

## Research review

# Combining host plant defence with targeted nutrition: key to durable control of hemiparasitic *Striga* in cereals in sub-Saharan Africa?

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## Summary

Host plant defence mechanisms (resistance and tolerance) and plant nutrition are two of the most widely proposed components for the control of hemiparasitic weeds of the genus *Striga* in tropical cereal production systems. Neither of the two components alone is effective enough to prevent parasitism and concomitant crop losses. This review explores the potential of improved plant nutrition, being the chemical constituent of soil fertility, to fortify the expression of plant inherent resistance and tolerance against *Striga*. Beyond reviewing advances in parasitic plant research, we assess relevant insights from phytopathology and plant physiology in the broader sense to identify opportunities and knowledge gaps and to develop the way forward regarding research and development of combining genetics and plant nutrition for the durable control of *Striga*.

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**Key words:** defence mechanisms, fertilizer, maize, rice, *Striga asiatica*, *S. hermonthica*, sorghum, witchweed.

## Introduction

Obligate hemiparasitic plants of the genus *Striga*, commonly known as witchweeds, pose a great threat to cereal production in sub-Saharan Africa (SSA) (Dugje *et al.*, 2006; Rodenburg *et al.*, 2010). Resource-poor smallholder farmers are particularly hard hit by these parasitic weeds, as they often grow cereal crops in *Striga*-prone areas characterized by poor soil fertility, and they frequently lack the knowledge or resources for effective *Striga* control options (Emechebe *et al.*, 2004; Tippe *et al.*, 2017).

The genus *Striga* is diverse, consisting of *c.* 28 species and six subspecies (Mohamed *et al.*, 2001). All but one of the weedy *Striga* species parasitize on monocotyledon plants. The exception is *S. gesnerioides*, which is specific to dicotyledon hosts. The most economically important species parasitizing cereal crops (e.g. maize, sorghum, rice, millet) are *S. hermonthica*, *S. asiatica*, *S. aspera* and *S. forbesii* (Parker, 2009). Monocotyledon-parasitizing species (i.e. the focus of this review and henceforward referred to as '*Striga*') have a low host specificity and can thus parasitize a broad range of plant species including native and introduced cultivated

crops such as wheat, sorghum, maize, millet or teff, sugarcane and also wild grasses (Vasey *et al.*, 2005; Welsh & Mohamed, 2011). *Striga* are observed in at least 44 countries in SSA (Rodenburg *et al.*, 2016). *Striga* are most widespread in West Africa, covering an estimated 64% of the arable land under cereals, followed by East and Central Africa, with 23% of land being infested (Gressel *et al.*, 2004).

Yield losses due to *Striga* result in a considerable economic impact. An estimated 293 000 tonnes of milled rice (worth US \$117 million) are lost annually because of *Striga* infestation of rainfed rice (Rodenburg *et al.*, 2016). High losses are also observed in sorghum and millet with an estimated combined annual loss of 8.6 M tonnes, and maize with an estimated annual loss of 2.1 M tonnes (Gressel *et al.*, 2004). Factors such as poor soil fertility and continuous monocropping greatly favour the spread and infestation by *Striga* in cereal-growing regions (Emechebe *et al.*, 2004).

A range of *Striga* management options have been developed in recent decades, but none of these provides durable control when deployed as stand-alone practices (Hearne, 2009; Bàrberi, 2019). For effective and durable *Striga* control, an integrated *Striga*

management approach that is affordable, easy to use and adaptable to smallholder farming systems is recommended. Oswald (2005) proposed that for an effective integrated approach, soil fertility management should be the central focus. Nitrogen-fixing legumes can be grown as covercrops or intercrops as a low-cost technique to improve soil fertility and reduce *Striga* infections in cereal crops (Reda *et al.*, 2005; Khan *et al.*, 2007; Tonitto & Ricker-Gilbert, 2016; Randrianjafizana *et al.*, 2018). Mineral fertilizers would enable more tailored crop nutrition in terms of quantities, composition, placement and timing. The use of mineral fertilizers and *Striga*-resistant or *Striga*-tolerant cultivars has shown to hold promise as a suitable combination for integrated *Striga* management (Tippe *et al.*, 2017). However, knowledge of the effects of macro- and micronutrients on host plant defence against *Striga*, required to develop the most effective approach, is limited.

In this review, we take a closer look at the identified host plant defence mechanisms against *Striga*. We then examine what is known about the effect of nutrients on these defence mechanisms, as this will help to tailor appropriate nutrient combinations providing an additive or even a synergistic effect. Beyond nutrient effects on the expression of resistance and tolerance against *Striga*, we consider relevant insights from phytopathology, where resistance is widely exploited and investigated, and look at the role of nutrients in plant physiological processes that are affected after *Striga* infection. Finally, we discuss potential nutrient delivery techniques that are cost-effective, efficient and easily adaptable to smallholder farming systems in SSA.

## *Striga* biology and host interactions

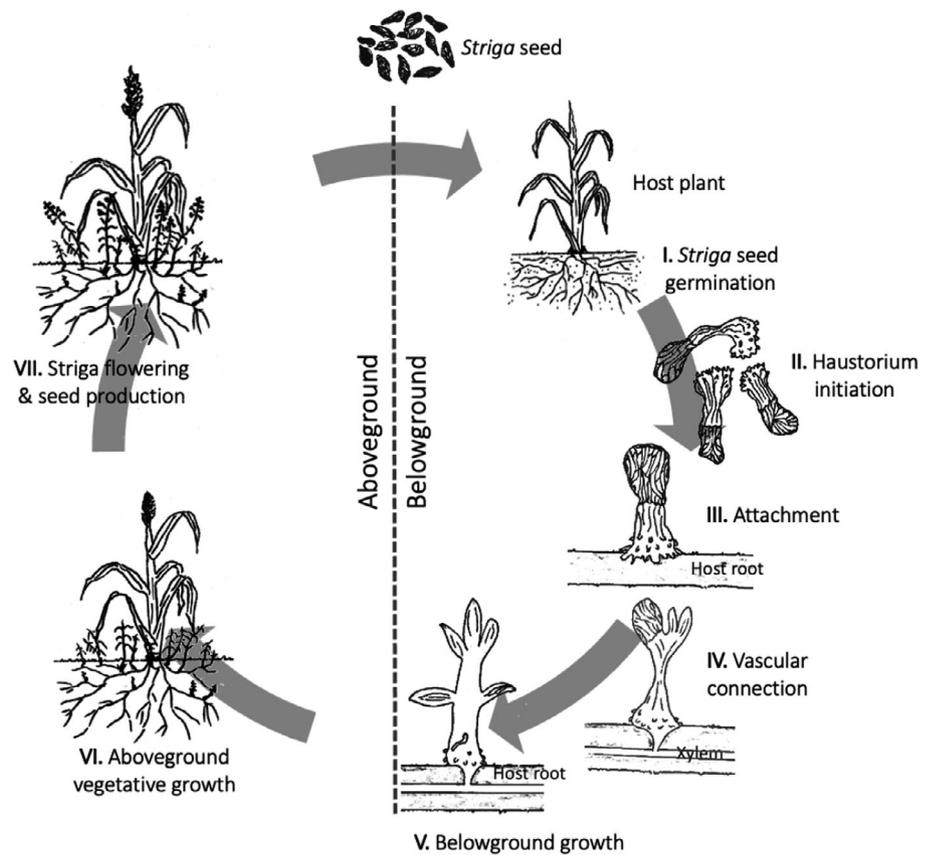
The success of *Striga* is based on its life cycle that is intricately synchronized with the host plant's cycle (Fig. 1), because of a suite of underlying molecular processes clearly outlined by Mutuku *et al.* (2020). First, *Striga* seed dormancy needs to be broken by a period (*c.* 10 d) of sufficiently moist soil conditions, usually achieved at the onset of a new rainy season. After this preconditioning, the actual seed germination of *Striga* (Fig. 1 stage I) depends on germination stimulants, secreted in the root exudates of both host and nonhost plants, such as dihydroquinones, ethylene sesquiterpene lactones, ethylene and strigolactones (Babiker & Hamboun, 1983; Bebawi, 1986; Bouwmeester *et al.*, 2003; Yoneyama *et al.*, 2010). Among them, strigolactones have been shown to be the most potent, inducing *Striga* seed germination at very low concentrations (Kim *et al.*, 2010; Yoneyama *et al.*, 2010). Once *Striga* seeds germinate, the seedlings grow chemotropically towards the host roots (Yoshida & Shirasu, 2009). *Striga* depend on the production of cues by the host root to start the formation of an intrusive structure, called haustorium (Yoshida *et al.*, 2016; Fig. 1 stage II). These host cues, called haustorium-inducing factors (HIFs), are diverse, and include phenolic (syringic and guanycl) acids, quinones (2,6-dimethoxy-*p*-benzoquinone) and flavonoid compounds (Yoshida *et al.*, 2016; Cui *et al.*, 2018; Goyet *et al.*, 2019). Below ground, seedlings of *Striga* recognize these metabolites and subsequently form a haustorium at the tip of the radicle that enables host root attachment (Fig. 1 stage III) and penetration (Hood *et al.*, 1997). Once penetration has occurred, the parasite cells differentiate to

