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Recommendations

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Advancing entomopathogenic fungi for improved management of *Phthorimaea (Tuta) absoluta* (Lepidoptera: Gelechiidae)

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Phthorimaea (*Tuta*) *absoluta* (Meyrick), a destructive pest of tomato, is currently mainly controlled using chemical insecticides. However, overdependence on chemical control induces resistance among *P. absoluta* populations and negatively impacts human health and the environment. Therefore, there is a need to adopt complementary pest control methods. Biological control of *P. absoluta* using integrated pest management (IPM) strategies incorporating entomopathogenic fungi (EPFs) holds great promise for suppressing pest populations and reducing insecticide applications. In this review, we discuss the relevance of EPFs in controlling *P. absoluta* and highlight their value as an integral component of IPM programs. The review provides an overview of strategies to address the challenges that limit research, development, wide-scale commercialization, and adoption of EPFs, particularly in sub-Saharan Africa. It also highlights technological advances that could improve the insecticidal activity of EPFs to harness their biocontrol potential fully. Further, the review recommends actionable measures for the broad and sustained application of EPFs as components of IPM programs for the control of *P. absoluta*.

Keywords: tomato leafminer, mycoinsecticide, biocontrol, pest management

The tomato leafminer, *Phthorimaea* (*Tuta*) *absoluta* (Meyrick, 1917) (Lepidoptera: Gelechiidae), has become an increasingly important pest of tomato (*Solanum lycopersicum* L.) since its first documented report in the African continent in 2008 (Desneux et al. 2010, Chang and Metz 2021). Native to South America, the pest continues to cause severe tomato losses in countries across Africa, Asia, Europe, and South America (Desneux et al. 2010, Mansour et al. 2018, Tarusikirwa et al. 2020, Zhang et al. 2020a, Acharya et al. 2023). The invasive populations of *P. absoluta* in Africa are believed to have originated from a single introduction in Morocco (Guillemaud et al. 2015). Presently, the pest's occurrence has been confirmed in approximately 37 African countries (Soares and Campos 2020, EPPO 2024), with yield losses ranging from 11% to 60% in greenhouses (Chermiti et al. 2009, Kinyanjui et al. 2021) and as high as 100% in open fields (Mohamed et al. 2012, Chidege et al. 2016). The establishment is also associated with increased crop protection expenditure costs and significant economic losses of tomatoes estimated at US$59.3 million (Kenya) and US$8.7 million (Zambia) per annum (Rwomushana et al. 2019). The larvae primarily feed on tomato leaves and shift to other plant parts, including young shoots, stems, buds, flowers, and fruits, under severe infestations. The pest also colonizes other cultivated and wild solanaceous plants, although the feeding damage is significantly higher in the primary host plant, the tomato (Silva et al. 2021). Field infestations of potato (*Solanum tuberosum* L.), black nightshade (*Solanum nigrum* L.), eggplant (*Solanum melongena* L.), and African eggplant (*Solanum aethiopicum* L.) have been reported in various African countries (Smith et al. 2018, Idriss et al. 2020, Mahlangu et al. 2022, Sawadogo et al. 2022).

Similar to other world regions, the control of *P. absoluta* in sub-Saharan Africa relies heavily on chemical insecticides to protect tomato plants against the pest's damage (Biondi et al. 2018, Mansour et al. 2018, Sawadogo et al. 2020, Desneux et al. 2022, Aboutalebian-Soureshjani et al. 2023, Karanu et al. 2024). This is attributed to the ease of use and availability of conventional insecticides, coupled with the inaccessibility of suitable and cost-effective complementary pest control options (Lykogianni et al. 2021, Colmenárez et al. 2022, Srinivasan et al. 2022). In addition, controlling pests using conventional insecticides has several appreciable advantages, including providing affordable and immediate pest reductions after application, thereby preventing significant pest-induced crop losses

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(Tarusikirwa et al. 2020). Although considerable efforts have been made to advocate for integrated pest management (IPM) programs, they are not adequately adopted to control *P. absoluta* across the region (Mansour et al. 2018, Srinivasan et al. 2022). Smallholder farmers may also have limited knowledge of IPM principles, such as pest identification, monitoring, prevention, and setting action thresholds, and thus resort to calendar-based insecticide applications to suppress pest populations (Colmenárez et al. 2022, Chepchirchir et al. 2023). These routine applications, often practiced throughout the tomato crop cycle, are costly for resource-constrained smallholder farmers (Rwomushana et al. 2019, Buragohain et al. 2021, Desneux et al. 2022).

Overreliance on (especially broad-spectrum) chemical insecticides is a principal concern due to potential associated adverse effects on beneficial insects, soil microbes, and other nontarget organisms (Hill et al. 2017, Rajak et al. 2023). In many sub-Saharan African countries, although pesticide use is regulated, counterfeit products are common in the market, coupled with other malpractices, including noncompliance with the label instructions, lack of or improper use of personal protective equipment, and unsafe disposal practices, impacting heavily on human health and the environment (Lykogianni et al. 2021, Tudi et al. 2021, Haggblade et al. 2023, Rajak et al. 2023, Yami et al. 2025). Additionally, the concealed feeding behavior of *P. absoluta* larvae protects them from exposure to contact insecticides, thus rendering several chemical pesticides ineffective (Agbessenou et al. 2020). The development of resistance among *P. absoluta* populations is also a contributing factor to the reduced control of the pest using conventional insecticides (Barati et al. 2018, Mansour et al. 2018, Aboutalebian-Soureshjani et al. 2023, Ma et al. 2024). Resistance results from, among other factors, repeated use of the same insecticide or insecticides with the same mode of action across multiple generations (Ong'onge et al. 2023, Prasannakumar et al. 2023). For instance, *P. absoluta* populations in Kenya have developed resistance to commonly used products such as emamectin benzoate, flubendiamide, and chlorantraniliprole (Ong'onge et al. 2023, Karanu et al. 2024). Further, Karanu et al. (2024) observed an exponential increase in resistance development, which is likely to render most commercially available insecticides ineffective against this pest.

Utilizing IPM strategies is a promising approach to suppressing *P. absoluta* populations while reducing the risks associated with the overuse of chemical insecticides (Buragohain et al. 2021, Desneux et al. 2022). Studies have also indicated that most tomato farmers are willing to adopt IPM strategies and technologies against this pest (Colmenárez et al. 2022, Chepchirchir et al. 2023). An ideal IPM program for *P. absoluta* comprises good agricultural practices, pheromone-based monitoring and mass trapping, host plant resistance, biological control using beneficial arthropods and microorganisms, and selective and judicious chemical control (Nderitu et al. 2020, Buragohain et al. 2021, Saeidi and Raeesi 2021, Desneux et al. 2022). Biological control using entomopathogenic fungi (EPFs) is a key component of IPM programs for *P. absoluta* (Rwomushana et al. 2019, Vivekanandhan et al. 2024b). These parasitic microbes are capable of infecting arthropods and possess several beneficial characteristics, including easy multiplication, host specificity, self-replication, and minimal risks of harmful residues (Liu et al. 2023).

Hypocrealean EPFs suppress the populations of insects such as fruit flies (Diptera: Tephritidae), aphids (Hemiptera: Aphididae), whiteflies (Hemiptera: Aleyrodidae), thrips (Thysanoptera: Thripidae), mealybugs (Hemiptera: Pseudococcidae), weevils (Coleoptera: Curculionidae), beetles (Coleoptera: Scarabaeidae), and the fall armyworm (Lepidoptera: Noctuidae) (De Faria and Wraight 2007, Ramanujam et al. 2020, Liu et al. 2023). Virulent strains in the genera *Metarhizium, Beauveria, Cordyceps* (formerly *Isaria* and *Paecilomyces*), *Purpureocillium, Akanthomyces* (previously *Lecanicillium* and *Verticillium*), and *Aspergillus* are also pathogenic to *P. absoluta* (Kepler et al. 2017, Akutse et al. 2020a, Chouikhi et al. 2022, Karaca et al. 2022, Zekeya et al. 2022a, 2022b). While most EPFs infect *P. absoluta* through the direct penetration of the cuticle, several *Beauveria, Metarhizium, Trichoderma*, and *Hypocrea* strains colonize tomato plants as endophytes, eliciting induced systemic resistance that enhances defense against the pest (Klieber and Reineke 2016, Agbessenou et al. 2020, Silva et al. 2020, Aynalem et al. 2022). Fungal strains capable of exhibiting pathogenicity through direct contact and endophytic colonization have been of great interest in recent studies, as they present a promising solution to manage *P. absoluta* larvae (Agbessenou et al. 2020, Zheng et al. 2023).

This review aims to provide information that promotes the use of EPFs as essential components of IPM programs for controlling *P. absoluta* across sub-Saharan Africa. The review discusses current knowledge on managing *P. absoluta* using EPFs and provides an overview of the multi-step process involved in commercializing these biocontrol products. The utilization of EPFs as components of IPM and their compatibility with other pest control methods have also been discussed. The review highlights several challenges hindering research, development, wide-scale commercialization, and adoption of EPFs and identifies strategies to address these issues. Additionally, the review discusses research innovations and technological advances to enhance the biocontrol activity of EPFs, as well as other strategic measures to increase their availability and adoption among farmers in sub-Saharan Africa.

