

Review Article

An overview of the potential role of microbial metabolites as greener fungicides for future sustainable plant diseases management

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Abstract: Fungal plant diseases can severely damage oil palm crops and compromise agricultural yields. To ensure a high crop yield while keeping the fungal pathogens at bay, microbial control to combat such diseases offers a more sustainable alternative to chemical control. It is safer to replace chemical fungicides with eco-friendly bio formulations containing living fungi or bacteria and their products to manage fungal infestations on plants, especially oil palm. This is because natural antagonistic microorganisms/substances form components of biofungicides and protect plants by various modes of action such as hyperparasitism, antibiosis and/or by induction of systemic resistance. Microbial agents' application in managing fungal plant diseases, especially oil palm crop diseases, promises a safer and sustainable agricultural system to control fungal phytopathogens while ecologically less polluting. This article briefly describes the different bioformulations and the mechanism of action of microbial agents to manage fungal phytopathogens of crops, especially in oil palm. A summary of various merits and demerits of biofungicides over synthetic ones and the future outlooks are also highlighted. Bio-based microbial agents for controlling fungal phytopathogens, especially in oil palm plants, appear to be a promising fungal pest management approach considering the growing need for sustainable practices in the agronomic sector.

Keywords: biofungicides, bioformulation, phytopathogens, microbial agent, fungicides

1. Introduction

The need for sustainable agriculture has grown exponentially over the years following the rise in

global crop demand. Due to this increasing demand, there is a growing concern as sustainable agriculture results from abiotic and biotic stressors. The latter involves infections by pathogenic microorganisms, such as bacteria, fungi, nematodes, and protozoa, while the former is due to unfavorable environmental conditions that hinder optimal plant growth (Fahad *et al.*, 2015; Martinez-Soto *et al.*, 2019; de Vilhena

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Araújo *et al.*, 2020; Rajwade *et al.*, 2020). Plants, including oil palm, are exceptional sessile organisms, unable to escape potential threats by various pathogens, arthropods, or adverse environmental conditions (Dean *et al.*, 2012; Varma *et al.*, 2015). Over 10,000 identified species of plant pathogenic fungi have been reported to severely damage global commercial crops (Horbach *et al.*, 2011; Cerda *et al.*, 2017; Khalili *et al.*, 2017; Khater *et al.*, 2017). The combined toll of crops infected by fungi contributes between 10-20% of annual yield losses (Bhattacharjee and Dey, 2014; Khalili *et al.*, 2016; Kumar *et al.*, 2016), and the losses are as high as 20-40% in susceptible cultivars (Kashyap *et al.*, 2017; Rajwade *et al.*, 2020).

In some Southeast Asian countries, such diseases accounted for a total economic loss of between RM225 million to 1.5 billion in a year (Onoja *et al.*, 2018; Onoja *et al.*, 2019). *Ganoderma* spp., *Phoma herbarum*, *Fusarium oxysporum* f. sp. *elaedis*, *Marasmius palmivorus*, *Phytophthora palmivora*, *Thielaviopsis paradoxa* are some of the pathogens that are affecting oil palm worldwide (Rees *et al.*, 2012; Alvarez *et al.*, 2012; Rusli *et al.*, 2015; Hanum *et al.*, 2016; Zheng *et al.*, 2017; Maizatul-Suriza *et al.*, 2021; Torres *et al.*, 2010).

A plethora of physical, cultural, chemical, and living systems are presently being used to control phytopathogens of the oil palm (Bargabus *et al.*, 2002, 2004; Benhamou, 2004; Heydari and Pessarakli, 2010; Borges Chagas *et al.*, 2015; Crozier *et al.*, 2015; Khalili *et al.*, 2016; Khalili *et al.*, 2018). Synthetic fungicides and bactericides are currently the preferred means of controlling fungal and bacterial phytopathogens (Heydari and Pessarakli, 2010). The synthetic chemicals used has raised concerns about their long-term impact on public health (Ge *et al.*, 2016; Basaid *et al.*, 2021), given the unprecedented liberation of high quantities of toxic compounds into the environment (Oruç, 2010; Chamorro *et al.*, 2015; Rubio-Canalejas *et al.*, 2016; Topal *et al.*, 2016; Pradana *et al.*, 2017; Tsatsakis *et al.*, 2017). Fortunately, we do have options to replace the chemicals with eco-friendly and

more sustainable ones through microbial control of plant diseases (Elmhirst *et al.*, 2011; Ramli *et al.*, 2016; Chauhan *et al.*, 2016; Khalili *et al.*, 2016; Gao *et al.*, 2018; Wallace *et al.*, 2018; Raymaekers *et al.*, 2020), and using their derivatives to formulate biopesticides. The concept of biopesticides was raised after the first green revolution, which principally reduced the arbitrary use and side effects of chemical pesticides. The methods employed for crop management are less harmful and are more sensible by capitalizing on a wide-ranging soil and rhizospheric microorganism to act as bio-stimulators for plants. On the other hand, antagonistic microorganisms help inhibit phytopathogens' growth (Lee *et al.*, 2006; Segarra *et al.*, 2010; Brotman *et al.*, 2012; Chauhan *et al.*, 2016). (Maheshwari, 2010). Biofungicides containing natural suppressor compounds to control plant diseases caused by fungi are fine examples of the first green revolution (Arora *et al.*, 2010; Maheshwari, 2010; Chauhan *et al.*, 2016).

Biofungicide" is defined as "specific preparations containing microorganism, fungi in particular" (Regnault-Roger and Philogène, 2008; Liu *et al.*, 2021). Specifically, bioformulated products derived from beneficial microorganisms (bacteria, fungi, yeast, and actinomycetes) or their metabolites (Bonaterra *et al.*, 2012) are increasingly popular as products for plant protection for both individual applications and within the Integrated Pest Management (IPM) in the modern-day agricultural system (Fontenelle *et al.*, 2011; Singh *et al.*, 2011; Harman *et al.*, 2012; Małolepsza *et al.*, 2017; Liu *et al.*, 2021). These naturally occurring substances curb the further proliferation of oil palm crop pathogens by various modes of action such as hyperparasitism and antibiosis, in conjunction with enhancing nutrition for crops and induced resistance.

Pertinently, the fungi/bacteria's ability to parasitize and inhibit other pathogenic microorganisms underlies the biocides' industrial success in controlling oil palm crop diseases by non-toxic mechanisms. Bioformulated products

have since progressed substantially in support of a greener agronomic pest management approach. Having said that, this review focuses on fungi and bacteria's biocides, considering their high diversity in infecting oil palm plants and a vast number of global crops. The review also highlights the different microbial formulations (fungicides and bactericides) and their mechanisms of action, and briefly the merits and demerits of biocides over synthetic ones.

