Trenchant microbiological-based approach for the control of *Striga*: Current practices and future prospects

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Striga species are obligate parasitic weeds most of which are members of the Orobanchaceae family. They are commonly associated with staple crops and constitute threats to food security, especially in Sub-Saharan Africa. They pose deleterious impacts on staple cereal crops like maize and pearl millet, resulting in 7–10 billion dollars yield losses or, in extreme infestations, entire crop losses. Farmers' limited knowledge about the weed (genetics, ecology, nature of the damage caused, complex life cycle, interactions with its host and associated microbes) and their attitude toward its control have negatively affected its management and sustainability. With the present *Striga* management such as mechanical, chemicals, cultural and biological measures, it is extremely difficult to achieve its active management due to nature of the association between host plants and parasites, which requires highly selective herbicides. The use of soil microbes has not been well explored in the management of *Striga* infection in African countries. However, many soil microorganisms have been considered viable biological control techniques for fighting parasitic weeds, due to their vast action and roles they play in the early stage of host-*Striga* interaction. Their application for pest control is well perceived to be cost-effective and eco-friendly. In this review, we gave a comprehensive overview of major knowledge gaps and challenges of smallholders in *Striga* management and highlighted major potentials of microbial-based approach with respect to the mechanisms of host-*Striga*-microbe interactions, and the metagenomics roles on *Striga* management that include understanding the microbe and microbial systems of *Striga*-infested soil.

KEYWORDS

parasitic weed, soil microbes, metagenomics, biological control, chemical control

1. Introduction

Parasitic weeds in the genus *Striga* have constituted a major threat to the cultivation of cereal crops such as sorghum, maize, pearl millet, and rice. *Striga* poses an imminent threat to food security because of up to 90% production loss it causes (Mounde et al., 2020). *Striga gesneriodes* are classified as holoparasites since they depend solely on the host

plants (i.e dicots) for nutrients, water, and carbon since they lack chlorophyll (Irving and Cameron, 2009). However, some other *Striga* species including *Striga hermontica* are obligate hemiparasite with the ability to photosynthesize; they fully depend on their host which is mainly cereals crops for nutrients and water, and partially for their carbon requirements. *Striga* survival depends on its ability to siphon nutrients and water from host crops to aid its own growth and development. The species have 5–7 days to attach to a suitable host for them to be established, or else the radicles will wither if their stored resource in the seeds is depleted (Mwangangi et al., 2021). *Striga* thus impairs the host plants *via* penetration and colonization of their root cells, thereby degrading the host function and productive values even before it emerges from the ground (Figure 1). Because of the further resource demand, *Striga* transitions from an independent to a host-dependent parasitic state. A parasitic association is created once *Striga* sp. successfully attaches to the host, in which it acts as a sink for the host's metabolites and water. Two separate techniques of resource retrieval are maintained, the first method is its unique capacity to maintain a constant high stomatal conductance, while the second technique is the accumulation of large quantities of osmotically active substances such as mineral ions, sugars, and alcohols such as mannitol (Shen et al., 2006).

Striga produce a large number of seeds, which can remain dormant for a long time, for instance, *Striga hermontica* produces up to 200,000 seeds and *S. asiatica* about 58,000 (Dafaallah and Babiker, 2016). The seeds are lightweight ($\sim$4–7 μg per seed) and are easily dispersed through the wind, agricultural tools and animals, which enrich the seed reserve in the soil. More so, they only germinate after exposure to hot and humid environments, and upon the secretion of strigolactones which is the germination stimulants produced by the host (Jamil et al., 2021). Infestation of *Striga* spp. is therefore prevalent in places with low soil fertility and rainfall, as well as in agricultural systems that practices intensive cultivation, poor crop management, or shortage of agricultural inputs (Ejeta, 2007).

In Sub-Sahara Africa (SSA), *Striga* are of food security concerns as they pose a deleterious impact on the production of staple cereal crops like maize and pearl millet. It results in 7–10 billion dollars yield losses, and could lead to entire crop losses in extreme infestations (Kountche et al., 2019). The production of cereal crops in SSA between 2017 and 2019 amounted to approximately 141 metric tons; however, *Striga* infestation reduced yield to as little as 1,000 kg ha^{-1}, making SSA one of the world's lowest producers (Kanampiu et al., 2018). Up till now, *Striga* has not been sustainably managed as a result of its peculiar nature which includes the production of large number of seeds, longevity, easy dispersal, variations in their genetic makeup, and the nature of damage caused (Spallek et al., 2013).

