Tripartite interaction between *Striga* spp., cereals, and plant root-associated microorganisms: a review

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Abstract

Striga spp. is a major threat to cereal and legume production, putting the food security and economy of smallholder farmers in sub-Saharan Africa at severe risk. This is manifested in the fact that *Striga* spp. infestation can result in up to 90% loss of both cereal and legume production. A consensus exists that there is yet no single measure to efficiently control *Striga* spp. This is mainly because of the limited fundamental knowledge of the genetics and ecology of *Striga* spp. and its interaction with its hosts and host root-associated microorganisms, including plant growth-promoting rhizobacteria (PGPR). Since *Striga* spp. is a root parasite, it is speculated that PGPR play a key role in controlling the emergence and development of *Striga* spp. At the same time, PGPR may exhibit beneficial effects on growth promotion of the host to strengthen its tolerance against *Striga* spp. attacks, while on the other hand, it may also induce, similar to biocontrol agents, direct suicidal effects on *Striga* spp. Such hypothesized associations between *Striga* spp., crops (e.g., cereals such as sorghum and maize), and PGPR remain largely unknown, and the central question remains if PGPR play an important role in the *Striga*-crop pathosystem. This knowledge gap is the central impetus of this review. It will elaborate the complex and fascinating tripartite ecological system of cereals, *Striga* spp. and root-associated microorgamisms. In a first step, the review will provide a comprehensive summary of the pairwise interactions between *Striga* spp. and cereals, cereals and PGPR, as well as *Striga* spp. and PGPR. This summary will then merge into the discussion about the yet limited knowledge of the tripartite interaction between cereals, *Striga* spp., and PGPR. This specifically includes the exploration of recent discoveries related to population genetics and the life cycle of *Striga* spp, host (cereal) defense responses to and mechanisms of *Striga* spp. infestation, as well as the inhibitory and stimulatory role of PGPR on *Striga* spp. seed germination. In a concluding section, remaining research gaps are identified and necessary research perspectives are provided to direct prospective research toward further understanding the relationship between the three biological components paving the avenue to develop biological and environmentally friendly measures to fight off the everlasting threat of *Striga* spp.

Key words: *Striga* spp., cereals, rhizosphere, plant growth-promoting rhizobacteria (PGPR), tripartite interaction, biological control

Review methodology: The first step taken in compiling this review article was the formulation of research questions and objectives relevant to this review. This step was the key because it provided a guide to the type of information that was needed. In addition, it informed the search for and selection of relevant literature, and its consequent analysis. The next step consisted of searching literature and making decisions about the suitability of material to be considered in the review. There was a deliberate effort to ensure that published literature on *Striga* and associated rhizosphere microorganisms in journal articles, books, databases, conference proceedings, personal communications, etc., was included in the review. The information gathered was summarized, combined, organized, and evidence extracted from the studies compared. Conclusions, knowledge gaps, and recommended future research directions were based on this all-inclusive knowledge base. The extracted data is therefore presented in a way that suggests a new contribution to the state-of-the-art knowledge.

Introduction

Daunting challenge of Striga *spp. infestation in sub-Saharan Africa*

Several flowering plants have developed parasitic associations with other members of the plant kingdom. Watling and Press [1] as well as Runo *et al.* [2] estimated that about 4,000 parasitic plant species exist, which are grouped in 13 families. Parasitic plants colonize the tissue of their hosts, where they demonstrate a remarkable efficiency in obtaining water as well as organic and inorganic resources [3, 4].

Parasitic plants of major agronomic significance belong to the genera *Cuscuta* spp., *Alectra* spp., *Orobanche* spp., and *Striga* spp. [4]. Currently, approximately 90 genera and 2,000 species of *Striga* spp. and *Orobanche* spp. are known. Both genera are grouped in the *Orobanchaceae* family, indicating a close phylogenetic relationship [5]. *Orobanche* spp. and *Striga gesnerioides* are holoparasites as they lack chlorophyll; hence, they depend fully on the host plants (i.e., dicots) for carbon, water, and nutrients [6–8]. *Striga* spp., on the other hand, is an obligate hemiparasite with photosynthetic abilities. It derives only a part of its carbon requirement from its host (e.g., mainly cereals) but depends fully on its host for water and nutrients [1, 9, 10].

In sub-Saharan Africa, the agronomically most important *Striga* spp. are *Striga hermonthica*, *Striga asiatica, Striga aspera*, and *Striga forbesii*. They parasitize a range of cereal crops, including sorghum (*Sorghum bicolor* L.), maize (*Zea mays* L.), pearl millet (*Pennisetum glaucum* L.), finger millet (*Eleusine coracana* L.), and rice (*Oryza* spp. L.). *Striga gesnerioides* parasitizes dicots, including cowpea *(Vigna unguiculata* L.*),* Bambara groundnut (*Vigna subterranea* L.*)*, tobacco (*Nicotiana tabacum* L.), and sweet potato (*Ipomoea batatas* L.) [11, 12]. Ejeta and Butler [13] ranked *Striga* spp. as the leading biotic constraint to cereal production in sub-Saharan Africa, with considerable losses in yield quality and quantity ranging from 30% to 90% [14]. Besides having a huge impact on agricultural commodities Parker [15], Striga spp. impacts have been estimated by Ejeta [16] as well as Scholes and Press [12] to lead to about 100 million people facing food insecurity, causing an economic damage equivalent to approximately 1 billion $US annually [17, 18].

