

Current progress in *Striga* management

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Update

Abstract

The *Striga*, particularly *S. hermonthica*, problem has become a major threat to food security, exacerbating hunger and poverty in many African countries. A number of *Striga* control strategies have been proposed and tested during the past decade, however, further research efforts are still needed to provide sustainable and effective solutions to the *Striga* problem. In this paper, we provide an update on the recent progress and the approaches used in *Striga* management, and highlight emerging opportunities for developing new technologies to control this enigmatic parasite.

Background

Striga species of the Orobanchaceae family are obligate root parasites that infest staple crops in sub-Saharan Africa (SSA), Middle East, and parts of Asia (Tank et al., 2006; Parker, 2012). *Striga hermonthica*, *Striga asiatica*, and *Striga gesnerioides* are the most economically important parasitic plants among the 42 known *Striga* species. The three species differ in their host specificity. *Striga hermonthica* and *S. asiatica* parasitize on cereals and sugarcane (*Saccharum officinarum*; Parker, 2009; Pennisi, 2010), while cowpea (*Vigna unguiculata*) is the main host of *S. gesnerioides* (Ohlson and Timko, 2020). The *Striga*, particularly *S. hermonthica*, problem has become a major threat to food security, exacerbating hunger, and poverty in many African countries (Pennisi, 2010; Khan et al., 2014). Although consequences are difficult to measure, a few estimates have indicated that *Striga* is affecting the life of more than 300 million people in Africa

and causing enormous yield losses with a value ranging from 7 to 10 billion US\$ annually (Emechebe et al., 2004; Gressel et al., 2004; Ejeta, 2007; Scholes and Press, 2008; Rodenburg et al., 2010). In heavily infested regions, farmers have been forced to abandon cereal cultivation and to switch to other less important crops (Atera et al., 2012a). The severity of *Striga* depends upon degree of infestation, seed viability, ecotypes, virulence, host crop susceptibility, climatic/edaphic factors, and cultural practices (Rodenburg et al., 2016).

Striga species are among the hardest parasitic plants to control (Berner et al., 1995; Nickrent and Musselman, 2004). Adaptability of *Striga* to a wide range of hosts and environmental conditions has made it one of the most widespread and successful parasitic plants (Mohamed et al., 2006). In addition, long-term management of *Striga* is hampered by the tremendous number and longevity of seeds, vast genetic

ADVANCES

- New sources of host resistance to *Striga* have been identified and will, together with modern genomics and breeding tools, enable generating of resistant varieties.
- The recently established *Striga* control technologies, such as push-pull, toothpick, and imidazolinone seed dressing have opened up new opportunities for smallholder farmers to overcome this parasite.
- The development of low-cost and efficient germination stimulants together with an application protocol for rain-fed agriculture has made the suicidal germination strategy a realistic approach.
- Molecular elucidation of strigolactone biosynthesis and perception has led to the development of new chemicals that disrupt the communication between *Striga* and its hosts.

variability, complex life cycle, and subterranean nature of damage (Joel, 2000; Huang et al., 2012a, b). Indeed, it is estimated that about 900,000 *S. hermonthica* plants can emerge from one hectare of infested sorghum field, which can add about 4.5×10^{10} seeds in one growing cycle (Bebawi et al., 1984). Very tiny (0.3 nm \times 0.15 nm) and light (4–7 μ g) *Striga* seeds are easily dispersible in nearby fields through wind, animals, and agricultural tools, thereby gradually enriching seed reserve in the soil (Ejeta, 2007). The seeds remain dormant for a long period and germinate only after exposure to hot and humid conditions followed by perception of host derived germination stimulants, mainly strigolactones (SLs; Yoneyama et al., 2010; Joel and Bar, 2013; Al-Babili and Bouwmeester, 2015). Following germination, *Striga* radicle grows toward host roots. The perception of host-derived haustorium-inducing factors (HIFs), such as 2,6-dimethoxy-1,4-benzoquinone, prevents further growth of the radicle and induces cell expansion and division, and proliferation of hair cells at its tip, forming a haustorium, a special invasive organ that penetrates host roots to enable siphoning off water, minerals, and nutrients. The vital role of the haustorium provides a rarely exploited option for controlling *Striga* by breeding varieties with low HIF release or developing compounds that specifically inhibit haustorium formation (Cechin and Press, 1993; Shen et al., 2006; Yoshida and Shirasu, 2012; Yoshida et al., 2016; Goyet et al., 2019).

Due to the persistence and severity of the *Striga* problem, there has been an extensive effort to develop simple, easy, and effective control strategies that can be employed either alone or integrated with existing approaches (Figure 1). In the past decade, intensive research on the interaction of *Striga* with its host at molecular level has opened up

opportunities to develop new management strategies. For sustainable *Striga* management, any control method should target at least one of the following goals (Figure 1): (1) PREVENTION: avoiding seed dispersal, for instance, by using clean crop seeds, tools, and fodder, controlling animal grazing or applying phytosanitary/quarantine measures; (2) CONTAINMENT: limiting new seed production by planting resistant (pre- and post-attachment, see below) varieties, using fertilizers, applying herbicides, employing a number of agronomic practices, such as hand weeding, deep sowing, burning, fallowing and soil solarization, and the application of chemicals that reduce the release of germination stimulants by the host; and (3) REDUCTION: reducing *Striga* seed bank accumulated in infested soils by employing cultural practices, such as trap cropping, inter cropping, and crop rotations, employing microbial agents that impact *Striga* and/or *Striga*/host interaction, applying synthetic germination stimulants in host's absence, and by developing specific inhibitors that block germination of preconditioned seeds and decrease their viability. Reduction of seed bank can be also achieved by planting resistant varieties that stimulate *Striga* seed germination, but withstand the parasitic attack (post-attachment resistance, see below). In this article, we provide an update on the recent progress and the approaches used in *Striga* management, and highlight emerging opportunities for developing new technologies to control this enigmatic parasite.