2. Microbial biocides

Microorganisms, viz. bacteria, fungi or protozoans, are potent ecological sources of many bioactive compounds (Kim *et al.*, 2020). The microorganisms are well-reported producers of fungicides (Islam *et al.*, 2005; Gupta and Dikshit, 2010) that can be used in formulations for more ecologically benign and sustainable pest management by non-toxic effects. The mechanisms are generally classified as plant-incorporated protectant fungicidal substances, where sustainable crop protection comes from secondary microbial metabolites (antibiotics) (Copping and Menn, 2000; Gupta and Dikshit, 2010). To date, groups of microbial metabolites to be used as microbial fungicides in crop management include; Blasticidin S, Kasugamycin, Polyoxins, Validamycins, Soraphen A, Strobilurin A, Fenpiclonil, Azoxystrobin, Tubercidin, Oudemansin A, Pyrrolnitrin, Nikkomycins, Phellinsin A, Arthrichitin, Aculeacin A, Abikoviromycin, Dihydroabikoviromycin, Verlamelin, Gloeosporone *et.c* (Vijayakumar *et al.*, 1996; Copping and Menn, 2000; Heaney *et al.*, 2000; Hwang *et al.*, 2000; Sierotzki *et al.*, 2000; Hwang *et al.*, 2001; Bartlett *et al.*, 2002; Kim *et al.*, 2002; Maruyama *et al.*, 2003; Lee *et al.*, 2004; Thines *et al.*, 2004; Lee *et al.*, 2005; Kim *et al.*, 2006). This article's following sub-sections further describe the above-mentioned microbial metabolites and their application in managing plant diseases. On another note, Nusaibah *et al.* (2016) reported that plant metabolites, mainly lipids and heterocyclic aromatic organic metabolites, could be potentially involved in early oil palm defense mechanisms against *G. boninense* infection.

2. 1. Blasticidin S and kasugamycin

Blasticidin S is an antibiotic derived from a microbial metabolite, capable of killing conidia or inhibiting conidial germination and mycelial growth of the pathogenic ascomycete fungi, *Magnaporthe* species. This substance has been used to control plant diseases caused by several fungal species. Blasticidin S binds to the peptidyl transferase center of bacterial 70S and eukaryotic 80S ribosomes which inhibits the release stage of translation termination in the metabolic pathway for protein synthesis (Copping and Duke, 2007; Law *et al.*, 2017; Chakraborty *et al.*, 2020).

Another similar metabolite, the kasugamycin, is an aminoglycoside antibiotic produced by *Streptomyces kasugensis*, which inhibits the mycelial growth of pathogenic *Magnaporthe grisea*. The compound is also effective against specific yeasts infesting crops (Copping and Menn, 2000; Pooja and Katoch, 2014; Law *et al.*, 2017). Another group of microbial antibiotics is polyoxins, belonging to the class of peptidyl nucleoside antibiotics. The amphoteric compounds are particular against phytopathogenic fungi, reportedly isolated from the culture of the branching filamentous, Gram-positive bacterium *Streptomyces cacaoi* (Li *et al.*, 2012). In addition, the metabolite suppresses cell wall chitin production in sensitive fungi such as *Aspergillus fumigatus*, *Rhizoctonia solani*, *Botrytis cinerea* and *Trichoderma viride* with no adverse effects on organisms with deficient chitinous cell walls (Li *et al.*, 2012; Lee and Kim, 2015). Polyoxins are also effective against fungal pathogens infecting vegetables and other fruit plants, such as grey mold caused by *Botrytis cinerea*, and the black spot disease which affect pears caused by *Alternaria kikuchiana* S. Tanaka fungus. Another microbial metabolite-derived fungicide, the validamycin, produced by *Streptomyces hygroscopicus* (Yu *et al.*, 2005; Zhou and Zhong, 2015) suppresses the activity of the enzyme trehalase. The glycoside hydrolase is crucial for converting trehalose to glucose by crop pathogens. Validamycin has been used with success to inhibit diseases caused by *Rhizoctonia solani*.

2. 2. Strobilurin A and Fenpiclonil

Strobilurin A comes from strobilurins, a class of microbial fungicides produced by a Basidiomycete fungus known as *Strobilurus tanacellus*. Strobilurins are broad-spectrum acting fungicides, active against fungal pathogens from all four taxonomic groups (Bartlett *et al.*, 2001). This group of substances inhibits fungal mitochondria activity by binding to the quinol oxidation (Qo) site in the cytochrome b (Brauer *et al.*, 2019; Feng *et al.*, 2020).

Fenpiclonil is another group of bioactive microbial metabolites that contains various functional groups such as dichlorobenzene, nitrile, and pyrrols (Kilani and Fillinger, 2016). The spectrum of antifungal activity of fenpiclonil is comparable to iprodione and tolclofos-methyl of the dicarboximide and aromatic hydrocarbon fungicides. Fenpiclonil is useful for inhibiting the growth of pathogenic Basidiomycetes, Deutromycetes, and Ascomycetes that cause seed-borne diseases. Fenpiclonil inhibits any transport-associated phosphorylation of glucose and eventually precedes a cascade of metabolic events leading to the fungicide's toxic action. Therefore, several phytopathogenic imperfect fungi's mycelial growth becomes impeded by the substantial accumulation of amino acids and sugars in their system, which are unavailable as components for growth (Jespers *et al.*, 1993; Kilani and Fillinger, 2016).

2. 3. Azoxystrobin and Soraphen A

Azoxystrobin is another metabolite-derived fungicide that blocks the spore germination of a wide-ranging type of pathogenic fungi (Ascomycetes, Basidiomycetes and Deutromycetes) Bartlett *et al.* (2002). The synthesis of this new fungicide was inspired by strobilurins produced by several species of Basidiomycete fungi. The problem of Azoxystrobin is that it is a xenobiotic and an accepted environmental contaminant. Azoxystrobin is a methoxy acrylate analog of the strobilurin, in which its fungicidal mode of an action precludes electron transport and energy production via oxidative phosphorylation which may interfere and block

the electron transfer between cytochromes b and c1, hindering mitochondrial respiration. A recent study found that metabonomic profiles of aquatic microbial communities exposed to azoxystrobin were profoundly altered. The affected microorganisms showed the most various metabolites due to changes in their metabolic pathways. The pathways involve were the citrate cycle, fatty acid biosynthesis, and purine metabolism, all of which responded to azoxystrobin toxicity (Zhang *et al.*, 2020).

Similarly, the macrolide of the myxobacterial metabolite Soraphen A (Park *et al.*, 2010) produced by *Sorangium cellulosum* (Koutsoudakis *et al.*, 2015) is exceptionally effective against powdery mildew fungus. Initially, it was discovered for its potent and broad-spectrum antifungal activity. Soraphen A is also a bacterial metabolite inhibitor of the Acetyl-CoA carboxylase (EC.6.4.1.2), which converts acetyl-CoA to malonyl-CoA. The enzyme is responsible for essential cellular metabolic processes like fatty acid synthesis and the β -oxidation of mitochondrial fatty acid. In other words, Soraphen A essentially interferes with fatty acid elongation or lipid biosynthesis of fungal pathogens. Unfortunately, there are issues with the safety of Soraphen following the discovery of its teratogenicity (Koutsoudakis *et al.*, 2015; Wang *et al.*, 2020).

2. 4. Oudemansins and Pyrrolnitrin

Oudemansin a fungicidal metabolite produced by the Basidiomycetes group of fungi especially, *Oudemansiella mucida* (Fernández-Ortuño *et al.*, 2010). The substance potently binds to the specific site on cytochrome b and inhibits the mitochondrial respiration of pathogenic fungi (Fernández-Ortuño *et al.*, 2010). Oudemansin is a fungicide component to treat plant diseases, for instance, powdery mildew and septoria leaf spot of plants.