Current control options of Striga *spp.*

Major efforts have been carried out to understand potential measures to control *Striga* spp. affecting various cereal and leguminous crops. Yet, no single control method with sufficient efficacy has been established [15, 19–21]. Several methods with inconsistent success and potential for adoption are anchored on cultural, mechanical, chemical, or biological means, including but not limited to hand weeding, crop rotation, trap cropping, deep or no tillage, use of herbicides and resistance breeding [22–24].

Alternatively, biological control of *Striga* spp. has been introduced as a promising, environmentally friendly technique [14, 25, 26]. There has been a great focus on the use of fungal microorganisms, where *Fusarium oxysporum* f.sp. *strigae* (Fos) strain "Foxy-2" proved valuable to control *Striga* spp. emergence by up to 95%, while increasing sorghum yields by almost 50% [27–29]. In Western Africa, the control efficacy was increased by combined use of "Foxy-2" and resistant varieties of affected cereals [29–31]). Avedi *et al.* [32] in Eastern Africa (Kenya), however, contradicted the effectiveness of "Foxy-2." Instead, "FK3," a different Fos isolate from Kenya, was effective in this case [33]. The disparity in the effectiveness of both Fos isolates against *Striga hermonthica* in Western Africa and Eastern Africa is yet to be understood. It was assumed that the inconsistent effectiveness of a specific Fos isolate against *Striga hermonthica* may be attributed to biotic factors such as the biocontrol isolate specificity [34], susceptibility pattern of weed genotypes [35], soil microbiota [36], including abiotic factors such as soil physicochemical properties [37] and climate [29, 38]. Hence, a fundamental understanding of the inconsistent effectiveness of "Foxy-2" and "FK3" recorded across agroecologies is yet to be given.

Knowledge gaps and review objectives

In any ecosystem, plants interact both mutually and antagonistically with other organisms, forming complex ecological associations [39, 40]. For a long time, many ecological studies focused largely on bipartite interactions between species (e.g., plant host-parasite). Over the last few years, this paradigm has shifted. An increasing number of studies have highlighted the importance of linking multiple interactions, including those connecting above- and below-ground biota, to understand ecological and evolutionary processes in nature [41, 42].

This includes the recognition of essential interactions between plant roots and microorganisms [43–45]. In this respect, plant growth-promoting rhizobacteria (PGPR) and also arbuscular mycorrhizal fungi (AMF) have a variety of essential functions ranging from improved uptake of immobile nutrients, protection of host from pathogens, and soil aggregation to promote plant growth [45–47]. There is ample information providing clear evidence for the positive role of soil biotic interactions in crop growth and *Striga* spp. management:

- A significant annual death rate of *Striga* spp. seeds in the field, as linked to microbial decay [48].
- Increased *Striga hermonthica* attachment to host crops in unpasteurized soils compared to pasteurized soils [49].
- Pathogenic effects of bacteria [50] and fungi [51] against *Striga* spp. seed germination.

- A reduced *Striga* spp. incidence with increased soil suppressiveness [52].
- Microorganisms benefit plant health and crop productivity, while in other cases, root exudates can prevent growth of harmful microorganisms [53–56].
- Soil microorganisms can cause decay of *Striga* spp. seeds through enzymatic and antibiotic activities [57].

Given that plant root-associated microorganisms play key ecological roles in nature, they might as well affect *Striga* spp. parasitism on cereals. Possible associations between *Striga* spp., cereals, and root-associated microorganisms remain, however, largely unknown, and the question whether these microorganisms play a role within the *Striga*-cereal pathosystem has not been answered completely. This knowledge gap is the central impetus of this review, which elaborates the complex and fascinating tripartite ecological system of cereals, *Striga* spp., and root-associated microorganisms.

In a first step, a comprehensive review of existing literature was undertaken on pairwise interactions between *Striga* spp. and cereals, cereals and root-associated microorganisms, as well as *Striga* spp. and root-associated microorganisms. In a second step, we emphasized the current knowledge of the tripartite interaction between cereals, *Striga* spp., and root-associated microorganisms. We highlighted recent discoveries related to population genetics and life cycle of *Striga* spp., host (cereal) defense responses and mechanisms to *Striga* spp. infestation, as well as the inhibitory and stimulatory role of the rhizosphere microbiome in *Striga* spp. seed germination. We concluded this review with novel approaches to study the complexity of the cereal-*Striga* spp. rhizosphere, which will translate into emerging opportunities to direct future research. Such improved understanding of tripartite interactions will be paramount in developing appropriate strategies for *Striga* spp. management with high level of efficacy.

Bipartite interaction between Striga spp. and cereals

Genetic structure in Striga *spp.*

Striga spp. is a genus that is made up of over 25 hemiparasitic member species that exhibit diversity in various forms, including but not limited to morphology, host, virulence, and mating systems [58]. The mating system in *Striga* spp. can serve as basis for understanding the diversity patterns, gene flow, and genetic population structure with respect to a peculiar *Striga* species [59, 60]. For instance, the two most economically important *Striga* species (namely *Striga hermonthica* and *Striga asiatica*) exhibit contrasting mating systems, which in turn determine the flow of genetic variation from one population to another. *Striga hermonthica* is an obligate allogamous (outcrossing) species [61], while *Striga asiatica* is primarily autogamous (selfing) [62]. In genetically structured populations, outcrossing species exhibit higher genetic variability within than among subpopulations. Conversely in selfing species, greater genetic variability is expected among than within subpopulations [63]. There is a general agreement on the influence of geography as the primary determinant of population structure in *Striga hermonthica*, through the support of higher gene flow between closer (i.e., within a structured subpopulation) than between distant (i.e., between subpopulations) populations, but host specificity is an unimportant basis for population structure. This phenomenon has been presented using different genetic marker systems, as in the case with enzyme electrophoresis [64, 65], amplified fragment length polymorphism (AFLP) [66], simple sequence repeats (SSR) [67], single nucleotide polymorphisms (SNP) [68], and expressed sequence tag-simple sequence repeats (EST-SSR) [69].

