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**REVIEW** **Open Access**

# Management of the *Striga* epidemics in pearl millet production: a review

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**Abstract**

Pearl millet (*Pennisetum glaucum* [L.] R. Br.) is a drought-resilient and nutritious staple food crop widely cultivated in arid and semi-arid regions. Worldwide, pearl millet is ranked the 6th most widely produced cereal crop after wheat, rice, maize, barley, and sorghum, with a total production of 30.5 million tons on 32.1 million hectares. In Burkina Faso, it is the 3rd widely cultivated crop next to sorghum and maize, with a mean yield of 0.8 ton $ha^{-1}$, far below the potential yield of 3.0 tons $ha^{-1}$ attributable to various production challenges. Among the production constraints, the parasitic weed *Striga* species, particularly *S. hermonthica* is endemic and causes up to 80% yield losses under heavy infestation. Different control methods (e.g., cultural practices, chemicals and bio-herbicides) have been recommended, but they have been largely ineffective due to diverse and complex problems, including the life cycle, seed production, and prolonged seed dormancy of *S. hermonthica*; poor access and cost of implementation. Breeding for host plant resistance presents a cost-effective, environmentally friendly and affordable method for smallholder farmers to control and reduce *Striga* infestations and improve pearl millet yields. Therefore, the objectives of this study were to present the impact of *S. hermonthica* damage on pearl millet production and productivity and assess the effectiveness of different management methods of *S. hermonthica* with an emphasis on host plant resistance. The first section of the review assesses the impact of *Striga* infestation on pearl millet production, followed by the developmental stages of *Striga*, *Striga* infestation and damage management strategies, breeding for *Striga* resistance and other *Striga* control methods. The paper summarises genetic resources, new breeding technologies, and innovations for the precision and speed breeding of *Striga*-resistant cultivars. The review will guide the use of the best breeding strategies and accelerate the breeding of new pearl millet cultivars that are best-performing and resistant to *S. hermonthica* to reduce damage incurred by *Striga* infestations on farmers' fields in Burkina Faso and related agro-ecologies.

**Keywords** Breeding methods, Pearl millet, *Striga* control methods, *Striga hermonthica*, Witchweed

## Background

Pearl millet (*Pennisetum glaucum* [L.] R. Br., $2n = 2x = 14$) is among the most nutritious and hardy cereal crops in arid and semi-arid regions. In sub-Saharan Africa (SSA), including Burkina Faso, pearl millet is the major cultivated crop after sorghum and maize (INSD 2021; FAOSTAT 2018). Pearl millet is remarkably tolerant to drought, low fertile and saline soils, and higher temperatures, making it the most reliable food supply in dry regions worldwide. Pearl millet is valued for its nutritional profiles and quality food and feed

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for human wellbeing. For instance, when compared to maize, pearl millet grain has 11–12.5% bio-available protein. The grain comprises higher concentrations of iron, zinc and micro-minerals, including magnesium, calcium, sodium and potassium (Ghatak et al. 2016; Owheruo et al. 2019).

The average productivity of pearl millet is generally low in Africa. In Burkina Faso, a mean grain yield of 0.8 ton ha$^{-1}$ is reported, comparatively lower than that for maize (1.7 ton ha$^{-1}$) and sorghum (1.0 ton ha$^{-1}$) (FAOSTAT 2022). The low productivity of pearl millet is attributable to the combined effect of several production constraints, including lack of improved varieties, *S. hermonthica* infestation, bird damage, severe drought, and poor soil health (Drabo et al. 2018; Rouamba et al. 2021). Rouamba et al. (2021) reported that *S. hermonthica* (Del.) Benth was identified to be the major constraint to pearl millet production in five regions of Burkina Faso.

The parasitic weed, *Striga* species, is the primary constraint to cereal and legume crop production in sub-Saharan Africa (SSA). It is the most noxious weed affecting sorghum, pearl millet, maize and cowpea (Ali et al. 2009). The following *Striga* species are mainly recognised: *S. hermonthica* and *S. asiatica*, which inflict heavy damage to the major cereal crops in SSA. Dafaallah (2019) reported that more than 50 million hectares of agricultural soils under cereal cultivation have been infested by *Striga* spp. in SSA. The yield losses in cereals due to *Striga* damage can rise to 80% depending on cultivar susceptibility and the degree of the infestation in SSA (Dafaallah 2019; Kamara et al. 2020). Crop failures and abandonment of cereal production are common in SSA due to high parasitism (Kamara et al. 2020). Most crop damage in *Striga*-infested fields occurs before *Striga* emergence, complicating effective parasite control (Dafaallah 2019). During 2017 to 2019, approximately 141 metric tons of cereal grains were produced from 22 million ha in SSA. A yield loss of 1,000 kg ha$^{-1}$ was reported due to *Striga* infestation during the same period (Kanampiu et al. 2018). Worldwide, biotic stress (i.e., diseases, pests, and parasitic weeds) is reported to cause about 30% yield loss in cereal crops (Savary et al. 2019). *Striga* weeds present the most devastating effect on Africa's major cereal and legume crop yield and quality losses. More than 50% of agricultural soils under cereal production is infested by *Striga* spp. in the region (Rodenburg et al. 2016). An estimated 8.6 million tons annual yield loss is incurred in sorghum and millet in the region (Mallu et al. 2021) for SSA. So far, no *Striga*-resistant pearl millet cultivars have been bred and deployed in SSA (Jamil et al. 2021; Rouamba et al. 2022). Kountche et al. (2013) identified six and Dayou et al. (2021) one pearl millet with relatively high yields and moderate resistance to *Striga*.

