New Phytologist

Review

Research review

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

Authors for correspondence:
Immaculate M. Mwangangi
Email: i.mwangangi@greenwich.ac.uk

Jonne Rodenburg
Email: j.rodenburg@greenwich.ac.uk

Received: *2 December 2020*
Accepted: *7 February 2021*

Immaculate M. Mwangangi[1], Lucie Büchi[1], Stephan M. Haefele[2], Lammert Bastiaans[3], Steven Runo[4] and Jonne Rodenburg[1]

[1]Natural Resources Institute, University of Greenwich, Chatham Maritime, Kent, ME4 4TB, UK; [2]Sustainable Agriculture Sciences Department, Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ, UK; [3]Centre for Crop Systems Analysis, Wageningen University & Research, Wageningen 6700 AK, the Netherlands; [4]Department of Biochemistry, Microbiology and Biotechnology, Kenyatta University, Nairobi 43844-0100, Kenya

New Phytologist (2021)
doi: 10.1111/nph.17271

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

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*.

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 refered 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; Randrianjafizanaka *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 guanycyl) 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 self-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_2 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_2 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

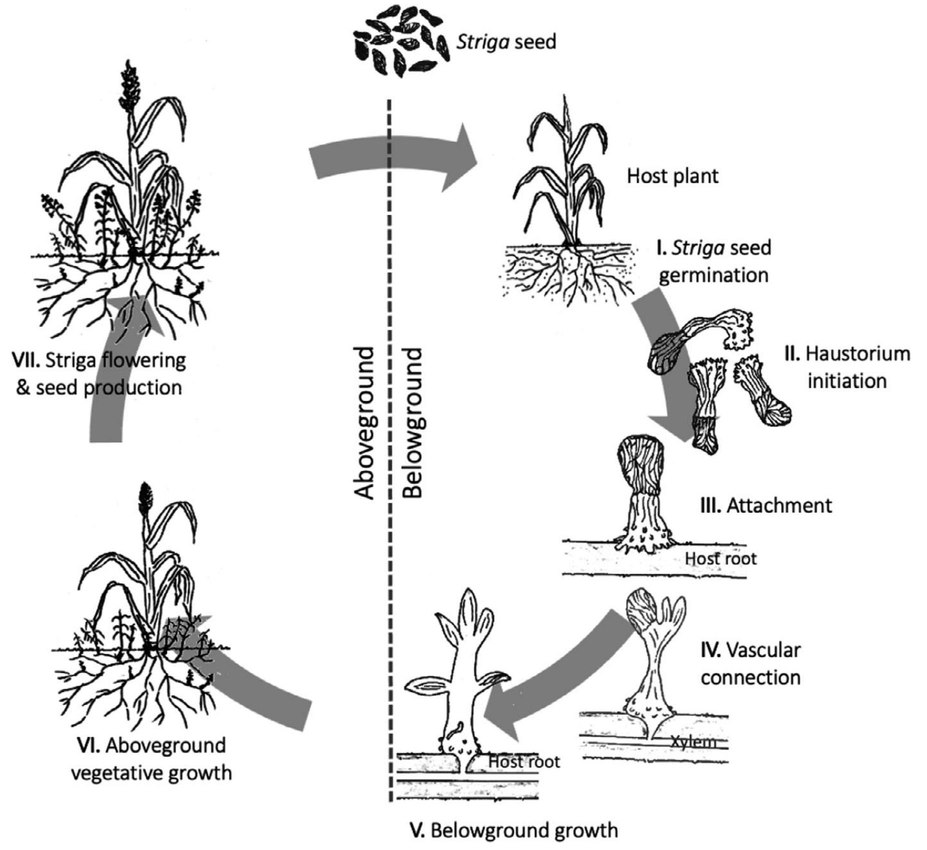


Fig. 1 Life cycle of *Striga*. Clockwise from the top: (I) *Striga* seeds in the soil germinate after a period of preconditioning and upon reception of cues of nearby host presence (exudates derived from the host roots); (II) when the *Striga* radicle is in close proximity of a host root, upon reception 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; Mohemed *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),

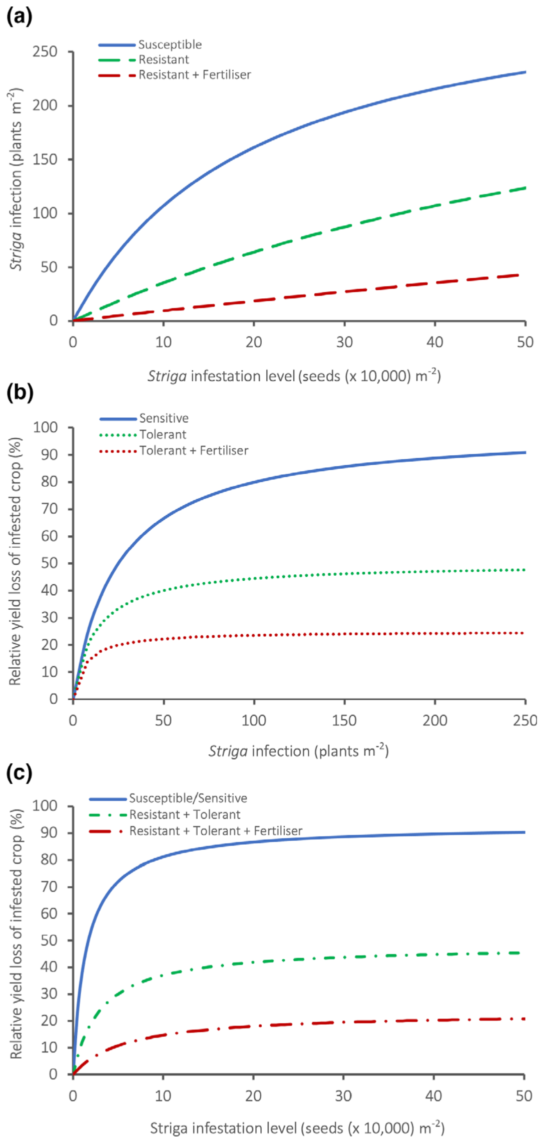


Fig. 2 Models of *Striga* control using improved cultivars and plant nutrition. (a) Using resistant cultivars will reduce *Striga* infection levels in a crop at any given infestation level. (b) Using tolerant cultivars will not affect *Striga* infection levels but will reduce *Striga*-inflicted relative 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	*Striga* species	Genotype	Reference(s)
LGS	Sorghum	*S. hermonthica*, *S. asiatica*	Framida, 555, IS9830, SRN39	El Hiweris (1987), Haussmann *et al*. (2000), Gobena *et al*. (2017)
	Rice	*S. hermonthica*	Super Basmati, TN-1, Anakila, CG14, NERICA-1	Jamil *et al*. (2011b, 2012)
LHIF	Wild sorghum	*S. asiatica*	PQ-434, IS14313, IS18803	Rich *et al*. (2004)
	Wild maize relative	*S. hermonthica*	*Tripsacum dactyloides*	Gurney *et al*. (2003)
Mechanical barriers	Rice	*S. hermonthica*	Nipponbare	Mutuku *et al*. (2019)
	Sorghum	*S. hermonthica*, *S. asiatica*	N-13, Framida, IS9830	Maiti *et al*. (1984), El Hiweris (1987)
	Wild sorghum	*S. hermonthica*	WSE-1, WSA-1, WSA-2	Mbuvi *et al*. (2017)
HR	Sorghum	*S. asiatica*	Framida, Dobbs	Mohamed *et al*. (2003)
	Wild sorghum	*S. asiatica*	P47121	Mohamed *et al*. (2003)
Antibiosis	Sorghum	*S. hermonthica*	Framida, IS9830	El Hiweris (1987)
IR	Maize	*S. hermonthica*	ZD05, KSTP	Amusan *et al*. (2008), Mutinda *et al*. (2018)
	Rice	*S. hermonthica*	Nipponbare, CG14, NERICA-1, NERICA-10	Gurney *et al*. (2006), Cissoko *et al*. (2011)
Tolerance	Sorghum	*S. hermonthica*	Framida, Tiemarifing, Ochuti, IS9830	El Hiweris (1987), Gurney *et al*. (1995), Van Ast *et al*. (2000), Rodenburg *et al*. (2008)
	Maize	*S. asiatica*	Staha, SC535, SC527, MQ623	Gurney *et al*. (2002), Nyakurwa *et al*. (2018)
		S. hermonthica	TZEEI 79, 74, Maseno Double Cobber, H511	Efron (1993), Oswald & Ransom (2004), Badu-Apraku & Oyekunle (2012)
	Rice	*S. asiatica*, *S. hermonthica*	Makassa, CG14, ACC102196	Rodenburg *et al*. (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 phenypropanoid 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 (Dennese *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.

