Advance in Biological Research, 2022, 3(1), 16-25
https://www.hillpublisher.com/journals/abr/
ISSN Online: 2635-0319

# Striga Biology and Its Management in Maize: A Review

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**How to cite this paper:** Nigus Belay. (2022). Striga Biology and Its Management in Maize: A Review. *Advance in Biological Research*, 3(1), 16-25.
DOI: 10.26855/abr.2022.05.001

**Received:** March 9, 2022
**Accepted:** April 8, 2022
**Published:** May 11, 2022

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## Abstract

Striga spp., S. hermonthica (Del.) Benth. and S. asiatica (L.) Kuntze are obligate root hemi-parasites belong to the family Orobanchaceae and cause devastating yield losses in maize production in sub-Saharan Africa (SSA). Control of striga is difficult due to the ability of the parasite to produce large number of seeds that can remain viable in the soil for more than 15 year and complex nature of the host-parasite relationship. This review presents an update on the recent knowledge on Striga biology, life cycle and management options in maize. Striga life cyle is complex and generally involves germination, attachment to host, haustorial formation, penetration and establishment of vascular connections, accumulation of nutrients, flowering and seed production. A number of Striga management strategies, such as cultural and agronomic practices, chemical control, biological control, host resistance and integrated Striga management (ISM), have been proposed during the past decade. ISM approach, through integrating Striga-resistant maize cultivars with other control methods, is considered the most economical and affordable for small-scale farmers. Novel genetic approaches such as marker assisted breeding, targeted gene editing or mutation breeding and RNA interference (RNAi) may allow the development of Striga resistant maize genotypes.

## Keywords

Striga, Haustoria, Strigolactones, Host resistance, Striga Management, Maize

## 1. Introduction

Maize (Zea mays L.) is the principal staple food crop that supports household and national food security in sub-Sahara Africa (SSA) [1]. Despite the enormous potential and crucial role that maize plays in SSA, its production and average yield per hectare are low when comparing to the global average production [2]. Maize production and productivity in SSA is challenged by drought, low fertility and the destructive parasitic weeds known as Striga hermonthica [3]. Among the biotic stresses, noxious parasitic weeds (Striga spp) are the most important biological constraints of maize production, particularly for smallholder farmers who cannot afford high inputs and other control measures [4]. Striga spp. has colonized over 50 million ha of arable land in SSA [5] and average yield losses due to Striga are estimated to range from 20% to 80% and complete yield losses under severe Striga infestation have also been reported [6]. Striga affect the life of more than 300 million people in Africa and cause economic damage worth US$10 billion annually [7]. Continuous depletion in soil fertility due to mono-cropping practice, build-up of Striga seed in the soil seed bank and increasing human population aggravates the Striga infestation in SSA [8, 9].

The parasite's lifecycle is intimately associated with its host to ensure its survival [8]. Striga is a metabolic sink for the host, deriving water and nutrients from its host's xylem [10] and infected crops can be heavily damaged, partly through phyto-toxins effects, before Striga emerge from the soil [11]. Plant stunting, chlorosis, firing of leaves around margins, poorly filled ears, wilting symptoms are observed on striga infested host under severe infestation [12]. Striga infestation reduces plant height, number of ears harvested, ear length, ear diameter and 1000-kernel weight and increases stalk lodging [13].

Control of Striga is difficult due to the ability of the parasite to produce a tremendous number of seeds that may remain viable in the soil for more than 15 year and the intimate physiological interaction of the parasite with host plants [14]. However, several control methods have been proposed for the control of parasitic weeds in maize that can be done either by a single control method or integrated two or more approaches [4, 9, 15]. The available Striga management strategies include cultural and agronomic practices (crop rotation with trap and catch cropping, fallowing, hand-pulling, fertilisation, intercropping), chemical (herbicides, seed dressing with Imazapyr and artificial seed germination stimulants), biological (fungi) and genetics and breeding (use of tolerant and resistant varieties).Therefore, this review focuses on the recent knowledges on Striga biology, life cycle and management options in maize.

## 2. The Striga Biology

### 2.1. Striga species, species distribution and host ranges

Species of the Striga genus, which belongs to the parasitic plant family Orobanchaceae, are obligate root hemi-parasites which depend on its host for survival for 4-6 weeks before shoot emergence from the soil, yet can probably manufacture its own food after emergence [16]. Striga's common name, "witchweed," is derived from the mysterious drought-like symptoms, wilting, and chlorosis seen in Striga-infected plants even before the parasite emerges from soil [17].