Contrarily, AFLP studies with *Striga asiatica* populations from Benin revealed a higher genetic variability within subpopulations, including a high extent of host specificity [70]. However, AFLP marker-based genetic diversity studies with Kenyan *Striga asiatica* populations did not show evidence of a subpopulation structure [71]. This disparity in genetic structure in both cases of *Striga asiatica* is due to the high diversity in the sampled *Striga asiatica* from Benin, which also exhibited a strong correlation between the geographic distance and the genetic distance between the subpopulations [70]. The Kenyan *Striga asiatica* collection established by Gethi *et al*. [71], on the other hand, manifested low genetic diversity with no relationship between genetic and geographic distance of the sampling locations. Gethi *et al*. [71] attributed the non-robustness of their markers to cover genomic regions containing virulence or pathogenicity genes as possible explanation for the low genetic diversity. This contradictory knowledge substantiates that the genetic diversity in *Striga* spp. is key to understand important phenotypic attributes associated with possible ecotypes of *Striga* spp., such as the contrasting response of *Striga hermonthica* to different Fos isolates (e.g., Foxy-2, FK3) in different geographic locations [32, 33].

Life cycle of Striga *spp.*

The life cycle of *Striga* spp. is harmonized with that of the host, starting from germination to maturity [72]. At early developmental stages, however, *Striga* spp. does not require the presence of a host. Accordingly, Joel *et al.* [73] divided the life cycle of *Striga* spp. into two phases: the independent, nonparasitic phase and the parasitic, host-dependent phase.

Independent, nonparasitic phase

The independent, nonparasitic phase is initialized when a *Striga* spp. seed germinates, culminates, and its radicle

(modified as haustrorium) attaches to the roots of its host. The host crop triggers *Striga* spp. germination and attachment through exudation of organic stimulants, including sesquiterpene lactones (SLs) (= strigolactones) [74–76]. Sesquiterpene lactones (SLs) are derived from carotenoids, found in the rhizosphere and secreted by plant roots in very small amounts [77, 78]. Many of these chemicals have been isolated and identified as a variety of SL-type compounds. They include strigol [79–81], sorgolactone [79, 82], sorgomol [83], as well as alectrol and orobanchol [84]. SLs facilitate the establishment of symbiotic and parasitic interactions [85, 86]. It is worthwhile noting that a considerable number of uncharacterized SLs exists, as was reported for sorghum and tomato [81].

By evolution, *Striga* spp. use strigolactones as a sensor to trigger the germination of its seeds, followed by attack of the host [87, 88]. However, the mechanism by which the SLs induce *Striga* spp. seed germination is still a subject of scientific debate. Xie *et al.* [89] proposed that SLs specificity and biological activities are influenced by their interaction with other molecules in the rhizosphere. The amount of SLs secreted by plants of the same species and variety depends very much on the nutritional status of the host, and is inversely correlated to soil fertility. Ayongwa *et al.* [90], Yoneyama *et al.* [91], and Jamil *et al.* [92] demonstrated that host plants growing in less fertile soils with deficiency in mineral nutrients (e.g., nitrogen and phosphorus) promoted the secretion of SLs compared to well-nourished plants. SLs secretion attracts AMF [93] to plants roots, by which a symbiotic relationship is established [94, 95], AMF spore germination is stimulated [96, 97], and hyphal branching in AMF through mitochondrial and mitotic activation induced [86, 98, 99]. As a response, AMF secrete N-acetylglucosamine and lipochitin-oligosaccharides [100–102], which activate a signaling pathway in the roots of the host. A symbiotic nutrient exchange follows after a successful communication network has been established [103].

Parasitic, host-dependent phase

Striga spp. must attach to a suitable host within a short time of 5–7 days. Otherwise, *Striga* spp. radicles exhaust their resource reserves stored in the seeds and die [104, 105]. This resource demand forces them to shift from the independent to the host-dependent, hence, parasitic phase. After attachment, host-derived secondary metabolites like flavonoids and quinines stimulate the formation of the haustorium, which is the physiological connection between the parasite and vascular vessels of the host plants [106]. Some of these compounds are phenolic in nature (e.g., 2,6-dimethyl-p-benzoquinone (DMBQ) [107]), and are released from host cell walls after stimulation by the *Striga* spp. radicle. Using a semagenetic strategy, *Striga* spp. provokes the host to synthesize signals necessary for its own development [108]. DMBQ initiates the transition from vegetative growth to haustorial development [109, 110]. Induction consists of rapid cell cycle arrest, redirection of cellular expansion from longitudinal to radial dimensions, and, ultimately, the formation of haustorial hairs on the periphery of the swelling root tip [111]. Up-regulation of genes encoding for expansins (i.e., *saExp1*, *saExp2*, and *SaExp3*) in *Striga* spp. are responsible for the haustorium formation [112]. Expansins enable cell expansion of root cells in *Striga* spp. haustoria by cleaving the hydrogen bonds within cells [113, 114].