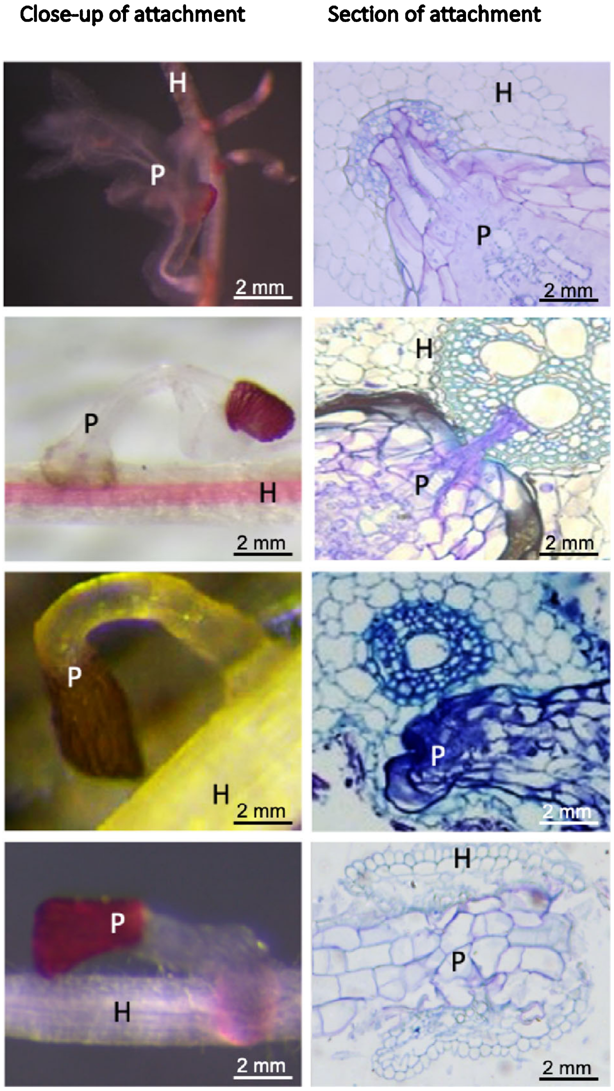


Fig. 3 Close-up and transverse sections of host root (H) – parasite (P) attachments, of the sorghum – *Striga hermonthica* association on day 9 postinfection (photos by SR and IMM) showing a susceptible (a) and three distinctly different resistant phenotypes (b–d). The histological analysis was carried 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 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 thouroughly 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 abberant protein phosphatase ShPP2C1 which enables *Striga* to loose 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 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