Although the genus Striga comprises more than 30 species, only five are presently of economic importance in Africa [18]. These are, in approximate order of economic importance in Africa, *S. hermonthica* (Del.) Benth., *S. asiatica* (L.) Kuntze, *S. gesnerioides* (Willd.) Vatke, *S. aspera* (Willd.) Benth., and *S. forbesii* Benth. *S. hermonthica* (Del.) Benth. and *S. asiatica* (L.) Kuntze (Figure 1) are the two most widespread and economically important species, which parasitize cereal crops [5, 19]. Striga asiatica is an autogamous (self-pollinating) species and genetic diversity analyses have shown distinct races of that species across their ranges [20]. In contrast, S. hermonthica is a highly out-crossing species, thus it is expected to show greater diversity within a population than seen in related autogamous species [21]. All except *S. gesnerioides* preferentially parasitize cereal crops such as maize (Zea mays), sorghum (Sorghum bicolor), rice (Oryza sativa) and millet [22]. Striga has been found attaching to non-traditional host crops such as Eragrostis tef, barley (Hodeum vulgare) and wheat (Triticum aestivum) [23]. *S. gesnerioides* is a parasite on dicotyledonous crops such as cowpea and other wild legumes [18].

**Figure 1.** ***Striga asiatica*** **(L.) Kuntze (left) and** ***Striga hermonthica*** **(Del.) Benth (right).**

Africa is thought to be the center of origin for Striga, originates from a region between Semien Mountains of Ethiopia and the Nubian Hills of Sudan, but has been reported in more than 40 countries [7]. With regard to specific species distribution, S. hermonthica's range extends throughout sub-Saharan African with particular prevalence in western, central, and eastern Africa, as well as parts of the south-western part of the Arabian Peninsula across the Red Sea and *Striga asiatica* (Asian witchweed) has a much wider geographical range, from Africa to South and East Asia down to Australia, and is also present in the United States since the 1950s [7, 24]. S. gesnerioides greatly limiting cowpea production in the West African countries of Mali, Burkina Faso, Niger, and Benin. S. aspera constrains maize and rice production in Sudan, Malawi, Nigeria, Cameroon, Ivory Coast, and Senegal [36].

### 2.2. The life cycle of Striga

Striga are annual, chlorophyll-bearing, root-parasitic plants that need a host plant for survival and its life cycle is complex and intimately linked with that of the host and generally involves germination, attachment to host, haustorial formation, penetration, establishment of vascular connections, accumulation of nutrients, flowering and seed production [9]. A generalized overview of the Striga life cycle is presented in Figure 2. Striga spp are very prolific seeder, with each plant capable of producing 10,000-200,000 very tiny (with dimensions of 0.3 and 0.15 mm.) and very light (weighing 4-7 µg) dust-like seeds such that they are easily dispersed by wind [7, 9, 25]. After dispersal, Striga seeds pass through a period of dormancy for several months. This period is commonly called after-ripening or post-harvest ripening, which is the period of time between shedding of the seeds of Striga and conditioning [26].

Striga seeds are released from dormancy through a process called conditioning or preconditioning during which favorable moisture and warm stratification must prevail before the seeds become responsive to the germination stimulants secreted by the host roots and some non-host plants [27]. The preconditioning of the seeds which requires a period of imbibitions of water for several weeks under humid and warm (25-35$^{o}$C) conditions [9]. Little is known about the biological mechanisms acting during conditioning of parasitic plant seeds except for a reported accumulation of Adenosine 3′,5′-cyclic monophosphate (cAMP) and gibberellins during preconditioning of Orobanche minor [28]. In the absence of appropriate germination conditions, the seed will become dormant but remain viable in the soil for many years [14].

