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Endophytic fungi: versatile partners for pest biocontrol, growth promotion, and climate change resilience in plants

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Plant-associated endophytic fungi (EFs) are emerging as a promising solution to advancing modern agriculture and fostering environmental sustainability, especially in the face of climate change scenarios. These fungi, either naturally residing in plants or introduced through artificial inoculation techniques, improve agricultural production due to their various roles in protecting and supporting host plants. The majority of EFs serve as natural biocontrol agents for a variety of agricultural pests, such as insects, phytopathogens, nematodes, and weeds. Notably, EFs produce secondary metabolites, trigger immune responses, modify plant defense gene expression, confer host plant resistance and/or tolerance, and regulate pest growth, populations, and survival to combat agricultural pests. Beyond controlling pests, EFs promote optimal plant growth, development, and resilience by aiding in the synthesis of vital compounds such as phytohormones and bioactive metabolites, nutrient acquisition, and fortifying plants against environmental stresses and climatic changes. Moreover, the mostly nonpathogenic nature of EFs, coupled with their high yield potential, environmental safety, and cost effectiveness, positions them as eco-friendly and economically viable alternatives to synthetic agrochemicals amidst rapid climate change scenarios. As a result, the promising horizon of EFs in agricultural production necessitates interdisciplinary study and microbial modulation approaches to optimize symbiotic plant-EF relationships and their potential for improved productivity. This review provides current and comprehensive insights into the practical applications and multifaceted benefits of EFs in pest management, plant growth promotion, and climate change resilience for future agricultural production improvements. The analysis reveals the potential of developing EFs into innovative bioformulations such as biofertilizers, biostimulants, and biopesticides, thereby paving the way for their integration into a sustainable and more resilient future agricultural system.

KEYWORDS

agricultural pests, colonization, growth promoters, mutualistic endophytes, nutrient acquisition

1 Introduction

Global food and nutrition security, in the face of rapid population growth and climate change, requires a sustainable food production approach addressing availability, access, utilization, and stability, ensuring livelihoods while preserving natural ecosystems and services (Giller et al., 2021). Agriculture, which is responsible for 90% of global food calories (Cassidy et al., 2013), will be at the forefront of transforming and/or reforming conventional practices by employing agroecological principles to address sustainability and environmental concerns within food systems. These concerns have led plant-associated microorganisms, particularly endophytic fungi (EFs), to emerge as a new frontier in agricultural production, achieving global demands for nutritious foods and eventually becoming fundamental to sustainable agriculture (Chitnis et al., 2020; Singh et al., 2021; Verma et al., 2022). In particular, EFs can reduce reliance on synthetic agrochemicals, which have a detrimental impact on agricultural productivity, ecosystems, and human health, thereby promoting environmentally friendly approaches for addressing food production challenges (Fadiji and Babalola, 2020; Rigobelo and Baron, 2021). Therefore, EFs are crucial for guaranteeing agricultural production and environmental sustainability.

The widespread application of EFs is revolutionizing the field of agriculture, primarily due to their remarkable capacity to support and protect host plants by producing beneficial bioactive molecules and acting as biocontrol agents to naturally regulate plant pest populations (Yan et al., 2019; Verma et al., 2022). These fungi colonize plants through root, stem, or leaf tissues and can occur naturally or be introduced into plants through seed coating, root dipping, and foliar spraying (Vega et al., 2008; Tefera and Vidal, 2009; Jain and Pundir, 2017). Most EFs are classified in the phyla *Oomucota*, *Ascomycota*, *Chytridiomycota*, and *Zygomocata* (Gul et al., 2014). Most of these important EFs are found in the orders *Hypocreales* (*Ascomycetes*) and *Entomophthorales* (Sharma et al., 2019). For instance, *Beauveria, Metarhizium, Paecilomyces, Aschersonia, Hirsutella,* and *Lecanicillium* are the most well-known fungal genera of these orders (Goettel, 2008). Mostly, they are formulated as *Beauveria bassiana*, *Metarhizium anisopliae*, and *Trichoderma* spp. propagules (Gul et al., 2014).

Endophytic functional groupings are diverse in ecological functions, host range, taxonomy, transmission, tissue specificity, and colonization patterns (Aamir et al., 2020). Based on ecological category/diversity/functional roles, EFs were grouped into two main categories: clavicipitaceous fungal endophytes (C-endophytes) and nonclavicipitaceous (NC-endophytes) fungal endophytes (Aremu et al., 2017). C-endophytes, also known as true endophytes, are host-specific and most common in the grass family Poaceae, which includes *Balansia* sp. and *Epichloë* sp., and often transmitted vertically through seeds, potentially resulting in an obligate association and higher rates of infection (Khiralla et al., 2016). These EFs are beneficial to the plant by improving plant growth and producing certain toxic chemicals against herbivory; however, they rely on the host plant species, environmental conditions, and genotype (Aremu et al., 2017). In contrast, NC endophytes are predominant and associated with both nonvascular and vascular plant species and are transmitted horizontally. These endophytes, including EFs such as *Lecanicillium lecanii*, *Beauveria bassiana*, *Metarhizium anisopliae,* and *Isaria* spp., can have impacts on several agricultural pests by antagonizing plant diseases and promoting plant growth (Jain and Pundir, 2017). However, until now, only a few species of EFs have been isolated, identified, characterized, and implemented in pest management.

Mutualistic endophytes, which are mostly fungal microbes that survive within plant tissues without adversely affecting the host, can promote plant growth and development while efficiently reducing agriculturally important pests, especially insects (Vega et al., 2008; Agbessenou et al., 2020), plant pathogens (Yan et al., 2019), and nematodes (Tolba et al., 2021). The mechanisms of EF colonization to suppress potential pests differ depending upon the species of EFs and the host plants to be colonized, and they can be employed in either direct or indirect ways (Quesada-Moraga et al., 2014; Zhang et al., 2019; Rajani et al., 2021). Furthermore, EFs are ubiquitous and have been demonstrated to improve host plant growth and tolerance against various abiotic stresses (Lata et al., 2018; Morsy et al., 2020). As a result, there is significant and developing interest in implementing them in agriculture as biocontrol agents of pests and plant growth and adaptation promoters (Molina-Montenegro et al., 2016; Mantzoukas and Eliopoulos, 2020). The use of EFs is also considered an alternative to synthetic insecticides (Sinno et al., 2020), eco-safety and lack of pathogenicity to plants (Mantzoukas and Eliopoulos, 2020), to reduce the impact of pesticides on living organisms and resistance development (Hernández-Rosas et al., 2020), less harmfulness to nontarget organisms, cost-effectiveness, high yield, and absence of harm to the environment (Mantzoukas and Eliopoulos, 2020). According to Yung et al. (2021), EFs are mostly nonpathogenic, with potential applications in organic matter mineralization, plant nutrition, biocontrol agents, crop productivity improvement, and sustainability while reducing chemical inputs, making them environmentally friendly tools that require integration and/or rotation with other alternatives. In addition, EFs also protect plants from different environmental stresses, such as drought, salinity and temperature (Lata et al., 2018; Morsy et al., 2020). However, their success depends on many factors, including their interactions, target host, and environment (Morales-Sánchez et al., 2020). The specific relationships between host plants and EFs, as well as the environment, could change throughout the plant's lifecycle based on environmental and intrinsic factors such as leaf traits, host chemistry, and leaf chemical profiles (Sinno et al., 2020). In general, despite their numerous benefits, the utilization of EFs in developing countries by farmers is limited. Nevertheless, these EFs are not yet sufficiently produced and/or available to fulfill farmers' demands even in developed countries. Hence, this review provides recent and comprehensive information on plant-fungal endophyte associations, the efficiency of EFs as pest biocontrol agents, growth promoters, and climate change resilience partners in plants.

2 Plant-fungal endophyte associations and related regulating factors

All plants appear to be symbiotic with fungal endophytes in natural ecosystems, which survive within plant tissues either throughout their lives or during a particular period of their lifespans without producing obvious damage and/or changing the morphology of their hosts. This makes the plant-fungal endophyte interaction a balanced antagonism where fungi survive by consuming nutrients from the plants, providing various benefits, while the host plants activate virulence mechanisms for colonization and host defenses (Baron et al., 2020). However, EFs inhabiting healthy plant tissues may convert from nonpathogenic to pathogenic modes when the plant is stressed (Galindo-Solís and Fernández, 2022). This diverse group of fungi can have a significant impact on plant families by conferring abiotic and biotic stress tolerance, boosting biomass while reducing water utilization, or decreasing fitness through resource allocation modifications (Khiralla et al., 2016). Through these positive relationships, plant growth, nutrition, and productivity can be improved (Behie and Bidochka, 2014) in various ways, such as providing nitrogen (N) to plants (Behie et al., 2015), acting as biocontrol agents (Akello and Sikora, 2012; Suryanarayanan, 2019; Huang et al., 2020), and improving tolerance to abiotic stress (Morsy et al., 2020). After successful colonization, EFs assist plants in producing plant hormones (phytohormones) and other bioactive compounds by promoting the production of secondary metabolites within plant tissues (Khan et al., 2019), enhancing tolerances to drought, salinity, and extreme temperature (Morsy et al., 2020), interfering with weed growth and germination and hindering the activities of insects, pathogens, and plant parasitic nematodes (Schouten, 2016; Sallam et al., 2021). What is interesting in a plant-fungal endophyte symbiotic relationship is that the plant itself helps fungal endophytes by offering shelter, nutrients, and seed spreading. In general, EFs are known to affect the biosynthesis of phytohormones, enzymes, and other bioactive compounds in plants (Satheesan and Sabu, 2020).