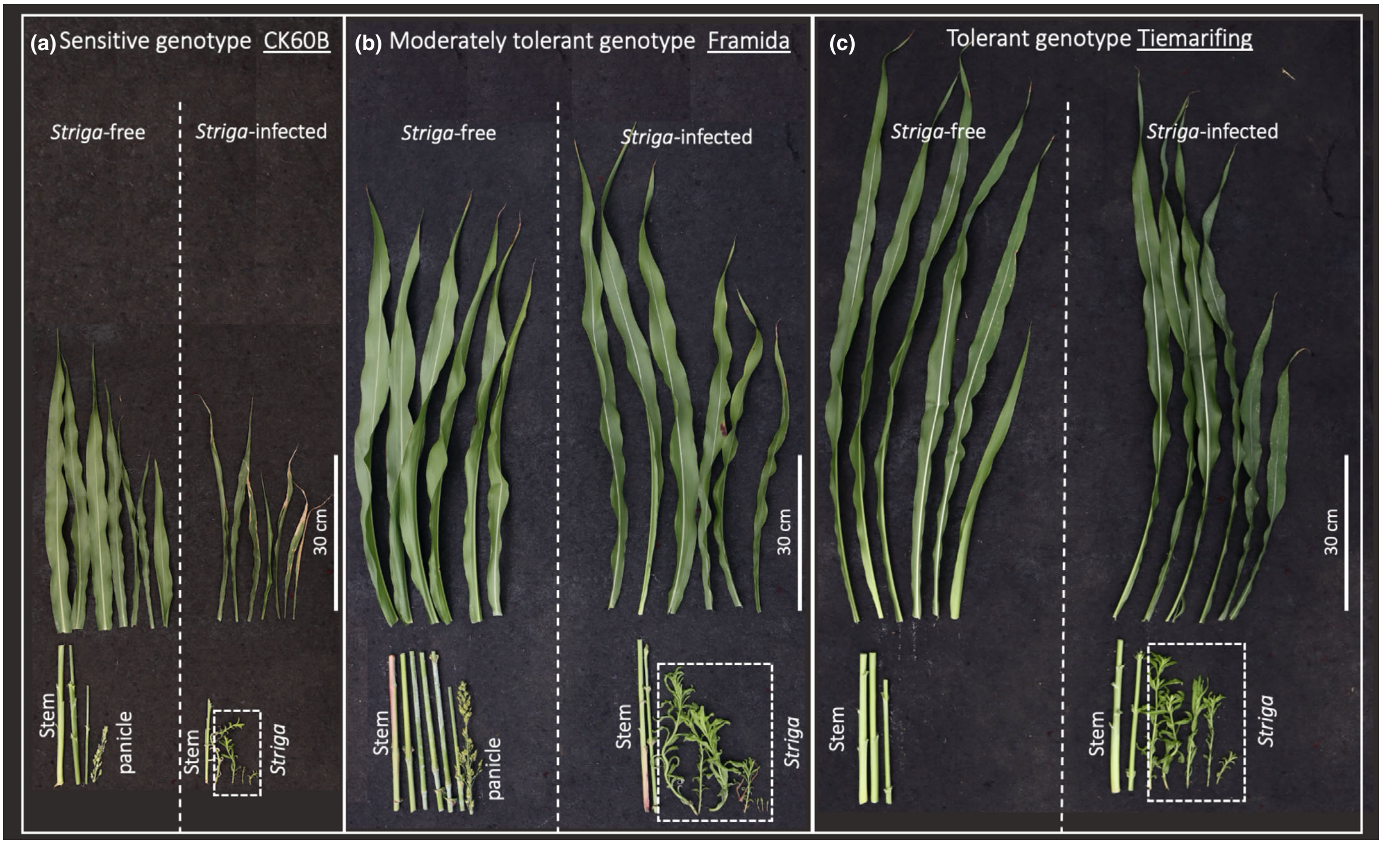


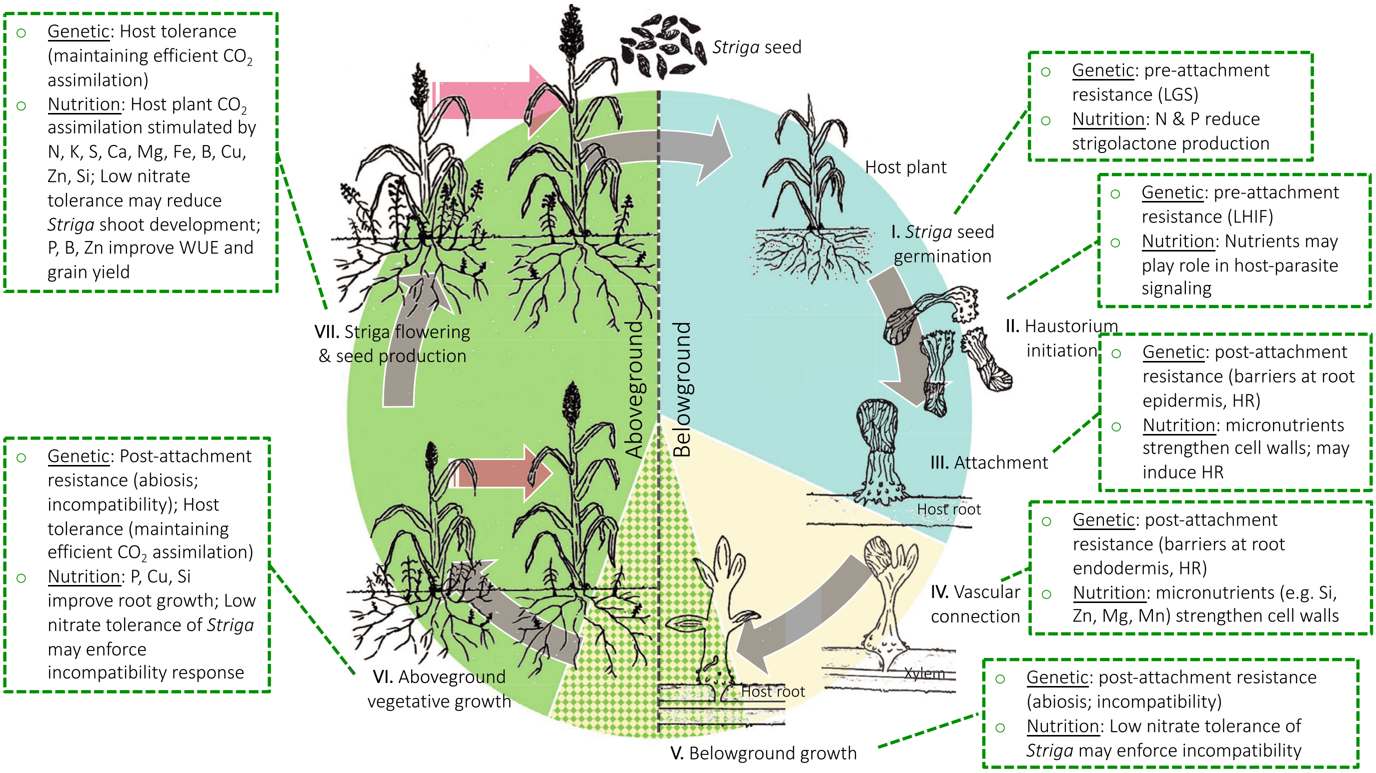
Fig. 4 Dissected shoots of host plants, and associated parasite (*Striga hermonthica*) load, of three sorghum genotypes demonstrating different levels of *Striga* tolerance at 89 d after sowing (at *Striga* infection levels that were similar based on parasite : host biomass ratio): (a) sensitive genotype 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; *Orobanche* 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; Peréz *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



- ○ Genetic: Host tolerance (maintaining efficient CO_2 assimilation)
- ○ Nutrition: Host plant CO_2 assimilation stimulated by N, K, S, Ca, Mg, Fe, B, Cu, Zn, Si; Low nitrate tolerance may reduce *Striga* shoot development; P, B, Zn improve WUE and grain yield

- ○ Genetic: pre-attachment resistance (LGS)
- ○ Nutrition: N & P reduce strigolactone production

- ○ Genetic: pre-attachment resistance (LHIF)
- ○ Nutrition: Nutrients may play role in host-parasite signaling

- ○ Genetic: post-attachment resistance (barriers at root epidermis, HR)
- ○ Nutrition: micronutrients strengthen cell walls; may induce HR

- ○ Genetic: Post-attachment resistance (abiosis; incompatibility); Host tolerance (maintaining efficient CO_2 assimilation)
- ○ Nutrition: P, Cu, Si improve root growth; Low nitrate tolerance of *Striga* may enforce incompatibility response

- ○ Genetic: post-attachment resistance (barriers at root endodermis, HR)
- ○ Nutrition: micronutrients (e.g. Si, Zn, Mg, Mn) strengthen cell walls

- ○ Genetic: post-attachment resistance (abiosis; incompatibility)
- ○ Nutrition: Low nitrate tolerance of *Striga* may enforce incompatibility

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_2 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_2 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 overlayed 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	*T. aestivum*	*Gaeumannomyces graminis*	Reduced infection	Brennan (1992)
	Z. mays	*Fusarium graminearum*	Decreased disease severity and mycotoxin accumulation	Reid *et al*. (2001)
		Aspergillus flavus	Reduction in aflatoxin	Payne (1989)
Potassium	*T. aestivum*	*Septoria tritici*	Inhibited spore germination	Mann *et al*. (2004)
		Erysiphe graminis f. sp. *tritici*	Induces osmotic effect on spore germination	Kettlewell *et al*. (2000)
Magnesium	*O. sativa*	*Monographella albescens*	Alleviated infection and preserved photosynthesis performance	Tatagiba *et al*. (2016)
Zinc	*T. turgidum*	*Drechslera tritici repentis*	Reduced leaf lesions	Simoglou & Dordas (2006)
	T. aestivum/ T. durum	*Fusarium solani*	Improved integrity of cell membrane and lowered oxidative damage	Khoshgoftarmanesh *et al*. (2010)
Manganese	*T. turgidum*	*Drechslera tritici repentis*	Reduced leaf lesions	Simoglou & Dordas (2006)
	T. aestivum	*G. graminis*	Decreased infection	Brennan (1992)
Boron	*T. turgidum*	*D. tritici-repentis*	Reduced leaf lesions	Simoglou & Dordas (2006)
Iron	*T. aestivum*	*Blumeria graminis* f. sp. *tritici*	Mediated oxidative burst	Liu *et al*. (2007)
Silicon	*T. aestivum*	*B. graminis*	Induced active localized cell defences	Belanger *et al*. (2003)
		Xanthomonas translucens pv. undulosa	Increased tissue lignification	Silva *et al*. (2010)
	O. sativa	*Magnaporthe grisea*	Increased cell silicification, lignification and defence-related enzymes	Cai *et al*. (2008)
		Rhizoctonia solani	Increased activities of defence enzymes	Schurt *et al*. (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^{-1} in Ghana to US \$1.5 kg^{-1} in landlocked Burundi (Cedrez *et al.*, 2020). High market prices of fertilizers can render their use unprofitable without subsidies (Theriault *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 optimizite 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	*T. aestivum*	Increased photosynthesis and antioxidant defence system	Abid *et al*. (2016)
		Increased accumulation of osmoprotectants and antioxidant enzyme activities	Shabbir *et al*. (2016)
		Increased water use efficiency, photosynthetic pigment and antioxidant enzyme activities	Agami *et al*. (2018)
	Z. mays	Enhanced photosynthetic capacity	Song *et al*. (2019)
Potassium	*S. bicolor*	Increased relative water content	Abdelhameid (2019)
	Z. mays	Increased water productivity and reduced susceptibility	Ul-Allah *et al*. (2020)
	T. aestivum	Increased water potential, Chl content and gas exchange	Wei *et al*. (2013)
Phosphorus	*S. bicolor*	Promoted accumulation of proline	Al-Karaki *et al*. (1996)
	T. aestivum	Promoted water use efficiency and grain yield	Kang *et al*. (2014)
Calcium	*Z. mays*	Increased photosynthesis, stomatal conductance, water potential	Naeem *et al*. (2018)
	T. aestivum	Increased growth, photosynthesis and decreased oxidative stress	Sewelam (2017)
	O. sativa	Inhibited Chl decline and rise of free proline	Nayek *et al*. (1983)
Sulphur	*Z. mays*	Increased gas exchange and antioxidant enzyme activities	Usmani *et al*. (2020)
Iron	*T. aestivum*	Increased photosynthesis and decreased oxidative stress	Adrees *et al*. (2020)
Boron	*T. aestivum*	Increased photosynthesis and water use efficiency	Karim *et al*. (2012)
		Reduced oxidative stress and increased Chl pigments	Abdel-Motagally & El-Zohri (2018)
Manganese	*T. aestivum*	Increased photosynthesis and water use efficiency	Karim *et al*. (2012)
	L. perenne	Inhibited lipid peroxidation, maintained membrane integrity and delayed senescence	Wang *et al*. (2010)
Copper	*T. aestivum*	Promoted elongation of root hairs and lateral root formation	Yang *et al*. (2018)
		Increased antioxidant activities, relative water content and stabilization of photosynthetic pigments	Taran *et al*. (2017)
	Z. mays	Increased antioxidant activities	Cetinkaya *et al*. (2014)
Zinc	*T. aestivum*	Increased photosynthesis and water use efficiency	Karim *et al*. (2012)
		Promoted elongation of root hairs and lateral root formation	Yang *et al*. (2018)
		Increased Chl levels and panicle emergence	Dimkpa *et al*. (2020)
		Increased antioxidant activities, relative water content and stabilization of photosynthetic pigments	Taran *et al*. (2017)
	S. bicolor	Fortified grains, promoted yield and increased plant development	Dimkpa *et al*. (2019)
Silicon	*O. sativa*	Increased photosynthetic rate, root and shoot biomass and sugar accumulation	Yang *et al*. (2019)
	T. aestivum	Increased antioxidant enzyme activities	Bukhari *et al*. (2015)
	Z. mays	Increased germination rate, and maintained higher relative water content	Zargar & Agnihotri (2013)
	S. bicolor	Increased shoot and root dry weight and Chl content	Ahmed *et al*. (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.

