalyptus camaldulensis* in Thailand. (A); spore suspension of *Pisolithus albus* (B); and *Eucalyptus camaldulensis* seedlings inoculated and uninoculated with *Pisolithus albus* spores (C). Scale bars A and C = 50 mm; B = 25 mm.

The spore inoculation of *Scleroderma albidum, S. areolatum, S. cepa*, and *S. citrinum*, could enhance height, shoot diameter, and dry biomass of *Eucalyptus globulus* and *E. urophylla* seedlings (Chen et al. 2006). Inoculation of *Lithocarpus urceolaris* seedlings with spores of *S. citrinum, S. columnare*, and *S. sinnamariense* resulted in taller stems with a thicker diameter compared to uninoculated seedlings (Alamsjah et al. 2015). The inoculation of *S. citrinum* and *S. columnare* spores showed potential to improve the growth of *Parapiptadenia rigida* (red angico) and *Shorea javanica* seedlings, respectively (Steffen et al. 2017, Handayani et al. 2018). Ouatiki et al. (2021) found that the growth and survival rates of *Pinus halepensis* in polymetallic-contaminated soil were improved by inoculation with *Scleroderma* sp. spores. Additionally, the growth performance, nutrient uptake, and survival rate of *Acacia mangium* and *Pinus arizonica* seedlings were improved by inoculation with *Pis. tinctorius* spores (Aggangan et al. 2010, Quiñónez-Martínez et al. 2023). *Shorea seminis* seedlings injected with *P. arhizus* spores displayed greater shoot height, plant biomass, and shoot nitrogen and phosphorus uptake (Turjaman et al. 2006). Notably, most *Pisolithus* and *Scleroderma* species are easy to isolate, grow quickly in culture, and have mycelia that can be used as inoculum for a variety of plants.

Mycelia of *Pis. tinctorius* and *S. sinnamariense* displayed phosphate-solubilising activities due to the production of organic acids, phosphomonoesterases (alkaline and acid phosphatases), phosphodiesterases, and phytases (Jayakumar & Tan 2005, Bechem 2011, Zhang et al. 2014a, Ruess et al. 2019, Tedersoo & Bahram 2019). Yuan et al. (2004) found that *Pis. microcarpus*, *Pis. tinctorius*, and *Pisolithus* sp. XC1 could mobilise potassium from clay minerals. Pure cultures of *Pis. albus* and *S. sinnamariense* were able to demonstrate detoxification by solubilising various toxic metals (Al, Co, Cd, Cu, Pb, and Zn) contained in minerals (Kumla et al. 2014). Pure cultures of *Pis. albus, Pis. tinctorius*, *Pis. orientalis*, and *S. sinnamariense* have been reported for their ability to produce indole-3-acetic acid (IAA), a phytohormone involved in mycorrhizal associations and promoting plant growth (Kumla et al. 2014, 2020, Niemi et al. 2002, Siri-in et al. 2014, Splivallo et al. 2009). Ditengou et al. (2000) found that the pure culture of *Pis. tinctorius* produced hypaphorine (an indole alkaloid compound) that regulates root hair elongation during ECM development.

Mycelial inoculants derived from pure cultures of *Pisolithus* and *Scleroderma* can be prepared using various methods, such as mycelial plugs, mycelial suspensions, and substrate carriers like cereal grains, peat moss, vermiculite, and alginate beads (Sanchez-Zabala et al. 2013, Gandini et al. 2015, Kumla et al. 2016, Wagner et al. 2019, Zuo et al. 2022). The inoculation of mycelial inoculants derived from *Pisolithus* and *Scleroderma* species enhanced the growth, drought tolerance, nutrient uptake, and survival rate of seedling plants, as shown in Table 3. These applications are mostly involved in plants such as *Eucalyptus grandis*, *Nothofagus dombeyi*, and *Quercus suber* (Alvarez et al. 2009, Canton et al. 2016, Sebastiana et al. 2018), *Acacia mangium* and *E. globulus* (Aggangan et al. 2010, Jourand et al. 2010), *P. pinaster, E. urophylla*, *Coccoloba uvifera* and *P. wallichiana* seedlings (Bandou et al. 2006, Sanchez-Zabala et al. 2013, Itoo & Reshi 2014, Gandini et al. 2015). However, before applying *Pisolithus* and *Scleroderma* species to target plants, it's important to consider and understand the specific associations between host plant species and the selected species that are known to form compatible ECM associations to assure the supply of high-quality seedlings for forestry (Kumla et al. 2016, Lofgren et al. 2018, Kennedy et al. 2020).

Table 4 Examples for the use of *Pisolithus* and *Scleroderma* treated on plants for forestry.

Fungal taxa	Type of inoculant	Treated plant	Result	Reference
Scleroderma areolatum	Mycelia entrapped in alginate beads	*Eucalyptus urophylla*	Enhanced plant growth and nitrogen, phosphorus and potassium uptake of seedlings	Gandini et al. (2015)
Pisolithus sp.	Mycelia on agar	*Pinus densiflora*	Protected seedlings under a toxic concentration of copper	Chen et al. (2015)

Fungal taxa	**Type of inoculant**	**Treated plant**	**Result**	**Reference**
Pisolithus tinctorius	Mycelia on agar	*Nothofagus dombeyi*	Enhanced shoot and root dry weights, foliar N and P concentrations, and root enzyme activities of seedlings	Alvarez et al. (2009)
Scleroderma citrinum	Mycelia on agar	*Pinus wallichiana* and *Cedrus deodara*	Increased shoot height, needle number, shoot and root biomass and survival of seedlings	Itoo & Reshi (2014)
Pisolithus arhizus	Mycelia on a mixture of vermiculite and peat moss	*Pinus pinaster*	Increased shoot height, shoot diameter, shoot and root biomass of seedlings	Sanchez-Zabala et al. (2013)
Pisolithus albus	Mycelia on a mixture of vermiculite and peat moss	*Acacia holosericea*	Enhanced shoot and root biomass of seedlings	André et al. (2004)
Pisolithus tinctorius	Mycelia on a mixture of vermiculite and peat moss	*Quercus suber*	Increased drought tolerance of seedlings	Sebastiana et al. (2018)
Pisolithus tinctorius	Spore suspension	*Acacia mangium*	Enhanced height, shoot diameter and dry biomass of seedlings	Aggangan et al. (2010)
Pisolithus tinctorius	Mycelia on agar	*Eucalyptus grandis*	Protected seedlings under a toxic concentration of manganese	Canton et al. (2016)
Scleroderma bermudense	Mycelia on a mixture of vermiculite and peat moss	*Coccoloba uvifera*	Increased salt tolerance and phosphorus uptake of seedlings	Bandou et al. (2006)
Scleroderma cepa, Scleroderma citrinum, Scleroderma albidum, Scleroderma areolatum	Spore suspension	*Eucalyptus globulus* and *E. urophylla*	Enhanced plant growth of seedlings	Chen et al. (2006)
Scleroderma sp.	Mycelia in liquid medium	*Castanea henryi*	Enhanced plant growth of seedlings and increased nitrogen, phosphorus, and potassium uptake in roots, stems, and leaves,	Zuo et al. (2022)
Scleroderma columnare	Spore suspension	*Shorea javanica*	Improved plant growth, plant height, shoot dry weight, total dry weight, and total leaf area	Handayani et al. (2018)
Scleroderma citrinum	Spore suspension	*Parapiptadenia rigida*	Enhanced plant growth, plant height and stem diameter	Steffen et al. (2017)
Scleroderma sp.	Spore suspension	*Pinus halepensis*	Enhanced plant growth and increased survival rate in polymetallic contaminated soil	Ouatiki et al. (2021)
Scleroderma sinnamariense, Scleroderma columnare and	Spore suspension	*Lithocarpus urceolaris*	Enhanced height, and shoot diameter of seedlings	Alamsjah et al. (2015)

Fungal taxa	Type of inoculant	Treated plant	Result	Reference
Scleroderma citrinum				
Pisolithus albus	Mycelia in liquid solution	*Eucalyptus globulus*	Enhanced plant growth and tolerance of nickel	Jourand et al. (2010)
Pisolithus arhizus	Spore suspension	*Shorea seminis*	Increased shoot height, biomass, shoot nitrogen content and phosphorus uptakes	Turjaman et al. (2006)
Pisolithus tinctorius	Spore suspension	*Pinus arizonica*	Enhanced survival rate and mineral uptake	Quiñónez-Martínez et al. (2023)

3.4 Future directions in fungal biofertilizers: challenges and advancements

Fungal biofertilizers are showing benefits in terms of crop production and ecosystem stability. Overall, they are the most promising input to the agricultural field. However, the application process and its sustainability are always challenged. One of the main concerns is that fungal biofertilisers are sensitive to environmental conditions. They require specific soil conditions such as pH, moisture, and organic matter for optimal activity (Hernández-Fernández et al. 2021, Ferreyra-Suarez et al. 2024). This limits their effectiveness in degraded or heavily fertilised soils. Another challenge is that fungal fertiliser requires time to establish. As fertilisers are introduced to living organisms, these fungi require time to colonise roots and develop a symbiotic relationship. Therefore, the application of biofertilizers delays visible growth benefits, which are slower than those of commercial chemical fertilisers. Also, for the optimum results, long-term application is required (Carvajal-Muñoz et al. 2012, Chakraborty & Akhtar 2021). The limit is to establish trust in biofertilizers and move farmers from conventional chemical fertilisers.

Mass production of fungal inocula is challenging since it is required to maintain viability, or else improper storage can reduce the shelf life (Herrmann and Lesueur 2013, Malusà et al 2016, Bagga et al. 2024, Fadiji et al. 2024) and lack of quality control has resulted in poor products, which affect the confidence of farmers (Herrmann & Lesueur 2013). Ecologically, these introduced fungi might have to compete with the native microbial community. However, one of the main problems with biofertilizers is a poor understanding of interactions between these introduced fungal species with other microbes and plants (Malusà et al. 2016). The competition with the native microbial community will be a struggle and could reduce the success of the inoculation (Čaušević et al. 2024, Kong et al. 2025). However, developing fungal inoculants from the same environment will help to overcome this matter.

Recent advancements have been made to address these challenges, based on genetic engineering policies and farmer adaptation strategies. Using genetic and metabolic engineering, fungal strains are being developed to improve nutrient solubilization, stress tolerance, and symbiotic efficiency. Likewise, *Aspergillus niger* strains with modified phosphatase genes have shown higher phosphate release (Peng et al. 2022, Ma et al. 2025). In addition, fungal species isolated from extreme environments could be utilised to develop beneficial microbes in degraded soils. For instance, Khan et al. (2022) showed that *Aspergillus terreus* from saline soils promotes barley growth under salt stress. Future work is open to incorporating CRISPR-Cas9 editing to knock out fungal genes that inhibit symbiosis and to genetically engineer fungi that confer solubilization, pathogen resistance, and other important traits (Yang et al. 2024).

To enhance the inoculant viability in introduced environments, nano-coating and biochar-based carriers are being used. For instance, use of nano-coated *Trichoderma harzianum* spores, coated with biodegradable polymers, to enhance their survival in acidic soils (Brondi et al. 2022, 2025). In addition, Biochar can serve as a favorable physical niche for arbuscular mycorrhizal fungi, facilitating colonization of biochar particles and providing protected microhabitats. Studies have shown direct AMF colonization of biochar and slower viability loss of inoculated spores in biochar substrates under controlled conditions (Minkosse et al. 2023, Neuberger et al. 2024). However, biofilm-biofertiliser, a combination of both fungi and bacteria, will be the best combatant to overcome inoculant survival. Co-inoculation of *Rhizophagus intraradices*, which is an arbuscular mycorrhizal fungus, with *Azospirillum brasilense* has been shown to increase maize yield by 20% compared to single inoculants (Rodríguez et al. 2023). Similarly, when *Piriformospora indica*, an endophytic fungus, was paired with Azotobacter, has increased wheat growth in nitrogen-deficient soils (Sing et al. 2022, Li et al. 2023). Therefore, future research should focus more on combining fungi with bacteria or other microbes to create multifunctional biofertilizers. Smart nanocarriers which release fungi only when root exudates are detected will be another approach for future advancements.

Even when such advancements are made, policies and farmers' acceptance are important facets in the future of biofertilizers. It is necessary to develop small-scale implementations to overcome farmers' acceptance. In India, the small-scale project, Paramparagat Krishi Vikas Yojana (PKVY), which subsidises AMF inoculants for organic farming, is an example of successful implementation (Acharya et al. 2020, Khobragade et al. 2024). Another example is promoting biofertilizers in the Great Mekong Region (GMR: China, Vietnam, Myanmar, Thailand, Cambodia and Lao PDR), where the majority of the population relies on agriculture and related industries (Atieno et al. 2020). Since this is an era of digitalisation and AI, digital platforms have to be essentially promoted for the required knowledge dissemination (Yadav et al. 2024).

4. Biocontrol agents

Biological control is currently making a huge impact on the agricultural sector as it moves towards organic and sustainable farming, particularly fungal biocontrol agents that play an important role by suppressing pests, pathogens, and weeds through diverse mechanisms (Peng et al. 2021, Pérez-Pizá et al. 2024). These fungi act as antibacterial and antifungal agents (Xu et al. 2015, Hyde et al. 2019, Liao et al. 2025), entomopathogenic fungi (Hyde et al. 2019, Wang et al. 2024), nematode-trapping fungi (Berhanu et al. 2024), and emerging agents for controlling mycoplasmas and viruses as well. Moreover, bioherbicidal fungi target weeds through phytotoxic compounds or direct tissue invasion (Htet et al. 2022), which is also an important aspect in the fungal biopesticide industry.

Ecologically, fungal biocontrol agents enhance biodiversity by reducing chemical pesticide use and promoting beneficial microbes (Barratt et al. 2018, Ayaz et al. 2023, Chaudhary et al. 2024). It also contributes by preventing soil and water contamination (Satapathy 2018). Biological control fungi reduce resistance development, which is a major problem associated with chemical pesticides (Rauf 2024, Wang et al. 2024, Diepenbrock et al. 2024). Therefore, the incorporation of fungal biological control agents not only promotes long-term agricultural sustainability but also lowers production costs and ecological sustainability.

Even though biological control is currently making a huge entrance, it is not a new strategy. Fungi as biological control agents have a long history. In the 1800s, silkworm populations in Europe and Asia were naturally decimated by *Beauveria bassiana*. This has led to the recognition of *B. bassiana* as a potential insect pathogen. Based on this, in the late 19th century, studies were conducted to understand its effect on crop pests like the Colorado potato beetle. In the late 1800s, Russian scientist Ilya Mechnikov identified the *Metarhizium anisopliae* as an entomopathogen of wheat cockchafer beetles. In the early 20th century, field trials in Australia and Africa demonstrated the effectiveness of *M. anisopliae* against locust plagues, which was the foundation for myco-insecticides. *Colletotrichum gloeosporioides* was the first commercially developed myco-herbicide. In the 1980s, the USDA developed "Collego" to control northern jointvetch weed in rice fields. In the 1950s–60s, researchers observed that *Arthrobotrys* and *Dactylella* species formed trapping structures to capture nematodes. These observations led to the protection of crops from root-knot and cyst nematodes without the use of chemicals. As an antibacterial agent, *Trichoderma viride* was among the first fungi to be identified for its antagonistic effects. It has shown an antagonistic effect against soil-borne plant pathogens. By the 1970s, commercial formulations of *Trichoderma* were developed for seed treatment and soil application. These major historical milestones highlight the ecological and economic value of fungi in sustainable agriculture.

4.1 The mode of action

Biological control agents have special characteristics/mechanisms to reduce/eradicate target organisms. The type of these variable mechanisms/characteristics is determined by both the biocontrol agent and the target organism and is categorised into four modes of action: competition, parasitism, antibiosis, and induced resistance (Junaid et al. 2013, Köhl et al. 2019). In theory, these modes could be specific, yet a given biocontrol agent might use one or more actions to control the target organism (Stiling & Cornelissen2005). These diverse mechanisms suppress pathogens and enhance plant health via direct and indirect interactions

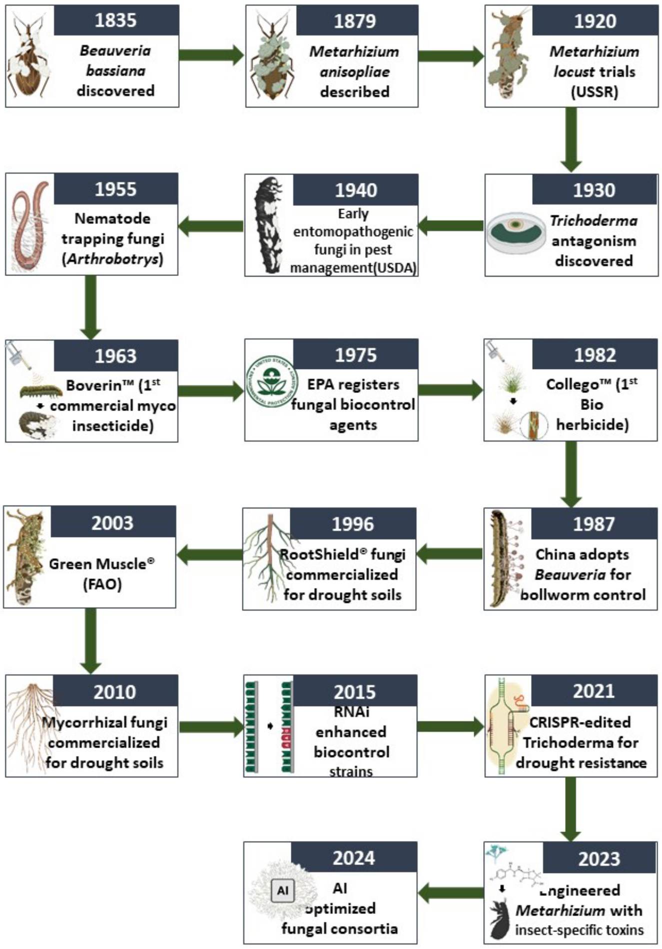

Figure 8 – Milestones of development of biocontrol agents.

1. Direct interactions
    a. *A. Antagonism:* Antibiosis is the process by which biological control agents produce antimicrobial metabolites. The metabolites include a wide range of antibiotics, toxins, and VOCs. Antibiotics such as gliotoxin and penicillin directly inhibit pathogens, and toxins like beauvericin and destruxins disrupt cellular functions. The VOCs act as long-distance inhibitors. Enzymes, including chitinases and proteases, degrade pathogen structures. *Trichoderma* produces chitinases and β-1,3-glucanases that hydrolyse *Fusarium* hyphae, and also, *Trichoderma* spp., secrete gliotoxin and viridin, suppressing *Fusarium* and *Rhizoctonia* (Vinale et al. 2008). Pseudozyma flocculosa produces flocculosin, effective against powdery mildew (Avis et al. 2001).
    b. *Mycoparasitism or Hyperparasitism:* Mycoparasitism is the process by which a fungus parasitises another fungus, which leads to its suppression or death. This

involves several key steps: (i) sensing and growth toward the target and then binding to the host hyphae via lectins or hydrophobic proteins. The pathogenic fungus uses enzymes (chitinases, proteases, β-1,3-glucanases) to breach the cell wall, followed by intracellular colonisation, leading to the death of the target fungus. As for the previous examples, *Trichoderma* species are one of the best examples of well-studied mycoparasites. They attack pathogens like *Rhizoctonia solani*, *Fusarium oxysporum*, *Pythium* spp., and *Sclerotinia sclerotiorum* using hyphal coiling, enzymatic activities, and antimicrobial peptides (Howell 2003). *Ampelomyces Quisqualis* produce haustoria to penetrate powdery mildew fungi belonging to *Podosphaera*, *Erysiphe*, and *Blumeria* (Németh 1991). Similarly, *Pythium oligandrum* also produced appressoria to penetrate *Pythium ultimum*, *Fusarium* spp. (Benhamou et al. 2012). *Coniothyrium minitans* attacks survival structures, sclerotia of *Sclerotinia sclerotiorum* by infecting and producing cell wall-degrading enzymes Whippset al. 2008). *Lecanicillium* species can act as dual biocontrol agents against Aphid Pathogens and Powdery Mildew, penetrating fungal spores and hyphae (Askary et al. 1998).

   c. *Competition for nutrition and space*: All organisms are in continuous competition for nutrients and space on their hosts. Although the competition is difficult to study, the metabolic patterns of yeasts related to Nitrogen, Iron and Sulphur make it easier to understand the mechanism of competitiveness (Freimoser et al. 2019). The antimicrobial fungi also compete with pathogenic species for nutrients and space. Most biocontrol agents rapidly and aggressively colonise plant surfaces, outcompeting pathogens for available resources. For example, *Trichoderma* compete with *Fusarium* for root niches (Alabouvette et al. 2009). Similarly, *Trichoderma* is a fast-growing fungus that occupies root niches, thereby blocking pathogen establishment. Additionally, *Trichoderma* upregulates sugar transporters (MSTs) to outcompete pathogens for root exudates.

2. Indirect mechanisms
   a. *Induce systemic resistance*: The innate immune system in plants recognises and responds to the presence of microorganisms (Chisholm et al. 2006, Jones & Dangl 2006) which induces the resistance systemically. This was used to develop the biocontrol agents and the fortifiers (Gozzo & Faoro 2013, Pieterse et al. 2014). Biocontrol agents can produce jasmonic acid, salicylic acid-like compounds that prime plant defence genes, enhancing resistance to subsequent pathogen infections. *Trichoderma* species secrete small effector proteins (e.g., Sm1/Epl1) that bind to plant receptors and activate MAPK cascades. This leads to the upregulation of pathogenesis-related (PR) genes (e.g., *PR-1*, *PDF1.2*), which enhance lignin deposition and phytoalexin production.
   b. *Endophytic colonisation:* Fungi with biological control characteristics could colonise intercellular spaces as endophytes. These species live inside the plant without causing any physical symptoms, while helping the plant through induced systemic resistance, antibiosis, the secretion of insecticidal metabolites, and the induction of tree tolerance. For example, entomopathogenic fungi like *Beauveria bassiana* colonise plants including Maize, cotton, coffee, and cocoa, as endophytes and produce beauvericin and oosporein, which kill all armyworms, and aphids and upregulate jasmonic acid (JA) defence pathways of the host (Donga et al. 2018). Sasan & Bidochka (2013) has shown that *Metarhizium robertsii*, which is an entomopathogenic fungus, could enhance drought tolerance in plants. Furthermore, endophytic colonisation of *Trichoderma* in maize roots has shown its potential to induce systemic resistance against Fusarium wilt (Harman et al. 2004). *Epichloë* (=*Neotyphodium*) species are well-known grass endophytes, which could produce alkaloids such as lolitrem B and

   peramine that are toxic to livestock pests. Because of this, *Epichloë coenophiala* has been commercially applied to pasture grasses (Schardl & Leuchtmann 2005). Non-pathogenic *Fusarium oxysporum* strains have shown hypovirulence against pathogenic *F. oxysporum* f. sp. cubense, causing Panama disease (Alabouvette et al. 2009)

   c. *Disruption of pathogen signalling:* Biological control fungi could interfere with pathogens by secreting inhibitory compounds, competition for signalling molecule receptors by disrupting their ability to coordinate virulence, sporulation, or biofilm formation. For instance. *Trichoderma* produce N-Acyl Homoserine Lactones (AHLs), which prevent bacterial virulence gene expression (Uroz et al. 2009). *Ampelomyces quisqualis* interferes with the mating-type (MAT) gene signalling of cucurbit powdery mildew (Kiss et al. 2004). *Clonostachys rosea* blocks protein signalling pathways and lowers toxin contamination in grains by *Fusarium graminearum* (Kosawang et al. 2014). Moreover, *Saccharomyces cerevisiae* degrades oxylipins, which regulate aflatoxin synthesis and sporulation of *Aspergillus flavus* (Affeldt et al. 2012, Yan et al. 2015).

3. *Hypovirulence:*
   Virus-mediated attenuation in fungal biocontrol. In here, the pathogenicity of fungi is reduced due to infection by mycoviruses. These infections lead to decreased sporulation, growth rate, toxin production, and impaired host colonisation. These mycoviruses disrupt signalling pathways, including those involved in secondary metabolite synthesis. Cryphonectria hypovirus 1 (CHV1) is a mycovirus belonging to Hypoviridae that affects *Cryphonectria parasitica*, which is the chestnut blight pathogen. Nuss (2005) has shown that CHV1 reduces fungal virulence by more than 90%, suppressing pigmentation and sporulation.

Nematode-trapping fungi are a fascinating group that employs specialised structures and biochemical strategies to capture and digest nematodes. These traps are categorised into two forms:

1. Adhesive Traps - sticky hyphae secrete extracellular polymers that immobilise nematodes. These hyphae may further develop adhesive knobs or branched networks to increase surface area. For example, *Arthrobotrys oligospora* expresses adhesins (e.g., AoMad1) on hyphal surfaces, mediated by G-protein signalling.
2. Constricting Rings - mechanical traps that rapidly inflate when nematodes pass through, effectively strangling them. After capturing the nematodes, the fungi secrete cuticle-degrading enzymes and produce nematocidal metabolites that may paralyse the nematodes before hyphal invasion.

Some fungi also exhibit endoparasitic strategies, producing spores that adhere to nematodes and then colonise them internally.

Compared to other biocontrol agents, entomopathogenic fungi have a well-defined pathogenic cycle. Initially, spores (conidia) attach to the insect cuticle via hydrophobic interactions or mucilage. Under favourable humidity and temperature, the spores germinate, forming germ tubes and appressoria. These structures secrete proteases, chitinases, and lipases that degrade the insect's exoskeleton. The appressoria also exerts mechanical pressure that aids penetration. Once inside, the hyphae switch to yeast-like blastospores and rapidly colonise the insect tissues. During this infection, the fungi escape insect immunity by masking their cell walls with hydrophobins. Upon successful colonisation, the fungi produce various toxins that kill the insect. After the host dies, hyphae emerge from the cadaver and produce new spores under high-humidity conditions.