However, for EFs to be effective symbionts of different plants (pests), they need to be capable of infecting, occupying, and establishing themselves in both organisms (Branine et al., 2019). Colonization by EFs may be systemic (Quesada-Moraga et al., 2014), restricted to some plant tissues (Wearn et al., 2012), or distributed throughout the plant parts (Behie et al., 2015). Both gene duplication (Wang and St Leger, 2007) and horizontal gene transfer (Zhang et al., 2019) are involved in the penetration and establishment of EFs inside both host plants (pests). However, environmental conditions, inoculation methods, season of sample collection, species of fungal endophytes, geographical location, and genotype of the host plant itself can influence EF colonization of host plants (; Tefera and Vidal, 2009; Morales-Sánchez et al., 2020; Wu et al., 2020). Furthermore, depending on the method of inoculation (seed coating, foliar spray of conidia, conidial suspension injection, radicle dressing, soil drenching, and root and rhizome immersion), EFs can vary in their ability to colonize different plant parts (Tefera and Vidal, 2009). Wei Q. Y. et al. (2020) found that leaf spraying of conidial suspension on tomato plants resulted in greater colonization by *B. bassiana* than seed dressing. Leaf inoculation using *B. bassiana* conidial suspensions has also been described as the most efficient method of colonizing sorghum plants, successfully delivering the fungal endophyte into leaves (Tefera and Vidal, 2009).

Several factors related to geographic factors and the ecological function of the host plant also exert an influence on the diversity, specificity, and specialization of EF communities (Aamir et al., 2020). A report on native Hawaiian plants coexisting along an altitudinal gradient, for instance, revealed distinct patterns of EF diversity, host specificity, and interaction specialization across various elevations, with less specialization and greater diversity occurring at extreme altitudes (Cobian et al., 2019). This suggests that associations between host plants and EFs are more specialized under intermediate conditions and less specific under ecological extremes. A study by Wu et al. (2020) found that certain key chemical components and growth patterns in *Dendrobium catenatum* were influenced by the integration of cultivar genetics and species of fungal endophyte. He et al. (2019) studied the genetic variation in the forb host *Oxytropis ochrocephala*, its interaction with EF *Alternaria oxytropis*, and swainsonine mycotoxin production, revealing that host genotype and precipitation significantly influenced population-scale swainsonine production. Similarly, Hughes et al. (2020) observed significant impacts from the root EF *Lulwoana* sp. on phenotypic traits across genotypes of *Spartina alterniflora*, suggesting that plant-EF associations can exert community- and ecosystem-level impacts on plant species. A recent study also revealed that host plant genotype and tissue type have a significant influence on fungal endophytic communities in wheat, with the effects of host genetics mostly limited to leaves and roots (Latz et al., 2021). Hence, studying the factors driving plant-fungal endophyte associations is crucial for optimizing their development as agricultural solutions, with a focus on colonization and related mechanisms, as well as ecological effects on fungal endophyte community assembly and host interactions.

3 Efficiency of endophytic fungi in agricultural pest biocontrol

Agricultural pests, such as pathogens (e.g., fungi, bacteria, viruses, and nematodes), insect pests, and weeds, impede crop growth and yields, necessitating a comprehensive approach to addressing food production, as well as environmental conservation challenges. Management techniques that involve overreliance on synthetic agrochemicals have resulted in the resistance and resurgence of pests and negative environmental outcomes such as pollution (Waqas et al., 2015a; Verma et al., 2022). Alternative strategies such as biocontrol agents utilizing EFs are more effective, sustainable, and environmentally friendly approaches to plant protection (Ambele et al., 2020; Ahmad Y. et al., 2020; Mota et al., 2021). This section presents comprehensive analyses of the efficacy of endophytic fungi in the biocontrol of agricultural pests, including insect pests, plant diseases, parasitic nematodes, and weeds.

3.1 Endophytic fungi against insect pests

Biological control strategies utilizing beneficial organisms have increasingly attracted interest in recent decades as a means to reduce dependence on synthetic pesticides. Endophytic fungi in particular show promise due to their ability to form mutualistic relationships with host plants, alter metabolism, strengthen stress tolerance, and protect against insect pest damage (Aamir et al., 2020). The mechanisms through which EFs colonize and reduce insect herbivore damage vary based on the crops, fungal endophytes, application methods, and target insects. In insect pests, colonization (as a mode of action) of EFs begins with the bonding of fungi to the host plant surface, followed by penetration through the host cuticle and proliferation within the body cavity, which is the mode of entry for most EFs (Vega et al., 2008). During insect invasion, after efficient adherence, conidia develop to form hyphae, and conidial surface proteins, such as *Metarhizium* adhesin genes, *MAD1* and *MAD2* of

M. anisopliae, and hydrophobin proteins (*hyd1* and *hyd2*) of *B. bassiana,* are needed for plant and insect attachment and to recognize insect-specific compounds that then degrade the insect cuticles. For instance, Wang and St Leger (2007) reported that in *Metarhizium robestsii*, the adhesive *MAD1* is essential for insect cuticles and *MAD2* in plant conidial spore adhesions. Then, degradation of the insect cuticle/plant cell wall allows EF access to plant/insect tissues, which is accomplished by enzymatic activity such as that of various proteases and the mechanical pressure exerted by specific infections of hyphal structures (such as appressoria; Barelli et al., 2016). The EF needs to escape the insect immune system to efficiently parasitize insects and kill them. Once the EF pierces the insect cuticle, it distributes the insect's hemolymph, where it divides into blastospores (yeast-like asexual spores), which collect nutrients in the hemocoel and generate particular insecticidal metabolites, leading to insect death (Fan et al., 2017). The mechanisms/modes of action by which EFs reduce insect herbivore injury in their host plants comprise antibiosis or pest avoidance/feeding deterrence (Vega et al., 2008), reduction of insect fitness, maximizing risks of predation and parasitism (Shymanovich and Faeth, 2018), reduction of insect survival (Lopez and Sword, 2015; Rasool et al., 2021), retardation of insect growth (Rondot and Reineke, 2019; Ahmad I. et al., 2020) and modification of plant defense gene expression (Ahmad I. et al., 2020). A possible mode of action could be direct defense or indirect plant defense by enhancing plant odors and attracting additional olfactory foraging natural enemies (Fuchs and Krauss, 2019).

Reductions in insect pest-induced plant damage were documented in a number of agricultural crop plants that were treated with EFs following effective colonization (Table 1). For instance, *Tuta absoluta* (Meyrick; Lepidoptera: Gelechiidae), which causes serious damage to tomato and nightshade (*Solanum scabrum*), was reduced when these plants were treated with *Trichoderma asperellum*, *Beauveria bassiana* (Balsamo) vullemin (Ascomycota: Hypocreales), and *Hypocrea lixii* (Agbessenou et al., 2020). In tomatoes, the use of *B. bassiana* was also effective in reducing the damage caused by *Helicoverpa armigera* (Toffa et al., 2021). A similar reduction in damage caused by bean stem maggot (*Ophiomyia phaseoli*) was reported in common bean (*Phaseolus vulgaris*) when *M. anisopliae* ICIPE 78 was used as a potential EF (Mutune et al., 2016). Similarly, *B. bassiana* colonizing tomato leaves also resulted in a reduction in the longevity of *T. absoluta* larvae and caused 50% mortality of all larval instars (Klieber and Reineke, 2016). Furthermore, EFs can be employed along with other insect pest management techniques, such as biological control agents acting as natural enemies (Akutse et al., 2013). Jaber and Araj (2018) reported that EFs such as *B. bassiana* and *Metarhizium brunneum* could be combined with the aphid endoparasitoid *Aphidius colemani* Viereck (Hymenoptera: Braconidae) for the control of the green peach aphid *Myzus persicae* Sulzer (*Homoptera*: Aphididae) in sweet pepper (*Capsicum annum*).

Several reports on insect pest damage reduction after the application of EFs to crops are also available (Quesada-Moraga et al., 2014; Muvea et al., 2015; Rondot and Reineke, 2019; Table 1). For example, the production of alkaloids by *Epichloë* species in diverse grass species accumulating in plants is toxic to numerous insect pests (Lugtenberg et al., 2016). Nodulisporic acid, produced by *Nodulisporium* sp., is another alkaloid molecule that is vital for preventing insect herbivory by activating glutamate, which results in the flow of chlorine ions through the chlorine channels of insect muscle and nerve cells, resulting in flaccid paralysis (Rigobelo and Baron, 2021). New insecticidal anthraquinone and chloramphenicol (Yuan et al., 2020) derivatives characterized from *Acremonium vitellinum* were reported to be effective against the cotton bollworm *Helicoverpa armigera* (Hübner; Lepidoptera: Noctuidae). In general, a wide range of secondary metabolites, such as polyketides exhibiting antibiotic activity, have been synthesized by fungal endophytes (Lugtenberg et al., 2016; Aamir et al., 2020). Therefore, insect pest management approaches could benefit from harnessing EFs given their low costs, high efficacy, safety for nontarget species and the environment, and potential to enrich agroecosystem biodiversity (Barelli et al., 2016).