After successful connection of *Striga* spp. to the host, a parasitic relationship is established, where the parasite becomes a sink for metabolites and water from the host [115]. The retrieval of resources is maintained by two distinct modes. The first strategy is its unique ability to maintain a high stomatal conductance (open stomata) at all times [116, 117]. Press *et al.* [105] and Seel *et al.* [118] reported that the stomatal conductance of a parasitic angiosperm is generally higher than that of its host. This circumstance reflects the phenomenon leading to a reduced stomatal conductance in *Striga* spp.-infested plants. It results in stomatal closure of the host, allowing the diversion of more water and nutrients in host plants, as was shown for sorghum [105] and maize [119]. *Striga* spp. lacks coupling of stomatal conductance to environmental conditions, a water-conserving strategy often employed by plants for growth during dry seasons [105]. The second strategy of *Striga* spp. is the accumulation of high amounts of osmotically active compounds comprising of mineral ions (e.g., potassium), sugars, and alcohols like mannitol [5, 120, 121]. In this case, open stomata elevate transpiration of the parasite that creates a high demand for water from the host. This is achieved by tapping the xylem or apoplast of the host. Osmotically active substances create a high negative water potential enabling the flow of solutes from the host to the parasite [122]. The impact of water loss on host plants is accelerated if the host is growing under water stress. Shah *et al.* [123] found stomata of *Striga hermonthica* and *Striga asiatica* to remain open until the relative water content of the parasite leaves is reduced to about 70%. These processes are particularly important for *Striga* spp. during its emergence phase, when its seedlings depend totally on their hosts for carbon, because of their inability to access light below ground [124]. For maize, Godwin *et al.* [125] found that *Striga* spp. derived all its carbon requirements and about 60% of nitrogen from the host crop prior to emergence. Other studies demonstrated that host-derived carbon accounts for up to 65% of *Striga* spp. in leaves of mature *Striga hermonthica* parasitizing sorghum [126–128]. The amount of withdrawn carbon decreases drastically when the parasite matures and becomes photosynthetically active.

It has been estimated that 20–80% of the parasite biomass is built at the expense of the hosts [124, 129, 130]. The resource withdrawal has a direct impact on crop performance and yield. Sorghum shoot yield reduction has

been found to vary between 77% and 86%, depending on the infesting *Striga* spp. species [105], while carbon withdrawal ranged between 28% and 35% [131]. This indicates that host yield reduction cannot only be explained by the carbon withdrawn by the parasite. This argument is corroborated by the fact that host biomass is not proportional to that of the parasite and amount of resources deprived. *Striga hermonthica* and *Striga asiatica* parasitizing grasses have been found to elicit a higher influence on their hosts causing a shoot-to-root ratio of 18% compared to *Striga gesnerioides* and *Orobanche* spp., having a much smaller influence on their broad-leaved hosts with a shoot-to-root ratio between 63% and 90% [132, 133]. Graves *et al*. [127] reported that competition between sorghum and *Striga hermonthica* for organic solutes may account for 20% reduction in host biomass. This loss of crop biomass is thus a clear indicator that not all resources derived from the host are consumed by the parasite [134]. It could be deduced that the parasite has by far a more detrimental effect on their hosts, in addition to simple draining of resources [135].

Besides such source-and-sink relationships, the loss of host crop biomass inflicted by *Striga* spp. infestation is also driven by disruption of photosynthesis and metabolism, hormonal imbalances, and toxins, where nitrogen levels have been found to be twice as high in *Striga* spp. than in its host, thus affecting host physiology including lower rates of photosynthesis [58]. In this case, Rodenburg *et al*. [136] showed reduced electron transport rates through photosystem II and photochemical quenching. Deterred photosynthesis is directly related to reduced stomatal conductance, a result of elevated levels of abscisic acid (ABA) in the cell sap [137–139]. High levels of ABA inhibit leaf expansion and shoot growth and promote more resource allocation to the roots at the expense of shoots of crops [140]. Disruption of the hormone stability of the host has been proposed as another cause of *Striga* spp. damage to hosts, especially cereals [137]. The disruption is generally set very early during the infestation process with decreased levels of auxin, cytokinin, and gibberellin production, while that of ABA is increased [137, 141]. Conversely, host plants might be affected by toxins produced by *Striga* spp. Host damage (i.e., stunting, chlorosis, wilting, etc.) by *Striga* spp. has been observed before the emergence of the *Striga* plants. Injecting uncharacterized crude *Striga* spp. extracts on young maize seedlings, Efron *et al*. [142] noted necrotic lesions at a distance from the site of injection. Additionally, injection of crude extracts from leaves and stems of *Striga* spp. was found to induce loss of chlorophyll and wilting in susceptible sorghum [13]. Although these experiments provide evidence that *Striga* spp. produce injurious toxins, these toxic chemicals remain to be characterized.

Although *Striga* spp. can fix carbon [105, 117, 143], its high respiratory rates enable the depletion of more carbon than it actually synthesizes. This fact reduces the net carbon gain, creating a huge demand for the resource from their hosts. Gurney *et al*. [139] determined lower photosynthetic rates in leaves of *Striga* spp. infested sorghum and maize plants, resulting in smaller leaf sizes of the hosts [117, 144, 145]. A study conducted by Inoue *et al*. [146] indicated a higher transpiration rate of *Striga hermonthica* than the host crop sorghum, even when water stress was achieved through higher stomatal density. The study concluded that severe damage to the host under drought may have been caused by increased stomatal opening, leading to enhanced water and nutrient withdrawals from the crop by the parasite. It has been estimated that more than 80% of sorghum growth reduction is due to the effect of *Striga* spp. on host photosynthesis [127] and reduced leaf expansion [139, 147, 148]. Watling and Press [1] have classified these as effects having direct influence on photosynthetic metabolism and indirect influence on host architecture by enhancing or reducing whole-plant carbon gain, reducing light capture, or altering the balance between photosynthetic and non-photosynthetic tissues. These deleterious effects of *Striga* spp. on host photosynthesis can be categorized in terms of direct resources abstraction (source-sink interactions) and indirect non-source-sink interactions [1, 149].