Understanding of *Striga* life cycle is essential in developing a long-term control strategy as this allows selection of most critical stage(s) that could be targeted in the design of novel control approach. Although, farmers' reluctance to embrace approved weed management in most instances has worsened the *Striga* problem, especially in Africa. One of such situations is the consistent monocropping that results in high infestation and accumulation of *Striga* seeds in the soil (Midega et al., 2017). The existing control measures of *Striga* can be employed either as individual
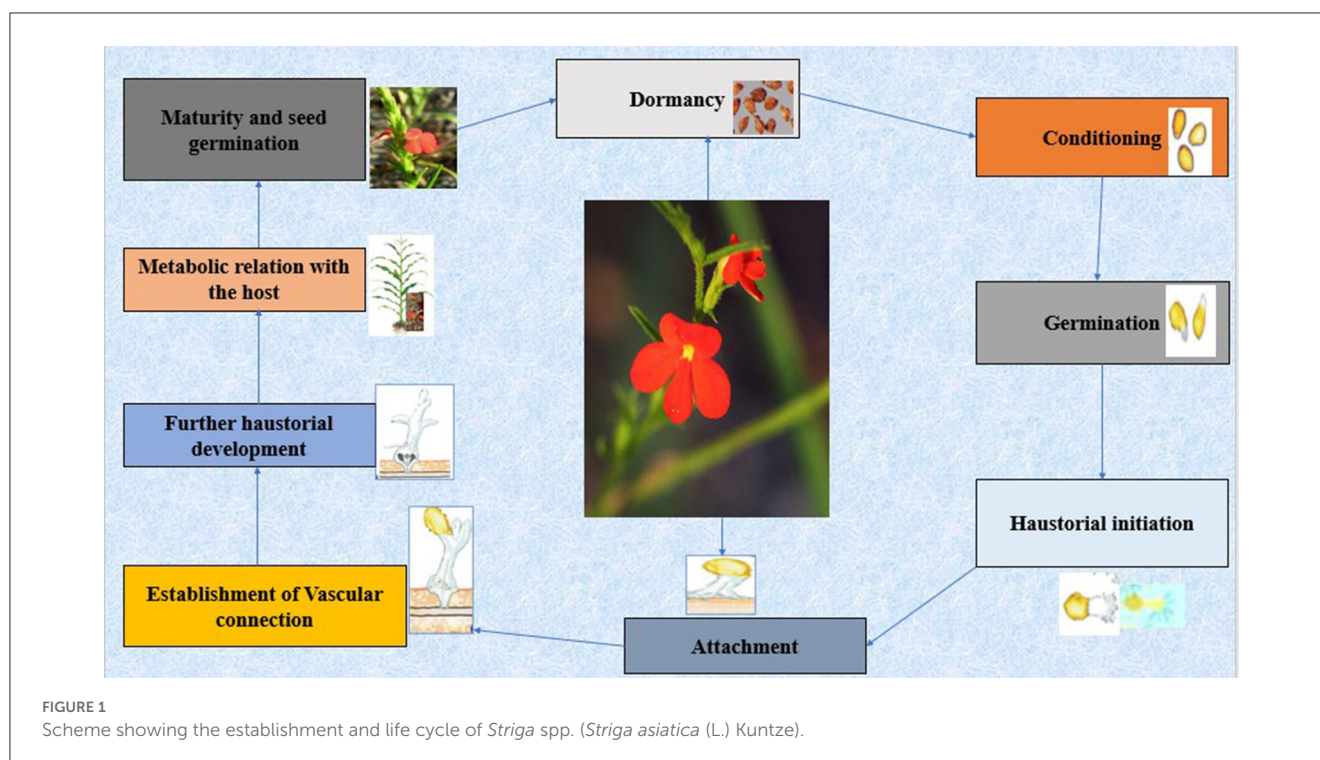
or integrated treatments. Some soil microbes have been reported to significantly cause reduction in *Striga* germination, emergence, and attachment (Hassan et al., 2009; Jamil et al., 2021). Some earlier studies have reported arbuscular mycorrhizal fungi (AMF) for their potential in the management of *Striga* infested fields (Birhane et al., 2018). They do not only promote growth and control *Striga* infection, but also participate in the absorption of phosphorus (P), micronutrients, and water from soil through extraradical hyphae (Aggarwal et al., 2011). However, there occur conficting views on the *Striga* and AMF relationship as another study reported the stimulation of AMF spore germination by strigolactones produced as root exudates of *Striga*, thereby suggesting the dependency of AMF growth on *Striga* (Steinkellner et al., 2007).