Entomopathogenic Fungi as Biocontrol Agents of *Phthorimaea absoluta*

Research efforts in sub-Saharan African countries have been geared toward the isolation of indigenous strains of *Beauveria bassiana* (Balsamo-Crivelli) Vuillemin *sensu lato* and *Metarhizium anisopliae* (Metschnikoff) Sorokin *sensu lato* and the evaluation of their pathogenicity against different developmental stages of *P. absoluta*. For instance, 3 virulent strains of *B. bassiana* isolated in Sudan exhibited mortality rates of up to 99% in third instar larvae (Hammad et al. 2022). Twelve indigenous *B. bassiana* strains native to Ethiopia caused up to 95% mortality in second and third instar larvae (Aynalem et al. 2021). Despite the remarkable pathogenicity demonstrated by *B. bassiana* strains, most experiments have been conducted only under laboratory conditions (Ndereyimana et al. 2019, Erasmus et al. 2021, Hammad et al. 2022). Therefore, field efficacy evaluations are necessary to determine the conidial germination, sporulation, persistence, and infection potential of these fungal strains under various environmental influences.

Additionally, while many indigenous isolates exhibit biocontrol activity almost comparable to the commercial *B. bassiana*

(Bals.) Vuill. strain R444 (Erasmus et al. 2021, Hammad et al. 2022), their level of development and commercialization remains relatively limited. Moreover, commercial strains, including *B. bassiana* (Bals.) Vuill. strains BB02 and J25, which reported high insecticidal activity against the populations of *P. absoluta* larvae and pupae in Rwanda and South Africa, are not specifically registered to control the pest (Ndereyimana et al. 2019, Erasmus et al. 2021). For this reason, a coordinated region-wide approach is essential to develop and commercialize the potent indigenous isolates and undertake research toward label extension for the promising commercial strains of *B. bassiana* to authorize their use in managing *P. absoluta*.

Metarhizium anisopliae sensu lato is a promising biocontrol agent for *P. absoluta* in sub-Saharan Africa. In Ethiopia, 6 of 13 native *M. anisopliae* strains pathogenic to *P. absoluta* recorded mortality rates of 80% to 95% of the second and third instar larvae (Ayele et al. 2020). Twelve *M. anisopliae* strains indigenous to Kenya were found to be pathogenic to *P. absoluta*, with the highest mortality rates recorded in adult moths treated with ICIPE 18 (95%), ICIPE 20 (88%), and ICIPE 665 (86%) (Akutse et al. 2020a). Additionally, these Kenyan strains significantly reduced pupation of fourth instar larvae and subsequent emergence of adult moths, with 100% mortality rates recorded in *P. absoluta* larvae treated with ICIPE 18. Commercial strains of *M. anisopliae* (Metschn.) Sorok, namely FCM Ar 23B3, ICIPE 69, and E9, exhibited high pathogenicity toward *P. absoluta*, causing 83% larval mortality (FCM Ar 23B3) and pupal mortality of 89% (E9) to 90% (ICIPE 69) in Rwanda and South Africa (Ndereyimana et al. 2019, Erasmus et al. 2021). Table 1 lists commercial EPFs that have exhibited pathogenicity against *P. absoluta* populations in Africa.

Besides laboratory evaluations, greenhouse and field experiments demonstrated that *M. anisopliae*-AAUM78 and *B. bassiana*-AAUB03 strains, native to Ethiopia, reduced the pest's damage on tomato leaves and fruits, resulting in an increase in the marketable fruit yield (Aynalem et al. 2022). A field trial in Uganda validated the insecticidal activity of an *M. anisopliae* strain ICIPE 20 against *P. absoluta*, as indicated by reduced crop damage and improved tomato yield (Akutse et al. 2020a, Kabaale et al. 2022). In addition, a commercial *M. anisopliae* strain ICIPE 69, not previously registered for *P. absoluta* control, significantly reduced damage to tomato leaves and fruits, and minimized yield losses in Tanzania and Uganda (Kabaale et al. 2022, Zekeya et al. 2022a). Commercial formulations of *B. bassiana* and *M. anisopliae* possess a unique advantage in terms of broad-spectrum insecticidal activity (Ndereyimana et al. 2019, 2020, Erasmus et al. 2021, Kabaale et al. 2022), highlighting the need to prioritize their screening against *P. absoluta* and promote the immediate use of efficacious strains. Further, while many indigenous isolates of *B. bassiana* and *M. anisopliae* exhibit entomopathogenicity against the populations of *P. absoluta* in Ethiopia, Kenya, Rwanda, South Africa, Sudan, Tanzania, and Uganda, most studies are still in the research phase, with minimal efforts to validate the biocontrol efficacy of the promising strains and develop them to the commercial level. Therefore, there is a need to bridge the evident gap in the research and development of EPFs in sub-Saharan Africa and set up measures to accelerate their commercialization.

Additionally, harnessing the biocontrol activity of other virulent species reported worldwide, despite the predominance of *B. bassiana* and *M. anisopliae* strains in sub-Saharan Africa, is essential. Examples of promising biocontrol agents against *P. absoluta* include *Metarhizium robertsii* (Metchnikoff) Sorokin in Ethiopia (Geremew et al. 2024), *Akanthomyces lecanii* (Zimm.) Spatafora, Kepler & B. Shrestha (formerly *Lecanicillium (Verticillium) lecanii*) in Egypt and Zambia (Kepler et al. 2017, Abdel-Raheem et al. 2020, Mazimba et al. 2022), *Aspergillus oryzae* (Ahlb.) and *Aspergillus flavus* (Ahlb.) in Tanzania (Zekeya et al. 2019, 2022b), and *Purpureocillium lilacinum* (Thom) Luangsa-ard, Houbraken, Hywel-Jones, and Samson in Sudan (Hammad et al. 2022). Other EPFs with reported insecticidal activity against *P. absoluta* include *Metarhizium flavoviride* Gams and Roszypal, *Metarhizium rileyi* (Farlow) Kepler, S. A. Rehner and Humber, and *Cordyceps fumosorosea* (Wize) in China (Zheng et al. 2023), *Simplicillium obclavatum* (W. Gams) Zare and Gams in India (Bali et al. 2023), and *C.*

Table 1. Examples of commercial entomopathogenic fungi used against *Phthorimaea absoluta* in Africa. R1 and R2 are registered in Tanzania and South Africa, respectively, for use against *Phthorimaea absoluta* and other insect pests

Species	Strain/isolate	Trade name	Experimental site (country)	Reference
Akanthomyces (Lecanicillium) muscarium	Ve6	Mycota	Tunisia	(Kepler et al. 2017, Chouikhi et al. 2022)
Aspergillus oryzae	BCA/IN/0005	Vuruga^{R1}	Tanzania	(Zekeya et al. 2019, 2022b)
Beauveria bassiana	R444	Bb-Protec	Tunisia	(Chouikhi et al. 2022)
	R444	Eco-Bb^{R2}	South Africa	(Erasmus et al. 2021)
	R444	Eco-Bb^{R2}	Sudan	(Hammad et al. 2022)
	BB02	Real Beauveria	South Africa	(Erasmus et al. 2021)
	ATCC 74040	Naturalis	Tunisia	(Chouikhi et al. 2022)
	J25	Beauvitech	Rwanda	(Ndereyimana et al. 2019)
	GHA	Botanigard	Rwanda	(Ndereyimana et al. 2019)
Metarhizium anisopliae	FCM Ar 23B3	Metatech	Rwanda	(Ndereyimana et al. 2019)
	E9	Metarril	South Africa	(Erasmus et al. 2021)
	ICIPE 69	Real Metarhizium 69	South Africa	(Erasmus et al. 2021)
	ICIPE 69	Campaign	Uganda, Tanzania	(Kabaale et al. 2022, Zekeya et al. 2022a)

fumosorosea and *P. lilacinum* in Turkey (Karaca et al. 2022). An isolate of *Clonostachys* sp. in Algeria (Mohamed Mahmoud et al. 2021) and a commercial strain of *L. muscarium* Zare and Gams, strain Ve6 (*Akanthomyces muscarius* (Petch) Spatafora, Kepler & B. Shrestha, comb. nov.) in Tunisia also demonstrated insecticidal effects against *P. absoluta* (Kepler et al. 2017, Chouikhi et al. 2022). These studies underscore the significant potential for increasing the availability of diverse mycoinsecticides against *P. absoluta* through extensive bioprospecting for virulent EPFs in sub-Saharan African countries.

Entomopathogenic Fungal Activity against *Phthorimaea absoluta*

The primary mode of action for EPFs against insects involves infection and pathogenic mechanisms, which require significant quantities of conidia to attach and penetrate the cuticle of the target host (Jaronski 2010, Wraight et al. 2010, Aynalem et al. 2021, Saminathan et al. 2025). *Metarhizium anisopliae sensu lato* and *B. bassiana sensu lato* produce adhesin proteins *Mad1* and hydrophobin *Adh2*, respectively, which are linked to conidial adhesion (Zhou et al. 2021, Ma et al. 2023). Cuticular penetration is achieved by forming penetrative structures and the hydrolytic activity of cuticle-degrading enzymes (Mannino et al. 2019, Ma et al. 2023, Zhang et al. 2025). EPFs also secrete a variety of toxic secondary metabolites (Zhang et al. 2020b, Pedrini 2022) to facilitate invasion, disrupt the host's immune reactions and physiological processes, and cause paralysis. *Beauveria bassiana* strains secrete, among other toxins, beauvericin, beauverolides, and bassianolide, while the pathogenicity of *Metarhizium* strains is associated with the production of a variety of destruxins with varying levels of insecticidal activity and virulence (Mannino et al. 2019, Amobonye et al. 2020, Pedrini 2022). A comprehensive process of infection by EPFs against insects, including conidial germination, production of penetrative structures, adhesins, hydrolytic enzymes, and secondary metabolites, as well as colonization in the hemolymph and hyphal extension, and conidiogenesis, has been described (Mascarin and Jaronski 2016, Litwin et al. 2020, Saminathan et al. 2025).