Host defense response and mechanisms

Host resistance is regarded as key to combating *Striga* spp. attack. This may occur at all development stages of the host [6, 150, 151]. However, utilization of host resistance is limited due to a lack of knowledge of the underlying genetic and phenotypic basis of the adaptation of *Striga* populations to new host resistance phenotypes [12]. Advanced knowledge would enable an anticipation of *Striga* spp. responses to selection imposed by resistant host crops, allowing host resistance phenotypes to be combined and integrated optimally in agroecosystems [152]. According to Joel *et al*. [115], the respective resistance mechanisms of the host include alteration of the host sap chemical composition to limit the water and assimilate flow or uptake by the parasite, hormonal imbalance, or toxicity to the parasite. Pérez-de-Luque *et al*. [153] classified host resistance responses into three mechanisms: pre-attachment, pre-haustorial and post-haustorial mechanisms.

Pre-attachment mechanisms

Pre-attachment resistance of the host appears during parasite germination and differentiation of the radicle into the haustorium, which takes place before the haustorium attaches to the host. The resistance mechanisms include absent or reduced production of germination stimulants (e.g., strigolactones) through carotenoid-pathway inhibitors in a resistant crop variety [22, 154]. This mechanism has been adopted for resistance breeding of sorghum against *Striga* spp. [16, 155, 156]. Similar results were observed in

several wild varieties of sorghum [157, 158]. Low production of germination stimulants or haustorium-inducing factors, such as DMBQ released by sorghum, revealed a high potential to inhibit haustorium growth [93, 159].

Striga spp. germination and attachment may take place, but seedlings may fail to form a haustorium. Therefore, seeds of *Striga* spp. can exhaust their resource reserves at early stages and die shortly afterward [154]. This low haustorial initiation may be attributed to the synthesis of inhibitors (e.g., phenolic acids) produced by the host [158] or low quantities of haustorium-inducing substances (e.g., strigolactones) [93, 160, 161]. Some resistant sorghum cultivars have demonstrated a hypersensitive reaction (HR) characterized by necrosis at the infestation [162]. Agrios [163] described HR with necrotic zones around the site of attempted infestation, which discourage further penetration into host roots. This leads to unsuccessful establishment and ultimate demise of the parasite [16, 155].

Moreover, plants reduce the level of infestation by minimizing their contact to parasitic seeds [164]. This is enabled by reduced root formation or deeper root systems since most parasitic seeds, including those of *Striga* spp., are found predominantly in the top layers of the soil [165, 166]. It has been revealed that reduced root growth may not necessarily lead to increased resistance against parasites [167]. Low production of germination stimulants could explain partly the resistance as demonstrated by resistant varieties, although other so far unknown compounds may have been responsible for the inhibition of *Striga* spp. germination [168]. Mohamed *et al.* [169] showed successful inhibition of *Striga* spp. germination in sorghum, although the causal agent for inhibition was not determined. Some germination inhibitors of *Orobanche* spp. operating in the rhizosphere of non-cereal crops level include trigoxazonane [170], Trichothecenes [171], 7-hydroxylated coumarins as well as naringenin and gallic acid [172, 173]. However, inhibitors operating in the *Striga*-cereal crop rhizosphere are yet to be discovered.

Pre-haustorial mechanisms

Host plants can cease the vascular connection with the parasite through physical or chemical prevention of parasite penetration [173, 174]. One of these strategies is manifested through the death of haustorial cells before connecting to the host vascular tissues [175]. Reduced nutrient flow to the haustorium or accumulation of phytotoxic compounds (e.g., phenolics and phytoalexins) and physical barriers to parasite penetration at the sites of infestation were found to inhibit haustorial development [176–178]. Inhibition of haustorium induction was caused by the presence of auxin [179]. In addition, structural changes on host cells suppress the level of infestation. These include cell wall thickening with structural carbohydrates of xylem vessels [180], protein cross-linking and suberization of cell walls, as was shown in *Orobanche* spp. [153, 174, 181]. Moreover, several *Orobanche* spp. hosts, such as tomato, produce high amounts of phenolic compounds to boost resistance and to minimize the incidence of infestation [165, 182, 183]. It needs to be emphasized that none of these chemical and structural responses have been documented so far in *Striga* spp.-infested cereals, offering an important field of fundamental research.

Post-haustorial mechanisms

Plants employ post-haustorial mechanisms after the parasite has established the vascular connection with the host. Death of parasite tubercles is the main indicator of these strategies. This happens either at the root cortex or endodermis, where further parasite development is hindered. Interruption of water and nutrient flow to the parasite happens when the resistant host vascular tissues are blocked by mucilage, causing tubercle death in *Orobanche* spp. [165, 180, 184]. This strategy is similar to that of pathogens causing vascular wilts in plants. However, Pérez-de-Luque *et al.* [185] proposed the need for further investigation to clarify these hypothesized relationships between genes responsible for wilt resistance to those offering resistance to plant parasites.