Host resistance

Deployment of resistant varieties is generally considered as the most economical, practical, and suitable long-term approach for controlling *Striga* (Hearne, 2009; Mandumbu et al., 2019). There are two main types of host resistance, that is, pre-attachment resistance resulting from SL profiles with low seed germinating activity, and post-attachment resistance that is based on hypersensitive response (HR)/incompatible response (IR). The recent identification of genes mediating the synthesis of different SLs opens up the possibility of modifying the SL profile of host plants by using genetic engineering and gene editing tools and, hence, increasing their resistance (Wakabayashi et al., 2019, 2020). Genetic resistance can be employed independently or as a central element of an integrated *Striga* management (ISM). Here, we present the latest knowledge on *Striga* resistance in maize (*Zea mays*), sorghum (*Sorghum bicolor*), pearl millet (*Pennisetum glaucum*), rice (*Oryza sativa*), and cowpea (*V. unguiculata*).

Maize has surpassed the traditional cereals in SSA, with the highest cultivation area of about 39 million ha in 2018 (FAOSTAT, 2018). Considering the importance of this crop, significant progress has been achieved in identifying a number of *Striga* resistant maize varieties and hybrids with different types of resistance (Akaogu et al., 2013, 2019; Badu-Apraku et al., 2019; Menkir and Meseke, 2019). For instance, Amusan et al. (2008) identified ZD05 a resistant maize inbred line that exhibits very low *Striga* attachments and high mortality of attached parasites, compared with the

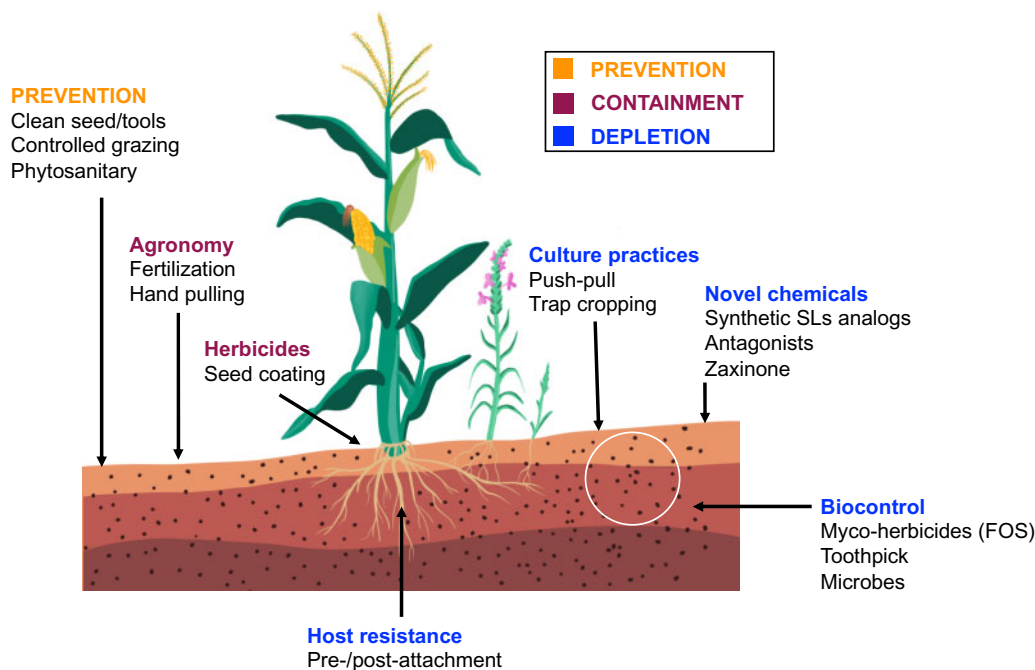


Figure 1 List of complementary approaches for *Striga* control. Methods depicted are used either for prevention and containment of *Striga* infestation, or for depletion of accumulated seed banks.

susceptible inbred line 5057. This resistance in ZD05 has been attributed to multilevel post-attachment barriers, particularly physiological or biochemical incompatibility to parasite growth and development. It is likely that this resistance is controlled by different genes that can be employed for durable and stable resistance. Similarly, Nyakurwa et al. (2018) compared quality protein maize (QPM) with non-QPM genotypes for *S. asiatica* resistance/tolerance under field/pot and agar gel assay conditions. They found several QPM genotypes with considerable levels of tolerance (i.e. no impairment of growth and yield despite of infestation), although they showed susceptibility similar to that of other genotypes in agar gel assays. However, the mechanisms underlying the tolerance of QPM genotypes remain elusive. In a similar study, Midega et al. (2016) evaluated six landraces for *Striga* infection under pot and natural field infestation and showed low *Striga* emergence, relative to hybrids.

In addition to investigating resistance in the field, a number of pre-attachment resistance studies based on SL analysis have been conducted in the past few years. For instance, Karaya et al. (2012) screened a collection of 420 maize landraces, populations, and inbred lines and identified several landraces with low *Striga* germinating activity and reduced release of the highly active strigol, however, without further investigation of responsible genetic factors. Later, the effect of SL composition on *Striga*/maize interaction was further demonstrated by comparing the two cultivars Pioneer 3253 (*Striga*-susceptible) and KSTP94 (resistant), which showed that 5-deoxystrigol was exclusively released by the susceptible variety, while sorgomol was the main SL in root exudates of the resistant one (Yoneyama et al., 2015). Interestingly, the two varieties were indistinguishable with respect to

arbuscular mycorrhizal (AM) symbiosis, indicating that the effect of SL composition on the interaction with AM fungi is different from that on *Striga* attack (Yoneyama et al., 2015). Furthermore, a study of *S. hermonthica* infestation using rhizotron unraveled the presence of post-attachment resistance in the aforementioned cultivar KSTP94, demonstrated by lower number of *Striga* attachments and biomass in comparison to the susceptible maize inbred line CML144 (Mutinda et al., 2018). Similarly, Gasura et al. (2019) evaluated 30 maize inbred lines for *S. asiatica* resistance in pots and using agar gel assays, and identified seven inbred lines with low germination stimulant production and decreased root attachment and emergence under pot conditions, while four inbred lines exhibited low *Striga* attachment.