The management of the *Striga* epidemics in pearl millet includes cultural practices (e.g., crop rotation, intercropping, optimal soil fertilization, moisture conservation methods, hand-weeding), herbicides, biological control agents (e.g., *Fusarium oxysporum* f.sp. *Strigae* [*FOS*]), resistance breeding and integrated *Striga* management (Kountche et al. 2013; Jamil et al. 2021; Rouamba et al. 2021; Rouamba et al. 2022). The primary cultural practices are less expensive to employ and helpful in reducing *Striga* seed bank and infestation. However, they are not widely adopted due to limited access, low farmer acceptance associated with labour shortage, less effective in reducing crop damage and limited access to finance (Murage et al. 2011; Goldwasser and Rodenburg 2013; Mahuku et al. 2017; Franke et al. 2018). According to Hearne (2009), Yoder and Scholes (2010) and Mandumbu et al. (2019), host-resistance is an economical, effective, sustainable approach for managing *Striga* under smallholder conditions.

Integrating different approaches enables effective *Striga* management. Combining host plant resistance with a biological control agent (e.g., *FOS*) effectively reduces *Striga* counts and emergence (Mrema et al. 2020; Shayanowako et al. 2020; Dossa et al. 2023). The biocontrol agent has been successfully used and integrated with resistance breeding in maize (Hassan et al. 2018; Baiyegunhi et al. 2019); Lobulu et al. 2019; Shayanowako et al. 2020; Yacoubou et al. 2021; David et al. 2022) and sorghum (Rebeka et al. 2013; Mrema et al. 2017; Belay 2018; Mrema et al. 2020; Begna 2021). However, this technology is yet to be explored in pearl millet production solo or in combination with other control methods in Burkina Faso and elsewhere. Therefore, the objectives of this study were to present the impact of *S. hermonthica* damage on pearl millet production and assess the effectiveness of different management methods of *S. hermonthica* with an emphasis on host plant resistance. The review discusses the impact of *Striga* infestation on pearl millet production, followed by the developmental stages of *Striga*, infestation and management strategies, breeding for *Striga* resistance and other *Striga* control methods. The paper summarises genetic resources, new breeding technologies, and innovations for developing *Striga*-resistant cultivars with precision and speed breeding methods.

## The impact of *Striga* on crop production

*Striga hermonthica* is an obligate and hemi parasitic weed of cereals and legumes. It is a major and continuing threat to crop production in SSA, the Middle East, and Asia (Parker 2012). *Striga* affects the livelihoods of millions of people in Africa and causes annual yield loss with a monetary value of 7–10 billion US$. Under severe infestation, *Striga* could lead to entire crop losses (Scholes and Press 2008; Rodenburg et al. 2010; Kountche et al. 2019). The parasite causes significant crop damage, such as stunted plant growth, leaf chlorosis, and reduction of the host's photosynthetic capacity. Due to *Striga* damage a productivity loss of 80% was reported in cereals, including pearl millet in SSA (Dafaallah 2019). Annual yield losses reaching 8.6 million tons have been reported in sorghum and pearl millet production (Mallu et al. 2021).

*Striga hermonthica* infestation causes up to 80% yield losses in pearl millet production in Burkina Faso (Rouamba et al. 2021). Wilson et al. (2004) reported grain losses in pearl millet due to *Striga* ranging between 10 and 95% depending on the susceptibility of the variety, agroecology and cultural practices. The salient features of *S. hermonthica* damage include stunted plant growth, yellowing and scorching of the leaves, and death of parasitized plants (Sibhatu 2016; Rouamba et al. 2021). A total crop loss with heavy infestations has been reported due to its pervasive nature of the weed (Mbuvi et al. 2017; Menkir et al. 2020). In West Africa, countries including Burkina Faso, Gambia, Mali, Niger, Nigeria, Senegal, and Togo are severely affected by the scourge of *Striga* (Jamil et al. 2022). Dawud (2018) reported an increasing trend in *S. hermonthica* occurrence and damage in pearl millet growing areas in Nigeria. Early-generation *Striga* control reduces yield losses and prevents subsequent spread to previously unaffected areas (Scholes and Press 2008; Kountche et al. 2016).

## Developmental stages of *Striga*

*Striga* can not survive and grow without the host plant (Cimmino et al. 2018). In 10 weeks after germination, *Striga* complete its life cycle (Yacoubou et al. 2021). The release of germination stimulants, mainly strigolactones (SLs), by the host plant's roots induces *Striga* seed germination (Yoneyama et al. 2010; Joel and Bar 2013; Al-Babili and Bouwmeester 2015). After successful germination, the radicle of *Striga* grows toward the host roots, during which the host perceives and produces chemicals such as 2,6-dimethoxy-1,4-benzoquinone. Host-derived haustorium-inducing factors inhibit the growth of the radicle, followed by cell division and enlargement and root hair proliferation (Goyet et al. 2019).

*Striga* penetrates the host epidermis by the distal cells of the haustorium (Spallek et al. 2013). The periclinal and anticlinal cells of the haustorium undergo series of cell divisions leading to *Striga* growth into the cortex of host plants to siphon water and nutrients (Hood et al. 1998; Yoshida et al. 2010). Up to 500,000 *Striga* seeds are produced per plant. The seeds remain dormant in the soil for 20 years (Lobulu et al. 2019).

## Management strategies of *Striga* infestation and damage

*Striga* grows in agricultural lands with low soil moisture and fertility associated with cereal monocropping, decreased fallow, and minimal input of organic or inorganic fertilizers (Groote et al. 2005). There are various strategies, solo or in combination recommended to manage *Striga.* The control measures can be grouped into cultural, chemical, biological, genetic and a combination of these (Mbwika et al. 2011; Sibhatu 2016).