Little is known about the mechanisms by which monocots respond to *Striga* spp. attacks [186]. It was suggested that host crops show reduced production of unidentified stimulants different from sorgoleone [157], activation of salicyclic acid and jasmonic acid, as well as electron transport signaling molecules [187]. Endodermal thickening, pericycle lignification, and silica crystal deposition have been observed in post-attachment resistance to *Striga hermonthica* in sorghum cultivars [188]. Moreover, Neumann *et al.* [189] revealed cell wall modifications such as collapsed and necrotic host cells appearing at the lateral site of the invading *Striga* spp. haustorium.

Bipartite interaction between cereals and plant growth-promoting rhizobacteria

In close association with plants, diverse bacterial and fungal genera provide a vital component of crop health and productivity. The narrow zone of soil surrounding closely the root system of a plant is referred to as the "rhizosphere," a hot-spot of microbial activity. There, the composition of the microbiome and its functional potential are strongly regulated by the constant release of plant-derived rhizodeposits. These include root exudates (e.g., amino acids, organic acids, carbohydrates, and sugars) and root debris [43, 190, 191]. The plant itself manipulates the rhizosphere according to its physiological requirements. Such cell-to-cell communication via quorum sensing regulates the root colonization by microorganisms [192]. Quorum sensing comprises intercellular signaling mechanisms that coordinate microbial behavior (i.e., density, activity, etc.) during host colonization [192, 193]. Plant-associated microorganisms, on the other hand,

employ the quorum-sensing mechanism to modulate and coordinate their individual interaction with plants.

There has been a widespread recognition of many bacteria living in the root environment being capable of promoting plant health and growth [43]. These root-associated bacteria are defined as plant growth-promoting rhizobacteria (PGPR). Well-studied examples refer to diverse bacterial genera, including *Azospirillum* sp., *Gluconacetobacter* sp., *Pseudomonas* sp., and *Rhizobium* sp., as well as some gram-positive genera, including *Bacillus* sp. and *Paenibacillus* sp. [194]. PGPR directly control plant growth through auxins, gibberellins, indole-3-acetic acid (IAA), and cytokinin phytohormone synthesis [194–196]. Specifically, IAA is important for shoot and root development as well as plant vigor [197, 198]. PGPR increase soil mineral bioavailability through diazotrophic (nonsymbiotic) atmospheric N_2 fixation [199–201] and phytate degradation to solubilize phosphate [202, 203].

An indirect effect of PGPR in promoting plant growth is the synthesis of ACC (1-aminocyclopropane-1-carboxylic acid) deaminase (EC 4.1.99.4), an enzyme that degrades ACC into α-Ketobutyric acid and ammonia [204, 205]. ACC is the precursor of the plant stress hormone ethylene [206–208], which is produced especially under abiotic stress conditions [209, 210]. The harmful effect of ethylene in plants is reflected in chlorosis, wilting, leaf senescence, and abscission [211, 212]. A significant amount of plant ACC might be released *in planta* or from the plant roots and subsequently taken up by plant-associated micro-organisms. Bal *et al*. [213], for example, demonstrated the effectiveness of plant-associated bacteria exhibiting ACC deaminase activity, such as *Alcaligenes* sp., *Bacillus* sp., and *Ochrobactrum* sp., in inducing salt stress tolerance in cereal crops, including but not limited to rice. Comparable findings were provided by Ali *et al*. [214], who showed a high level of salt stress tolerance of tomato plants after treatment with ACC deaminase-active *Pseudomonas fluorescens*, while Zahir *et al*. [215] proved *Pseudomonas* sp. to partially mitigate the effect of drought stress on legume growth via enhanced ACC deaminase activity. Other indirect mechanisms of PGPR in supporting cereal growth involve the secretion of siderophores to sequester and solubilize iron [216, 217], including the synthesis of polyamines (e.g., spermidine), which are important for regulating the transport/exchange of bioactive ions essential for cell survival (e.g., Ca^{2+}, Na^{+}, and K^{+}) needed for maintaining membrane potential and controlling intracellular pH, and modulating ATPase that metabolizes ATP into ADP. It should be noted that spermidine is also the precursor of spermine and thermospermine, which both contribute to tolerance against drought and salinity in plants [218–220].

Furthermore, another striking indirect effect of PGPR is the support of plant growth via production of extracellular hydrolytic enzymes (e.g., chitinase, glucanase, proteinase, and cellulose) that can degrade the cell wall of phytopathogens [221–223]. Similarly, the biological control potential of PGPR to fight off crop pests and diseases was approved by PGPR-derived antibiotics and antifungal metabolites acting as biopesticides and bioherbicides [221, 224]. Among cereal crops, bacteria with effective disease control properties were identified in the rhizospheres of sorghum and maize [225].

Bipartite interaction between *Striga* spp. and PGPR

The interaction between PGPR and *Striga* spp. occurs at any stage of its life cycle, ranging from germination and haustorium establishment to maturity. Identification of bacteria inducing parasitic weed germination or inducing suicidal effects in the absence of the host has gained a huge research interest. In this respect, two major scenarios are expected when *Striga* spp. seeds interact with PGPR: their germination could be (1) enhanced or (2) inhibited.

Enhanced germination

During *Striga* spp. germination, strigolactones act as elicitors of ethylene biosynthesis, leading to subsequent seed germination [226]. Ethylene produced by *Pseudomonas syringae* and *Klebsiella* sp. was found to stimulate *Striga* spp. germination [227–229], where the former bacterium was also shown to induce suicidal germination of *Striga* spp. seeds.