4.2 *Trichoderma* as a biological control agent

Trichoderma is a cosmopolitan fungal genus belonging to Sordariomycetes (Hyde et al. 2024, Tan et al. 2025). They are abundant in high-humid ecosystems such as agricultural soils, forests, and grasslands (Zhao et al. 2023b, Tan et al. 2024, Hyde et al. 2024). With the exponential expansion in the field of taxonomy, as many as 50 new *Trichoderma* species are being identified annually (Cai & Druzhinina 2021, Huang et al. 2024b), reflecting their important roles in various fields. *Trichoderma* has experienced significant ecological and evolutionary shifts. It has transitioned from a parasite of plant-decomposing fungi to a saprotroph, then to a mycoparasite, and finally to a plant symbiont (Woo et al. 2023). Over time, it has become an opportunistic plant coloniser (Woo et al. 2023). These transitions have led to the acquisition of genes for carbohydrate hydrolysis and the ability to parasitise a diversity of fungi, nematodes, and even some insects. *Trichoderma* species are highly adept at colonising plant roots and acting as endophytes. Their opportunistic nature allows them to thrive in various environments, competing for resources and modifying ecological conditions to their advantage (Druzhinina et al. 2011, Woo et al. 2023).

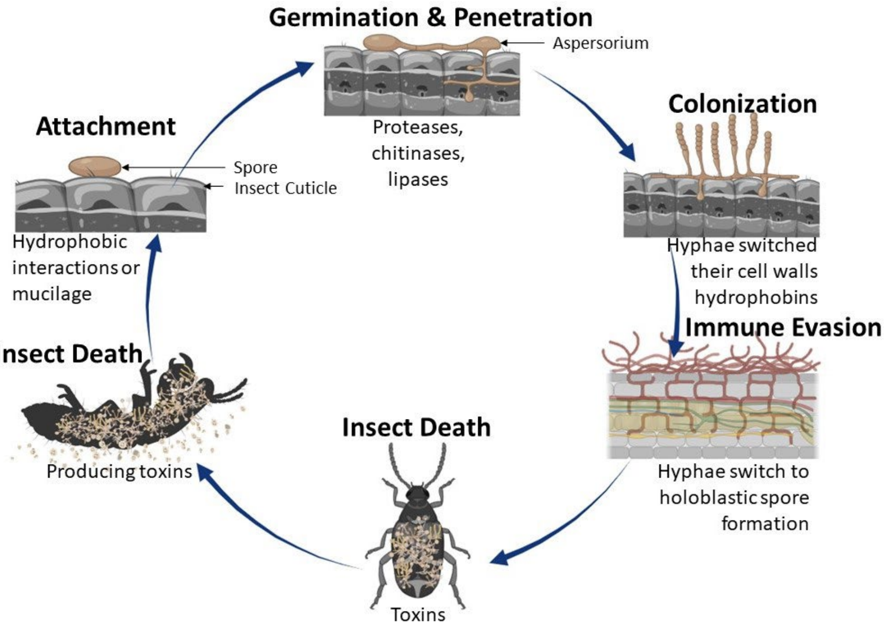

Figure 9 – Mode of action by entomopathogenic Fungi

Trichoderma is increasingly recognised as a key component in sustainable agricultural practices, contributing to eco-sustainable agriculture by reducing the need for chemical pesticides and fertilisers. Commercial formulations of *Trichoderma* are widely used as biopesticides, biostimulants, and biofertilizers, enhancing crop yields and quality. *Trichoderma harzianum* T-22 (renamed as *Trichoderma afroharzianum*) is widely used as a biocontrol agent in agriculture to protect crops against various soil-borne diseases such as damping-off caused by *Pythium* spp., Rhizoctonia root rot, Fusarium wilt, and Sclerotinia rot (Harman et al. 2004). Other *Trichoderma* species such as *T. citrinoviride*, *T. ghanense*, *T. guizhouense*, *T. koningiopsis*, *T. virens*, also show great potential in controlling plant diseases, especially some soil-borne diseases (Luo et al. 2023, Tao et al. 2023a, Woo et al. 2023). Research continues to explore the potential of *Trichoderma* to improve soil health, remediate contaminated sites, and promote crop resilience to climate change. The development of innovative formulations and application methods, such as seed coatings and time-release technologies, further enhances the practical use of *Trichoderma* in modern agriculture (Ramírez-Valdespino et al. 2019). By leveraging *Trichoderma*'s ability to induce systemic resistance and promote plant growth, their applications not only enhance crop productivity but also contribute to environmental sustainability.

Trichoderma functions as a direct biological control agent by parasitising pathogens and producing secondary metabolites that inhibit their growth. These species secrete cell wall-degrading enzymes and volatile organic compounds that can suppress pathogens and even attract natural enemies of insect pests. For example, *Trichoderma* species produce chitinases, glucanases, and proteases that degrade the cell walls of pathogenic fungi, thereby reducing their virulence. Additionally, *Trichoderma* can produce secondary metabolites such as gliovirin and trichothecenes, which have antimicrobial properties and can inhibit the growth of various plant pathogens (Howell & Stipanovic, 1983, Malmierca et al. 2012). Klaiklay et al. (2019) isolated 13 trichothecenes compounds from *T. brevicompactum*. Malmierca et al. (2016) proved that trichothecenes and aspinolides produced by *T. arundinaceum* can regulate the expression of *Botrytis cinerea* genes involved in virulence and growth. Competition for ecological niches and resources is also important for *Trichoderma*'s biocontrol efficacy, contributing to its colonisation of soil, rhizosphere, and even endosphere. Luo et al. (2023, 2025) found that both *T. koningiopsis* (Tk905) and *T. azadirachtae* (Ta3302) can grow quickly and compete with pathogens for the ecological niches in soil, rhizosphere and even for the colonisation of the host plant.

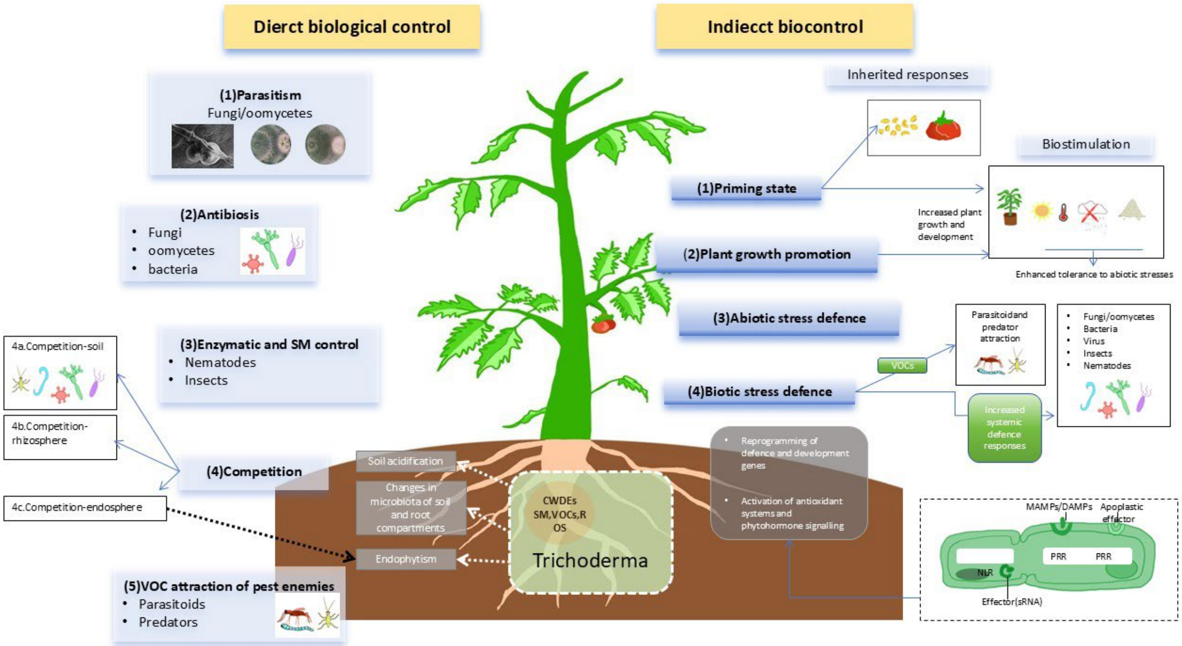

Figure 10 –Direct and indirect mode of action of *Trichoderma* as a biocontrol agent.

Indirectly, *Trichoderma* primes plant defences, enhancing systemic resistance through the activation of phytohormone pathways. This priming allows plants to respond more rapidly and effectively to subsequent pathogen attacks. *Trichoderma* species also promote plant growth by producing phytohormones and improving nutrient uptake, contributing to overall plant health and stress tolerance (Pieterse et al. 2014). The elicitors produced by *Trichoderma*, such as xylanase (EIX) and cerato-platanin (Sm1), act as signalling molecules that trigger the plant's immune responses. These elicitors activate pattern recognition receptors (PRRs) in plant cells, leading to the production of reactive oxygen species (ROS), antimicrobial secondary metabolites, and pathogenesis-related proteins (PRs) (Boller & Felix, 2009, Dodds & Rathjen, 2010).

Trichoderma plays a crucial role in enhancing plant defence mechanisms through the induction of systemic resistance. This process involves the activation of phytohormone pathways, particularly jasmonic acid (JA) and ethylene (ET), which prime plants to respond more rapidly and effectively to subsequent pathogen attacks (Pieterse et al. 2014). *Trichoderma* species have been shown to induce systemic resistance in various crops, including cucumber, maize, and tomato (Segarra et al. 2007, Martínez-Medina et al. 2017). The development of high-throughput sequencing technologies, gene editing tools, and multi-omics approaches has provided new tools and methods to study complex interactions. These advancements enable a deeper understanding of the signalling pathways and molecular mechanisms involved in *Trichoderma*-induced resistance. Further research into the tripartite interactions of "*Trichoderma*-pathogen-host plant" will not only elucidate the underlying mechanisms of *Trichoderma*'s biocontrol activity but also pave the way for the development of more effective and sustainable biocontrol strategies in agriculture.

4.3 *Chaetomium* is at the beginning of a new era in biological control

Chaetomium (Chaetomiaceae, Sordariales, Sordariomycetes, Ascomycota) accommodate around 50 species known for producing various bioactive secondary metabolites (Ibrahim et al. 2021, Dwibedi et al. 2023). The first reported application of *Chaetomium* as an antagonist to control plant pathogens was by Tveit & Moore (1954), who found that *C. globosum* and *C. cochliodes* grown on the surface of oat seeds could control *Helminthosporium victoriae*. To date, *Chaetomium* has emerged as a source of a wide range of bioactive natural chemicals and over 500 compounds with diverse chemistry have been isolated and identified, more than 100 secondary metabolites with varied beneficial qualities, such as anticancer, cytotoxic, antimalarial, and enzyme inhibitory actions, have been reported (Dwibedi et al. 2023, Rao et al. 2023). Among *Chaetomium* species, *C. globosum* is one of the most extensively studied species in its bioactive potential (Ashwini 2019). Several *Chaetomium* species are reportedly antagonistic to the growth of various phytopathogens, especially soil-borne and seed-borne (Marwah et al. 2007, Zhang & Yang 2007).

Mechanism of biological control

Chaetomium species compete with phytopathogens for nutrients and space in the rhizosphere or on plant surfaces through antagonism (Park 1960, Zhang & Yang 2007). They reduce pathogen populations, limiting their ability to establish infections (Park 1960, Zhang & Yang 2007). Competition for nutrients with *Fusarium graminearum* has been reported by Chang & Kommendahl (1968) using *C. globosum* coated maize seeds. Di Pietro et al. (1992) reported evidence that *C. globosum* can produce and release certain antibiotics to suppress the damping-off of sugar-beet caused by *Pythium ultimum*. Chaetoblobosin C, produced by *C. globosum*, can suppress plant pathogens' growth by disrupting cellular processes, while making this species a very potent antagonist of various soil microbiota (Soytong et al. 2001, Dhingra et al. 2003, Aggarwal et al. 2004, Abdel-Azeem 2020). Some *Chaetomium* species are capable of secreting hydrolytic enzymes (chitinases and glucanases) to degrade the cell walls of phytopathogens (Liu et al. 2008).

Current trends

Endophyte *Chaetomium* strains are gaining attention as potential biocontrol agents and biofertilizers due to their ability to colonise plant tissues and provide various benefits without harming the host plant (Kaewchai et al. 2009, Elshahawy & Khattab 2022). Many such studies have reported antagonistic ability of the endophytic *Chaetomium* strains toward various bacterial and fungal pathogens, such as species of *Alternaria*, *Botrytis*, *Erwinia*, *Fusarium*, *Lophodermium*, *Rhizoctonia*, *Sclerotinia, Sphaeropsis*, *Pestalotiopsis, Phomopsis*, *Pseudomonas*, *Pythium*, and *Pyrenophora* (Xu et al. 2014, Abdel-Azeem et al. 2021, Nongthombam & Mutum 2024) in both *in vitro* and *in vivo*. The root endophyte *Chaetomium cupreum* has been reported to promote plant growth and detoxify aluminium when *Miscanthus sinensis* was grown at an acidic mine site (Haruma et al. 2018). The endophyte, *Chaetoimum globosum* encourages the growth of maize plants and cucumbers (Elshahawy & Khattab 2022, Tian et al. 2022). Antimalarial and cytotoxic compounds (Azaphilones and Depsidones) were extracted from the fungus *C. brasiliense* and C. *longirostre* (Khumkomkhet et al. 2009, Panthama et al. 2011). In addition, *Chaetoimum* species have also been reported to show promising anticancer activity, such as *C. cupreum* extracts against human breast cancer (Wani et al. 2020), *C. globosum* natural product suppresses tumour growth and metastasis in gastric cancer (Guan et al. 2023), and *C. nigricolor* against breast carcinoma cell line (Nongthombam & Mutum 2024).

However, continued research and clinical studies are essential to fully understand their mechanisms and translate these findings into effective cancer treatments.

State of the commercial application

Chaetomium-based biofungicides and biostimulants are used for integrated plant disease management (Kaewchai et al. 2009, Soytong et al. 2021). Effective strains of *Chaetomium* have been formulated into bio-pellets and bio-powders for the biological control of plant diseases. These formulations are patented and registered under the names Ketomium® and BIOKUPRUM™ (Soytong et al. 2001, Mehnaz 2016). Ketomium® contains 22 strains of *C. globosum* and *C. cupreum* in the form of spore powder or pellets. The recipe for BIOKUPRUM™ is a wettable powder containing 2 ×106 CFU/g. It can be applied either on seeds and tubers or as a foliar spray. In addition to protecting plants from bacterial and fungal infections that cause rots, rusts, and leaf spots, BIOKUPRUMTM and Ketomium® also produce substantial amounts of Ergosterol, which can enhance the humus layer in soils, thereby increasing soil fertility (Soytong et al. 2001, Mehnaz et al. 2016).

Challenges

Chaetomium species share similar characteristics with other genera in Chaetomiaceae, such as *Achaetomiella*, *Arcopilus*, *Dichotomopilus*, and *Humicola* (Wang et al. 2016b). Therefore, correct species identification is necessary to develop *Chaetomium* species as biocontrol agents. *Chaetomium* species exhibit complex, sometimes variable morphological characters, making them difficult to identify solely on morphological grounds. However, current species identification is based on ITS, LSU, *rpb2,* and *tub2,* and has shown considerable similarity among *Chaetomium* species, questioning the current species delimitation methods. Thus, there is a necessity to develop a comprehensive genomic database to overcome species delineation issues (Wang et al. 2022a, Yang et al. 2024). *Chaetomium* is a cosmopolitan genus, despite its known significant ecological roles and diverse habitats (Abdel-Azeem et al. 2020). Demonstrating the efficacy of *Chaetomium*-derived compounds in *vivo* (in living organisms) can be challenging, and results from *in vitro* studies often do not directly translate to *in vivo* systems (Harvey 2008). Like *Chaetomium*, the complex mechanisms behind its antagonistic effects need to be further explored (Seethapathy et al. 2022). Meanwhile, when those *Chaetomium*-derived metabolites are used as versatile weapons against numerous plant pathogens and soil microorganisms, their potential indiscriminate use could threaten ecosystem stability, as sterigmatocystin has been shown to become toxic, posing challenges to their use and requiring thorough safety assessments (Rank et al. 2011).

4.4 Yeasts for sustainable disease management in agroecosystems

Yeast is a eukaryotic, unicellular fungal assemblage with a wide range of habits. The specific budding ability of yeasts gave them unique characteristics to support their biocontrol ability. Due to the symbiotic and antagonistic nature of the yeast, it became a good source for biocontrol (Freimoser et al. 2019). Yeast has long been used as a model in biotechnology and medical mycology. However, the yeast in agricultural aspects must be widely investigated. It is worth investigating the major characteristics which support using yeasts in green agriculture. Yeasts are highly diverse and distributed among a wide range of fungal taxa, naturally occurring as antagonists in the photosphere, epiphytes, or mutuals (Freimoser et al. 2019). For green agricultural purposes, rapid generation, genetic stability and rapid colonisation are important. As eukaryotes, yeasts show complex genetic stability. Certain yeast strains contain a high-copy 2 µm plasmid, which can be important in biotechnological aspects such as gene editing (Peter et al. 2018). However, several yeast strains do not contain plasmids. Hence, unlike most bacteria, the yeasts do not transfer or acquire plasmids. Thereby, yeasts do not exchange factors such as antibiotic resistance, pathogenicity (disease-causing genes), and toxin production. Nevertheless, horizontal gene transfer is less frequent in yeasts. This makes the yeasts safer and stable biocontrol agents. As a sum, rapid colonisation (increasing the competition for nutrients), biofilm formation, antimicrobial compounds production (VOCs and toxins), secretion of enzymes, mycoparasitism and inducing the plant's immunity make the yeast a highly successful potent biocontrol agent for green agricultural purposes (Fanning & Mitchell 2012, Pandin et al. 2017, Rossouw et al. 2018, Verstrepen & Klis 2006).

Mechanisms of disease suppression by Yeasts

Yeasts show different biocontrol mechanisms. The combined effects of these mechanisms increase the efficiency of the biocontrol.

Competition for nutrients and space against phytopathogens – Metschnikowia reukaufi is a yeast closely related to certain biocontrol species, reported with duplication of nitrogen transporter and metabolism genes, causing priority effects and acting as a driver of competitiveness (Dhami et al. 2016). Synthesis of iron-binding molecules to deprive competing organisms is a common mechanism among eukaryotes and prokaryotes (Barber & Elde 2015, Johnson 2008). Interestingly, the higher demand for iron in biocontrol yeasts is recognised as an important mode of action (Spadaro & Droby 2016). Yeasts such as *M. pulcherrima* form cyclic dipeptide, pulcherriminic acid, which complexes with iron (GoreLloyd et al. 2019). Several components of the sulphur assimilation pathways are absent in certain yeasts, and these yeasts tend to acquire methionine from their prey (Junker et al. 2019), which also proves the competitiveness of yeasts in their habitat (Junker et al. 2019). Further, yeasts are either strongly or weakly antagonistic against most fungi and control the mycobiome in their habitat (Hilber-Bodmer et al. 2017).

Biofilm formation – The yeast biofilms initiate with the adhesion of individual cells on the desired surface through cell wall modifications, secretion of an extracellular matrix, and often the formation of hyphae or pseudohyphae (Cavalheiro & Teixeira 2018, Costa-Orlandi et al. 2017). The biofilm formation on phyllo- and carpospheres is considered an important mode of action. Further, studies by Millan et al. (2024) investigated the attachment of *Pichia* spp. to pathogenic *Botrytis cinerea* mycelia. Hence, yeast biofilms on the host surface increase the competition for space and on wounds, fasten the healing process or on the mycelium to suppress the pathogen (Millan et al. 2024).

Production of volatile compounds – Volatiles produced by *Aureobasidium pullulans* proved efficient in reducing the growth and infection by *Botrytis cinerea, Colletotrichum acutatum, Penicillium expansum, P. digitatum and P. italicum* both *in vitro* and *in planta* (Di Francesco et al. 2014). Current research on yeast VOC revealed that a plethora of *Alternaria* spp., *Aspergillus* spp., *Fusarium* spp., and *Penicillium* spp. suppressed, and the mycotoxin production was inhibited by VOC (Oufensou et al. 2023). However, the mode of action is yet to be understood. Interestingly, Yeast VOCs are often non-toxic, and most of them are recognised as GRAS (Generally Regarded as Safe) (Mari et al. 2016).

Toxin production – Due to their relatively low production of harmful secondary metabolites, yeasts are considered as a safer biocontrol agent (Freimoser et al. 2019). The production of toxins causes most of the antagonistic behaviours of yeasts. Certain compounds, such as aureobasidins, liamocins, 2-propylacrylic acid, 2-methylenesuccinic acid, are known as toxins which induce the antagonistic behaviour of *Aureobasidium pullulans* against bacteria and fungi (Prasongsuk et al. 2018, Price et al. 2013, 2017, Takesako et al. 1991, Zain et al. 2009). Most of the toxins produced by biocontrol yeast are proteinaceous killer toxins. Certain toxins inhibit or kill plant pathogenic fungi and are proposed for plant protection (Corbaci & Ucar 2018, Liu et al. 2015, Marquina et al. 2002, Perez et al. 2016). However, investigations are needed to understand the effects of these toxins on other beneficial microorganisms (phyllosphere & soil microbiota), and to assess human consumption safety (Freimoser et al. 2019).

Mycoparasitism – Recent studies by Millan et al. (2024) observed the strong adhesion of *Pichia* spp. on pathogenic *Botrytis cinerea* mycelium. Similar effects were observed by Wisniewski et al. (1991), and interestingly, *Pichia guilliermondii* caused the hyphal collapse in the plant pathogen *Botrytis* *cinerea*. The effect was assumed to be due to the hydrolytic enzymes, such as glucanases. Further, Ustilaginomycete *Pseudozyma aphidis* parasitises on powdery mildew pathogen *Podosphaera xanthii* and *Botrytis cinerea* (Calderon et al. 2019, Gafni et al. 2015). Parasitism through feeding on the prey was observed in *Saccharomycopsis* feeding on *Penicillium* spp. (Junker et al. 2017, 2018, 2019, Lachance & Pang 1997, Pimenta et al. 2008). However, mycoparasitism is poorly studied in yeast.

Induction of systemic resistance in plants – The biocontrol yeasts induce systemic resistance against a broad range of pathogens (Freimoser et al. 2019). *Candida saitoana*, *C. oleophila, Metschnikowia* spp., *Rhodosporidium paludigenum,* and *Saccharomyces cerevisiae* induce an innate immune response against phyllosphere pathogens in fruits (Freimoser et al. 2019). The induction of the resistance can be due to the production of reactive oxygen species (Macarisin et al. 2010) or yeast cell components (De Miccolis et al. 2019). The dead yeast cells can also induce resistance. Resistance inducers such as salicylic acid or rhamnolipids can also be formulated together with biocontrol agents to enhance the activity (Freimoser et al. 2019).

Secretion of enzymes – Chitinolytic enzyme secretion was observed with *Aureobasidium, Candida, Debaryomyces, Metschnikowia, Meyerozyma, Pichia, Saccharomyces, Tilletiopsis,* and *Wickerhamomyces.* However, in certain cases, such as *Saccharomycopsis,* chitinase expression requires the presence of prey cells (Freimoser et al. 2019). Chito-oligosaccharides from chitin degradation are potent inducers of plant immune responses (Kombrink et al. 2011, Langner & Gohre 2015, Liu et al. 2012, 2014). *Glucanases Glucans* are a major component in fungal cell walls and exoglucanases are involved in cell wall modification, cell adhesion, and killer toxin resistance (Adams 2004, Jiang et al. 1995, Tsai et al. 2011, Xu et al. 2013). The glucanases activity was observed through overexpression or deletion analyses. The deletion of genes involved in glucanase production significantly reduced the biocontrol activity in certain yeasts such as *Candida oleophila* and *Wickerhamomyces anomalus* (Bar-Shimon et al. 2004, Friel et al. 2007, Grevesse et al. 2003). Exoglucanase activity is directly involved in antagonistic activity (Lopes et al. 2015; Zhang et al. 2011). Proteases are important virulence factors in entomopathogenic fungi. Certain studies have suggested a concentration-dependent inhibitory effect of these pathogens on apple (Banani et al. 2014, Zhang et al. 2012). Protease activity has also been reported in the genera *Metschnikowia, Pichia, and Wickerhamomyces.* The enzymatic activities of the yeast with biocontrol ability were observed in various in vitro experiments. However, the mechanisms are yet to be identified.

Yeast biocontrol agents and products

Candida capable of inhibiting plant pathogens are readily available in natural habitats. *Candida oleophila* was the first commercial biocontrol agent with multiple antifungal activities. Apart from the competition for nutrients and space, secretion of hydrolytic enzymes: proteases, chitinases and glucanases, and VOC production implicated in antifungal activity (Bar-Shimon et al. 2004, Huang et al. 2011, Segal et al. 2002). Furthermore, biofilm formation, high osmotolerance, induction of host resistance, and direct parasitism on the pathogen also contributed to the biocontrol activity of this yeast (Droby & Chalutz 1994, Droby et al. 2002, El Ghaouth et al. 2003, Wisniewski et al. 1995, 2007). The activity of *C. oleophila* can be enhanced with buffers (calcium chloride, bicarbonate), chitosan, or lysozyme (Droby et al. 1998, 2003a, b; El-Ghaouth &Wilson 2002; Scherm et al. 2003; Wilson & El-Ghaouth 2002). *Candida oleophila* strains I-182 was developed under Aspire® and Nexy®, respectively. Nexy® was the first biocontrol yeast registered against a postharvest disease (Wisniewski et al. 2007), and *C. oleophila* strain O has been approved as a plant protection agent in Europe in 2013 (European Commission Health & Consumers Directorate-General 2013; European Food Safety Authority (EFSA) 2015a).