Recently, a genome-wide association study for *S. hermonthica* resistance in maize identified significant loci on chromosomes 3, 9, and 10, which are related to plant defense. A total of 24 single nucleotide polymorphisms (SNPs; under *Striga* infested conditions) and 11 SNPs (under *Striga*-free conditions) showed significant association with grain yield and number of ears per plant. The identified loci and candidate genes (*GRMZM2G060216*, *GRMZM2G057243*, and *GRMZM2G164743*) could be excellent breeding source for the development of *Striga*-resistant maize genotypes through marker-assisted selection (MAS) in SSA (Adewale et al., 2020). Moreover, as mentioned above, the ability of cultivars, such as KSTP94, to resist *Striga* infestation at pre- and post-attachment stages makes them a very suitable genetic source for resistance breeding. In addition, the identification of genetic factors underlying the resistance will allow stacking them by using

genetic engineering/genome editing technologies to generate highly resistant varieties to *Striga* infestation.

Sorghum is the second most important cereal crop after maize in SSA. It was grown on about 30 million ha in 2018 (FAOSTAT, 2018). In the past two decades, significant progress has been made with the identification and characterization of quantitative trait loci (QTLs) associated with *Striga* resistance in this cereal. Initially, Haussmann et al. (2004) detected QTLs in recombinant inbred lines derived from the cross between IS9830 and N13. By deploying MAS techniques, some QTLs have been transferred into elite sorghum varieties, leading to the development of sorghum cultivars with improved resistance to *Striga* (Ejeta, 2007). Moreover, by using 328 recombinant inbred lines, derived from a cross between SRN39 (low germination stimulant) and Shanqui Red (high germination stimulant) sorghum, Satish et al. (2012) fine mapped *LOW GERMINATION STIMULANT 1* (*LGS1*) locus to a 400-kb region on chromosome 5. Interestingly, it was later demonstrated that mutations in *LGS1* (*lgs1-1* to *lgs1-5* mutants) lead to a change in the stereochemistry of released SLs, replacing the dominant SL 5-deoxystrigol by the less active orobanchol (Gobena et al., 2017). These findings were confirmed by Mohamed et al. (2018) who showed that sorghum genotypes with high release of 5-deoxystrigol are more susceptible to *Striga*, compared to orobanchol releasing genotypes. More importantly, *LGS1*-mediated (loss-of-function) resistance was further characterized in various sorghum landraces with respect to *S. hermonthica* diversity and geographic distribution (Bellis et al., 2020). These authors reported that *LGS1* loss-of-function mutations are adaptive and widely distributed among African landraces across a large region of highly *Striga* infestation in Africa. Using gene-edited sorghum lines, it has been further shown that the degree of *LGS1*-mediated resistance depends on parasite genotype and abiotic environment (Bellis et al., 2020). In addition to the well-characterized pre-attachment mechanism, few reports documented the presence of strong HR or incompatibility-based post-attachment resistance (Mohamed et al., 2010a, 2010b; Mbuvi et al., 2017).

Pearl millet was cultivated on around 22 million ha during 2018, making it the third most important cereal after maize and sorghum in SSA (FAOSTAT, 2018). However, with paucity of reliable and adapted resistance donor sources, research and breeding for *Striga* resistance in pearl millet is still challenging, compared with other cereals (Wilson et al., 2000, 2004; Kountche et al., 2013; Sattler et al., 2018). Although several studies have been conducted to characterize mechanisms and inheritance of resistance to *Striga* in other cereals (Amusan et al., 2008; Cissoko et al., 2011; Jamil et al., 2011a; Satish et al., 2012), knowledge on individual resistance mechanisms, their genetic and physiological basis are still lacking in pearl millet. To fill this gap and by deploying a genotyping-by-sequencing approach, a genetic map of SNP markers together with single sequence repeats was constructed using a segregating population derived from a cross between a wild relative, resistant to *Striga* (Wilson et al.,

2004) and a cultivated-susceptible pearl millet parent (Moumouni et al., 2015). The availability of such genomic resources will help in identifying and mapping QTLs associated with *Striga* resistance, which can be deployed in a MAS. Also, using conventional field based breeding, significant progress has been made with the identification of six varieties (M141, M239, M029, M197, M017, and KBH), showing higher yield and less *Striga* susceptibility (Kountche et al., 2013). The response to five cycles of phenotypic recurrent selection for *Striga* resistance was evaluated in a diversified pearl millet gene pool developed from these varieties (Kountche et al., 2013). The authors also reported the development of the first *Striga*-resistant experimental varieties (Kountche et al., 2013).

Rice was grown in 2018 on about 14 million ha in SSA (FAOSTAT, 2018). Both, pre- and post-attachment resistances were detected in this cereal. The Nipponbare rice cultivar shows strong post-attachment resistance to *S. hermonthica*, likely because of its incapability to build xylem–xylem connections with the parasite (Gurney et al., 2006). To shed light on the genes underlying this resistance, the response of Nipponbare and the susceptible cultivar IAC 165 was investigated using gene expression profiling. This study unraveled an association of the induction of defense genes with resistance, and of that of genes involved in nutrient transport, amino acid metabolism and abiotic stress response with susceptibility (Swarbrick et al., 2008). Genes induced in the resistant cultivar include three with unknown function, which are localized within a major resistance QTL on chromosome 12 and might have a significant contribution to the resistance (Swarbrick et al., 2008). In another study, three *Striga* resistance QTLs were detected in Koshihikari–Kasalath back-cross inbred lines. A QTL of major effect was verified and narrowed down and could be, therefore, a good target for MAS (Swarbrick et al., 2009). *Striga* attack on the resistant rice cultivar Nipponbare is accompanied by an accumulation of lignin, guaiacyl, and syringyl at the site of *Striga* infection and by induction of phenylpropanoid pathway genes. The role of lignification in Nipponbare post-attachment resistance was demonstrated through manipulation of genes regulating lignin composition, which led to *Striga* susceptibility in this cultivar (Mutuku et al., 2019). Besides this structural barrier, post-attachment resistance also depends on a change in the level of defense hormones. Transcriptome analysis of infested roots indicated an involvement of the plant hormones jasmonic acid (JA) and salicylic acid (SA) in *Striga* post-attachment resistance. Mutant analysis confirmed the role of JA, but not that of salicylic acid. However, *WRKY45* knock-down—a regulator of the SA/benzothiadiazole-mediated defense response—can lead to *Striga* susceptibility. This phenotype (susceptibility) could be rescued by exogenous JA application, indicating that *WRKY45* contributes to *Striga* defense by modulating the interaction between JA and SA and positively regulating SA/benzothiadiazole and JA pathways (Mutuku et al., 2015).