Acknowledgements

This work was funded by the UK Royal Society – GCRF International Collaborations award to JR and SR (Grant CA\R1\191195) and the Research England 'Expanding Excellence in England' (E3)-funded FaNSI programme of the NRI.

ORCID

Lammert Bastiaans https://orcid.org/0000-0002-8465-3003
Lucie Büchi https://orcid.org/0000-0002-1935-6176
Stephan M. Haefele https://orcid.org/0000-0003-0389-8373
Immaculate M. Mwangangi https://orcid.org/0000-0002-6381-2108
Jonne Rodenburg https://orcid.org/0000-0001-9059-9253
Steven Runo https://orcid.org/0000-0002-9043-2338

References

Abdelhameid N. 2019. Effect of mycorrhizal inoculation and potassium fertilization on grain yield and nutrient uptake of sweet sorghum cultivated under water stress in calcareous soil. *Egyptian Journal of Soil Science* **60**: 17–29.

Abdel-Motagally FMF, El-Zohri M. 2018. Improvement of wheat yield grown under drought stress by boron foliar application at different growth stages. *Journal of the Saudi Society of Agricultural Sciences* **17**: 178–185.

Abid M, Tian Z, Ata-Ul-Karim ST, Cui Y, Liu Y, Zahoor R, Jiang D, Dai T. 2016. Nitrogen nutrition improves the potential of wheat (*Triticum aestivum* L.) to alleviate the effects of drought stress during vegetative growth periods. *Frontiers in Plant Science* **7**: 981.

Ackroyd RD, Graves JD. 1997. The regulation of the water potential gradient in the host and parasite relationship between *Sorghum bicolor* and *Striga hermonthica*. *Annals of Botany* **80**: 649–656.

Adrees M, Khan ZS, Ali S, Hafeez M, Khalid S, ur Rehman MZ, Hussain A, Hussain K, Shahid Chatha SA, Rizwan M. 2020. Simultaneous mitigation of cadmium and drought stress in wheat by soil application of iron nanoparticles. *Chemosphere* **238**: 124681.

Agami RA, Alamri SAM, Abd El-Mageed TA, Abousekken MSM, Hashem M. 2018. Role of exogenous nitrogen supply in alleviating the deficit irrigation stress in wheat plants. *Agricultural Water Management* **210**: 261–270.

Ahmed M, Fayyaz-ul-Hassen QU, Aqeel AM. 2011. Silicon application and drought tolerance mechanism of sorghum. *African Journal of Agricultural Research* **6**: 594–607.

Al-Karaki GN, Clark RB, Sullivan CY. 1996. Phosphorus nutrition and water stress effects on proline accumulation in sorghum and bean. *Journal of Plant Physiology* **148**: 745–751.

Amusan IO, Rich PJ, Menkir A, Housley T, Ejeta G. 2008. Resistance to *Striga hermonthica* in a maize inbred line derived from *Zea diploperennis*. *New Phytologist* **178**: 157–166.

Babiker AG, Hamboun AM. 1983. Factors affecting the activity of ethephon in stimulating seed germination of *Striga hermonthica* (Del.) Benth. *Weed Research* **23**: 125–131.

Badu-Apraku B, Oyekunle M. 2012. Genetic analysis of grain yield and other traits of extra-early yellow maize inbreds and hybrid performance under contrasting environments. *Field Crops Research* **129**: 99–110.

Bàrberi P. 2019. Ecological weed management in Sub-Saharan Africa: prospects and implications on other agroecosystem services. In: Sparks DL, ed. *Advances in agronomy*. London, UK: Elsevier Science, 219–264.

Bebawi FF. 1986. Efficacy of ethylene as a germination stimulant of *Striga hermonthica*. *Weed Science Society of America* **34**: 694–698.

Bebawi FF, Eplee RE, Harris CE, Norris RS. 1984. Longevity of witchweed (*Striga asiatica*) seed. *Weed Science* **32**: 494–497.

Bélanger RR, Benhamou N, Menzies JG. 2003. Cytological evidence of an active role of silicon in wheat resistance to powdery mildew (*Blumeria graminis* f. sp. *tritici*). *Phytopathology* **93**: 402–412.

Berner DK, Kling JG, Singh BB. 1995. *Striga* research and control. A perspective from Africa. *Plant Disease* **79**: 652–660.

Bindraban PS, Dimkpa CO, Nagarajan L, Roy A, Rabbinge R. 2015. Revisiting fertilisers and fertilisation strategies for improved nutrient uptake by plants. *Biology and Fertility of Soils* **51**: 897–911.

Bindraban PS, Dimkpa CO, White JC, Franklin FA, Melse-Boonstra A, Koele N, Pandey R, Rodenburg J, Senthilkumar K, Demokritou P *et al.* 2020. Safeguarding human and planetary health demands a fertilizer sector transformation. *Plants, People, Planet* **2**: 302–309.

Boukar I, Hess DE, Payne WA. 1996. Dynamics of moisture, nitrogen, and striga infestation on pearl millet transpiration and growth. *Breeding Oilseed Crops for Sustainable Production: Opportunities and Constraints* **88**: 523–549.

Bouwmeester HJ, Matusova R, Zhongkui S, Beale MH. 2003. Secondary metabolite signalling in host–parasitic plant interactions. *Current Opinion in Plant Biology* **6**: 358–364.

Brennan RF. 1992. The role of manganese and nitrogen nutrition in the susceptibility of wheat plants to take-all in Western Australia. *Fertilizer Research* **31**: 35–41.

Bukhari MA, Ashraf MY, Ahmad R, Waraich EA, Hameed M. 2015. Improving drought tolerance potential in wheat (*Triticuma estivum* L.) through exogenous silicon supply. *Pakistan Journal of Botany* **47**: 1641–1648.

Burke WJ, Frossard E, Kabwe S, Jayne TS. 2019. Understanding fertilizer adoption and effectiveness on maize in Zambia. *Food Policy* **86**: 12.

Cai K, Gao D, Luo S, Zeng R, Yang J, Zhu X. 2008. Physiological and cytological mechanisms of silicon-induced resistance in rice against blast disease. *Physiologia Plantarum* **134**: 324–333.

Cechin I, Press MC. 1993a. Nitrogen relations of the sorghum–*Striga hermonthica* hostparasite association: growth and photosynthesis. *Plant, Cell & Environment* **16**: 237–247.

Cechin I, Press MC. 1993b. Nitrogen relations of the sorghum–*Striga hermonthica* host–parasite association: germination, attachment and early growth. *New Phytologist* **124**: 681–687.

Cedrez CB, Chamberlin J, Guo Z, Hijmans RJ. 2020. Spatial variation in fertilizer prices in Sub-Saharan Africa. *PLoS ONE* **15**: 20.

Cetinkaya H, Seckin DB, Tasci E. 2014. Investigation of comparative regulation on antioxidant enzyme system under copper treatment and drought stress in maize (*Zea mays* L.). *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* **42**: 363–371.

Cissoko M, Boisnard A, Rodenburg J, Press MC, Scholes JD. 2011. New Rice for Africa (NERICA) cultivars exhibit different levels of post-attachment resistance against the parasitic weeds *Striga hermonthica* and *Striga asiatica*. *New Phytologist* **192**: 952–963.

Cui S, Wada S, Tobimatsu Y, Takeda Y, Saucet SB, Takano T, Umezawa T, Shirasu K, Yoshida S. 2018. Host lignin composition affects haustorium induction in the parasitic plants *Phtheirospermum japonicum* and *Striga hermonthica*. *New Phytologist* **218**: 710–723.

Czarnecki O, Yang J, Weston DJ, Tuskan GA, Chen JG. 2013. A dual role of strigolactones in phosphate acquisition and utilization in plants. *International Journal of Molecular Sciences* **14**: 7681–7701.

Denness L, McKenna JF, Segonzac C, Wormit A, Madhou P, Bennett M, Mansfield J, Zipfel C, Hamann T. 2011. Cell wall damage-induced lignin biosynthesis is regulated by a reactive oxygen species- and jasmonic acid-dependent process in arabidopsis. *Plant Physiology* **156**: 1364–1374.

Dimkpa CO, Andrews J, Sanabria J, Bindraban PS, Singh U, Elmer WH, Gardea-Torresdey JL, White JC. 2020. Interactive effects of drought, organic fertilizer, and zinc oxide nanoscale and bulk particles on wheat performance and grain nutrient accumulation. *Science of the Total Environment* **722**: 137808.