Aureobasidium pullulans strains, DSM 14940 (CF 10) and DSM 14941 (CF 40), are registered against the fireblight disease caused by *Erwinia amylovora* and postharvest diseases (European Food

Safety Authority (EFSA) 2013). Two strains were formulated as a wettable powder under the product name Blossom-Protect® and tested under field conditions at different sites and over several years (Kunz 2004, Kunz & Haug 2006, Kunz et al. 2011, Seibold et al. 2004). These two strains were further developed against postharvest diseases of apple under Boni-Protect® (Weiss & Mögel 2006). They are further used against storage and rot diseases of strawberries; plum and sour cherries are being studied (Holb & Kunz 2013, Weiss et al. 2014). The mode of action involves competition for space and nutrients. However, proteases, chitinases might also be involved (Freimoser et al. 2019).

Antifungal activity of *Metschnikowia* mediated by a range of mechanisms: competition for nutrients, secretion of glucanases and chitinases, and the production of VOCs (Banani et al. 2015, Dhami et al. 2016, Gore-Lloyd et al. 2019, Hershkovitz et al. 2013, Saravanakumar et al. 2008, Sipiczki 2006, Zajc et al. 2019). Inducing the oxidative burst in plant tissues activates the plant's defined responses (Hershkovitz et al. 2012, Macarisin et al. 2010). *Metschnikowia fructicola* isolate NRRL Y-30752 was developed and registered as a biocontrol product for preventing postharvest diseases, particularly in sweet potato and carrot (Eshel et al. 2009, Kurtzman & Droby 2001, Wisniewski & Droby 2012) and approved by the European Food Safety Authority (EFSA) (European Food Safety Authority (EFSA) 2015c, 2017).

Saccharomyces cerevisiae isolate BY4741 shows antifungal activity against filamentous fungi (Hilber-Bodmer et al. 2017). The mycotoxin-removing activity of *S. cerevisiae* is due to adsorption of toxins to cell walls, stress responses to the toxin, as well as transcriptional downregulation of polyketide synthesis (Cubaiu et al. 2012, Oporto et al. 2019). Further, the killer toxin activity, hydrolytic enzymes, as well as VOCs are involved. *Saccharomyces cerevisiae* shows biocontrol activity against soilborne fungal pathogens such as *Fusarium, Rhizoctonia* or *Sclerotium* (Shalaby & ElNady 2008). The comprehensive transcriptome confirmed that strain LAS117 induces the gene expression against fungal attack (De Miccolis Angelini et al. 2019). The registered products are Romeo® and cerevisane® (European Food Safety Authority (EFSA) 2015b). These are used as systemic resistance against powdery and downy mildew in grapes, fruits and vegetables.

With all regards, yeasts are highly effective biocontrol agents for green agriculture. However, studies are needed in broad aspects to understand the mechanisms of their biocontrol activities (Fernandez-San Millan et al. 2024). The biocontrol activities of yeasts are highly strain-specific (Fernandez-San Millan et al. 2023). Further, their behaviour changes drastically from *in vitro* to *in vivo*. The classic experiments, such as dual culture and inhibitory assays, screen the active strains. However, a broader understanding of the mode of action is needed for developing effective and efficient biocontrol products (Fernandez-San Millan et al. 2024). This addresses the requirement of omics-based studies on yeast to develop effective biocontrol products towards green agriculture.

4.5 Entomopathogenic *Beauveria bassiana*, a silver bullet mycopesticide in today's world

Beauveria bassiana: in the Loop

When it comes to the entomopathogenic fungi, no introduction is needed for *Beauveria bassiana* as it is one of the most well-known and frequently recorded fungi with the ability to infect a wide range of insects (over 700 species) along with their cosmopolitan distribution (Xiao et al. 2012, Irsad et al. 2023). *Beauveria bassiana* is an ascomycetous fungus that belongs to Cordycipitaceae (Hypocreales, Sordariomycetes). Eighty-one *Beauveria* epithets are listed in Index Fungorum (August 2025), which is higher than the previously known 25 species (Solano-González et al. 2023). *Beauveria bassiana* was first recognised for its entomopathogenic ability by the Italian scientist Agostinio Bassi in 1835 as the cause of the devastating muscardine disease of silkworms (*Bombyx mori*). In the 1880s, Metchnikoff began working on *Metarhizium anisopliae* against grain beetles and was among the first scientists to suggest the potential for managing insect pests with entomopathogenic fungi (Irsad et al. 2023). Like many other entomopathogenic fungi, *B. bassiana* infects the insects mainly through cuticular penetration (Fig. 11). They produce numerous toxins such as bassianin, bassianolide, beauvericin and analogues, beauverolides, calcium oxalate crystals, oosporein, oxalic acid, and tenellin increase their virulence and speed up the infection (Wang et al. 2021a). However, the exact details of the mechanism of the fungus in destroying the insects are yet to be understood.

Nevertheless, the current understanding of its potential to kill a broad range of crop pests, *Beauveria bassiana,* has been used in agricultural systems in many countries to control pests. As per the latest experimental evidence based on molecular data, it has been recognised that *B. bassiana* encompasses cryptic lineages adapted to specific hosts or ecologies and not exactly the generalist as originally identified with a worldwide distribution (Wang et al. 2022b). In this section, we brief on their potential applicability to controlling pests, current trends in pest control, commercial applications, and challenges yet to be resolved.

Recent studies on Beauveria bassiana in controlling a wide variety of insect pests in agriculture

The application of *Beauveria bassiana* in the current agriculture field is extremely important not only because of its zero or minimum environmental pollution but also for its superior toxicity against a plethora of insect groups, further supplemented with easy application (Wang et al. 2022b). The use of *B. bassiana* is more effective than that of other biocontrol agents like parasitoids (Saito and Buitenhuis, 2024). *Beauveria bassiana* has been reported in its control over the main insect groups, namely, *Coleoptera*, *Diptera*, *Hemiptera*, *Hymenoptera*, and *Lepidoptera* (Singh et al. 2015a). In a most recent study, Sarker et al. (2024) recognised that a new strain AAD16 of *Beauveria bassiana*, can control the Japanese coleopterans. They have isolated the fungus from the Japanese rhinoceros beetle, *Allomyrina dichotoma* (L.) (Coleoptera: Scarabaeidae) and found it to be effective in controlling larvae of *Allomyrina dichotoma*, *Monochamus alternatus,* and *Tenebrio molitor*. Further, Sarker et al. (2024) have compared the biocontrol ability of the new strain of the previously isolated strain ARP14. The results showed that strain AAD16 was superior to the previously isolated strain. Similarly, Zemek et al. (2021) recorded several new native strains that show very positive results in controlling the Colorado potato beetle, *Leptinotarsa decemlineata.*

Aedes notoscriptus (*Diptera*), responsible for causing health issues for livestock animals, was tested with *B. bassiana* by Paris et al. (2023). They have found that the mortality of the adult mosquitoes was four times higher with the application of *B. bassiana*, suggesting a promising future. In another study, Hajek et al. (2023) found that *B. bassiana* was able to control the Invasive hemipteran Spotted Lanternfly, *Lycorma delicatula*. Idrees et al. (2022), López et al. (2022), and Soth et al. (2022) have shown the importance of the use of *B. bassiana* against lepidopteran pests, Fall armyworm (*Spodoptera frugiperda*, *Cydalima perspectalis*), and diamondback moth (*Plutella xylostella*), respectively.

Current study trends

Several studies have also shown the effectiveness of *B. bassiana* together with other biocontrol agents. Wakil et al. (2023) tested *B. bassiana* along with the entomopathogenic nematode, *Steinernema carpocapsae*. The results showed that co-infection shows higher mortality at all exposure intervals than with single treatments over several pests, which include *Cryptolestes ferrugineus*, *Oryzaephilus surinamensis*, *Rhyzopertha dominica*, *Sitophilus oryzae*, *Tribolium castaneum*, and *Trogoderma granarium*. Further, a maximum mortality rate (over 90%) was recorded on *Rhyzopertha dominica* (96.62%) and *Sitophilus oryzae* (90.48%). In contrast, Soth et al. (2022) experimented with the combined application of different *Beauveria species, viz. B. bassiana, B. caledonica, B. malawiensis,* and *B. pseudobassiana,* against *P. xylostella.* They have found that even though the individual strains were of low virulence, the combined applications achieved higher mortality rates by killing the targeted pest faster than the highly virulent combinations and isolates. Further, the combined application of *B. bassiana* with other bacterial pathogens capable of causing diseases on pests has been variously acknowledged (Johnson et al. 2019).

Mao et al. (2023) demonstrated the increase in the biocontrol ability of *Beauveria bassiana* using CRISPR-Cas9-mediated gene editing. They have transformed the fungus with the *get* gene, which plays a role in deactivating 20-hydroxyecdysone. The 20-hydroxyecdysone is a key hormone in insect development, and the results were significant as they observed the transgenic fungus killing more silkworms of 2nd instar larvae than the wild-type with a shorter LT_{50} time. Compared to the wild type, larvae dropped to approximately 20% (day one of the second instar silkworm infection of *B. bassiana*) and 26.4% (day two of the second instar silkworm infection of *B. bassiana*). Further, it showed a higher mortality rate before moulting. Another trend in studies is the potential application of the fungus in controlling pests and other phytopathogenic diseases (Sinno et al. 2021). Several studies have also tested the field survivability and better substrates for the fungus to stay active for the longest duration (Kaiser et al. 2019, Zamora-Avilés et al. 2022, Gu et al. 2023b).

Recent advances in genomics have significantly deepened the understanding of *Beauveria bassiana,* revealing its genetic composition that underlies its ability to infect and kill a wide range of insect hosts. Whole-genome sequencing has identified thousands of genes involved in virulence, including those encoding hydrolytic enzymes such as chitinases, proteases, and lipases that facilitate cuticular penetration. In addition to that, genes responsible for the biosynthesis of potent secondary metabolites like beauvericin, bassianolide, oosporein, and tenellin, which disrupt insect physiology and immune responses, have also been identified. Additionally, surface proteins such as hydrophobins aid in spore adhesion and immune evasion, while stress response genes contribute to fungal resilience under field conditions. Comparative genomic studies have revealed strain-specific variations in these virulence factors, suggesting the existence of cryptic lineages adapted to particular hosts or ecological niches.

This new insight helps in precise strain selection and targeted pest control. These genomic tools not only allow for the development of more effective fungal strains but also enable the integration of multi-omics strategies to better understand host-pathogen interactions.

State of the commercial application

The commercial application of *Beauveria bassiana* runs several decades behind; for example, the Indian Insecticide Act of 1968 has amended its schedule to incorporate *B. bassiana* as a biopesticide for commercial production. This revision was published in the Indian Gazette on March 26, 1999 (Singh et al. 2015a). However, the developments are still taking place, for instance, on 20 July 2017, *B. bassiana* strain 203, a new active substance for bioformulation (under Article 7 of Regulation (EC) No 1107/2009 of the European Parliament and the Council, the rapporteur Member State -RMS, Netherlands) has been approved to be applied (EFSA et al. 2020). Nonetheless, there are plenty of trade names available in the market having *B. bassiana* various strains, e.g., Agronova, Ballve´ria, Bb Moscas, Beauveria JCO, Biostop F, BotaniGard, Bouveriz WP, Bovebio, Bovemax EC, Boveril WP PL63, Daman, Eco-Bb, Granada, Mirabiol, Mycotrol-O, Nativo 2 SC, Racer, Trichobass-L, Trichobass-P, etc (Mascarin & Jaronski 2016).

Challenges

One of the main considerations would be the screening of selected fungal strains to recognise whether they are species-specific or generalists, as some fungal strains could have negative effects on beneficial insects such as honeybees (Omuse et al. 2022). Another challenge in the application of *Beauveria bassiana* would be the reduction of its virulence over time. The virus infections can cause hypovirulence in the fungus, causing resultant decreases in cuticular penetration, growth of hyphae, and toxin metabolism (Zhang et al. 2023). Apart from that, changes in the microclimate, application of other synthetic pesticides and fertilisers, and competition between other associated microflora could impart reductions in efficacy. Overall, accounting, survivability, and stability of the fungus under field conditions are difficult to predict, hindering complete acceptance of its usage in the field (Gu et al. 2023b).

Conclusions

For more than a century, the entomopathogenic fungus *Beauveria bassiana* has been reputed for its biocontrol ability of insect pests. Despite the common drawbacks of using biocontrol agents, *B. bassiana* has been formulated to be applied in commercial farming systems. So far, no considerable negative impacts have been recorded in the use of this fungus. Therefore, along with other benefits, it has been recognised as a better alternative to synthetic pesticides more promising bio-controlling results. Combined application with other biocontrol agents should be considered. Utilisation of modern biotechnological approaches could become more advantageous for the development of more virulent strains. Furthermore, it is required to develop quick and reliable methods to understand the colonisation/spread, survival, and persistence of the fungus after application in the field. This would be essential for the sustenance of biological control in pest management.

4.3 *Metarhizium* species as a microbial pesticide in green agriculture

Metarhizium belongs to Clavicipitaceae in Hypocreales (Sordariomycetes) (Chen et al. 2019, Castrillo & Indexed 2020, Hyde et al. 2024). *Metarhizium* is a well-known entomopathogenic fungus widely used as an alternative to chemical pesticides in agricultural pest management (Driver et al. 2000, Lovett & Leger 2015, Leger & Wang 2020). Approximately, there are over 700 entomopathogenic fungal species representing 90 genera belonging to different major fungal groups of Ascomycota (Roberts & Humber 1981, Leger et al. 2011). Among those 700 species, only 12 have been commercialised, with 34% of them being based on *Metarhizium* species (Sani et al. 2020, de Faria & Wraight, 2007). The most researched and applied species as biopesticides include *M. anisopliae, M. brunneum, M. acridum, M. robertsii,* and *M. rileyi* (Bischoff et al. 2009, Castro et al. 2018, Mongkolsamrit et al. 2020). The host specialisation and environmental adaptability of each *Metarhizium* species are variable (Chen et al. 2017). *Metarhizium* can infect a wide range of insects. For instance, *M. robertsii* is known to infect *Coleoptera* (beetles), *Lepidoptera* (butterflies and moths), *Diptera* (flies), *Hemiptera* (true bugs), and *Orthoptera* (locusts and grasshoppers) (Wen et al. 2015, 2017, Zha et al. 2020). In contrast, some species, such as *M. acridum,* are specialised in infecting only grasshoppers and locusts (Wang et al. 2016a, Chen et al. 2017). Certain strains of *Metarhizium* play a vital role in targeted biological control within sustainable agriculture, contributing to environmentally friendly pest management strategies (Aw & Hue 2017, Zhang et al. 2024). The infection cycle of *Metarhizium* can be categorised into adhesion, germination, appressorium formation, penetration and sporulation (Figure 11) (Fang et al. 2009, Gabarty et al. 2014, Muller et al. 2023). Fungi like *Metarhizium* live in soil near the plant roots and affect other microorganisms. This means that *Metarhizium* not only kill insects, but it also has other important roles in the soil there so they which need elaborating through more research (Liu et al. 2022b, Wei et al. 2022).

Phylogenetic analyses suggest that *Metarhizium* originated from plant roots approximately 300 million years ago, with its pathogenicity against nematodes and insects evolving around 180 million years ago (Gao et al. 2011, Moonjely & Bidochka 2019, Sheng et al. 2022). The potential of bio-pesticides as a biological control agent (BCA) has been recognised for more than a century to reduce the use of chemical pesticides (Hussain et al. 2022, Pednekar & Rajan 2024). Historically, the application of *Metarhizium* as a biocontrol agent against agricultural pests has demonstrated the environmental benefits over synthetic pesticides (Fang et al. 2012, Guo et al. 2024, Chowdhury et al. 2024). The mostly used entomopathogenic fungus is *Metarhizium anisopliae*, which was first discovered by Metschnikoff in 1879 (Metschnikoff 1879). This got its place established as a biocontrol agent in the green pesticide approach (Steinhaus 1956, Zimmermann et al. 1995, Pattemore et al. 2014, Kobmoo et al. 2024). It was demonstrated that *M. anisoplia* infects more than 200 insect species in green agriculture. Most of the studies have reported that *M. anisoplia* has a 90% to 97% mortality rate that causes infection in pests (Zhang et al. 2014b, Wang et al. 2019a). *Metarhizium* species have a dual purpose in which they not only infect the insects but also promote the growth of plants in agricultural environments (Elena et al. 2011). They play a crucial role in biological pest control through the production of mycotoxins, which can effectively reduce pest populations in agricultural areas. (Zhang et al. 2014b, Kepler et al. 2015, Sani et al. 2020).

Metarhizium species are used in a number of formulations, such as sprays and granules, in managing pests that pose threats to crop health (Castro et al. 2018, Sani et al. 2020, Kamga et al. 2022, Liao et al. 2023). Innovative techniques like spray-drying and air-drying are being employed to create stable powder formulations of *M. robertsii*, which exhibit prolonged efficacy under different environmental conditions (Iwanicki et al. 2021). The conidia of *M. rileyi* are now utilised as drones for excellent pest control in large-scale agriculture (Faria et al. 2022). Combining *Metarhizium* with other chemicals or biopesticides has been shown to enhance biocontrol efficacy and overall pest management (Irsad et al. 2023). The infection process of *Metarhizium* begins with fungal spores adhering to the insect's cuticle and secreting enzymes to penetrate it. Subsequently, the spores germinate, penetrate the exoskeleton, and proliferate within the insect, ultimately causing its demise (Figure 11) (Roberts & Leger 2004, Wang & Leger 2007a, Guo et al. 2017).

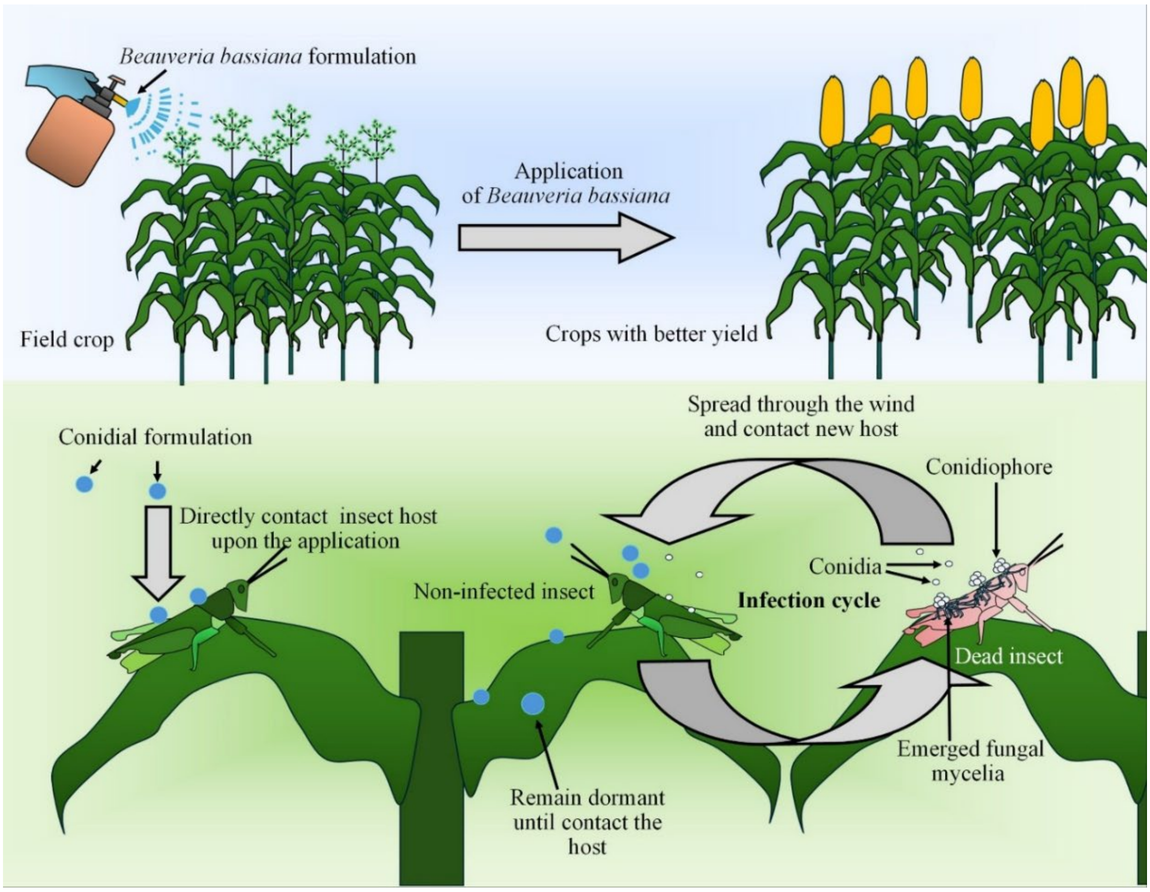

Figure 11 – Application of *Beauveria bassiana* in the control of pests. The fungalus formulations are available as emulsions or wettable powders. The conidia are generally included in the formulations. With the field application, the conidia directly contact insects and start infecting them, causing the death of the insects. The conidiospores emerge from insect cadavers, and the released conidia start to disseminate through the wind, continuing the infection to the new hosts. The control of insect pests in an eco-friendly manner leads to a better-quality harvest (adapted from Mascarin & Jaronski 2016, Ortiz-Urquiza 2021, Pedrini 2022, Ma et al. 2024).

Historical applications of Metarhizium as a biocontrol agent

Metarhizium as a microbial pesticide in green agriculture

Metarhizium species have demonstrated the ability to effectively manage insect pests in sustainable green agriculture, reducing reliance on chemical pesticides and promoting healthier ecosystems and stronger agricultural practices (Fenibo et al. 2022, Yarzábal et al. 2024). Particularly, species like *M. anisopliae* and *M. brunneum* have been utilised to control severe agricultural pests like locusts, beetles, whiteflies, termites, and caterpillars (Yitaferu et al. 2006, Aw & Hue 2017, Francis 2019, Gu et al. 2023a, Ma et al. 2024). *Metarhizium anisopliae* and *M. acridum* are host-specific, killing only the targeted pest without endangering non-target species and can control pest populations in green agriculture (Zhang et al. 2019a, 2023, Du et al. 2024a). *Metarhizium insopliae* ICIPE 18 and M. insopliae ICIPE 20 showed strong pathogenicity against adults of Phthorimaea absoluta (Maingi et al. 2023). *Metarhizium,* when used in conjunction with other biological control agents, can effectively suppress soil pests for extended periods, creating a favourable environment for crops (Zhao et al. 2023a). The combination of *M. acridum* with different weather conditions has shown promise in improving pest control and reducing the need for harmful chemicals (Kamga et al. 2022).

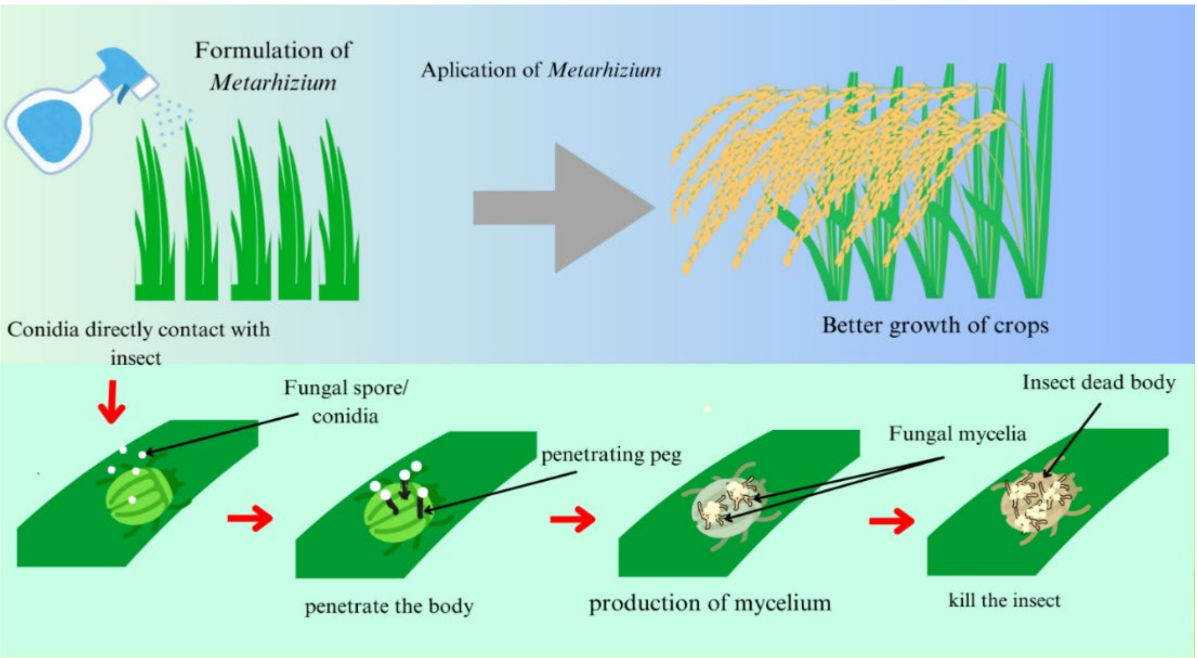

Figure 12 – Application of *Metarhizium* spp. for pest control in agricultural fields**.**

Metarhizium demonstrates high adaptability to various environmental conditions, from tropical to temperate regions, making it an asset in biological control (Rodríguez & Coy-Barrera 2023). Spores of *Metarhizium* are mostly found in undisturbed pasture soil and waiting for a susceptible insect host (Roberts & Leger 2004, Leger 2008). *Metarhizium* could utilise a variety of nutrients with the changing of soil structure (Leger & Wang 2020, Stone & Bidochka 2020, Reingold et al. 2024). *Metarhizium* species survive and withstand high-temperature fluctuation, UV radiation and changing moisture (Liu et al. 2023a, Mishra et al. 2023, Yarzábal et al. 2024). Many studies highlight the potential of *Metarhizium* as a supportable solution for insect pest control in diverse climates (Kamga et al. 2022, Wei et al. 2024).