Gibberellic acid primes *Striga* spp. seeds prior to germination [230] and subsequent germination [231]. Studies have demonstrated that *Striga* spp. parasitism can be prevented through application of gibberellin synthesis inhibitors into the soil [232]. Evidence was further given by Zehhar *et al.* [233] who reported that treatment of *Orobanche ramosa* preconditioned seeds with inhibitors of gibberellins or ethylene biosynthesis resulted in inhibition of seed germination in the presence of the germination stimulant GR24. Further research will be needed to explore additional molecules with comparable antagonism toward *Striga* germination.

Inhibited germination

PGPR can inhibit *Striga* spp. seed germination and attachment to the host. Hassan and Babiker [197] has noted that low levels of germination, haustorium initiation, and attachment are important factors that may lead to reduced or delayed emergence of *Striga* spp., when exposed to PGPR. Various modes of action have been suggested. These include interruption of germination, radicle growth, and haustorium-inducing signals, together with disorientation of the radicle from the host root or reduced attachment [234]. The key stages in the life cycle of *Striga* spp. are controlled by hormones and, therefore,

several PGPR were shown to affect early stages of parasitic growth [197].

There is scarce information on the causes of bacteria-induced germination inhibition in *Striga* spp. Phytohormones and lipophilic compounds released by *Azospirillum brasilense* are known to cause reductions in germination, radicle growth, and cell differentiation [50]. Phytotoxic substances (characterized as a complex of peptides, fatty acid esters, and lipopolysaccharides) are other biochemicals produced by PGPR that inhibit seed germination and radicle elongation of weeds [235]. Inhibition of *Striga* app. seed germination and radicle elongation have been also attributed to breakdown and chemical alteration of the germination stimulant GR24, including the production of strigolactone-like hormones that inhibit radicle elongation, or produce GR24 inhibitors [234]. Enhanced control of *Striga* spp. can be expected if appropriate identification of the factors that are associated with bacterial inhibition of radicle elongation will be conducted. This will provide the necessary baseline to facilitate the selection of PGPR isolates with potential to control the *Striga* spp. Some PGPR have been reported to produce yet-to-be identified substances that inhibit germination or suppress radicle development in parasitic weeds, including broomrape (*Orobanche aegyptiaca* and *Orobanche cernua*). Examples are *Pseudomonas aeruginosa* QUBC1, *Pseudomonas fluorescens* QUBC3, *Bacillus atrophaeus* QUBC16, and *Bacillus subtilis* QUBC18 [234]. Radicle growth inhibition in broomrape was also shown by *Azospirillum brasilense* [236], while ethylene-mediated suicidal germination in *Striga* spp. was verified by ethylene-producing *Pseudomonas syringae* pv. *glycinea* [228, 237]. In addition, germination suppression in *Striga hermonthica* was approved for sorghum root inoculated with *Bacillus subtilis* GBO3, *Bacillus amyloliquefaciens* FZB42, and *Burkholderia phytofirmans* PsJN [238].

Other mechanisms include growth hormones detrimental to *Striga* spp. development. For instance, *Azospirillum* sp. caused hormonal imbalance in the parasitic weed, leading to poor radicle development. Some of these hormones include IAA [239, 240]. Likewise, PGPR-derived auxin was shown to cause strong inhibition to attachment and haustorium development. This was related to their antagonistic nature with cytokinins and benzoquinone, both of which favor the two processes [179]. It could be speculated that PGPR such as *Azospirillum brasilense*, *Azotobacter* sp., *Pseudomonas putida*, and *Klebsiella* sp., which are known as auxin producers [227], may be used as inoculants to efficiently inhibit the attachment process of *Striga* spp.

Tripartite interaction between cereals, Striga spp., and root-associated microorganisms

Though exclusively bipartite interactions between the three biological components have been discussed with regard to the control of *Striga* spp., less attention has been given to the tripartite interaction between cereals (e.g., sorghum and maize), *Striga* spp., and root-associated microorganisms, including PGPR and AMF. This extended ecological understanding will provide relevant avenues to develop applicable control measures for *Striga* spp.

One of the best examples studied so far is the close interaction of AMF with a cereal host crop and *Striga* spp. Studies by Gworgwor and Weber [241] as well as Lendzemo [242] indicated reduced *Striga* spp. germination and emergence in consequence of AMF treatment on sorghum cultivated. The low *Striga* spp. germination resulted from reduced strigolactone production as well as structural and chemical changes on AMF-colonized plants roots. Lendzemo [242] suggested that AMF inoculation on sorghum roots might have interfered with the exudation patterns of strigolactones. In turn, this led to poor stimulation of *Striga* spp. seed germination (see section "Independent, nonparasitic phase") [93].

It has been acknowledged that sufficient crop nutrition (specifically phosphorus) reduces strigolactone exudation, resulting in minimal *Striga* spp. germination and parasitism. Moreover, AMF generally improve phosphorus uptake by crop with positive feedback on growth and health, compensating partially the effects of *Striga* spp. attack [242]. Likewise, AMF mitigate hormones secreted by *Striga* spp., which are detrimental to the crop, including auxins [72] and ABA [137, 138]. Root parasitic weeds have likely evolved a mechanism to hijack this communication signal and turn it into a germination-inducing signal to respond in the presence of a suitable host. Shubha *et al.* [243] and Chimmalagi *et al.* [244] reported improved chlorophyll content in AMF-inoculated plants. The physiological parameters such as photosynthetic rate and stomatal conductivity of sugarcane have been enhanced and *Striga* spp. biomass reduced following AMF inoculation [244]. This was attributed to the conversion of strigolactones to mycoradicin in AMF-colonized host plant. Mycoradicin does not support *Striga* spp. germination and emergence [245].