3.2 Endophytic fungi against plant diseases and parasitic nematodes

Fungal endophytes can act as biocontrol agents by stimulating the plant's inherent defense molecules and defending themselves or by producing bioactive compounds with the ability to kill or prevent pathogen attacks on their own (Jaber and Araj, 2018; Huang et al., 2020). These bioactive compounds have antifungal and antibacterial properties and include terpenoids, flavonoids, alkaloids, quinols, chlorinated compounds, peptides, steroids, polyketides, phenols, and other VOCs (Moraes et al., 2020; Lu et al., 2021). As a result, several crop plants treated with EFs showed reductions in plant damage from a variety of plant diseases and plant-parasitic nematodes following effective colonization (Tables 2**,** 3). In a recent study, *Fusarium oxysporum* f. sp. *cucumerinum*, which causes wilt in cucumber, was treated with 30 species of EFs, of which *Penicillium* sp. and *Hypocrea* sp. were reported to be effective at hindering the mycelial colony growth of diseases and successfully suppressing wilt severity in cucumber (Abro et al., 2019). Recent studies have indicated that endophytic *Trichoderma* has the capacity to reduce the incidence of red root rot disease caused by *Ganoderma philippii* in *Acacia mangium* seedlings (Gafur, 2023; Gafur et al., 2023). Sallam et al. (2021) also reported the antagonistic activity of *T. longibrachiatum*, *T. asperellum*, and *T. atroviride* against *R. solani*a, and the three EF isolates produced pectinase and chitinase and solubilized phosphorus (P) in soybean plants. Similarly, *M. brunneum* and *B. bassiana* colonize wheat, leading to a reduction in disease incidence, severity, and development against *F. culmorum,* the causal agent of crown and root rot, following plant colonization (Jaber, 2018). Furthermore, Billar de Almeida et al. (2010) also reported the possibility of using EFs for the management of grapevine trunk diseases, which are very important and widespread fungal diseases impacting grapevines. Several other reports on plant–pathogen suppression following the treatment of crops with EFs are well documented (Hassanein et al., 2020; Zanudin et al., 2020; Aldinary et al., 2021; Mota et al., 2021; Table 2).

Much is unclear regarding the particular mode of action by which these fungi combat nematodes in most scenarios; however, they are most likely highly diverse. EFs can kill cells directly and impede cell development, obscure them when finding their host, immobilize and attack resources, repel nematodes, or use a combination of these modes of action (Schouten, 2016). For example, Swarnakumari and Kalaiarasan (2017) found that *Purpureocillium lilacinum* and *Pochonia chlamydosporia* can attach, penetrate, colonize, and finally condense egg contents in root-knot nematodes, *Meloidogyne* spp., and stop

TABLE 1 EFs used against agricultural insect pests described in diverse field crops.

Crop	Fungal endophytes	Application methods	Target insect	References
Theobroma cacao	*B. bassiana*	Seed soaking, soil drench and foliar spray	*Odontotermes* spp.	Ambele et al. (2020)
Solanum lycopersicum	*B. bassiana*	Leaf spray	*Bemisia tabaci*	Wei Q. Y. et al. (2020)
Vicia faba	*B. bassiana* and *Hypocrea lixii*	Seed inoculation	*Liriomyza huidobrensis*	Akutse et al. (2013)
S. lycopersicum and *Solanum scabrum*	*Trichoderma asperellum*, *B. bassiana* and *H. lixii*	Seed inoculation	*T. absoluta*	Agbessenou et al. (2020)
Phaseolus vulgaris	*M. anisopliae* and *B. bassiana*	Seed inoculation	*Ophiomyia* spp.	Mutune et al. (2016)
Corchorus capsularis	*B. bassiana*	Seed inoculation	*Apion corchori*	Biswas et al. (2013)
Gossypium hirsutum	*B. bassiana* and *Purpureocillium lilacinum*	Seed inoculation	*Helicoverpa zea*	Lopez and Sword (2015)
S. lycopersicum	*B. bassiana*	Injection, solid substrate root dip, and direct foliar application	*H. armigera*	Qayyum et al. (2015)
Zea mays	*B. bassiana*	Seed dressing, topical application and stem injection	*Sesamia calamistis*	Cherry et al. (2004)
Musa spp.	*B. bassiana*	dipping roots	*Cosmopolites sordidus*	Akello et al. (2007)
Coffea arabica	*B. bassiana*		*Hypothenemus hampei*	Vega et al. (2008)
Allium cepa	*Clonostachys rosea*, *Trichoderma asperellum*, *Trichoderma atroviride*, *Trichoderma harzianum*, *Hypocrea lixii* and *Fusarium* sp.,	Seed or seedling inoculation	*Thrips tabaci*	Muvea et al. (2015)
G. hirsutum	*B. bassiana*, *Lecanicillium lecanii*	Leaf discs immersion	*Aphis gossypii*	Gurulingappa et al. (2010)
V. faba and *P. vulgaris*	Beauveria, Hypocrea, Gibberella, Fusarium and Trichoderma isolates	Seed inoculation	*Liriomyza huidobrensis*	Akutse et al. (2013)
Triticum aestivum	*B. bassiana*, *Aspergillus parasiticus*	-	nymphs	Gurulingappa et al. (2010)
Wild barley	*Neotyphodium coenophialum*		*Rhopalosiphum padi* and *Metopopophium dirhodum* and *Mayetiola destructor*	Clement et al. (2005)
G. hirsutum	*Purpureocillium lilacinum* (Formerly *Paecilomyces lilacinus* and *B. bassiana*)	Seed inoculation	*Aphis gossypii*	Lopez and Sword (2015)
V. faba	*Trichoderma asperellum*, *Gibberella moniliformis* and *B. bassiana*, *M. anisioplaie* and *Hypocrea lixi*	Seed inoculation	*Acyrthosiphon pisum* and *Aphis fabae*	Akello and Sikora (2012)
Cucumis melo	*Fusarium oxysporum*	Seed inoculation	*Aphis gossypii*	Menjivar (2010)
Capsicum annum	*F. oxysporum*	Seed inoculation	*Myzus persicae*	Menjivar (2010)
T. aestivum	*M. brunneum* and *M. robertsii*	Seed inoculation	*Tenebrio molitor*	Keyser et al. (2014)
C. annum	*B. bassiana* and *M. brunneum*	Soil drenching	*Myzus persicae*	Jaber and Araj (2018)
S. lycopersicum	*B. bassiana*	Plant growth substrate	*Trialeurodes vaporariorum*,	Barra-Bucarei et al. (2020)
Vitis vinifera	*B. bassiana*	Leave inoculated feeding	*Aphis illinoisensis*	Sayed et al. (2020)

development at the gastrula stage. An additional example is the EF *Acremonium implicatum* from tomato root galls, which suppresses egg hatching and inhibits the development of root galls by the nematode *M. incognita* (Tian et al., 2014). Furthermore, an EF isolated from *Cucumis melo* root, which was characterized as *P. brefeldianum,* was also reported to be effective in reducing the severity and gall numbers caused by *M. incognita* (Miao et al., 2019). Apart from this, EFs can also produce different nematocidal secondary metabolites against different nematode species. For instance, chaetoglobosin A synthesized by *Chaetomium globosum* controls *M. incognita* (Khan

TABLE 2 **EFs used against plant pathogens and their effects on plant diseases.**

Crop	Fungal endophytes	Target pathogens	References
Cucumis sativus	*Penicillium* sp. and *Hypocrea* sp.	*Fusarium oxysporum* f. sp. *cucumerinum*	Abro et al. (2019)
G. hirsutum	*Fusarium solani*	*Verticillium dahliae*	Wei et al. (2019)
T. cacao	*Colletotrichum gloeosporioides, Clonostachys rosea and Botryosphaeria ribis*	*Moniliophthora perniciosa*, *Phytophthora palmivora* and *Moniliophthora roreri*	Mejía et al. (2008)
C. sativus	*Streptomyces rimosus*	*Fusarium oxysporum* f. sp. *cucumerinum*	Lu et al. (2016)
Musa spp.	*Streptomyces* sp.	*Fusarium oxysporum* f. sp. *cubense* Tropical Race 4	Wei Y. et al. (2020)
S. lycopersicum	*Streptomyces* sp.	*Ralstonia solanacearum*	Le et al. (2021)
Citrus aurantiifolia var. 'Bears'	*Xylaria adscendens*, and *Trichoderma atroviride*	*Colletotrichum acutatum*	Muñoz-Guerrero et al. (2021)
Musa spp.	*Streptomyces* sp.	*F. oxyspoum* f. sp. *cubense*	Zou et al. (2021)
C. sativus	*Fusarium, Chaetomium, Colletotrichum* and *Acrocalymma*	*Rhizoctonia solani, Sclerotinia sclerotiorum*, and *Fusarium oxysporum* f. sp. *cucumerinum*	Huang et al. (2020)
G. max	*Trichoderma longibrachiatum S12, T. asperellum S11, and T. atroviride PHYTAT7*	*Rhizoctonia solani*	Sallam et al. (2021)
S. lycopersicum	*Aspergillus alabamensis, Aspergillus tubingensis and Aspergillus oryzae*	Fusarium wilt	Aldinary et al. (2021)
P. vulgaris	*Induratia* spp.	*Colletotrichum lindemuthianum*, *Sclerotinia sclerotiorum* and *Pseudocercospora griseola*	Mota et al. (2021)
T. aestivum	*Fusarium subglutinans*	*Fusarium semitectum, Aspergillus petrakii*	Hassanein et al. (2020)
T. aestivum	*B. bassiana, M. brunneum*	*Fusarium culmorum*	Jaber (2018)
Z. mays	*M. anisopliae, Trichoderma harzianum*	*Sugarcane mosaic virus/Maize lethal necrosis*	Kiarie et al. (2020)
P. vulgaris	*Trichoderma* spp.	*Fusarium solani*	Toghueo et al. (2016)
Hordeum vulgare	*Fusarium equiseti* and *Pochonia chlamydosporia*	*Gaeumannomyces graminis* var. tritici	Maciá-Vicente et al. (2009)
Traditional rice varieties	Absidia and Acremonium	*Magnaporthe grisea*, the causative agent of rice blast disease	Atugala and Deshappriya (2015)
Solanum melongena	*Helicomyces* spp., *Rhizopus* sp., *Mucor* sp., and *Penicillium* sp.	*F. oxysporum*	Nuraini et al. (2017)
Capsicum annuum	*Cercospora nicotianae, Curvularia* sp., *Fusarium* sp.	*Pepper yellow leaf curl virus*	Lestari et al. (2018)

et al., 2019), while the production of VOCs by *Daldinia cf. concentrica* affects the viability of *M. javanica* (Liarzi et al., 2016). As indicated in Table 3, several reports have revealed the positive impact of EFs on plant growth and their nematicidal effects on diverse species of nematodes (Yan et al., 2011; Liarzi et al., 2016; Bajaj et al., 2017; Zhou et al., 2018; Farhat et al., 2022).