form tracheary elements that establish the vascular connection to the host plant xylem (Fig. 1 stage IV) within 48–72 h (Dörr, 1997; Hood *et al.*, 1997). *Striga* acquire water, carbon and nutrients from the host plant through this xylem bridge.

Following its successful initial establishment, the parasite forms secondary attachments to other roots and starts growing upwards (Fig. 1 stage V), emerging above the soil *c.* 4 wk later. Following emergence, the plants produce leaf Chl that enable them to photosynthesize (Press *et al.*, 1991). The *Striga* plants then grow vegetatively (Fig. 1 stage VI), whereby they exhibit a high transpiration rate due to their near-continuous open leaf stomata (Shah *et al.*, 1987). Once above ground, *Striga* plants develop for another 4 wk and then produce flowers, followed by pollination, seed capsule formation and seed dispersal (Fig. 1 stage VII) (Webb & Smith, 1996). A small number of *Striga* species, including *S. hermonthica*, are strictly cross-pollinated (allogamous) but most others, such as *S. asiatica*, are self-pollinated (autogamous). To ensure successful survival, a single *Striga* plant produces over 50 000 tiny seeds that are easily dispersed by wind and rain. Seeds of *Striga* are long-lived in the soil seed bank (Bebawi *et al.*, 1984; Van Mourik *et al.*, 2005), which contributes to the difficulty of controlling this weed.

Above ground, plants of *Striga* photosynthesize but are not sufficient in terms of carbon assimilation (Shah *et al.*, 1987; Press *et al.*, 1991). Comparison of *S. hermonthica* to its close nonparasitic relative, snapdragon (*Antirrhinum majus*), revealed the parasite has CO<sub>2</sub> assimilation rates of < 40% on a Chl basis and 20% on a whole leaf basis of that of the nonparasitic plant (Shah *et al.*, 1987). Consequently, an estimated 85% of the carbon needs of mature *Striga* plants are fulfilled by the parasitized host plant (Press & Stewart, 1987; Press *et al.*, 1987; Shah *et al.*, 1987; Graves *et al.*, 1990). At the same time, *Striga* parasitism diminishes the host plant photosynthesis rate (Press & Stewart, 1987; Press *et al.*, 1987). The complete mechanistic background of the suppression of host photosynthesis by the parasite has yet to be elucidated. However, studies suggest it might be due to the increased secretion of ABA by *Striga* to the rhizosphere that suppresses the host growth and immunity (Fujioka *et al.*, 2019a). *Striga*-infected host plants also have elevated ABA levels in their xylem sap resulting in a reduction of the stomatal conductance rate (Frost *et al.*, 1997).

The siphoning of resources and reduced CO<sub>2</sub> fixation following infection by *Striga* are accompanied by stunted growth, and an increased root : shoot ratio of the host plant (Gurney *et al.*, 1995, 1999; Dörr, 1997; Rank *et al.*, 2004). These effects, as well as yet unelucidated phytotoxic effects manifested by chlorosis, necrosis and desiccation, cause negative feedback loops on host performance (Spallek *et al.*, 2013). Because of the high transpirational pull of the attached *Striga* plants, the infected host plants also experience drought stress, which further induces host leaf stomatal closure (Inoue *et al.*, 2013). The transpiration gap between *Striga* and the host plant promotes the flow of nutrients and water from the hosts to the parasite (Dörr, 1997) together with host metabolites. Similarly, through the host–parasite xylem bridge, *Striga* transfer toxic secondary metabolites such as iridoid glycosides to the host plants but their function as well as the mechanism of their action is unknown (Rank *et al.*, 2004). In addition, the recently identified



**Fig. 1** Life cycle of *Striga*. Clockwise from the top: (I) *Striga* seeds in the soil germinate after a period of preconditioning and upon reception of cues of nearby host presence (exudates derived from the host roots); (II) when the *Striga* radicle is in close proximity of a host root, upon reception of a second type of host cue, it forms a haustorium that enables the parasite to (III) attach to a host root and penetrate root tissue to form a (IV) vascular connection (xylem bridge); the parasite will then (V) grow below ground and emerge above ground after 2–4 wk; (VI) once above ground it produces Chl and turns green; a period of around 4 wk of vegetative growth is followed by (VII) flowering, pollination and seed-capsule production; each seed capsule produces hundreds of small (dust-like) seeds that are then shattered and returned to the soil to replenish the seedbank.

horizontal transfer of genes and transposons from host plants to *Striga* that aid in parasitism might occur through the host xylem bridge (Yoshida *et al.*, 2019).

The dependence of *Striga* on host signals, penetrable host tissue, xylem vessels and the ability to withdraw water, nutrients and carbon from the host plant provide entry points for genetically driven defence mechanisms. Host plant defence mechanisms are based on the production of less active strigolactones and HIFs, impairment of the parasite attachment and establishment of the vascular connection, or mitigation of negative parasitism effects (Yoshida & Shirasu, 2009). These defence mechanisms are presented in more detail in the next section, after which emphasis will be on how macro- and micronutrients might fortify the expression of these defence mechanisms. The combination of inherent defence and targeted host plant nutrition could potentially reduce parasite success and increase host plant performance, providing a solid basis for durable control.