Ahonsi *et al.* [246] indicated the ability of *Pseudomonas fluorescens* and *Pseudomonas putida* in reducing *Striga* spp. emergence in the presence of maize hosts. This was corroborated by Ahonsi *et al.* [237] who observed in cowpea and soybean rhizospheres that certain *Pseudomonas* sp. minimize *Striga* spp. infestation, either individually or in combination with N_2-fixing *Bradyrhizobium japonicum*. Miché *et al.* [50] revealed the inhibition of *Striga* spp. germination after *Azospirillum brasilense* treatment, while the growth of the host crop (i.e., sorghum) was promoted. Similar findings were given by Babalola [247] confirming beneficial effects of selected PGPR (e.g., *Bacillus* sp. and *Pseudomonas putida*) against *Striga* spp., while promoting sorghum growth. Suppressed *Striga* spp. emergence and haustorium development was attributed to PGPR-derived auxin and auxin-like compounds [179, 227]. Crops infested by *Striga* spp. generally show low IAA levels [141]. To counteract such low IAA levels, Hassan and Babiker [197]

showed for both resistant and susceptible sorghum varieties that inoculation of PGPR (e.g., *Pseudomonas putida*, *Azospirillum brasilense*, *Azospirillum amazonas*, and *Bradyrhizobium japonicum*) delayed and reduced *Striga* spp. incidence.

Mounde *et al.* [238] identified *Bacillus subtilis* GBO3 and *Bacillus amyloliquefaciens* FZB42 to promote sorghum growth, while inhibiting *Striga hermonthica* germination. Tubercle formation was significantly suppressed in comparison to non-inoculated controls, confirming the bioherbicidal potential of the two PGPR. It has been proposed that seed germination inhibition was initialized by certain unidentified metabolites, which may compete for binding sites with the germination stimulants (e.g., strigolactone) [236]. Strigolactone is produced by the host primarily for regulating its above-ground architecture (shoot branching) [98] and to stimulate the branching and root attachment of AMF [96]. In strigolactone-dependent plants, the receptive site DWARF14 hydrolyzes the strigolactone molecule. Strigolactone induces the interaction between DWARF14 and a repressor DELLA protein (i.e., DWARF53). This repressor protein is degraded in a strigolactone/DWARF14/DWARF53/Skp1-Cullin-F-box protein (SCF) complex through the 26S proteasome, ultimately resulting in the germination of *Striga* spp. [248, 249]. The disruption of DWARF14 protein by mutation or other means (e.g., PGPR-derived inhibitors) results in the inability of the receptor to transduce the strigolactone signal. Yoshimura *et al*. [250] identified a novel compound DL1, which is a potent inhibitor of the strigolactone-receptive site DWARF14. Knowledge of the identity of peculiar metabolic compounds produced by PGPR, which can effectively block DWARF14, will improve the efficiency in controlling *Striga* spp. by the suggested PGPR metabolic bioherbicidal approach.

Concluding remarks and future research direction

This review has presented the current knowledge on the multiple interactions that occur in the rhizosphere of cereal crops (e.g., sorghum and maize) and its close associations with *Striga* spp. and root-associated microorganisms (e.g., bacteria and fungi). From an ecological viewpoint, the discussion about the reviewed tripartite interactions has to be extended to quadripartite interactions, since AMF as critical biological agents in the plant rhizosphere play, besides PGPR, a unique role in suppressing the emergence of *Striga* spp. and in promoting the growth of affected crops [244, 251].

The full understanding of these complex interactions remains incomplete due to the difficulty of studying below-ground processes under controlled yet realistic conditions. For instance, while the structural chemistry of strigolactones is known, the mechanisms underlying its low production under enhanced host mineral nutrition, particularly nitrogen and phosphorus, remains elusive. In this regard, this review stressed the relationship between carbon and nitrogen accumulation by *Striga* spp. at different growth stages. The amount of carbon withdrawn depends heavily on the concentration of nitrogen in the soil. No explanation is available yet on the inverse relationship between nitrogen amount in soils and carbon withdrawal from the host by *Striga* spp. Certainly, a scientific explanation through research is needed.

It was further proposed that low haustorial initiation is a result of the host that produces inhibitors [158] or low amounts of haustorium-inducing factors [93, 160, 161]. In addition, the reduced translocation of organic resources from the host to the parasite was discussed, although the factors causing the reduced translocation remain elusive. Further research is needed to better understand the cause-effect of reduced translocation of assimilates in *Striga* spp.-infested plants. In this respect, phytotoxic substances are increasingly recognized to be responsible for low parasitic seed germination and radicle elongation. These substances must be characterized and their inhibitory mechanisms on germination, radicle elongation, and haustorial initiation further understood.

Plants or microbiota can alter their behavior in response to other organisms at different omics-levels. Advanced approaches such as genomics, transcriptomics, proteomics, metabolomics, and epigenomics will reveal more information about the ecology of rhizospheres and the principal compounds, genes, functions, and mechanisms that inform the discussed tri- and quadripartite interaction and demonstrate their usefulness under diverse environments [252, 253]. Thus, native AMF species and PGPR associated with plant roots could form an efficient *Striga* spp. control system to be integrated with other *Striga* spp. management strategies. This integrated research strategy and knowledge enhancement will contribute greatly to the development of biological and environmentally friendly measures to fight off the everlasting threat of *Striga* spp.

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