The primary possible mechanisms of plant disease and plant-parasitic nematode suppression differ depending on the EF species. Several mechanisms through which these plant-EF associations benefit the host to shape resistance against various pathogens and nematodes have been suggested (Schouten, 2016; Swarnakumari and Kalaiarasan, 2017; Sallam et al., 2021). Mechanisms could occur through the direct inhibition of pathogens, such as competition for resources (space and nutrients), mycoparasitism and antibiosis (Rajani et al., 2021), and indirect inhibition by induced systemic resistance (ISR) and the induction of secondary metabolites (Rajani et al., 2021; Urooj et al., 2021). For instance, *B. bassiana* can endophytically inhabit a wide range of plant species and has been reported to diminish and limit the growth and development of various soilborne plant diseases *in vitro*, such as *Pythium*, *Rhizoctonia*, and *Fusarium*. *Beauveria* spp. are known to produce an array of bioactive metabolites, which in turn induce systemic resistance and limit the growth of fungal pathogens. Moreover, the defense responses of the EF *Piriformospora indica*, which causes sheath blight disease, against *Rhizoctonia solani* were able to disease the severity of the disease by limiting levels of hydrogen peroxide (H_2O_2) and increasing the activity of antioxidants such as superoxide dismutase (SOD) in rice crops (Nassimi and Taheri, 2017). Induced resistance by EF elicitors against early blight diseases caused by *Alternaria solani* in tomatoes was recently demonstrated by increasing certain enzymatic activities, such as lipoxygenase, peroxidase, polyphenol oxidase, and phenyl ammonia-lyase, when tomato seeds were treated with fungal colony-forming units (CFU)

TABLE 3 Effect of fungal endophytes against plant parasitic nematodes (PPNs) in diverse crops.

Crop	Fungal endophytes	Target PPN	Effects on PPN	References
S. lycopersicum	*Daldinia cf. concentrica*	*Meloidogyne javanica*	Reduced the viability of the second-stage juveniles (j2s) and decreased eggs hatching	Liarzi et al. (2016)
Musa spp.	*Fusarium oxysporum*	*Pratylenchus goodeyi* and *Helicotylenchus multicinctus*	Nematode population densities were reduced by >45%; Percentage root necrosis was reduced by >20% as a result improved yield	Waweru et al. (2014)
S. lycopersicum	*Trichoderma asperellum*	*Meloidogyne* spp.	Reducing root galling severity by 47% and nematode reproduction by 67%, respectively, and significantly inhibiting egg hatch by up to 85%	Affokpon et al. (2018)
C. sativus	Chaetomium Ch1001	*Meloidogyne incognita*	Produced compounds affect the motility of the second-stage juveniles of *M. incognita* reduced galls formed	Yan et al. (2011)
S. lycopersicum	*T. asperellum* and *F. oxysporum*	*M. incognita*	Reduced root-knot nematode egg densities by 35–46%	Bogner et al. (2016)
S. lycopersicum	*Acremonium implicatum*	*M. incognita*	96.0% of second-stage juveniles of *M. incognita* were killed by a culture, suppressed egg hatching, with only 36.3% of treated eggs hatching, inhibited the formation of root galls, reduced the nematode population in soil	Tian et al. (2014)
S. lycopersicum	*Pochonia chlamydosporia*	*M. incognita*	Enhanced defense gene expression	Tolba et al. (2021)
Piper nigrum	*Annulohypoxylon nitens, Daldinia eschscholtzii, Fusarium* spp., *Ceriporia lacerata, Diaporthe* sp. and *Phomopsis* sp.	*Phytophthora capsici, Radopholus similis*	The highest mortality of up to 60%	Sreeja et al. (2016)
Musa spp.	*F. oxysporum*	*R. similis, Pratylenchus goodeyi* and *Helicotylenchus multicinctus*	Higher nematode mortality	Van Dessel et al. (2011)
Glycine max	*Piriformospora indica*	*Globodera* spp. and *Heterodera* spp.	Egg density was significantly decreased and had a strong growth- and yield-promoting effect in soybean	Bajaj et al. (2017)
Solanum tuberosum	*P. fluorescens, P. putida, P. syxantha, P. aurantiacea*	*Globodera rostochiensis*	Nematode multiplication reduced by 40.7–42.2%	Trifonova et al. (2014)
Musa spp.	*F. oxysporum*	*R. similis*	Reduced root penetrations by *R. similis*	Vu et al. (2006)
Oryza sativa	*F. moniliforme*	*Meloidogyne graminicola*		Le et al. (2016)

and different concentrations of crude oligosaccharide (CO) of EF; as a result, the vegetative and reproductive parameters of tomato were enhanced (Sujatha et al., 2021). Several research findings have reported that EFs can induce resistance in various crops against insects (Kiarie et al., 2020), nematodes (Swarnakumari and Kalaiarasan, 2017), phytopathogens (Muvea et al., 2015; Galletti et al., 2020; Urooj et al., 2021), and abiotic stresses (Lata et al., 2018; Morsy et al., 2020; Singh et al., 2021).

Some filamentous fungi, such as *Trichoderma*, act on plant-parasitic nematodes directly and indirectly through antibiosis, production of lytic enzymes, parasitism, paralysis, competition, improving nutrient and water absorption, modifying plant root morphology and/or rhizosphere interactions, and inducing resistance by initiating hormone-mediated responses, such as salicylic acid, jasmonic acid, and strigolactone, for plant defense (Poveda et al., 2020). As a direct mechanism, for instance, *Acremonium implicatum* antagonized the colonization of *Meloidogyne incognita* Chitwood nematodes in tomato (*Solanum lycopersicum*; Tian et al., 2014), and *Penicillium brefeldianum* antagonized the colonization of *M. incognita* nematodes in *Cucumis melo* (Miao et al., 2019). EFs can also produce different nematocidal secondary metabolites that can act indirectly against different nematode species. For instance, it was revealed that chaetoglobosin A formed by *Chaetomium globosum* acted against the root-knot nematode *M. incognita* (Khan et al., 2019), and volatile organic compounds (VOCs) released by *Daldinia cf. concentrica* acted against *M. javanica* in tomatoes (Liarzi et al., 2016).

3.3 Endophytic fungi as weed biocontrol agents

Weeds are among the undesired plants that grow alongside crops in the field, competing for nutrients and space, as well as hosting pathogens that attack crop plants and reduce production (Asim et al., 2022). Fungal endophytes have been shown to have bioherbicidal potential that suppresses and controls weeds while simultaneously stimulating crop plant growth, making them particularly suited for this use due to their dual benefits (Suryanarayanan, 2019; Ahmad Y. et al., 2020). Therefore, the use of EFs provides a more effective and environmentally sound approach to weed control than either synthetic herbicides, which pose risks to human and environmental health, or other biocontrol agents whose long-term efficacy relies upon persistence in introduced settings. The biocontrol of *Orobanche* using EFs such as *Ulocladium* spp. and *Fusarium* spp. resulted in 90% control in tomato and 90–97% control in watermelon, while other EFs, such as *Rhizoctonia*, *Alternaria*, and *Sclerotinia,* were also effective (Nemat Alla et al., 2008). Earlier studies have shown the effective biocontrol of *Convolvulus arvensis*, *Chenopodium album*, and *Avena fatua* through various EF species, with these weeds exhibiting substantial reductions in growth and germination when sprayed or inoculated with EF culture filtrates (Tunali et al., 2009; Akbar and Javaid, 2012).