Researchers, with the advancements in the "omics" technologies have been able to better understand the diversity of soil microbial communities and their functional traits, which are significant ways of defining microbiological parameters (Zhou et al., 2022). Analysis of functional microbial diversity has shown how adaptable microorganisms interact with their environment, identifying trophic linkages, microbes interaction, their participation in biogeochemical cycles, and their responses to environmental changes. The rapid advancement of sequencing technologies, combined with bioinformatic tools enhances the feasibility of large-scale microbial ecology investigations, which also allows a better understanding of the composition and roles of microbes in different ecosystems (Tedersoo et al., 2021).

2. Current trends in *Striga* management

Striga species often affect various crops, especially cereal crops, and there have been significant efforts made to fully understand their controls. However, no single method of control has been found to be sufficiently effective (Mounde et al., 2020). Conventional approach of weed management is an age-long practice which entails the diversification agricultural operations to reduce dependency on chemical inputs while maintaining buoyant crop outputs and efficient ecosystem services (Rao et al., 2017). Weeding using hand tools are other common conventional method of managing *Striga* in SSA since majority of the farmers are smallholders. Also, the intercropping of cereal with legumes has been widely engaged to enhance soil fertility in relation to N$_2$ fixation. Other conventional approaches are land fallowing and crop rotation (Kerr et al., 2007). Integrated management of *Striga* is commonly advocated for and entails the combination of management methods that can work synergistically. Such include the use of *Striga*-resistant cultivars, arbuscular mycorrhizal fungi (AMF), mycoherbicidal biocontrol, improved tillage, intercropping with legumes, and fertilizer inputs (Babalola and Odhiambo, 2008; Bàrberi, 2019). Cultural methods such as rotation and cultivar selection in weed management are well established in many agricultural systems. However, alternative control measures are necessary, including biological control, which is promising, cost-effective, and safe for the environment.

Mycoherbicides are biological agents that have high host specificity, aggression, and ease of mass manufacturing, long storage life, and genetic diversity that make them effective against

FIGURE 1
Scheme showing the establishment and life cycle of *Striga* spp. (*Striga asiatica* (L.) Kuntze).

Striga (Babalola, 2010b; Zarafi and Dauda, 2019). In recent time, attention have been focused on fungal microorganisms as mycoherbicides against *Striga*, where *Fusarium oxysporum* f. f.sp. *Strigae* (Fos) strain "Foxy-2" has proven to reduce the establishment of *Striga* spp. by 95% while increasing sorghum yields by approximately 50% (Babalola and Odhiambo, 2008). Bàrberi (2019) confirmed the effectiveness of mycoherbicides developed from *Fusarium oxysporum* to inhibit *Striga* which decreases its seed bank in infected soils and its adhesion to cereals. High amounts of the poisonous amino acids L-tyrosin and L-leucine, which are toxic to *Striga* but not to maize are produced by some *F. oxysporum* and this interferes with the strictly regulated homeostasis of free amino acids. Also, soil microbes convert methionine secreted by *F. oxysporum* strains into germination stimulant ethylene which results in *Striga* seeds germinating suicidally (Babalola et al., 2007; Jamil et al., 2021; David et al., 2022). Watson (2013) proposed that *Striga* treatment could be accomplished in the field by seed coating with *F. oxysporum* (FOXY2). It was observed that for easy application and duration, FOXY2 and PSM197 were combined in a granular formulation and *Striga* emergence was reduced up to 75% in sorghum and maize crops (Beed et al., 2007). However, despite the significance of this findings, *F. oxysporum* has not been commercially employed by farmers in managing *Striga* infested field because of its host specificity. The host specificity of most *Fusarium* species has been recorded at the genus or species level. An instance of this is the efficacy of Isolate Foxy 2 against *S. hermonthica* and *S. asiatica* in the screenhouse trials. Also, the high genetic variability of *Striga* spp. may impact the efficacy of the *F. oxysporum*-bioherbicide. Therefore, to establish the effectiveness of *F. oxysporum* f. sp. striga isolates, there is need for its evaluations against multiple *Striga* populations from different hosts and across different environments,

whereas, the vegetative compatibility grouping pattern of the isolates of *Fusarium* species differs in relation to their host range (Beed et al., 2007). Furthermore, the ineffectiveness of the organism as a single control method could discourage its widespread application, as no single control method has been found successful in managing the *Striga* menace (Joel, 2000). This thereby showcasee a gap in the knowledge of *Striga* biology, its host-parasite interaction and the genetic basis of host resistance. Whereas, a combination of methods have proved effective, an instance of such was the combined application of *Fusarium oxysporum*-based mycoherbicide and host resistance which significantly reduced *Striga* prevalence and increased crop yield (Mrema et al., 2020).