A screen for pre-attachment resistance unraveled NEW RICE for Africa (NERICA) cultivars, such as NERICA1, and their parent CG14, which release low amounts of SLs (Jamil et al., 2011a). In another study, rice high tillering cultivars, for example, Super Basmati or TN1, showed low SL production and *Striga* infection, in contrast to low tillering rice varieties, for example, IAC-165 or IAC-1246 (Jamil et al., 2012a). Interestingly, Cissoko et al. (2011) reported that the above-mentioned NERICA cultivars also exhibited post-attachment resistance to *S. hermonthica* and *S. asiatica*, caused by incompatibility response or lack of xylem–xylem connections to rice endodermis. Both resistance studies were further validated and confirmed under field conditions (Atera et al., 2012b; Rodenburg et al., 2015, 2017). Similarly, the upland rice variety Umgar was characterized by pre- and post-attachment resistance to *S. hermonthica* under lab, pot, and field conditions (Samejima et al., 2016a).

Cowpea is an important vegetable and food legume in many African countries but its yield is severely affected by *Striga gesnerioides* (Parker, 2009). About seven distinct races of *S. gesnerioides* (SG1–SG6 and SG4z) were classified based on their genetics and parasitism on cowpea in West Africa (Botanga and Timko, 2005; Botanga and Timko 2007). Cowpea resistance to *S. gesnerioides* is conferred by single dominant genes in a race-specific manner (Timko and Singh, 2008; Timko et al., 2012). In addition, many cowpea landraces and local accessions possess post-attachment resistance that is based on HR at the site of attachment (Timko and Singh, 2008). Indeed, Li and Timko (2009) identified and characterized RSG3-301 from the cowpea cultivar B301, which is involved in *S. gesnerioides* resistance. Silencing of RSG3-301 in B301 plants caused susceptibility to *S. gesnerioides* race SG3 due to reduced HR. These findings led to the conclusion that the race-specific *Striga* resistance in cowpea is likely an effector-triggered immunity that activates intracellular NLR proteins (RSG3-301) upon the recognition of pathogen/parasite effectors. Supporting the race-specific interactions in *S. gesnerioides*–cowpea associations, the cultivar B301 was, however, susceptible to the *S. gesnerioides* race SG4z producing a small soluble effector protein at high amounts in haustoria, which is transferred to the host root (Huang et al., 2012a, b). This protein can suppress the host innate immunity by binding to a host BTB-BACK domain-containing ubiquitin E3 ligase homolog POB1 (POZ/BTB containing protein 1). Overexpression of VuPOB1 led to a reduction of SG4z parasitism due to increased HR, while its silencing caused susceptibility, suggesting that VuPOB1 might be a positive regulator of the HR response (Su et al., 2020). As mentioned above, *S. gesnerioides* races and their distribution are dynamic systems, influenced by genetic drift and gene flow. Ohlson and Timko (2020) recently investigated *S. gesnerioides* diversity and known sources of resistance in cowpea. They collected 58 unique *S. gesnerioides* populations from 9 West African countries and screened 7 cowpea lines for resistance. Results obtained showed that none of the cowpea lines was resistant to all *S.*

gesnerioides populations and that there is no *S. gesnerioides* population that can overcome the resistance of all seven cowpea lines. Analysis of single sequence repeats of the *Striga* populations unraveled high differentiation and suggested that genetic relatedness is generally a result of geographic proximity rather than of host compatibility. This study indicates that generating a broad-spectrum and durable *S. gesnerioides* cowpea-resistant lines requires stacking of multiple resistance genes (Ohlson and Timko, 2020).

In a field study in Nigeria, Muranaka et al. (2011) evaluated the susceptibility of different cultivars toward *S. gesnerioides* race SG3, which confirmed the resistance of the cultivars B301, IT97K-499-35, and IT98K-205-8. In a further field study performed in Burkina Faso, Tignegre et al. (2013) identified 11 cowpea genotypes with resistance to several *S. gesnerioides* races. Similarly, Omoigui et al. (2017) identified two high-resistant varieties, that is, UAM09 1046-6-1 and UAM09 1046-6-2, in the dry savanna agro-system in Nigeria, by phenotypic screening and using biplot analysis.

Cultural and agronomic practices

Trap cropping, sowing of false host such as cowpea, groundnut, sesame, and cotton to stimulate suicidal germination and to improve soil fertility were reported to be an effective way of seed bank depletion (Atera et al., 2013; Goldwasser and Rodenburg, 2013). Combining trap crops and nitrogen fertilizers was also reported to significantly decrease *Striga* seed bank (Tadesse, 2018). Cover cropping, sowing crops for the protection and enrichment of the soil showed *Striga* suppression directly through mulching, induction of suicidal germination, or its shading effect (Pickett et al., 2010; Goldwasser and Rodenburg, 2013; Randrianjafizana et al., 2018). Intercropping of cereals with legumes or a trap crop such as *Desmodium spp.* (Push–Pull) reduced *Striga* emergence by improving soil fertility, organic matter, and soil moisture content and releasing allelochemicals, such as C-glycosylflavonoids, isoflavanones, isoschaftoside, phenolics, 3,4-dihydroxybenzoic acid, which might impact *Striga* germination, growth, or development (Makoi and Ndakidem, 2012; Khan et al., 2014; Pickett et al., 2014; Hooper et al., 2015; Midega et al., 2017; Hailu et al., 2018). A combination of herbicide-resistant maize varieties intercropped with legumes appeared more effective against *Striga* (Kanampiu et al., 2018).