Current trends of Metarhizium *in commercial application*

Metarhizium is commercially available in the form of spores or fungal conidia, often produced through genetic engineering for enhanced properties (Jaronsk & Mascarin 2017, Sun et al. 2023). These products are used for soil treatment, pest infection, and reducing the use of chemical pesticides (Zhou et al. 2020, Tudi et al. 2021, Nowak et al. 2024). Biotechnological advancements have led to the development of *Metarhizium* strains with rapid killing rates and adaptability to different climates (Guo et al. 2017, Tang et al. 2024). Scientists focus on genetic engineering to modify specific genes that produce insecticidal peptides influencing host immunity, thus improving the virulence of *M. anisopliae* (McGraw & O'neill 2013, Wang 2019c, Lovett 2019, Vidhate et al. 2021, Peng et al. 2022b).

Recent studies have witnessed the utilisation of 68 *Metarhizium* strains as biocontrol agents in several countries (Tupe et al. 2017, Brunner-Mendoza et al. 2019, Villamizar et al. 2021). Furthermore, *M. anisopliae* oil formulations have been shown to reduce fertility and blood feeding in adult malarial vectors, i.e., *Anopheles gambiae* (Shoukat et al. 2020, Peng et al. 2022b). Understanding how pests may develop resistance to fungal infections is crucial for maintaining the effectiveness of *Metarhizium* products over time (Leger & Wang 2020, Tang et al. 2024). To prevent the development of resistance, different strains of *Metarhizium* can be rotated or combined with other control agents (Beys-da-Silva et al. 2020).

Conclusion

Metarhizium is one of the entomopathogenic fungi that provides a clearer understanding of biological pest control. It could efficiently target a wide variety of agricultural pests while minimising harm to non-target species. Through historical application and ongoing genetic research, *Metarhizium* has the potential to become a keystone of Integrated Pest Management strategies. Continuous research and development in genetic and construction advancements will no doubt expand the potential applications of *Metarhizium* in pest management. Its adaptability to various climates and compatibility with other biocontrol agents enhance its utility in sustainable agriculture. However, challenges such as pest resistance and the need for a deeper understanding of host-pathogen interactions must be addressed. Further research must focus on maximising the effectiveness of *Metarhizium* and its lifespan in agro ecosystems for its sustained use, contributing more to the sustainable approaches to pest management in agriculture.

Future perspectives

Metarhizium has great potential for sustainable agriculture through its contribution as an eco-friendly alternative to chemical pesticides, playing a key role in future pest management approaches like Integrated Pest Management (Thakur et al. 2021). The specificity and long-term insect pest control must allow *Metarihzium* to be a perfect contender in the reduction of ecological impact (Hokkanen & Menzler-Hokkanen 2024). Despite its advantages, there are still gaps in our understanding of *Metarhizium*, such as host-pathogen coevolution, the effects of climate change on its efficacy, and its interactions with soil microbiomes (Singh et al. 2015a). Investigating them is needed to improve the adaptability and performance of *Metarihizium* in varied agroecosystems (Dev et al. 2021). Further research is needed to explore modern biotechnological approaches, such as gene transformation, in combination with chemical products and entomopathogens, to enhance the effectiveness of *Metarhizium*.

4.7 *Glomus* species for the biocontrol of plant parasitic nematodes

Plant-parasitic nematodes represent a significant biotic threat to global agriculture, severely limiting crop productivity and threatening food security worldwide (Bernard et al. 2017, Feyisa 2021). These microscopic, worm-like pathogens (Schmitt & Sipes 1998) primarily inhabit soil and cause extensive direct damage by feeding on plant roots and also predisposing plants to secondary infections (Powell 2012). Globally, plant-parasitic nematodes are estimated to reduce crop yields by 12.3%, resulting in annual economic losses of approximately USD 157 billion (Singh et al. 2015b). In light of their devastating impact, developing effective nematode management strategies is important for safeguarding agricultural productivity and ensuring long-term food security.

The traditional method of controlling plant parasitic nematodes has primarily relied upon chemically synthesised nematicides, which pose serious risks to both human health and the environment (Mendoza-de Gives 2022, Ansari & Saleem 2023). Therefore, non-chemical approaches, including crop rotation, fallowing, addition of soil organic amendments, resistant cultivars, and biological control, have been proposed as reduced-risk approaches for managing plant parasitic nematodes (Mendoza-de Gives 2022). With the advancement of green agriculture, biological control has emerged as a promising strategy in plant parasitic nematode management (Mokrini et al. 2024), and several microorganisms are being used as biological control agents in plant parasitic nematode management (Ruanpanun & Chamswarng 2016, Ma et al. 2017, Haarith et al. 2020, Mokrini et al. 2024).

Glomus species stands out as a multifunctional fungal group, representing the predominant and largest genus in the phylum Glomeromycota (Rodrigues & Rodrigues 2020). Members of Glomeromycota are grouped into arbuscular mycorrhizal fungi (AMF) as they establish symbiotic associations with plant roots, forming specific structures known as arbuscules within the plant cells (Parniske 2008). In this section, we discuss how *Glomus* species are utilised in the biocontrol of plant parasitic nematodes, their underlying mechanisms, ecological impact, and economic implications in modern farming, contributing to global food security and sustainable agriculture.

Glomus species used in the biocontrol of plant parasitic nematodes

Several *Glomus* species, including *G. aggregatum*, *G. clarum*, *G. coronatum*, *G. etunicatum*, *G. fasciculatum*, *G. intraradices*, *G. mosseae*, *G. versiforme*, and *G. viscosum,* have been shown to successfully control various plant parasitic nematodes on different hosts (Table 5). Among these, *G. intraradices* and *G. mosseae* are widely utilised in the biocontrol of plant parasitic nematodes. However, the selection of a *Glomus* sp. for nematode biocontrol and its success may depend on the type of nematode, plant species involved, environmental conditions, the time of application, and the duration of exposure to the nematode (Talavera et al. 2001).

Studies have demonstrated that there are differences in the effectiveness of different *Glomus* species on a particular host(s) affected by particular plant parasitic nematodes. For instance, Zhang et al. (2008) showed that *G. mosseae* and *G. versiforme* are more effective than *G. intraradices* in the suppression of *Meloidogyne incognita* on cucumber. Forge et al. (2001) suggested that *G. mosseae* is more effective among *G. aggregatum*, *G. clarum*, *G. etunicatum*, *G. intraradices*, and *G. versiforme* in the biocontrol of *Pratylenchus penetrans* on apple. Also, there are some reports with no or insufficient biocontrol effects of *Glomus* spp. on certain plant parasitic nematodes (Strobel et al. 1982; Elsen et al. 2003a; Rumbos et al. 2006). Considering the timing of application, many studies recommend inoculating the biocontrol agent (*Glomus* sp.) during the nursery stage, before exposure to the plant parasitic nematode in the field (Calvet et al. 2001, Talavera et al. 2001, Castillo et al. 2006). This allows *Glomus* spp. sufficient time to establish within the root cells (Calvet et al. 2001), as they typically require 2-4 weeks to penetrate plant roots, whereas nematodes can penetrate within a few hours (Talavera et al. 2001). Furthermore, it is also crucial to evaluate *Glomus* spp. for their capacity to improve nutrient absorption and promote growth, along with their effectiveness in suppressing nematodes, before recommending them as biocontrol agents (Habte et al. 1999).

Table 5: *Glomus* spp. used in the biocontrol of plant parasitic nematodes on different host plants

***Glomus* species**	**Nematode Species**	**Host plant**	**Reference**
G. aggregatum	*Pratylenchus penetrans*	Apple	Forge et al. (2001)
G. clarum	*P. coffeae*	Coffee	Vaast et al. (1997)
	P. penetrans	Apple	Forge et al. (2001)
G. coronatum	*Meloidogyne incognita*	Tomato	Diedhiou et al. (2003)
G. etunicatum	*P. penetrans*	Apple	Forge et al. (2001)

***Glomus* species**	**Nematode Species**	**Host plant**	**Reference**
G. fasciculatum	*Rotylenchulus reniformis*	Tomato	Sitaramaiah & Sikora (1982)
G. intraradices	*P. penetrans*	Apple	Forge et al. (2001)
	Meloidogyne incognita	Cucumber	Zhang et al. (2008)
	Xiphinema index	Grapevine	Hao et al. (2012)
	M. incognita and *M. javanica*	Olive	Castillo et al. (2006)
	M. javanica	Peach almond hybrid GF-677	Calvet et al. (2001)
	Nacobbus aberrans	Tomato	Lax et al. (2011)
	P. coffeae	Carrot	Elsen et al. (2003c)
G. mosseae	*M. incognita*	Banana	Jaizme-Vega et al. (1997)
	P. coffeae	Banana	Elsen et al. (2003a)
	Radopholus similis	Banana	Elsen et al. (2003b)
	M. incognita and *M. javanica*	Olive	Castillo et al. (2006)
	M. incognita	Tomato	Talavera et al. (2001), Vos et al. (2012a)
	P. penetrans	Tomato	Vos et al. (2012b)
	P. penetrans	Apple	Forge et al. (2001)
G. versiforme	*P. penetrans*	Apple	Forge et al. (2001)
G. viscosum	*M. incognita* and *M. javanica*	Olive	Castillo et al. (2006)

Mechanisms involved in nematode biocontrol of Glomus spp.

Understanding the underlying mechanisms of resistance against plant parasitic nematodes could be utilised to enhance the efficacy of utilising *Glomus* species as biocontrol agents. Four main mechanisms have been identified in the biocontrol of plant parasitic nematodes by AMF, including enhanced plant tolerance, direct competition for nutrients and space, induced systemic resistance, and altered rhizosphere interactions (Schouteden et al. 2015). *Glomus* spp., as a group of AMFs, also employs these mechanisms in nematode biocontrol (Table 5).

Species belonging to *Glomus* can improve host tolerance and enhance plant resistance against nematode infestations. This is an indirect mechanism, achieved by promoting the plant nutritional state (Benedetti et al. 2021) and/or rendering root tissues unfavourable as a food source for plant parasitic nematodes through physiological changes (Calvet et al. 2001). *Glomus* species compete with plant parasitic nematodes for space and nutrients by early establishment within host root cells. The limited space and malnutrition among females reduce the reproduction of plant parasitic nematodes (Talavera et al. 2001). Induced systemic resistance is a plant-mediated response against plant parasitic nematodes, where *Glomus* species induce biochemical changes in the plant, leading to the production of defence compounds and signalling molecules. These changes trigger systemic resistance throughout the plant, reducing its susceptibility to nematode attacks (Elsen et al. 2008, Vos et al. 2012b). During symbiosis, *Glomus* species induce the secretion of specific root exudates that alter the composition of the rhizosphere (Vos et al. 2012c). Some of these exudates negatively impact nematode host-finding behaviour and subsequent root penetration, providing pre-inflectional protection against plant parasitic nematodes (Vos et al. 2012a). The mechanism involved may vary depending on the specific nematode species involved, and the same *Glomus* sp. may exhibit different mechanisms (Table 6).

Table 6: Different mechanisms involved in the nematode biocontrol of *Glomus* spp.

Mechanism		***Glomus* sp.**	**PPN involved**	**Reference**
Enhanced plant tolerance	Improving plant nutrition	*G. intraradices*	*P. vulnus*	Calvet et al. (1995)
	Improving plant growth	*G. intraradices, G. mosseae,* and *G. viscosum*	*M. incognita* and *M. javanica*	Castillo et al. (2006)
	Altering the root morphology	*G. intraradices, G. mosseae and G. etunicatum*	*M. javanica*	Calvet et al. (2001)

Mechanism		***Glomus* sp.**	**PPN involved**	**Reference**
Competition for nutrients and space	Reducing egg production of nematode by limiting available food resources	*G. fasciculatum*	*R. reniformis*	Sitaramaiah & Sikora (1982)
	Suppressing reproduction by competition for penetration and/or nutrient sites.	*G. intraradices*	*P. coffeae*	Elsen et al. (2003c)
Induced systemic resistance	Enhanced transcriptional activity of the class III chitinase gene	*G. versiforme*	*M. incognita*	Li et al. (2006)
	Up-regulation of host genes involved in defence, signal transduction and protein synthesis and modification	*G. mosseae*	*M. incognita*	(Vos et al. 2013)
	Up-regulation of defence-related host genes	*G. intraradices*	*X. index*	Hao et al. (2012)
Altered rhizosphere interactions	Inducing root exudates that negatively affecting nematode host finding and subsequent root penetration	*G. mosseae and G. intraradices*	*R. similis*	Vos et al. (2012a)
	Reduction of root penetration	*G. mosseae*	*M. incognita*	Vos et al. (2012c)

Ecological and economic implications of Glomus spp. in nematode biocontrol in modern farming

In addition to managing plant parasitic nematodes, the use of *Glomus* species offers various ecological benefits by promoting soil health and biodiversity. Glomalin, a soil protein secreted by AMF, originally discovered in soils associated with *Glomus* spp., plays a vital role in soil health by enhancing soil aggregation (Gupta 2020). This improves soil structure, providing a stable environment for microbial communities, enhancing nutrient cycling, and soil fertility (Pal & Pandey, 2014, Hamel 2004). A greenhouse experiment conducted by Siddiqui & Akhtar (2007) demonstrated that better plant parasitic nematode control could be achieved by incorporating *G. mosseae* with organic fertiliser. According to their findings, poultry manure along with *G. mosseae* proved to be the most effective combination in controlling *M. incognita* in tomatoes. Furthermore, biological control using *Glomus* species promotes biodiversity by reducing the need for synthetic nematicides, in general.

Oyekanmi et al. (2007) demonstrated that the use of *G. mosseae* alone or in combination with different biocontrol agents could achieve equal or better control of root-knot nematodes compared to the synthetic nematicide carbofuran. This suggests that *Glomus* species could serve as a cost-effective alternative for nematode control. Commercial bio-fertilisers containing *Glomus* spp. are available in certain countries (Talavera et al. 2001), or farmers can produce their own inocula on-farm, using the trap-culture method (Madhushan et al. 2021). Additionally, as previously mentioned, *Glomus* spp., being a multifunctional group of fungi, offers various benefits to host plants while managing plant parasitic nematode populations. For example, *G. mosseae*, a well-known nematode biocontrol agent, can enhance plant nutrition (Jaizme-Vega et al. 1997) and mitigate soil salinity (Sheng 2008, Al-Khaliel 2010), drought stress (Ruiz-Lozano 1995, Ganjeali 2018), and heavy metal toxicity (Zhang et al. 2006). Therefore, farmers could achieve increased crop yields and profits through enhanced plant productivity and reduced nematode damage. Overall, *Glomus* species exhibit significant potential in managing plant parasitic nematodes across various plant hosts. However, research on *Glomus* spp. for nematode control seems relatively limited in the past decade. Moreover, the potential of *Glomus* spp. in controlling nematodes affecting staple food crops remains largely unexplored. Given the importance of nematode control and the ecological and economic benefits associated with *Glomus* spp., they emerge as promising candidates for integration into sustainable agriculture. This work will inspire further research and commercialisation of *Glomus* spp. for application in green agriculture.

4.7 Fungi against plant viruses and viroids

Plant viruses are obligate pathogens composed of single- or double-stranded RNA or DNA, exhibiting diverse replication strategies, encapsulated within a protein shell, and lacking intrinsic metabolism (Hull 2013). Viroids, in contrast, are exogenous, single-stranded, circular non-coding RNAs (Randles 2003). Currently, around 1,600 plant virus species are recognised, classified into 158 genera and 22 families (ICTV 2023), whereas only 44 viroids have been identified, belonging to two families: Pospiviroidae and Avsunviroidae (Ma et al. 2023). Both viruses and viroids are highly infectious and cause significant yield and quality losses in wild and cultivated plants. Plant viral diseases are estimated to cause global yield losses of 10–15% (Savary et al. 2019), though losses can range from 0% to 100% depending on infection sources, vector dynamics, and environmental conditions (Rao & Reddy 2020). Viruses account for nearly 47% of emerging and re-emerging plant pathogens worldwide (Anderson et al. 2004, Jones 2021). Unlike other pathogens, viruses cannot be cured post-infection, and their spread is often rapid and unpredictable due to vector-dependent transmission (Dietzgen et al. 2016, Dáder et al. 2017, Jia et al. 2018). Thus, plant virus disease management relies on preventive, cultural, genetic, and biotechnological strategies, with biological control emerging as a sustainable alternative, particularly when host resistance or chemical treatments are ineffective (Collinge et al. 2022). In this section, we explore the potential of fungi in mitigating plant virus and viroid diseases.

Emerging plant viruses, including begomoviruses (Geminiviridae), criniviruses (Closteroviridae), tospoviruses (Bunyaviridae), and potyviruses (Potyviridae), pose a growing threat to global agriculture. These pathogens are primarily transmitted by insect vectors such as whiteflies, thrips, and aphids. The spread of plant viruses is accelerated by viral genetic evolution, expanding vector populations, agricultural intensification, and climate change (Navas-Castillo et al. 2011, Tatineni & Hein 2023, Jeger et al. 2023). The whitefly *Bemisia tabaci* is a key vector, transmitting over 400 plant viruses across multiple genera, including *Begomovirus*, *Crinivirus*, and *Torradovirus* (Ghosh & Ghanim 2021, Thesnim et al. 2023). Effective management of *B. tabaci* can be achieved using entomopathogenic fungi (EPF) such as *Ashersonia* spp., *Beauveria bassiana*, *Isaria fumosorosea, Metarhizium anisopliae*, and *Verticillium lecanii* (Wang et al. 2007b, Panyasiri et al. 2007, Borisade 2015, Abdel-Raheem & Lamya 2016, Zhang et al. 2017). Additionally, *Akanthomyces muscarius, B. bassiana, I. javanica,* and *M. brunneum* demonstrate significant potential as biocontrol agents against aphids, inducing high mortality rates, with some strains achieving up to 100% mortality within days of application. Their efficacy stems from direct infection and the action of secondary metabolites with aphid-specific toxicity (Erol et al. 2020, Kang et al. 2018, Kim et al. 2013). Additionally, *I. javanica*, isolated from Q-type *B. tabaci* (the primary vector of tomato yellow leaf curl virus, TYLCV), demonstrated degradation of the TYLCV capsid protein (CP). Fungal fermentation with the virus resulted in higher CP degradation activity in the supernatant than in the precipitate. Furthermore, treatment with *I. javanica* reduced the disease index in tomato plants infected by viruliferous Q-type whiteflies (Sun et al. 2021).

Beyond direct application of fungi for virus vector control, emerging research on antiviral properties of fungi has shown promising results. Several plant viruses, including barley yellow dwarf virus (BYDV), cucumber mosaic virus (CMV), groundnut bud necrosis virus (GBNV), iris yellow spot virus (IYSV), maize chlorotic mottle virus (MCMV), pepper leaf curl virus (PeLCV), potato virus X (PVX), potato virus Y (PVY), sugarcane mosaic virus (SCMV), tobacco mosaic virus (TMV), tomato mosaic virus (ToMV), TYLCV, and zucchini yellow mosaic virus (ZYMV), as well as chrysanthemum stunt viroid (CSVd), have been studied in plant-fungi-virus interactions.

Recent studies have identified diverse fungal-derived compounds with potent antiviral activity against plant viruses, particularly TMV, a major RNA-based plant pathogen. Peptaibols, such as peptavirins A and B from an unidentified fungus (Yun et al. 2000) and *Apiocrea* sp. (Yeo et al. 2002), inhibited TMV infection by 74–79% at 10 µg/mL. Similarly, Hrip1, a hypersensitive response-inducing protein from *Alternaria tenuissima*, triggered systemic acquired resistance against TMV through multi-scale defence signalling (Kulye et al. 2012). Polysaccharides from *Penicillium chrysogenum* (PCPS) and peptidogalactomannan (pGM) from *Cladosporium herbarum* upregulated phenylpropanoid (PAL, 4CL) and pathogenesis-related (*PR-1a*, *PR-2*, *PR-3*, *PR-5*) genes, enhancing TMV resistance (Fu et al. 2020, Montebianco et al. 2020). Trichokonins from *Trichoderma pseudokoningii* (Luo et al. 2010) and glucosylceramides (GlcCer) from *Fusarium oxysporum* (Bernardino et al. 2020) further demonstrated antiviral efficacy by priming PAL, peroxidase (POD), and PR gene expression. Additionally, *P. oxalicum* yielded 2-(4-hydroxybenzoyl) quinazolin-4(3H)-one, a novel anti-TMV compound (Shen et al. 2013). These findings highlight fungi as rich sources of antiviral agents acting via direct inhibition or host defence induction.

Notably, the *pac1* gene, encoding a dsRNA-specific RNase from *Schizosaccharomyces pombe*, has been successfully employed to engineer viral resistance in transgenic plants. Watanabe et al. (1995) first demonstrated its efficacy against ToMV, CMV, and PVY, while Milŏsevíc et al. (2013) extended these findings by conferring resistance to tomato spotted wilt virus (TSWV) in transgenic tobacco and *Impatiens walleriana*. Further expanding its utility, Ogawa et al. (2005) achieved dual resistance against TSWV and CSVd in transgenic chrysanthemum, underscoring the broad-spectrum potential of *pac1*-mediated RNA interference in plant pathogen defence.

Additionally, Elsharkawy (2019) reported that both barley grain inoculum and the cell-free filtrate of *Phoma* sp. effectively reduced CMV severity in *Arabidopsis thaliana* and cucumber plants. Similarly, culture filtrate from *Penicillium simplicissimum* was shown to mitigate CMV infection in *A. thaliana* and tobacco (*Nicotiana tabacum*), correlating with upregulated expression of defence genes in both salicylic acid (SA) and jasmonic acid/ethylene (JA/ET) signalling pathways (Elsharkawy et al. 2012). Marine fungi have also demonstrated antiviral activity, with crude extracts from *P. oxalicum* and *Neosartorya fischeri* exhibiting inhibitory effects against TMV (Shen et al. 2009). These findings collectively underscore the broad-spectrum antiviral capabilities of fungal metabolites, acting through both direct inhibition and host defence priming.

Aspergillus tubingensis from *Brucea javanica* and *Phomopsis* sp.-derived exopolysaccharides as endophytes showed potent anti-TMV activity through metabolite production (Tan et al. 2015, 2017). Vector-mediated viral transmission can also be disrupted, as demonstrated by *Hypocrea lixii* in onion plants, which reduced *Thrips tabaci* populations and IYSV transmission via antixenotic effects and suppressed viral replication (Muvea et al. 2014, 2018). Similarly, *Neotyphodium uncinatum* in meadow ryegrass decreased aphid vectors and BYDV incidence (Lehtonen et al. 2006). Additional studies show that *Paecilomyces variotii* extracts activate salicylic acid (SA)-mediated RNA silencing against PVX and TMV (Peng et al. 2020), while endophytic *B. bassiana* in squash plants reduced ZYMV severity (Jaber & Salem 2014). Collectively, these findings highlight endophytes' multifaceted roles in antiviral defence, spanning direct pathogen inhibition, vector suppression, and host immunity priming.

Studies demonstrate that *Trichoderma* species suppress viral infections through direct antagonism and SR induction. For instance, *T. hamatum* from tomato rhizosphere reduced Tomato Mosaic Virus accumulation by 84.69% while upregulating defence-related genes (*HQT*, *CHS*, *PR-1*, *PR-7*) in infected plants (Abdelkhalek et al. 2022). Similarly, endophytic *T. harzianum*, *T. polysporum*, and *T. atroviride* suppressed PeLCV via SA-mediated SAR and gliotoxin production (Mukherjee et al. 2012, Rochal et al. 2021). Virus-specific effects were observed in maize, where *T. harzianum* and *Metarhizium anisopliae* reduced SCMV titers but not MCMV (Kiarie et al. 2020). Further, *T. harzianum* activates jasmonic acid/ethylene and SA pathways against CMV in tomato (Vitti et al. 2016), while cell-free extracts of T. harzianum, T. *viride*, and *T. longisporum* inhibit TMV in *Nicotiana glutinosa*, with combined acetone-ethyl alcohol extracts showing the highest efficacy (Kolase & Sawant 2007). Collectively, these findings highlight the multifaceted antiviral mechanisms of *Trichoderma*, involving induced resistance, secondary metabolites, and pathogen-specific suppression.

Studies show that mushroom-derived metabolites have direct anti-virus activities. Purified lectin AAL from edible mushroom *Agrocybe aegerita* inhibited TMV infection on *Nicotiana glutinosa* (Sun et al. 2003). Fu et al. (2002, 2003) demonstrated TMV inhibition rates of protein extracts from *Pleurotus citrinopileatus* (50%) and *P. eryngii* (upto 99%). Zhang et al. (2005) showed that polysaccharides from edible fungi (*Flammulina velutipes*, *Lentinula edodes*, and *Pleurotus ostreatus*) inhibited TMV and CMV infecting *Chenopodium amaranticolor,* with the highest inhibition of *P. ostreatus* extracts. An alkaline protein (Y3; Wu et al. 2003) and a polysaccharide (Wu et al. 2007), both purified from *Coprinus comatus*, have been documented to exhibit strong antiviral activity against TMV. Wang et al. (2013) found that sulfated lentinan (sLNT) from *Lentinus edodes* showed stronger dose-dependent antiviral activity against TMV than native LNT, demonstrating that sulfation enhances its efficacy. Sangeetha et al. (2020) evaluated the antiviral activity of culture filtrates from *Coprinopsis cinerea*, *Ganoderma lucidum*, and *Lentinula edodes* in cowpea and tomato plants against GBNV. Among these, G. lucidum demonstrated the most promising inhibitory effects against GBNV infection.