A clear understanding of the diverse modes of action of EPFs, including the role of hydrolytic enzymes and secondary metabolites as virulence factors (Valero-Jiménez et al. 2016, Pedrini 2022, Karthi et al. 2024), is crucial for optimizing their insecticidal activity against *P. absoluta*. Virulence is typically associated with high intrahost growth rates and horizontal transmission of conidial infections, which induce significant mortality in the pest populations (Akutse et al. 2020a). Pathogenicity is also exhibited against all life stages of the pest (Vivekanandhan et al. 2024b). However, most studies investigating the insecticidal activities of EPFs have focused on the larvicidal effects, while little research has reported ovicidal (Chouikhi et al. 2022), pupicidal (Erasmus et al. 2021), and adulticidal (Akutse et al. 2020a) activities. Biological control of EPFs is achieved through the inundative application of fungal conidia via foliar sprays or soil drenches (Mascarin and Jaronski 2016, Erasmus et al. 2021, Kabaale et al. 2022). This approach, however, can expose the infective spores to unfavorable environmental variables, which negatively affect the field efficacy and persistence of most EPFs (Jaronski 2010, McGuire and Northfield 2020, Quesada-Moraga et al. 2024). For example, Agbessenou et al. (2021) demonstrated that temperature variability can limit the field applicability of 3 *M. anisopliae* strains, ICIPE 18, 20, and 665, which have previously proved pathogenic to *P. absoluta* within laboratory environments. Other environmental factors that negatively impact spore survival and entomopathogenicity in the field include sunlight, relative humidity, and rainfall (Jaronski 2010, Quesada-Moraga et al. 2024).

Fortunately, several EPFs colonize tomato plants endophytically and confer systemic resistance against *P. absoluta* (Agbessenou et al. 2020, Mohamed Mahmoud et al. 2021, Hammad et al. 2022, Zheng et al. 2023, Geremew et al. 2024). Using fungal endophytes can significantly reduce the adverse effects caused by abiotic stressors, including low infection rates and persistence in the field. However, relatively few endophytic strains have been reported in sub-Saharan Africa, underscoring the need to strengthen research and development efforts in this region. Fungal endophytes induce harmful effects on pests indirectly through nonpathogenic mechanisms, such as antibiosis, antixenosis, and induced systemic resistance (Akutse et al. 2020b, Bamisile et al. 2021a, Samal et al. 2022, Panwar and Szczepaniec 2024). They improve the growth of their host plants and promote protection against insect pests and pathogens by stimulating the production of secondary metabolites with pesticidal properties (Fadiji and Babalola 2020, Samal et al. 2022, Panwar and Szczepaniec 2024). Endophytic colonization is achieved using various artificial inoculation techniques, including foliar application, stem injection, soaking seeds, dipping seedling roots in conidial suspensions, and soil drenching, which exhibit variable levels of efficiency (Mantzoukas and Eliopoulos 2020, Silva et al. 2020, Zheng et al. 2023). For instance, seed soaking and soil drenching techniques were employed to endophytically colonize tomato plants with native strains of *B. bassiana* and *P. lilacinum* in Sudan (Hammad et al. 2022). Strains of *B. bassiana*, *Trichoderma* spp., *Fusarium proliferatum*, and *Hypocrea lixii*, native to Kenya, were inoculated in tomato plants through seed soaking (Agbessenou et al. 2020). However, in the same study, all the tested *M. anisopliae* strains failed to colonize tomato plants after seed inoculation. Nevertheless, an isolate of *M. anisopliae* in China demonstrated successful endophytic colonization in tomato plants using the seed coating method (Zheng et al. 2023). In Argentina, an endophytic *B. bassiana* was successfully inoculated in tomato plants using leaf spraying, seed inoculation, and root dipping techniques, with leaf spraying achieving the highest percentage of colonization (Allegrucci et al. 2017). Conversely, conventional inoculation techniques, including foliar application, seed soaking, soil drenching, and stem injection, failed to achieve endophytic colonization of a *B. bassiana* strain in Brazil, with seedling inoculation emerging as the only efficient technique (Silva et al. 2020). These laboratory evaluations emphasize the importance of sound knowledge of the taxonomic identity of fungal endophytes and their suitable inoculation techniques, which are essential for successful colonization and establishment in the target hosts.

Endophytic colonization can be systemic or localized within specific plant tissues (Bamisile et al. 2018, Mengistu 2020). In particular, foliar endophytes residing within leaf tissues play a significant role in minimizing crop damage through oviposition and feeding deterrence on tomato leaves, which are the preferential sites for *P. absoluta* (Desneux et al. 2010, Bamisile et al. 2018). Besides reducing crop damage, endophytic EPFs induce damaging effects on the pest's fitness and survival by negatively impacting its growth and development, fecundity, and reproductive output (Klieber and Reineke 2016, Agbessenou et al. 2020, Aravinthraju et al. 2024, Panwar and Szczepaniec 2024). For example, colonization of endophytic strains *B. bassiana* ICIPE 706, *Trichoderma asperellum* M2RT4, and *H. lixii* F3ST1 in tomato plants significantly reduced oviposition, leaf mining, pupation, and adult emergence of *P. absoluta* (Agbessenou et al. 2020). Further, Agbessenou et al. (2022) showed that the endophytic strain *T. asperellum* M2RT4 triggered the production of a key defense phytohormone (Z)-jasmone that reduced the leafmining activity of *P. absoluta* larvae and activated both the salicylic and jasmonic acid defense pathways. The ongoing research on endophytic colonization of EPFs presents a promising strategy for managing *P. absoluta*. However, field validation studies are required to ascertain their environmental competence and suitability as biocontrol agents. Continued research is necessary to advance our understanding of the biotic and abiotic factors that influence the colonization of endophytic EPFs (Bamisile et al. 2018, Mengistu 2020). Allegrucci et al. (2017) also noted that endophytic colonization in plant systems decreases over time, underscoring the need for further studies to assess their efficacy and persistence throughout the plant growth cycle. Additionally, the molecular mechanisms underlying endophyte-mediated resistance in tomato plants against *P. absoluta* remain to be determined. Multiple modes of action have been proposed, including the induction of systemic resistance through hormonal signaling, gene expression, and recognition of microbe-associated molecular patterns (Khare et al. 2018, Adeleke et al. 2022, Samal et al. 2022). Determining the action mechanisms of endophytic EPFs, besides the production of phytohormones (Agbessenou et al. 2022), within the tomato system is crucial for their application as biocontrol agents of *P. absoluta*.

Research and Development of Entomopathogenic Fungi for *Phthorimaea absoluta* Control

Isolation, Identification, and Pathogenicity Screening

The development of EPFs into commercial products is a multistep process that involves isolation, species identification, pathogenicity screening, field efficacy trials, mass production, formulation, toxicology and ecotoxicology testing, and product registration (Montesinos 2003, Samal et al. 2022, Chaudhary et al. 2024). The first step entails the isolation of EPFs from their natural habitats to obtain pure fungal cultures for subsequent procedures (Bali et al. 2022b, Dos Reis et al. 2022, Hammad et al. 2022). Hypocrealean EPFs are easily cultivated on artificial isolation media and mass-produced on artificial substrates (Akutse et al. 2020b, Rajula et al. 2020, Liu et al. 2023), making them valuable pest control agents against *P. absoluta*. The predominant *B. bassiana* and *M. anisopliae* strains are frequently isolated using the soil dilution plate method and cultured on selective media that favor the growth of the target fungus, while aseptic techniques are employed to minimize the growth of contaminants (Ayele et al. 2020, Aynalem et al. 2021, Hammad et al. 2022). Insect bait method using the larvae of the greater wax moth *Galleria mellonella* L. has also been employed to selectively isolate EPFs from soil samples, including *Beauveria*, *Metarhizium*, *P. lilacinum*, and *S. obclavatum* species (Ayele et al. 2020, Bali et al. 2022b, Hammad et al. 2022, Bali et al. 2023). Endophytic EPFs are mainly isolated from plant tissues using the classical fragment plating technique, which involves surface sterilization and culturing of small plant fragments on artificial media (Mohamed Mahmoud et al. 2021, Dos Reis et al. 2022, El-Maraghy et al. 2023, Liao et al. 2025).

Although classical cultivation methods are instrumental in fungal isolation, many pathogenic and endophytic taxa of EPFs are unculturable, while some cultured isolates do not grow properly on artificial media, showing very low sporulation or endophytic colonization rates, often inadequate for subsequent bioassays (Bamisile et al. 2021b, Dos Reis et al. 2022, Liu et al. 2023, Liao et al. 2025). Slow growth rates of fungal cultures, inadequate production, and low-quality conidia are among the major limiting factors to the development and commercialization of most EPFs (Faria et al. 2015, Muñiz-Paredes et al. 2017, Liao et al. 2025). Consequently, the drawbacks of traditional techniques limit the potential applications of EPFs in insect pest management programs. This necessitates the exploration of complements, such as culture-independent methods and other advancing technologies, to increase the diversity of exploitable isolates. The traditional approaches of isolating EPFs in pure cultures are also labor-intensive and skill-intensive, requiring a lot of manual handling activities (Ayele et al. 2020, Bali et al. 2022b). Additionally, fungal cultures are prone to contamination from other microorganisms if not produced and maintained under sterile conditions. Another obstacle to the successful inoculation and colonization of fungal endophytes in the target host plants involves ineffective surface sterilization procedures (Dos Reis et al. 2022, Liao et al. 2025). These challenges highlight the need for innovative approaches to improve the isolation procedures and maximize the exploitation of a broad arsenal of EPFs against *P. absoluta*.