### Host plant defence mechanisms against *Striga*

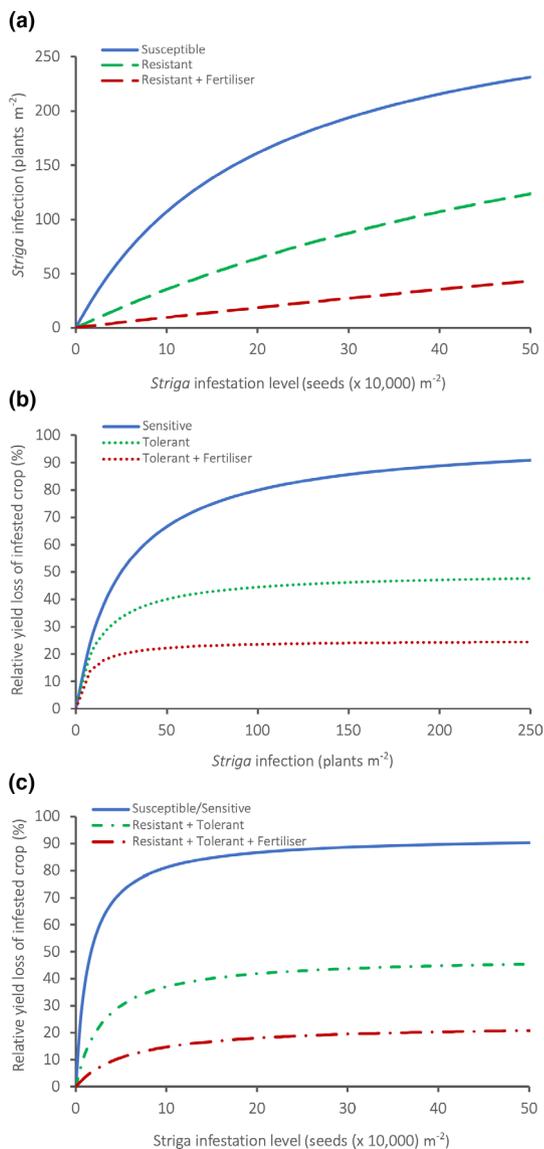
Host plant defence mechanisms against *Striga* comprise two broad categories, resistance and tolerance. *Striga* resistance mechanisms lead to relatively reduced *Striga* infection levels of the host plant (Fig. 2a) while tolerance refers to the ability of the host plant to sustain parasitic infection with reduced negative effects (Fig. 2b; Rodenburg & Bastiaans, 2011). To date, except for nonhost resistance, complete resistance to *Striga* has not been documented, and only partial resistance exists in various hosts (Table 1).

### Preattachment resistance

Preattachment resistance includes all mechanisms that affect *Striga* life-cycle stages until attachment (i.e. parasite seed germination and haustorium formation). Two main types of preattachment resistance mechanisms exist. First, some host crop genotypes produce lower quantities or less active forms of germination stimulants (e.g. strigolactones); this mechanism is referred to as low germination stimulant resistance (LGS) (Hess *et al.*, 1992; Jamil *et al.*, 2011a; Gobena *et al.*, 2017; Mohamed *et al.*, 2018). Another mechanism is the production of lower quantities of HIFs (LHIF) (Rich *et al.*, 2004; Table 1). These mechanisms impair *Striga* germination or attachment to host roots and thereby prevent parasitism. *Striga* endosperm resources can only support seedling growth for 3–7 d after germination and failure to attach and establish a parasitic relation with suitable host plants within that time frame leads to death of the seedlings (Ramaiah *et al.*, 1991; Berner *et al.*, 1995; Runo & Kuria, 2018).

### Postattachment resistance

All resistance mechanisms that intervene after the first contact between the haustorium and a host root are categorized as postattachment resistance. These mechanisms hinder penetration of the haustorium through the root epidermis or they impair the necessary formation of the host xylem-bridge to support successful *Striga* parasitism (Fig. 3). Hypersensitive responses are expressed as necrosis of the host cell at the point of *Striga* attachment (Fig. 3b),



**Fig. 2** Models of *Striga* control using improved cultivars and plant nutrition. (a) Using resistant cultivars will reduce *Striga* infection levels in a crop at any given infestation level. (b) Using tolerant cultivars will not affect *Striga* infection levels but will reduce *Striga*-inflicted relative yield losses of a crop at any given infection level, and fertilizer application will further reduce relative yield loss. (c) Applied in combination, both genetic defence mechanisms relax the relationship between *Striga* soil infestation level and relative crop yield loss. Fertilization is expected to reinforce the effects of inherited resistance and tolerance mechanisms, but more research is needed to expand on preliminary research findings and the translation into an effective and affordable fertilization strategy.

resulting in death of the parasite, as observed in sorghum genotypes Framida and Dobbs (Mohamed *et al.*, 2003). Mechanical barriers in the epidermal region (Kavuluko *et al.*, 2020) or the cortex (Mbuvi *et al.*, 2017) may prevent *Striga* penetration to the endodermal region (Mutuku *et al.*, 2019; Fig. 3c). The barriers can be imposed by deposition of lignin at the interface between *Striga* and its host, as observed in resistant sorghum and rice genotypes (Maiti *et al.*, 1984; Cissoko *et al.*, 2011; Mbuvi *et al.*, 2017; Mutuku *et al.*, 2019; Kavuluko *et al.*, 2020) (Table 1). The *Striga*

haustorium is arrested within the host root tissue before it successfully establishes parasitism due to lignin deposition that acts as a mechanical barrier. However, even when the parasite reaches the endodermis, the parasite can fail to recognize the host xylem and establish a viable vascular connection (Fig. 3d). An incompatibility response impairs further growth and development of *Striga* following attachment as observed in the maize inbred line ZD05 (Gurney *et al.*, 2006; Amusan *et al.*, 2008). The mechanistic background of the incompatibility response is not known yet. Antibiosis involves the transfer of toxic compounds from the host plant to the *Striga* resulting in growth impairment (El Hiweris, 1987). However, what these toxic compounds are and how they impair parasite growth is not yet entirely understood. There is also no conclusive evidence yet that incompatibility response and antibiosis are two distinctly different mechanisms.

## Tolerance

Resistance is always only partial, implying that the likelihood of *Striga* infections can never be entirely excluded. This leads to two major shortcomings of resistance: resistance can break down in a few generations resulting from the high genetic variation within *Striga* populations allowing the development of a population of adapted ecotypes (Unachukwu *et al.*, 2017; Joel *et al.*, 2018; Mutuku *et al.*, 2020); and partially resistant cultivars that become infected by *Striga* can still suffer severe grain yield losses. It is therefore important for a crop genotype to combine resistance with a sufficient degree of tolerance. As shown in Fig. 2(b), host plant tolerance is characterized by mitigated crop yield losses caused by *Striga* infection, and this is shown to be related to the maintenance of functional levels of photosynthesis, Chl fluorescence and stomatal conductance (Gurney *et al.*, 2002; Rodenburg *et al.*, 2008, 2017). Various studies have identified genotypes of host plants with relative tolerance, resulting in relatively low *Striga*-induced impacts on host plant biomass (Fig. 4) and yields (Table 1). The occurrence of resistance and tolerance in a given cultivar is independent, implying that observed resistance in a cultivar does not provide any clue on its level of tolerance (Rodenburg *et al.*, 2006). Tolerance as a stand-alone mechanism is not very useful as it does not reduce *Striga* infection and reproduction rates. Tolerance should therefore be backed up by some level of resistance to reduce the infection level and prevent a parasitic seed bank from building up in the soil (Rodenburg & Bastiaans, 2011). Stacking different resistance mechanisms through breeding could result in cultivars with more durable forms of resistance, and adding a certain level of tolerance to that would result in an additional yield 'safety net' for farmers (Rodenburg & Bastiaans, 2011).