Germination of Striga seeds requires the presence of specific secondary metabolites that are exuded from roots of host plant and some non-host plants [17, 29]. There are several classes of germination stimulants; strigolactones are the most common [29] and are present in the exudates of many cereals species [30]. Strigolactones are a class of carotenoid-derived plant hormones involved in regulating root and shoot branching and promote aspects of arbuscular mycorrhizae symbiosis [31] and under stressful conditions plant roots exude strigolactone hormone to promote induction of hyphal branching of arbuscular mycorrhizal (AM) fungi, presumably to attract them in low-nutrient environments [32] (Figure 3). To date there are over 30 known strigolactones that have been characterized from plant root exudates [33]. The first strigolactone, strigol, initially discovered from the root exudates of cotton (Gossypium hirsutum L.) [34] and later identified in the root exudates of several true Striga hosts (proso millet and maize and, in trace amounts, in sorghum[35]. About 20 years later, sorgolactone was identified in the root exudates of sorghum as germination stimulant of Striga asiatica and S. hermonthica [35].

Once germination has been triggered, a radicle emerges from the seed, reaching a length of a few millimeters up to 1 cm [36]. The Perception by the parasite of host-derived compounds, called haustorium-inducing factors (HIFs), such as 2,6-dimethoxy-1,4-benzoquinone, subsequently results in the formation of a special invasive organ, the pre-haustorium, characterized by the swelling of the radicle tip and proliferation of haustorial hairs on the surface [37]. Upon contact with the host root, the pre-haustorium develops intrusive cells that penetrates the host root cortex and endodermis [38], eventually forming the haustorium, a physiological bridge between the vascular system of the parasite and that of the host (parasite host xylem-xylem connection) through which the parasite withdraws water, minerals and nutrients [29, 39]. Subsequently, the Striga further develops belowground for a few weeks before emerging from the soil and emerge above the ground, develop chlorophyllous shoots, and produce flowers and set seeds which remain viable in the soil for 20 years or even more, thus completing its life-cycle [9].

## 3. Striga managemet options in maize

### 3.1. Cultural and agronomic practices

#### 3.1.1. Hand pulling/Hand weeding

Hand pulling/Hand weeding, uprooting by hand or hand tools, is the most common and widely practiced traditional Striga control method in maize due to its low cost particularly in fields with a relatively low Striga infestation [15]. Hand weeding prior to flowering and seed production is recommended to prevent further seed setting and to reduce soil Striga seed bank [41]. However, hand weeding is less effective because it is time consuming, labour intensive and much of the damage to the host occurs before emerging aboveground [9, 15].

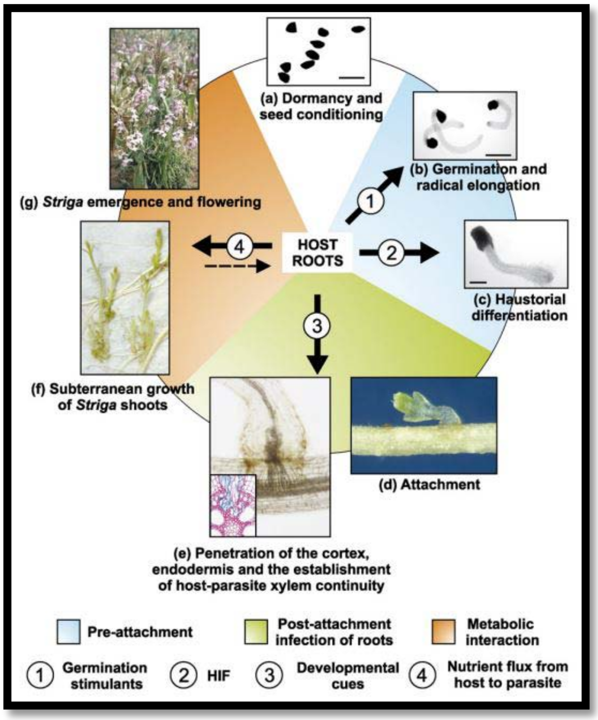


**Figure 2. The life cycle of Striga. (a) Each Striga seeds which are viable for up to 20 years. (b) Following a period of pre-conditioning seeds germinate in response to germination stimulants present in host root exudates. (c) Elongation of the Striga radical and haustorial initiation factors (HIF) initiates haustoriogenesis leading to the formation of the functional attachment organ. (d) The haustorium attaches to the host root by means of sticky haustorial hairs. (e) haustorium divide to form a wedge and penetrate through the host root cortex and endodermis. Parasite cells then form intrusions into the xylem vessels of the host. (f) Once xylem continuity with the host has been established the parasite haustorium undergoes further differentiation and cotyledon leaves are formed 1-2 days later. (g) The Striga shoot emerges above ground and flowers and sets seed approximately 6 weeks later. Source: [5].**