Accurate species identification of isolated EPFs and their corresponding strains is crucial for their exploitation in pest control. The identification of pathogenic and endophytic fungal isolates is based primarily on adequate observation of their essential macroscopic and microscopic morphological characteristics (Agbessenou et al. 2020, Akutse et al. 2020a, Dos Reis et al. 2022, Hammad et al. 2022, Bali et al. 2023, El-Maraghy et al. 2023, Vivekanandhan et al. 2024a). Therefore, adequate knowledge of key diagnostic characteristics, such as colony morphology and the size and shape of conidia of different fungal species, is of the utmost importance to accurate identification of EPFs. Molecular biology techniques are also progressively being employed to complement classical light microscopy in the characterization of pathogenic and endophytic species (Ayele et al. 2020, Aynalem et al. 2021, Bali et al. 2022b, Dos Reis et al. 2022, Hammad et al. 2022). The combined use of classical microbiological methods and molecular techniques is necessary for subsequent analyses of pure cultures, including genetic variability and phylogenetics, whole genome sequencing and functional genomics studies, as well as elucidating the molecular mechanisms underlying pathogenicity and endophytism of EPFs (Gebremariam et al. 2021, Wang et al. 2021, Dos Reis et al. 2022, Hammad et al. 2022, Ayilara et al. 2023). Employment of fungal metagenomics also provides insights into the diversity, community structure, and interactions of fungi within their natural ecosystems and envisages suitable locations for microbial bioprospecting of EPFs (Dos Reis et al. 2022, Sun et al. 2022).

Robust pathogenicity screening allows for the selection of virulent strains that can effectively suppress pest populations. Standard protocols are followed to determine pathogenicity and select suitable candidates for field efficacy evaluations, as evidenced by conidial germination and proliferation, extensive hyphal growth on infected insects, and fungal-induced mortality (Mwamburi 2016, Agbessenou et al. 2020). Accordingly, studies investigating pathogenicity report the biological characteristics of EPFs, such as conidial viability, vegetative growth, germination and sporulation rates, pathogenesis, and virulence (Ayele et al. 2020, Aynalem et al. 2021, Gebremariam et al. 2021). Besides selecting efficacious fungal strains for development, the screening procedure also helps determine the optimal number of spores at which the highest mortality rates of the pest are achieved, as well as estimate the best concentrations to make a lethal infection for field applications (Aynalem et al. 2021, Erasmus et al. 2021). Screening also involves characterizing isolates based on their biochemical properties, particularly the production of cuticle-degrading enzymes such as proteases and chitinases (Hussien et al. 2021, Mohamed Mahmoud et al. 2021, El-Maraghy et al. 2023). Crucial characteristics for defining the virulence of endophytic fungi include conidial viability, colonization rates, improved plant defense, and reduced pest damage (Klieber and Reineke 2016, Agbessenou et al. 2020, Aravinthraju et al. 2024). By using molecular approaches, classical methods employing germination assessment can be complemented by quantitative real-time PCR, which has a potential application in evaluating spore viability by identifying target genes and quantifying their expression during conidial germination and entomopathogenesis (Chen et al. 2018). Additionally, important functional genes involved in virulence can be identified through transcriptome analysis of differential gene expression (Chen et al. 2018, Ding et al. 2020). Mass spectrometry-based proteomics can also provide further insights into the functional role of proteins involved in the infection process (Bali et al. 2022a).

Field Efficacy Evaluation of Entomopathogenic Fungi

High efficacy and good persistence in the field are among the essential factors to guarantee the effectiveness of EPFs. Therefore, efficacy achieved within controlled laboratory conditions requires field validation studies that consider EPFs as components of ecosystems. This is because the performance of most strains is subject to environmental influences, including temperature, relative humidity, rainfall, solar ultraviolet (UV) radiation, and oxidative and osmotic stressors (Jaronski 2010, De Jesus Seabra et al. 2024, Quesada-Moraga et al. 2024). Variations of these pertinent environmental parameters within agroecosystems negatively impact the virulence of EPFs, limiting their use at a commercial level. For instance, deviations from the optimal growth temperatures limit the virulence and persistence of *Beauveria* and *Metarhizium* strains, characterized by reduced rates of conidial germination, vegetative growth, sporulation, and survival (Acheampong et al. 2020a, Agbessenou et al. 2021). Additionally, exposure of EPFs to UV radiation has adverse effects on conidial germination, efficacy, and persistence in the field (Braga et al. 2015, Fernandes et al. 2015, Acheampong et al. 2020b). However, studies have also reported UV-tolerant strains (Braga et al. 2015, Fernandes et al. 2015), which serve as suitable candidates for the development of commercial biocontrol agents. Other environmental factors influencing the virulence of EPFs have been identified (Jaronski 2010, Wu et al. 2020). Unfortunately, little information is available on the influence of environmental variables on conidial infectivity and persistence of EPFs with promising biocontrol activity against *P. absoluta*. A better understanding of their tolerance to different environmental conditions can ensure optimized field efficacy and facilitate the exploitation of more effective strains.

Additionally, optimal performance and persistence of EPFs in the field can be achieved by employing temperature-dependent modelling and spatial predictions to identify suitable areas for their use (Agbessenou et al. 2021, Boaventura et al. 2025). These predictive mathematical models can be used to assess the optimum temperature for the growth of EPFs as well as model and predict their virulence against the targeted pest populations under different environmental influences. Agbessenou et al. (2021) showed that different agroecological zones in Kenya, Tanzania, and Uganda have conducive temperature regimes for optimal growth and virulence of *M. anisopliae* strains ICIPE 18 and 20. Their findings are particularly relevant to the application of *M. anisopliae*-based mycoinsecticides for managing *P. absoluta* and other insect pests in the region (Tumuhaise et al. 2018, Akutse et al. 2020a, Kabaale et al. 2022, Zekeya et al. 2022a). Most importantly, *Beauveria* and *Metarhizium* strains exhibit significant intraspecific genotype and phenotype variability, which affects, among other things, their virulence potential under varied field conditions (Agbessenou et al. 2021, Quesada-Moraga et al. 2024). Therefore, evaluating the environmental tolerance of each candidate strain selected for biological control of *P. absoluta* and modelling their environmental suitability can guarantee the development of effective mycoinsecticides to control this pest.

Mass Production and Formulation of Entomopathogenic Fungi

Fungal strains selected for mycoinsecticide development must demonstrate the capacity for mass production, indicated by rapid fungal growth and high sporulation rates, to ensure sufficient amounts of conidia for inundative releases (Muñiz-Paredes et al. 2017, Mascarin et al. 2024a). Most mycoinsecticidal products are mass-produced through solid-state fermentation to produce aerial conidia on starch-rich substrates (Mascarin and Jaronski 2016, Jaronski and Mascarin 2017, Méndez-González et al. 2022). However, several studies have proposed the employment of submerged liquid fermentation to produce infective propagules, such as blastospores, submerged conidia, and microsclerotia (Jaronski and Mascarin 2017, Silva et al. 2022, Mascarin et al. 2024a). Other studies have explored biphasic fermentation, where solid- and liquid-state fermentations are combined to mass-produce dry aerial conidia from blastospore-based inoculum (Seema et al. 2013, Santos et al. 2021, Gao et al. 2025). Overall, for the commercial development of EPFs, the preferred method of mass production must ensure the delivery of adequate quantities of high-quality conidia or other infective propagules. Other critical success factors to consider for commercial production of EPFs include, among others, ease of scalability and downstream processing, efficient and cost-effective processes, reduced processing time, minimal risks of microbial contamination, and sustained conidial stability with repeated subculturing (Hussien et al. 2021, Méndez-González et al. 2022, Mascarin et al. 2024a, Gao et al. 2025). Additionally, while most hypocrealean EPFs are relatively easy to produce in large quantities, there is a need to explore technological innovations to facilitate the mass production of entomophthoralean species, which also have a high potential for insect pest control but are more challenging to mass-produce using the classical methods (Mascarin et al. 2024a).

Besides selecting effective fungal strains with high environmental tolerance, mycoinsecticide development also demands formulations that maintain the storage stability of infective propagules, strengthen their infectivity, and protect them from environmental influences (Lei et al. 2022, 2023, Méndez-González et al. 2022, Mathulwe et al. 2023, Saminathan et al. 2025). The most common formulations of EPFs include powders, liquids, and granules (Akutse et al. 2020b, Saminathan et al. 2025). However, considering climate change effects encompassing rising temperatures and extreme rainfall as well as potential sensitivity of EPFs to climate variability and other abiotic stressors (Acheampong et al. 2020a, 2020b, Rangel et al. 2023, Saminathan et al. 2025), innovative formulations are increasingly developed to improve their biocontrol activity and shelf life, and provide natural protection against the stressors (Paixão et al. 2017, Chaudhary et al. 2024, Quesada-Moraga et al. 2024). For instance, oil-based formulations, including emulsions and vegetable and mineral oils, have several advantages, including enhanced efficacy, improved tolerance against UV radiation and high temperatures, improved adhesion of spores to the pest cuticle, and increased persistence in the field (De Oliveira et al. 2018, Kaiser et al. 2019, Acheampong et al. 2020b, Lei et al. 2022, 2023, Saminathan et al. 2025). Formulations based on emulsifiable oils can also offer EPFs a significant protective effect against certain chemical fungicides (Lopes et al. 2011, Samal et al. 2023). Additionally, the utilization of biopolymer-based formulations of EPFs incorporating alginate, starch, and chitosan is essential to safeguard the viability and infectivity of conidia against environmental stressors and enhance product stability (Felizatti et al. 2021, Baldiviezo et al. 2023, Friuli et al. 2023, De Jesus Seabra et al. 2024).