## The role of nutrition in fortifying resistance and tolerance against *Striga*

In the following section, we present the state of the art regarding the role of nutrients in host plant defence against *Striga*. Because this is a rather narrow field of research, we then broaden this overview by presenting knowledge of plant nutrition effects on plant defence

**Table 1** Defence mechanisms (resistance and tolerance) against *Striga* in cereal host species.

Defence mechanism	Host plant species	<i>Striga</i> species	Genotype	Reference(s)
LGS	Sorghum	<i>S. hermonthica</i> , <i>S. asiatica</i>	Framida, 555, IS9830, SRN39	El Hiweris (1987), Haussmann <i>et al.</i> (2000), Gobena <i>et al.</i> (2017)
	Rice	<i>S. hermonthica</i>	Super Basmati, TN-1, Anakila, CG14, NERICA-1	Jamil <i>et al.</i> (2011b, 2012)
LHIF	Wild sorghum	<i>S. asiatica</i>	PQ-434, IS14313, IS18803	Rich <i>et al.</i> (2004)
	Wild maize relative	<i>S. hermonthica</i>	<i>Tripsacum dactyloides</i>	Gurney <i>et al.</i> (2003)
Mechanical barriers	Rice	<i>S. hermonthica</i>	Nipponbare	Mutuku <i>et al.</i> (2019)
	Sorghum	<i>S. hermonthica</i> , <i>S. asiatica</i>	N-13, Framida, IS9830	Maiti <i>et al.</i> (1984), El Hiweris (1987)
	Wild sorghum	<i>S. hermonthica</i>	WSE-1, WSA-1, WSA-2	Mbui <i>et al.</i> (2017)
HR	Sorghum	<i>S. asiatica</i>	Framida, Dobbs	Mohamed <i>et al.</i> (2003)
	Wild sorghum	<i>S. asiatica</i>	P47121	Mohamed <i>et al.</i> (2003)
Antibiosis	Sorghum	<i>S. hermonthica</i>	Framida, IS9830	El Hiweris (1987)
IR	Maize	<i>S. hermonthica</i>	ZD05, KSTP	Amusan <i>et al.</i> (2008), Mutinda <i>et al.</i> (2018)
	Rice	<i>S. hermonthica</i>	Nipponbare, CG14, NERICA-1, NERICA-10	Gurney <i>et al.</i> (2006), Cissoko <i>et al.</i> (2011)
Tolerance	Sorghum	<i>S. hermonthica</i>	Framida, Tiemarifing, Ochuti, IS9830	El Hiweris (1987), Gurney <i>et al.</i> (1995), Van Ast <i>et al.</i> (2000), Rodenburg <i>et al.</i> (2008)
	Maize	<i>S. asiatica</i> <i>S. hermonthica</i>	Staha, SC535, SC527, MQ623 TZEEI 79, 74, Maseno Double Cobber, H511	Gurney <i>et al.</i> (2002), Nyakurwa <i>et al.</i> (2018) Efron (1993), Oswald & Ransom (2004), Badu-Apraku & Oyekunle (2012)
	Rice	<i>S. asiatica</i> , <i>S. hermonthica</i>	Makassa, CG14, ACC102196	Rodenburg <i>et al.</i> (2017)

LGS, low germination stimulant production; LHIF, low haustorium initiation factor production; HR, hypersensitive response; IR, incompatibility response.

responses to other pathogenic infections, resembling *Striga* infections, as well as on plant physiological mechanisms that are affected by *Striga* infection. A last section discusses advances in fertilizer delivery methods that may have relevance for *Striga* control.

## Striga resistance

*Striga* germination and haustorium formation are two steps of the life cycle that can be disrupted by improved host nutrition (Fig. 5 stages I and II). Strigolactones are secreted to foster a symbiotic relationship between the host plant and arbuscular mycorrhizal fungi (AMF) for phosphorus assimilation in poorly fertile soils (Yoneyama *et al.*, 2010). *Striga* capitalizes on this symbiotic relationship by detecting the presence of strigolactones, to induce seed germination. The extent to which host plants produce these compounds is a function of the deficiency of macronutrients (mainly nitrogen (N) and phosphorus (P)) in the soil. Compensating for soil nutrient deficiency by the use of (N and P) fertilizer application has been shown to limit strigolactone exudation, leading to lower *Striga* germination (e.g. Czarnecki *et al.*, 2013; Yoneyama, 2020; Cechin & Press, 1993; Yoneyama *et al.*, 2007; Jamil *et al.*, 2012, 2014). To date, there is limited understanding of the interaction of plant nutrition with other *Striga* germination stimulants (dihydroquinones, sesquiterpene lactones, ethylene) as studies have so far focused on strigolactones. Similarly, there is limited research on the effects of fertilizers on the production of HIFs (Fig. 5 stage II). However, following the recent elucidation of the role of lignin pathway in the synthesis of HIFs (Cui *et al.*, 2018), targeting the phenylpropanoid pathway by specific nutrients (i.e. N, P, potassium (K) and calcium (Ca)) (Eppendorfer & Eggum, 1994;

Entry *et al.*, 1998; Fritz *et al.*, 2006; Teixeira *et al.*, 2006; Wang *et al.*, 2015; Ziegler *et al.*, 2016; Zhang *et al.*, 2017), probably enhances *LHIF* resistance. Moreover, upregulating lignin deposition by improved host nutrition may also benefit mechanical resistance at the root epi- and endodermis levels (Fig. 5 stages III and IV). This would involve targeting overexpression of jasmonic acid (JA), which regulates the lignin biosynthesis pathway (Denese *et al.*, 2011) by improved host nutrition. To date, the hypersensitive response is the most well understood resistance mechanism. The salicylic acid (SA) pathway is involved in this type of response and a few nutrients (i.e. silicon (Si), magnesium (Mg) and P) that potentially enhance this have been identified (Reuveni & Reuveni, 1998; Fauteux, *et al.*, 2006; Imada *et al.*, 2016; Wang *et al.*, 2017). We found only one study that reported a negative effect of fertilizers on the parasite physiology stages beyond establishment of the vascular connection (Igbinnosa *et al.*, 1996) but the actual mechanisms are not yet resolved (Fig. 5 stages V and VI).

## Striga tolerance

Studies have shown that the application of nutrients improves the physiological performance of an infected host plant and alleviates detrimental effects of parasitism. A *Striga* plant siphons nutrients from the host plant by decreasing the host leaf osmotic pressure and maintaining high osmotic pressure at its leaf epidermal cells (Gworgwor & Weber, 1991). *Striga* maintains higher osmotic pressure than its host by having a higher transpiration rate that results in low water potential. This causes the host plant to lower its transpiration rate and osmotic pressure in order to conserve the

## Description

(a)

Susceptible interaction between parasite and host (genotype IS18800). Parasite attaches to the host root, penetrates the endodermis and establishes a xylem–xylem connection.

(b)

The parasite attaches to the host (genotype IS41724) root but experiences a hypersensitive response at the endodermis preventing a xylem–xylem connection.

(c)

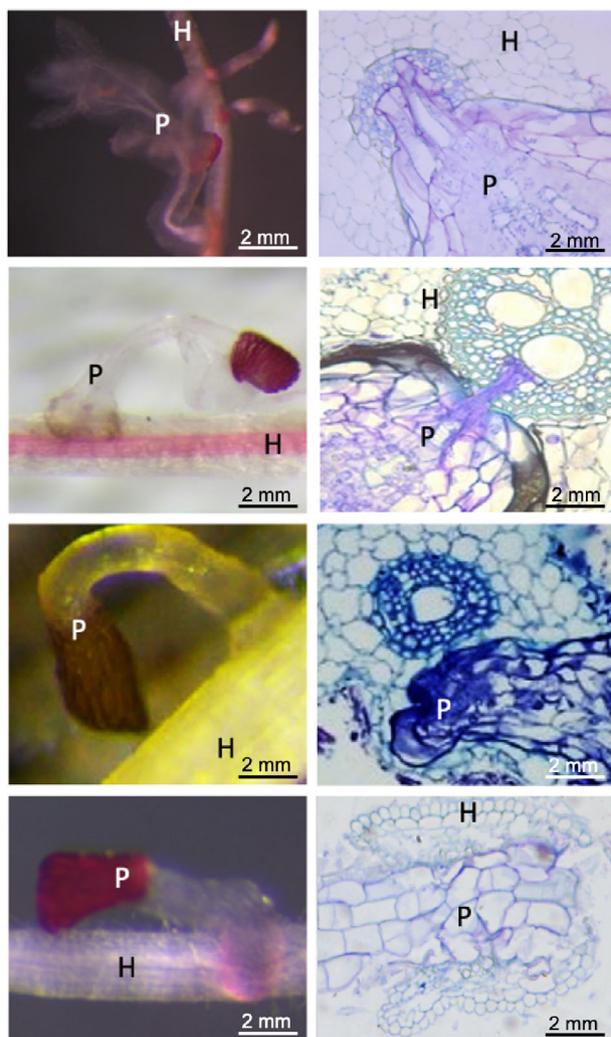
The parasite attaches to the host (maize–sorghum hybrid) root but a mechanical barrier at the cortex prevents penetration into the root endodermis.