Several studies have indicated the potential of AMF in alleviating *Striga* infection. The AMF enhance cereal growth to withstand *Striga* damage and facilitate host plant's uptake of micronutrients, water, and phosphorus (P) from soil through extraradical fungal hyphae (Olowe et al., 2018). The strigolactones (SLs) exudation by the host in the soil is ultimately reduced by the increased uptake of P via symbiotic interactions by AM fungi, thereby reducing *Striga* infection (Aquino et al., 2021). Furthermore, rate of *Striga* infestation is equally lowered by the soil microbes through their release of amino acids such as methionine or by the producing secondary metabolites such as trichothecenes which may interfere with SL perception. Also, there is evidence of fungal degradation by Strigolactone, which may result to decrease in *Striga* germination and the release of root exudates (Jamil et al., 2021) (Table 1). Soil microbes are potential biological control tools for combating *Striga* because of their cost-effectiveness and eco-friendliness approach. However, abiotic and biotic factors under field conditions can alter the efficacy of this approach (Berner et al., 2003).

TABLE 1 Tripartite interaction between host plant, *Striga* spp., and associated microorganisms.

(Micro)organism	Parasite	Host plant	Impact on *Striga*	References
Fusarium oxysporum f.sp. *Strigae*	*Striga hermonthica*	Maize, sugarcane, sorghum, and millet	Reduce the occurrence of *Striga* infestation.	(Babalola et al., 2007; Babalola and Odhiambo, 2008; Nzioki et al., 2016; Jamil et al., 2021; David et al., 2022)
Pseudomonas syringae pv *glycinea*	*Striga aspera, S. gesnerioides* and *S. hermonthica*	Cowpea	Stimulate germination in *Striga* spp	(Berner et al., 1999; Jamil et al., 2021)
AM fungi	*Striga hermonthica*	Maize and sorghum	Low strigolactone production resulted in low *Striga* spp. germination.	(Lendzemo et al., 2007; Tulu et al., 2021; Yilma and Bekele, 2021; David et al., 2022)
Bradyrhizobium	*Striga gesnerioides*	Cowpea	Depressed *Striga* count	(Abdullahi et al., 2022)
Pseudomonas fluorescens and *Pseudomonas putida*	*S. hermonthica*	Maize	Limiting the spread of *Striga* spp.	(Ahonsi et al., 2002; Yilma and Bekele, 2021)
Gigaspora spp, *Glomus epigaeum, G. macrocarpum, G. occulatum*	*S. gesnerioides*	*Lepidagathis hamiltoniana*	Limit stimulation of *Striga* seed germination	(Kamble and Agre, 2014)
Pseudomonas spp, *Bradyrhizobium japonicum*	*S. hermontica*	Soybean and cowpea	*Striga* infestation was reduced.	(Ahonsi et al., 2003; Yilma and Bekele, 2021)
Azospirillum brasilense	*Striga* sp.	Sorghum	Germination of *Striga* is inhibited.	(Bouillant et al., 1997; Yilma and Bekele, 2021)
Pseudomonas putida and *Bacillus* sp.	*S. hermonthica*	Sorghum	*Striga* spp. emergence and haustorium development are suppressed.	(Babalola and Akindolire, 2011; Kushwaha et al., 2020)
Azospirillum brasilense, Bradyrhizobium japonicum, Pseudomonas putida, and *Azospirillum amazonas*	*S. hermontica*	Sorghum	*Striga Incidence has been delayed and reduced.*	(Hassan et al., 2009; Mounde et al., 2020)
Bacillus amyloliquefaciens FZB42 t, and *Bacillus subtilis* GBO3	*S. hermonthica*	Sorghum	Inhibiting the growth of *Striga hermonthica*	(Mounde et al., 2015; Anteyi and Rasche, 2021)

