

# Control – the *Striga* conundrum

Sarah J Hearne\*

## Abstract

There is a wide range of existing and potential control options for *Striga*. This paper describes and discusses many of the control options, with a focus on technology limitations, adoption limitations (real or potential) and, in the case of novel technologies, development limitations. The paper addresses the question as to why, after many years of research, control method testing, piloting and technology dissemination, the wide-scale effective control of *Striga hermonthica* (Del.) Benth. and *Striga asiatica* (L.) Kuntze is so elusive. Limitations, including variable technology reliability, poor access to control technology, costs (monetary, labour, skills) associated with control technology, limited practicality of methods and poor information, all hamper the adoption and impact of existing control methods. Some of the same issues may impact upon novel control technologies, and this needs careful consideration. Additional issues surround other potential technologies, especially so in the case of transgenic approaches. Suggestions are made as to how the impasse of effective *Striga* control can be overcome. More effective use of integrated control approaches, improved crop germplasm phenotyping, enhanced understanding of the host/non-host – parasite interaction and better integration and communication among the parasitic plant research, development and extension community are among the suggestions made.

© 2009 Society of Chemical Industry

**Keywords:** *Striga*; cultural control; breeding; biological control; transgenic; adoption

## 1 INTRODUCTION

The life cycles of the noxious cereal weeds *Striga hermonthica* (Del.) Benth. and *Striga asiatica* (L.) Kuntze (herein generically termed *Striga*), are complex, coevolving with many hosts to comprise a series of discrete steps that are tightly coupled with host biochemistry, life cycle and genotype.<sup>1,2</sup> For example, the seed germination and development of the penetrating organ, the haustorium, are initiated by specific chemical cues contained in the root exudates of potential host species.<sup>3–6</sup> The germination of *Striga* is tightly defined by spatial relation with potential host roots. This spatial relationship between host roots and *Striga* seed germination is reflected by the distance from the host root where germination stimulant is still active, i.e. concentrated enough to elicit germination.<sup>7</sup> Concentrations of stimulant required to initiate germination are in the range  $10^{-10}$ – $10^{-15}$  mole  $m^{-3}$ .<sup>8</sup> The carbohydrate and lipid reserves of *S. hermonthica* seed, used for germination, radicle growth and haustorial initiation, are low in comparison with other plants.<sup>3,9</sup> On account of this, germinated seedlings will lose their capacity to form competent haustoria within 3–5 days. Therefore, the concentration-dependent spatial limitation of *Striga* seed germination ensures proximity to a potential host root.

*Striga hermonthica* plants have a high reproductive capacity, producing 10 000–200 000 seeds per plant. *Striga* seeds are small (0.3 mm × 0.15 mm), light (4–7 µg fresh weight) and are easily dispersed by wind, water, animals and agricultural practices (e.g. transmitted by implements such as ploughs). The viability of *Striga* seed has been determined to be for as little as two seasons through to 5–10 years and beyond.<sup>3,10</sup> Soil chemistry, soil flora and fauna will all have a role in governing viability. In addition, *Striga* seed reserves may be important determinants of seed viability over time, although the relative investment in seed reserve versus seed number in *Striga* is unclear. The large capacity for seed production, which would be exacerbated by lengthy viability,

creates conditions for high numbers of *Striga* seed in the soil seed bank in areas where the plant is endemic.

Over the years, many promising *Striga* control methods have been suggested in various formats, some suggestions appearing in multiple incarnations. Some control methods have been evaluated in on-station and on-farm trials, and a sample of these has been deployed in specific localities across sub-Saharan Africa.<sup>11</sup> In spite of all this valuable work, adoption and utility of control methods are limited; yield loss attributable to *Striga* is acute, perhaps even exacerbated, ranging from 35 to 72% in some studies.<sup>12–14</sup> It is increasingly obvious that there is no magic bullet for *Striga* control.

This review discusses the range of potential current and potential *Striga* control technologies, their strengths and weaknesses and the need to formulate integrated *Striga* management practices that are easy for farmers to adopt and implement. The scientific and structural barriers to the development and deployment of novel control options are described.

## 2 AVAILABLE AND POTENTIAL CONTROL METHODS

There are numerous control methods and agents that have been developed or suggested, as summarised in Table 1, with some of the perceived technical and adoption limitations.