Endophytic fungi exhibit multiple weed control mechanisms, impacting germination and subsequent growth stages and various physiological and biochemical processes. For example, absorbed fungal metabolites may damage seed cell membranes and disrupt vital processes such as amylase activity and cell division, delaying or preventing germination (Moura et al., 2020). Additionally, intercellular root colonization releases toxic substances, hindering germination and growth by suppressing photosynthesis and phytohormones while enhancing ROS and stress hormones such as ethylene and abscisic acid (Asim et al., 2022). For instance, *Diaporthe phaseolorum*, *T. spirale*, and *P. simplicissimum* have been shown to play crucial roles in reducing photosynthesis and growth in *Ipomoea grandifolia* and *Senna occidentalis* through different hydrolytic enzyme production (Moura et al., 2020). Daba et al. (2021) demonstrated that conidial suspensions of EFs exhibit varying herbicidal activities against weed germination and growth, with the herbicidal actions of applied conidia or exudates during fungal growth reducing germination and growth by up to 65%. Asim et al. (2022) also reported that *F. oxysporum* controlled *A. fatua* by reducing seed germination, vigor index, root length, shoot length, fresh weight, and dry weight by up to 95%, 100%, 64.21%, 62.5%, 73.68%, and 99%, respectively. Ahmad Y. et al. (2020) found that *Alternaria* spp. and *Drechslera* spp. reduced *C. album* germination by 57 and 75% and *A. fatua* germination by 44% and 31%, respectively. Bashir et al. (2018) also reported that secondary metabolites of *Aspergillus niger* significantly decreased the germination and shoot and root biomass of parthenium weeds by 90%, 57%, and 68%, respectively, when using original metabolites.

Endophytic fungi-secreted phytotoxic compounds such as holdysenterine and drechslerol-C, isolated from *Drechslera* spp. and cyclic tetrapeptide isolated from *Alternaria* spp. have reduced germination, growth, and chlorophyll content, leading to chlorosis, cell damage, and necrosis in *C. album, A. fatua, C. arvensis*, and *Rumex dentatus* (Akbar and Javaid, 2012; Ahmad Y. et al., 2020). Host-specific phytotoxic compounds called chenopodolans have been reported in the EF *Phoma chenopodiicola* for effective biocontrol of *C. album* (Ahmad Y. et al., 2020). These phytotoxic compounds usually cause the appearance of necrotic spots surrounded by chlorosis and cell damage on the leaves of target weeds and lack toxicity on nontarget cultivated and wild plants (Cimmino et al., 2015). Cyclic tetrapeptide and AAL toxins from *Alternaria* spp. also inhibited chlorophyll contents, caused cell damage and electrolyte leakage, and interfered with overall plant metabolism by producing reactive oxygen species, ultimately leading to chlorosis and cell death (Ahmad Y. et al., 2020). Studies have demonstrated that conidial suspensions of *Aspergillus* spp. have variable herbicidal activities against weed germination and growth, with applied conidia or exudates during fungal growth reducing germination and growth by up to 65% (Bashir et al., 2018; Daba et al., 2021).

Herbicidal compounds secreted by EFs have also been found to potentially compromise cell membrane integrity, resulting in increased permeability, solute leakage, and elevated electrolyte leakage, significantly impacting the overall health and functionality of the affected weeds. For instance, EF-produced phytotoxic compounds, such as bisanthraquinones, octahydronaphthalenes, alkaloids, and molecules possessing chemical scaffolds, are capable of absorbing electrons and affecting redox processes (Ahmad Y. et al., 2020; Moura et al., 2020). EF *F. oxysporum* also produces polyphenols that reduce *A. fatua* growth, including quercetagetin, isovitexin, calycosin, dihydroxy-dimethoxyisoflavone, naringenine, vitaxin, cis-cafatric acid, caffeoyl-D-glucose, and p-dyroxy benzoic acid (Asim et al., 2022). Some of these chemicals have also shown allelopathic and herbicidal activity against *A. retroflexus*, *P. oleracea*, *C. album*, and *Abutilon theophrasti* (Boselli et al., 2021). Cimmino et al. (2015) also found that nonproteic toxic amino acids from the culture of *Ascochyta caulina* cause cell harm and necrosis in the leaves of *C. album*, finally causing electrolyte leakage. Toxins such as indole 3-acetic acid (IAA) isolated from *A. alternata* were also found to damage cells, cause chlorosis and induce electrolyte leakage in various weed species, demonstrating their potential as natural herbicides (Ahmad Y. et al., 2020). Suryanarayanan (2019) reported that EFs produce metabolites that exhibit herbicidal activities and induce chlorosis, finally causing necrosis in *Lemna minor*. The herbicidal effects of various species of EFs on different weeds, as well as the compounds released by these EFs and their effects on the host weeds, are shown in Table 4.

TABLE 4 Use of endophytic fungi in weed control and management.

Crops	Fungal endophytes	Compounds released by the EFs	Target weeds	Effects on the weeds	References
T. aestivum	*F. oxisporum*	Isovitexin, calycosin, quercetagetin, and dihydroxy-dimethoxyisoflavone	*Avena fatua*	Inhibited the growth of *A. fatua* by the biomass of the fungus in the soil	Asim et al. (2022)
	Drechslera holmii, D. biseptata and D. australiensis	Metabolites such as holadysenterine, de-O-methyldiaporthin, drazepinone, Ophiobolin E, 8-epi-ophiobolin J, di-(2-ethyl-hexyl)-phthalate, and 2,4-dichlorophenoxyacetic acid	*Rumex dentatus*	Reduced germination, shoot and root growth, and shoot and root fresh and dry biomasses (For instance, metabolites of *Drechslera* spp. suppressed the weed germination, shoot length, shoot dry biomass, root length and root biomass by 12%–56%, 73%–85%, 72%–88%, 82%–94% and 77%–88%, respectively)	Akbar and Javaid (2012) and Akbar et al. (2020)
	Drechslera spp. (*D. hawaiiensis*, *D. holmii*, *D. biseptata*, and *D. australiensis*)	Metabolites and herbicidal constituents, like ophiobolin A, 6-epi-ophiobolin A, anhydro-6-epiophiobolin A, ophiobolin I, and drazepinone	*Chenopodium album* and *A. fatua*	Reduced germination and root and shoot growth and biomass	Akbar and Javaid (2010, 2012)
Parthenium hysterophorus	*Alternaria*, *Aspergillus*, and *Drechslera* spp.	Phytotoxic compounds like holadysenterine and drechslerol-C, nonproteic toxic amino acid, AAL toxins, cyclic tetrapeptide, reactive oxygen species (ROS), and other bioactive compounds	*C. album*, *A. fatua*, and *Convolvulus arvensis*	Reduced germination, shoot and root length, and plant biomass, and other growth parameters, phytotoxic effects, increased leaf relative electrolyte leakage, reduced biochemical and physiological processes like cellular respiration and chlorophyll contents, chlorosis, and necrosis	Ahmad Y. et al. (2020)
C. arabica	*Aspergillus niger* and *Trichoderma* spp. (*T. asperlium*, *T. atroviride*, *T. hamatum*, *T. harzanium*, *T. longibrachatum* and *T. viride*)	Phytotoxins and other compounds with herbicidal constituents and inhibitory potential found in fungal conidia suspensions	*Bidens pilosa* (Asteraceae)	Inhibited germination percentage and index, plumule and radicle length, seedling vigor index, and overall early growth of the weed	Daba et al. (2021)
Helianthus annus	*Aspergillus alliaceus*	Phenolic substances such as gallic acid, catechin, syringic acid, p-coumaric acid, syringic acid, caffeic acid, and abscisic acid	*Orobanche cernua*	Reduced synthesis and disrupted balances of hormones (abscisic acid, salicylic acid, and jasmonic acid), damaged free radicals and protein synthesis metabolism, inhibited antioxidant enzymes, and weakened apoptosis-based plant defense reactions eventually leading to a slow and continuous death	Aybeke (2020)
	F. oxysporum	Secondary metabolites such as phenols (catechin, syringic acid, caffeic acid and p-coumaric acid), flavonoids, ROS, and antioxidant enzymes such as Mn-superoxide dismutase and Zn-superoxide dismutase	*O. cernua*	Hormonal disorders, lethal physiological damages, and induced phenol synthesis, accumulation and oxidation causing typical symptoms of tissue browning finally killing the weed quickly	Aybeke (2017)
	Aspergillus alliaceus	Phenols, phytoalexins, mucilaginous substances (mucilage), mycotoxins (ocratoxin A), lignin-like reddish-brown droplets (safranin-stained droplets), and carbohydrate-derived products (nonesterified pectins)	*O. cernua*	Collapse of outer cells of various tissues, thickenings, lignification and disintegration of cell wall, breakdown and disintegration of organelles and cytoplasm, deformations of cellular and pollen grains, destruction of seed hilum, embryo and endosperm finally causing tissues disappearance, leaf necrosis, and reduction of weed attachments, tubercles, and emergent shoots	Aybeke et al. (2014)

(Continued)

TABLE 4 (Continued)

Crops	Fungal endophytes	Compounds released by the EFs	Target weeds	Effects on the weeds	References
V. faba and *S. lycopersicum*	*F. oxysporum* (Foxy I and Foxy II)	Microconidia and chlamydospores	Orobanche spp. (*O. crenata* and *O. ramosa*)	Decreased germination, attachments, tubercles, emerged shoots, shoot height and dry weight (For instance, application of isolate Foxy I and Foxy II, respectively, reduced *invitro* germination by 80 and 76% in *O. crenata* and by 77 and 76% in *O. ramosa*)	Nemat Alla et al. (2008)
S. lycopersicum, *Brassica oleracea*, and *Nicotiana tabacum*	*Fusarium* spp.	Various secondary metabolites	*Orobanche ramosa*	Reduced number, length, and fresh and dry weights of shoots (by approximately 60%) and number of tubercles attached to the roots of host plants (by more than 70%)	Boari and Vurro (2004)

4 Efficiency of endophytic fungi in plant growth promotion

4.1 Endophytic fungi as inducers of plant growth-promoting phytohormones

Fungal endophytes are microorganisms that enhance plant growth and development either directly through secreting or stimulating vast arrays of phytohormones (Bilal et al., 2018; Yan et al., 2019; Rajani et al., 2021). They can actively or passively regulate plant growth by enhancing the production of plant hormones such as auxin, gibberellic acid (GA), abscisins, ethylene, and IAA (Lata et al., 2018; White et al., 2019; Rigobelo and Baron, 2021). Due to their ability to produce enzymes and other bioactive compounds, EFs such as *Penicillium, Piriformospora indica, Sebacina vermifera*, and *Colletotrichum* have more potent plant growth-promoting abilities even in unfavorable environments (Kaur, 2020). A diverse range of phytohormones and phytohormone signaling pathways are utilized in mediating PGP, resulting in greater root growth and, ultimately, higher yield and biomass (Bilal et al., 2018; Abro et al., 2019; Fadiji and Babalola, 2020). Some common plant growth hormones produced by different fungal endophytes in different plants are presented in Table 5. Aamir et al. (2020) further delineated that the most common mechanisms by which EFs provide benefits to plants have been achieved by siderophore production, solubilization of phosphates, N fixation, phytohormones such as IAA production, and 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity. Various mechanisms by which EFs benefit their host plants are presented in Figure 1.