Formulations of EPFs can be applied as foliar sprays to target the egg and larval stages of *P. absoluta* or as soil drenches targeting the late larval instars and pupae (Akutse et al. 2020a, Erasmus et al. 2021, Kabaale et al. 2022, Irsad et al. 2023). Further, Erasmus et al. (2021) observed that soil drenches suppressed the emergence of *P. absoluta* adult moths and reduced the fecundity of females emerging from the affected pupae. These authors also reported that emulsifiable suspensions of *B. bassiana* and *M. anisopliae* caused higher mortality of *P. absoluta* pupae than wettable powders, supportive of the phenomenon that oily formulations exhibit improved bioefficacy compared to water-based suspensions (Paixão et al. 2017, Acheampong et al. 2020b). While the observed differences in pupal mortality could also be attributed to varying efficacy levels of the strains studied (Agbessenou et al. 2021, Quesada-Moraga et al. 2024), previous studies corroborate that oil-based formulations maintain the viability and pathogenicity of EPFs and enhance their tolerance against high temperatures and UV radiation (De Oliveira et al. 2018, Kaiser et al. 2019, Mathulwe et al. 2023).

Other vital factors to consider during the mass production and formulation of EPFs are the inoculum delivery approach and suitable preservation methods. Screening for the most effective inoculation technique is essential to inform the best mode of application and achieve optimal field efficacy. For instance, foliar spraying of endophytic *B. bassiana* strains can achieve dual biocontrol activity against *P. absoluta*, characterized by colonization in tomato plants and infectivity of the larval instars (Klieber and Reineke 2016, Mohamed Mahmoud et al. 2021). Although other inoculation techniques, such as seed inoculation, are effective in delivering fungal inoculum, most commercial formulations are applied as foliar sprays, perhaps due to the relative ease of application, as most farmers are accustomed to using sprayable chemical insecticides. Nevertheless, Akutse et al. (2020a) proposed the field application of dry conidia of *M. anisopliae* through an autodissemination device in an "attract and infect" approach to target the adult moths of *P. absoluta*. Erasmus et al. (2021) also recommended the application of *B. bassiana* and *M. anisopliae* conidia as soil drenches to target the pupation phase of the pest.

Commercialization and Registration of Entomopathogenic Fungi for *Phthorimaea absoluta* Control

After selecting a suitable fungal strain, the following steps involve registering and introducing the mycoinsecticide to the market. In the recent past, the path to successful commercialization in sub-Saharan Africa has proved challenging due to biological constraints inherent to EPFs and other technological and regulatory limitations. This also explains the significant gaps in laboratory-based research on EPFs, efficacy evaluations at semi-field and field conditions, and the development of commercial products in the region. There are a few products registered for *P. absoluta* control, despite the worldwide availability of commercial strains of *Beauveria, Metarhizium, Akanthomyces* (*Lecanicillium*), and *Cordyceps* (*Isaria)* species (Table 1) (Kepler et al. 2017, Maina et al. 2018, Akutse et al. 2020b, Bamisile et al. 2021a). This highlights the need to strengthen the research for the development of mycoinsecticides in sub-Saharan Africa. Nevertheless, countries like South Africa and Tanzania have achieved significant progress in developing and commercializing EPFs against *P. absoluta*, such as *A. oryzae* and *B. bassiana* strain R444 (Table 1) (Erasmus et al. 2021, Zekeya et al. 2022b). Akutse et al. (2020b) also reported that, by 2020, several strains of *M. anisopliae*, *H. lixii*, and *Trichoderma* species, native to Kenya, were in the development pipeline for commercial use against *P. absoluta*.

Among the critical factors to consider when selecting a commercial strain are high conidial vigor and pathogenicity, capacity for mass production, storage stability, and environmental competence to ascertain conidial viability and high rates of virulence and infectivity under field conditions (Faria et al. 2015, Akutse et al. 2020a, Agbessenou et al. 2021, Quesada-Moraga et al. 2024). Further, given that mycoinsecticides face substantial competition from chemical pesticides, their success in the market hinges on efficacy and cost-effectiveness, which foster their commercial interest and user acceptance among the public. Fortunately, recent advances in mass production and formulation technologies for EPFs have overcome several challenges related to field efficacy and persistence of mycoinsecticides, thereby stimulating their commercial development. Another critical factor for a successful mycoinsecticide is its commercial viability, which is mainly determined by its production efficiency (Chaudhary et al. 2024). This factor underscores the need for optimized and cost-effective mass production and formulation processes to maximize product efficacy, minimize production costs, and generate sustainable revenues.

Unfortunately, while there is a growing commercial interest in mycoinsecticides, several inherent attributes of EPFs limit their broad utility. These include short shelf life under non-refrigerated conditions, potential degradation of live inoculum during storage and transportation, and unstable biocontrol effects (Faria et al. 2015, Kumar et al. 2021). Proper preservation methods can overcome these limitations by maintaining the genetic integrity of conidial cultures over time and guaranteeing the reliable availability of commercial formulations and viable stocks for mass production (Oliveira et al. 2011, Ayala-Zermeño et al. 2023). Common preservation methods include constant subculturing, storage in distilled water, mineral oil, saline solution, or grains at room temperature, cool storage, and deep freezing (Oliveira et al. 2011). Freeze-drying, ultra-freezing, and cryopreservation are the best methods for the long-term preservation of fungal cultures (Ayala-Zermeño et al. 2023, Saminathan et al. 2025), although their usage is restricted due to high costs. Proper drying of conidia after harvesting is also crucial for a good shelf life and stability of EPFs (Jaronski and Mascarin 2017). This is particularly relevant in sub-Saharan Africa, as solid-state fermentation is currently the primary mass production method of aerial conidia for commercial use, and the fermentation process can encompass low-technology bioreactors for the small- to medium-sized enterprises, or high-technology bioreactors for the large multinational companies (Jaronski and Mascarin 2017, Méndez-González et al. 2025). The production of microsclerotial granules also holds promise for storage-stable formulations with sustained shelf life under cool temperatures and unrefrigerated storage conditions (Jaronski and Mascarin 2017, Mascarin et al. 2024a). Jeong et al. (2022) also recommended using modified atmosphere packaging technology to extend the shelf life of fungal conidia. Moreover, encapsulated formulations of *B. bassiana* and *M. anisopliae* are being developed, exhibiting enhanced bioinsecticidal activities and extended shelf life beyond the typical 3 to 6 months (Felizatti et al. 2021, Sarma et al. 2023, De Jesus Seabra et al. 2024, Shahbaz et al. 2024).

Mycoinsecticides, like other pest control products, are subject to registration and approval. The regulatory frameworks and registration regulations for new products vary by country but can be drafted in alignment with global standards, such as the Organisation for Economic Co-operation and Development guidelines (Ashaolu et al. 2022, Karaoğlan et al. 2024). The registration process, conducted by a regulating authority, evaluates scientific data demonstrating the product's efficacy and performs risk assessments to ensure the safety of the fungal strain involved (Karaoğlan et al. 2024). An application package for biopesticide registration includes, among other things, a comprehensive technical dossier consisting of the identity and biological attributes of the fungus, efficacy trials and performance data demonstrating efficacy on the target pest, risk assessment analyses on toxicological and ecotoxicological effects, and compliant label recommendations. After assessment and meeting the regulatory standards, the mycoinsecticide is approved for sale and use. Lengthy and costly registration procedures, as well as other limitations imposed by policies and regulations, are among the constraints for the wide-scale commercialization of EPFs, contributing to few products on the market across sub-Saharan Africa (Ndolo et al. 2019, Ashaolu et al. 2022). Nevertheless, several countries have made efforts to navigate the regulatory barriers for microbial biopesticides, as evidenced by the development of certain research results into commercial products (Akutse et al. 2020a, 2020b, Zekeya et al. 2022a, 2022b). Moreover, aligning regulatory frameworks with international standards and harmonizing registration regulations within the region can improve the registration process for EPFs and help overcome some of the regulatory hurdles for all the involved countries (Ndolo et al. 2019, Ashaolu et al. 2022).

Utilization of Entomopathogenic Fungi as Components of IPM in *Phthorimaea absoluta* Control

Exclusive use of mycoinsecticides is often insufficient to control *P. absoluta* effectively, and, therefore, for sustainable management of this pest, an integrated approach is necessary. This requires a better understanding of the compatibility potential of the virulent strains with different pest control methods to develop practical IPM strategies that effectively reduce the pest's damaging effects. These include pheromone-based mass trapping, arthropod and microbial control agents, cultural control practices, and chemical control using selective insecticides (Mansour et al. 2018, Desneux et al. 2022). Besides integrating EPFs with these pest control tools, adequate knowledge and resources are required to develop and implement the IPM programs, as well as effective communication tools for knowledge dissemination (Dara 2019). This knowledge is also essential for achieving optimal synergistic or additive interactions and avoiding antagonism between IPM components. For example, a combination of an *M. anisopliae* strain and egg endoparasitoid *Trichogramma brassicae* Bezdenko yielded an additive effect on *P. absoluta* egg mortality when applied sequentially and a synergistic effect when applied simultaneously (Nozad-Bonab et al. 2021). Similarly, Mama Sambo et al. (2022) observed that a sequential combination of an *M. anisopliae* strain and a larval endoparasitoid *Dolichogenidea gelechiidivoris* (Marsh), whereby the fungus was first applied to an infested tomato plant, followed by the release of the parasitoid, had an additive impact that yielded high mortality of *P. absoluta*. Additionally, the combined application of a *B. bassiana* strain and a larval ectoparasitoid, *Necremnus tutae* Ribes & Bernardo, showed an additive effect on the larval mortality of *P. absoluta* (Lisi et al. 2024). These laboratory evaluations demonstrate that EPFs and parasitoids are compatible, and the complementary utilization of these 2 biocontrol agents can potentially increase the efficacy of IPM programs for *P. absoluta*.