During a screen house trial, four PGPR inhibited *Striga* infestation in sorghum, and the strain *Bacillus subtilis* GBO3 resulted in the death of 35%-59% of *Striga* tubercles emergence and a 23% decrease in *Striga* attachment (Samejima and Sugimoto, 2018). In another study, the significant decrease of *Striga* seed germinating activity of sorghum root exudates following treatment with *Pseudomonas* suspensions, may have resulted from SLs degradation (Jamil et al., 2021). As shown for some isolates of *Bacillus, Streptomyces* and *Rhizobium* genera, the production of compounds with antibiotic activity and of extracellular enzymes, such as xylanases, pectinases, and amylases, can directly cause *Striga* seed decay (Neondo et al., 2017). Soil microbe could also inhibit *Striga* by releasing amino acids such as methionine or through secondary metabolites production such as β-lactone derivatives that may affect SL perception. SL was found to be degraded by fungi in several investigations, which may have a negative impact on the ability of produced exudates to germinate *Striga* (Brun et al., 2018). PGPR, AMF and strains of bacteria are considered to be economical, promising and environmentally friendly (Babalola, 2010a; Le Mire et al., 2016). However, the effectiveness of this approach can be affected by a number a of stress factors under field conditions. Thus, the choice of inoculum media, suitable formulations, storage, mass production, shelf life, consistency, compatibility with the host plants, and maintenance of their activity in infected soils are to be taken in to consideration (Vassileva et al., 2021). In-depth study and field-testing under various climatic and environmental circumstances are still necessary for the validation and further development of this microbes-based biocontrol strategy.

3. Understanding the tripartite dynamism: *Striga* spp. and rhizospheric organisms associated with cereals

The tripartite interaction of the cereals, *Striga* spp. and rhizospheric microorganisms such as arbuscular mycorrhizal fungi (AMF) and PGPR, has not been sufficiently researched despite the scientific exploration of their bipartite relationship (Mounde et al., 2020). Whereas the in-depth ecological knowledge of this interaction will open up opportunities to create *Striga* species-specific management strategies. The interaction of AMF, a cereal host crop and *Striga* spp. is one of the most suitable references of the tripartite interaction researched thus far, and is evident in the reduced germination and emergence of *Striga* spp. in an AMF treated sorghum field (Bàrberi, 2019; Mwangangi et al., 2021). Strigolactone is a multifunctional plant hormone that is involved in a variety of internal and external functions in plants including

the promotion of arbuscular mycorrhizal symbiosis, stimulating the growth of parasitic plants, determining plant architecture and acting as a developmental and environmental signal (Torres-Vera et al., 2014). The Important plant recognition cues for AMF have been reported as the strigolactones present in root exudates and causing hyphal branching in AMF (Basu et al., 2018). The root exudates of mycorrhizal host and nonhost plant species contain at least nine strigolactones, including strigol, sorgolactone, orobanchol, strigyl acetate, 5-deoxystrigol, orobanchyl acetate, epi-orobanchol, sorgomol, and solanacol (Soto-Cruz et al., 2021). The host plant produces more strigolactones to promote the growth of fungi and the establishment of symbioses under the nutrient deficient conditions. More so, some species, in particular root parasitic plants, are able to detect strigolactones as a signal of host presence in the rhizosphere and as a result promotes a parasitic association (López-Ráez et al., 2011). In line with some earlier reports, the effect of strigolactone on the later stage of the AMF—plant interaction is dependent on the plant type involved, as further root colonization by AMF is reduced in mycorrhizal plants compared to the non-mycorrhizal plants. Whereas, the inhibition in the rate of Striga spp. germination has been associated to the reduction in striglactone production caused by the structural and chemical alterations in the roots of AMF-colonized plants that disrupts strigolactone exudation patterns, thereby leading to poor stimulation of Striga spp. seed germination (Steinkellner et al., 2007; Abdelhalim et al., 2019). This can be further affirmed in some earlier reports of the root exudates of the mycorrhizal maize and sorghum plants which induced lower Striga seed germination when compared to the control plants. Similarly, the in vitro branching of AMF was more stimulated by the root exudates from non-mycorrhizal cucumber plants than by exudates from the mycorrhizal cucumber plants (Steinkellner et al., 2007; Fernández-Aparicio et al., 2011).

Certain plant families, such as the Brassicaceae, Chenopodiaceae, and lupins (an exception in the mycorrhizal host family of the Leguminosae), are listed as mycorrhizal nonhost plants, despite the fact that the majority of terrestrial plants are hosts for mycorrhizal fungi. While some data suggest that some mycorrhizal nonhost plants' root exudates include substances that are antagonistic to mycorrhizal fungi, other data suggest that other mycorrhizal nonhost plants' root exudates lack crucial signals for mycorrhizal fungi to colonize their roots (García-Garrido et al., 2009; Wang et al., 2022).