Auxins, gibberellins, and cytokinins synthesize EF and are known to serve as chemical mediators and signaling molecules for plant growth (Baron et al., 2020). Endophytic fungi, such as *F. fujikuroi*, *Serendipita indica*, and *Piriformospora indica*, can produce phytohormones such as indole-3-acetic acid (IAA), cytokinin, and gibberellic acid, suggesting that they can regulate host signaling and influence physiological and metabolic activities (Liu et al., 2021). However, PGP is primarily driven by IAA, which positively impacts shoot and root development, including responses to tropism, cell division, cell elongation, vascular tissue differentiation, and root formation (Airin et al., 2023). Khan et al. (2008) found that bioactive gibberellins such as GA1, GA3, GA4, and GA7 in *P. citrinum* IR-3-3, EF isolated from dune plants, improved seedling length and growth in Waito-c rice dwarf mutant and sandy plant *Atriplex gmelinii*. Bader et al. (2020) studied *Trichoderma* strains from soils of Argentine Pampas, revealing high phytohormone production capacities and significantly improved plant height, fresh and dry biomass, chlorophyll content, and higher surface area in inoculated tomato seeds after 45 days. Baron et al. (2020) found that *P. lilacinum*, *P. lavendulum*, and *Metarhizium marquandii* can produce IAA in soybean, bean, and maize, promoting growth by improving parameters such as dry matter, attributed to endophytic colonization of the plants. As a result, sustainable agriculture could rely largely on endophytic fungi, which possess the unique ability to thrive and colonize host plant tissues, promoting the production of various phytohormones with biological activities.

4.2 Endophytic fungi as modulators of nutrient acquisition by plants

Fungal endophytes can also boost plant growth indirectly by assisting the plant in acquiring nutrients (Bilal et al., 2018; Yan et al., 2019; Rajani et al., 2021). In previous studies, EFs that dwell in host plants without developing obvious symptoms have been noted to play an important role in boosting plant growth by aiding nutrient absorption (Molina-Montenegro et al., 2016; Abro et al., 2019; Huang et al., 2020). These microorganisms are capable of enhancing agricultural productivity by increasing plant access to nutrients [N, P, K, Zn, iron (Fe), etc.] producing plant hormones, reducing ethylene, or increasing the water acquisition rate (Baron et al., 2018; Abro et al., 2019; Huang et al., 2020). Various nutrient transporters and processes of translocation have been confirmed in different plants infected with EFs. For instance, the nutrient acquisition mechanism employed by EFs includes the release of nutrients from insects that are decayed by microbes (Behie and Bidochka, 2014; White et al., 2019). This has been confirmed by Behie and Bidochka (2014), who reported the EF transfer of N from insects by some EF species, namely, *M. guizhouense, M. flavoviridae, M. robertsii, M. brunneum, M. acridum, Akanthomyces (=Lecanicillium) lecanii and B. bassiana*, *P. vulgaris* (common bean), *G. max* (soybean), *P. virgatum* (switchgrass), and *T. aestivum* (wheat). In this regard, Rigobelo and Baron (2021) showed that some species of EF can kill the larvae of insects and colonize plants endophytically, facilitating the transfer of nutrients from insects to these plants.

Fungal endophytes also help in the biodegradation of the litter of their host plants and decomposition of organic components,

TABLE 5 Examples of common phytohormones produced by EFs reported in various host plants.

Crop	Fungal endophytes	Phytohormone	References
S. lycopersicum	*Curvularia lunata* and *Nigrospora sphaerica*	Indole 3-acetic acid (IAA)	Saad and Badry (2020)
H. annuus	*Penicillium citrinum* and *Aspergillus terreus*	IAA and GAs	Waqas et al. (2015a)
V. faba	*Aspergillus niger* and *Penicillium chrysosporium*	Abscisic acid (ABA) and ethylene	El-Mahdy et al. (2021)
C. sativus	Combinations of different EFs	IAA and GAs	Syamsia et al. (2021)
G. max	*Paecilomyces formosus* and *Penicillium funiculosum*	GAs and IAA	Bilal et al. (2020)
G. max	*Porostereum spadiceum*	GAs	Hamayun et al. (2017)
G. max, *V. faba* and *Z. mays*	*Purpureocillium lilacinum*, *Purpureocillium lavendulum* and *Metarhizium marquandii*	IAA and solubilize P from fluorapatite	Baron et al. (2020)

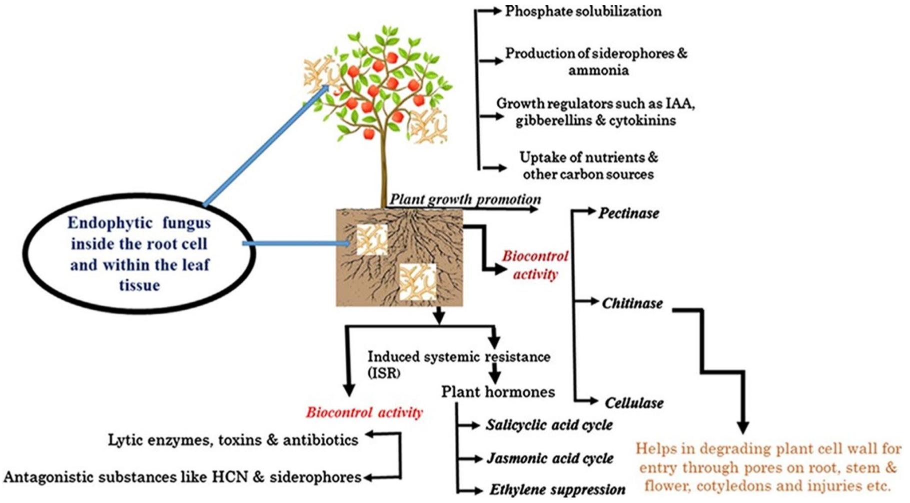

FIGURE 1
The functional dimension of EFs that localize inside living plant root tissues and within root cells and the mechanisms by which they benefit their host plants. Adapted from Aamir et al. (2020).

comprising cellulose, lignin, and hemicelluloses, which enable nutrient cycling (Lata et al., 2018). As reported by Behie and Bidochka (2014), EFs such as *Heteroconium chaetospira* have been shown to transfer N gained from decayed OM in the soil to *Brassica campestris* roots and increase N uptake efficiency. Yang et al. (2014) also indicated that fungal endophyte *Phomopsis liquidambari* colonization increases N, P, S, Zn, and Mg availability and significantly increases plant root length, root number, height, number of buds, chlorophyll levels and biomass in rice. Lugtenberg et al. (2016) revealed that *P. indica* increased shoot dry weight and grain yield and appeared to trigger flowering earlier at low temperatures under the lowest nutrient input, therefore helping to decrease fertilizer inputs while maintaining reasonable yields.

In nutrient acquisition, a process known as the 'rhizophagy cycle' enables EFs to access nutrients in the soil and then transport them back to the plants, where they penetrate the root cells at the tips of the roots closest to the nutrient exudate zone, where the growing root epidermal cells possess thin cell walls (Lata et al., 2018; White et al., 2019; Rigobelo and Baron, 2021; Singh et al., 2021). Rhizophagy symbiosis is a mutualism that involves nutrition exchange between plants and their EF partners (White et al., 2018, 2019; Rigobelo and Baron, 2021), and this process has been hypothesized by White et al. (2018, 2019), as depicted in Figure 2. Nutrient mining by EFs in the rhizophagy cycle, according to Kumar et al. (2020), involves three major steps: (1) Plant roots exudate organic acids, such as malic, citric, and acetic acids, into the soil, which bind with metals found in the soil (Mg^{2+}, Fe^{3+}, Mn^{2+}, Co^{2+}, Cu^{2+}, Co^{2+}, Ni^{2+}, etc.); (2) the EFs eventually possess transporters that attach to these organic acid-metal complexes and transfer them into the EF cells; and (3) finally, EFs return to plant roots and enter root cells, where they oxidatively take nitrogen and micronutrients, including Fe, Zn, and Mg, from microbes and eject them back into the soil from root hair tips to acquire more nutrients.