## Cultural control method

In Burkina Faso, smallholders routinely use cultural practices to manage *Striga* (Fig. 1). Cultural practices to control *Striga* include hand-weeding (Rouamba et al. 2021), cereals and legumes intercropping (Lee and Thierfelder 2017; Mutyambai et al. 2019; Jamil et al. 2021), soil moisture management (Rouamba et al. 2021), mixed cropping and crop rotation (Kuyah et al. 2021), cover cropping (Randrianjafizanaka et al. 2018; Rich 2020), push–pull technology (Niassy et al. 2022), and soil fertilization (Dawud 2017). Cultural control strategies aid in reducing *Striga* seed proliferation and slow down seed germination and growth (Silberg et al. 2021). Push–pull' is an approach that involves intercropping fields with a repellent and an attractant trap plant. The push–pull technology was developed to control *Striga* in resource-poor farming systems by repelling the weed from the major food crops while simultaneously attracting it to a trap crop (Ndayisaba et al. 2020). The method explores an allelopathic effect of the intercrop root exudates in suppressing the germination of *Striga* seed (Khan et al. 2010). For instance, the root secretes of Desmodium promote *Striga* seed germination and prevent the attachment of the young plants to host roots through radical growth inhibition. This system results in the depletion of *Striga* seed bank (Ndayisaba et al. 2020). However, most cultural control strategies are perceived as unaffordable, labour-intensive, or incompatible with other farm operations (Sibhatu 2016) and have thus not been applied widely. Hand weeding is widely practised by smallholder farmers using family labour. However, this method is laborious, time-consuming, and less efficient to reduce *Striga* seed bank and crop damage (Mahuku et al. 2017). Integrated *Striga* management (ISM) is the most effective way to control *S. hermonthica* (Magallon-Servín et al. 2020). Nevertheless, smallholder farmers do not use ISM due to limited access to a combination of resources (David et al. 2022).

## Chemical control

Strigolactones and related chemical compounds are methods of choice in *Striga* management in pearl millet

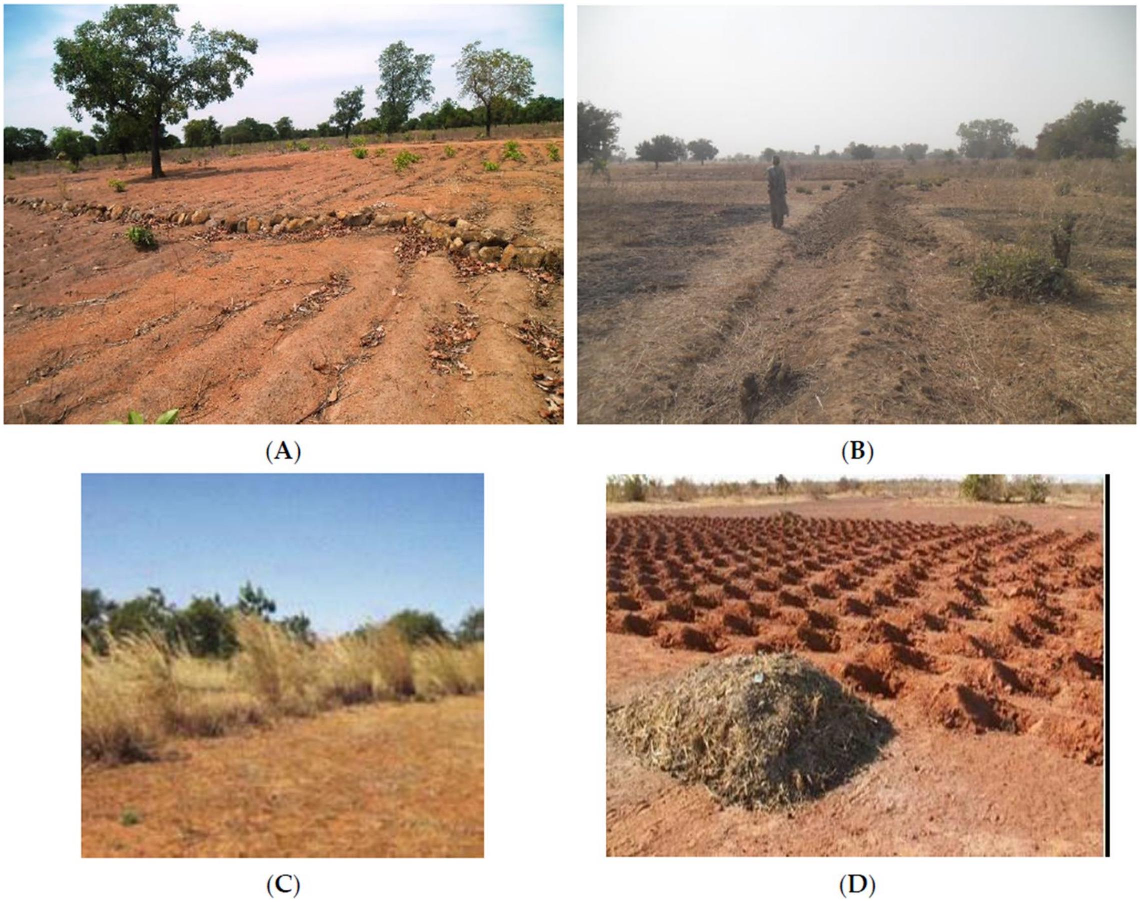

**Fig. 1** Photos depicting cultural practices used by smallholder farmers in Burkina Faso to control *Striga hermonthica* infestation in pearl millet fields. **A** = terraces to conserve soil moisture, **B** = ridge planting, **C** = use of grass strips as *Striga* push, and **D** = use of micro plots or planting holes (locally referred to as zaï) to grow healthy and vigorous pearl millet seedlings (Rouamba et al. 2021)

and sorghum production. This method involves the use of different chemicals such as dihydrosorogoleone, sesquiterpene and kinetin (Babalola and Odhiambo 2008; Cardoso et al. 2011; Zwanenburg et al. 2016). Known as suicidal germination stimulants for parasitic plants, SLs hold promises for *Striga* control (Zwanenburg et al. 2016). The SL analogue MP16 reduced *Striga* emergence by 97% under greenhouse conditions. The Nijmegen-1 analogue rendered 40% and 60% reductions of *Striga* emergence in pearl millet and sorghum fields, respectively, compared to the standard chemical GR-24. Though this method has been highly successful in greenhouse trials, it is still expensive for small-scale farmers (Samejima et al. 2016; Zwanenburg et al. 2016; Kountche et al. 2019).