Pyrrolnitrin is a metabolite produced by the *Pseudomonas* species and has been demonstrated effective in combating several phytopathogenic diseases and against soil and seed-borne plant diseases (Pawar *et al.*, 2019). Pyrrolnitrin can inhibit *Botrytis cinerea*'s growth, *Magnaporthe*

grisea, and *Sclerotinia sclerotium*, pathogens that cause stem rot. The substance interferes with the terminal electron transport system and inhibits the phytopathogens' cellular respiration, including dermatophytic fungi (Selin *et al.*, 2009; Nandi *et al.*, 2015). Likewise, the naturally occurring nucleoside-peptide antibiotics, nikkomycins, produced by *Streptomyces ansochromogens* (Liao *et al.*, 2010), are, in fact, uridine diphosphate-N-acetyl glucosamine substrate analogs for biological activities of chitin synthases (Zhang and Miller, 1999; Feng *et al.*, 2014). This group of compounds is effective against filamentous fungi (yeast), insects, and acarids (Feng *et al.*, 2014). Their bioactivity against different pathogenic fungi comes from their formidable competitive inhibition of chitin synthases, which affect chitin cell-wall synthesis, interfering with mycelial growth (Liao *et al.*, 2010; Feng *et al.*, 2014).

2. 5. Phellinsin and Arthrichitin

The phenolic lignin antifungal metabolite Phellinsin, is produced by the *Phellinus* species of fungi (Hwang *et al.*, 2000). It exhibits biological activities against chitin synthases I and II in various pathogens, for example, *Saccharomyces cerevisiae*, *Rhizoctonia solani*, *Collectotrichum lagenarium*, *Pyricularia oryzae*, and *Aspergillus fumigatus*. It is worth mentioning here that chitin synthase I is a non-essential repair enzyme of damaged chitin, while chitin synthase II is an essential enzyme to form the primary septum between mother and daughter cells in pathogenic microbes. Interfering the enzymes' cellular function thus precludes the upkeep and preservation of cellular chitin in the pathogens. Therefore, specific inhibitors of the two enzymes make interesting bioactive substances in developing antifungal agents (Hwang *et al.*, 2000; Sridhar and Deshmukh, 2019).

Arthrichitin is a cyclodepsipeptide which forms another bioactive substance produced by *Arthrinium phaeospermum* (Vijayakumar *et al.*, 1996; Moussa *et al.*, 2020). This metabolite is a potent chitin synthesis inhibitor used for inhibiting further proliferation of grey mold plant diseases

caused by *Magnaporthe grisea* and *Botritis cinerea*, respectively (Lee and Kim, 2015).

2. 6. Abikoviromycin and Dihydroabikoviromycin

Pathogenic fungi such as *Magnaporthe grisea* and *Colletotrichum lagenarium* species are well known as producers of pentaketide derivatives such as abikoviromycin and dihydroabikoviromycin which are known antibiotics Maruyama *et al.* (2003). The two substances have been potent in suppressing polyketide synthase in melanin biosynthesis by the pathogenic *Colletotrichum lagenarium* (Dembitsky and Kilimnik, 2016). Both compounds' actions interfere with the ability of fungus' to produce melanin, and hence it becomes susceptible to the deactivation of UV from the sun. Verlamelin, like the cyclic lipodepsipeptide, is a metabolite produced by *Acremonium strictum* (Kim *et al.*, 2002; Lee and Kim, 2015; Mao *et al.*, 2015). The compound exhibits exceptional in vitro and in vivo antifungal activity against an array of powdery mildew diseases instigated by *Alternaria brassicae*, *Fusarium avenaceum*, *Rhizoctonia solani*, *Phythium pythioides*, *Marasmius oreades*, *Sclerotinia sclerotiorum*, *Leptosphaeria maculans* and *Blumeria graminis*. In vivo, verlamelin demonstrated intense protective and curative activities, predominantly against barley powdery mildew.

2. 7. Aculeacin A and Gloeosporone

Aspergillus aculeatus produces the novel antifungal antibiotic Aculeacin A, successfully inhibits the growth of yeast, and various species of bacteria and filamentous fungi (Mizuno *et al.*, 1977; Yamaguchi *et al.*, 1982; Wang *et al.*, 2017) by inhibiting the synthesis of β -1,3-glucan Wang *et al.* (2017). Lastly, the fungicide gloeosporone produced by *Colletotrichum gloeosporioides* Chapla *et al.* (2014) has been shown to inhibit conidia germination of *Colletotrichum* species. This self inhibitor of germination also showed promising application as a plant protectant against plant pathogenic fungi Adam *et al.* (2014). The chemical structure of some microbial fungicides is depicted in Fig. 1.

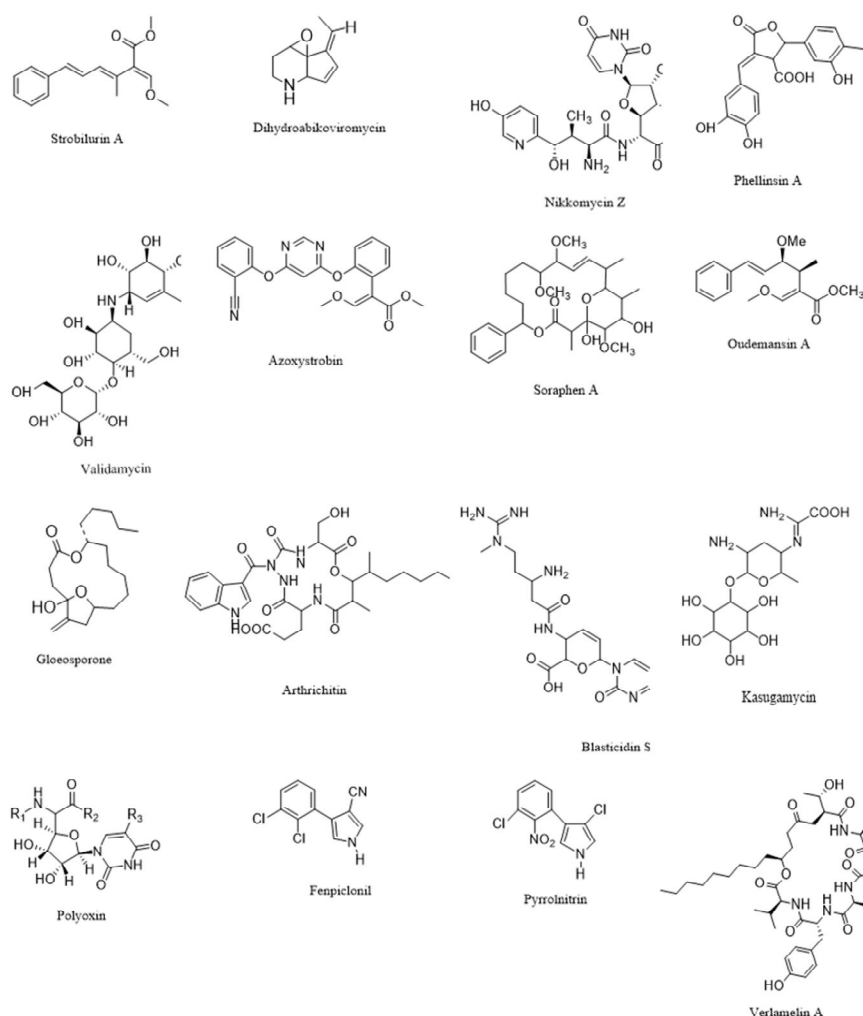


Figure 1 Chemical structure of some fungicidal compounds of microbial origin.

It is clear that microbial metabolites with antifungal potential significantly influence disease management in the agricultural sector, championing a more gentle and natural way to protect and rid the crops of diseases. The plus point of using microbial metabolites is that they are relatively easy to obtain by cultivating suitable and cost-effective substrates; hence, they can be more economical. Moreover, the use of novel microbial fungicides to combat and manage plant diseases offers a long-term and sustainable approach to crop protection. It is also an alternative approach to wean the agricultural community from their heavy dependence on hazardous synthetic fungicides.