The rhizophagy cycle involves EFs transitioning between the EF/intracellular protoplast phase of the plant root cells and the free-living walled phase of soils, acquiring nutrients in the soil and oxidatively extracting them from the EF/intracellular protoplast phase (White

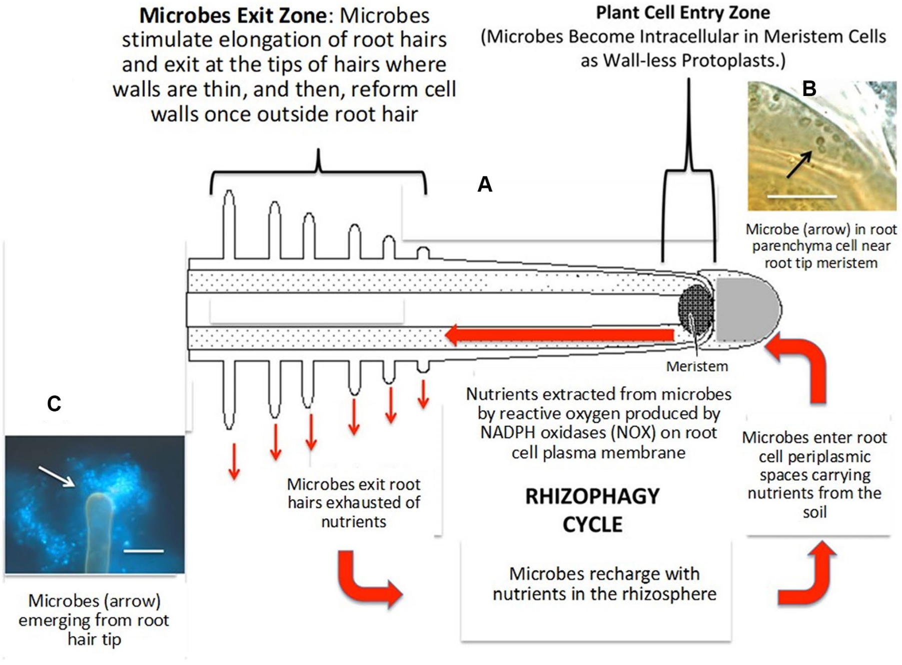

FIGURE 2
Diagram of the rhizophagy cycle showing microbes entering root cells at the plant root tip meristem and exiting root cells at the tips of elongating root hairs **(A)**, microbes (arrow) in the periplasmic space of parenchyma cells near the plant root tip meristem **(B)** and microbes (arrow) emerging from the plant root hair tip **(C)**. Adapted from White et al. (2019).

et al., 2019; Kumar et al., 2020). In this cycle, EFs enhance root exudates and change their composition, which boosts microbial activity and nutrient mining. These root exudates contain proteins, vitamins, enzymes, phenolic acids, flavonoids, fatty acids, tannins, nucleotides, alkaloids, steroids, terpenoids, and polyacetylenes in addition to organic acids (White et al., 2018, 2019). Plants use their symbiotic EF to transport nutrients from the soils into the periplasmic spaces of their root cells, liberate nutrients via oxidation, and deposit used EF back into the rhizosphere by extending root hairs. This process has been found to improve nutrient transport into plants, assisting with nutrient acquisition from symbiotic EFs that sequester soil nutrients utilizing siderophores (White et al., 2018). Yung et al. (2021) further delineated that EFs act as the prey of roots in rhizophagy and serve to nourish plant nutrition and growth by improving the mineral nutrition and root elemental composition of host plants. For instance, Yung et al. (2021) reported that EFs, particularly DBF60 (*Metapochonia rubescens*), DBF79 (*Alternaria thlaspis*), DBF81 (*Trichoderma harzianum*), and DBF107 (*Cladosporium* sp.), isolated from various plant parts improved the root elemental contents of P, K, Mg, Ca, and S by up to five times in some cases.

Furthermore, EFs produce extracellular enzymes such as pectinase, cellulase, lipase, laccase, proteinase, phosphatase, and xylanase, which aid in the breakdown of macromolecules such as sugar-based polymers, lignin, organic phosphate, proteins, and carbohydrates to micromolecules accessible to plants (Kaur, 2020). In particular, EF chitinase enzymes play a vigorous role in the degradation and cycling of C and N from chitin molecules obtained from insect exoskeletons, crustacean shells, and fungal cell walls (White et al., 2019; Kaur, 2020). Chen et al. (2018) showed that *Epichloë festucae* var. *lolii* alleviated nutrient deficiency in ryegrass by promoting root metabolic activity and decreasing the stoichiometric ratios of C:N, C:P, and N:P in leaves and roots and the Cu content of roots. This EF also increased the concentration of C, N, P, K, Ca, Mg, Fe, and Mn, the dry weight of leaves and roots, the Cu content of leaves and root activity in the absence of fertilization. Overall, EFs have been confirmed to be a safe option for achieving sustainable farming due to their ability to increase the transfer of access to nutrients and other essential compounds (Lata et al., 2018; Fadiji and Babalola, 2020; Rigobelo and Baron, 2021; Singh et al., 2021).

5 Endophytic fungi conferring plant resilience under climate change conditions

Sustainable agricultural goals aim to address climate change as a significant impediment to food security for an increasing global population, emphasizing the need for climate-resilient production systems as a key dimension of sustainability. Climate change-driven abiotic stresses, such as climatic variability, drought, salinity, heat, osmotic stress, and nutrient shortages, are increasingly affecting and limiting agricultural productivity in this century (Ferus et al., 2019; Fontana et al., 2021). According to Singh et al. (2021), increasing drought, temperature, and soil salinity and decreasing water availability are growing challenges for improvements in crop production. Endophytic fungi, which inhabit almost all plants in natural Earth's ecosystems, provide different benefits to boost crop performance, yield, and resilience to environmental stresses, hence mitigating the negative effects of climate change (Hereme et al., 2020; Verma et al., 2022). Consequently, the integration of EFs is perhaps a beneficial approach for both mitigating the effects of climate change on main crops and growing agricultural production on marginal lands. Thus, the use of EFs would be a promising approach for improving agricultural productivity by decreasing the reliance on harmful agrochemicals. For example, Tian et al. (2021) noted that after crossbreeding wild rice (African and Asian wild rice) species with grown rice accessions, wild rice contains more root EFs than the cultivated parent rice used to produce crosses in the first generations (F1 offspring), which opens up new research areas for the impacts of breeding on the inheritance of EFs in successive generations. Similarly, Abdelrazek et al. (2020) reported that carrot genotypes affected EF abundance and suggested the possibility of using EFs in carrot breeding programs for improvements in the health and yield of crops. Wang et al. (2020) also reported that *Fusarium* head blight (FHB) resistance gene Fhb7 (Fhb7) introgressions in wheat confer resistance to both FHB and crown rot in varied wheat backgrounds, offering a solution for *Fusarium* resistance breeding.

Several laboratory and greenhouse experiments have strongly indicated that endophytes could be used to mitigate stresses in agricultural crops to increase productivity (Chitnis et al., 2020; Singh et al., 2021), as demonstrated in Table 6. The colonization of EFs usually triggers physiological changes in plants, imparting tolerance to various abiotic (oxidative, drought, salinity, high temperature, high CO_2, and metal toxicity) stresses (Lata et al., 2018; Morsy et al., 2020; Verma et al., 2022). EFs can enhance plant resilience to climate change by promoting the plant's own molecule production and/or by producing several compounds on their own, which are crucial for adaptation to adverse environmental conditions (Lata et al., 2018; Morsy et al., 2020). In most cases, EFs aid host plants in responding to stresses by regulating plant growth and development using bioactive substances that can work together with hosts for better performance. They secrete phytohormones, saponins, triterpenoids, ginsenosides, proteolytic enzymes, growth hormones, phosphate-solubilizing factors, active volatile and nonvolatile metabolites, IAA, and ACC deaminase during stress to enhance plant growth and enable plants to overcome abiotic stresses (Moraes et al., 2020; Jagannath et al., 2021; Lu et al., 2021). According to Verma et al. (2022), *T. atroviride*, *T. polysporum*, and *T. harzianum*, which inhabit *Phaseolus vulgaris,* phosphate solubilizing factors, exude proteolytic enzymes, and active volatile and nonvolatile compounds that enhance plant growth and improve abiotic stress tolerance. Secondary metabolites such as flavonoids, phenylpropanoids, phytoalexins, and carotenoids are found in stressed plants inoculated with EFs, and they help plants tolerate abiotic stress by acting as antioxidants that scavenge ROS (Kaur, 2020; Jagannath et al., 2021). In a recent study, EFs increased the phenol and proline contents in drought-salinity-exposed plants, where phenols signal symbioses, while proline, a stress-associated amino acid, improves drought tolerance by regulating macromolecule stabilization and redox homeostasis (Ballesteros et al., 2023).