## Biological control

Biocontrol agents are vital to controlling major crop pests and diseases. They are ecologically friendly and have added benefits to soil health compared to crop protection chemicals. (Raklami et al. 2019; Jabborova et al. 2020). Biological control method is a deliberate use of living organisms to suppress parasitic plants, plant diseases and insect pests. Herbivorous insects, microorganisms (e.g., fungi), and smothering plants are vital biocontrol agents against weeds. *Fusarium oxysporum* f.sp. *Strigae* [*FOS*], host-specific fungi, is highly pathogenic against *S. hermonthica* (Mrema et al. 2020). *FOS* is soil-borne and has shown immense potential to control the emergence and reproduction of *Striga* sp. (Zarafi et al. 2015). Plant toxic compounds such as fumonisin B1 are produced by *FOS* that can kill *Striga* plants before it penetrate the roots of their host (Elzein and Kroschel 2004; Rebeka 2007). Pathogenic fungi are host-specific, highly destructive, easy to reproduce, and genetically divergent (Ciotola et al. 2000). Rebeka (2007) and Elzein et al. (2008) reported the pathogenicity and host specificity of *FOS* to *Striga* without any adverse effects on major cereal crops (Elzein et al. 2010; Rebeka et al. 2013; Mrema et al. 2018). Planting *FOS* treated seeds of the host allow reproduction of the fungus in the rhizosphere of the young host plants inhibiting the growth and development of *Striga* plants (Rebeka 2007).

Another class of biological agents is the *Arbuscular mycorrhizal* (AM) fungus. The AM enhances crop performance, providing adequate protection against *Striga* and facilitating the assimilation of phosphorus (P), water, and micronutrients from the soil by the companion crops. The use of AM-treated maize decreased the incidence of *S. hermonthica* and increased plants' nitrogen (N) and P uptake (Bonfante and Genre 2010; Samejima and Sugimoto 2018). Artificial inoculation of sorghum seeds with *Bacillus subtilis*, *B. amyloliquefaciens*, and *Burkholderia phytofirmans* reportedly reduced *Striga* infestation by 47% (Mounde et al. 2015). *Bacillus* and *Streptomyces* species-derived enzymes, such as xylanases, pectinase, and amylases damaged *Striga* seeds.

## Host plant resistance

Host resistance is the most economical approach to control *Striga* because resistant cultivars can be grown with limited production input (Hess and Ejeta 1992). *Striga* resistance is defined as the ability of the host to prevent *Striga* attachment and development while yielding reasonably well than the susceptible genotypes (Ramaiah 1987; Ejeta et al. 1993). Conversely, tolerance is the ability of the host to maintain high yield compared to susceptible check (Haussmann et al. 2000; Rodenburg et al. 2005; Hearne 2009). Host resistance has not been fully utilized in breeding programs due to the partial resistance conferred by major genes (Ramaiah 1987; Wilson et al. 2004; Mwangangi et al. 2021; Rouamba et al. 2022). Plants employ different mechanisms to resist and tolerate *Striga* infestation (Anitha et al. 2020).

## Integrated *Striga* management

Integration of multiple control methods, also referred to as integrated *Striga* management (ISM) are efficient and economical to control *Striga,* including under smallholder farmers' conditions (Tesso et al. 2007). Figure 2 depicts tri-trophic interactions for integrated *Striga* control through resistant genotypes compatible with a biocontrol agent (*FOS*). The picture portrays the underlying mechanisms and principles of integrating the *Striga*-resistant genotype with *FOS* treatment. The system reportedly enhances the effectiveness of the biocontrol agent with ultimate yield gains in sorghum and maize. An ISM is considered the most cost-effective and environmentally friendly and can quickly be adopted by smallholder pearl millet farmers (Joel 2000; Hearne 2009).

## Components of host plant resistance

### *Root architecture*

Field resistance to *Striga* parasites is attributed to root architecture and physiology. Plant roots serve as mechanical barriers that may resist haustorial attachment or avoid contact with pests held in seed banks (Ejeta 2000; Gurney et al. 2003). Antibiosis and hypersensitivity to *Striga* infection are due to active resistance functions in

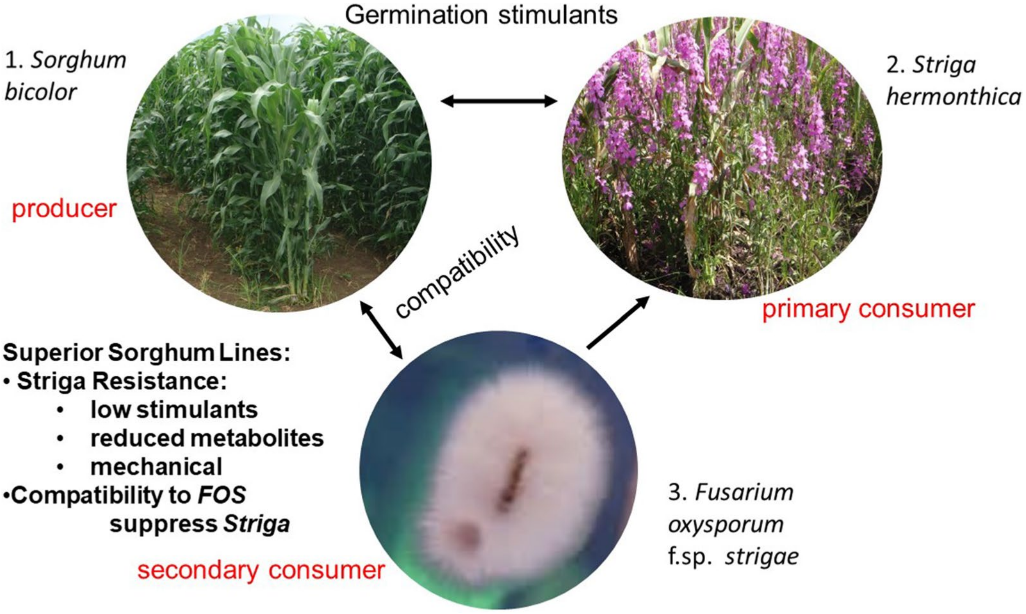

**Fig. 2** Schematic presentation of tri-trophic interactions for integrated control of *Striga* through resistant host compatible with a biocontrol agent *Fusarium oxysporum* f.sp. *Strigae* [*FOS*]