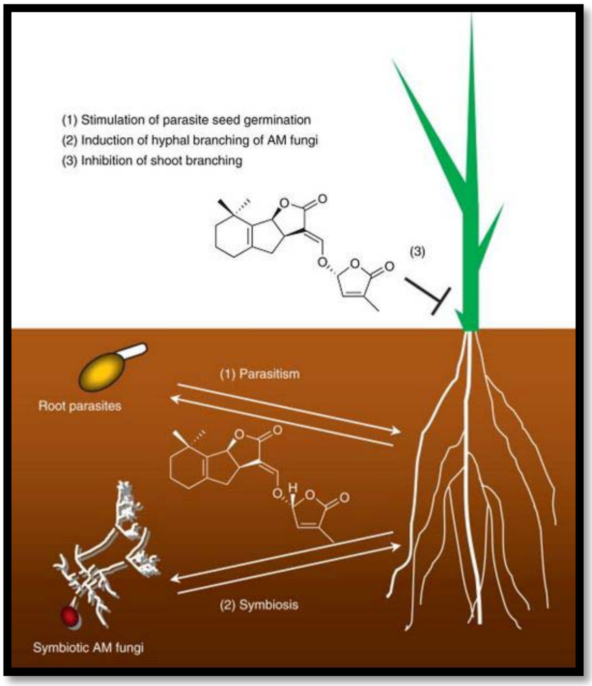


**Figure 3. Biological functions of strigolactones. Source: [40].**

#### 3.1.2. Phytosanitary Measures

A number of preventive measures must be taken to avoid spreading the infestation into neighboring fields by avoiding seed dispersal, for instance, by using clean crop seeds, tools, and fodder, controlling animal grazing and irrigation or flooding should not come from ponds, canals or reservoirs that are located adjacent to infested fields [9].

#### 3.1.3. Crop rotation and fallow

Crop rotation of Striga infested land with non-susceptible crops (with trap and catch crops) is a cheap and effective way to control Striga and boost maize and overall farm productivity [42]. Population of Striga seed in the soil can be reduced by trap cropping, sowing of non-host crops (mostly legumes) such as cowpea, groundnut, soyabean, pigeon pea, sunflower, sesame, and cotton to induce suicidal germination of Striga seeds and to improve soil fertility [43]. Catch crops are susceptible cereals such as Sudan grass (*Sorghum sudanense* L.) which may be grown at the beginning of the season or in short rains prior to the main season, to stimulate germination of Striga [44]. However, they need to be destroyed before the Striga flower and set seed.

According to Rao and Gacheru [45], leguminous trees and shrubs used as candidates for managed fallow into areas where the soils are severely depleted and have the potential to increase soil fertility and/or cause suicidal germination of Striga seeds and thereby help to reduce the level of Striga infestation. In moderately striga-infested fields, fallows planted with Desmodium distortum, Sesbania sesban, Sesbania cinerascens, Crotalaria grahamiana and Tephrosia vogelii reduced Striga infestation by 40-72% and increased maize grain yield by 224-316% compared with continuous maize [46].

#### 3.1.4. Intercropping /Push-pull

Intercropping cereals (hosts) with legumes (non-hosts of Striga) and other crops is a common practice in most areas of Africa, and is a potentially viable and low-cost metod of controlling the hemiparasitic weed Striga [47]. Studies in Kenya shows that intercropping maize with cowpea and sweet potato can significantly reduce the emergence of Striga [48]. Similarly, intercropping tolerant maize varieties with either soybean or groundnut proved to be a successful strategy to reduce Striga interference and increase crop yield in the northern Guinea savannah of Nigeria [49].

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 [50]. Push-pull, where maize is intercropped with silverleaf and greenleaf desmodium (Desmodium uncinatum and D. intortum, respectively), provided significant control of Striga and enhanced grain yield in western Kenya through allelopathic effects [51]. Similarly, Midega et al. [52] reported significant reduction in Striga count when maize intercropped with desmodium.

#### 3.1.5. Fertilizer application

Nitrogen (N) and phosphorus (P) have been identified as the main deficient nutrients [53] and higher striga infestation has been found to be closely linked with this deficiency [54]. Many studies have reported a decrease of Striga infestation with the application of N and P nutrients to cereals on soils of low fertility [55]. The reduction of Striga infestation of rice upon fertilizer application is likely caused by a decrease in SL exudation [56]. Rice releases more strigolactones upon lower availability of N and P hence inducing more Striga germination which results in higher Striga infection. Similarly, greenhouse study showed that maize secretes strigolactones upon N and P deficiency [57].