Dimkpa CO, Bindraban PS. 2016. Fortification of micronutrients for efficient agronomic production: a review. *Agronomy for Sustainable Development* **36**: 1–26.

Dimkpa CO, Singh U, Bindraban PS, Elmer WH, Gardea-Torresdey JL, White JC. 2019. Zinc oxide nanoparticles alleviate drought-induced alterations in sorghum performance, nutrient acquisition, and grain fortification. *Science of the Total Environment* **688**: 926–934.

Dordas C. 2009. Role of nutrients in controlling plant diseases in sustainable agriculture: a review. *Sustainable Agriculture* **28**: 443–460.

Dörr I. 1997. How *Striga* parasitizes its host: a TEM and SEM study. *Annals of Botany* **79**: 463–472.

Dugje IY, Kamara AY, Omoigui LO. 2006. Infestation of crop fields by *Striga* species in the savanna zones of northeast Nigeria. *Agriculture, Ecosystem & Environment* **116**: 251–254.

Efron Y. 1993. Screening maize for tolerance to *Striga hermonthica*. *Plant Breeding* **110**: 192–200.

El Hiweris SO. 1987. Nature of resistance to *Striga hermonthica* (Del.) Benth. parasitism in some *Sorghum vulgare* (Pers.) cultivars. *Weed Research* **27**: 305–311.

Emechebe AM, Ellis-Jones J, Schulz S, Chikoye D, Douthwaite B, Kureh I, Tarawali G, Hussaini MA, Kormawa P, Sanni A. 2004. Farmers perception of the *Striga* problem and its control in northern Nigeria. *Experimental Agriculture* **40**: 215–232.

Entry JA, Runion GB, Prior SA, Mitchell RJ, Rogers HH. 1998. Influence of CO_2 enrichment and nitrogen fertilization on tissue chemistry and carbon allocation in longleaf pine seedlings. *Plant and Soil* **200**: 3–11.

Eppendorfer WH, Eggum BO. 1994. Effects of sulphur, nitrogen, phosphorus, potassium, and water stress on dietary fibre fractions, starch, amino acids and on the biological value of potato protein. *Plant Foods for Human Nutrition* **45**: 299–313.

Eskandari S, Höfte H, Zhang T. 2020. Foliar manganese spray induces the resistance of cucumber to *Colletotrichum lagenarium*. *Journal of Plant Physiology* **246–247**: 153129.

Fauteux F, Chain F, Belzile F, Menzies JG, Bélanger RR. 2006. The protective role of silicon in the Arabidopsis–powdery mildew pathosystem. *Proceedings of the National Academy of Sciences, USA* **103**: 17554–17559.

Fritz C, Palacios-Rojas N, Feil R, Stitt M. 2006. Regulation of secondary metabolism by the carbon-nitrogen status in tobacco: nitrate inhibits large sectors of phenylpropanoid metabolism. *The Plant Journal* **46**: 533–548.

Frost DL, Gurney AL, Press MC, Scholes JD. 1997. *Striga hermonthica* reduces photosynthesis in sorghum : the importance of stomatai limitations and a potentiai role for ABA? *Plant, Cell & Environment* **20**: 483–492.

Fujioka H, Samejima H, Suzuki H, Mizutani M, Okamoto M, Sugimoto Y. 2019a. Aberrant protein phosphatase 2C leads to abscisic acid insensitivity and high transpiration in parasitic *Striga*. *Nature Plants* **5**: 258–262.

Fujioka H, Samejima H, Mizutani M, Okamoto M, Fujioka H, Samejima H, Mizutani M, Okamoto M. 2019b. How does *Striga hermonthica* bewitch its hosts? *Plant Signaling & Behavior* **14**: 1–2.

Ghassemi S, Farhangi-Abriz S, Faegi-Analou R, Ghorbanpour M, Lajayer BA. 2018. Monitoring cell energy, physiological functions and grain yield in field-grown mung bean exposed to exogenously applied polyamines under drought stress. *Journal of Soil Science and Plant Nutrition* **18**: 1108–1125.

Glazebrook J. 2005. Contrasting mechanisms of defense against biotrophic and necrotrophic pathogens. *Annual Review of Phytopathology* **43**: 205–227.

Gobena D, Shimels M, Rich PJ, Ruyter-Spira C, Bouwmeester H, Kanuganti S, Mengiste T, Ejeta G. 2017. Mutation in sorghum *LOW GERMINATION STIMULANT 1* alters strigolactones and causes *Striga* resistance. *Proceedings of the National Academy of Sciences, USA* **114**: 4471–4476.

Goyet V, Wada S, Cui S, Wakatake T, Shirasu K, Montiel G, Simier P, Yoshida S. 2019. Haustorium inducing factors for parasitic orobanchaceae. *Frontiers in Plant Science* **10**: 1056.

Graves JD, Wylde A, Press MC, Stewart GR. 1990. Growth and carbon allocation in *Pennisetum typhoides* infected with the parasitic angiosperm *Striga hermonthica*. *Plant, Cell & Environment* **13**: 367–373.

Gressel J, Hanafi A, Head G, Marasas W, Obilana B, Ochanda J, Souissi T, Tzotzos G. 2004. Major heretofore intractable biotic constraints to African food security that may be amenable to novel biotechnological solutions. *Crop Protection* **23**: 661–689.

Gurney AL, Grimanelli, D, Kanampiu, F, Hoisington, D, Scholes, JD & Press, MC. 2003. Novel sources of resistance to *Striga hermonthica* in *Tripsacum dactyloides*, a wild relative of maize. *New Phytologist* **160**: 557–568.

Gurney AL, Press MC, Ransom JK. 1995. The parasitic angiosperm *Striga hermonthica* can reduce photosynthesis of its sorghum and maize hosts in the field. *Journal of Experimental Botany* **46**: 1817–1823.

Gurney AL, Press MC, Scholes JD. 1999. Infection time and density influence the response of sorghum to the parasitic angiosperm *Striga hermonthica*. *New Phytologist* **143**: 573–580.

Gurney AL, Slate J, Press MC, Scholes JD. 2006. A novel form of resistance in rice to the angiosperm parasite *Striga hermonthica*. *New Phytologist* **169**: 199–208.

Gurney AL, Taylor A, Mbwaga A, Scholes JD, Press MC. 2002. Do maize cultivars demonstrate tolerance to the parasitic weed *Striga asiatica*? *Weed Research* **42**: 299–306.

Gworgwor NA, Weber HC. 1991. Effect of N-application on Sorghum growth, *Striga* infestation and the osmotic pressure of the parasite in relation to the host. *Journal of Plant Physiology* **139**: 194–198.

Haussmann BIG, Hess DE, Reddy BVS, Welz HG, Geiger HH. 2000. Analysis of resistance to *Striga hermonthica* in diallel crosses of sorghum. *Euphytica* **116**: 33–40.

Hayashi K, Abdoulaye T, Gerard B, Bationo A. 2008. Evaluation of application timing in fertilizer micro-dosing technology on millet production in Niger, West Africa. *Nutrient Cycling in Agroecosystems* **8**: 257–265.

Hearne SJ. 2009. Control – the *Striga* conundrum. *Pest Management Science* **65**: 603–614.

Heath MC. 2000. Hypersensitive response-related death. *Plant Molecular Biology* **44**: 321–334.

Hess DE, Ejeta G, Butler LG. 1992. Selecting sorghum genotypes expressing a quantitative biosynthetic trait that confers resistance to *Striga*. *Phytochemistry* **31**: 493–497.

Hiraoka Y, Sugimoto Y. 2008. Molecular responses of sorghum to purple witchweed (*Striga hermonthica*) parasitism. *Weed Science* **56**: 356–363.

Hood ME, Condon JM, Timko MP, Riopel JL. 1997. Primary haustorial development of *Striga asiatica* on host and nonhost species. *American Phytopathological Society* **88**: 70–75.

Hu W, Tian SB, Di Q, Duan SH, Dai K. 2018. Effects of exogenous calcium on mesophyll cell ultrastructure, gas exchange, and photosystem II in tobacco (*Nicotiana tabacum* Linn.) under drought stress. *Photosynthetica* **56**: 1204–1211.

Igbinnosa I, Cardwell KF, Okonkwo SNC. 1996. The effect of nitrogen on the growth and development of giant witchweed, *Striga hermonthica* Benth. Effect on cultured germinated seedlings in host absence. *European Journal of Plant Pathology* **102**: 77–86.