Integrating different fungal species has proven successful for *B. bassiana* and *M. anisopliae* strains in controlling *P. absoluta*. These strains have targeted insect pests (De Faria and Wraight 2007, Maina et al. 2018, Akutse et al. 2020b), and their compatibility with other microbial agents and arthropod biocontrol agents can broaden their insecticidal spectra within IPM programs to target a greater number of insect pests attacking tomato plants. Aynalem et al. (2022) reported that the field application of *B. bassiana* and *M. anisopliae* strains on tomato plants enhanced their insecticidal efficiency against the pest, resulting in significant reductions in leaf and fruit damage. Further, the authors demonstrated that fungal strains are compatible with the bacterium Bacillus *thuringiensis*, and a consortium of fungal and bacterial biocontrol agents, applied with a relatively lower dose of chlorphenapyr insecticide, significantly reduced *P. absoluta* infestations. However, more caution is necessary when combining chemical insecticides and EPFs, as several active ingredients inhibit the growth and development of the latter (Alizadeh et al. 2007, Roberti et al. 2017, Litwin et al. 2020). For instance, copper-based fungicides, mostly recommended in IPM programs, require further compatibility studies to understand their interaction with mycoinsecticides, as research has demonstrated some toxic effects of copper oxide on EPFs (Kouassi et al. 2003, Celar and Kos 2020, Litwin et al. 2020).

Several studies have reported negative effects of fungicides on the germination, sporulation, and survival rates of *Metarhizium, Beauveria, Cordyceps* (*Isaria*), *Purpureocillium*, and *Akanthomyces* (*Lecanicillium*) strains (Silva et al. 2013, Kepler et al. 2017, Samal et al. 2023, Aravinthraju et al. 2024). Moreover, exposure to certain chemical pesticides, often regarded as compatible with EPFs, was reported to reduce the growth of *B. bassiana* and *M. anisopliae* strains, thus necessitating integration at sublethal doses to suppress their damaging effects on the biocontrol agents (Alizadeh et al. 2007, Silva et al. 2013, Nasiya-Beegum and Madhu 2019, Gavya et al. 2023, Aravinthraju et al. 2024). While a few studies have explored the compatibility of EPFs with chemical insecticides against *P. absoluta*, research on other insect pests has shown that their combined applications have varied outcomes, including additive, synergistic, and antagonistic effects on the mortality of the target pest (Nawaz et al. 2022, Ribeiro et al. 2023, Samal et al. 2023, Dearlove et al. 2024). The synergistic effects on *P. absoluta* control could be optimized further by the integrative use of compatible chemical pesticides at sublethal concentrations and ensuring adequate application intervals between biological and chemical pest control (Samal et al. 2023, Aravinthraju et al. 2024). This literature underscores the need for more specialized research on *P. absoluta* to understand the interaction of potent EPFs with chemical pesticides, commonly used against tomato pests and diseases, as their compatibility is based on several pertinent variables, including species and strain selection, the active ingredient and concentration of chemical pesticide(s) applied, and the timing of applications.

Previous studies have demonstrated that *M. anisopliae* strains ICIPE 18, 20, 69, and 665 are compatible with commercial sex pheromone lures for *P. absoluta* (Akutse et al. 2020a, Zekeya et al. 2022a). Thus, both present essential components of IPM programs. In addition, a combined application of commercial *B. bassiana* and azadirachtin formulations significantly reduced the levels of *P. absoluta* infestation on tomato leaves and fruits, achieving a high crop yield under greenhouse conditions in Kuwait (Jallow et al. 2019). These findings establish that EPFs and botanical insecticides are compatible components within IPM programs. The concentration of each bioinsecticide applied, however, should be considered carefully to achieve good mycoinsecticides-botanicals compatibility and maximal control of the pest, as dose-dependent interactions, yielding both positive and negative results, have been observed between a strain of *B. bassiana* and pyrethrum in the control of fall armyworm larvae (Harte et al. 2024). The studies discussed herein indicate that when determining the best combinations to develop an effective and feasible IPM program for *P. absoluta*, it is necessary to consider all suitable control methods, such as parasitoids, pheromone-based monitoring and mass trapping, botanicals, and compatible pesticides. Overall, the successful incorporation of EPFs as an integral component of IPM programs requires concerted efforts to leverage their prospects of compatibility with these pest control methods (Bamisile et al. 2021a, Smagghe et al. 2023, Aravinthraju et al. 2024, Rivera-Alonso et al. 2024, Vivekanandhan et al. 2024b).

Challenges Limiting Research, Development, Wide-Scale Commercialization, and Utilization of Entomopathogenic Fungi

Based on the literature discussed herein, many challenges, including biological, technological, and regulatory constraints, hinder the research, development, commercialization, and registration of EPFs as biocontrol agents. Furthermore, their utilization is still limited due to market challenges, such as limited accessibility and availability of products, as well as low user acceptance. Overcoming these challenges is necessary to fully realize the biocontrol potential of EPFs against *P. absoluta*.

Primarily, cost-effective and efficient mass production of EPFs remains critical for a continuous and sufficient supply of good-quality inoculum (Mascarin and Jaronski 2016, Akutse et al. 2020b). However, repeated mass production, involving successive subculturing of fungal strains in artificial medium, can lead to phenotypic degeneration of cultures, altered genetic make-up, and reduced conidial yield and virulence (Oliveira et al. 2011, Muñiz-Paredes et al. 2017, Hussien et al. 2021, Behle et al. 2023), rendering the products commercially unviable. Another problem in the mass production of EPFs is the susceptibility of the fungal inoculum to microbial contaminants, resulting in a consequent reduction in field performance (Mascarin et al. 2024a). These challenges underscore the importance of technical capacity and strict adherence to standardized protocols and quality control procedures to ensure consistent and replicable outcomes, prevent the proliferation of contaminants on the culture media, and maintain high conidial quality and viability (Mwamburi 2016, Agbessenou et al. 2020, Hammad et al. 2022). Sensitivity to abiotic stressors and consequent variability of field efficacy and persistence (Wu et al. 2020, Rangel et al. 2023, Quesada-Moraga et al. 2024) are also major limiting factors for commercial mycoinsecticides. Further, their formulations constitute living preparations of fungal inoculum that require specific storage facilities to maintain their conidial viability, thereby limiting their utility in remote areas (Rangel et al. 2023). Their inherent short shelf life at room temperature is also a significant bottleneck in the development and commercialization of EPFs.

Substantial capital investments and the requirement for controlled and sterile mass production and formulation environments impede the commercial production of mycoinsecticides, particularly for small- to medium-sized enterprises (Rajula et al. 2020, Mascarin et al. 2024a). Consequently, limited availability and relatively high prices of mycoinsecticides limit consumer acceptance, particularly among small-scale farmers primarily involved in tomato production in sub-Saharan Africa. To improve their availability at national and regional levels, it is necessary to support the utilization of feasible mass production techniques, such as solid-state and biphasic fermentations of effective *B. bassiana* and *M. anisopliae* strains (Seema et al. 2013, Jaronski and Mascarin

2017, Akutse et al. 2020b). Additionally, local production systems, involving small-scale production by farmers and cottage industries, offer avenues to improve the availability of EPFs among locals at relatively low cost (Harman et al. 2010, Seema et al. 2013). Given that EPFs are inundative biocontrol agents, repeated applications are required to suppress recurring *P. absoluta* populations effectively, which can significantly increase crop protection costs and make competing products more viable for farmers. Additionally, mycoinsecticides have slower biocontrol effects (Maina et al. 2018, Rajula et al. 2020) than fast-acting chemical insecticides, negatively influencing farmers' preferences. Moreover, due to environmental influences, most EPFs display inconsistent field performance (Kumar et al. 2021, Quesada-Moraga et al. 2024).

Further, while the host specificity of EPFs makes them ideal candidates in biological control due to the targeted selection of insect pests and minimal side effects to nontargets (Maina et al. 2018, Akutse et al. 2020b, Zhang et al. 2025), this trait can also be a disadvantage that limits the broad applicability of fungal strains with narrow host ranges compared with broad-spectrum insecticides. For this reason, the selection of EPFs for *P. absoluta* control needs to favor generalist strains, including *B. bassiana*, *C. fumosorosea*, and *M. anisopliae*, that exhibit pathogenicity not only to the target pest but also to multiple pest species attacking tomato plants (De Faria and Wraight 2007, Ndereyimana et al. 2019, Erasmus et al. 2021). Effective implementation of IPM programs for *P. absoluta* also requires optimized EPFs-chemical insecticides combinations for synergistic action against the pest. While several pesticide active ingredients act synergistically with EPFs, others inhibit conidial germination and growth, thereby adversely impacting IPM. Besides, limited information is available on the potential synergistic or antagonistic interactions between EPFs and chemical insecticides commonly used against *P. absoluta*. Considering that compatibility is product-specific, screening procedures, both in vitro and field trials, should be prioritized to inform the acceptable doses of chemical insecticides, optimal conditions for germination and mycelial growth, tolerance to various active ingredients, and the selection of the best combinations with minimal or no suppressive effects. Additionally, adequate knowledge of proper application techniques and suitable intervals is required, as most EPFs are sensitive to chemical pesticides, and positive pest control outcomes can only be achieved when these 2 products are applied appropriately (Aynalem et al. 2022, Nawaz et al. 2022). For example, applying EPFs a few days before applying chemical insecticides synergizes the insecticidal activity of the fungal strains (Kouassi et al. 2003, Aravinthraju et al. 2024). It is also important for farmers to read and follow the directions on product labels for both mycoinsecticides and chemical insecticides, particularly regarding compatibility and required intervals, to optimize their efficacy against the pest. The application method, seed inoculation or foliar sprays, is equally important for the successful colonization of endophytic EPFs within plant tissues.