(d)

The parasite attaches to the host (genotypes IS9830) root, penetrates cortex and endodermis but fails to recognise the host xylem leading to no parasitism.

## Close-up of attachment

## Section of attachment



**Fig. 3** Close-up and transverse sections of host root (H) – parasite (P) attachments, of the sorghum – *Striga hermonthica* association on day 9 postinfection (photos by SR and IMM) showing a susceptible (a) and three distinctly different resistant phenotypes (b–d). The histological analysis was carried according to Kavuluko *et al.* (2020). Sections of host roots infected with *Striga* were excised, fixed in Carnoy's fixative and stained with 100% safranin for 5 min. The tissues were then destained with choral hydrate ( $2.5 \text{ g ml}^{-1}$ ) for 12 h. The fixed tissues were infiltrated with 100% Technovit and embedded after 3 d. The embedded tissues were mounted onto wooden blocks using a Technovit 3040 kit according to the manufacturer's instructions. The tissues were sectioned using a Leica RM 2145 microtome and the cut sections were stained with 0.1% toluidine blue O dye in 100 mM phosphate buffer for 120 s and rinsed thoroughly with distilled water. The dried slides were covered with coverslips using DePex (BDH, Poole, UK), observed and photographed using a Leica DM100 microscope fitted with a Leica MC190 HD camera.

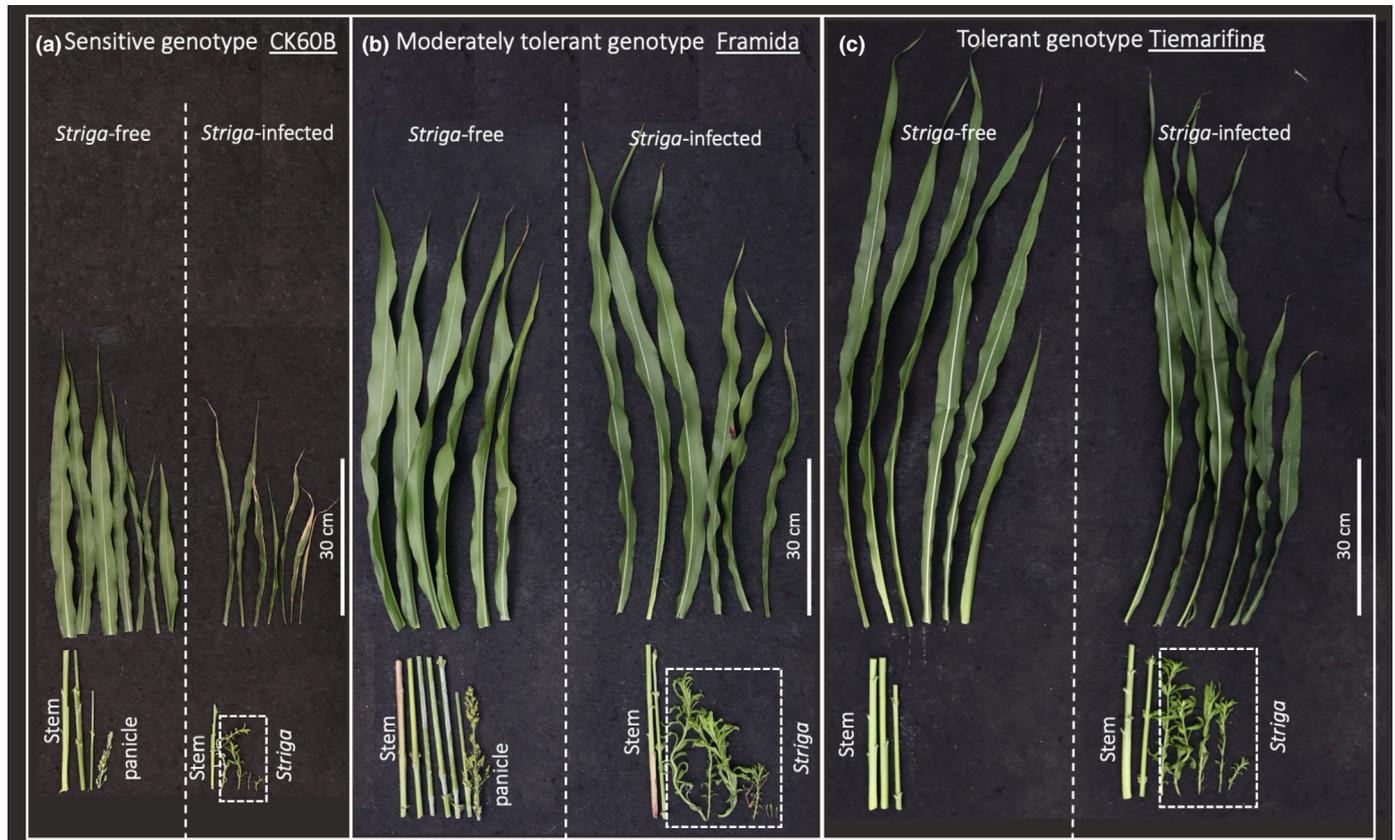
limited water resources (Ackroyd & Graves, 1997). However, at an optimum nitrogen rate this siphoning of nutrients is impaired by a lowering of the osmotic pressure of *Striga* and a simultaneous increase of the osmotic pressure of the host to near-equal values (Gworgwor & Weber, 1991). Another mechanism to facilitate the flow of water and nutrients used by the parasite is reduction of the host plant transpiration rate while maintaining a high transpiration itself (Inoue *et al.*, 2013). The high transpiration rate is positively regulated by an aberrant protein phosphatase ShPP2C1 which enables *Striga* to lose sensitivity to ABA during water stress (Fujioka *et al.*, 2019b). However, fertilizer application increases the transpiration rate of the host plant, resulting in a lower rate of water and nutrient transfer to the parasite. For example, the application of nitrogen fertilizer to pearl millet infected with *S. hermonthica* revealed an increase of the transpiration rate at different levels of infections, indicating increased stomatal conductance and  $\text{CO}_2$  fixation (Fig. 5 stage VII) (Press *et al.*, 1987; Boukar *et al.*, 1996). Potassium, which is present in high concentrations in *Striga* leaves, is another macronutrient that potentially plays an important role in the parasite's acquisition of solutes from the host plant, by its effect

on stomatal conductance via maintaining a high stomatal aperture (Smith & Stewart, 1990; Press *et al.*, 1991).

A combination of nitrogen fertilizer and tolerant sorghum genotypes has been shown to result in higher yield and good agronomic traits (Showemimo *et al.*, 2002). Photosynthesis and underlying processes have been shown to be associated with a *Striga* tolerance phenotype (Rodenburg *et al.*, 2008, 2017). Moreover, *Striga* parasitism depends on the host plant for carbon supply because its own photosynthesis is insufficient (Press & Stewart, 1987; Press *et al.*, 1987). At high foliar applications of nitrogen to host plants infected by *S. hermonthica*, the heterotrophic carbon dependency of *Striga* on the host reduces while the autotrophic carbon fixation of *Striga* increases (Cechin & Press, 1993). As a result, the host plant can use more of its assimilated carbon for its own growth and development.