Imada K, Sakai S, Kajihara H, Tanaka S, Ito S. 2016. Magnesium oxide nanoparticles induce systemic resistance in tomato against bacterial wilt disease. *Plant Pathology* **65**: 551–560.

Inoue T, Yamauchi Y, Eltayeb AH, Samejima H, Babiker AGT, Sugimoto Y. 2013. Gas exchange of root hemi-parasite *Striga hermonthica* and its host *Sorghum bicolor* under short-term soil water stress. *Biologia Plantarum* **57**: 773–777.

Jamil M, Charnikhova T, Cardoso C, Jamil T, Ueno K, Verstappen F, Asami T, Bouwmeester HJ. 2011a. Quantification of the relationship between strigolactones and *Striga hermonthica* infection in rice under varying levels of nitrogen and phosphorus. *Weed Research* **51**: 373–385.

Jamil M, Charnikhova T, Houshyani B, Van Ast A, Bouwmeester HJ. 2012. Genetic variation in strigolactone production and tillering in rice and its effect on *Striga hermonthica* infection. *Planta* **235**: 473–484.

Jamil M, Charnikhova T, Verstappen F, Ali Z, Wainwright H, Bouwmeester HJ. 2014. Effect of phosphate-based seed priming on strigolactone production and *Striga hermonthica* infection in cereals. *Weed Research* **54**: 307–313.

Jamil M, Rodenburg J, Charnikhova T, Bouwmeester HJ. 2011b. Pre-attachment *Striga hermonthica* resistance of New Rice for Africa (NERICA) cultivars based on low strigolactone production. *New Phytologist* **192**: 964–975.

Joel KA, Runo S, Muchugi A. 2018. Genetic diversity and virulence of *Striga hermonthica* from Kenya and Uganda on selected sorghum varieties. *Nusantara Bioscience* **10**: 111–120.

Kang L, Yue S, Li S. 2014. Effects of phosphorus application in different soil layers on root growth, yield, and water-use efficiency of winter wheat grown under semi-arid conditions. *Journal of Integrative Agriculture* **13**: 2028–2039.

Karim MR, Zhang YQ, Zhao RR, Chen XP, Zhang FS, Zou CQ. 2012. Alleviation of drought stress in winter wheat by late foliar application of zinc, boron, and manganese. *Journal of Plant Nutrition and Soil Science* **175**: 142–151.

Kavuluko J, Kibe M, Sugut I, Kibet W, Masanga J, Mutinda S, Wamalwa M, Magomere T, Odeny D, Runo S. 2020. GWAS provides biological insights into mechanisms of the parasitic plant (*Striga*) resistance in Sorghum. *BMC Plant Biology*. doi: 10.21203/rs.3.rs-54024/v1.

Kettlewell PS, Cook JW, Parry DW. 2000. Evidence for an osmotic mechanism in the control of powdery mildew disease of wheat by foliar-applied potassium chloride. *European Journal of Plant Pathology* **106**: 297–300.

Khan Z, Midega C, Hassanali A, Pickett J, Wadhams L. 2007. Assessment of different legumes for the control of *Striga hermonthica* in maize and sorghum. *Crop Science* **47**: 730–734.

Khoshgoftarmanesh AH, Kabiri S, Shariatmadari H, Sharifnabi B, Schulin R. 2010. Zinc nutrition effect on the tolerance of wheat genotypes to Fusarium root-rot disease in a solution culture experiment. *Soil Science and Plant Nutrition* **56**: 234–243.

Kihara J, Nziguheba G, Zingore S, Coulibaly A, Esilaba A, Kabambe V, Njoroge S, Palm C, Huising J. 2016. Understanding variability in crop response to fertilizer and amendments in sub-Saharan Africa. *Agriculture, Ecosystems and Environment* **229**: 1–12.

Kim H Il, Xie X, Kim HS, Chun JC, Yoneyama K, Nomura T, Takeuchi Y, Yoneyama K. 2010. Structure–activity relationship of naturally occurring strigolactones in *Orobanche minor* seed germination stimulation. *Journal of Pesticide Science* **35**: 344–347.

Kokla A, Melnyk CW. 2018. Developing a thief: haustoria formation in parasitic plants. *Developmental Biology* **442**: 53–59.

Kusumoto D, Goldwasser Y, Xie X, Yoneyama K, Takeuchi Y, Yoneyama K. 2007. Resistance of red clover (*Trifolium pratense*) to the root parasitic plant *Orobanche minor* is activated by salicylate but not by jasmonate. *Annals of Botany* **100**: 537–544.

Lambers H. 1983. "The functional equilibrium", nibbling on the edges of a paradigm. *Netherlands Journal of Agricultural Science* **31**: 305–311.

Letousey P, De Zélicourt A, Vieira Dos Santos C, Thoiron S, Monteau F, Simier P, Thalouarn P, Delavault P. 2007. Molecular analysis of resistance mechanisms to *Orobanche cumana* in sunflower. *Plant Pathology* **56**: 536–546.

Liu G, Greenshields DL, Sammynaiken R, Hirji RN, Selvaraj G, Wei Y. 2007. Targeted alterations in iron homeostasis underlie plant defense responses. *Journal of Cell Science* **120**: 596–605.

Ma C, Borgatta J, De La Torre-Roche R, Zuverza-Mena N, White JC, Hamers RJ, Elmer WH. 2019. Time-dependent transcriptional response of tomato (*Solanum lycopersicum* L.) to Cu nanoparticle exposure upon infection with *Fusarium oxysporum* f. sp. *lycopersici*. *ACS Sustainable Chemistry and Engineering* **7**: 10064–10074.

Mahdavi KA, Masoud SJ, Amini DM, Rezvan S, Damavandi A. 2020. Sesame (*Sesame indicum* L.) biochemical and physiological responses as affected by applying chemical, biological, and nano-fertilizers in field water stress conditions. *Journal of Plant Nutrition* **43**: 456–475.

Maiti RK, Ramaiah KV, Bisen SS, Chidley VL. 1984. A comparative study of the haustorial development of *Striga asiatica* (L.) Kuntze on sorghum cultivars. *Annals of Botany* **54**: 447–457.

Mann RL, Kettlewell PS, Jenkinson P. 2004. Effect of foliar-applied potassium chloride on septoria leaf blotch of winter wheat. *Plant Pathology* **53**: 653–659.

Mayer AM. 2006. Pathogenesis by fungi and by parasitic plants: similarities and differences. *Phytoparasitica* **34**: 3–16.

Mbuvi DA, Masiga CW, Kuria E, Masanga J, Wamalwa M, Mohame A, Odeny DA, Hamza N, Timko MP, Runo S. 2017. Novel sources of witchweed (*Striga*) resistance from wild sorghum accessions. *Frontiers in Plant Science* **8**: 116.

Mikkelsen RL. 2011. The "4R" nutrient stewardship framework for horticulture. *Horttechnology* **21**: 658–662.

Misiko M, Tittonell P, Giller KE, Richards P. 2011. Strengthening understanding and perceptions of mineral fertilizer use among smallholder farmers: evidence from collective trials in western Kenya. *Agriculture and Human Values* **28**: 27–38.

Mitsumasu K, Seto Y, Yoshida S. 2015. Apoplastic interactions between plants and plant root intruders. *Frontiers in Plant Science* **6**: 1–17.

Mohamed A, Ellicott A, Housley TL, Ejeta G. 2003. Hypersensitive response to *Striga* infection in sorghum. *Crop Science* **43**: 1320–1324.

Mohamed KI, Musselman LJ, Riches CR, Mohamed KI, John L, Riches CR. 2001. The genus *Striga* (Scrophulariaceae) in Africa. *Annals of the Missouri Botanical Garden* **88**: 60–103.

Mohemed N, Charnikhova T, Fradin EF, Rienstra J, Babiker AGT, Bouwmeester HJ. 2018. Genetic variation in *Sorghum bicolor* strigolactones and their role in resistance against *Striga hermonthica*. *Journal of Experimental Botany* **69**: 2415–2430.

Mutinda SM, Masanga J, Mutuku JM, Runo S, Alakonya A. 2018. KSTP 94, an open-pollinated maize variety has postattachment resistance to purple witchweed (*Striga hermonthica*). *Weed Science* **66**: 525–529.

Mutuku JM, Cui S, Hori C, Takeda Y, Tobimatsu Y, Nakabayashi R, Mori T, Saito K, Demura T, Umezawa T *et al.* 2019. The structural integrity of lignin is crucial for resistance against *Striga hermonthica* parasitism in rice. *Plant Physiology* **179**: 1796-1809.