Despite promising laboratory results demonstrating fungal applications against plant viruses, including direct antagonism, bioactive compound extraction, transgenic approaches, and endophytic colonisation, field-scale implementation remains limited, with only entomopathogenic fungi (e.g., *B. bassiana*) seeing widespread use for vector management. Key challenges include incomplete mechanistic understanding modes of action of fungal metabolites (e.g., RNA degradation, immune priming), strain- and host-dependent efficacy (e.g., anti-viral specificity of *Trichoderma harzianum*, Kiarie et al. 2020), and variable endophyte colonisation under environmental stresses. Field performance is further hindered by fungal metabolite instability (e.g., UV sensitivity), lack of scalable production protocols, and undefined non-target effects on ecosystems. Regulatory barriers also impede commercialisation, particularly for transgenic strategies (e.g., pac1 crops, Ogawa et al. 2005). Future priorities include omics-driven discovery of antifungal mechanisms, structural optimisation of compounds (e.g., sulfated lentinan), and combinatorial therapies (e.g., *Trichoderma* + *Penicillium* metabolites) to broaden antiviral spectra. Nano formulations, engineered endophytes, and IPM integration (e.g., Hypocrea lixii for thrips control) could enhance field durability, while public-private partnerships must address regulatory and adoption bottlenecks.

4.8 Fungi against phytoplasmas

Phytoplasmas, a group of cell wall-less, pleomorphic bacteria in the class Mollicutes (Doi et al. 1967, Hogenhout et al. 2008), are destructive plant pathogens that cause significant yield losses in diverse crops globally (Lee et al. 2000, Bertaccini 2007). These obligate parasites colonise exclusively the phloem sieve elements of host plants and are transmitted by phloem-feeding hemipteran vectors, including leafhoppers (Cicadellidae), planthoppers (Fulgoromorpha), and psyllids (Psyllidae) (Weintraub & Beanland 2006, Lee & Davis 1992). Their confinement to the phloem, a tissue inherently resistant to microbial colonisation due to its high turgor pressure, callose deposition, and nutrient composition, limits direct antagonism by endophytic fungi (Lee & Davis 1992). However, the inoculation of endophytic fungi, which asymptomatically colonise plant tissues while often conferring host benefits (Wen et al. 2022), represents a promising biocontrol strategy against phytoplasma diseases.

Endophytic fungi can induce systemic resistance in host plants, enhancing defence mechanisms against phytoplasma infection through structural and biochemical modifications. Notably, callose deposition, a key physical barrier, can restrict pathogen movement within the vascular system. Musetti et al. (2007) demonstrated this phenomenon in *Catharanthus roseus* infected with apple proliferation phytoplasma, where inoculation with *Aureobasidium pullulans* and *Epicoccum nigrum* triggered pronounced callose accumulation and P-protein aggregation in phloem sieve tubes, contrasting with the minimal deposition observed in untreated controls. Further supporting these findings, Musetti et al. (2011) reported that E. *nigrum* treatment significantly alleviated phytoplasma symptoms in *Catharanthus roseus*, restoring normal flower morphology and reducing pathogen titers, as quantified by real-time PCR. These studies collectively highlight the potential of endophytic fungi to mitigate phytoplasma infections through induced host resistance.

Indirect phytoplasma control can be achieved by targeting their insect vectors using entomopathogenic fungi, which parasitise and kill arthropod hosts (Bihal et al. 2023). Moussa et al. (2021) demonstrated this approach by applying spore suspensions of *Beauveria bassiana*, *Isaria fumosorosea*, *Lecanicillium muscarium,* and *Metarhizium anisopliae* to *Hyalesthes obsoletus*

(Hemiptera: Cixiidae), the vector of *Candidatus* Phytoplasma solani, the causative agent of bois noir disease. Among these, *I. fumosorosea* exhibited the highest efficacy, underscoring its potential as a biocontrol agent. Similarly, Görg et al. (2021) reported successful infection of *Cacopsylla* sp. (Hemiptera: Psyllidae), the vector of *Ca*. Phytoplasma mali (causing apple proliferation disease), using *Pandora* sp., further supports the utility of fungal-based vector control. Kernasa et al. (2021) expanded these findings by testing *B. bassiana* and *M. anisopliae* against *Yamatotettix flavovittatus* (Hemiptera: Cicadellidae), a vector of sugarcane white leaf phytoplasma, with *B. bassiana* inducing significantly higher vector mortality. Collectively, these studies highlight entomopathogenic fungi as promising tools for disrupting phytoplasma transmission through vector suppression.

Despite promising advances, critical knowledge gaps hinder the widespread application of fungi for phytoplasma control. Key research limitations include incomplete understanding of endophytic fungal colonisation dynamics in phloem tissue - the exclusive niche of phytoplasmas, unclear mechanisms of localised resistance induction, insufficient field validation of entomopathogenic fungi across diverse agroecological conditions, and unresolved synergies between direct (endophyte-mediated) and indirect (vector-targeting) strategies for integrated disease management. Future research should prioritise multi-omics approaches to elucidate phloem-specific defence priming by endophytes, formulation optimisation for entomopathogenic fungi, combined applications of endophytes and entomopathogens to simultaneously target phytoplasmas and vectors, and assessment of long-term ecological impacts on soil microbiomes and pollinator health to ensure sustainable deployment.

4.9 Fungal herbicides

Weeds can cause a significant threat to agricultural productivity by competing with crops for essential nutrients, ultimately reducing their yield (Scareow 2022, Horvath et al. 2023). When weeds and crops compete for nutrients, crop production declines (Hasanuzzaman 2015). Therefore, controlling weed growth in agricultural areas is essential, and herbicide application has become an important tool in agriculture. There are many ways to manage weeds, and fungi have emerged as an interesting agent that can naturally reduce weed density (Htet et al. 2022). Mycoherbicides are becoming popular as fungal herbicides. Mycoherbicides are formulated from effective fungal agents to manage the growth of weeds (Radi & Banaei-Moghaddam 2020, Golijan et al. 2023, Rengasamy et al. 2023, Kurose et al. 2024). Several fungi have been studied and used as mycoherbicides, including *Alternaria*, *Colletotrichum*, *Fusarium*, *Phoma*, and *Puccinia* (Fauzi 2009, Hebbar et al. 1998, Abdessemed et al. 2021, Rai et al. 2021). Among them, *Colletotrichum* is one such interesting agent (McRae & Stevens 1990*,* Templeton 1992, Boyette et al. 1993, Singh et al. 2010, Masi et al. 2017,2018*,* Xu et al. 2019).

Colletotrichum species as a Mycoherbicide

Colletotrichum was introduced by Corda (1831) and belongs to Glomerellaceae, Glomerellales, Sordariomycetes (Maharachchikumbura et al. 2015). It comprises a diverse group of species (Jayawardena et al. 2021). Members of *Colletotrichum* are plant pathogens causing anthracnose disease in a wide range of host plants, including fruits, vegetables, and ornamental plants (Than et al. 2008, Talhinhas & Baroncelli 2021, Liu et al. 2024). *Colletotrichum* species also exhibit different life modes, which can switch lifestyles (O'Connell et al. 2012). The macroscopic morphology of *Colletotrichum* species can be recognised by the mucilaginous masses of conidia with pink- or salmon-coloured, acervuli associated with anthracnose lesions under humid conditions (Guo et al. 2022, Wu et al. 2023). The microscopic morphology of *Colletotrichum* species is characterised by acervuli producing dark brown setae and hyaline, aseptate conidia that germinate to form appressoria (Lenné et al. 1984, Callan & Carris 2004, Norphanphoun & Hyde 2023). Many studies have focused on *Colletotrichum* species, including plant pathology, fungal ecology, and biotechnology (Damm et al. 2010, De Silva et al. 2017, Chakraborty & Ray 2021, Gupta et al. 2022). A comprehensive understanding of the biology and interactions of *Colletotrichum* species with their hosts can provide an efficient disease control plan for green agriculture (Chakraborty & Ray 2021, Zakaria 2021). Furthermore, investigating the ability of specific *Colletotrichum* strains to biocontrol weeds promotes the development of sustainable weed management strategies (Shi et al. 2021).

Colletotrichum gloeosporioides is one of the important species within the genus *Colletotrichum*. While many strains of *C. gloeosporioides* are known plant pathogens causing anthracnose disease in various crops, certain strains have been explored for their potential as biocontrol agents against weeds (Templeton 1992, Masi et al. 2018, Xu et al. 2019). Three commercial mycoherbicides, BioMal, Collego and Lubao have been developed from *C. gloeosporioides* strains for the biological control of different weeds, viz. *Aeschynomene virginica*, *A. indica*, *Cuscutae australis, C. campestris, Malva pusilla*, *M. palviflora*, and *Sesbania exaltata* (Chakraborty & Ray 2021). Other *Colletotrichum* species, such as *C. dematium*, *C. higginsianum*, *C. orbiculare*, *C. coccodes*, and *C. truncatum*, have also shown potential herbicidal actions against different weeds (McRae & Stevens 1990, Templeton 1992, Boyette et al. 1993, Singh et al. 2010, Masi et al. 2017).

The process for mycoherbicide production involves isolating and cultivating particular strains of fungi that have shown herbicidal effects on targeted weed species (Ellison et al. 2008, Fauzi 2009, Ireland et al. 2019, Anderson et al. 2010, Rengasamy et al. 2023, Kurose et al. 2024). Once these fungi are identified and grown in the laboratory, they can be formulated into products for use in agriculture or environmental contexts (Berestetskiy & Sokornova 2018). However, the process, from selecting the right fungal agents for their application, can be time-consuming (Berestetskiy & Sokornova 2018). *Collectotrichum gloeosporioides* f. sp. *malvae* is an effective agent for controlling round-leaved mallow (*Malva pusilla*) (Wei et al. 1997, Mortensen & Makowsaki 1997, Makowski & Mortensen 1998). Makowski & Mortensen (1998) stated that a major challenge to the development of mycoherbicides is the time and expertise required for the cultivation, storage, and preservation of *Colletotrichum* spores for future use. Even though some *Colletotrichum* species have potential herbicidal activity, there are fewer registered mycoherbicides derived from these species due to the labour and time-intensive process (Chakraborty & Ray 2021).

As traditional chemical herbicides can have harmful effects on ecosystems, human health, and biodiversity, the bioherbicide market is growing in demand (Cox et al. 2000, Ustuner et al. 2020, Brühl and Zaller 2021). However, many factors can slow down the market growth unless technological advancements or improved formulations are developed to address these issues (Boyetchko 2004, Pottinger et al. 2004, Htet et al. 2022, Aneja 2024). The bioherbicide Collego™ is an interesting example of market fluctuations in bioherbicides. It was initially removed from the market due to low commercial demand, reflecting the challenges in gaining widespread adoption for such products at the time (Aneja 2024). However, it was reintroduced in 2006 under the name Lock Down® following renewed interest, driven by the increasing demand for environmentally friendly alternatives and the growing awareness of sustainable agricultural practices (Bailey 2014, Aneja 2024). Mycoherbicide use may increase further if market demand rises. However, there are still several production and shelf-life issues that raise serious questions about the future of mycoherbicides.

5. Circular agriculture and agroforestry

5.1 From waste to wealth: integrating mycelium composites into circular agricultural practices

Why Agriculture Needs a Circular Model

For most of its history, farming has followed a straight-line logic: extract raw materials, turn them into products, then discard what is left (Knickel et al. 2009). This "take–make–waste" pathway has supported economic growth, yet it has also accelerated resource exhaustion, soil erosion, water shortages, and an ever-growing mountain of agricultural refuse (Mukherjee et al. 2019, Kohphaisansombat et al. 2024). A circular economy reverses this logic. It aims to keep resources cycling through the system, capturing their maximum value before nutrients and materials are regenerated (Morseletto 2020). In agriculture, this means closing loops, reducing waste, recycling nutrients, and valorising residues rather than treating them as liabilities (Ellen MacArthur Foundation, 2013). Fungal mycelium, the thread-like network that decomposes organic matter in nature, is emerging as a key enabler of this new paradigm. Modern biotechnology can steer mycelial growth through crop residues, turning low-value waste into high-value, fully bio-based composites

(Talbot et al. 2008, Wattanavichean et al. 2025). This section explains the science behind those materials and shows how they can underpin a genuinely circular farming economy.

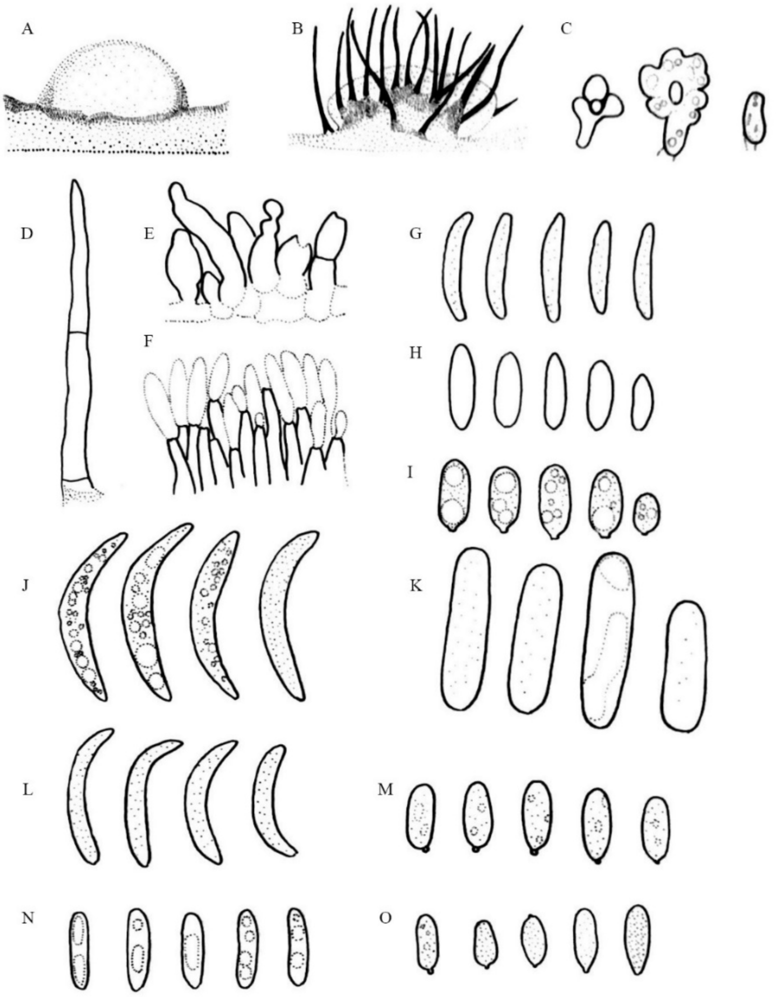

Figure 13 – *Colletotrichum* spp. (redrawn from Marin-Felix et al. 2017). A. Conidiomata of *C. acutatum* (ex-type CBS 112996), B. Conidiomata of *C. destructivum* (ex-type CBS 136228), C. Appressoria of *C. americae-borealis* (CBS 136855), D. Setae of *C. torulosum* (ex-type CBS 128544), E. Conidiogenous cells of *C. Brasiliense* (ex-type CBS 128501), F. Conidiogenous cells of *C. scovillei* (ex-type CBS 126529), G. Conidia of *C. dematium* (ex-type CBS 125.25), H. Conidia of *C. acutatum* (ex-type CBS 112996), I. Conidia of *C. boninense* (ex-type CBS 123755), J. Conidia of *C. graminicola* (ex-epitype CBS 130836). K. Conidia of *C. gigasporum* (ex-type CBS 133266), L. Conidia of *C. truncatum* (ex-type CBS 151.35), M. Conidia of *C. gloeosporiodes* (ex-type CBS 1362999), N. Conidia of *C. destructivum* (ex-type CBS 136228), O. Conidia of *C. orbiculare* (ex-type CBS 570.97).

Agricultural waste: a resource in disguise

The agricultural sector generates vast quantities of organic residues annually, including lignocellulosic crop remains (e.g., straw, stover, husks), animal manures, and agro-industrial by-products such as fruit peels, brewers' spent grain, and pulp waste (Smil 1999, Shah et al. 2017, Van Hung et al. 2020). Rice straw and corn stover alone contribute hundreds of millions of metric tons per year globally, of which a significant fraction is underutilised or improperly disposed of. Standard practices, such as open field burning and landfill disposal not only squander valuable biomass but also release considerable amounts of particulate matter, carbon dioxide (CO_2), methane (CH_4), and other greenhouse gases, thereby exacerbating air pollution and climate change (Raza et al. 2022, IPCC 2019).

Anaerobic degradation of organic matter in unmanaged settings can yield high methane emissions, while nutrient leaching from manure contributes to eutrophication and aquatic ecosystem degradation (Carpenter et al. 1998). The heterogeneous composition and decentralised nature of these waste streams present logistical challenges for valorisation. Nonetheless, their biochemical richness, particularly in cellulose, hemicellulose, and lignin, makes them highly suitable for conversion via microbial or fungal bioprocesses (Broda 1992).

Fungal biotechnology, particularly using filamentous fungi such as *Pleurotus ostreatus* and *Ganoderma lucidum*, has demonstrated strong potential for utilising diverse agricultural wastes as substrates for mycelial growth. Successful examples include valorisation of spent coffee grounds, bamboo residues, sawdust, rice husks, and even problematic biomasses such as *Eichhornia crassipes* (water hyacinth) (Benchaphong et al. 2025, Kohphaisansombat et al. 2024, Sangkawanna et al. 2025). These applications not only divert organic waste from polluting endpoints but also contribute to the production of functional biocomposites with economic and environmental value. Reframing agricultural residues as feedstocks within a circular bioeconomy thus offers a dual benefit: mitigating environmental externalities and fostering sustainable material innovation.

Mycelium composites: the science and the solution

At the core of mycelium-based composites lies the remarkable enzymatic and structural functionality of filamentous fungi. Mycelium, the vegetative growth of fungi, comprises a dense network of hyphae, microscopic filaments capable of penetrating and colonising organic substrates. Through the secretion of extracellular enzymes, these hyphae decompose complex biopolymers into absorbable nutrients (Shakir et al. 2025, Wattanavichean et al. 2025). When cultivated on lignocellulosic agricultural residues, the expanding hyphal network interlocks substrate particles, forming a cohesive, fibrous matrix. This natural, energy-efficient process creates a self-assembling biocomposite, wherein mycelium functions as a biological adhesive that binds the substrate without synthetic binders (Wattanavichean et al. 2025).

The fabrication of mycelium composites follows a relatively simple yet highly adaptable sequence. Initially, lignocellulosic feedstocks such as sawdust, corn stalks, or cotton by-products are cleaned, shredded, and thermally treated to suppress microbial contamination. The substrate is then inoculated with fungal species selected for their robust colonisation and binding capacity, commonly *Ganoderma lucidum* and *Pleurotus ostreatus* (Soh et al. 2021).

Comparative studies have also assessed the performance of species such as *Trichoderma virens* on varied substrate blends, optimising mechanical and morphological outcomes (Benchaphong et al. 2025). Following inoculation, the substrate is shaped in moulds and incubated under controlled environmental conditions to facilitate hyphal proliferation. Once colonisation is complete, the composite is dehydrated, typically via heat treatment, to arrest fungal growth, stabilise form, and improve durability. Incorporation of natural reinforcements such as pineapple leaf fibre further enhances tensile and flexural properties (Kohphaisansombat et al. 2024).

These biocomposites combine low weight with notable structural strength and thermal stability. Critically, they are fully biodegradable, decomposing without leaving persistent waste. Compared to conventional materials such as plastics, foams, or concrete, mycelium composites require substantially lower energy inputs during production, thereby reducing their carbon footprint. Their inherent cellular architecture provides excellent thermal and acoustic insulation, intrinsic fire resistance, and potential for water resistance or buoyancy depending on formulation (Antinori et al. 2020). These multifaceted properties establish mycelium composites as a transformative material class for sustainable manufacturing across diverse sectors.

Applications and impact in circular agriculture

The multifunctionality of mycelium-based composites supports their integration across numerous sectors, reinforcing circular economy frameworks in both agriculture and industry. A key application lies in sustainable packaging. Mycelium foams serve as biodegradable, compostable substitutes for petroleum-derived polymers such as expanded polystyrene, which are environmentally persistent and challenging to recycle (Holt et al. 2012, Yang et al. 2021).

In the built environment, mycelium composites are gaining traction as eco-conscious alternatives to synthetic insulation materials. Their intrinsic thermal and acoustic insulation capabilities, low energy consumption during manufacture, and fire-retardant properties make them suitable for panels, bricks, and architectural components. Their compatibility with digital fabrication and mould-based growth processes enables on-demand, form-specific production, reducing material waste and construction time (Bitting et al. 2022).

The circular value of these materials extends beyond their primary lifecycle. Following composite fabrication, the residual substrate, now enriched with fungal biomass and partially decomposed lignocellulose, can be repurposed as a soil amendment or biofertilizer, enhancing nutrient cycling and soil organic carbon. This integration exemplifies a closed-loop system: agricultural waste fuels composite production, and the spent biomass reinvests into agroecosystems. A notable demonstration includes the development of mycelium-based Thai *krathongs* incorporating embedded plant seeds, which combine cultural relevance with ecological restoration goals (Sangkawanna et al. 2025).

Emerging innovations continue to expand the utility of mycelium materials. These include fungal-based leather analogues (e.g., Mylo™ by Bolt Threads), bio-fabricated textiles, furniture, and sculptural art objects (Amobonye et al. 2023). The modular growth behaviour of mycelium enables customizable designs, facilitating both aesthetic and functional versatility. As research advances and commercialisation accelerates, mycelium technology is transitioning from niche to mainstream, offering a robust platform for low-impact, regenerative material systems across diverse applications (Wattanavichean et al. 2025).

Challenges, opportunities, and outure oerspectives

Despite the clear potential of mycelium composites, several technical and systemic challenges hinder their large-scale deployment. A major limitation is the scalability of production systems. While laboratory and pilot-scale fabrication are well-established, translating these processes to industrial volumes necessitates substantial investment in infrastructure, automation, and process control (Vandelook et al. 2021). Variability in substrate quality, fungal strain physiology, and environmental parameters can result in inconsistent product performance, posing challenges for applications demanding standardised mechanical and physical properties. Additionally, the regulatory landscape for novel biomaterials remains underdeveloped, creating uncertainty around safety, certification, and market access. Public awareness and consumer acceptance are also evolving factors; targeted education and outreach are essential to overcome misconceptions and foster market confidence (Bonenberg et al. 2023, Lewandowska et al. 2024).

Nevertheless, the opportunities presented by mycelium technology are extensive and compelling. Ongoing research into strain selection, metabolic engineering, and substrate optimisation is expanding the functional properties of composites, enhancing durability, water resistance, and tunable biodegradability. Advancements in bioreactor technology, modular growth systems, and decentralised fabrication models are poised to reduce production costs and carbon emissions (Jones et al. 2020). Localised use of region-specific agricultural residues further aligns with circular economy principles by transforming biomass waste into high-value products, thus generating socio-economic benefits at the community level.

Policy interventions will play a critical role in accelerating the adoption of mycelium composites. These include subsidies for sustainable material innovation, tax incentives for bio-based product development, and regulatory frameworks that favour biodegradable alternatives over petrochemical counterparts. Strategic investments in demonstration facilities and public-private partnerships can bridge the gap between R&D and market readiness (Sydor et al. 2022). Cross-sectoral collaboration among farmers, biotechnologists, waste processors, and manufacturers will be key to establishing resilient supply chains and scaling production capacity (Meyer et al. 2020).

In conclusion, mycelium composites represent a transformative material platform capable of addressing urgent environmental and economic challenges. As global awareness of the limitations of linear production systems grows, demand for regenerative, low-carbon materials will intensify. Mycelium-based solutions provide a biologically aligned approach to resource management, converting waste streams into value-added outputs, supporting soil health, and enabling sustainable design. This mycological innovation is not merely a material advancement, but a paradigm shift toward ecological integration and circular economy resilience (Alemu et al. 2022, Abdelhady et al. 2023, Angelova et al. 2021).

5.2 The roles of field mushroom cultivation in circular agriculture

Circular agriculture emerged as a sustainable farming model that aims to maximise resource efficiency, minimise waste, and promote environmental sustainability. Compared with conventional agriculture, which often relies on linear processes with significant waste generation, circular agriculture integrates ecological principles to create closed-loop systems where outputs from one process become input for another (Grimm & Wösten 2018, Haque et al. 2023). This approach is particularly relevant as global agricultural practices adapt to growing resource constraints, environmental degradation, and climate change. Field mushroom cultivation plays an integral role in circular agriculture through dual mechanisms: economically, converting agricultural and organic waste in situ into valuable food resources (Dhiman et al. 2022, Hu et al. 2021); ecologically, it enhances soil ecosystem connectivity via mycelial network expansion, functional microbiome coupling, and environmental adaptation (Adebayo et al. 2014, Hibbett et al. 2000, Ogwu et al. 2025). In this section, we present four distinct field methodologies for mushroom cultivation as case studies, demonstrating their contributions to sustainable food systems and soil productivity (Fig. 14).

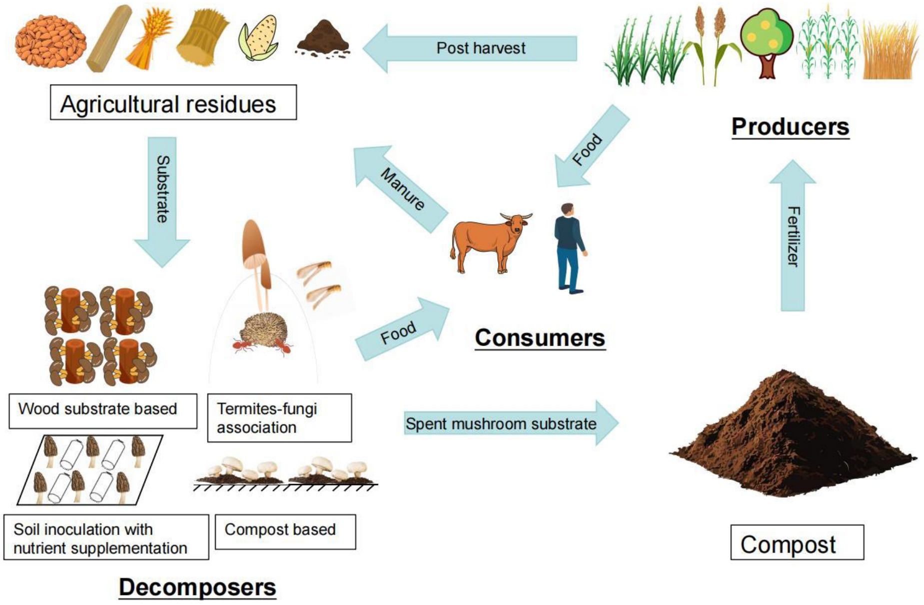

Figure 14 – Field mushroom cultivation in the circular agriculture system.