Fallow and crop rotation were found not only to improve soil fertility and crop yield, but also to lower *Striga* infestation in Cameroon (Ayongwa et al., 2010). In a similar study, a reduction in *Striga* seed bank through fallowing was reported in Mali and Niger (Van Mourik et al., 2011). Rotation of a nonhost legume crop can considerably reduce the *Striga* seedbank in infested fields, leading to decreased infestation and significantly enhanced yield, compared with continuous cereal cultivation (Franke et al., 2018). Recently, Kountche et al. (2019) suggested field partitioning into two sections where suicidal germination agents (see below) and existing integrated *Striga* and soil management practices can be rotated to sustain *Striga* seed bank reduction. Hand

pulling, uprooting *Striga* by hand or hand tools, is still considered as the cheapest traditional *Striga* control method (Goldwasser and Rodenburg, 2013). It is recommended to apply this method before *Striga* flowering, to prevent further seed setting and seed bank accumulation (Ayongwa et al., 2010; Sibhatu, 2016). However, hand weeding is laborious, time-consuming and less effective in reducing damage to standing crop (Mahuku et al., 2017). Fertilizer application and organic amendments showed a negative impact on *Striga* emergence (Ayongwa et al., 2011). The reduction of *Striga* infestation of rice upon fertilizer application is likely caused by a decrease in SL exudation (Jamil et al., 2011b). Similarly, nitrogen–phosphate–potassium fertilizer, micro-dosing of di-ammonium phosphate, and phosphate-based seed priming have been shown to reduce SL release and *Striga* parasitism in sorghum, pearl millet, and rice (Jamil et al., 2012b, 2014a, 2014b; Isah et al., 2013).

Recently, combining conservation agriculture practices, such as cover cropping and fertilizer applications, with *Striga*-resistant varieties was found to alleviate *Striga* impact on rice and maize (Abdallah et al., 2015; Rodenburg et al., 2020). Although most of the cultural practices are less expensive and helpful in reducing parasitic seed bank and improving soil fertility and soil texture, they are constrained by low farmer acceptance, the need for introducing additional crops, labor forces, and financial resources (Murage et al., 2011).

Biocontrol by microbiome

Myc-herbicides developed from the fungus *Fusarium oxysporum* showed *Striga* inhibition by reducing its attachment to cereals and decreasing seed bank in infested soils (Rebeka et al., 2013; Zimmermann et al., 2016; Bärberi, 2019). Some *F. oxysporum* strains produce high amounts of the amino acids L-leucine and L-tyrosine which are toxic to *Striga*—but not to maize—as they disrupt the tightly regulated free amino acid homeostasis. In addition, methionine released by *F. oxysporum* strains can be converted by soil microbes into the germination stimulant ethylene, causing suicidal germination of *Striga* seeds (Nzioki et al., 2016; Rubiales et al., 2018). Seed coating with *F. oxysporum* (FOXY2) was proposed as an effective way to deal with *Striga* under field conditions (Elzein et al., 2010; Ndambi et al., 2011, 2012; Rebeka et al., 2013; Watson, 2013). Later PSM197 and FOXY2 were encapsulated in a granular formulation (PESTA) for easy application/longevity, and a reduction of 75% in *Striga* emergence was observed in maize and sorghum crops (Schaub et al., 2006). FOXY2 was further classified as *F. oxysporum* f. sp. *strigae* (FOS) based on its highly selective inhibition of *S. asiatica* and *S. hermonthica* emergence (Mrema et al., 2018; 2020; Shayanowako et al., 2020). The characteristics that make mycoherbicides striking bio-agents against *Striga* include host specificity, high aggressiveness, easy mass production, genetic diversity, and long storage life (Rebeka et al., 2013; Nzioki et al., 2016). Fungal delivery of primary inoculum on toothpick, multiplication of secondary field inoculum and farmers training are key

components of this approach (Nzioki et al., 2016). The application of FOXY T14 led to an increase of 42%–56% in crop yield and reduction of 80% in *Striga* infestation under experimental conditions. However, *F. oxysporum* has not been extensively used in real fields, which might be due to a low effectiveness (Nzioki et al., 2016). Moreover, *F. oxysporum* might cause diseases, such as *Fusarium* wilt and dieback, in solanaceous crops (Zarafi et al., 2015).

Soil microbes like plant growth-promoting bacteria (PGPR), employment of AM fungi and some bacterial strains caused considerable reduction in *Striga* germination, attachment, and emergence (Lendzemo et al., 2009; Babalola, 2010; Hassan and Babiker, 2011; Mazaheri-Naeini et al., 2015). The potential of AM fungi in alleviating *Striga* infection has been indicated in a number of studies (Akiyama et al., 2005; Lendzemo et al., 2006; Bouwmeester et al., 2007; Xie et al., 2010). AM fungi not only enhance cereal growth and performance to withstand *Striga* damage but also facilitate host plant's uptake of water, phosphorus (P), and micronutrients from the soil through the wide net of extraradical fungal hyphae (Bonfante and Genre, 2010). Increased uptake of P through symbiotic interaction by AM fungi could ultimately reduce SLs exudation by the host in the soil, thereby lowering *Striga* infection (Lendzemo et al., 2007; López-Ráez et al., 2011).