Despite mycoinsecticides being considered safe owing to their minimal adverse effects on human health, nontarget organisms, and the environment, associated biosafety concerns of several EPFs that produce secondary metabolites with hazardous effects (Zekeya et al. 2019, Zhang et al. 2020b, Bamisile et al. 2021a, 2021b, Wang et al. 2021, Wend et al. 2024) need to be addressed through case-by-case risk assessments to ascertain their safety. Other challenges, besides technical hurdles, include a lack of adequate regulatory frameworks to support EPFs in most sub-Saharan African countries, and inadequate knowledge of the mode of action and use of mycoinsecticides, as well as practical inexperience among farmers (Ndolo et al. 2019, Ashaolu et al. 2022, Chepchirchir et al. 2023). Barriers to obtaining regulatory approvals, such as high costs of product registration, restrictive regulations, and lengthy procedures, can prevent promising fungal strains from reaching the commercial level (Harman et al. 2010, Ndolo et al. 2019, Ashaolu et al. 2022) and hence should be addressed to accelerate the commercialization of potent EPFs in the region.

Strategies for Advancing Research, Development, Commercialization, and Utilization of Entomopathogenic Fungi

The essential role of EPFs in controlling *P. absoluta* in modern agriculture underscores the importance of a range of research advancements and innovative strategies to overcome the challenges presented herein and open up new paradigms in mass production, formulation, and commercialization of both pathogenic and endophytic strains (Fig. 1). Most importantly, the success of biotechnological innovations to advance EPFs will require support from the governments and favorable regulatory environments. Therefore, it is necessary for sub-Saharan African countries to develop and implement robust regulatory frameworks and policies supportive of EPFs and IPM innovations to drive the development and commercialization of mycoinsecticides as well as improve their affordability and use across the region (Ndolo et al. 2019, Srinivasan et al. 2022). While most countries have limited access to innovative technologies, there is a need to leverage international collaborations with developed countries for increased knowledge and technology sharing in relation to the research and development of EPFs. Additionally, strategic collaborations between researchers and local governments, as well as the private sector, are pivotal to the commercial success of EPFs (Harman et al. 2010, Akutse et al. 2020b).

Adequate funding is necessary to overcome the challenges related to the high costs of acquiring, implementing, and scaling up innovative technologies, as well as to advance the research and development of EPFs. For example, financial resources are required to sustain innovative microbiological techniques for improving spore yield and infectivity of fungal cultures. Supportive measures are also necessary to bridge the significant gap between basic and applied research of native EPFs in sub-Saharan Africa and promote their development to the level of commercial production. Laboratory research has demonstrated that sub-Saharan Africa has a diverse array of species and strains that can be developed to increase the chances of success of biological control of *P. absoluta* populations within the region. This is due to the anticipated temporal and geographic congruence of isolated indigenous EPFs, their potential tolerance to environmental influences, and consequently, their desirable field efficacy and persistence (Agbessenou et al. 2021, Quesada-Moraga et al. 2024). The use of region-specific strains also circumvents the possible environmental inadaptability of the introduced strains (McGuire and Northfield 2020, Agbessenou et al. 2021, Quesada-Moraga et al. 2024).

Advances in biotechnology hold promising solutions to addressing the technological challenges limiting the efficiency of EPFs by improving their conidial viability, virulence, shelf

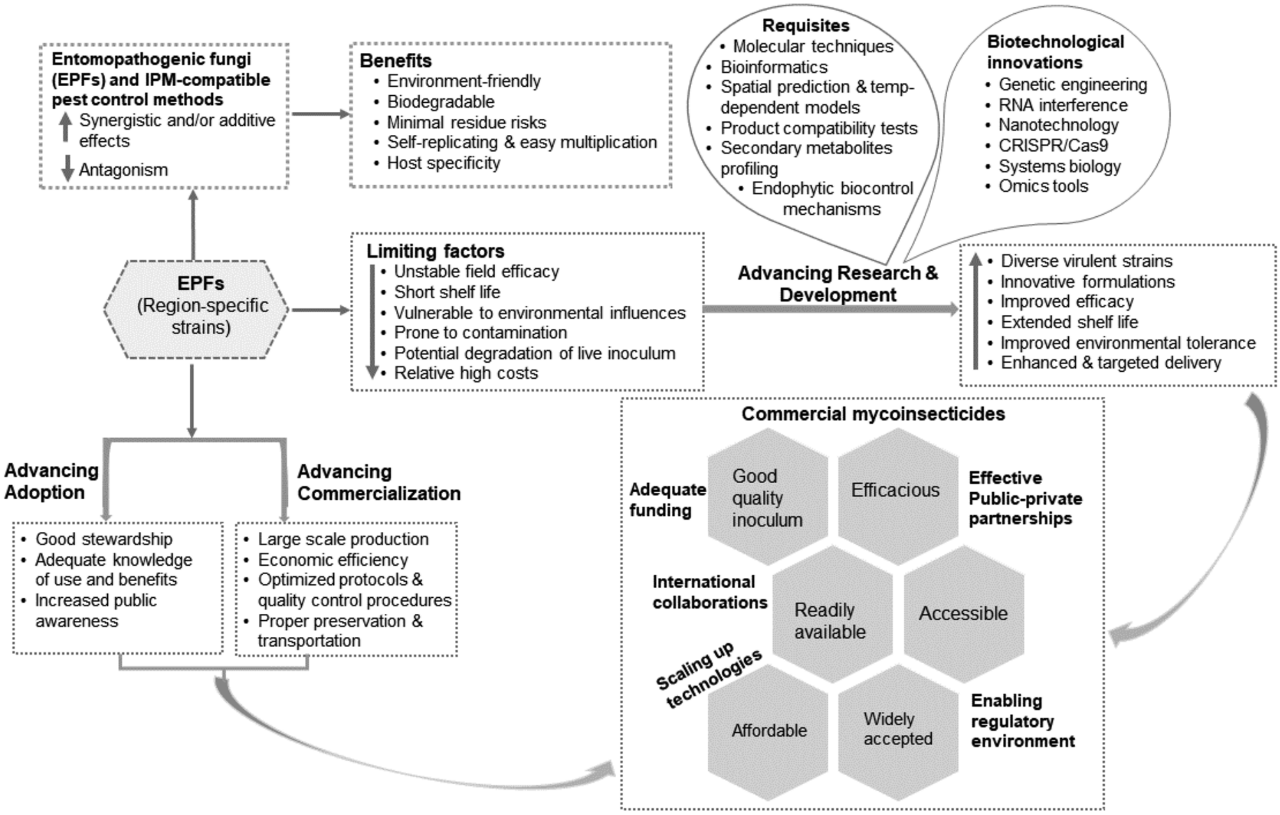

Fig. 1. A holistic approach to fully harnessing the biocontrol potential of entomopathogenic fungi for sustainable management of *Phthorimaea absoluta*.

life, and field efficacy. For instance, potent EPFs can be genetically engineered to overexpress surface-active hydrophobin proteins and hydrolytic enzymes, including proteases, chitinases, and protease-chitinase fusion to yield strains with enhanced insecticidal activity against *P. absoluta*, as has been previously observed on other insect pests (Fan et al. 2007, Singh and Kaur 2020). Through genetic engineering, the tolerance of EPFs to UV damage can be improved, resulting in a significant increase in virulence of the transgenic strains against *P. absoluta*, as previously observed in a genetically modified *B. bassiana* strain against lepidopteran and coleopteran larvae (Shang et al. 2012). The majority of genetically improved fungal strains exhibit characteristics such as improved conidial quality, increased virulence, enhanced tolerance to environmental influences, and increased persistence in the field (Muñiz-Paredes et al. 2017, Méndez-González et al. 2022, Karthi et al. 2024). Genetic engineering approaches can also potentially increase tolerance to chemical pesticides in EPFs (Samal et al. 2023). However, it is necessary to address the many challenges limiting the applicability of genetically modified EPFs to optimize their biocontrol against *P. absoluta*. For example, mass production of transgenic EPFs remains a challenge, and there are safety concerns that enhanced virulence through genetic engineering, particularly recombinant endophytic fungi, could have adverse effects on nontarget organisms, including natural enemies and beneficial insects (Muñiz-Paredes et al. 2017, Sankar and Rani 2018).

Advanced technologies, such as RNA interference (RNAi) and nanotechnology, can be utilized to develop formulations with enhanced insecticidal virulence against *P. absoluta*, improved environmental tolerance, and longer shelf life (Bihal et al. 2023, Han et al. 2023, Irsad et al. 2023, Zhang et al. 2023). RNAi is a mechanism of posttranscriptional gene silencing that holds promise as a highly targeted approach to crop protection. A double-stranded RNA (dsRNA) is delivered through various techniques, including injection, feeding, topical application, and integration into transgenic plants. The employment of RNAi remarkably improved the virulence of *B. bassiana* against aphids (Zhang et al. 2023), presenting this technology as an attractive strategy for controlling *P. absoluta*. Nanotechnology is a promising tool for enhancing efficacy, improving stability, extending shelf life, and ensuring safe delivery of mycoinsecticides (Bihal et al. 2023). Several nanoparticles based on EPFs, including silver, selenium, iron, titanium, and zinc, have demonstrated biocontrol potential against a range of insect pests, including lepidopteran larvae (Yosri et al. 2018, Bihal et al. 2023). These findings, therefore, indicate that nanoformulations of EPFs can provide selective and targeted management of *P. absoluta* larvae.