the host plants barring the contact of the parasite with the host. Haustorial interference with the host's root surface causes biochemical responses that cause histological changes, such as necrosis of the host's root cells to prevent penetration of distal cells of *Striga*. A genotype with hypersensitive resistant mechanisms inhibits parasitic attachment and growth and deprives its access to nourishment to reach maturity (Ejeta 2000). However, the host in a given environment might succumb to one *Striga* population but resist another community of the same parasite (David et al. 2022). Hence, reliance on root architectural resistance alone may be insufficient and unreliable. Furthermore, host plants escape infestation by reduced root biomass production and root architecture that avoids the soil layer in which the parasite seeds are more common (Wegmann et al. 1991).

#### Stay-green trait

High photo-inhibition rates per unit leaf are typical on most cereals infested by *Striga* spp. Therefore, maintaining high photosynthetic efficiency under heavy *Striga* infestation is key to increasing tolerance levels to the parasite (Gurney et al. 2003). The stay-green or delayed senescence trait determines the ability of plants to keep their leaves in the active photosynthetic stage to sustain photo-assimilate production and reproductive efficiency under biotic and abiotic stress conditions. *Striga* damage and drought symptoms exhibit rapid leaf senescence and degeneration of leaf chlorophyll. Augmenting the stay-green trait with other *Striga* resistance components may increase host defence and boost yield gains. Ribaut et al. (2009) and Luche et al. (2015) reported that gains in grain yield under *Striga* infestation have been associated with delayed senescence. Delayed senescence is expressed in two forms, namely functional and non-functional stay green characteristics. Functional stay-green plants continue to grow under conditions that lead to senescence in the wild type (Thomas and Howarth 2000). Non-functional stay-green plants are defective in the breakdown of chlorophyll and remain green even though chloroplasts are no longer photosynthetically active (Thomas and Howarth 2000). The former is relevant to *Striga* tolerance as mutants with functional "stay-green" have prolonged photosynthetic activity and delayed senescence than standard genotypes. In maize, genomic regions conferring stay-green have been mapped within the genome. Three stay-green QTLs, *qsg-1, qsg-4, and qsg-8*, have been identified under low nitrogen conditions (Ribeiro et al. 2018), showing the importance of the stay-green trait in *Striga* populations. In pearl millet two stay-green QTLs (Xibmsp09/AP10.2, and Xibmcp09/AP10.1) have been identified and four markers on chromosome 6 were reportedly associated with stay-green trait (Singh and Nara 2023).

#### Escape

The ability of genotypes to complete the reproductive life cycle before peak pest pressure, moisture deficit or disease outbreak is defined as 'escape'. Selection for *Striga* escape through early maturity can reduce yield loss due to the parasites and their derived phytotoxins (Rich and Ejeta 2008). Evaluating drought-tolerant extra early germplasm under *Striga* infestation is fundamental in breeding for early maturity. Ultra-early cultivars that complete their life cycle before the continuous effects of multiple *Striga* infestations are required where terminal drought stress jointly occurs with the parasite (Wegmann et al. 1991).

#### Striga resistance genes

*Striga* resistance is conditioned by a chain of signals elicited by the host plant. The inheritance of crop traits associated with *Striga* resistance are not conclusively known. Some modest success are reported in sorghum and only brief progress in pearl millet. Kountche et al. (2013) reported quantitative resistance to *S. hermonthica* using cultivated pearl millet gene pool under field evaluations. Pearl millet landraces such as M141, M239, M029, M197, M017, KBH, and 29Aw have been reported to possess *Striga* resistance genes (Kountche et al. 2013, Dayou et al. 2021). The introgression of multiple resistance genes in a single cultivar would provide more robust resistance to *Striga* (Kountche et al. 2016). Although conventional breeding has significantly contributed to *Striga* resistance, particularly in sorghum and pearl millet, this approach has not been fully deployed due to the complex quantitative resistance to *Striga*. Thus, the development of molecular markers offer an opportunity to identify resistant genes in wild relatives and resistant varieties of related species (Ejeta and Gressel 2007; Rispail et al. 2007). This may facilitate the pyramiding of multiple resistance genes into the agronomically superior and locally adapted *Striga* susceptible varieties (Kountche et al. 2016). Marker-assisted backcross has been used to introgress *Striga*-resistant genes from *Striga*-resistant lines (N13, SRN 39, Framida and Hakika) to farmers preferred lines (Gadam and Kari Mtama-1) that are susceptible to *Striga* in sorghum (Muchira 2022). Novel resistance genes were identified in the wild perennial maize, *Zea diploperennis*. The candidate genes were introgressed into early- and extra-early-maturing maize inbreds (Amegbor et al. 2017). Early-maturing *Striga*-resistant and drought-tolerant maize inbred line, TZdEI 352, derived from a cross between TZEW Pop DT STR and *Z. diploperennis* had increased grain yield and durable *Striga* resistance/tolerance (Akaogu et al. 2019).

## Screening for *Striga* resistance in pearl millet

Several screening techniques were reported (Berner et al. 1997; Haussmann et al. 2000). These included double-pot, Pasteur pipette, root-slope, sandwich, and antihaustorial. Screening in pots requires growing the host in pots artificially inoculated with *Striga* seeds. *Striga* infestation in pots is more definite than in artificially infested fields (Rao et al. 1983). The agar-gel assay developed by Hess and Ejeta (1992) provides a relatively easy means for screening host genotypes for low *Striga* seed germination stimulant production. These screening techniques used in other crops can be adapted to screen pearl millet for *Striga* resistance breeding.