In a screening study, four PGPR suppressed *Striga* infestation in sorghum. Moreover, application of the strain *B. subtilis* GBO3 led to the death of 35%–59% of emerging *Striga* tubercles and to a 23% reduction in *Striga* attachment (Mounde et al., 2015). *Striga* seed germinating activity of sorghum root exudates decreased significantly upon treatment with *Pseudomonas* bacterial suspensions, which might be due to degradation of SLs (Ali et al., 2013). As shown for 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). In addition, soil microbes could impact *Striga* by releasing amino acids, such as tyrosine, leucine, and/or methionine (Vurro et al., 2009) or by producing secondary metabolites, such as anthranilic acid, β -lactone derivatives sesquiterpenoids, tricothecenes, which might interfere with SL perception (Tyc et al., 2017). Similarly, there is some evidence for SL degradation by fungi, which might lead to reduction in *Striga* germinating activity of released exudates (Boari et al., 2016). The germinating activity of root exudates and, hence, infestation by *Striga* can be also affected by soil microbes that modulate root architecture and growth (Huang et al., 2014).

The usage of soil microbes (AM fungi, PGPR, and other bacterial strains) is now considered as a promising, cost-effective, and environmentally safe approach for combating *Striga* (Watson, 2013; Samejima and Sugimoto, 2018). However, a number of biotic and abiotic factors can affect the efficacy of this approach, especially under field conditions. Finding a suitable inoculum medium, its mass

production, suitable formulation, storage, shelf-life, consistency, and compatibility of applied microbes with the host, and the maintenance of their activity in infested soils must be taken into consideration. The validation and further development of this microbes-based biocontrol approach still requires intensive research and field testing under varying climatic and edaphic conditions (Müller-Stöver et al., 2016; Mohammadi, 2019).

Use of herbicides and suicidal agents

Seed coating of imazapyr-resistant maize with imidazolinone herbicides, such as imazapyr, imazapic, pyriathiobac, and imazaquin, caused a reduction in *Striga* emergence throughout the planting season and led to a three- to four-fold increase in maize yield (Menkir et al., 2010; Chikoye et al., 2011; Habimana et al., 2014; Makumbi et al., 2015). Similarly, treatment of cowpea seeds with imazaquin at 0.24 kg a.i. ha⁻¹ significantly decreased *Striga* infection in different cowpea genotypes (Lado et al., 2018). Albeit promising results, availability of IR resistance seeds to the farmers, application technology, the risk of generating resistance in *Striga* itself, and the impact on environment are important issues that need to be considered (Ransom et al., 2012).

Application of synthetic germination stimulants to deplete *Striga* seed bank in infested soils by inducing suicidal germination in the absence of host has recently gained a lot of attention (Samejima et al., 2016b; Zwanenburg et al., 2016; Kountche et al., 2019). Several SL analogs (Fig. 2) have been developed and evaluated (Xie et al., 2010; Mwakaboko and

Zwanenburg, 2011; Kgosi et al., 2012; Boyer et al., 2014; Screpanti et al., 2016; Vurro et al., 2016; Jamil et al., 2018, 2020; Uruguchi et al., 2018; Prandi and McElean, 2019). Functional tests revealed large variation in the efficiency of these analogs in exerting different SL functions, including the induction of *Striga* seed germination under lab conditions. Generally, SL analogs/mimics are quite variable in their structure but have in common the D-ring and ether bridge characteristic for natural SLs (Zwanenburg and Mwakaboko, 2011; Fukui et al., 2013, 2017; Cala et al., 2016; Takahashi et al., 2016; Oancea et al., 2017; Jamil et al., 2020). Structure–activity relationship studies have shown that minor structure modification can lead to significant changes in the biological activity (Cohen et al., 2013; Zwanenburg et al., 2013; Jamil et al., 2018, 2019, 2020). Following the discovery of the central SL biosynthesis intermediate carlactone (Alder et al., 2012), a carlactone-based SL analog, nitro-phenlactone was developed. Nitro-phenlactone showed high parasitic seed germinating activity in *Phelipanche ramosa*, which was at least comparable to GR24, but not in *Striga* (Jia et al., 2016). Subsequently, a series of carlactonoic acid-based analogs, called methyl-phenlactonoates (MPs), were developed and tested (Jamil et al., 2018, 2020). The three analogs MP1, MP3 and MP16 showed high suicidal germination activity on *S. hermonthica* in lab, greenhouse and field trials performed in Burkina Faso (Jamil et al., 2018, 2020; Kountche et al., 2019). Similarly, a carbamate-derived SL analog T-010 was applied in an infested field in Sudan, which led to a significant reduction in *Striga* emergence and better growth of