3. *Trichoderma* species as potent microbial fungicides

So far, the most common groups of fungi used as microbial fungicides to combat plant diseases include the *Trichoderma* spp., *Botrytis* spp., *Sclerotinia*, *Cladosporium*, *Oxysporium*, *Gladiolus*, *Ampelomyces*, *Candida*, and *Coniothyrium* species (Elad, 2000; Freeman *et al.*, 2004; Vinale *et al.*, 2008; Patel and Saraf, 2017). The past decade has witnessed the *Trichoderma* spp. being the prevalent fungal species for antagonistic tests against other fungal phytopathogens (Chaube *et al.*, 2004; Sundram *et al.*, 2008; Bogumił *et al.*, 2013; Keswani *et al.*, 2014; Soliman *et al.*, 2015).

Hence, their physical characteristics have been rigorously described (Divya and Sadasivan, 2016) and their biochemical and molecular characteristics. *Trichoderma* species are well-reported accomplished producers of microbial compounds and inhibiting the plant diseases directly or by inducing plant resistance response (Shetab Booshehri, 2014).

Despite the potential use of *Trichoderma* spp. as biocontrol agents, these facultative fungal saprophytes are industrially used to synthesize enzymes and produce bio fungicides, bio-fertilizers, and soil amendments (Mohammed *et al.*, 2014; Khalili *et al.*, 2016). *Trichoderma* spp. are outstanding transformation agents of the soil microenvironment. Their rhizosphere delivers a cocktail of polysaccharides, chlorophenols, and enzymes that degrade hydrocarbons (Harman *et al.*, 2004; Das and Chandran, 2011). Also, the *Trichoderma* spp. have been reported to parasitize other microorganisms while some species produce antibiotics effective against plant diseases (Howell, 2003; Vinale *et al.*, 2008; Kumar *et al.*, 2017). Different species of *Trichoderma* produce a variety of antimicrobial metabolites showing good antibiotic activity against various fungal pathogens (Moutassem *et al.*, 2020). Likewise, several fungal species also produce several plant defenses stimulating substances associated with molecular patterns such as xylanase, swollenins, peptaibols, and cerato-platanins (Harman *et al.*, 2004; Shores *et al.*, 2010; Druzhinina *et al.*, 2011; Nitta *et al.*, 2012; Khalili *et al.*, 2016). These substances induce the plant defense response by altering the microfloral composition around the plant rhizosphere. Consequently, the changes improve the soil nutrients' solubility and promote fibrous plant roots (Harman, 2000).

Perhaps one of *Trichoderma*'s remarkable traits is its robustness and the ability to remain mostly unaffected by exposure to many toxic compounds produced by the soil microflora in the rhizosphere. The fungus is also resistant to many herbicides, antibiotics, and fungicides applied by farmers (Sjaarda *et al.*, 2015; Khalili *et al.*, 2016). For instance, *T. harzianum* produce low levels of cell-wall degrading enzymes (CWDEs) such as β -glucosidase and

chitinases into the environment. The produced CWDEs then beneficially hydrolyze the fungal pathogens' cell walls upon contact (Khalili *et al.*, 2016), with the concomitant liberation of cell wall products. Another defense mechanism of the *T. harzianum* where the products instigate expression of a mycoparasitic gene system, which causes the antagonistic fungus to grow and coil in the direction of the pathogenic fungi (Hermosa *et al.*, 2013).

4. Modes of action in microbial biological control agents

The fundamental factor in achieving a sufficient decline of plant diseases hinges on the modes of action of the antagonistic microorganism (Bonaterra *et al.*, 2012; Rania *et al.*, 2016). Microbial biological control agents' activity is wide-ranging, where some interact with plants by inducing resistance without any direct interaction with the target pathogen. In contrast, certain microorganisms accommodate the growth of other microorganisms by providing nutrients. Alternatively, certain fungi compete for nutrients and exhibit antibiosis and hyperparasitism (Köhl *et al.*, 2019; Peters *et al.*, 2020; Singh, 2014; Singh *et al.*, 2014; Vasebi *et al.*, 2013). The mechanisms of action between microbial agents and the host in controlling plant pathogens are described in Fig. 2.

4. 1. Induction of systemic host resistance

It is a plant defense system prompted by biological or chemical inducers that shields the non-exposed plant parts against any impending attack by pathogenic microbes viz. fungi, bacteria, or herbivorous insects (Kuč, 1982; Van Loon *et al.*, 1998; Choudhary *et al.*, 2007; Pieterse *et al.*, 2014; Mauch-Mani *et al.*, 2017; Zhang *et al.*, 2017). Currently, two major types of induced resistance are known to exist; namely, i) a localized induced systemic resistance (ISR) triggered by root-colonizing mutualistic microbes such as *Pseudomonas fluorescence*, *Paenibacillus polymyxa*, or *Trichoderma* sp (Bargabus *et al.*, 2002, 2004; Alfano *et al.*, 2007; Bae *et al.*, 2011) and ii) a systemic acquired resistance (SAR) triggered

by plant pathogens (Sequeira, 1983; Champigny *et al.*, 2011; Pieterse *et al.*, 2014). According to the disease's nature, plants can instigate a distinct defense pathway (Garcia-Brugger *et al.*, 2006). For instance, when a phytopathogen kills the host tissue and feeds on the remains (necrotrophs), this triggers a dependent response by the release of jasmonic acid (JA) and ethylene (ET). On the contrary, the liberation of salicylic acid (SA) triggers a dependent response when a phytopathogen feeds on a living host tissue (biotrophs) (Wu *et al.*, 2012; Thakur and Sohal, 2013).

In the modern perspective of the plant immune system, the pathogen-induced systemic acquired resistance (SAR) is activated upon local triggering of a pattern-triggered immunity or effector-triggered immunity response (Mishina and Zeier, 2007; Vleeshouwers *et al.*, 2014; Wiesel *et al.*, 2014). This response elevates the level of the hormone salicylic acid (SA) essential for a SAR in the systemic tissue (Vernooij *et al.*, 1994; van Loon *et al.*, 2006; Vlot *et al.*, 2009). The organized triggering of pathogenesis-related genes and the encoded pathogenesis-related

proteins with antimicrobial activity also need to initiate SAR. Despite the SA, it is essential to note that other metabolites involved in the long-distance SAR include methyl ester of dehydroabietinal, diterpenoid, a glycerol-3-phosphate-dependent factor, azelaic acid, as well as pipecolic acid. Also, a redox-regulated protein non-expressor of PR (pathogenesis-related) genes 1 (NPR1) in a SAR act as a transcriptional coactivator of a large set of PR genes upon triggering (Dong, 2004; Pieterse *et al.*, 2012; Pajerowska-Mukhtar *et al.*, 2013; Vlot *et al.*, 2009; Lyu *et al.*, 2016). Similarly, the signaling of herbivore-induced resistance in plants is triggered upon the release of plant-derived signals such as damage-associated molecular patterns (DAMPs), herbivore-associated molecular patterns (HAMPs) and elicitors secreted from the insect's oral at the site of tissue injury (Mithöfer and Boland, 2008; Heil, 2009; Wu and Baldwin, 2010; Hogenhout and Bos, 2011). Consequently, a reduced JA signaling pathway also triggers many JA-responsive genes (Memelink, 2009; Pieterse *et al.*, 2012; Martínez-Medina *et al.*, 2017).