### Defence mechanisms against other pathogens

To gain more insight into the potential effect of nutrition and fertilizer use on defence against *Striga*, we gathered evidence from



**Fig. 4** Dissected shoots of host plants, and associated parasite (*Striga hermonthica*) load, of three sorghum genotypes demonstrating different levels of *Striga* tolerance at 89 d after sowing (at *Striga* infection levels that were similar based on parasite : host biomass ratio): (a) sensitive genotype CK60B showing severe leaf and stem reductions and no panicle formation due to *Striga* infection; (b) moderately tolerant genotype Framida showing strongly reduced stem lengths, slightly reduced leaf biomass and no (or delayed) panicle formation due to *Striga* infection; (c) tolerant genotype Tiemarifing showing only slightly reduced stem length and leaf biomass due to *Striga* infection.

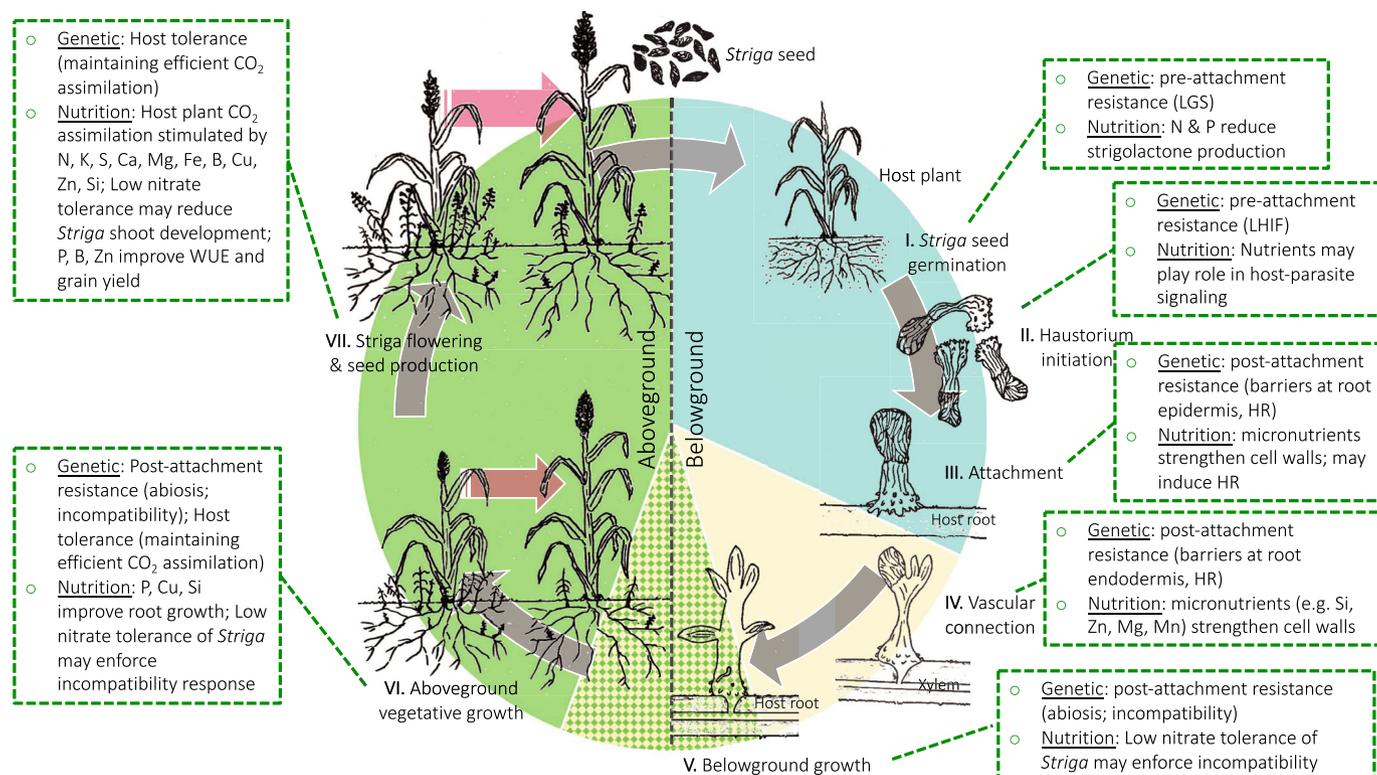
defence mechanisms against other pathogens (e.g. broomrape, nematode, fungal and bacterial infections) that have shown similarities (Heath, 2000; Vieira Dos Santos *et al.*, 2003; Glazebrook, 2005; Kusumoto *et al.*, 2007; Letousey *et al.*, 2007; Hiraoka & Sugimoto, 2008; Swarbrick *et al.*, 2008).

The formation of an haustorium followed by intra- and intercellular penetration to establish vascular connections with the host is observed in other parasitic weeds (e.g. broomrapes; *Orobancha* spp. and *Phelipanche* spp.) and biotrophic fungi (Petre & Kamoun, 2014; Mitsumasu *et al.*, 2015; Kokla & Melnyk, 2018; Goyet *et al.*, 2019). Similar to *Striga*, parasitic nematodes and biotrophic fungi utilize cell wall degradation enzymes to establish successful penetration of the host plants (Mayer, 2006; Mitsumasu *et al.*, 2015). The beneficial effects of nutrients on plant defence responses to biotrophic, hemibiotrophic and necrotrophic pathogens have been demonstrated in both Poaceae and non-Poaceae species (Table 2; Supporting Information Table S1). Nutrients enhance similar defence response pathways in different plant species against a wide array of attacking pathogens. For example, the application of nutrients significantly enhances plant immunity against root and foliar bacterial and fungal pathogens (Ma *et al.*, 2019; Eskandari *et al.*, 2020; Pérez *et al.*, 2020). Other studies in plant pathology have shown that

nutrients play important roles in hypersensitive responses and the formation of mechanical barriers against bacterial and fungal infections (Reuveni & Reuveni, 1998; Imada *et al.*, 2016; Yang *et al.*, 2018). This effect can be positive or negative. Hypersensitive responses could be moderated or aggravated by boron, manganese, copper, nitrogen, phosphorous and potassium (Fig. 5 stage III) (Reuveni & Reuveni, 1998; Reuveni *et al.*, 2000). For example, potassium induced systemic resistance against powdery mildew in cucumber and magnesium against bacterial wilt in tomato (Reuveni *et al.*, 2000; Imada *et al.*, 2016). Similarly, enhanced lignification or formation of phenolic compounds to strengthen cell wall resistance at the root endodermis level could be stimulated by essential nutrients such as zinc, boron and manganese (Fig. 5 stages II and IV) (Dordas, 2009; Eskandari *et al.*, 2020). Identification of key nutrients in mechanical and hypersensitive response pathways holds the potential for developing fertilizers to enhance postattachment *Striga* resistance.

### Plant physiological responses

Nutrients, such as manganese, copper, zinc, iron, magnesium and boron, have proven to play an important role in plant photosynthesis pathways (Dordas, 2009; Dimkpa & Bindraban, 2016; Yang