Mutuku JM, Cui S, Yoshida S. 2020. Orobanchaceae parasite–host interactions. *New Phytologist* **2001**: 3–29.

Naeem M, Naeem MS, Ahmad R, Ihsan MZ, Ashraf MY, Hussain Y, Fahad S. 2018. Foliar calcium spray confers drought stress tolerance in maize via modulation of plant growth, water relations, proline content and hydrogen peroxide activity. *Archives of Agronomy and Soil Science* **64**: 116–131.

Nayek B, Biswas AK, Choudhuri MA. 1983. Effect of calcium on water-stress-induced biochemical changes and yield of field-grown rice. *Biologia Plantarum* **25**: 117–123.

Nyakurwa CS, Gasura E, Setimela PS, Mabasa S, Rugare JT, Mutsvanga S. 2018. Reaction of new quality protein maize genotypes to *Striga asiatica*. *Crop Science* **58**: 1201–1218.

Oprica I, Mihai CT, Lungip M, Badea IA. 2014. A new eco-friendly foliar fertilizer with bone glue suitable for crops of maize and sunflower. *Revista de Chimie* **65**: 1–7.

Oswald A. 2005. *Striga* control-technologies and their dissemination. *Crop Protection* **24**: 333–342.

Oswald A, Ransom JK. 2004. Response of maize varieties to *Striga* infestation. *Crop Protection* **23**: 89–94.

Parker C. 2009. Observations on the current status of orobanche and *Striga* problems worldwide. *Pest Management Science* **65**: 453–459.

Payne GA. 1989. Increased aflatoxin contamination in nitrogen-stressed corn. *Plant Disease* **73**: 556.

Peréz CDP, De La To RR, Zuverza-Mena N, Ma C, Shen Y, White JC, Pozza EA, Pozza AAA, Elmer WH. 2020. Metalloid and metal oxide nanoparticles suppress sudden death syndrome of soybean. *Journal of Agricultural and Food Chemistry* **68**: 177–187.

Petre B, Kamoun S. 2014. How do filamentous pathogens deliver effector proteins into plant cells? *PLoS Biology* **12**: 2.

Press MC, Smith S, Stewart GR. 1991. Carbon acquisition and assimilation in parasitic plants. *Functional Ecology* **5**: 278–283.

Press MC, Stewart GR. 1987. Growth and photosynthesis in *Sorghum bicolor* infected with *Striga hermonthica*. *Annals of Botany* **60**: 657–662.

Press MC, Tuohy JM, Stewart GR. 1987. Gas exchange characteristics of the sorghum–*Striga* host–parasite association. *Plant Physiology* **84**: 814–819.

Ramaiah KV, Chidley VL, House LR. 1991. A time-course study of early establishment stages of parasitic angiosperm *Striga asiatica* on susceptible sorghum roots. *Annals of Applied Biology* **118**: 403–410.

Randrianjafizanaka MT, Autfray P, Andrianaivo AP, Ramonta IR, Rodenburg J. 2018. Combined effects of cover crops, mulch, zero-tillage and resistant varieties on *Striga asiatica* (L.) Kuntze in rice–maize rotation systems. *Agriculture, Ecosystems and Environment* **256**: 23–33.

Rank C, Rasmussen LS, Jensen SR, Pierce S, Press MC, Scholes JD. 2004. Cytotoxic constituents of *Alectra* and *Striga* species. *Weed Research* **44**: 265–270.

Reda F, Verkleij J, Ernst W. 2005. Intercropping for the improvement of sorghum yield, soil fertility and *Striga* control in the subsistence agriculture region of tigray (Northern Ethiopia). *Journal of Agronomy and Crop Science* **191**: 10–19.

Reid LM, Zhu X, Ma BL. 2001. Crop rotation and nitrogen effects on maize susceptibility to gibberella (*Fusarium graminearum*) ear rot. *Plant and Soil* **237**: 1–14.

Reuveni R, Dor G, Raviv M, Reuveni M, Tuzun S. 2000. Systemic resistance against *Sphaerotheca fuliginea* in cucumber plants exposed to phosphate in hydroponics system, and its control by foliar spray of mono-potassium phosphate. *Crop Protection* **19**: 355–361.

Reuveni R, Reuveni M. 1998. Local and systemic control of powdery mildew (*Leveillula taurica*) on pepper plants by foliar spray of mono-potassium phosphate. *Scientia Agricola* **17**: 703–709.

Reuveni R, Reuveni M. 1998. Foliar-fertilizer therapy – a concept in integrated pest management. *Crop Protection* **17**: 111–118.

Rich PJ, Grenier C, Ejeta G. 2004. *Striga* resistance in the wild relatives of sorghum. *Crop Science* **44**: 2221–2229.

Rietra RPJ, Heinen M, Dimkpa CO, Bindraban PS. 2017. Effects of nutrient antagonism and synergism on yield and fertilizer use efficiency. *Communications in Soil Science and Plant Analysis* **48**: 1895–1920.

Rodenburg J, Bastiaans L, Kropff MJ. 2006. Characterization of host tolerance to *Striga hermonthica*. *Euphytica* **147**: 353–365.

Rodenburg J, Bastiaans L, Schapendonk AHCM, Van Der Putten PEL, Van Ast A, Dingemanse NJ, Haussmann BIG. 2008. CO_2-assimilation and chlorophyll fluorescence as indirect selection criteria for host tolerance against *Striga*. *Euphytica* **160**: 75–87.

Rodenburg J, Bastiaans L. 2011. Host-plant defence against *Striga* spp.: reconsidering the role of tolerance. *Weed Research* **51**: 438–441.

Rodenburg J, Cissoko M, Kayongo N, Dieng I, Bisikwa J, Irakiza R, Masoka I, Midega CAO, Scholes JD. 2017. Genetic variation and host–parasite specificity of *Striga* resistance and tolerance in rice: the need for predictive breeding. *New Phytologist* **21**: 1267–1280.

Rodenburg J, Demont M, Zwart SJ, Bastiaans L. 2016. Agriculture, ecosystems and environment parasitic weed incidence and related economic losses in rice in Africa. *Agriculture, Ecosystems and Environment* **235**: 306–317.

Rodenburg J, Riches CR, Kayeke JM. 2010. Addressing current and future problems of parasitic weeds in rice. *Crop Protection* **29**: 210–221.

Runo S, Kuria EK. 2018. Habits of a highly successful cereal killer, *Striga. PLoS Pathology* **14**: 2–7.

Schurt DA, Cruz MFA, Nascimento KJT, Filippi MCC, Rodrigues FA. 2014. Silicon potentiates the activities of defense enzymes in the leaf sheaths of rice plants infected by *Rhizoctonia solani. Tropical Plant Pathology* **39**: 457–463.

Sebnie W, Mengesha M, Girmay G, Feyisa T, Asgedom B, Beza G, Dejene D. 2020. Evaluation of micro-dosing fertilizer application on sorghum (*Sorghum bicholor* L) production at Wag-Lasta Areas of Amhara Region, Ethiopia. *Scientific Reports* **10**: 6–11.

Sewelam N. 2017. Study of the interactive effects of calcium and abscisic acid on drought stressed *Triticum aestivum* seedlings. *Egyptian Journal of Botany* **57**: 215–232.

Shabbir RN, Waraich EA, Ali H, Nawaz F, Ashraf MY, Ahmad R, Awan MI, Ahmad S, Irfan M, Hussain S *et al.* 2016. Supplemental exogenous NPK application alters biochemical processes to improve yield and drought tolerance in wheat (*Triticum aestivum* L.). *Environmental Science and Pollution Research* **23**: 2651–2662.

Shah N, Smirnoff N, Stewart GR. 1987. Photosynthesis and stomatal characteristics of *Striga hermonthica* in relation to its parasitic habit. *Physiologia Plantarum* **69**: 699–703.

Showemimo FA, Kimbeng CA, Alabi SO. 2002. Genotypic response of sorghum cultivars to nitrogen fertilization in the control of *Striga hermonthica. Crop Protection* **21**: 867–870.

Silva IT, Rodrigues FÁ, Oliveira JR, Pereira SC, Andrade CCL, Silveira PR, Conceição MM. 2010. Wheat resistance to bacterial leaf streak mediated by silicon. *Journal of Phytopathology* **158**: 253–262.

Simoglou KB, Dordas C. 2006. Effect of foliar applied boron, manganese and zinc on tan spot in winter durum wheat. *Crop Protection* **25**: 657–663.