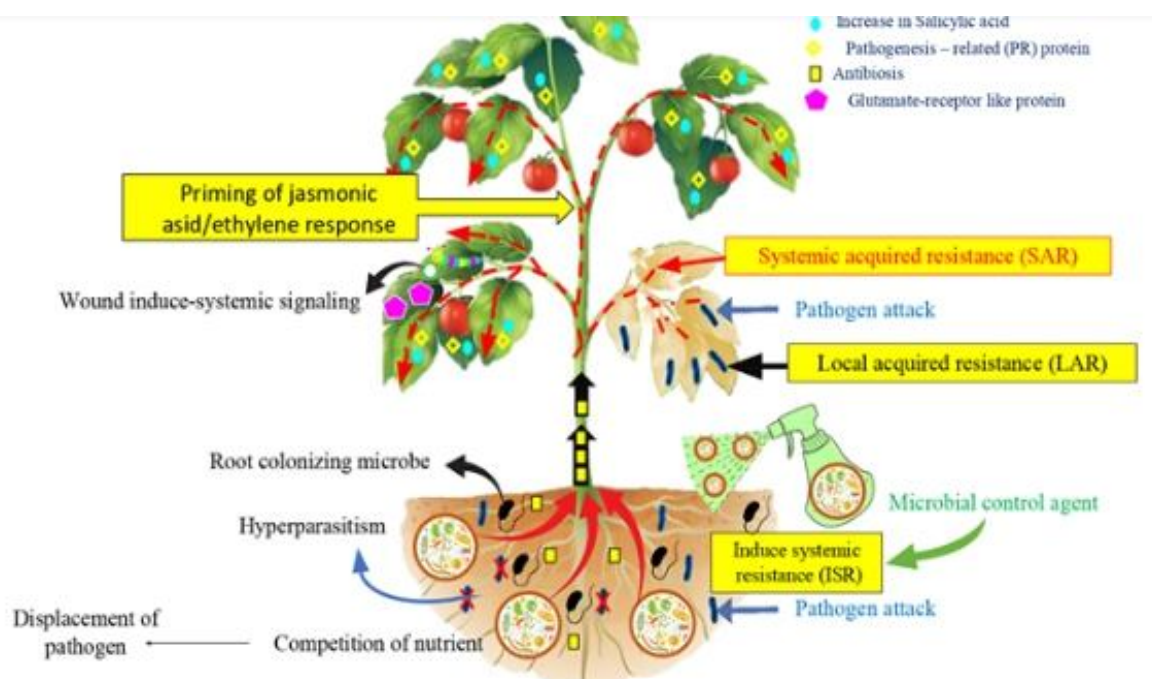


Figure 2 Mechanisms of action of microbial agents for the control of plant pathogens (Abbasi *et al.*, 2014; Heydari and Pessarakli, 2010).

Likewise, the glutamate receptor-like proteins are essential for triggering wound-induced-systemic signaling and facilitating wound-induced surface potential modifications (Mousavi *et al.*, 2013). As a result, the dormant signaling components' levels are enhanced, and systemic immunity is developed alongside a potentiated expression of pathogenesis-related genes 1 (PR-1). Priming is also related to chromatin changes in the promoters of DNA-binding proteins in the transcription factor gene family like the WRKY. This gene plays a significant role in plant defense to biotic and abiotic stresses, seed dormancy, seed germination, and some plant developmental processes (Jaskiewicz *et al.*, 2011; Pieterse *et al.*, 2012; Wu *et al.*, 2012). The induced systemic resistance signaling pathway is illustrated in Fig. 3.

4. 2. Competition

Antagonist microorganisms showing nutrient competition mechanism of action have a vast host range modulation of environmental conditions due to the micro-niche potential affecting various less competitive pathogens (Di Francesco *et al.*, 2017). Competition at the initial stage of interaction with the pathogen depends heavily on the availability of growth factors, timing, and antagonist (Kessel *et al.*, 2005). Hence, competitive microorganisms are germane participants in microbial control via the mechanism of action for competition growth factor. Competition between microorganisms resulting from the shortage or limited growth factors, such as nutrients and space, can critically affect the pathogen's development (Howell, 2003; Benítez *et al.*, 2004; Viterbo *et al.*, 2007). Competition for three above-said components can lead to the eventual displacement of the pathogen. Rapid growth and substrate colonization are highly significant aspects that dictate the survival of the microorganism. Various crop pathogenic fungi develop an ingenious method of continued feeding association with their host's living cells (Köhl *et al.*, 2019), rather than killing the host cells as a portion of the infection process, ensuring successful colonization. Certain species of pathogenic fungi attack the host plant tissue and utilize the existing nutrients, although the majority are colonizers that destroy host tissues.

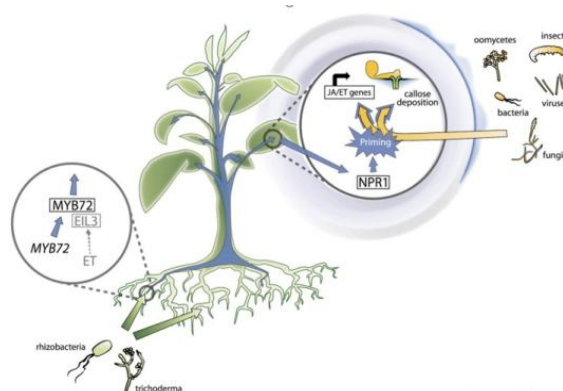


Figure 3 Schematic representation showing the induced systemic resistance (ISR) signaling pathway. Recognition of microbe-associated molecular patterns (MAMPs) of beneficial rhizosphere-colonizing microorganisms, such as *Pseudomonas fluorescens* rhizosphere-colonizing microorganisms, such as *P. fluorescens* WCS417 or *Trichoderma asperellum* T34, leads to local activation of the transcription factor gene MYB72 in the roots. Subsequently, MYB72 putatively interacts with the ethylene-insensitive-like transcription factor 3 (EIL3). Downstream of, or in parallel with MYB72/EIL3, a so-far unidentified ET signaling component is required in the roots for ISR onset in the leaves. The ISR signal transduction cascade requires NPR1, probably in the systemic tissue. Systematically, induction of ISR is associated with priming for enhanced expression of a set of jasmonic acid-responsive and/or ethylene-responsive genes and increased callose-containing papillae formation at the site of attempted pathogen entry. As depicted on the right side of Figure 3, attack by pathogens or insects activates defense responses in the plant (yellow arrows) is accelerated in ISR-primed plants (combined blue and yellow arrows) (Adapted with permission from Van Wees *et al.*, 2008).

Interestingly, the same strategy has been observed in non-pathogenic fungi to better compete for existing nutrients and space. Likewise, non-pathogenic fungi that can survive on the dead organic matter also have the upper hand in substrate competition (Köhl and Fokkema, 1998; Köhl *et al.*, 2019). Specific microbial control agents can compete with other fungi for growth factors and essential elements present in the soil and around the rhizosphere (Irtwange, 2006). They do so by

altering the surrounding acidity of the soil so that pathogens are unable to grow (Benítez *et al.*, 2004).