**Fig. 5** The role of host plant genetics and nutrition in the host–*Striga* interaction. I. *Striga* seed germination: a host plant growing in a poorly fertile soil secretes strigolactones to promote AMF symbiosis for P assimilation but *Striga* seeds perceive strigolactones as germination stimulants. Genetic resistance based on low germination stimulant production (LGS) may reduce the parasite germination rate; similarly, improved host plant nutrition (macronutrients: N and P) reduce strigolactone production and thus germination. II. Haustorium initiation: germinated *Striga* seedlings grow chemotropically towards host roots and perceive haustorium induction factors (HIFs) for haustorium formation, enabling attachment to the host plant roots. Host plant genotypes producing smaller amounts of HIFs exhibit preattachment resistance (called LHIF). III. Attachment: mechanical barriers at the root epidermis or a hypersensitive response (HR) may provide a host plant with postattachment resistance, as it discourages parasite penetration and impairs establishment of parasitism. Micronutrients may stimulate both forms of preattachment resistance. IV. Vascular connection: other forms of postattachment resistance may be exhibited by barriers at the root endodermis, inhibiting establishment of the vascular connection (xylem bridge), or beyond this point by host incompatibility responses or antibiosis (V. Belowground growth). Micronutrients play a role in cell wall strengthening, while host plant nitrate concentrations may impair parasite development. Once the vascular connection is established, in addition to postattachment resistance incompatibility and antibiosis, genetic host plant tolerance becomes an important factor as it contributes to the maintenance of host plant CO<sub>2</sub> assimilation rates. Macro- and micronutrients support healthy host root growth and metabolism. VI. Aboveground vegetative growth: the *Striga* plants then emerge above ground, produce Chl and growth vegetatively. In this stage, host plant tolerance becomes the sole remaining *Striga* defence mechanism. VII. *Striga* flowering and seed production: the parasite produces flowers and eventually seeds. Host plant tolerance and a range of macro- and micronutrients play an important role in host plant performance by maintaining high water use efficiency (WUE) and CO<sub>2</sub> assimilation rates at this stage. *Striga* shoot development may be impaired by nitrogen fertilizer. The *Striga* seeds are dispersed and deposited back to the soil where they form an inoculum for a new parasite cycle. Background colours indicate the host plant defence stage, starting with preattachment resistance (blue), moving to postattachment resistance (yellow and yellow–green) and to tolerance (yellow–green and green). The overlap between the latter two stages is indicated by a yellow background overlaid by green dots. LGS, low germination stimulant; LHIF, low haustorium-inducing factors; HR, hypersensitive response; WUE, water use efficiency.

*et al.*, 2018) and therefore also have the potential to mitigate negative *Striga* effects on host plants (Fig. 5 stage VII).

There is a remarkable correspondence between the physiological symptoms caused by *Striga* infection and the symptoms following drought stress (Ghassemi *et al.*, 2018; Hu *et al.*, 2018). In the absence of an adequate water supply, the leaf stomata close, causing a decrease in the transpiration rate. The reduced transpiration rate causes a shortage of water and nutrients in the shoot and, following the principal of the ‘functional equilibrium’ (Lambers, 1983), the plant allocates a higher quantity of newly produced assimilates to the roots. These assimilates are used for the production of additional root material that might help overcome the relative lack of water and nutrients in the aboveground parts. *Striga* infection

creates identical symptoms. In this case the hormonal regulation of stomatal closure might be regarded as a strategy of the parasite to generate a flow of assimilates towards the root system of the plant, of which the parasite also benefits. Consequently, the nutrients that alleviate drought stress in plants hold the potential for alleviating the drought stress-induced symptoms by *Striga* infection and hence to confer and enhance *Striga* tolerance. In particular, they might help in generating a reduced carbon flow to the roots (Fig. 5 stage VI). Drought stress symptoms of the host plant following *Striga* infection also compromise physiological performances by reducing leaf Chl (*a* and *b*) and Chl content index, and by increasing leaf temperature (Ghassemi *et al.*, 2018). In addition, drought is known to impede the plants’ ability to absorb and transfer nutrients,

**Table 2** The role of nutrients in plant defence mechanisms against pathogenic infections in cereal crops (*Triticum aestivum*, *Triticum durum*, *Triticum turgidum*, *Oryza sativa*, *Zea mays*).

Element	Host species	Pathogen	Mechanism of action	Reference
Nitrogen	<i>T. aestivum</i>	<i>Gaeumannomyces graminis</i>	Reduced infection	Brennan (1992)
	<i>Z. mays</i>	<i>Fusarium graminearum</i>	Decreased disease severity and mycotoxin accumulation	Reid <i>et al.</i> (2001)
		<i>Aspergillus flavus</i>	Reduction in aflatoxin	Payne (1989)
Potassium	<i>T. aestivum</i>	<i>Septoria tritici</i>	Inhibited spore germination	Mann <i>et al.</i> (2004)
		<i>Erysiphe graminis</i> f. sp. <i>tritici</i>	Induces osmotic effect on spore germination	Kettlewell <i>et al.</i> (2000)
Magnesium	<i>O. sativa</i>	<i>Monographella albescens</i>	Alleviated infection and preserved photosynthesis performance	Tatagiba <i>et al.</i> (2016)
Zinc	<i>T. turgidum</i>	<i>Drechslera tritici repentis</i>	Reduced leaf lesions	Simoglou & Dordas (2006)
	<i>T. aestivum</i> / <i>T. durum</i>	<i>Fusarium solani</i>	Improved integrity of cell membrane and lowered oxidative damage	Khoshgoftarmanesh <i>et al.</i> (2010)
Manganese	<i>T. turgidum</i>	<i>Drechslera tritici repentis</i>	Reduced leaf lesions	Simoglou & Dordas (2006)
	<i>T. aestivum</i>	<i>G. graminis</i>	Decreased infection	Brennan (1992)
Boron	<i>T. turgidum</i>	<i>D. tritici-repentis</i>	Reduced leaf lesions	Simoglou & Dordas (2006)
Iron	<i>T. aestivum</i>	<i>Blumeria graminis</i> f. sp. <i>tritici</i>	Mediated oxidative burst	Liu <i>et al.</i> (2007)
Silicon	<i>T. aestivum</i>	<i>B. graminis</i>	Induced active localized cell defences	Belanger <i>et al.</i> (2003)
		<i>Xanthomonas translucens</i> pv. <i>undulosa</i>	Increased tissue lignification	Silva <i>et al.</i> (2010)
	<i>O. sativa</i>	<i>Magnaporthe grisea</i>	Increased cell silicification, lignification and defence-related enzymes	Cai <i>et al.</i> (2008)
		<i>Rhizoctonia solani</i>	Increased activities of defence enzymes	Schurt <i>et al.</i> (2014)

impairing nutrient access (Mahdavi *et al.*, 2020). Various nutrients (i.e. P, N, K, Mg, Zn, Mn, B, Cu, Ca, S and Si) have therefore been shown to be important in alleviating plant drought stress (Tables 3, S2).

### Nutrient delivery techniques

Fertilizer prices vary greatly across SSA. For urea, for instance, prices range from US \$0.8 kg<sup>-1</sup> in Ghana to US \$1.5 kg<sup>-1</sup> in landlocked Burundi (Cedrez *et al.*, 2020). High market prices of fertilizers can render their use unprofitable without subsidies (Therault *et al.*, 2018). Even if fertilizers are affordable, due to the uncertainty of outcomes of fertilizer applications, farmers may still be reluctant to make such investments (Burke *et al.*, 2019). Indeed, farmers in *Striga*-infested areas across Africa often indicate that fertilizers represent a relatively high cost in their farm budgets that they are not always willing to bear (Emechebe *et al.*, 2004; Misiko *et al.*, 2011; Tippe *et al.*, 2017). Because of the smallholder farm context of the *Striga* conundrum, it is imperative to assess and optimize the efficiency and cost effectiveness of delivery techniques when focusing on the application of nutrients to enhance *Striga* resistance and tolerance. Integrating the '4R' nutrient approach, which involves precise targeting at the Right place and Right time with the Right nutrient combination at the Right rate to ensure low costs and high effectiveness of fertilizer application, is recommended (e.g. Mikkelsen, 2011). Improving fertilizer efficacy has indeed been suggested recently as a means to address the persistent low fertilizer use, and concomitant low crop yields, in Africa (Burke *et al.*, 2019). Determination of an efficient delivery strategy is also crucial to minimize loss of nutrients to the environment or unavailability in the soil (Bindraban *et al.*, 2020). For effective use of nutrients for *Striga* control, delivery of nutrients should perhaps be targeted to the (host) plant and not to the soil.