1. *Compost-based mushroom cultivation*

Compost-based mushroom cultivation gained significant traction in rural communities due to its minimal infrastructure requirements for substrate preparation, sterilisation, and environmental conditions control, while concurrently enhancing the yields in low-input agricultural settings (Bandara et al. 2021). During the composting process, resident microorganisms, particularly bacteria, accelerate the degradation of cellulose, hemicellulose, and lignin, thereby facilitating the efficient absorption of carbon sources by the mushrooms (Guo et al. 2021, Wei et al. 2018). Hu et al. (2021) listed eight species that have been cultivated in fields and facilitate interactions between soil ecosystems and compost through fungal hyphae, viz. *Agaricus bisporus*, *A. subrufescens*, *Coprinopsis cinerea*, *Phallus impudicus*, *Lepista sordida*, *Stropharia rugosoannulata*, *Pleurotus flabellatus*, and *Volvariella volvaceae*.

Among *Agaricus* species, the button mushroom (*A. bisporus*) and almond mushroom (*A. subrufescens*) are the most common species that use compost-based production methods (Dias et al. 2013, Llarena-Hernández et al. 2014, Simsek et al. 2008). The substrate mixture containing wheat straw, rice straw, and poultry manure is prepared in a two-phase fermentation process (I and II). In phase I (PI), the agricultural residue is compiled and watered until it gets enough water content (about 70%), then the microbial activity generates heat up to around 80 °C in the centre of the pile, breaking down carbohydrates and reducing ammonia (Zhang et al. 2019b). During this stage, the metabolic activity of the thermophilic microflora will create a more selective substrate for mycelium colonisation and frequent turning is conducted to ensure even decomposition and aeration. After the compost colour turns brown and a strong smell of ammonia is released, the composting process to a pasteurisation process (phase II, PII). In PII, pasteurisation with around 45–50°C kills pests, pathogens and competitor fungi; also, thermophilic microbes convert extra ammonia into absorbable protein with controlled aeration and temperature regulation (Colmenares-Cruz et al. 2017). Phase II takes about 10 days, ensures better substrate for high yield of mushroom production, and prevents contamination.

After the compost cools to around 25 °C, spawning at a rate of 2%-5% of dry weight is conducted in the field. *Agaricus* species will colonise the substrate in around 15–25 days, and a 2–5cm layer of casing soil is covered to maintain the humidity (to cover the substrate with casing soil soon after spawning, if the climate conditions are not ideal for mycelium growth in the field). After the mycelium colonises the compost (Vos et al. 2017), it impacts the biomass and composition of bacteria in the compost, accompanied by degradation of 50% of the lignin, with an additional decomposition of 15% of the xylan and 10% of the cellulose (Jurak et al. 2015) and shows pesticide residues degradation in soil system (Du et al. 2025). After 30–60 days, the first flush of harvest will appear (Fig. 15a).

2. *Wood substrate-based mushroom cultivation*

Wood substrate-based mushroom cultivation refers to growing mushrooms on a non-composted woody substrate, transforming low-value lignocellulosic waste into nutritious food and soil amendments. *Lentinula edodes* (shiitake) and *Pleurotus citrinopileatus* (golden oyster mushroom) are widely cultivated species around the world, thriving on lignin-rich waste such as wood logs, wood chips and agricultural residues (Royes et al. 2017, Tao & Zheng 2023).

Logs from hardwood tree species such as white birch (*Betula pubescens* Ehrh.), alder (*Alnus incana* (L.) Moench), aspen (*Populus tremula* L.), oak (*Quercus* spp.), beech (*Fagus* spp.), and Hornbeam (*Carpinus* spp.) are cut, drilled, and inoculated with shiitake spawn (Chen et al. 2022). Then the logs are stacked in the shaded, humid forest for 6–12 months for mycelial colonisation. After that, the fruiting occurs after soaking the logs in cold water to induce the primordia. The traditional wood log cultivation for *Lentinula edodes* yields 2–3 flushes per year, for 3–5 years (Fig. 15b). Compared to new-cut wood logs, spent logs are liable to degrade into humus and improve forest soil after mushroom harvest (Wei et al. 2020). Shiitake can selectively degrade lignin and hemicellulose while preserving cellulose (Chen et al. 2022). The spent substrate is composted for urban vegetable gardens or fertiliser for crops, or orchards.

3. *Termites-fungi association for Termitomyces spp.*

The mutualistic relationship between fungus-growing termites (*Macrotermitinae*) and their fungi (*Termitomyces* spp.) drives a sustainable way for highly prized mushroom cultivation. The termite workers construct elaborate mounds with specialised chambers, called a fungal comb, where they cultivate *Termitomyces* spp. With the inoculation of fungal mycelium, worker termites collect and pre-digest plant materials like wood debris, corn straw, and cow dung, creating an ideal nutrient-rich substrate for spores of *Termitomyces* (Pal et al. 2013, Wood & Thomas, 1989). This association allows termites to thrive on indigestible cellulose, while fungal mycelium benefits from a stable and nutritious environment (Gomathi et al. 2019, Schalk et al. 2021).

In practice, cultivating *Termitomyces* spp. by termites offers significant economic and ecological benefits, aligning with circular agricultural principles. To increase the efficiency of *Termitomyces* cultivation, male and female termite alates were matched to generate new termite colonies in the fields that have not been treated with pesticides and built their kingdom, while after the fungal spores or mycelium were inoculated, and the agricultural waste, like corn straw as substrate was gathered by smallholder farmers and put near the termites' mounds. *Termitomyces* convert termite-processed biomass and form the mushrooms, while the metabolic heat and CO2 regulate the microclimate inside the mounds (Wood & Thomas 1989). It takes around 2–3 years for farmers to get fruiting bodies of *Termitomyces* to harvest after a match of termites, inoculation of spores or mycelium, and substrate provision (Fig. 15c)

Smallholder farmers leverage the symbiosis by semi-domesticating termite colonies near villages and obtain a steady supply of highly prized *Termitomyces* mushrooms. During the cultivation process, the termite-fungi system efficiently decomposes and utilises agricultural straw, meanwhile it promotes soil fertility and carbon sequestration to increase crop yield in a dry climate (Evans et al. 2011), as termite mounds enhance nutrient cycling in degraded land and soils (Chen et al. 2023b; Jouquet et al. 2011; Sileshi, 2016).

4. *Soil inoculation with nutrient supplementation for Morchella spp.*

The cultivation of morel mushrooms (*Morchella* spp.) has long been a challenge due to their complex life cycle and symbiotic relationships with soil microbes (Tan et al. 2021). However, the advancements in cultivation techniques based on soil inoculation combined with exogenous nutrient supplementation have revolutionised morel farming, making the cultivation of morels sustainable and fostering the development of circular agriculture (Zhang et al. 2023, Fu et al. 2025).

For the preparation of morel cultivation, a robust strain with mass mycelium production is the basis for the fruiting body formation of the fungus (Liu et al. 2023b). Besides, farmers need to prepare the substrate with fewer competing microorganisms, such as sandy soil (Tan et al. 2021, Zhang et al. 2023). A liquid or grain substrate-based *Morchella* inoculum is then introduced into the soil, often accompanied by nutrient-rich supplements such as wheat bran, rice husk, humus, or specially formulated nutrient bags on the surface of the soil (Fig. 15d), after the mycelium grows onto the soil surface (Tan et al. 2021). The supplements provide the necessary carbohydrates and nitrogen resources to stimulate mycelial growth and primordia formation, triggering more fruiting in the field (Tan et al. 2019, 2021).

The key technique of *Morchella* spp., cultivation is the use of exogenous nutrient bags (Yan et al. 2025). These bags, filled with agricultural waste, were placed onto soil beds when the mycelial growth appears on the soil (Fig. 15d). As the mycelium colonises the substrate, it absorbs the nutrients from these bags and enhances the speed and yield of mushroom production. After the morel harvest, the spent substrate is ploughed back into the soil, improving its structure and fertility for subsequent crops (Pintarič et al. 2024). Soil inoculation and nutrient supplementation offer new opportunities for sustainable agriculture, yielding farmers highly prized mushrooms and enhancing the health of the field ecosystem (Huang et al. 2024a).

5.3 Truffles in agroforestry: a sustainable path for high-value crop production

Edible truffles, as ectomycorrhizal filamentous fungi, play a vital role in forest ecosystems through their symbiotic relationship with a wide range of host trees (Guerin-Laguette 2021). Beyond their ecological importance, truffles have historically been collected from forests as they are a highly valued gourmet food and flavouring item, appreciated worldwide for their unique flavour and aroma (Fan et al. 2022, Lee et al. 2020, Payen et al. 2014). Recent studies have revealed the therapeutic effects of truffles, demonstrating antibacterial, anticancer, anti-inflammatory, antioxidant, cytotoxic, hepatoprotective, and immunomodulatory activities (Khalifa et al. 2019, Lee et al. 2020). Cultivation of truffles was initiated in Europe in the 1970s and, in the last 50 years, has spread to other countries with appropriate climatic conditions (Hall et al. 2017, Zambonelli et al. 2015). Truffieres are a green way to diversify agricultural production and benefit the environment (Fischer et al. 2017). While some large commercial plantations have been established, these require considerable financial resources to develop, and it is common for truffiers (Figure 17) to be small (one-half acre to several acres in the United States) and to complement other agricultural outputs from the area (Benucci et al. 2013, Kaiser & Ernst 2016) .

Figure 15 – Case studies of field mushroom cultivation. a. compost-based cultivation of *Agaricus surufescens*, b. log-cultivation of *Lentinula edodes*, c. termites-fungi association of *Termitomyces* spp., d. Soil inoculation with nutrient supplementation for *Morchella* spp.

The economic value of Truffle cultivation

The most frequently cultivated truffle species are *Tuber aestivum*, *T. borchii*, *T. indicum,* and *T. melanosporum* (Benucci et al. 2013), and success has recently been reported for the most valuable species *T. magnatum,* in Spain (Bach et al. 2021). Among these, *T. melanosporum* is the dominant cultivated species, with reported market prices reaching several thousand Australian dollars per kilogram (Adamo, 2025). Truffles are rich in nutrients (carbohydrates, proteins, fats, minerals, lipids, and amino acids) and contain phenols, terpenes, polysaccharides, and phytosterols (Lee et al. 2020). However, the volatile organic compounds (VOCs) linked to flavour and aroma are the key to their high standing in gastronomy (Lee et al, 2020, Patel et al. 2017). Truffles have traditionally been consumed in salads, pasta, and egg dishes, but value-added products have been developed, including cheese, oils, honey and sauces (Patel 2012, Tejedor-Calvo et al. 2023).

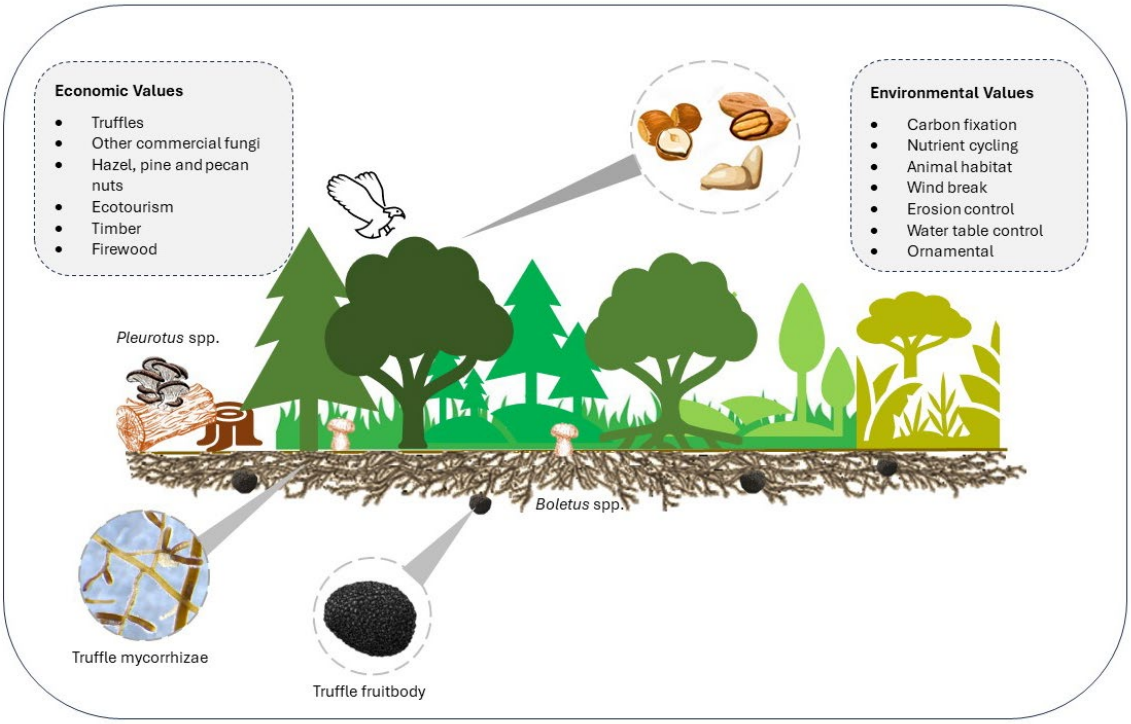

Figure 16 – Case studies of field mushroom cultivation Truffiere: Synergy of mycoforestry and agroforestry.

In addition to the economic return from the truffles themselves, some host species may also produce commercial products that are of environmental value (Table 6). Hazel nuts and pecans are suitable hosts for some truffle species, and their nuts provide an additional income stream. Some softwood species, such as *Pinus* spp., can also be hosts and provide timber and edible seeds (Benucci et al. 2013). Some species are ornamental (De Rigo et al. 2016) or can be harvested for animal fodder (De Rigo et al. 2016, Perevolotsky et al. 1993) or for dye extraction (Deveoglu et al. 2012) without detriment to truffle output.

Ecotourism can be a further financial reward from truffle cultivation. Truffle hunting in natural forests has a long history in many cultures, but in Europe, climate change, soil acidification, overharvesting and poor forest management have made this increasingly difficult (Čejka et al. 2020, García-Montero et al. 2009, Oliach et al. 2021). However, truffle hunting and truffle-tasting experiences in truffieres are growing in popularity (Benucci et al. 2013).

A combination of truffles with other edible or commercially valuable fungi is also possible. There is potential for the concepts of 'myco-forestry' (Thomas & Jump, 2023) to be applied in truffieres, and future research should establish suitable combinations of host species and the mix of truffle species with other commercially valuable mycorrhizal or saprobic fungi, which could assure optimal production of both the host tree and fungi.

The environmental value of Truffle cultivation

Truffiers can contribute to increase tree cover, which is essential to slowing climate change. Host plants and the truffles contribute to carbon sequestration as soil carbon or long-lived woody biomass (Benucci et al. 2013). Truffiers are environmentally friendly as they require little fertiliser. The ectomycorrhizal fungus enhances the availability of limiting nutrients such as nitrogen and phosphorus from the soil to the plant (Zambonelli et al. 2015). In addition, they are generally and relatively pest and disease-free, requiring little in the way of pesticides, fungicides and herbicides compared to other agricultural or horticultural produce (Vishwanathan et al. 2020).

The incorporation of truffle cultivation into a farming system can yield many other ecological benefits. The deep-rooted perennial hosts will help prevent rising water tables resulting from shallow-rooted annual crops such as cereals (George et al. 1999). They enhance the farm landscape, provide windbreaks, help stabilise soil and provide wind and water erosion protection (DeBell, 1990, Benucci et al. 2013,).

A truffiere is not a biodiverse region the volatile compounds that *Tuber* species produce can reduce seed germination and cause root inhibition of other species, resulting in the creation of a virtually vegetation-free brûlé (burnt area) under the host canopy (Tarkka & Piechulla 2007). However, the hosts provide food and shelter for the fauna. Truffles are a food source for humans and many animals, such as rabbits, wild boars, squirrels, mice, armadillos, rat-kangaroos and small marsupials. In natural forests, animals are essential for spore dispersal and truffieres must be fenced to preclude their predation (Benucci et al. 2013, Zambonelli et al. 2015).

Table 6. Truffle (*Tuber* spp.) host plants and their values.

Host species	Food	Timber	Medicinal Value	Host species	Food	Timber	Medicinal Value
Angiosperms				**Gymnosperms**			
Alnus cordata[26]		√[9]		*Abies alba*[13,23]		√[2]	
Betula pendula[23]		√[6]		*Cedrus atlantica*[26]		√[3]	√[3]
Carya illinoinensis[4]	√[4,8]	√[8]		*C. deodara*[26]			√[5]
Castanea sativa[13,23]	√[1]	√[1]	√[1]	*Picea excelsa*[26]			√[7]
Cistus spp.[26]			√[25]	*Pinus armandii*[26]		√[27]	
Corylus avellana[4]	√[4]		√[21]	*P. brutia*[26]			√[24]
C. colurna[26]			√[21]	*P. halepensis*[4]		√[4]	
Populus trichocarpa[4]		√[4,10]		*P. nigra*[4]		√[4]	
Quercus cerris[4]		√[4]		*P. pinaster*[26]		√[20]	√[15]
Q. ilex[4]		√[4]	√[12]	*P. pinea*[4]	√[4]	√[4]	√[24]
Q. petraea[4]		√[4]		*P. strobus*[26]	√[11]		√[11]
Q. pubescens[4]		√[4]		*P. sylvestris*[26]		√[19]	
Q. robur[4]		√[4]		*P. taeda*[4]		√[4]	
Salix alba[26]			√[18]	*Pseudotsuga menziesii*[4]		√[4]	
Tilia cordata[4]		√[4]	√[17]				
T. platyphyllos[4]		√[4]	√[22]				
Ulmus spp.[26]		√[14]	√[16]				

(Aglietti et al. 2022)[1], (Ancuceanu et al. 2023)[2], (Belkacem et al. 2021)[3], (Benucci et al. 2012)[4], (Bisht et al. 2021)[5], (Cameron et al. 1995)[6], (Canillac & Mourey, 2001)[7], (Casales et al. 2018)[8], (Caudullo & Mauri, 2016)[9], (DeBell, 1990)[10], (Gendron et al. 2014)[11], (Güllüce et al. 2004)[12], (Hall et al. 2007)[13], (Han et al. 2019)[14], (Iravani & Zolfaghari, 2011)[15], (Kang et al. 2019)[16], (Kusiak et al. 2022)[17], (Maistro et al. 2019)[18], (Mátyás et al. 2004)[19], (Riesco Muñoz et al. 2014)[20], (Riethmüller et al. 2014)[21], (Selvi, 2020)[22], (Stobbe et al. 2012)[23], (Ulukanli et al. 2014)[24], (Zalegh et al. 2021)[25], (Zambonelli et al. 2016)[26], (Zheng et al. 2017)[27]

Conclusion and future perspectives

The establishment of truffieres or their addition to diversify farm output is a prime example of fungi contributing to green agriculture. The establishment of truffieres is very costly, and several years could elapse before a return can be expected, but the value of truffles far exceeds most other agricultural products. Truffles offer carbon-negative food production, and the host trees provide many ecological and environmental services. In the future, combinations of truffles with other commercially valuable fungi may increase financial returns and could expand the production season.

6. Fungi in agricultural waste management and soil rehabilitation

6.1 Enzyme cocktails derived from *Aspergillus* and *Trichoderma* for biorefinery conversion of agricultural waste

The growing demand for renewable and sustainable energy sources has spurred interest in developing biorefineries that utilise various biomass feedstocks, including agricultural waste. These wastes, such as corn stover, wheat straw, and sugarcane bagasse, are abundant and renewable lignocellulosic biomass sources that can be converted into biofuels, biochemicals, and biomaterials through biochemical conversion processes (Usmani et al. 2021). However, the efficient conversion of lignocellulosic biomass presents significant challenges due to its complex and recalcitrant structure, necessitating the synergistic action of multiple enzymes to break down its major components: cellulose, hemicellulose, and lignin (Abolore et al. 2024). Recently, fungi, particularly the genera *Aspergillus* and *Trichoderma*, have emerged as promising sources of enzyme cocktails for the efficient conversion of agricultural wastes in biorefineries. These fungi are well-known for their ability to produce a diverse array of lignocellulolytic enzymes, including cellulases, hemicellulases, and lignin-degrading enzymes, which work synergistically to degrade the complex plant cell wall components (Intasit et al. 2021).

Lignocellulosic biomass and enzyme requirements

Agricultural wastes, such as corn stover, wheat straw, and sugarcane bagasse, are materials that primarily consist of cellulose, hemicellulose, and lignin, which are tightly bound together in a complex matrix (Blasi et al. 2023). The efficient conversion of lignocellulosic biomass into fermentable sugars requires the synergistic action of multiple enzymes to overcome its recalcitrance and maximise the release of fermentable sugars.

Cellulose and cellulases

Cellulose is the main structural component of plant cell walls and the most abundant renewable biopolymer on Earth. It is a linear polymer composed of D-glucose units linked by β-1,4-glycosidic bonds. The crystalline structure and extensive hydrogen bonding within cellulose fibrils contribute to its recalcitrance and resistance to enzymatic hydrolysis (McNamara et al. 2015). The complete hydrolysis of cellulose requires the synergistic action of three types of cellulases: a) Endoglucanases - these enzymes randomly cleave the internal β-1,4-glycosidic bonds within the amorphous regions of cellulose, creating new chain ends; b) Exoglucanases (cellobiohydrolases) - these enzymes act on the reducing or non-reducing ends of the cellulose chains, progressively releasing cellobiose units; and c) β-glucosidases - these enzymes hydrolyze cellobiose and soluble cellooligosaccharides into glucose monomers, preventing product inhibition of other cellulases. The efficient hydrolysis of cellulose requires the synergistic action of these three enzyme classes, as well as the presence of accessory enzymes that disrupt the crystalline structure of cellulose (Behera et al. 2017).

Hemicellulose and hemicellulases

Hemicellulose is a heteropolymer composed of various sugar monomers, including xylose, arabinose, mannose, galactose, and glucuronic acid. The composition and structure of hemicellulose vary among different plant species, but it is typically composed of a backbone of xylan or mannan decorated with various side chains (Lu et al. 2021). The enzymatic hydrolysis of hemicellulose requires a diverse array of hemicellulases, including; a) Xylanases - these enzymes catalyze the hydrolysis of the xylan backbone by cleaving β-1,4-glycosidic bonds, b) Mannanases: These enzymes hydrolyze the mannan backbone of certain hemicelluloses, and c) Accessory enzymes - these include arabinofuranosidases, xylosidases, glucuronidases, and others that remove side groups and facilitate the complete breakdown of hemicellulose into monomeric sugars. The synergistic action of various hemicellulases is essential for the efficient conversion of hemicellulose into fermentable sugars (Shrivastava et al. 2023).

Lignin and lignin-degrading enzymes

Lignin is a complex aromatic polymer composed of phenylpropanoid units cross-linked in a three-dimensional network. It encrusts and protects the cellulose and hemicellulose components in plant cell walls, contributing significantly to biomass recalcitrance (Shah et al. 2022). The degradation of lignin requires the action of various oxidative enzymes, including; a) Laccases - these copper-containing enzymes catalyze the oxidation of phenolic compounds and can degrade lignin in the presence of mediator compounds, b) Peroxidases - these enzymes, such as lignin peroxidases (LiP) and manganese peroxidases (MnP), catalyze the oxidation of non-phenolic lignin structures through the formation of reactive oxygen species, and c) Auxiliary enzymes - these include oxidoreductases, such as aryl-alcohol oxidases and glyoxal oxidases, which generate hydrogen peroxide required for peroxidase activity (Wang et al. 2018b). The efficient degradation of lignin often requires the synergistic action of multiple lignin-degrading enzymes, as well as the involvement of low-molecular-weight mediators and accessory enzymes (Janusz et al. 2017).

Aspergillus and Trichoderma: potent enzyme producers

The complexity of lignocellulosic biomass necessitates a well-coordinated action of various enzyme classes, including cellulases, hemicellulases, and lignin-degrading enzymes, to overcome the recalcitrance and achieve efficient conversion into fermentable sugars. *Aspergillus* and *Trichoderma* species are known to produce diverse arrays of these enzymes, making them attractive candidates for biorefinery applications. *Aspergillus* species, such as *A. niger*, *A. fumigatus*, and *A. terreus*, are widely studied for their potential in enzyme production. These fungi are known to produce a diverse array of cellulases, hemicellulases, and accessory enzymes, including xylanases, arabinofuranosidases, and feruloyl esterases (Ntana et al. 2020). These enzymes work synergistically to break down the complex polysaccharides present in agricultural wastes. *Aspergillus niger* is particularly noteworthy in its ability to produce high levels of various enzymes, including cellulases, xylanases, amylases, and pectinases (Bakare et al. 2022). This versatility makes *A. niger* a valuable source of enzyme cocktails for biorefinery applications. Additionally, the well-established fermentation technology and genetic tools available for *A. niger* facilitate further optimisation and genetic engineering of enzyme production (Gao et al. 2023).

Trichoderma species, including *T. reesei*, *T. harzianum*, and *T. longibrachiatum*, are prolific producers of cellulases and hemicellulases (Ghadi et al. 2014). *Trichoderma reesei*, in particular, is widely studied and employed for its high cellulolytic activity and ability to secrete a complete set of cellulases, making it a preferred choice for industrial enzyme production (Druzhinina & Kubicek 2017). *Trichoderma reesei* is known to produce high levels of cellobiohydrolases (CBH I and CBH II), endoglucanases (EG I and EG II), and β-glucosidases, which work synergistically to efficiently hydrolyze cellulose (Lee et al. 2022). Additionally, *T. reesei* produces various hemicellulases, including xylanases and mannanases, which contribute to the degradation of hemicellulose in agricultural wastes. Other *Trichoderma* species, such as *T. harzianum* and *T. longibrachiatum*, have also shown promising potential for the production of cellulases, hemicellulases, and lignin-degrading enzymes, further expanding the repertoire of enzyme cocktails available for biorefinery applications (Guigón-López et al. 2014; Guruk & Karaaslan 2020).