Another competitive method involves the availability of free nutrients in fruit plant lesions to stimulate infection by different fruit diseases (Calvo-Garrido *et al.*, 2014; Di Francesco *et al.*, 2016). Highly competitive microbial agents must occupy such a niche to survive and quickly consume the growth factors (sugars, pollen, and plant exudates on plant surfaces) so that pathogens cannot infect the host (Köhl *et al.*, 2019). Competition for carbohydrates and other nitrogen sources, including amino acids, plays a significant role in determining the interactions between the pathogen and the antagonists (Spadaro and Droby, 2016). Ferric iron limiting factor is another competing microbial component among the pathogens and antagonists. Several microorganisms were documented to be capable of producing different low molecular weight siderophores with a high affinity for ferric iron (Raaijmakers *et al.*, 1995; van Loon, 2000; Whipps, 2001; Lugtenberg and Kamilova, 2009; Segarra *et al.*, 2010; Di Francesco *et al.*, 2016; Rania *et al.*, 2016; Lugtenberg *et al.*, 2017). This exceptional microbial ability can potentially inhibit plant diseases via iron competition. This mechanism of action lowers iron availability to the pathogen (van Loon, 2000; Whipps, 2001; Wilhite *et al.*, 2001; Lugtenberg and Kamilova, 2009).

4. 3. Hyperparasitism

Parasitism is the direct competitive association between two living organisms in which one organism obtains nutrients from the other host organism. In the situation whereby the host organism is also a parasite, as in plant disease, the association is hyperparasitism or mycoparasitism (Köhl *et al.*, 2019). A specific microbial agent launches a direct attack on the pathogen and inhibits or kills it. Hyperparasitism is made up of an array of activities such as i) the chemotrophic growth of the antagonist over the host, ii) recognition of the host mycoparasite, iii) attachment, iv) excretion of extracellular

enzymes, v) lysis, and vi) the exploitation of the host (Whipps, 2001; Benítez *et al.*, 2004; Viterbo *et al.*, 2007). This sort of competitive association is regarded as a direct form of antagonism involving the growth of a microbial agent towards the target organism, coiling, attacking, and finally disrupting the target pathogen's cell wall or membrane by secreting enzymes (Altomare *et al.*, 1999; Junaid *et al.*, 2013; Khalili *et al.*, 2016). Similarly, mycoparasitism supports the hyperparasite's survival by relying on the living host fungus by gaining nutrients from the host cells through parasitic fungal hyphae. The parasite then coils and penetrates its host's tissue and absorbs nutrients without killing the host (Jeffries, 1995; Gomes *et al.*, 2015).

The most studied hyperparasites are the genera *Clonostachys* and *Trichoderma*, which possess unique features to facilitate attachment and host infection. The fungi then inhibit the hosts by producing cell wall degradation enzymes (CWDEs) (Khalili *et al.*, 2019; Kabbage *et al.*, 2015), often alongside the production of antimicrobial secondary metabolites (Harman *et al.*, 2004; Harman, 2006; Mukherjee *et al.*, 2012; Karlsson *et al.*, 2017; Nygren *et al.*, 2018), triggered by the close contact with the host cell. The lytic action of the CWDEs punches holes in the cell wall and subsequently disrupts the cytoplasm of the parasitic fungus. The same disruptive mechanism occurs during hyperparasitic activity (Viterbo *et al.*, 2007; Zhang *et al.*, 2017). Enzymes known for such an action are the chitinase, β -1,3-glucanase, and protease or, in the case of hyperparasites of oomycote, is the cellulase (Harman *et al.*, 2004; Harman, 2006; Mukherjee *et al.*, 2012; Khalili *et al.*, 2016; Karlsson *et al.*, 2017; Nygren *et al.*, 2018; Köhl *et al.*, 2019). CWDEs are also responsible for killing or inhibiting mycelial growth and spore germination of plant pathogenic fungi (Benítez *et al.*, 2004; Lin *et al.*, 2007). The examples of hyperparasitism or mycoparasitism association of *Trichoderma* strains against the pathogenic fungus-like organism *Phytophthora cactorum*, and pathogenic fungi *S. sclerotiorum* in a dual culture is depicted in Figs. 4 and 5, respectively.

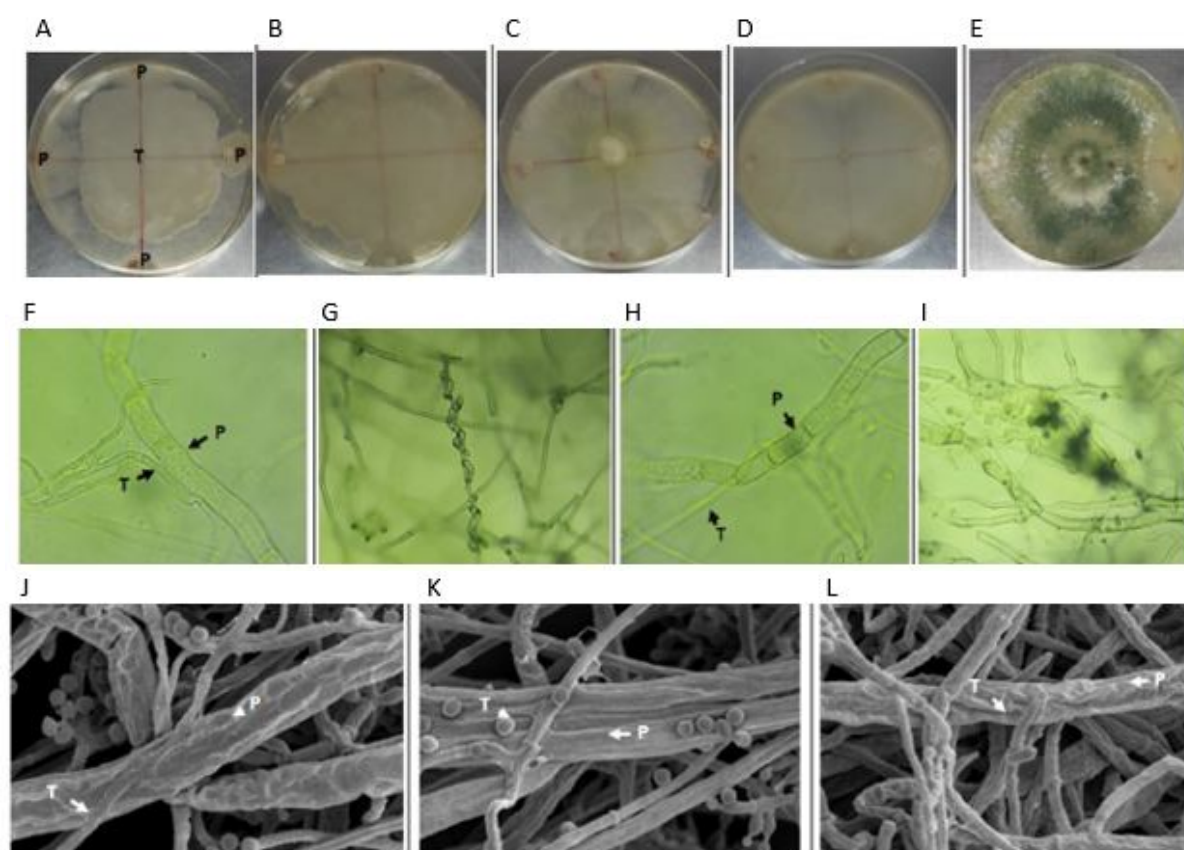


Figure 4 Microphotographs (A-I) and (J-L) scanning electron microscopic representation showing the mycoparasitism of *Trichoderma* strains to *P. cactorum* in dual cultures. (A = no invasion on the pathogen colony, B = invasion on $\frac{1}{4}$ of the pathogen colony, C = invasion on $\frac{1}{2}$ of the pathogen colony, D = total invasion on the pathogen colony, E = total invasion and sporulation on the pathogen colony; (F-I) optical microscope (40x objective) of the interaction zone, F = Adhered hyphae growth. G-H = hyphae coiling. I= vacuolated hyphae; (J-L) scanning electron microscope of interaction zone, J = isolate of *T. atroviride*, K = *T. brevicompactum* and L = *Trichoderma harzianum* growing near the hyphae of the phytophthora pathogen) (Adapted with permission from Sánchez *et al.*, 2019).