Fungal endophytes also indirectly promote plant growth by inducing resistance and promoting antibiotic, secondary metabolite, and siderophore production, which protects plants against abiotic stressors (Singh et al., 2021). Thus, root EF can be leveraged as a biotechnological tool to sustain high ecophysiology and productivity in abiotic stressors (Molina-Montenegro et al., 2016; Ferus et al., 2019). In areas under drought conditions, for instance, EFs offer benefits that are related to reduced lipid peroxidation, higher proline levels, and ion homeostasis upregulation or downregulation (Molina-Montenegro et al., 2016; Morsy et al., 2020). Studies have revealed that EFS confers drought tolerance in crops through enhanced photosynthesis, improved water use efficiency (Dastogeer, 2018; Hereme et al., 2020), improved nutrition and root development (Dastogeer, 2018), and induced stress-responsive gene expression (Molina-Montenegro et al., 2016; Hereme et al., 2020). For instance, under water stress conditions, EFs increased chlorophyll content, total biomass, net photosynthesis, relative water contents, and stomatal conductance in plants compared to nonstressed conditions (Dastogeer, 2018; Ismail et al., 2020). Additionally, EFs also aid plant adaptation to drought endurance by secreting phytohormones, exopolysaccharides, ROS, 1-aminocyclopropane-1-carboxylate deaminase, and volatile compounds while altering root morphology and biosynthesizing anti-stress metabolites (Fontana et al., 2021). Ismail et al. (2020) isolated the EF *A. violaceofuscus* from the fern *Dryopteris flix* L. and found that its culture filtrate had a higher concentration of secondary metabolites that improved plant height, chlorophyll contents, soybean seedlings, and sunflower biomass under drought and heat stresses. Drought and heat stresses can also be mediated by

TABLE 6 Endophytic fungi conferring abiotic stress resistance in various plants.

Fungal endophytes	Host plant	Abiotic stress	References
P. indica	*Hordeum vulgare*	Salinity stress	Baltruschat et al. (2008)
Trichoderma sp.	*T. cacao, Brassica rapa* subsp. Pekinensis and *H. vulgare*,	Salinity and Drought stress	Chhipa and Deshmukh (2019)
Curvularia protuberate	*Lycopersicon esculentum*	Temperature stress	Rodriguez et al. (2008)
Paecilomyces formosus LWL1	*Oryza sativa* subsp. Japonica	Temperature stress	Waqas et al. (2015b)
Chaetomium globosum and *Penicillium resedanum*	*Capsicum annum*	Drought stress	Khan et al. (2014)
Penicillium brevicompactum	*Hordeum vulgare*	Drought stress	Chhipa and Deshmukh (2019)
P. indica	*Brassica rapa* subsp. Pekinensis	Drought stress	Sun et al. (2010)
Penicillium roqueforti Thom	*Triticum*	Heavy metal stress	Ikram et al. (2018)
Exophialapisciphila	*Zea Mays*	Heavy metal stress	Wang et al. (2016)
Acrocalymma vagum	*N. tabacum*	Heavy metal stress	Jin et al. (2018)

EFs through mitogen-activated protein kinase (MAPK) and heat shock proteins (HSPs), respectively (Lata et al., 2018).

Fungal endophytes also have the potential to mitigate soil salinity stresses in various crops (Badawy et al., 2021; Moghaddam et al., 2021). Some of the strategies mediated by EFs to mitigate salt (other abiotic) stresses include (1) proline accumulation within cells (Badawy et al., 2021; Gupta et al., 2021); (2) modulation of plant hormones/phytohormones (Gul et al., 2014; Baron et al., 2020; Illescas et al., 2021); (3) maintenance of ionic homeostasis by modulating ion accumulation, ensuring a low cytosolic Na+:K+ ratio and advancing nutrient uptake in plants (Gupta et al., 2021); (4) accumulation of glycine betaine and polyols (Khan et al., 2011); and (5) production of extracellular enzymes (Jagannath et al., 2021). For instance, *Induratia* spp. isolated from coffee plants also produce remarkable amounts of extracellular enzymes, such as protease, cellulase, lipase, phosphates and amylase (Monteiro et al., 2020). A recent study examined 203 EFs from 29 species from *Baliospermum montanum* tissues for extracellular enzymes and showed that 83% of isolates produced amylase, 79% cellulase, 77% phosphatase, 72% protease, and 59% lipase (Jagannath et al., 2021).

Furthermore, EFs can support host plants in responding to various stresses through the involvement and expression of mutualistic genes (Monteiro et al., 2020; Jagannath et al., 2021; Lu et al., 2021). In particular, EFs can upregulate genes involved in secondary metabolite production, osmotic regulation, ion transport, stress signaling pathways, and the synthesis of antistress metabolites and scavenger molecules (Lata et al., 2018; Chitnis et al., 2020; Harman et al., 2021). For instance, Verma et al. (2022) reported that wheat EF altered stress-related gene expression to enhance drought tolerance, while rice EF modified antioxidant defense gene expression to improve oxidative stress tolerance. Several transcriptomic and metabolomic studies have also indicated the involvement of mutualistic gene products in various plant growth and abiotic stressor adaptation pathways. A recent study by Toppo et al. (2023) revealed that *T. longibrachiatum* T6 upregulated the expression of actin, POD, SOD, and CAT biosynthetic genes to reduce salt stress in wheat seedlings, while *T. harzianum* upregulated CsAPX and CsGR genes in cucumber seedlings, mitigating various abiotic stresses. Abdelaziz et al. (2017) also showed that EF can help salt-stressed plants from osmotic stress by regulating the expression of the *P5CS* gene (pyroline-5-carboxylate synthase), which is involved in the biosynthesis of proline, starch-degrading enzyme activation, and glucan-water dikinase. Toppo et al. (2023) further observed that *P. funiculosum* LHL06 upregulates the *GA1, GA3, GA4, GA7*, and *GA9* genes to reduce metal toxicity by modulating hormonal concentration while downregulating the stress mitigation-related genes *G6PDH, GmGST3, GmGST8* and *GmSOD1[Cu–Zn]*. Fungal endophytes such as *Paecilomyces formosus* LHL10 and *P. funiculosum* LHL06 have also shown increased transcript expression of the *GmHsp90A2* and *GmHsp90A1* genes to enhance soybean growth under high temperature and drought stress (Bilal et al., 2020). In addition, MAPK genes are also key players in the MAPK pathway, which is responsible for producing ROS, signaling pathways, and the synthesis of antioxidants in EFs to help their host plants cope with abiotic stresses (Ogbe et al., 2020). In general, EFs demonstrate remarkable promise as a means to safeguard global agriculture and food security amidst climate change through their multifaceted abilities to promote plant growth and strengthen host plant resilience against environmental stresses.

6 Research gaps and future perspectives

Increasing threats to global food security from climate change, population growth, and multiple stress factors emphasize the urgent need to boost crop yields in vulnerable environments. Fungal endophytes show promise through direct and indirect mechanisms that promote plant growth, pest protection, and climate adaptation, offering a cost-effective and environmentally friendly alternative to improving food production and promoting sustainable agriculture practices. However, their agricultural application remains limited due to regulatory standards and difficulties with mass production, inoculant efficacy, and resistance from consumers and farmers (Khiralla et al., 2016; Ballesteros et al., 2023). Secondary metabolite production from EFs is effective at small-scale setts, but large-scale production has been unsuccessful due to poor yields and performance, particularly for functional polysaccharide biosynthesis. A deeper understanding of EF-produced metabolite structures, microbial interactions, and plant support and/or protective mechanisms could aid integrated management approaches, thereby improving production and benefiting the environment. Further research is also needed on EF manipulation of host morphology and physiology to assess the application potential. Fundamentally, elucidating complex relationships between EFs, crops, soil variables, and soil/plant microbiomes and how these influence morphological, physiological and biochemical responses is essential to optimize EF-mediated adaptations and strengthen sustainable agriculture amid climate threats.

There is also a knowledge gap about how biotic and abiotic stressors may alter plant-EF interactions, potentially leading to mutualistic or parasitic partnerships (Kamran et al., 2021), warranting comprehensive analysis of influential factors to determine the possible interactions. The competition between native microbiomes and introduced EFs, particularly in extreme environments, may lead to decreased effectiveness or negative impacts (Aremu et al., 2017), necessitating studies to confirm effects and identify potential shifts in EF efficacy. Comprehensive metabolomics, genomics, proteomics, and transcriptomics analyses could better elucidate these complex interactions, as well as the diversity and beneficial traits of EFs (Kamran et al., 2021; Verma et al., 2022). Furthermore, EF bioactivity, source, kind, and inoculant production need to be considered when determining the optimal quantity of EFs for plant growth, health, and climate change resilience. Overall, the ultimate goal should be translating endophytes into bioinoculants, biofertilizers and other products using interdisciplinary research and microbial modulation. Despite these aims, smallholder farms remain crucial for global food security, accounting for 50%–70% of global food production (Giller et al., 2021); hence, future efforts must integrate beneficial microbes such as EFs into smallholder agriculture to ensure urgent agricultural transformation.

7 Conclusion

Endophytic fungi are promising tools that can be used as biocontrol agents to regulate plant pest populations, enhance plant growth, and promote plant resilience against the challenges imposed by climate change. These microbes are greatly effective against agriculturally important pests, including insects, plant diseases, nematodes and weeds, while simultaneously having the potential to promote host plant growth and tolerance to various biotic and abiotic stresses. Thus, EFs have enormous potential to be used as effective and eco-friendly replacements for synthetic fertilizers and pesticides in agriculture under rapid climate change scenarios. Overall, EFs can be considered a key device in managing biotic and abiotic stresses due to the production of biologically active substances against both stresses by activating valuable products for agricultural production under rapid climate change scenarios. Generally, species-specific identification of EFs and characterization of their signaling, promotion and stress mitigation mechanisms, development and shelf-life enhancement components as climate-smart biocontrol agents and biofertilizers are highly imperative in agriculture under rapid climate change scenarios.

Author contributions

TF: Conceptualization, Investigation, Methodology, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. EK: Conceptualization, Investigation, Methodology, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. TT: Conceptualization, Resources, Supervision, Writing – original draft, Writing – review & editing. ZB: Conceptualization, Resources, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

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