Other innovative bioformulations based on EPFs, including bioencapsulation, tablet formulations, microemulsions, and oil dispersions, also have a competitive advantage in *P. absoluta* control in relation to improved shelf life, better delivery systems, consistent field performance, and enhanced tolerance to abiotic stressors (Felizatti et al. 2021, Friuli et al. 2023, Sarma et al. 2023, De Jesus Seabra et al. 2024, Saminathan et al. 2025). Biotechnological advancements, including UV-protectant formulations and targeted delivery approaches, can further broaden the opportunities for future mycoinsecticide applications (Acheampong et al. 2020b, Mascarin et al. 2024a). Concerted efforts should also be geared toward boosting oil-based and microsclerotia granule formulations, as they exhibit better stability at room, fridge, and freezer temperatures without significantly losing their viability and infectivity (De Oliveira et al. 2018, Akutse et al. 2020b, Mathulwe et al. 2023, Mascarin et al. 2024a). Further, using these formulations can increase the tolerance of EPFs to environmental stressors and improve their compatibility with chemical pesticides (Lopes et al. 2011, Samal et al. 2023). Additionally, the successful employment of clustered regularly interspaced short palindromic repeats (CRISPR) and CRISPR-associated protein 9 (Cas9) for genome editing in *B. bassiana* strains (Chen et al. 2017, Mascarin et al. 2024b) indicates that the CRISPR/Cas9 system has a more significant role in future genome engineering of EPFs and serves as a promising avenue for improving the virulence of mycoinsecticide formulations.

Endophytic fungi influence insect performance through the production of phytohormones and secondary metabolites (Bamisile et al. 2021b, Agbessenou et al. 2022, Liao et al. 2025); therefore, advanced research is needed to understand endophytic-mediated interactions, including direct effects of fungal endophytes on the survival and fitness of the natural enemies of *P. absoluta*. This necessitates the application of advanced biotechnological techniques and approaches, such as high-throughput sequencing, systems biology, and omics tools, including genomics, transcriptomics, proteomics, and metabolomics (Samal et al. 2022, Liao et al. 2025). Moreover, insights into the intrinsic functions of bioactive secondary metabolites involved in endophytism can facilitate the identification and development of important compounds for crop protection applications. For example, Vivekanandhan et al. (2024a) demonstrated that bioactive chemical compounds derived from *B. bassiana* are toxic to *P. absoluta* larvae and can be potentially developed into novel insecticides to combat the pest. The ability of EPFs to produce a wide array of secondary metabolites and enzymes has increased their interest in biotechnological applications as potential producers of biocatalysts and other biochemicals (Amobonye et al. 2020, Zhang et al. 2020b, Pedrini 2022, Liao et al. 2025).

Compatibility of EPFs with parasitoids, predatory mirids, and *B. thuringiensis* has yielded additive and synergistic effects against *P. absoluta* and a range of insect pests (Nozad-Bonab et al. 2021, Aynalem et al. 2022, Mama Sambo et al. 2022, Smagghe et al. 2023, Lisi et al. 2024, Rivera-Alonso et al. 2024). However, concerns persist about the negative effects of fungal endophytism on the natural enemies of insect pests that feed on endophyte-colonized plants (Bamisile et al. 2018, Aravinthraju et al. 2024, Panwar and Szczepaniec 2024). Therefore, further efforts should focus on translating the positive research findings into practical applications while addressing the concerns about the potential negative impacts of endophytic fungi on natural enemies. Additionally, good compatibility of EPFs with chemical insecticides used against *P. absoluta* is crucial for the success of IPM programs. Tomato plants are also susceptible to multiple insect pests and pathogens, and are subject to frequent applications of different pest control products. Therefore, adequate knowledge of various classes of chemical pesticides that exhibit good compatibility with EPFs could inform the choice of suitable products to incorporate in IPM programs for controlling *P. absoluta* and other tomato pests. In addition, there are prospects for the integrated use of fungal endophytes and autodissemination of pathogenic strains for the control of *P. absoluta*, as this combination has displayed significant biocontrol efficacy against the pest under field conditions (Gathage et al. 2016, Agbessenou et al. 2020, Akutse et al. 2020a). The successful application of dsRNAs spray on crops to enhance the virulence of *B. bassiana* Bb07 strain against several aphid species (Zhang et al. 2023) also indicates prospects for future integration of EPFs and RNAi to improve the virulence of fungal strains that have already exhibited pathogenicity against *P. absoluta* and enhance their biocontrol activity.

Advancing the commercialization of EPFs requires mass production systems with optimal efficiency and high economic viability to attract financial investments from the private sector (Fig. 1). To achieve this, it is necessary for governments to incentivize the private sector by supporting research and innovation, as well as reducing the costs associated with product registration and regulatory approvals. Prospective increases in commercialization efforts are likely to ease the availability of mycoinsecticides and reduce their costs, thereby supporting their economic relevance and increasing their acceptance among farmers. More importantly, advancing the adoption of EPFs through good stewardship is crucial for driving sustainability (Fig. 1). This involves providing technical knowledge on EPFs as pest control products and encouraging farmers to adhere to the guidelines on the labels related to their handling, use, and storage. Good stewardship also focuses on the proper application technique and correct timing to safeguard field efficacy against restrictive environmental influences and achieve maximum crop protection benefits. For instance, adopting best practices such as following product labels and applying mycoinsecticides when solar UV radiation is low and relative humidity is high guarantees the delivery of sufficient conidia to the target and adequate efficacy. Well-tailored training on the bioecology of *P. absoluta* and the best application techniques based on the pest's behavior can increase the efficiency of inoculum delivery and ensure sufficient conidia contact with the most susceptible life stages. For example, foliar application of mycoinsecticides on the upper and middle sections of tomato plants targets the eggs and young larvae of *P. absoluta*, while dust and soil drenches aim to control the soil-dwelling life stages of the pest. The "attract and infect" approach using dry conidia takes advantage of the mating behavior of male moths, which are attracted to the sex pheromone lures in the autodissemination devices, become infected with conidia, and spread the fungus while mating with the females (Akutse et al. 2020a). Nevertheless, sprayable formulations are more advantageous, as they do not require special equipment and can be applied easily or with minimal modifications based on conventional pest control practices.

Improved knowledge among farmers about the necessity, mode of action, and benefits of EPFs could also increase their level of acceptance and adoption as an integral component of IPM programs (Dara 2019, Colmenárez et al. 2022, Chepchirchir et al. 2023). This can be achieved through increased sensitization in outreach programs, including farmers' field days, farmer field schools, dissemination programs, periodic training, and field demonstrations of successful IPM programs based on EPFs, to facilitate effective technology transfer to the farmers and enhance sustained adoption (Dara 2019, Colmenárez et al. 2022, Irsad et al. 2023). Although advanced technologies, such as RNAi, nanoformulations, transgenic, and genome edited strains, are currently beyond the reach of farmers in sub-Saharan Africa, it is essential to empower them with knowledge and skills to exploit commercially available mycoinsecticides within IPM programs by leveraging synergistic interactions of specific fungal strains with other microbial agents, arthropod biocontrol agents, and sublethal doses of botanicals and chemical pesticides. Moreover, increasing awareness among policymakers, governments, farmers, and the public on using EPFs as vital components of IPM programs and the importance of complementing chemical pesticides is necessary to break existing market barriers and make mycoinsecticides as popular as other competing products.

Conclusion

EPFs hold great potential as biocontrol agents for *P. absoluta* control in sub-Saharan Africa. Their integration into IPM programs has become essential for sustainable pest control and reduced dependence on chemical pesticides. However, the success of EPFs demands a holistic approach to address the challenges that limit their widespread development and use, including inconsistent product performance, biological and technical constraints, regulatory barriers, and market limitations. This review highlights the significant progress made toward harnessing the potential of research innovations and technological advancements to break through certain biological and technical challenges and pave the way for the development and commercialization of efficacious mycoinsecticides. The ongoing research has opened up prospects of exploiting new pathogenic and endophytic fungal strains with improved sporulation and virulence. Additionally, recent advancements in formulation technology are enabling the development of improved and stable mycoinsecticides with greater efficacy, extended shelf life, increased tolerance to environmental influences, as well as enhanced inoculum delivery and field efficacy.

With technological interventions such as genetic engineering, omics technologies, RNAi, nanotechnology, and the CRISPR/Cas9 system, there are prospects of bridging the gap between research and product development of EPFs. Nevertheless, for sub-Saharan African countries to advance EPFs and leverage innovative technologies, deliberate efforts must be made to stimulate the uptake of necessary interventions. These include increased collaborations to facilitate knowledge sharing and the application of technologies, adequate resource allocation, strengthened regulatory frameworks, and building technical capacity to support the development and commercialization of innovative products. To advance adoption, key driving factors include empowering smallholder farmers, increasing the availability and accessibility of reliable products, strong product and technological stewardship, optimizing the compatibility of EPFs with IPM components, and increasing public awareness of the benefits of EPFs. Such concerted efforts will increase the utilization of EPFs in IPM programs and contribute to the sustainable management of *P. absoluta* in sub-Saharan Africa.

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Author Contributions

Grace Kinyanjui (Conceptualization, Methodology, Visualization, Writing—original draft, Writing—review & editing [equal]), Kahsay Tadesse Mawcha (Conceptualization, Resources, Visualization, Writing—original draft, Writing—review & editing [equal]), and Dennis Ndolo (Conceptualization [equal], Resources [equal], Supervision [lead], Validation [lead], Writing—review & editing [equal])

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Conflicts of Interest

The author declares no conflict of interest.

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