## Breeding for *Striga* resistance

### *Conventional breeding*

Considerable efforts have been made in breeding cereals for *Striga* resistance, and modest progress has been achieved in developing improved varieties (Yacoubou et al. 2021). Identifying potential sources of resistance is the first procedure of all *Striga* resistance breeding programmes. Crossing complementary parents with resistance genes and agronomic traits followed by recurrent selection increases the integration of *Striga* resistance genes. This method will build polygenic resistance, durable, and effective over time for the control of *Striga* (Menkir and Kling 2007). Recurrent selection has been used to develop the first experimental pearl millet *Striga*-resistant variety (Kounche et al. 2013). In maize breeding, *Striga* damage symptoms and counts were reduced by 3% and 10% per cycle of recurrent selection, and grain yield increased by 16% (Menkir et al. 2004). The half-sib as well as full-sib selection schemes are ways to develop composite populations with moderate resistance to *S. hermonthica* by allowing few *Striga* attachments compared to susceptible genotypes (Hallauer 1992; John and Sleeper 1995; Menkir et al. 2004). Conversely, the availability of donor parents with *Striga* resistance could facilitate the introgression of a favourable gene using backcrossing (Badu-Apraku et al. 2017).

### *Marker-assisted selection*

Molecular marker techniques are complementary genomic resource in traditional plant breeding and genetic analysis. Marker-assisted selection (MAS) is an indirect selection procedure to identify a trait of interest (e.g., *Striga* resistance) based on a molecular marker linked to the phenotypic trait (Ribaut et al. 2001). MAS allow the selection of better-performing genotypes at early generations (Yacoubou et al. 2021). Using simple sequence repeats (SSRs) and single nucleotide polymorphisms (SNPs) markers, some elite genotypes for the breeding of *Striga* resistance were selected, and new markers have been identified, which significantly contributed to the differentiation of *Striga* tolerant and susceptible genotypes (Bawa et al. 2015; Shayanowako et al. 2018). Quantitative trait locus (QTL) for *S. hermonthica* resistance from local populations have been successfully transferred through backcross breeding into adaptable maize populations using MAS (Rich and Ejeta 2008). *Striga* resistance QTL were discovered in sorghum and rice (Atera et al. 2015; Yasir and Abdalla 2013; Yohannes et al. 2016; Ali et al. 2016) while SNPs markers associated with *Striga* emergence count were reported by Dawud et al. (2018) in pearl millet. Haussmann et al. (2004) identified and mapped QTL associated with *Striga*-resistance in the sorghum variety, N13, where a mechanical barrier is the suggested mechanism of *Striga* resistance. The identification of *Striga*-resistance QTL for pearl millet will ease the transfer of candidate genes into adaptable pearl millet varieties.

Developing a marker-assisted selection scheme for enhancing quantitative *Striga* resistance in pearl millet shortens the breeding cycle. Due to low genotyping costs (Elshire et al. 2011), more significant numbers of entries could be screened for markers linked to resistance alleles, followed by field phenotyping of a selected subset of the entries with an increased selection intensity. When the field phenotyping method successfully differentiates the tested entries, the results can be re-calibrated to have the marker-based selection index (Kountche et al. 2013).

## Genetic resources of pearl millet for *Striga* resistance and economic traits

### *Landraces*

Landraces are novel sources of genetic variation for breeding based on their desirable genetic compositions for agronomic and quality attributes. Many accessions of pearl millet are curated in limited gene banks and databases globally (Table 1). There is a need to screen for large numbers of memberships to identify the required and desirable germplasm and genes for breeding. The first selfed generation ($S_1$) gene pool is more efficient for utilising landraces when limited genetic information is available. The $S_1$ gene pools are mixtures of selfed individuals from a more significant number of accessions, allowing for a more efficient evaluation of germplasm (Burton 1978; Hanna 1990). Furthermore, the $S_1$ gene pools allow to assess large populations and select the desired trait (s) more readily. Genetic diversity analyses in landraces offer possibilities of pearl millet breeding of open-pollinated and hybrid varieties (Langridge 2005; Varshney and Tuberosa 2007). In pearl millet (Wilson

**Table 1** Number of accessions curated and important gene banks and databases of pearl millet

| Number of accessions | Institution/Country | References |
|---|---|---|
| 3,082 | Southern African Development Community (SADC)/Matopos, Zimbabwe | Monyo1998; Upadhyaya et al. 2012 |
| 22,288 | International Crops Research Institute for the Semi-Arid Tropics (ICRISAT)/Patancheru, India | Mathur 2012 |
| 3,968 | Institute of Research for Development (IRD)/France | |
| 3,821 | Canadian Genetic Resources (CGR)/Saskatoon, Canada | |
| 1,283 | Germplasm Resource Information Network (GRIN)/Beltsville, USA | Yadav et al. 2007 |
| Number of accessions as sources of resistance | | |
| 6 | International Crops Research Institute for the Semi-Arid Tropics (ICRISAT)/Niamey, Niger | Kountche et al. 2013 |
| 1 | International Crops Research Institute for the Semi-Arid Tropics (ICRISAT)/Niamey, Niger | Dayou et al. 2021 |
| 4 | United States Department of Agriculture-Agricultural Research Service/Washington, America | Wilson et al. 2004 |
| 6 | International Crops Research Institute for the Semi-Arid Tropics (ICRISAT)/Ouagadougou, Upper Volta | Roger and Ramaiah 1981 |
| 2 | Institute of Environment and Agricultural Research (INERA)/Ouagadougou, Burkina Faso | Rouamba et al. 2022 |
| 2 | International Institute of Tropical Agriculture (IITA)/Ibadan, Nigeria | Kim et al. 1994 |

et al. 2004) and maize (Rich and Ejeta 2008), wild relative genotypes have been used as *Striga* resistance sources for variety development.