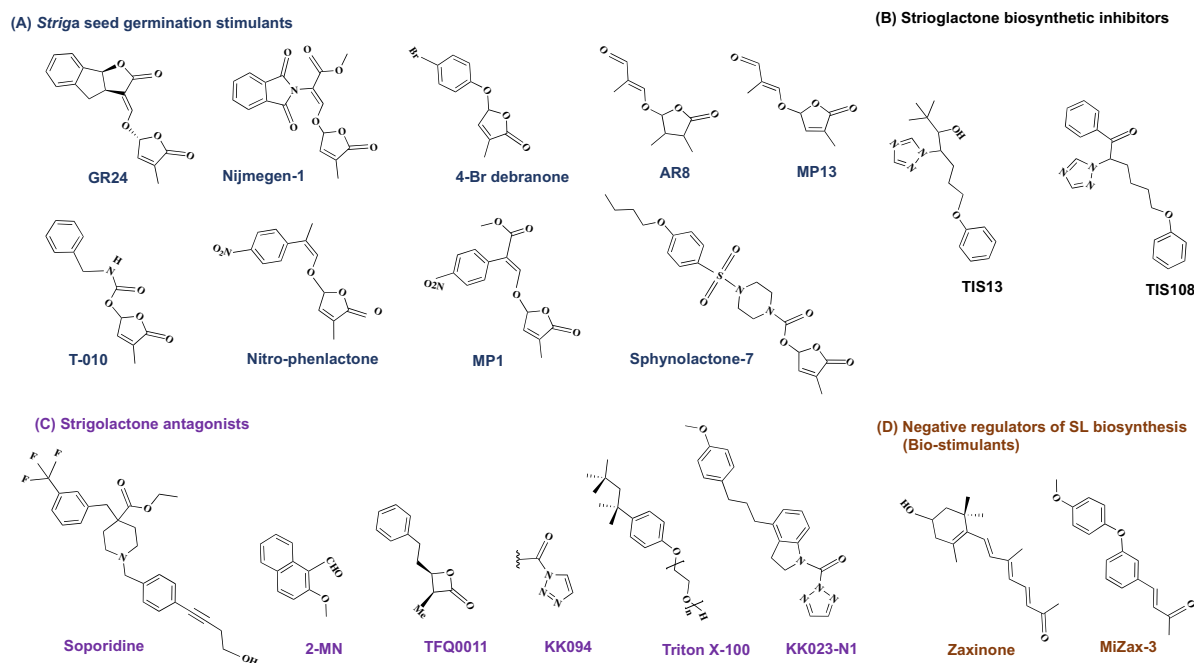


Figure 2 Structure of germination stimulants and further chemicals used in *Striga* control. A, Structure of the SL analogs GR24, Nijmegen-1, 4-Br debranone, AR8, MP13, Nitro-phenlactone, MP1, and Sphynolactone-7. B, Structure of TIS13, TIS108, two inhibitors of SL biosynthesis. C, Structure of the SL antagonists Soporidine, 2-methoxy-1-naphthaldehyde, TFQ0011, KK094, Triton X-100, and KK023-N1. D, Structure of zaxinone and its mimic MiZax-3, which act as growth-promoting compounds (biostimulants) and negative regulator of SL biosynthesis at transcript level in rice.

sorghum (Samejima et al., 2016b). Recently, a chemical screen for SL agonists, followed by structural modifications, led to a highly active compound that triggers *Striga* seed germination under lab conditions at femtomolar range concentrations (Uraguchi et al., 2018). However, the question about the activity of this analog in field is still open.

Although a large number of synthetic stimulants have been developed and proposed for usage as suicidal germination agents, there are only very few studies that assess the practicability and success of the suicidal germination approach and the activity of these stimulants in infested fields (Samejima et al., 2016b; Zwanenburg et al., 2016; Kountche et al., 2019). Indeed, the evaluation of the synthetic-stimulant-based suicidal germination strategy requires an application protocol suitable for infested regions in Africa, in addition to efficient and easy-to-synthesize SL analogs. Such a protocol needs to include an appropriate formulation and to account for local conditions, including less developed infrastructure. Given the water scarcity in the Sahel zone, the realization of the suicidal germination concept in the arid and semi-arid *Striga*-infested regions in SSA requires also a method that does not consume large amounts of water. Recently, Kountche et al. (2019) established a pipeline for assessing the germinating activity of SL analogs, which includes tests under lab conditions and in greenhouse, and mini and large field trials in Africa. For application in field, they developed a protocol for rain-fed agriculture, which requires a minimum of water and exploits rainfall for diluting and distributing of sprayed SL analogs. Following this protocol, the application of three SL analogs, that is, MP1, MP3, Nijmegen-1, at a final concentration below one micromole led to an up to 55% and 65% reduction in *Striga* emergence in an infested sorghum and pearl millet field, respectively (Kountche et al., 2019). These results and the study of Samejima et al. (2016b) demonstrate that the suicidal germination is a practicable and promising strategy to deplete *Striga* seed banks in infested African fields.

Development of novel chemicals for *Striga* control

Recent knowledge on SL biosynthesis and perception, and the availability of sequenced genomes have paved the way for developing new alternatives to combat root parasitic plants by chemicals, which decrease host SL release by inhibiting biosynthetic enzymes, down-regulating related transcripts, or blocking SL perception in the parasite.

Inhibitors of SL biosynthesis reported so far target either the formation of carotenoids, the precursor of SLs, or SL biosynthesis itself. Application of fluridone or norflurazon, which inhibit the desaturation of phytoene in carotenoid biosynthesis (Zheng et al., 2020), to rice plants decreased SL production and, hence, *Striga* germination (Jamil et al., 2010). However, treatment with carotenoid biosynthesis inhibitors may cause unwanted effects, given the diverse functions of carotenoids (Felemban et al., 2019; Zheng et al., 2020). Ito et al. (2011) developed the triazole-derivative TIS13 as inhibitor of SL biosynthesis and demonstrated its effect in decreasing rice SL release. On the basis of these results, a new set of structurally

related SL biosynthesis inhibitor candidates were synthesized, including TIS108 that showed considerable reduction in the release of *Striga* germination stimulants without affecting the host (Ito et al., 2013). Further development of TIS108 led to KK05 that caused higher reduction of 4-deoxyorobanchol release in rice exudates (Kawada et al., 2019).