4. 4. Antibiosis

The most powerful mechanism of action by microorganisms in plant disease control is the antimicrobial metabolites they produce (Raaijmakers and Mazzola, 2012). Utilization of microbial metabolites is considered to be a feasible and desirable for the control of various plant diseases (Bahraminejad *et al.*, 2015; Nouredine *et al.*, 2019). Microbial antibiosis destroys microorganisms by producing specific or non-specific metabolites or antibiotics that inhibit the growth of another microorganism (Benítez *et al.*, 2004; Irtwange, 2006; Haggag and Mohamed, 2007; Viterbo *et al.*, 2007). Antibiotics are organic low-molecular-weight secondary metabolites

produced by microorganisms, and the substances are lethal to the growth or metabolic activities of other competing microorganisms (Aminov, 2017; Lugtenberg *et al.*, 2017). A microorganism's ability to produce multiple classes of antibiotics that differentially obstruct an array of pathogens can substantially improve microbial control (Chaube *et al.*, 2004; Junaid *et al.*, 2013). This is because most antibiotics are made only when the microbial population reaches specific thresholds (Köhl *et al.*, 2019). In most cases, microorganisms release minimal quantities of antibiotics into the environment. Approximately 2900 and 4900, antibiotics were isolated from bacteria and fungi, respectively (Berdy, 2005).

Researchers have identified several antimicrobial metabolites that can significantly inhibit the growth of plant pathogens (Lewis *et al.*, 1989; Handelsman and Stabb, 1996) by either obstructing spore germination (fungistasis), or by inhibiting the growth of pathogen (antibiosis) (Benítez *et al.*, 2004; Haggag and Mohamed, 2007). The excellent microbial control activity of the *Trichoderma*

and *Gliocladium* genera stems from their antimicrobial metabolites, including alamethicins, gliotoxin, viridol, and harzianic acid, which inhibit plant pathogens by various modes of action (Handelsman and Stabb, 1996). For better suppressive effect, the antimicrobial metabolites can be used in synergy with CWDEs to manage plant diseases (Benítez *et al.*, 2004; Woo and Lorito, 2007; Vinale *et al.*, 2008).

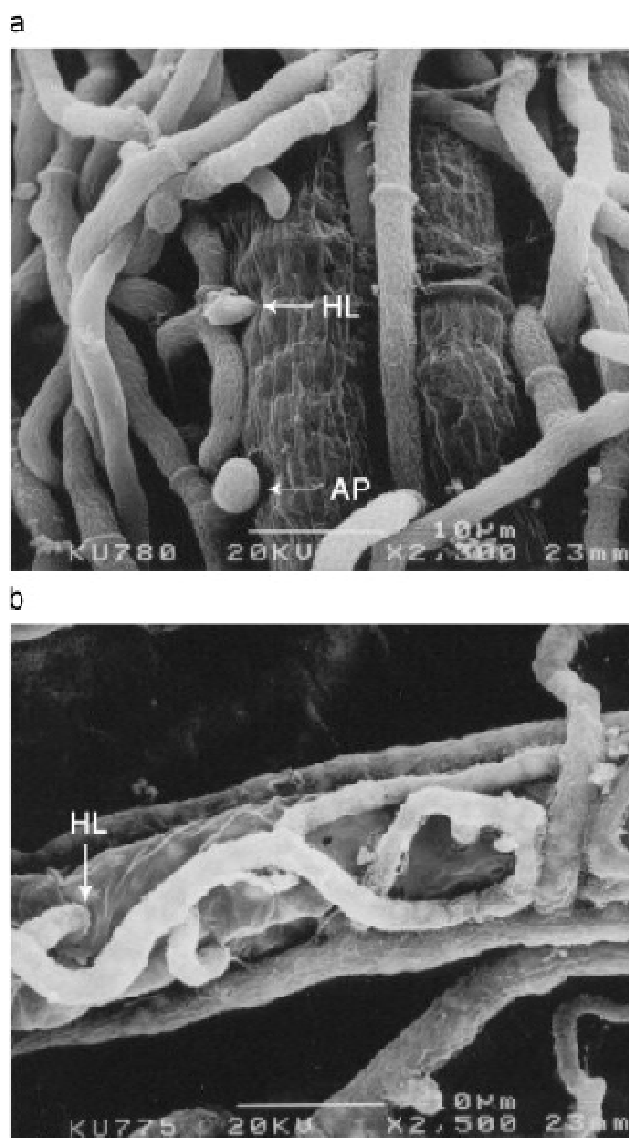


Figure 5 Scanning electron microscopic representation of *T. harzianum* hyphae attached to *S. sclerotiorum* hypha using scanning electron microscope x 2,300 and x 2, 500. (a) “Hook- like” (HL) and “appressorial-like” (AP) structures on *S. sclerotiorum* hypha (x 2,300 magnification) and (b) attachment, coiling, and penetration of *T. harzianum* hyphae into *S. sclerotiorum* hypha (2,500 x magnification). Adapted with permission from (Abdullah *et al.*, 2008).

However, the in-situ use of antibiotics in the soil environment for disease management may prove to be a challenging endeavor. Considering the half-life of antibiotics produced by the microbial control agents may vary according to the type of metabolite made, decomposition, and the possible physical and/or chemical inactivation of the substances (Mudgal *et al.*, 2013; Arseneault and Filion, 2017). Furthermore, antimicrobial metabolites also control microbial interactions in the soil and plant surfaces (Raaijmakers and Mazzola, 2012). Small quantities of the substances are known to participate in plant cell-to-cell communication, signaling, microbial community interaction, and biofilm regulation. Long-distance interaction among the soil organisms, plus

predators and bacteria, also occurs through antimicrobial metabolites intermediaries (Raaijmakers and Mazzola, 2012). Also, surface-active bacterial antimicrobial metabolites, viz. lipopeptides, facilitate bacteria's movement by modifying the viscosity of immediate surfaces to guide the bacteria towards nutrient-rich surfaces. The same substances also change the availability of water on leaf surfaces to destabilize plant disease development. Other bacterial antimicrobial metabolites such as 2,4-diacetylphloroglucinol and redox-active antibiotics can affect the nutritional status and promote plant growth activities (Köhl *et al.*, 2019). The advantages of microbial fungicides over other synthetic chemical fungicides are described in Table 1.