### 3.2. Chemical controls

#### 3.2.1. Herbicides

Dicamba and 2, 4-D are the most widely used herbicides against Striga [15]. Dicamba, as a post-emergence herbicide, has been shown to control Striga when applied soon after attachment, but timing is very critical to maximize its effectiveness [58], whereas 2, 4-D is sprayed several times directly on the parasites during the growing season to prevent further Striga seed production, because Striga seedlings that are still in their subterranean stage are unaffected by it [59]. However, because of the cost and the technology needed, none of these chemicals are accessible to small-scale subsistence farmers in Africa [60].

#### 3.2.2. Herbicide-treated maize seed

Coating of nontransgenic, imidazolinoneresistant (IR) maize seed with a formulation of imidazolinone herbicide imazapyr, for early Striga control before or during attachment to the maize roots caused a reduction in Striga emergence throughout the planting season and led to a three- to four-fold increase in maize yield [47, 61]. Tolerant maize germplasm contains a double recessive natural mutation conferring resistance to the ALS inhibiting herbicides. Development of herbicide-resistant maize started in 1996 at CIMMYT with incorporation of the IR gene into three CIMMYT maize inbred lines CML202, CML204, and CML206 through backcrossing using a temperate Pioneer hybrid PH3245-IR as the source of the IR gene [9]. Unlike the use of conventional herbicides that are sprayed on the maize crop, seed coating with herbicides acts before or at the time of Striga attachment to the maize root and prevents the phytotoxic effect of Striga on the plant before the parasite emerges from the soil [6].

#### 3.2.3. Germination stimulants as target for striga weed management.

Suicidal seed germination of Striga seeds in the absence of a suitable host by application of synthetic germination stimulants to deplete Striga seed bank is a promising option in combating Striga [62]. An outstanding example with this approach is the use of ethylene gas, a known plant hormone that induces parasitic seed germination,which is injected into the soil under high pressure using special sophisticated equipment in North Carolina to eradicate *S. asiatica* [63]. However, this approach cannot be applied in sub-Saharan Africa, because the equipment for bringing this gas into the soil is expensive [9]. Hence, application of Strigolactones (SLs) or SL analogs appears attractive because of their safety, decomposition in the soil within a short period of time and their high biological activity at a very low rate [62].

The GR compounds constitute the first series of SL analogues which are structurally related to the natural stimulant Strigolactone and GR24 the most potent active synthetic germination stimulants as natural strigol [64]. A series of SLs analogs can be used to develop a protocol for implementing the suicidal germination strategy for combating Striga in sub-Saharan Africa, such as the GR series (GR5 and GR7), Nijmegen-1 and MP series ( MP1, MP3 and MP16) [62].

### 3.3. Biological control

The use of pathogenic fungus as mycoherbicides, particularly fungus Fusarium oxysporum, has a potential of Striga control by reducing its attachment to cereals and minimizing striga seed bank in soils [65]. Fungi possess several advantages compared to other microorganisms as bioherbicides, given that they are usually host specific, highly aggressive, easy to mass produce and diverse in terms of number of isolates [66]. Studies have shown that F.oxysporum isolates M12-4A, PSM197 and Foxy 2 are host restricted and only infect plants in the genus Striga, and thus constitute the formae speciales strigae [67]. Seed coating with F. oxysporum (FOXY2) was proposed as an effective way to deal with Striga under field conditions [65]. Encapsulated propagules of Fusarium oxysporum (Foxy 2 or PSM 197) in “Pesta” granules during storage has been proposed [68] and reduced Stiga emergence by 75 % in maize and sorghum [69].