Adequate crop nutrition, particularly phosphate, have been found to inhibit strigolactone exudation, with a minimal impact on the germination and parasitism of Striga spp. (Chesterfield et al., 2020). Additionally, AMF enhances crop phosphorus absorption with favorable response on plant growth and health, thereby partially offsetting the parasitic impacts of Striga spp. The secretion of some detrimental hormones by Striga spp. such as auxins and ABA are mitigated by AMF, hence, it is possible that root parasitic weeds have developed a method to intercept the communication signal and transform it into a germination-inducing signal to react when a suitable host is present (Mounde et al., 2020). This is validated by the study of Mutsvanga et al. (2022) which reported higher chlorophyll contents in plants treated with AMF. Also, upon AMF inoculation, the physiological indicators including stomatal

conductivity and photosynthetic rate was reportedly improved, while the biomass of Striga spp. decreased. This was attributed to the host plant that had been colonized by AMF thereby converting strigolactones to mycoradicin, whereas mycoradicin does not support the emergence and germination of Striga spp. (Manjunatha et al., 2018). Conversely, strigolactones production have been reported to stimulate the spore germination of AMF, and thereby aids in AMF growths (Besserer et al., 2006).

Strigolactones have been found in the root exudates of wide range of plants, and they do not only serve as signals for AMF but also for other fungi, especially soilborne fungi.(García-Garrido et al., 2009). According to Ahonsi et al. (2002), Pseudomonas fluorescens and Pseudomonas putida can prevent Striga spp. from emerging when maize hosts are present. This was supported by the report that certain Pseudomonas species, either alone or in combination with N_2-fixing Bradyrhizobium japonicum, reduced Striga spp. infestation in cowpea and soybean rhizospheres (Ahonsi et al., 2003). After being treated with Azospirillum brasilense, Striga spp. germination was inhibited, whereas development of the host crop (sorghum) was encouraged (Abbes et al., 2019). Similar results showing the favorable benefits of certain PGPR (such as Pseudomonas putida and Bacillus sp.) against Striga spp. while encouraging the growth of sorghum was reported by Babalola (2010b), more so auxin and auxin-like chemicals generated by PGPR were shown to suppress Striga spp. emergence and haustorium development.

Striga spp. infested crops typically have low IAA levels (Mounde et al., 2020). Hassan et al. (2009) demonstrated that the inoculation of PGPR (such as Azospirillum brasilense, Pseudomonas putida, Bradyrhizobium japonicum and Azospirillum amazonas) delayed and reduced the incidence of Striga spp. for both resistant and susceptible sorghum varieties to counteract such low IAA levels. Bacillus subtilis GBO3 and Bacillus amyloliquefaciens FZB42 were reported to support sorghum growth while preventing the germination of Striga hermonthica (Mounde et al., 2015). The two PGPR's ability to reduce tubercle development as compared to non-inoculated controls provides evidence of their bioherbicidal properties. Some unexplained metabolites, which may compete with the germination stimulants for binding sites, have been postulated to be the origin of seed germination suppression (e.g., strigolactone). Strigolactone is predominantly generated by the host to promote AMF branching and root attachment and to control its above-ground architecture i.e., shoot branching (Jamil et al., 2011). The receptive site DWARF14 hydrolyzes the strigolactone molecule in strigolactone-dependent plants. The repressor DELLA protein interacts with DWARF14 when stigolactone is present (i.e., DWARF53) (Hu et al., 2017). The 26S proteasome breaks down this repressor protein in a combination with strigolactone, DWARF14, DWARF53, and Skp1-Cullin-F-box protein (SCF), which eventually leads to the germination of Striga spp. (Kaniganti et al., 2022). The DWARF14 protein is disrupted by mutation or other methods (such as PGPR-derived inhibitors), which prevents the receptor from transducing the strigolactone signal (Mounde et al., 2020). A new chemical called DL1 that is a powerful inhibitor of the strigolactone-receptive site DWARF14 was identified. Understanding the specific metabolic substances generated by PGPR, which may successfully inhibit

DWARF14, would increase the effectiveness of the recommended PGPR metabolic bioherbicidal method in controlling *Striga* spp. (Mounde et al., 2020) (Table 1).