Table 1 Merits and demerits of microbial fungicides versus synthetic chemical fungicides.

| Microbial fungicides merits | Synthetic chemical fungicides merits |
|--|--|
| Microbial biofungicides are non-toxic and non-pathogenic to target organisms and the wellbeing offered is their greatest strength. | Synthetic chemical fungicides are profitable and economical to control pests. Small labor involvement is necessary, and they can be applied and treated in large spaces rapidly and efficiently. |
| The success of microbial is specific to a single group of species of pests. Therefore, it will not disturb beneficial living organisms. | Synthetic chemical fungicides can control all pests with the variant in nature of action and perseverance. |
| Microbial bio fungicides can be used in many environments, including banned chemical fungicides in the agricultural system. | Production of high-quality agricultural products. |
| Remains of microbial biofungicides are always non-harmful, even when close to the harvesting time of the crops. | Production of food mainly for the non-agricultural population by the small population of agricultural producers. |
| Biofungicides can control fungi and certain pathogenic microbes in the pest population or its habitat. They also provide control over succeeding generations. | Synthetic chemical fungicides are merely obtainable in massive amounts, at high quality and affordable price. |
| Robust selectivity and protection for humans and animals. | Fungicides are frequently utilized to end the spread of the pest. |
| The impact of microbial fungicides on the ecological environment is sporadic. | Synthetic chemicals play a significant role in the stoppage of pests to an individual or human population at large. |
| Utilization of robust agricultural products. | Synthetic chemicals can be used for a wide range of pest control auctions. |
| Microbial fungicides demerits | Synthetic chemical fungicides demerits |
| Due to the specificity of action, biofungicides may control only the fungi present in a field and may not prevent other types of pests in treated areas; this can cause continuous damage to the diseases. | Decrease in beneficial living organisms due to the harmful effects of chemical fungicides to non-target pests leading to changes in biodiversity of an area and disturbing the natural biological stability. |
| As heat, UV light, and desiccation decrease microbial biofungicides, the provision of supply systems becomes an essential factor. | Implications of sprays and vapor of chemical fungicides can cause severe problems to a different plant, water, and general pollution to the environment. |
| Special preparation (formulations) of microbial fungicides and storage techniques are required. Thus, shelf life is a constraint, given their short lives. | Due to the persistent use of chemical fungicides in agricultural systems, the chemical residues can reach underground aquifers and contaminate the water bodies. |
| Slow acting. | Health risks to those that apply the agrochemicals. |

5. Future outlook

The increasing global preference for safer and ecologically friendly alternatives to plant disease management, especially in oil palm, requires the scientific community's concerted effort to develop novel and valuable biofungicides. Considering the fear of the hazardous effects of synthetic chemicals on plants and human health. More choices of biofungicides must be made available to the farming community to develop a more sustainable agronomic practice and better manage the present and future plant diseases (Wallace *et al.*, 2018). Correspondingly, the development of biofungicides/pesticides may not be too problematic, given the push in the right direction. Therefore, the search for effective antagonistic microorganisms to battle crop diseases has continued over the past few decades. Many effective microorganisms have been identified, and their data are available in several databases.

However, the bottleneck will probably be the unwillingness of large pesticide companies to utilize bio-based fungicides/pesticides. So, it has to do with the unfamiliarity for the technology to mass-produce biofungicides, as well as the prohibitive manufacturing cost. Additionally, the uncertainty in the effectiveness of biofungicides to curb plant diseases, albeit short-term or long-term, is something that manufacturers and farmers may not be willing to experience. The government must address the issues mentioned above, where national policy/agenda changes may prove mandatory to motivate or entice both parties to embrace biofungicides. Special incentives and tax relief should be given to parties agreeing to adopt a more sustainable agronomic approach.

Furthermore, commercially available biofungicides at affordable prices can positively impact the economy and possibly reduce food production costs (Abbey *et al.*, 2019). Even the partial switch to biofungicides by the agricultural community in phytopathogens management would translate into the lower user of synthetic fungicides. Biocides will have progressive consequences on organic crop production systems and alleviate the negative impacts of synthetic chemicals on the environment (Koul, 2012; Abbey *et al.*, 2019).

The need for safer foods and downstream food products increases microbial biopesticide formulations with effective antagonism and good stability (Keswani *et al.*, 2016). Hence, the main concern when developing new biofungicides is the shelf life, where longevity and high stability of the bio-products during storage are essential factors to be considered before their application in the fields. An extra detail of microbial agents' preparation is required when dealing with living organisms and their metabolites. Nonetheless, long-term preservation of bioactive compounds is now possible with the scientific advancement in nanotechnology. The technology currently permits ecological friendly microbial suspension to be prepared in various forms, namely nanocapsule, nanoemulsion, and nanosuspension (Glare *et al.*, 2012; Kashyap *et al.*, 2017). The bioactive ingredients are better protected and result in a controlled release of the substances into the environment. This approach provides a more extended in-situ protection on the plants and reduces the likelihood of the bioactive compounds' rapid leaching into the ground. It is expected that modern farming systems gradually adopt the extension of microbial agent formulations from a single microorganism-based formulation to microbial or metabolite consortium-based formulations and migrate from wettable powder and suspension formulations to liquid dispersible particles. Using a consortium of microbes or metabolites may offer a broader range of inhibitory/killing over different kinds of crop pathogens. In a nutshell, the switch to biofungicides in the modern agricultural system will facilitate the production of more natural, healthy, and safe foods and enable the farming community to satisfy consumer demands.

Declaration of competing interest

No potential conflicts of interest were reported by the authors.

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مروری بر نقش بالقوه متابولیت‌های میکروبی به‌عنوان قارچ‌کش‌های سبز به‌منظور مدیریت پایدار بیماری‌های گیاهی در آینده

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چکیده: بیماری‌های قارچی می‌تواند به‌شدت به گیاهان نخل روغنی آسیب وارد نماید و موجب به‌خطر افتادن عملکرد گردد. برای اطمینان از داشتن عملکرد بالا به‌همراه محافظت در برابر بیمارگرهای قارچی، کنترل میکروبی برای چنین بیماری‌هایی به‌عنوان جایگزین پایدارتر نسبت به کنترل شیمیایی پیشنهاد می‌شود. جایگزینی قارچ‌کش‌های شیمیایی با فرمولاسیون‌های زیستی سازگار با محیط زیست که حاوی قارچ‌ها یا باکتری‌های زنده و متابولیت‌های آن‌ها است، روش امن‌تر برای مدیریت آلودگی‌های قارچی در گیاهان به‌خصوص نخل روغنی می‌باشد. چراکه میکروارگانیزم‌ها/مواد آنتاگونیستی طبیعی تشکیل‌دهنده اجزای قارچ‌کش‌های زیستی می‌باشند و از گیاهان با نحوه عمل متفاوت از جمله هیپرپارازیتسم، آنتی‌بیوز و یا القای مقاومت سیستمیک محافظت می‌کنند. کاربرد عوامل میکروبی در مدیریت بیماری‌های قارچی گیاهان به‌ویژه بیماری‌های نخل روغنی نوید یک سیستم کشاورزی امن و پایدار برای کنترل بیمارگرهای قارچی گیاهان را می‌دهد که از نظر اکولوژیکی آلودگی کمی دارد. مقاله حاضر به‌طور خلاصه فرمولاسیون‌های مختلف و مکانیسم عمل عوامل میکروبی برای مدیریت بیمارگرهای قارچی گیاهان به‌ویژه نخل روغنی را شرح می‌دهد. همچنین خلاصه‌ای از مزایا و معایب قارچ‌کش‌های زیستی نسبت به انواع شیمیایی و چشم‌انداز آینده آورده شده است. به‌نظر می‌رسد کاربرد عوامل میکروبی زیستی برای کنترل بیمارگرهای قارچی گیاهان به‌ویژه در گیاهان نخل روغنی، یک رویکرد امیدوارکننده برای مدیریت عوامل قارچی با توجه به نیاز روزافزون به روش‌های پایدار در بخش کشاورزی می‌باشد.

واژگان کلیدی: قارچ‌کش‌های زیستی، فرمولاسیون زیستی، بیمارگرهای گیاهی، عوامل میکروبی، قارچ‌کش‌ها