SL antagonists, which specifically inhibit *Striga* SL perception, are a promising tool that could be applied in the presence of the host, enabling *Striga* control throughout the cropping season and complementing the suicidal germination strategy employed in host's absence. The development of specific germination inhibitors has become possible through the identification of *Striga* SL receptors, particularly the most sensitive one ShHTL7, which are involved in *Striga* seed germination and differ from the receptors mediating SL response in host plants (Toh et al., 2015). *Striga* SL receptors that regulate seed germination are supposed to have evolved from the homolog receptor KAI2 that perceives karrikins, smoke derived compounds mimicking a yet unidentified plant growth regulator inducing seed germination in nonparasitic plants (Toh et al., 2014; Waters et al., 2014; Conn and Nelson, 2016). Thus, the *Striga* ShHTL7 can replace KAI2 and mediate SL-dependent seed germination in *Arabidopsis kai2* mutant (Holbrook-Smith et al., 2016). This capability allowed the establishment of a high-throughput screening for chemicals that block the *Striga* ShHTL7 receptor and act as SL antagonists, which led to the identification of soporidine (SOP; Holbrook-Smith et al., 2016). Evaluation of SOP activity on *Striga* seed germination indicated its capability to block this process (Tsuchiya et al., 2018). A serendipity discovery of a potent SL antagonist that specifically blocks *Striga* ShHTL7 was recently reported (Hameed et al., 2018). The authors aimed at elucidating the structure of ShHTL7 by crystallography and found the receptor tightly bound to the detergent Triton X-100 usually used in protein purification. Functional studies confirmed that Triton X-100 is a SL antagonist that specifically blocks the *Striga* ShHTL7, but not host SL receptors, and reduce *Striga* infestation in greenhouse (Hameed et al., 2018). SOP and Triton X-100 can be considered as lead compounds for the development of efficient *Striga* herbicides that act by inhibiting seed germination. An improvement of Triton X-100 efficiency might be achieved by modifying it to become a covalently binding SL antagonist. Similarly, 2-methoxy-1-naphthaldehyde as an SL antagonist (Mashita et al., 2016) or simple β -lactones (TFQ0011) that act as covalent and high-efficient inhibitors of SL receptors have been developed based on the general SL perception mechanism (Xiang et al., 2017). Triazole urea compounds, such as KK094, that covalently bind to nonparasitic plant SL receptors have been recently produced and shown to efficiently inhibit rice SL perception (Nakamura et al., 2019). A combination of structural elements of Triton X-100 and KK094 or β -lactone inhibitors might lead to highly efficient *Striga*-specific herbicides. The recently developed Triton X-100/KK094 hybrid structure KK023-N1

(Figure 2) is an example for such compounds (Randa et al., manuscript under review).

Zaxinone is a natural growth-regulating apocarotenoid metabolite that has been recently shown to be required for normal rice growth and development. In addition, application of this compound promotes rice root growth and downregulates SL biosynthesis at the transcript level (Wang et al., 2019). A greenhouse study demonstrated that zaxinone application can alleviate *Striga* infestation (Wang et al., 2019). These activities point to zaxinone as a suitable candidate for reducing *Striga* infestation by accelerating host growth improving its performance and decreasing parasitic seed germination. Very recently, a series of easy-to-synthesize Mimics of Zaxinone (MiZax) have been developed and tested in lab and greenhouse. This study unraveled MiZax3 and MiZax5 as potent zaxinone mimics that promote rice growth, reduce SL release and decrease *Striga* infestation (Wang et al., 2020). The simple synthesis protocol and high efficacy make MiZax very promising candidates for field application.

Integrated *Striga* management

Effective *Striga* management cannot be achieved by a single control method and requires the integration of different approaches (Figure 1; Ejeta, 2007; Sibhatu, 2016). For instance, complementing host resistance with the use of *F. oxysporum* caused effective *Striga* reduction (Mrema et al., 2020; Shayanowako et al., 2020). Similarly, the reduction in *Striga* infestation achieved through seed coating of imazapyr-resistant hybrid maize can be significantly further increased by exploiting maize *Striga*-resistance (Kamara et al., 2020). As a further example, a cereal-legume crop rotation can be combined with the application of synthetic germination stimulants to deplete accumulated seed bank in infested soils (Hailu et al., 2018; Kountche et al., 2019). It can be also anticipated that the integration of suicidal germination technology with *Striga*-specific herbicides and/or zaxinone analogs can be very effective in dealing with the *Striga* problem in African agriculture.

Concluding remarks and perspectives

A number of *Striga* control strategies have been proposed and tested during the past decade; however, further research efforts are still needed to provide sustainable and effective solutions to the *Striga* problem (see Outstanding Questions).

First, further understanding of the molecular and genetic basis of host resistance and host–parasite interaction is needed to breed crops with durable resistance. Use of genomic resources and modern tools, such as targeted gene editing or mutation breeding, can translate this knowledge into resistant crops. Second, rotation and/or intercropping with false host are important and cost-effective components of *Striga* management. This approach can be a vital element in existing ISM in SSA. Third, farmers willingness, commitment and planning, labor, capital, and input availability in particular cropping system are important factors for the

OUTSTANDING QUESTIONS

- What are the molecular factors underlying *Striga* resistance?
- How can we efficiently mobilize the existing omics tools to breed durable *Striga*-resistant varieties?
- What determines the stereochemistry of released strigolactones?
- Can we design a microbiome community to suppress *Striga* impact and enhance host crop productivity in sub-Saharan Africa?
- What is the impact of synthetic germination stimulants and strigolactone-related novel chemicals on soil fauna and flora?

effectiveness of push–pull, seed coating, or toothpick/FOS technologies. Compatibility to climatic and soil factors, farmers awareness, dissemination of information, and transfer of technology to smallholders' farmers are essential factors that need further attention. Fourth, the effectiveness of novel chemicals (SL analogs, antagonists, bio-stimulants) might depend upon formulation and method and time of application. A suitable formulation of efficient compounds, mass scale, low-cost synthesis, and practical field application for rain-fed African agriculture are crucial, particularly for seed bank depletion by suicidal agents. Moreover, impact of these chemicals on soil fauna and flora, soil structure, persistency, and residual effects on environment must be investigated prior to their release for on-farm application. Last, but not least, a smart package of technology integrating *Striga*-resistant cultivars with either fertilizers, mycoherbicides, herbicide-based seed coating, or new chemicals still needs to be worked out to achieve complete and robust control of *Striga*.

Acknowledgments

We highly appreciate and acknowledge the help of Justin Braguy, KAUST, in designing and improving Figure 1.

Funding

This study was supported by the Bill & Melinda Gates Foundation Grant (OPP1194472) and the King Abdullah University of Science and Technology (KAUST).

Conflict of interest statement. None declared.

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