4. Metagenomics approaches for the detection and surveillance of *Striga* infested agricultural soil

The genomic assemblages of microbes isolated directly from their environment, without the requirement for preliminary growing under laboratory conditions, are referred to as metagenomics (Handelsman, 2004). Metagenomics provides a generally unbiased assessment of a community's functional (metabolic) capacity as well as its structure (species richness and distribution) (Hugenholtz and Tyson, 2008; Olowe et al., 2023). The DNA extracted from the environment eliminates the necessity for single isolate culturing. In this case, the diversity of microbial strains recovered from the environment increases when DNA is extracted directly from the environment. Metagenomics comprises of parallel sequencing of microbial metagenomes while functional screens can be used to find clones that have genes that code for biosynthesis of natural products and secondary metabolites, which are usually phytotoxic, enzymes and antimicrobial agents that can be used in weed management (Kao-Kniffin et al., 2013).

Metagenomics approaches have been employed by chemical and pharmaceutical industries to screen for novel enzymes and antibiotics. Similar functional screens can be used to find weed-suppressive chemicals that target a wide range of plant stages. The sheer diversity of bacterial and fungal genomes in soil provides a reservoir of genes that code for herbicidal chemical synthesis and resistance to herbicides. As a result, metagenomics techniques can be used to develop two approaches to weed management: (1) the isolation of novel herbicides produced by vector–hosts expressing the biosynthetic gene clusters, and (2) the identification of herbicide resistance genes in vector–hosts exposed to high levels of a herbicide (Kao-Kniffin et al., 2013). The greater possibility to uncover new biosynthetic gene clusters derived from soil microorganisms is one advantage of conducting a metagenomics-based functional screen in weed management (Kao-Kniffin et al., 2013). Structural and functional screens of sequences from the host could be established in order to uncover compounds with new modes of action (Westwood et al., 2018). Then selected clones or strains can be evaluated on a bigger scale in the greenhouse at a later period. The herbicides must be capable of controlling numerous weed targets rather than just one in order to gain widespread acceptability and importance. Their effectiveness should be based on specific stable gene activities or metabolites that can function in the field despite modest changes in environmental temperature and moisture (Westwood et al., 2018).

The discovery of genes and metabolites responsible for the generation of herbicidal chemicals is possible using high-throughput sequencing techniques, advanced computational tools, and metabolomics analysis (Kao-Kniffin et al., 2013; Trognitz et al., 2016). These techniques aimed at improving the screening of microbial generated herbicides have the potential to improve *Striga* control in a variety of crops and can help improve integrated weed management programs that include bioherbicides and other natural products. Many biosynthetic gene clusters for recognized natural products are arranged into operons with promoters and regulatory sites. While sequence-based screening is useful for analyzing key genes, functional screening based on host expression is best for discovering natural products like new herbicides (Kao-Kniffin et al., 2013). Phylogenetic or functional analyses are commonly analyzed from DNA isolated from environmental sources. Microbial function is investigated using a number of techniques that focus on genes or gene clusters that code for chemicals and proteins. The likelihood of finding a target varies depending on the gene or activity of interest (Kao-Kniffin et al., 2013).

To reduce the population density of the target weed or organism, biological control approaches most usually rely on (micro) organisms or natural chemicals. The traditional biological or inoculative strategy that is widely used entails introducing a natural enemy from its native range to a new location where the weed or pest is a problem. The biocontrol agent is released into the new habitat, and it takes time for the biocontrol organism to build up a population large enough to control the weed or pest. The introduced population is kept alive for a very long time (Trognitz et al., 2016). The research and development of novel herbicides based on natural chemicals, such as microorganisms byproducts or plant extracts is one promising area and herbicidal activity has only been tested on a limited percentage of the world's microbes and plant biodiversity (Westwood et al., 2018). Soil microbes, such as plant growth-promoting bacteria, the application of arbuscular mycorrhizae fungi, and some bacterial strains, significantly reduced *Striga* germination, adhesion, and emergence (Rocha et al., 2019). For example, strains of *Pseudomonas putida* and *P. fluorescens* have been used to suppress the germination of *Striga hermonthica* seeds (Ahonsi et al., 2002). Approaches to actively use microbial strains in weed management are still in their infancy with most biocontrol agents directed toward the above ground parts of plants (Müller-Stöver et al., 2016). More so, some of the limiting factors in the current application of metagenomics method for microbiological management of *Striga* include the possibility of the sequencing process to miss low-abundance microbes, inability to completely extract the DNA of the environmental microorganisms, while the sequencing data including species annotation and functional analysis may not be evaluated as a result of the inadequacies in many microbial database. Hence, the urgent need for a sequencing platform with long reads and high accuracy (Zhang et al., 2021). However, some prospective bioherbicidal strains have been successfully used to attack plants at various phases of development (Müller-Stöver et al., 2016). We are currently in the era of "omics" (genomics, proteomics, metagenomics, metabolomics, transcriptomics etc) that may enable new approaches in the management of weeds, including *Striga*. Computational, biochemical, and molecular approaches, including protein modeling and crystallography, can predict target-site resistance mutations and give early resistance screening prior to the herbicide's commercialization (Shaner and Beckie, 2014).