Smith S, Stewart GR. 1990. Effect of potassium levels on the stomatal behavior of the hemi-parasite *Striga hermonthica. Plant Physiology* **94**: 1472–1476.

Song Y, Li J, Liu M, Meng Z, Liu K, Sui N. 2019. Nitrogen increases drought tolerance in maize seedlings. *Functional Plant Biology* **46**: 350–359.

Spallek T, Mutuku M, Shirasu K. 2013. Pathogen profile. The genus *Striga*: a witch profile. *Molecular Plant Pathology* **14**: 861–869.

Swarbrick PJ, Huang K, Liu G, Slate J, Press MC, Scholes JD. 2008. Global patterns of gene expression in rice cultivars undergoing a susceptible or resistant interaction with the parasitic plant *Striga hermonthica. New Phytologist* **179**: 515–529.

Taran N, Storozhenko V, Svietlova N, Batsmanova L, Shvartau V, Kovalenko M. 2017. Effect of zinc and copper nanoparticles on drought resistance of wheat seedlings. *Nanoscale Research Letters* **12**: 60.

Tatagiba SD, DaMatta FM, Rodrigues FA. 2016. Magnesium decreases leaf scald symptoms on rice leaves and preserves their photosynthetic performance. *Plant Physiology and Biochemistry* **108**: 49–56.

Teixeira AF, De Bastos AA, Ferrarese-Filho O, de Lourdes Lucio Ferrarese M. 2006. Role of calcium on phenolic compounds and enzymes related to lignification in soybean (*Glycine max* L.) root growth. *Plant Growth Regulation* **49**: 69–76.

Theriault V, Smale M, Haider H. 2018. Economic incentives to use fertilizer on maize under differing agro-ecological conditions in Burkina Faso. *Food Security* **10**: 1263–1277.

Tippe DE, Rodenburg J, Schut M, Van Ast A, Kayeke J, Bastiaans L. 2017. Farmers' knowledge, use and preferences of parasitic weed management strategies in rain-fed rice production systems. *Crop Protection* **99**: 93–107.

Tonitto C, Ricker-Gilbert JE. 2016. Nutrient management in African sorghum cropping systems: applying meta-analysis to assess yield and profitability. *Agronomy for Sustainable Development* **36**: 10.

Ul-Allah S, Ijaz M, Nawaz A, Sattar A, Sher A, Naeem M, Shahzad U, Farooq U, Nawaz F. 2020. Potassium application improves grain yield and maize hybrids. *Plants* **9**: 75.

Unachukwu NN, Menkir A, Rabbi IY, Oluoch M, Muranaka S, Elzein A, Odhiambo G, Farombi EO, Gedil M. 2017. Genetic diversity and population structure of *Striga hermonthica* populations from Kenya and Nigeria. *Weed Research* **57**: 293–302.

Usmani MM, Nawaz F, Majeed S, Shehzad MA, Ahmad KS, Akhtar G, Aqib M, Shabbir RN. 2020. Sulfate-mediated drought tolerance in maize involves regulation at physiological and biochemical levels. *Scientific Reports* **10**: 1147.

Van Ast A, Bastiaans L, Kropff MJ. 2000. A comparative study on *Striga hermonthica* interaction with a sensitive and a tolerant sorghum cultivar. *Weed Research* **40**: 479–493.

Van Mourik TA, Stomph TJ, Murdoch AJ. 2005. Why high seed densities within buried mesh bags may overestimate depletion rates of soil seed banks. *Journal of Applied Ecology* **42**: 299–305.

Vasey RA, Scholes JD, Press MC. 2005. Wheat (*Triticum aestivum*) is susceptible to the parasitic angiosperm *Striga hermonthica*, a major cereal pathogen in Africa. *American Phytopathological Society* **95**: 294–300.

Vieira Dos Santos C, Delavault P, Letousey P, Thalouarn P. 2003. Identification by suppression subtractive hybridization and expression analysis of *Arabidopsis thaliana* putative defence genes during *Orobanche ramosa* infection. *Physiological and Molecular Plant Pathology* **6**: 297–303.

Wang C, Ruan RW, Yuan XH, Hu D, Yang H, Li Y, Yi ZL. 2015. Effects of nitrogen fertilizer and planting density on the lignin synthesis in the culm in relation to lodging resistance of buckwheat. *Plant Production Science* **18**: 218–227.

Wang M, Gao L, Dong S, Sun Y, Shen Q, Guo S. 2017. Role of silicon on plant–pathogen interactions. *Frontiers in Plant Science* **8**: 1–14.

Wang Y, Wang K, Shao X-Q. 2010. Manganese delays the senescence induced by drought in perennial ryegrass (*Lolium perenne* L.). *African Journal of Agricultural Research* **5**: 3035–3040.

Webb M, Smith MC. 1996. Biology of *Striga hermonthica* (Scrophulariaceae) in Sahelian Mali: effects on pearl millet yield and prospects of control. *Weed Research* **36**: 203–211.

Wei J, Li C, Li Y, Jiang G, Cheng G, Zheng Y. 2013. Effects of external potassium (K) supply on drought tolerances of two contrasting winter wheat cultivars. *PLoS ONE* **8**: 1–11.

Welsh AB, Mohamed KI. 2011. Genetic diversity of *Striga hermonthica* populations in Ethiopia: evaluating the role of geography and host specificity in shaping population structure. *International Journal of Plant Sciences* **172**: 773–782.

Yang KY, Doxey S, McLean JE, Britt D, Watson A, Al Qassy D, Jacobson A, Anderson AJ. 2018. Remodeling of root morphology by CuO and ZnO nanoparticles: effects on drought tolerance for plants colonized by a beneficial pseudomonad. *Botany-Botanique* **96**: 175–186.

Yang R, Howe JA, Golden BR. 2019. Calcium silicate slag reduces drought stress in rice (*Oryza sativa* L.). *Journal of Agronomy and Crop Science* **205**: 353–361.

Yoneyama K. 2020. How do strigolactones ameliorate nutrient. *Cold Spring Harbor Perspectives in Biology* **11**: a034686.

Yoneyama K, Awad AA, Xie X, Yoneyama K, Takeuchi Y. 2010. Strigolactones as germination stimulants for root parasitic plants. *Plant and Cell Physiology* **51**: 1095–1103.

Yoneyama K, Xie X, Kusumoto D, Sekimoto H, Sugimoto Y, Takeuchi Y, Yoneyama K. 2007. Nitrogen deficiency as well as phosphorus deficiency in sorghum promotes the production and exudation of 5-deoxystrigol, the host recognition signal for arbuscular mycorrhizal fungi and root parasites. *Planta* **22**: 125–132.

Yoshida S, Cui S, Ichihashi Y, Shirasu K. 2016. The haustorium, a specialized invasive organ in parasitic plants. *Annual Review of Plant Biology* **67**: 643–667.

Yoshida S, Kim S, Wafula EK, Claude W, Choi D, Yoshida S, Kim S, Wafula EK, Tanskanen J, Kim Y *et al.* 2019. Genome sequence of *Striga asiatica* provides insight into the evolution of plant parasitism. *Current Biology* **29**: 3041–3052.

Yoshida S, Shirasu K. 2009. Multiple layers of incompatibility to the parasitic witchweed, *Striga hermonthica*. *New Phytologist* **183**: 180–189.

Zargar SM, Agnihotri A. 2013. Impact of silicon on various agro-morphological and physiological parameters in maize and revealing its role in enhancing water stress tolerance. *Emirates Journal of Food and Agriculture* **25**: 138–141.

Zhang W, Wu L, Ding Y, Yao X, Wu X, Weng F, Li G, Liu Z, Tang S, Ding C *et al.* 2017. Nitrogen fertilizer application affects lodging resistance by altering secondary cell wall synthesis in japonica rice (*Oryza sativa*). *Journal of Plant Research* **130**: 859–871.

Ziegler J, Schmidt S, Chutia R, Müller J, Böttcher C, Strehmel N, Scheel D, Abel S. 2016. Non-targeted profiling of semi-polar metabolites in Arabidopsis root exudates uncovers a role for coumarin secretion and lignification during the local response to phosphate limitation. *Journal of Experimental Botany* **67**: 1421–1432.

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 zhennan*, *Nicotiana tabacum*, *Beta vulgaris*, *Arabidopsis thaliana*, *Sesamum indicum*, *Melissa officinalis*, *Solanum lycopersicum*, *Vitis vinifera*, *Gossypium hirsutum*, *Pisum sativum*) to nutrients during water stress.