### 3.4. Host resistance

The development of cultivars with tolerance and resistance is considered the most economic, practical, effective, and environmentally friendly and long-term approach for controlling Striga [70]. According to Kim [71], striga resistance refers to the ability of host plants to reduce or limit the number of Striga attachments, while tolerance refers to the ability of host plants to withstand the effects of the parasites already attached. Striga resistance in maize could be sourced from wild-grass relatives like Zea diploperennis and Tripsacum dactyloides [72]. Such efforts have led to the development of Striga-resistant inbred line ZD05 suitable for integration in breeding programmes in Western Africa [13] and open-pollinated maize variety KSTP’94' used by farmers in Eastern Africa [73]. Plant resistance to parasitic plants can be defined as pre-attachment and postattachment resistance [74]. Pre-attachment resistance resulting from SL profiles with low seed germinating activity or when Striga receptors that perceive germination stimulants are insensitive to the strigolactone produced by the host [73]. Pre-attachment resistance can also be due to reduced haustorium induction factors [75]. Pre-attachment resistance has been shown in 'KSTP’94', for S. hermonthica management [76]. This maize variety was shown to produce low amounts of sorgomol, a strigolactone that does not efficiently induce S. hermonthica germination [77]. Post-attachment resistance is based on hypersensitive response (HR)/incompatible response (IR) that prevent the Striga haustorium from connecting to the host’s xylem [72]. Amusan et al. [72] reported that Striga on the susceptible maize genotype usually penetrates the xylem and shows substantial internal haustorial development as compared the resistant genotype, where the parasite penetrates the host root cortex but does not form parasite-host xylem-xylem connections. The resistant maize inbred line (ZD05) derived from a backcross containing Z. diploperennis germplasm (a wild relative of maize) exhibits very low Striga attachments and high mortality of attached parasites, compared with the 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. Recently, post-attachment Striga resistance has been shown in the 'KSTP’94', maize open-pollinated variety [73].

The development of molecular markers associated with resistance to Striga has offered a promising way to rapidly accumulate several resistance genes [78]. Recently, using quantitative trait loci (QTL) mapping approach, Badu-Apraku et al. [1] identified 12 QTLs associated with four Striga resistance/tolerance traits in maize, explaining 3.2 to 34.9 % of the phenotypic variance. A genome-wide association analysis study for S. hermonthica resistance in maize identified 24 single nucleotide polymorphisms (SNPS ) markers associated with Striga resistance traits under Striga infestation on chromosomes 3, 9, and 10 [79]. These authors also identified candidate putative genes GRMZM2GO60216, GRMZM2GO57243, GRMZMZ2G164743, on chromosomes 3, 9 and 10, respectively, could be excellent breeding source for the development of Striga-resistant maize genotypes through marker-assisted selection (MAS).

A recent advanced genetic approach proposed for developing host-derived resistance against S. hermonthica is the use of RNA interference (RNAi), i.e., the transformation of the host crop with RNAi sequences targeted at critical Striga genes [80]. However the application constrained by lack of efficient high throughput screening protocols for silencing and by sub optimal delivery of siRNAs into the parasite.

### 3.5. Integrated Striga management (ISM)

Several control approaches (cultural and agronomic, chemical, use of resistant varieties, and biological) have been proposed for striga management, but there is no single control method that can successfully solve the Striga problem [81]. However, integrated Striga management approach (the combination of two or more the aforementioned control methods) is considered the most economical and afordable for small-scale farmers who cannot afford high inputs control options [7,41]. Haussmann et al. [19] suggested a combined action with containment and sanitation, using direct and indirect measures to prevent the damage caused by Striga, and with means to eradicate the Striga seed bank in infested soils. Combination between host resistance and Fusarium oxysporum-based mycoherbicide caused effective Striga reduction and increased crop yield [82]. 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 [83]. 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 [84].

## 4. Conclusion

Despite control of Striga is difficult due to the complex life cycle, different control options have been developed. However, the level of success in controlling this noxious parasitic weed is still inadequate. An integrated management approaches have a great potential in reducing striga infestation compared to single control method and attention should be given in testing and identifying promising and compatible control methods through integrating Striga-resistant cultivars with either fertilizers, myco-herbicides, crop rotation, intercropping/push-pull, herbicide-based seed coating, or synthetic germination stimulants to achieve effective Striga control. So far, only a few maize varieties with durable resistance to Striga have been developed through conventional breeding, and genetic resources for resistance genes are inadequate. Hence, more studies are needed to understand the parasite biology, molecular and genetic basis of host resistance and host–parasite interaction to breed crops with durable resistance. Application of biotechnological tools, such as marker assisted breeding, targeted gene editing or mutation breeding and RNA interference (RNAi) may allow the development of Striga resistant maize genotypes.

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