Today, the repertoire of data generated by completely sequenced genomes and *Striga* sequencing programs, as well as high-throughput technologies for transcriptome analysis, present

a way to supplement more traditional *Striga* management approaches. This has increased our understanding of microbe-weed interactions, which have impact on decision making, particularly during the microbe selection stage, as well as biocontrol approaches. Such information is crucial in guiding genetic alterations to improve the efficacy and tolerance of bioherbicides (Morin, 2020).

5. Future perspectives in *Striga* management

Overcoming the menace caused by *Striga* is still a major concern to farmers all over the world in ensuring food security. Hence, it is important to source new, affordable, effective, durable, and integrated control strategies. Identifying and exploring potential beneficial microorganisms that affect and destroy (i) germination of *Striga* seed (ii) formation of the haustorium, and (iii) attachment which often reduces the infection of *Striga* as a generic, effective, and eco-friendly technique to improve crop production is important. The nature of *Striga*'s life cycle and the mechanism of host infection propels the use of a microbial-based bio-control agent for the depletion of the seed bank. As a result, the isolation of microbes and understanding of seed-microorganism interactions, as well as the isolation and assessment of the tripartite relationships (*Striga*, plant, and microorganisms), will have significant implications on weed management methods in the future which are aimed at depleting seed banks and increasing the production of crop by peasant farmers.

Furthermore, to create crops with long-lasting resistance, further research into the genetic and molecular underpinnings of host resistance and host-parasite association is required. This knowledge may be translated into resistant crops using genomic resources and current technologies like targeted gene editing and mutant breeding. Intercropping and crop rotation alongside fake hosts are significant and cheaper *Striga* control techniques. This technique has the potential to be a critical component of present integrated *Striga* management in sub-Saharan Africa. Furthermore, for toothpick/FOS, push-pull, and seed coating technologies to be effective, farmers' planning, willingness, and commitment, alongside capital, labor, and availability of input in a specific cropping system are critical. Compatibility of soil and climate, farmer knowledge, information distribution, and technology transfer to smallholder farmers are all important variables that need to be further addressed. In addition, the efficacy of new compounds (bio-stimulants, and antagonists) may be influenced by their formulation, application technique, and timing. For rain-fed African agriculture, a proper formulation of effective chemicals, large scale, low-cost synthesis, and their application in the field is critical, most especially for seed bank depletion by biocontrol agents. Furthermore, before their on-farm application, the influence of these compounds on soil flora and fauna, soil structure, persistency, and residual impacts on the environment must be examined. Finally, a smart technological package combining *Striga*-resistant cultivars with mycoherbicides, fertilizers, herbicide-dependent seed coating, or new chemicals is still needed to accomplish a comprehensive and reliable *Striga* management. In addition, it is expected that more sequencing data will be accessible for meta-analyses, allowing researchers to delve deeper into more intricate evolutionary concerns and the fundamental mechanisms underlying complex characteristics like metabolic herbicide resistance and control, which would even contribute better to *Striga* management.

6. Conclusion

Cereals constitute a major staple food crop across the globe, and is strategic to attaining the Sustainable Development Goal (SDG) of ending hunger by the year 2030. However, *Striga* constitutes a major setback to cereal productions. This review explores the conventional and the current trends in *Striga* management. Considering the current deviation from the use of chemical herbicides to an eco-friendly alternative, the contribution of beneficial soil microbes in revitalizing agricultural soils and managing the invading *Striga* species are promising but yet untapped solutions. Hence, the interaction of the tripartite; host-*Striga*-microbe was discussed. Furthermore, the application of current biotechnological approaches such as metagenomics are essential tool in exploring weed-suppressive microbe-based chemicals that target a wide range of plant stages. This new approach also uncovers new biosynthetic gene clusters derived from soil microorganisms. Generally, there is need for more scientific investigation aimed at depleting *Striga* seed banks and increasing the crop production by taking advantage of the genetic and molecular underpinnings of host resistance in designing an appropriate host control measure.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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