Three techniques (i.e. seed coating, microdosing and foliar application) stand out in their potential for efficiency and cost-effectiveness, making them feasible for adaptation by smallholder farmers for *Striga* control. Complex interactions between the soil and nutrients might reduce availability and impair delivery of nutrients to the host plants, resulting in a limited effect and hence higher dosage requirements when fertilizers are applied directly to the soil (Kihara *et al.*, 2016; Rietra *et al.*, 2017). Seed coating of host plant seeds with nutrients ensures that the emerging radicle has direct contact with nutrients for use during germination. Similarly, microdosing (i.e. application of reduced and more affordable quantities of fertilizer with the seed) may ensure effective delivery of nutrients to the plant and, therefore, increase fertilizer use efficiency and productivity at minimum input quantities (Hayashi *et al.*, 2008; Sebnie *et al.*, 2020). Foliar application of nutrients is another option. Despite the restricted amounts that can be applied and the danger of foliar burn, foliar spraying circumvents the complex antagonistic interactions of soil and nutrients by directly delivering the nutrients to the plant (Oprica *et al.*, 2014; Bindraban *et al.*, 2015). Foliar application has the potential additional advantage of the physical distance between the parasite (at the root level) and the crop canopy where they are applied. Whether this or other delivery methods indeed pay off requires further investigation.

### Conclusions and perspectives

While the potential for combining host plant resistance and tolerance with targeted plant nutrition to enhance *Striga* control is promising, this review has identified several knowledge gaps. There is limited information on the effects of nutrients on preattachment resistance based on a lower production of HIFs, postattachment resistance and tolerance against *Striga*. Moreover, most studies have focused on nitrogen and phosphorus effects on the *Striga*-host

**Table 3** Physiological responses of cereal crops and perennial ryegrass (*Triticum aestivum*, *Zea mays*, *Sorghum bicolor*, *Oryza sativa*, *Lolium perenne*) to nutrients during water stress.

Element	Species	Mechanism of action	Reference
Nitrogen	<i>T. aestivum</i>	Increased photosynthesis and antioxidant defence system	Abid <i>et al.</i> (2016)
		Increased accumulation of osmoprotectants and antioxidant enzyme activities	Shabbir <i>et al.</i> (2016)
		Increased water use efficiency, photosynthetic pigment and antioxidant enzyme activities	Agami <i>et al.</i> (2018)
Potassium	<i>Z. mays</i>	Enhanced photosynthetic capacity	Song <i>et al.</i> (2019)
	<i>S. bicolor</i>	Increased relative water content	Abdelhameid (2019)
Phosphorus	<i>Z. mays</i>	Increased water productivity and reduced susceptibility	Ul-Allah <i>et al.</i> (2020)
	<i>T. aestivum</i>	Increased water potential, Chl content and gas exchange	Wei <i>et al.</i> (2013)
	<i>S. bicolor</i>	Promoted accumulation of proline	Al-Karaki <i>et al.</i> (1996)
Calcium	<i>T. aestivum</i>	Promoted water use efficiency and grain yield	Kang <i>et al.</i> (2014)
	<i>Z. mays</i>	Increased photosynthesis, stomatal conductance, water potential	Naem <i>et al.</i> (2018)
	<i>T. aestivum</i>	Increased growth, photosynthesis and decreased oxidative stress	Sewelam (2017)
Sulphur	<i>O. sativa</i>	Inhibited Chl decline and rise of free proline	Nayek <i>et al.</i> (1983)
Iron	<i>Z. mays</i>	Increased gas exchange and antioxidant enzyme activities	Usmani <i>et al.</i> (2020)
Boron	<i>T. aestivum</i>	Increased photosynthesis and decreased oxidative stress	Adrees <i>et al.</i> (2020)
		Increased photosynthesis and water use efficiency	Karim <i>et al.</i> (2012)
Manganese	<i>T. aestivum</i>	Reduced oxidative stress and increased Chl pigments	Abdel-Motagally & El-Zohri (2018)
		Increased photosynthesis and water use efficiency	Karim <i>et al.</i> (2012)
		Inhibited lipid peroxidation, maintained membrane integrity and delayed senescence	Wang <i>et al.</i> (2010)
Copper	<i>T. aestivum</i>	Promoted elongation of root hairs and lateral root formation	Yang <i>et al.</i> (2018)
		Increased antioxidant activities, relative water content and stabilization of photosynthetic pigments	Taran <i>et al.</i> (2017)
Zinc	<i>Z. mays</i>	Increased antioxidant activities	Cetinkaya <i>et al.</i> (2014)
	<i>T. aestivum</i>	Increased photosynthesis and water use efficiency	Karim <i>et al.</i> (2012)
		Promoted elongation of root hairs and lateral root formation	Yang <i>et al.</i> (2018)
		Increased Chl levels and panicle emergence	Dimkpa <i>et al.</i> (2020)
Silicon	<i>T. aestivum</i>	Increased antioxidant activities, relative water content and stabilization of photosynthetic pigments	Taran <i>et al.</i> (2017)
		Fortified grains, promoted yield and increased plant development	Dimkpa <i>et al.</i> (2019)
		Increased photosynthetic rate, root and shoot biomass and sugar accumulation	Yang <i>et al.</i> (2019)
		Increased antioxidant enzyme activities	Bukhari <i>et al.</i> (2015)
		Increased germination rate, and maintained higher relative water content	Zargar & Agnihotri (2013)
	<i>S. bicolor</i>	Increased shoot and root dry weight and Chl content	Ahmed <i>et al.</i> (2011)

interaction, while overlooking other macro- and micronutrients. While a few functional nutrients have been identified in the SA pathway underlying the hypersensitive response, further determination of the roles of other macro- and micronutrients to enhance this resistance mechanism would be useful. In addition, the mechanisms of the incompatibility response and antibiosis resistance in *Striga* control need to be better understood before informed suggestions on the role of plant nutrients can be made and investigated. This requires the identification of precise physiological and biochemical pathways that can form targets for resistance-enhancing host plant nutrition.

*Striga* tolerance, expressed by host plants that are able to maintain a relatively undisturbed functional equilibrium between shoot and root, can potentially be enhanced by nutrients that strengthen associated traits such as the maintenance of high photosynthesis levels by enhanced stomatal conductance, or the alleviation of drought effects by enhanced water use efficiency or root growth and functioning. However, all this requires much more research.

The combination of some nutrients might also have an antagonistic effect, and thereby weaken the host plant defence. Therefore, once effective nutrients for enhanced resistance and

tolerance are identified, interaction effects (i.e. synergies and antagonisms) and optimal dosages need to be studied to develop effective compositions of fertilizers.

The next step would then be to identify or develop the most effective delivery technique. Foliar spraying of fertilizers could potentially have a more direct effect on leaf photosynthesis and thereby increase *Striga* tolerance, but negative effects on the leaves, such as burning, need to be avoided. Moreover, it is important to further investigate the effectiveness of foliar spray as failures in nutrient transport from the leaves to the rest of the plant have been observed. In addition, the best spraying timings and technique should be established to prevent concomitant and superfluous fertilization of aboveground *Striga* plants. In general, possible fertilizer delivery solutions need to be determined and their feasibility and effectiveness need to be carefully tested.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Table S1** The role of nutrients in plant defence mechanisms against pathogenic infections in noncereal crops (*Malus domestica*, *Cucumis sativa*, *Capsicum annuum*, *Pinus resinosa*, *Solanum lycopersicum*, *Glycine max*, *Citrullus lanatus*, *Solanum melongena*).

**Table S2** Physiological responses of noncereal species (*Helianthus annuus*, *Nicotiana rustica*, *Eucalyptus grandis*, *Phoebe zhenan*, *Nicotiana tabacum*, *Beta vulgaris*, *Arabidopsis thaliana*, *Sesamum indicum*, *Melissa officinalis*, *Solanum lycopersicum*, *Vitis vinifera*, *Gossypium hirsutum*, *Pisum sativum*) to nutrients during water stress.

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