### *Mutant selections*

Kiruki et al. (2006) reported the first *Striga*-resistant mutant maize varieties (K9908, K9910 and K9911). The varieties had stable performances in *Striga*-infested fields in western Kenya. A mutation at LGS1 locus causes quantitative and qualitative alterations in the SL content of root exudates, significantly reducing the germination stimulant's action without negatively impacting productivity (Gobena et al. 2017). Nikièma et al. (2020) identified seven *Striga*-resistant mutants (SA38M5, SA188M6, GK715M4, GK225M5, IC47M5, IC83M5 and IC17M6) among sorghum mutants generated from gamma irradiation. For the performance and estimation of the genetic variability study, M3 population of pearl millet treated with different doses of gamma rays showed high heritability for panicle diameter, number of nodes per plant and stem diameter (Maryono et al. 2020). Induced mutation is a powerful tool in pre-breeding in pearl millet to generate new breeding populations to identify *Striga*-resistant mutants and cultivar development.

### *Hybrid varieties*

Hybrid varieties are man-made entities developed by crossing two genetically distant breeding lines. They represent the first generation ($F_1$) originating from the cross. In pearl millet, hybrids are developed as follows: (i) development of inbred lines in the various original populations, (ii) test crosses between the different inbred lines to find the best hybrids, and (iii) production of hybrid seed for the market (Arncken and Dierauer 2006). Hybrid seed production requires efficient cross-pollination methods to keep production costs low (Duvick 2009). Pearl millet hybrids outperformed landraces by 10–15% (Yadav and Rai 2013). However, the new hybrids could not be adopted because of the lack of efficient seed production programs and their limited genetic superiority (Yadav et al. 2021). Hybrids are known and desirable for their high productivity and quality. However, they have shown reduced disease resistance compared to open-pollinated varieties (OPVs) with innate defence traits (Schroeder et al. 2013). It is, therefore, vital to understand the parents' genetic makeup by combining ability analyses to develop hybrids with enhanced resistance to *S. hermonthica* (Yacoubou et al. 2021). Pearl millet hybrid derived from crosses between *S. hermonthica* resistant and susceptible parents were reported to be susceptible due to the recessive genes conditioning resistance which were masked by dominant genes (Haussmann et al. 2000; Rouamba et al. 2022). Hess and Ejeta (1992) and Kling et al. (2000) reported that heterosis can offer tolerance to *Striga* in sorghum and maize. Maize hybrid varieties with *Striga* resistance have been reported by Menkir et al. (2004) and Karaya et al. (2012). This suggested that hybrid breeding can offer *Striga* resistance which can also be exploited in pearl millet breeding.

### *Synthetic varieties*

A synthetic variety is derived from an open-pollinated population (Lonnquist 1949). Synthetics can be formed by inter-crossing selfed plants or lines that are subsequently maintained by mass selection. A synthetic variety designates a genetic pool derived from open-pollination or controlled crosses of all possible combinations among several genotypes subjected to a combining ability test. The progenitors of a synthetic variety could be inbred or mass-selected populations (Mandal 2014). The merit of synthetics has been observed in sorghum cultivars and demonstrated an average superiority of 18% for grain yield under *Striga* infestation (Haussmann et al. 2000). Host plant damage was significantly reduced in synthetic maize populations resistant to *Striga* (Kim et al. 1998). Synthetic varieties partially utilize heterosis because some inbreeding occurs to open pollination in later generations (Mohammed 2013). Being a cross-pollinated crop, developing pearl millet synthetic variety with *Striga* resistance may contribute to *Strig*a-resistance stability over time.

## Genomic-assisted breeding

### *Quantitative trait loci (QTL) analysis*

Quantitative traits are useful to plant breeders. Most of the economic traits have quantitative inheritance. A QTL is a region on the genome that may comprise one or more functional genes. In maize, the resistance to *S. hermonthica* is regulated by polygenes or QTL with small additive genetic contributions (Rodenburg et al. 2006; Shayanowako et al. 2020). QTL related to *Striga* damage rating and *Striga* emergence count have been identified in maize by Badu-Apraku et al. (2020), including *qepp-3, qepp-8.1, qsd-5.1, and qsc-3.1*. Identifying QTL associated with *Striga*-resistance facilitate the rapid development of *Striga*-resistant pearl millet genotypes using MAS. The polygenic nature of host–parasite relationship and its interaction with environmental factors after validation necessitate the use of MAS (Gedil and Menkir 2019). No significant research and development has been done on the detection of QTL or minor genes for *Striga* resistance in SSA (Yacoubou et al. 2021). MAS used in maize may serve as a model tool in pearl millet *Striga* resistance breeding programs.

### *Next-generation sequencing (NGS)*

Next-generation and conventional sequencing technology have been used to elucidate the molecular events underlying *Striga* resistance (Yoshida et al. 2010). *Striga* genomes have a typical complex angiosperm genome with a size of 615 Mb for *S. asiatica,*1425 Mb for *S. hermonthica* and 2460 Mb for *S. forbesii*, suggesting several polyploidization events (Schneeweiss et al. 2004). Next-generation sequencing technology has increased available transcriptional data for *S. hermonthica* and related species (Spallek et al. 2013).

Genomics-assisted breeding is one of the most promising developments that have implications for imparting genetic gains in pearl millet breeding. Genomic selection improves the breeding program's precision and efficiency (Yadav et al. 2021). Through whole-genome resequencing of Pearl Millet Inbred Germplasm Association Panel, mapping population parents, and elite hybrid parental lines more than > 32 million repositories of genome-wide SNPs were developed (Varshney et al. 2017). The genomic and genetic resources enable the development of genetic maps and rapidly deploying genes of agronomic importance. Also, it allows resequencing lines to mine and map genes of interest in pearl millet (Yadav et al. 2021). NGS based on the repository of genome-wide SNPs could substantially accelerate knowledge in *Striga*-resistance breeding to deliver pearl millet varieties with *Striga* resistance and farmers' preferred traits. The inherent biases and ambiguous alignment of repetitive genetic and nongenetic elements lead to highly fragmented draft genome assemblies that may hinder the use of NGS and complicate studies of hidden indels and structural variants (Sedlazeck et al. 2018). Gobena et al. (2017) reported transcriptome data on *S. hermonthica* plants of different development stages through NGS analysis. A new gene (*WKRY45*) in rice and an RNA-seq in finger millet were reported to be associated with *Striga* resistance (Yoshida and Shirasu 2012; Mutuku et al. 2015).