The potency of these fungal enzymes lies not only in their own capabilities but also in their synergistic interactions. When combined in a cocktail, enzymes from *Aspergillus* and *Trichoderma* work together to achieve a more comprehensive breakdown of agricultural waste than what could be achieved with enzymes from a single source (Intasit et al. 2021). This synergy enables the efficient conversion of diverse agricultural residues into fermentable sugars and other valuable products.

Advantages of Aspergillus and Trichoderma enzyme cocktails

The enzyme cocktails derived from *Aspergillus* and *Trichoderma* species offer several advantages for biorefinery applications; i) Broad substrate specificity - these fungi can produce enzymes capable of hydrolyzing a wide range of substrates, including cellulose, hemicellulose, and lignin, making them suitable for diverse agricultural waste feedstocks (Blasi et al. 2023), ii) High enzymatic activity and stability - the enzymes produced by these fungi often exhibit high specific activity and stability under harsh conditions, such as elevated temperatures and extreme pH, which are commonly encountered during biomass pretreatment and hydrolysis processes (Dahiya et al. 2024), iii) Cost-effective production - *Aspergillus* and *Trichoderma* species can be cultivated on inexpensive substrates, such as agricultural residues or industrial by-products, reducing the overall cost of enzyme production (Sakhuja et al. 2021), iv) Genetic engineering potential - the genomes of these fungi have been extensively studied, enabling genetic engineering approaches to improve enzyme production, stability, and activity for specific applications (Gao et al. 2023), Synergistic action - the diverse array of enzymes produced by *Aspergillus* and *Trichoderma* species can act synergistically, enhancing the overall efficiency of biomass degradation and sugar release (Intasit et al. 2021).

Biorefinery applications

Enzyme cocktails derived from *Aspergillus* and *Trichoderma* species find applications in various stages of the biorefinery process, including pre-treatment, saccharification, and fermentation. In the pre-treatment stage, lignin-degrading enzymes, such as laccases and peroxidases, can facilitate the removal of lignin, improving the accessibility to cellulose and hemicellulose for subsequent enzymatic hydrolysis (Tiwari et al. 2023). *Aspergillus* species, like *A. niger*, are known to produce significant amounts of these lignin-degrading enzymes, making them valuable for pre-treatment processes (Liu 2021). During saccharification, cellulases and hemicellulases catalyze the breakdown of cellulose and hemicellulose into fermentable sugars, which can be further converted into biofuels (e.g., ethanol, butanol) or other valuable chemicals through fermentation processes (Blasi et al. 2023). The efficient cellulase systems produced by *Trichoderma* species, such as *T. reesei*, are particularly useful for the saccharification of pre-treated biomass (Intasit et al. 2021). Some *Trichoderma* species can also produce enzymes like xylanases and β-glucosidases, which can enhance the efficiency of fermentation processes by removing inhibitors or improving sugar utilisation (Ajijolakewu et al. 2017). Additionally, certain *Aspergillus* species, like *A. niger*, can produce enzymes involved in the degradation of inhibitory compounds, further improving the fermentation process (Cui et al. 2021).

Studies have shown that enzyme cocktails can significantly increase the conversion of pretreated lignocellulosic biomass into fermentable sugars. For instance, research by Florencio et al. (2016) demonstrated that a specifically designed enzyme cocktail from *A. niger* and *T. reesei* achieved saccharification yields of up to 80% from sugarcane bagasse. This translates to a substantial increase in biofuel or bioproduct output per unit of waste processed. Compared to traditional methods that rely on harsh chemicals or high temperatures, enzyme cocktails offer a more sustainable and cost-effective approach. A study by Galbe and Zacchi (2002) estimated that the enzymatic conversion of lignocellulosic biomass to ethanol could be achieved for \$0.30 - \$0.40 per litre, highlighting the economic viability of this technology. Table 7 provides a comparison of the key enzymes produced by *Aspergillus* and *Trichoderma* species and their potential applications in biorefineries.

Enzyme cocktails derived from *Aspergillus* and *Trichoderma* are revolutionising the biorefinery industry, enabling the conversion of agricultural waste into a diverse range of valuable products such as:

1. Biofuel Production: These enzyme cocktails play a critical role in second-generation (2G) bioethanol production. They efficiently break down the complex carbohydrates in agricultural residues like corn stover, sugarcane bagasse, and straw into fermentable sugars. These sugars can then be fermented by microorganisms to produce ethanol, a biofuel alternative to gasoline (Robak & Balcerek 2018).
2. Biogas Production: Anaerobic digestion is a process that converts organic matter into biogas, a mixture of methane and carbon dioxide. However, lignin in agricultural waste hinders the process by limiting microbial access to cellulose. Enzymes from *Aspergillus* and *Trichoderma* can be used for the pre-treatment of the waste. These enzymes break down lignin, making cellulose more accessible to microbes responsible for biogas production, thereby enhancing biogas yields (Kubiak et al. 2023).

3. Production of High-Value Chemicals: Agricultural waste harbours untapped potential for various high-value chemicals. Enzymes from these fungi can be used to deconstruct the waste into specific components. For instance, xylanases can convert xylan in the waste into xylose, a crucial precursor for bioplastics production (Bueno et al. 2023). Additionally, enzymes can be used to unlock fermentable sugars from the waste, which can then be further processed into a variety of bio-based chemicals. This approach offers a sustainable alternative to traditional chemical production methods.
4. Animal Feed Production: Lignocellulosic biomass from agricultural waste can be a potential source of animal feed. However, its complex carbohydrates reduce digestibility. Pre-treatment with the enzymes of *Aspergillus* and *Trichoderma* can enhance the digestibility of the feedstock by breaking down these complex carbohydrates. This leads to improved nutrient utilization and overall feed quality for animals (Liu et al. 2023b).
5. Mushroom Cultivation: Agricultural waste can be used as a substrate for cultivating mushrooms. Pre-treatment with these enzyme cocktails can improve the efficiency of nutrient utilization by mushrooms. This can lead to higher yields and potentially unlock the cultivation of novel types of mushrooms with unique properties (Shankar et al. 2024).

While enzyme cocktails derived from *Aspergillus* and *Trichoderma* species present promising solutions for biorefinery conversion of agricultural waste, several challenges must be addressed to facilitate their widespread adoption and optimise their efficiency. The inherent recalcitrance of lignocellulosic biomass, stemming from the complex and tightly bound structure of cellulose, hemicellulose, and lignin, poses a significant obstacle for enzymatic hydrolysis, necessitating efficient pre-treatment methods and the development of more potent enzyme cocktails. Additionally, the presence of inhibitory compounds such as phenolic compounds, furan derivatives, and organic acids can impede enzyme activity and stability during the biorefinery process, requiring strategies to mitigate enzyme inhibition. Despite the potential for cost-effective production using inexpensive substrates, overall enzyme production costs, including fermentation, downstream processing, and purification, remain a limiting factor for large-scale applications, emphasising the need for optimisation of enzyme production processes and more efficient production systems. Moreover, harsh conditions encountered during biomass pre-treatment and hydrolysis, such as high temperatures, extreme pH, and inhibitor presence, can lead to enzyme inactivation and reduced stability, underscoring the challenge of improving enzyme stability and robustness through protein engineering or immobilisation techniques. Furthermore, while the synergistic action of enzymes is acknowledged, the precise mechanisms and optimal ratios of different enzymes for efficient biomass degradation are not fully understood, highlighting the necessity of further research to tailor enzyme cocktails for specific biomass feedstocks. Looking ahead, advances in genomics and systems biology can aid in the rational design of improved strains and optimised enzyme cocktails, while techniques such as protein engineering and directed evolution offer opportunities to enhance enzymatic performance. Consolidated bioprocessing (CBP), enzyme immobilisation and recycling, and integration with other technologies represent promising avenues for enhancing the efficiency and sustainability of biorefinery systems.

Table 7. The key enzymes produced by *Aspergillus* and *Trichoderma* species and their potential applications in biorefineries.

Feature	***Aspergillus***	***Trichoderma***
Dominant Enzyme Activity	Cellulase, Hemicellulase, Lignin-degrading enzymes (some species)	Cellulase, Hemicellulase, β-glucosidase
Key Species for Biorefinery Applications	*A. niger*, *A. oryzae*, *A. terreus*	*T. reesei*, *T. virgatum*, *T. longibrachiatum*, *T. harzianum*
Target Biorefinery Products	Biofuels (ethanol), Biogas, Bioplastics, High-Value Chemicals, Animal Feed	Biofuels (ethanol), Biogas, Bioplastics, High-Value Chemicals

Feature	*Aspergillus*	*Trichoderma*
Advantages	High production of cellulases and hemicellulases Produces lignin-degrading enzymes (*A. niger*, *A. terreus*) for enhanced pretreatment Generally well-established and cost-effective production	Superior cellulase activity for efficient saccharification Some species produce β-glucosidase for improved sugar utilisation Can contribute to fermentation by degrading inhibitors (some species)
Disadvantages	Lower cellulase activity compared to *Trichoderma* (except *A. niger*) Limited β-glucosidase production in some species	Lower lignin-degrading enzyme production compared to *Aspergillus*
Applications in Biorefinery	Pretreatment and enzymatic hydrolysis for biofuel production May contribute to fermentation by degrading inhibitors (some species) Pretreatment for biogas production Pretreatment for animal feed digestibility Enzyme deconstruction for high-value chemical production	Enzymatic hydrolysis for biofuel production May improve fermentation efficiency by removing inhibitors or utilising specific sugars (some species) Pretreatment for biogas production Enzyme deconstruction for high-value chemical production

6.2 Role of soil fungi in the revegetation of mine-affected lands

The introduction of native mycorrhizal fungi alongside plant seeds accelerates the recovery of diverse vegetation in post-mining environments, aiding in the restoration of ecological balance and supporting plant resilience (Vahter et al. 2020). Studies have shown that mycorrhizal partnerships represent a promising strategy for the successful revegetation and rehabilitation of degraded mine sites. Notable ectomycorrhizal fungi found in mine lands and waste dumps, and heaps are *Cenococcum geophilum*, *Laccaria* spp., *Pisolithus tinctorius*, *Suillus* spp., *Thelephora terrestris*, and *Inocybe* spp. These fungi help rehabilitate disturbed soils by promoting nutrient uptake and enhancing soil structure (Danielson, 1985). In addition, VAM species commonly found on mine grounds include *Acaulospora laevis*, *Glomus* spp., *Scutellospora gregaria* and *Scutellospora pellucida*.

Rhizophagus irregularis, an arbuscular mycorrhizal fungus, which enhances the resistance of *Sophora viciifolia* to arsenic, supporting plant growth in mining-affected areas by improving stress tolerance mechanisms (Zhang et al. 2022). However, in post-mining soils, *R. intraradices* significantly reduces both above and belowground plant biomass and microbial respiration, affecting plant community formation in disturbed environments (Ardestani et al. 2019). Additionally, this species also aids in the phytoremediation of lead-contaminated soils, promoting lead uptake in *Parkinsonia aculeata* (Gonzalez-Villalobos et al. 2021). *Glomus* species could improve nitrogen and mineral uptake under stress conditions (He et al. 2017, Abdelhameid et al. 2020). *Glomus macrocarpum* has been reported as a dominant species that supplies essential nutrients and water, although its limited diversity indicates ongoing disturbance in mines (Borges et al. 2014). In addition, *G. etunicatum* and *G. versiforme*, have shown enhanced plant growth, nitrogen uptake, and heavy metal tolerance in coal mine spoil banks (Zhao et al. 2013). Furthermore, it has been shown that *Glomus* spp. can improve sunflower growth and copper accumulation in Cu-contaminated soils (Castañón-Silva et al. 2013) and increase phytoremediation efficiency while reducing lead toxicity in *Hyoscyamus niger* (Karimi et al. 2013). Additionally, they enhance mycorrhizal colonisation, critical for seedling establishment in disturbed mine sites (Vézina et al. 2012), and *Glomus intraradices* supports *Tagetes erecta* growth in chromium-contaminated soils (Wartanto et al. 2020).

Various soil fungi have shown remarkable applications in post-mining environments. *Pisolithus tinctorius* enhances plant growth in contaminated soils, showing high copper tolerance, which aids in nutrient accumulation and heavy metal phytostabilisation (Wen et al. 2017). Additionally, *P. tinctorius* inoculation reduces leaf temperature, improves water availability, and strengthens plant defence mechanisms under water stress, making it a promising option for dry land restoration programmes (Lorente et al. 2021). *Cenococcum geophilum* is another example of revegetation of mining-affected has tolerance of cadmium (Cd), making it an asset in phytoremediation and ecological rebuilding in contaminated regions (Peter et al. 2016, Shi et al. 2022). This species also reportedly improves soil phytoremediation by promoting plant growth and metal absorption, particularly in copper-contaminated soils, further contributing to effective revegetation (Wen et al. 2017). In post-coal mining sites, *Acaulospora mellea* (*Acaulosporaceae*) is crucial for nutrient uptake, plant growth, and soil adaptability, enhancing plant tolerance to harsh conditions and aiding revegetation efforts (Wulandari et al. 2024). As a major genus of Arbuscular Mycorrhizal Fungi, *Acaulospora* sp. significantly contributes to the revegetation of mining-affected areas by promoting plant growth and ecosystem restoration (Salim et al. 2019). *Gigaspora margarita* is another example which enhances host plant resistance to mercury and nutrient accumulation (Ekamawanti et al. 2014). It is a promising option for phytoremediation, particularly in heavy metal-contaminated soils and mine tailings, due to its potential for lead remediation (Ferrer et al. 2022).

Considering the plant factors, *Acacia mangium*, *Mimosa caesalpiniaefolia*, and *Schinus terebinthifolia*, which respond well to mycorrhizal inoculation, organic compost, and thermophosphate, are excellent for afforestation in mining regions (Mendes et al. 2010, Yang et al. 2015). Similarly, *Imperata cylindrica*, when associated with AMF, shows enhanced eco-physiological traits in mining areas, aiding in ecological restoration and improving soil conditions (Jia et al. 2023). Bi et al. (2018) demonstrated that AMF-containing plants exhibit better growth, root development, and soil quality improvement, making them appropriate for afforestation in mining sites. AMF plants contribute to forming plant communities and soil recovery processes, which is beneficial for afforestation in mining regions (Teixeira et al. 2017). In nickel post-mine land studies, AMF plants are highlighted for their symbiotic connections that support plant growth under challenging soil conditions (Prayudyaningsih et al. 2019). Moreover, AMF-associated plants are advantageous for afforestation in mining-affected areas as they can thrive in phosphate-rich soils, aiding ecosystem restoration (Ducousso-Détrez et al. 2012). They also enhance soil enzyme activity and carbon sequestration in reclaimed mine soils, contributing significantly to ecological restoration efforts (Qian et al. 2012). Mycorrhizae are often absent in mining-affected sites with low nutrient levels, causing delays in vegetative community establishment. Inoculating these sites with mycorrhizae can enhance productivity by improving interactions with native plant species used in revegetation and accelerate the recovery of mine waste areas.

5. Application of fungi in livestock and aquaculture

Beyond their conventional roles in soil fertility and biocontrol, fungi are demonstrating novel and unexpected potential across various facets of agriculture. These include sustainable livestock feed, methane mitigation, disease control, and aquaculture enhancement. This section explores the expanding frontier of fungal applications in agricultural systems, supported by recent research and commercial innovations.

Fungal applications in livestock

Fungal mycoproteins offer a promising alternative to conventional protein sources like soy and fishmeal. These conventional animal-feeding sources are associated with deforestation, overfishing, and high carbon footprints. *Fusarium venenatum*, used in Quorn™, is a well-known fungal protein source that yields a protein content of 40–50%, exceeding that of soybean (30–40%). This species can be cultivated on agricultural waste products such as wheat straw and molasses in bioreactors, enabling a circular and sustainable feed system. Several companies are pioneering fungal protein production for animal feed: Deep Branch (UK) produces *Proton*™, a single-cell protein derived from *Fusarium* species using captured CO_2. Calysta (USA) manufactures *FeedKind*®, a protein derived from methane-utilising microbes. Unibio (Denmark) generates *Uniprotein*® from natural gas for use in aquaculture. In addition to mycoproteins, residual biomass from mushroom cultivation (e.g., *Pleurotus* and *Lentinula* spp.) has been used as a fibre-rich feed additive. Canadian farms report cost reductions of 15–20% when incorporating mushroom substrate residues into cattle feed.

Fungi contribute to livestock health by enhancing gut function and reducing dependence on antibiotics. *Saccharomyces cerevisiae* has demonstrated efficacy in improving digestion and nutrient uptake in ruminants, pigs, and poultry (Sampath et al. 2021, Hoque et al. 2021, Comi et al. 2025). Serval studied has found that dairy cows supplemented with *S. cerevisiae* produced more milk and had a lower incidence of acidosis (Desnoyers et al 2021, Sun et al. 2021, Xiang et al. 2025). Additionally, yeast-derived beta-glucans have shown immunomodulatory effects For example, For example, a *Saccharomyces cerevisiae*-derived postbiotic significantly reduced *Salmonella enterica* prevalence and load in broiler ceca in a commercial farm study, and multi-species probiotic supplementation has been shown to lower cecal *Salmonella* detection relative to untreated group (Neveling et al. 2020, Chaney et al. 2022, Shaji et al 2023). Commercial products such as Diamond V's fermented yeast extracts and Alltech's *Yea-Sacc®* are widely used in the USA. In aquaculture, *Cordyceps militaris* spent mushroom substrate has used as in-feed antibiotics in *Labeo rohita* to *Aeromonas hydrophila* (Devi et al. 2024).

Certain fungi exhibit strong antiparasitic properties. *Duddingtonia flagrans*, a nematode-trapping fungus, has been incorporated into livestock diets. Its spores pass through the digestive tract and germinate in manure, where they capture and kill nematode larvae (Larsen 2000). Field trials indicated a reduction in parasitic load in sheep (Paraud et al. 2018). BioWorma®, a commercial product based on *D. flagrans*, is now used in Australia and New Zealand, reportedly reducing chemical dewormer use.

Livestock, particularly ruminants, are major contributors to anthropogenic methane emissions. On average, a cow emits 150–200 litres of methane per day. To address this, research has focused on dietary interventions involving fungi and other microbial additives. *Asparagopsis taxiformis*, a red macroalga, when included in cattle feed, has been shown to reduce enteric methane emissions without affecting milk yield (Roque et al. 2021). Companies like FutureFeed (Australia) and Symbrosia (USA) are commercialising Asparagopsis-based feed products. Anaerobic gut fungi such as *Neocallimastix frontalis* have shown promise in enhancing fiber digestion while influencing methane emissions in ruminants (Wei et al. 2022, Kovács et al. 2025).

Fungal applications in aquaculture

Fungal products are also being adopted in aquaculture systems to enhance growth and disease resistance. *Saccharomyces cerevisiae* and *Aspergillus oryzae* are commonly added to aquafeed, with reported improvements in fish growth rates and immunity. Several studies have shown that the incorporation of *Aspergillus oryzae*-fermented feed increased tilapia growth over fishmeal-based diets (Dawood et al. 2020, Ismail et al. 2021). *Saccharomyces cerevisiae* supplementation has been shown to enhance disease resistance in shrimp and tilapia (Novozymes, Denmark). In aquaculture water remediation, *Aspergillus niger* has been utilised to reduce ammonia and nitrate levels, improving water quality in fishponds (Dawood et al. 2020). Vietnamese shrimp farms have incorporated fungal-treated water systems to prevent disease outbreaks.

Certain fungi, particularly chytrids, have demonstrated the ability to parasitise and control harmful algal blooms, including cyanobacteria. This offers a biological alternative to chemical algaecides such as copper sulfate. While still experimental, fungal "algaecides" hold promise for the sustainable management of freshwater aquaculture systems. The integration of fungi into livestock and aquaculture systems presents a sustainable pathway to improve feed efficiency, reduce environmental impact, and promote animal health. Key advances include that mycoprotein replacing soy and fishmeal with equal or superior performance (Macusi et al. 2023, Madhulika et al. 2025), Yeast probiotics reducing antibiotic use and improving growth metrics, Methane reduction through fungal feed additives and gut-modulating fungi, Fungal bioremediation for aquaculture water quality and disease control.

However, challenges remain in terms of long-term safety, regulatory approval (especially for genetically modified strains), and economic scalability. Despite these hurdles, fungi are poised to play a pivotal role in the future of sustainable agriculture.

7. Emerging applications of fungi in agricultural practices

As a sustainable agricultural practice, bio-fumigation utilises natural compounds to control soil-borne threats (Srivastava & Ghatak 2017, Ziedan 2022). *Brassicaceae* plants such as mustard and radish have been used as traditional biofumigants (Santos et al. 2020, Baysal-Gurel et al 2020). These plants produce isothiocyanates during decomposition, which act as natural fumigants with pesticidal properties (Szczygłowska et al. 2011, Baysal-Gurel et al 2020). In recent years, fungi have emerged as potent bio-fumigating agents. *Muscodor albus* (*Xylariaceae*, Sordariomycetes) is an ascomycetous fungus isolated initially as an endophyte from *Cinnamomum zeylanicum* in Honduras (Samarakoon et al. 2020, Hyde et al. 2024). This species produces a wide range of antimicrobial volatile organic compounds (VOCs) (Strobel 2006, Saxena & Strobel 2021). Additionally, *Trichoderma* spp. are known to produce similar VOCs, making fungal bio-fumigation a promising, eco-friendly alternative to chemical fumigants; i.e. *T. afroharzianum* against *Fusarium* infections in fresh chillies (Khruengsai et al 2021), control damping-off of *Pinus radiata* caused by *Fusarium* (Morales-Rodríguez et al. 2018), and Galletti et al. (2008) found that when *Brassica carinata* seed meal was combined with *Trichoderma,* it resulted in more efficient control of *Pythium ultimum.*

Several fungal species have also been used to remove pollutants from water through enzymatic degradation and biosorption. For example, *Stropharia rugosoannulata* has been employed to filter *E. coli* from stormwater (Thomas et al 2009, Taylor et al. 2015, Sen et al. 2023). *Pleurotus* species have been used to remove textile dyes and phenolic compounds (Kunjadia et al. 2016, Kumar et al. 2022), while *Ganoderma* species have shown potential in degrading petroleum hydrocarbons (Mohammadi-Sichani et al. 2019, Torres-Farradá et al. 2019). Furthermore, mycelium has been integrated into engineered frameworks such as filter beds and floating rafts to create myco-remediation units, designed to treat contaminated soil and water (Rosa 2021, Buratti 2024). For instance, floating myco-rafts have been developed for nutrient and pathogen removal in wetlands (Grosshans et al. 2019, Huth et al. 2021, Sen et al. 2023), straw bale myco-barriers are used in Oregon forests to intercept logging runoff (Grosshans et al. 2019, Sen et al. 2023), and myco-reactors are being trialled in South America to treat mine-polluted water (Hu et al. 2020). These small-scale, but low-cost applications offer valuable contributions to ecosystem restoration.

In addition, fungi are being utilised to develop biodegradable agricultural materials. Potential has been shown that common fungal genera such as *Agaricus*, *Cyclocybe*, *Fomitopsis*, *Ganoderma*, *Pleurotus*, *Phaeolus*, *Piptoporus*, *Polyporus*, *Pycnoporus*, and *Trametes* could be used to develop mycelium composites as eco-friendly alternatives to plastic mulch and packaging (Aiduang et al. 2022). *Trichoderma harzianum* seed coating has been used in India and Israel to enhance disease resistance and seedling vigour (Kumar et al. 2015, Vijaykumar 2023, Chandrika et al. 2024).

6. CRISPR gene editing in sustainable agriculture: future and challenges

Genome editing is an important aspect of fungal biotechnology as it allows the introduction of desirable traits or the removal of unwanted traits, providing a distinct advantage in the ever-changing landscape of agriculture and food production in a world impacted by increasing food demand, climate change, and escalating environmental challenges. Among the vast applications of genome editing are plants gaining disease resistance, increased yield, and adaptability to diverse climates, and reduced reliance on agrochemicals by introducing superior biocontrol agents, which open avenues for sustainable agricultural practices. There are many tools introduced and being introduced where genome editing has provided promising results for a sustainable and greener future. One such tool is the CRISPR/Cas system, a modified version of an adaptive immune mechanism in prokaryotes.

CRISPR (Clustered Regularly Interspaced Short Palindromic Repeats)/Cas (CRISPR-associated nuclease) technology allows for precise, efficient, and multiplexed gene editing in eukaryotic organisms, including fungi (Song et al. 2019, Liao et al. 2022). The integration of CRISPR-Cas gene editing into fungi is a revolutionary toolkit for advancing fungal biotechnology. CRISPR-Cas gene facilitates targeted gene modification, which will help the rapid development of improved traits for biocontrol, nutrient cycling, protein production, and stress resilience (Liao et al. 2022; Wang et al. 2022c, KhokharVoytas et al. 2023). In this section, we are discussing potential applications, regulatory, and socio-economic challenges while using CRISPR-edited fungi in sustainable agriculture.