## Genetic engineering and genome editing

### *Genetic engineering*

Genetic engineering involves integrating genetic material through transformation followed by selection. Genetic engineering permits the transfer of resistance genes from any organism into a reference crop. Genetic engineering can be deployed to integrate resistance genes against *Striga,* including the strigolactone content of the host plant. Genetic resistance can either be adopted solo or as part of an integrated management system (Jamil et al. 2021; Kavuluko et al. 2021; Muchira et al. 2021; Mallu et al. 2022). In *Striga* resistance breeding, the main limitation to employing genetic engineering is lack of well-defined resistance genes (Haussmann et al. 2000). The RNA interference (RNAi) technology has been explored as a genetic tool for engineering host plants with resistance against parasitic weeds. The RNAi technology can transform host plants with a plasmid encoding a double-stranded hairpin RNA (hpRNA) targeted against one or more *Striga* resistance genes (Runo et al. 2011; Yoder et al. 2009).

### *Genome editing*

Genome editing (also referred to as gene editing) is a set of tools enabling editing genes to enhance the genetic expression of an organism. It manipulates the specific gene loci to gain genome modifications, such as insertions, deletions or point mutations. Genome editing techniques were developed in the late 1990s with the discovery of homing and zinc-finger endonucleases, which direct DNA cleavage to particular sites within a genome. The three main genome editing tools currently used are ZFNs, TALENs, and CRISPR/Cas9 (ASSAF 2016). CRISPR-Cas9 is the most accurate and efficient genome editing technique (Barrangou 2015). Butt et al. (2018) reported that CRISPR/Cas9 system in translational research can be used for target improvement of plant architectural trait. The study showed that targeted engineering of CCD7 could improve crop yield and lower the risk of *Striga* infestation by increasing the number of tillers while significantly reducing *Striga* germination in rice.

### Limitations of the reviewed studies and potential sources of bias

Research efforts in *S. hermonthica* resistance breeding in pearl millet are limited compared to other major cereal crops (Mudereri et al. 2020; Stanley et al. 2021). Dossa et al. (2023) conducted a meta-analysis and summarised the most effective methods for *Striga* control. However, the authors only found one report for pearl millet and finger millet compared to 46 and 18 for maize and sorghum, respectively. The sparse studies available on pearl millet and finger millet could hinder drawing plausible conclusions of *Striga* resistance breeding efforts of the two important crops. Therefore, data presented based on the findings of maize and sorghum might be a source of bias until more research is conducted and robust data presented revealing the interaction of pearl millet and *Striga* to guide breeding and genetic analysis. The wide range of hosts of *S. hermonthica*, including primary hosts (e.g., cereal crops) and alternative hosts (e.g., grasses) may complicate its management and control methods. Genomic resources and innovations can reveal the molecular and genetic bases of host resistance and host–parasite interaction for the precision of pearl millet with durable *Striga* resistance (Jamil et al. 2021). Further, new genetic and genomic resources and safe and sustainable control strategies, including beneficial microorganisms, should be explored to control the scourge of *Striga* infestation (Olowe et al. 2023).

## Conclusion and outlook

Pearl millet yield in SSA is low due to various biotic and abiotic factors. *Striga* causes yield loss of up to 100% in heavily infested fields. Cultural practices, chemical and biocontrol agent control measures are recommended for *Striga* management. However, the methods were not widely adopted by smallholder farmers because of their unavailability or high cost and *Striga*'s complex life cycle and prolonged seed dormancy in farmlands. *Striga* resistance varieties are cost-effective, environmentally friendly and affordable for smallholder farmers to control and reduce *Striga* infestations and improve pearl millet yields. Furthermore, integrated *Striga* management involving pearl millet genotypes with *Striga*-resistance and *FOS* compatibility is the most cost-effective, and environmentally friendly and can quickly be adopted by smallholder pearl millet farmers. Information presented in this review, including genetic resources, new breeding technologies, and innovations, assists in the precision and speed breeding of *Striga*-resistant cultivars. Overall, the review will guide the use of the best breeding strategies and accelerate the development of new pearl millet cultivars that are high yielding and resistant to *S. hermonthica* to reduce damage incurred by *Striga* infestations on farmers' fields in Burkina Faso and similar agro-ecologies. There is a need for training pearl millet farmers about the occurrence, distribution, and management of *S, hermonthica*. Furthermore, pearl millet is an under-researched crop needing research and development priority and policymakers' support to enhance the crop's production and productivity through breeding *Striga*-resistant varieties using new genetic and genomic resources.

#### Abbreviations

| | |
|---|---|
| AM | Arbuscular mycorrhizal |
| CGR | Canadian genetic resources |
| *FOS* | *Fusarium oxysporum* F.sp. *Strigae* |
| GRIN | Germplasm Resource Information Network |
| IRD | Institute of Research for Development |
| ISM | Integrated *Striga* management |
| ICRISAT | International Crops Research Institute for the Semi-Arid Tropics |
| MAS | Marker-assisted selection |
| NGS | Next-generation sequencing |
| OPVs | Open-pollinated varieties |
| QTL | Quantitative trait loci |
| SSRs | Simple sequence repeats |
| SNPs | Single nucleotide polymorphisms |
| SADC | Southern African Development Community |
| SLs | Strigolactones |
| SSA | Sub-Saharan Africa |

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## Publisher's Note