The CRISPR/Cas system is highly versatile, enabling it to be used in many ways to confer immunity and resistance against important pathogenic fungi in a relatively sustainable manner. The introduction of avirulent mutants of important fungal pathogens created using CRISPR/Cas to compete with the pathogenic fungi in the field, while priming the plant against them, has been conducted for many important phytopathogenic fungi (Harishchandra et al. 2021). Additionally, enhanced biocontrol capabilities are observed in CRISPR/Cas edited fungi when genes in specific metabolic pathways were targeted (Muñoz et al. 2019). With CRISPR-Cas gene editing, genes of important fungal species associated with biological control, such as *Trichoderma*, *Beauveria*, and *Metarhizium* species, could improve antagonistic activities, enhance rhizosphere colonisation, and prolong survival under field conditions (Mukherjee et al. 2012). As given in the previous sections, *Fusarium venenatum* has been modified via CRISPR to optimise amino acid biosynthesis and to increase biomass productivity, which facilitates the use of *F. venenatum* as mycoprotein, an alternative to soy or fishmeal (Finnigan et al. 2019). CRISPR can also be used to knock out or activate genes that are responsible for the synthesis of important biochemicals such as antibiotics, siderophores, or mycotoxin suppressors in beneficial fungi such as *Aspergillus* and *Penicillium*. With the increasing temperature and climate change, stress tolerance and resilience are important aspects of green agriculture. Thus, with the help of CRISPR-Cas gene editing, it is possible to engineer fungi to withstand pH, salinity, temperature, and other extreme environmental conditions that can be successfully used as biocontrol agents in drought-prone and stressed agroecosystems where successful biocontrol is relatively difficult.

Furthermore, CRISPR could be used as a rapid, field-deployable detection system. Wang et al. (2025) have used CRISPR/Cas12a to develop a rapid detection tool for Grapevine Botryosphaeria Dieback. In this study, the authors have integrated Recombinase Polymerase Amplification (RPA), CRISPR/Cas12a, and Lateral Flow Dipstick (LFD) technology. This assay could be completed in less than 60 minutes, is highly sensitive as it could detect as little as 1 pg/mL DNA and is very specific while making it a powerful tool for early pathogen detection and management in vineyards.

Even though this gene editing sounds fascinating and has potential, applications of bioengineered fungi still face multiple hurdles. We are far behind and stuck with regulations and policy barriers. Countries that derive policies from process-based regulation (e.g., EU) consider CRISPR/Cas edited organisms as GMOs while countries the derive policies from product-based regulation (e.g., Argentina, Australia, Brazil, Japan, South America USA) do not consider them as GMOs if the final product does not contain foreign DNA and mimics natural variation (Ahmad et al. 2023). Some countries (Brazil and USA) treat certain CRISPR-edited organisms differently from GMOs, yet the EU has a strong opinion regarding GMOs (Eckerstorfer et al. 2019). Nevertheless, in China, CRISPR-edited organisms are linked with the misconception of perceived similarity to GMOs by the public. This is affecting the adoption of CRISPR in the agri-food sector, especially in organic or sustainable food systems.

Apart from barriers at the policy level, fungi also show their barriers to CRISPR editing. The most important phytopathogenic genera, *Alternaria*, *Colletotrichum*, *Fusarium* and others, are difficult to transform or regenerate. Even though CRISPR is the most precise gene-editing tool so far, it has also shown unintended off-target mutations, which could affect the stability, efficacy, and safety (Zhang,2021). Another limiting factor in gene editing is the limited genomic resources and annotation. For most of the non-model phytopathogenic fungi, quality genome resources are limited. This can slow down gene editing and their functional validation (Idnurm & Meyer 2018).

Potentially, more advanced genome editing tools such as CRISPR/Cas12 and CRISPR/Cas13 can be used for precision gene editing to overcome some challenges faced by the CRISPR/Cas9 system, which offers distinct advantages over the traditional CRISPR/Cas9 system. Cas12 can create staggered double-strand breaks, which may improve the efficiency of homology-directed repair (HDR) when integrating donor DNA, potentially leading to more precise edits (Shen et al. 2024, Hassane et al. 2025).

Overcoming these challenges is not an easy task, yet it is a possibility. To overcome technical challenges of CRISPR variants, such as base editors, and CRISPRi/a systems could be used to reduce off-target effects. This will allow gene regulation without DNA cleavage. CRISPR gene editing has the potential to revolutionise sustainable agriculture, yet lots of challenges remain to be addressed. These challenges could only be overcome with interdisciplinary research, policy development and public engagement.

9. Smart farming with AI: transforming agriculture for a greener, and sustainable future

The agricultural sector is under immense pressure to meet the rising global food demand, exacerbated by the continuous growth of the human population, exponential environmental changes and negative environmental impacts from conventional farming (Tilman et al. 2011, Tudi et al. 2021, Biswas et al. 2025). To reduce the impact of these factors, innovatively and sustainably improving the efficiency of farming practices is crucial (Sood et al. 2024). The integration of artificial intelligence (AI) in agriculture, incorporating aspects of machine learning, deep learning, remote sensing, and predictive analytics, has been on the rise over the last few years (Bhagat et al. 2022). The main reason for this shift is the information-based transformative solutions provided to address the most pressing challenges in agricultural production. The data and information analysed by AI can be used to reduce the environmental impact by reducing water, fertiliser, and pesticide consumption while increasing productivity (Lakshmi et al. 2020, Getahun et al 2024). The information processed by AI technologies can also help optimise resource use and build greater resilience to climate change (Chen et al. 2023b, Rane et al. 2024). The use of these technologies has reduced the risk of human error through accurate, data-driven decision-making, introducing precision, consistency, and actionable insights (Arya 2024).

The 21st-century agricultural practices are moving towards “Digital Agricultural Revolution” or “Smart Farming” with the development of AI, the Internet of Things (IoT), Big Data, and Cloud Computing (Araújo et al. 2023, Sørensen et al. 2025). The applications of AI-driven technologies in sustainable agricultural practices are vast and comprehensive (Ali et al. 2025). Some examples include precision farming (Alazzai et al. 2024), soil and crop health monitoring (Kothari et al. 2024), predictive analytics, robotics and automation, early disease detection, and many more (Adewusi et al. 2024). Precision agriculture, also known as precision farming, and related practices such as smart farming are becoming dominant research fields in the current global landscape of sustainability-focused ideologies in farming and food production (Garcia-Vazquez et al. 2021). Through real-time, data-driven decision-making and analysis from sensors, drones, and satellites, resource use efficiency is boosted (Bhavani et al. 2024, Babbar et al. 2025). For example, AI-controlled irrigation systems monitor soil moisture and weather patterns to optimise water use, thereby reducing water waste (Adewusi et al. 2024). Additionally, sensors and image processing systems utilising data from technologies such as hyperspectral imaging can accurately analyse plant health, enabling early disease detection (Thomas et al. 2018, Terentev et al. 2022). The uses of AI in agricultural practices apply to all stages from pre-production to supply chain management, making it a highly useful tool in sustainable farming practices of the future (Sood et al. 2024). A significant area of AI being utilised in agriculture is detection, management, and other broader applications of fungi, including important phytopathogenic fungi as well as beneficial fungal organisms.

AI for improved crop productivity and fungal pathogen management

Crop productivity increases when timely efforts are made to ensure plant health. This can be achieved through early disease detection, understanding aspects to improve crop yield and quality, and weed management. AI has been successfully used to resolve problems encompassing all these areas. Data obtained from Unmanned Aerial Vehicles/Drones, Satellites, and Ground-based/Handheld Sensors and Vehicles can all provide important data from vast areas that could be overwhelming to analyse manually. Therefore, AI-driven analytical methods are helpful for efficiently using this data to improve crop productivity.

Timely disease detection is an important aspect of agriculture as plant health is directly responsible for the quality and yield of the harvest. Therefore, sustainable farming practices require efficient, rapid, and accurate monitoring of crop health. For early disease detection, data derived from optical sensors, non-optical devices, and integrated systems can be successfully used with higher efficiency when aspects of AI technology are used to analyse the data. By analysing visual patterns from data obtained from different devices, AI-powered systems can identify signs of infections at very early, often asymptomatic stages. This can assist in timely and precise interventions to reduce disease spreading and minimise the use of agrochemicals. Most of these techniques are also non-invasive, thus helpful in sustainable farming practices.

Conventional equipment and methods can be made more efficient by incorporating AI-based technologies. Time-lapse images from traditional microscopic imaging, along with Convolutional Neural Networks and Support Vector Machines, have been used for automated disease diagnosis more efficiently as they can detect temporal morphological changes with great precision (Mansourvar et al. 2025; Shi et al. 2025). For example, microscopy combined with high-accuracy machine learning classification models, such as Support Vector Machines, can differentiate similar morphologies of fungal spores with up to 97.5% overall accuracy in *Lasiodiplodia brasiliensis*, *L. crassispora, L. exigua,* and *L. gilanensis* on grapevines (Shi et al. 2025). Similarly, microscopic images combined with AI technology were used to distinguish three *Trichoderma* species, including *T. harzianum*, *T. atroviride*, and *T. virens,* and the accuracy of correct detection was up to 95.38% in a random sample (Soltani Nezhad et al. 2024).

Furthermore, visual images captured by DSLR and RGB cameras combined with deep learning were successfully used to detect powdery mildew disease on strawberry leaves (Shin et al. 2021) and an array of diseases affecting guavas (Almadhor et al. 2021) more efficiently than using conventional disease detection methods. In another study, near-infrared spectroscopy and machine learning models were used to detect Verticillium wilt of potatoes (Shin et al. 2023). Not only can these technologies be applicable for disease detection at the laboratory level, but mobile devices equipped with cameras can also be used to provide a practical and cost-effective solution for rapid and accurate disease detection (Ahmed & Reddy 2021, Kumar et al. 2023b).

Hyperspectral and Multispectral Imaging can be used to monitor crop conditions, including diseases (Thomas et al. 2018, Terentev et al. 2022). Early disease detection in plants with a Hyperspectral Imaging System combined with AI, Machine Learning, and Deep Learning was achieved by processing complex spectral data and identifying subtle physiological changes before they become visible to the human eye (Pane et al. 2021). Both hyperspectral imaging and multispectral imaging can also be used to compute vegetation indices (VIs), such as the Normalised Difference Vegetation Index (NDVI), which are indicators of plant health (Liakos et al. 2018). Combined with HSI, thermal imaging can be used to detect plants under stress by measuring temperature variations that indicate physiological changes (Thomas et al. 2018). Hyperspectral imaging combined with machine learning can also be used to optimise the monitoring of the effects of the biocontrol agents and their effect on the environment they are being used on (Cabanás & Mercado-Blanco 2025). Additionally, a combination of Hyperspectral Imaging System, Machine Learning, and short-wave infrared (SWIR) with an electric nose (E-Nose) apparatus can be used to detect volatile compounds emitted by plants and assess plant physiological changes under abiotic or biotic stress (Fuentes et al. 2021). In the study conducted by Pane et al. (2021), they used data obtained through Hyperspectral Imaging System to evaluate the efficiency of biocontrol agents to control soil-borne fungal pathogens affecting baby leaf vegetables. Early identification of Oil Palm and Basal Stem Rot (BSR) disease was achieved using spectral reflectance data collected before visible symptoms appear, combined with AI technologies and a Hyperspectral Imaging System (Terentev et al. 2022). Sweet Pepper and Tomato Spotted Wilt Virus detection at early stages was also successfully conducted using AI technologies combined with AI (Gu et al. 2019, Wang et al. 2019b).

Another potential use of machine learning and deep learning to improve plan health is to leverage data from Internet of Things (IoT)- based systems (Ogubuike et al. 2021, Naqvi et al. 2025).

Smart sensory devices and remote sensing technologies in the IoT network collect diverse data about the plant and its environment. This data, in the form of images, strings, and numbers, is stored on cloud platforms, which can then be transformed into actionable insights using AI-based technologies to improve plant health. This can be highly useful for early disease and pest detection and diagnosis, and for the timely application of biological control agents to sustainably control disease and prevent sudden outbreaks and emerging pathogens (Mana et al. 2024). These technologies have become more accessible by using systems with low computational demand and can even be used as mobile smartphone applications (Ogubuike et al. 2021, da Silva et al. 2023, Christakakis et al. 2024; Sulaiman et al. 2025).

The use of multispectral and hyperspectral images, combined with AI, can accurately detect and discriminate between crops and weeds. This can be used to reduce the use of herbicides in cultivation areas by developing targeted weed destruction tools and robots (Binch & Fox 2017, Murad et al. 2023). Deep learning models such as SegNet are trained to separate weeds from crop images, which can be a highly useful step in disease diagnosis and segmentation (Rathore et al. 2022). To optimise economic benefits, understanding crop yield is highly important for farmers to plan agricultural work efficiently. Data from satellite images, weather data, and other agronomic information, analysed by AI models such as Artificial Neural Networks (ANNs) and Convolutional Neural Networks (CNNs), can be used to predict crop yields with high accuracy (Liakos et al. 2018, Bhagat et al. 2022).

In addition to early disease detection, sustainable agricultural practices rely on biological control agents (BCAs) to improve plant health and control certain phytopathogens. AI can be used to select and optimise certain BCAs and assess their efficacy. The biocontrol efficacy of *Trichoderma* spp. against soil-borne fungal diseases in baby leaf vegetables was successful using Artificial Neural Networks (ANNs) applied to hyperspectral image data (Pane et al. 2021). Additionally, AI technologies can assist in calculating the optimal dosage, timing, and distribution of BCAs to improve their efficiency at the field level by accounting for conditions that would otherwise reduce their efficacy, as observed in *in-vitro* studies (Cabanás & Mercado-Blanco 2025).

AI for food safety: mycotoxin management and fungal growth prediction

Mycotoxin contamination is a major concern for food safety, but common detection methods based on chromatographic separation, often combined with mass spectrometry, can be time-consuming. AI technologies can be used to attain zero contamination in food supply chains to ensure consumer safety (Aggarwal et al. 2024, Naseem & Rizwan 2025). Various strategies using AI technologies to manage toxigenic fungi, including their ability to proliferate in food and produce mycotoxins, are already being studied extensively (Mateo et al. 2025).

The ability to predict and any toxigenic tendencies of fungal pathogens can be highly important in ensuring food safety. This can also help limit crop loss. AI models such as extreme gradient boosted trees (XGBoost) have been successful in predicting growth rates of *Fusarium culmorum* and *F. proliferatum* and their mycotoxin production (zearalenone and fumonisin) under various environmental conditions as well as under different fungicide treatments (Tarazona et al. 2021). Also, screening techniques for fungal contaminants in food products can be highly useful for ensuring food safety. In one study using a combination of ML and HSI, the presence of *Penicillium* sp. in brown rice was detected with a 93.4% accuracy in a rapid, chemical-free and non-destructive manner (Siripatrawan et al. 2024). Additionally, AI technologies can also be used to distinguish between edible and poisonous fungi, ensuring safe consumption of mushroom food products (Singh & Sharma 2024).

Limitations and challenges of AI-driven agricultural technologies

AI-driven technologies have become hot topics across every discipline; however, whether these technologies can be transferred worldwide remains a central question in low- and middle-income regions. The most significant barrier is the high capital investment. AI-enabled infrastructure, including sensors, drones, hyperspectral cameras, cloud computing platforms, and high-performance hardware, requires initial investment with specialised labour costs as well. AI tools often require technical literacy and specialised expertise skills that are not universally available among farmers and extension workers (Pinski & Benlian 2024, Gu & Ericson 2025). More than 80% of farms globally are dominated by smallholder farmers in developing countries (FAO 2021, Rose et al. 2023). These costs are creating inequalities between technologically advanced farming systems and resource-limited agricultural communities. However, it is worth noting that this is not only an issue for AI-driven technologies; it's also a significant hurdle to the broader use of fungi and fungal products in agriculture, where capital remains a considerable challenge. Operational and maintenance costs will be added to capital costs, further increasing production costs (Mukherjee 2022, Aijaz et al. 2025). In many rural regions, including parts of Africa, South and Southeast Asia, and Latin America, limited digital infrastructure, unstable electricity supply, and poor internet coverage significantly constrain the practical deployment of AI-based agricultural solutions (Trendov et al. 2019, Mwansa et al. 2025).

So far, the AI systems have been developed using datasets from controlled environments or well-resourced agricultural systems. This highlighted the limited availability of high-quality, region-specific datasets. Current databases may not adequately represent the heterogeneity of crops, pathogens, climates, and farming practices in developing regions (Kamilaris et al. 2018,). This directly affects fungal disease detection, where pathogen diversity and symptom expression vary widely across agroecological zones (Agrios 2005, Burdon & Thrall 2009). The rate of technological advancement is not always the same as the rate of development of policy and institutional frameworks. One growing concern is that technology developers, rather than farmers, perceive the benefits (Bronson et al. 2022, Duncan et al. 2022).

Overall, AI-driven precision agriculture operates optimally (Kamilaris et al. 2018, Aijaz et al. 2025), but in farming systems that are already economically vulnerable, as increased production costs may outweigh productivity gains, undermining the long-term viability of AI adoption. Thus, it is necessary to develop low-cost technological innovations, inclusive policy frameworks, capacity building, and context-specific system design.

10. Green does not always mean safe: ecological and commercial challenges of fungal bioproducts

While fungi offer many promising benefits for green agriculture, their use is not always positive. In particular, fungal inoculants may lead to mycotoxin production, allergenicity, ecological disruption, and reduced commercial viability. Fungal genera such as *Aspergillus* and *Penicillium* are well known for mycotoxins and allergenic spores. Mycotoxins such as aflatoxins, ochratoxin A, fumonisins, and other secondary metabolites pose serious risks to human and animal health, including carcinogenic, mutagenic, teratogenic, immunotoxic, hepatotoxic, nephrotoxic, and neurotoxic effects (Imran et al.2020, Awuchi et al. 2022, Bunny et al. 2024, Magembe 2025). In non-agricultural or non-organic systems, these fungi colonise and biosynthesise toxins, thereby increasing mycotoxin risk (Abdel-Dullah et al. 2025). Climate change has been a catalyst by creating favourable temperature and humidity for toxigenic fungi, thereby increasing aflatoxin prevalence in many agroecosystems (Bunny et al. 2024). Furthermore, airborne conidia of toxigenic fungi can act as potential allergens, directly causing respiratory illness among farming communities. Early detection and mycotoxin surveillance using machine-learning-assisted monitoring are becoming an aspect, yet they come at a high cost (Inglis et al. 2024). Therefore, it is necessary to conduct strain-level screening and toxicological risk assessment before the large-scale deployment of fungal inoculants (Mshelia et al. 2023, Yazid et al. 2023). Beyond the direct health effects described above, fungal inoculants may also pose ecological risks when introduced into complex soil ecosystems. Cornell et al. (2021) has discussed that microbial biofertilizers can significantly reshape native bacterial and fungal communities, which is different for fungal and bacterial communities. This could result in displacement or suppression of the indigenous beneficial microbial community (Mazzola et al. 2017), which could affect long-term nutrient cycling, soil resilience, and sustainability (Gufwan et al. 2025), and an effect on non-target organisms should be highly concerning (Lynch & Thomas 2000).

The commercial success of fungal microbial products has been challenged several times over the years. This has been directly linked with formulation inconsistency, ecological risks, and secondary-metabolite toxicity (Ghorui et al. 2025). Future developments must prioritise strain-level screening for toxigenic potential, comprehensive ecological risk assessment, robust formulation technologies, long-term field validation, and harmonised regulatory oversight (Mshelia et al. 2023, Ghorui et al. 2025). These integrated validations can realise the full potential of fungal-based technologies without compromising food safety, environmental integrity, or economic sustainability.

11. Fungi in future of sustainable agriculture: a decade ahead

Within the next decade, global food production will need to be resilient, regenerative, and decentralised in response to escalating climate change, soil degradation, pesticide resistance, biodiversity loss, and the rising demand for safe food. A single innovation cannot meet this demand; it must be addressed through a combination of technologies and biological strategies, in which fungi are emerging as key agents of sustainability. Fungi are among the oldest and most diverse organisms on the planet (Blackwell 2011, Berbee et al. 2017, Kartawik et al. 2024). From ancient times to modern agriculture, fungi have demonstrated remarkable roles across multiple dimensions of sustainable farming (Field et al. 2018; Hyde et al. 2019). In the coming decade, the sustainability of soil fertility is expected to increasingly depend on fungal biofertilizers and mycorrhizal networks (Bhardwaj et al. 2014, Igiehon & Babalola 2017, Ntsomboh-Ntsefong et al. 2025). The commercial application of these biofertilizers will help restore soil fertility and reduce dependency on synthetic fertilisers.

With the current momentum in research and development on fungal biocontrol agents, fungi-based natural alternatives to synthetic pesticides are projected to capture a significant share of the global market in the next decade (Singh et al. 2023, Saldaña-Mendoza et al. 2025). Advances in genome editing and strain optimisation will make biocontrol agents more specific, targeting precise crop-pathogen interactions (Singh et al. 2024, Garg et al. 2025, Gómez-Lama Cabanás & Mercado-Blanco 2025). As a result, reduced use of synthetic pesticides will enhance food safety and lower environmental toxicity. Climate change is amplifying pest and disease incidences (Skendžić et al. 2021, Alfizar, & Nasution 2024), while extreme environmental conditions are threatening global food security (Ericksen et al. 2009, Mehrabi et al. 2022). In the next decade, global warming is unlikely to slow down; it will continue to intensify, contributing to desertification, increased salinity, and abiotic stress such as heat and drought (Le Houérou 1996, Chaudhry & Sidhu 2022). Isolating and enhancing fungal taxa from extreme environments, especially endophytes from deserts and saline ecosystems (Moghaddam et al. 2021, Nurrahma et al. 2024), could offer valuable solutions for improving plant resilience while addressing these stresses. Additionally, fungi play a crucial role in soil carbon stabilisation by producing stable organic matter (Khatoon et al. 2017, Tunlid et al. 2022). Thus, fungal composting can contribute actively to climate change mitigation through carbon sequestration (Malyan et al. 2019, de Goede et al. 2025).

Although not directly related to food production, fungi also have major potential in sustainable biomaterials. Mycelium-based biodegradable films, mulches, and seed coatings are currently being developed to reduce plastic and non-degradable materials in agroecosystems (Bandopadhyay et al. 2018, , Carneiro et al. 2025). These innovations support the transition toward a circular economy with a minimal environmental footprint. Fungal applications in agriculture can extend far beyond traditional farming practices. Fungi could be harnessed as myco-filters, mycoprotein sources, myco-remediation units, and even bioluminescent fungi-based lighting systems for regenerative urban food systems (de Souza Filho et al. 2019, Mnkandla & Otomo 2021, Ke & Tsa 2022). Although this sector is still emerging, it holds immense potential. Over the next decade, fungi could reshape agroecology through applications such as fungal biosensors for soil monitoring, customised fungal strains, and the revival of indigenous, fungi-based farming practices (Jain et al. 2021, de Sousa et al. 205).

Despite these immense potentials, challenges and barriers remain. Developing fungal inoculants, whether as biocontrol agents or biofertilizers, faces regulatory restrictions (Bharti & Suryavansh 2021, Santos et al. 2024). Standardising strain performance across diverse ecosystems is essential but difficult. Shifting farmer and public perceptions toward fungal-based agriculture is another hurdle, especially given misconceptions and the fact that fungal products do not offer immediate results (Thambugala et al. 2020, Palmieri et al. 2022, Ranout et al. 2025). Moreover, fungal products are currently not cost-effective (Palmieri et al. 2022, Thirumeni et al. 2024), which affects scalability and economic viability.

CONCLUSION

Based on the concepts discussed throughout this review, the next decade of sustainable agriculture will be defined by regenerative practices, with fungi positioned at the centre of this transformation. Arbuscular mycorrhizal fungi deliver multiple ecosystem services, yet their benefits cannot be viewed in isolation as simple biological inputs. Agricultural management practices and broader agroecosystem dynamics inherently shape their performance. Likewise, *Trichoderma* one of the most extensively studied filamentous fungal genera has emerged as a cornerstone of green agriculture, owing to its roles in growth promotion, antagonism, and environmental resilience. Beyond these well-established taxa, many newly described and understudied fungal species offer promising functions in plant productivity and biological control.

Conventional profit-driven farming has long followed a take–make–waste paradigm, accelerating resource depletion and waste accumulation. Integrating fungi within a circular bioeconomy provides a pathway to retain biological value, regenerate nutrients, and reduce system-level inefficiencies. Advances in molecular technologies have expanded the functional capabilities and precision application of fungal strains; however, progress remains constrained by societal and regulatory barriers surrounding genetically modified organisms.

Despite major strides in fungal genomics, microbial ecology, and formulation science, translating laboratory success into consistent field performance remains a significant bottleneck. Constraints arise from scalability challenges, high production costs, regulatory fragmentation, and limited farmer adoption. Industrial-scale fungal biopesticide production requires high-density sporulation, long-term viability, and formulation stability under variable storage and transport conditions. Many strains exhibit reduced sporulation, inconsistent metabolite profiles, and diminished competitive fitness when shifting from controlled laboratory cultures to industrial fermentation systems. These physiological shifts often compromise rhizosphere competence and soil colonisation following field application.

Production economics remain among the most significant limitations. Fungal biopesticides require sterilised fermentation facilities, specialised downstream processing, drying and stabilisation steps, cold-chain storage, and rigorous quality control. These contribute to cost structures that surpass those of conventional synthetic pesticides. In addition, the biological nature of fungal strains often limits intellectual property protection, thereby constraining private-sector investment. As a result, innovations frequently stall during early commercialisation phases, especially given the longer timeframes required for biologicals to establish efficacy compared with systemic chemical pesticides. Regulatory complexity further impedes widespread deployment. Although fungal inoculants are broadly regarded as environmentally safe, they are still subject to extensive toxicological, ecological, and non-target risk assessments. Regulatory pathways vary widely across jurisdictions, with some countries evaluating fungal products under chemical pesticide rules while others adopt microbial- or fertiliser-specific frameworks. This inconsistency delays approval timelines and increases compliance costs.

Despite these challenges, the potential of fungi in soil health restoration, crop resilience, and sustainable disease management remains profound. Fungi should no longer be perceived solely as biocontrol agents. They are fundamental ecological engineers that sustain nutrient cycling, enhance plant adaptability, and contribute to the regeneration of agricultural landscapes. Harnessing their full potential will require integrated agronomic practices, supportive regulatory environments, strategic investment, and continued scientific innovation.

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STATEMENTS AND DECLARATIONS

The authors declare no conflicts of interest regarding this article.

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