### 2.1 Current technologies

The currently deployed control methods fit into two broad categories: cultural control and seed-based technologies.

\* Correspondence to: Sarah J Hearne, IITA Ltd, Carolyn House, 26 Dingwall Road, Croydon CR9 3EE, UK. E-mail: shearne@cgiar.org

International Institute of Tropical Agriculture (IITA), Croydon, UK

**Table 1.** (A) Available and (B) potential *Striga* control methods and their perceived limitations, potential for adoption and impact

Control method/agent	Perceived limitations	Potential for adoption	Potential for impact	Refs
<b>A</b>				
Crop rotation	Land availability; farmers' reliance on grain staples Long time to a perceivable impact in farmers' fields Cultivation has to fit into the current cropping/agrarian system and tools Availability and cost of intercrop seed Use of intercrop by farmers Limited utility if neighbours do not also adopt Varied response of <i>Striga</i> and host productivity to rotation crop	If the break crop is high value/adds value, fits into the current cropping/agrarian system and the seed is available locally, then the potential is moderate to high Otherwise, the adoption potential is low to moderate	Variable; rotation crop specific	18,76,77,78
Intercropping (including agroforestry)/catch cropping and trap cropping	Cultivation has to fit into the current cropping system and tools Availability and cost of intercrop seed Limited utility if neighbours do not also adopt Varied response of <i>Striga</i> and host productivity to intercrop	If the intercrop is high value/adds value, fits into the current cropping/agrarian system and the seed is available locally, then the potential is moderate to high Otherwise, the adoption potential is low to moderate	Variable; intercrop specific	17,18,79,80,81
Late planting/deep planting/transplanting host	May not fit with cropping practices and tools Increased labour requirement Availability of <i>Striga</i> -free nursery Varied <i>Striga</i> and host productivity complicated by soil management techniques	Limited	Deep planting may have high potential in conservation agriculture/no-till systems Limited in general	22,82,83,84
Soil fertilisation, organic and inorganic	Availability and cost of input Labour cost in application Variability in impact on <i>Striga</i> /host performance			85,86,87
Herbicide seed dressing <sup>a</sup>	Dressed seed needs to be bought by farmers each season Availability and cost of dressed seed Agronomic performance/farmer preference of herbicide-tolerant host Herbicide lowering innate soil <i>Striga</i> suppressiveness	If available and affordable, moderate/high	High where available	14,18,42,88,89
Host resistance/tolerance from within crop species	Variable impact on <i>Striga</i> /host performance, depending on the specific tolerance/resistance mechanism May be <i>Striga</i> genotype interactions that limit performance	High if available	High/moderate if available	18,21,34,39,90

**Table 1.** (Continued)

Control method/agent	Perceived limitations	Potential for adoption	Potential for impact	Refs
Host resistance/tolerance from wide cross	<i>Striga</i> genotype interactions untested Farmers need access to improved seed	High if the seed is available	High/moderate	31,91
B				
Host resistance/tolerance from within crop species	Variable impact on <i>Striga</i> /host performance, depending on the specific tolerance/resistance mechanism May be <i>Striga</i> genotype interactions that limit performance	High if available	High/moderate if available	18,21,28,34,90
Host resistance/tolerance from wide cross	Screening for resistance is laborious Introgressing traits can be very difficult/impossible via conventional methods and carry significant genetic drag <i>Striga</i> genotype interactions untested Time to develop	High if available	High/moderate if available	32,92,93,94
<i>Fusarium</i> biocontrol	Variable control levels Variable response of host productivity More investment needed in improving formulations and field application techniques			95,96,97,98
Genetic transformation of <i>Striga</i> biological control agents	Not tested Development cost National legislation and testing Public acceptance Deployment of technology	Unknown	Unknown	52,99
Arbuscular mycorrhiza	Not fully evaluated Application technology and input not available	Unknown	Unknown	53,54
Genetic transformation of host	No tolerance/resistance genes validated in the crop species Development cost National legislation and testing Public acceptance	Variable	High/moderate if available	60,63,100
Genetic transformation of <i>Striga</i>	Not tested Development cost National legislation and testing Public acceptance Deployment of technology	Unknown	Unknown	66

<sup>a</sup> Being scaled out across Africa.

Cultural control includes crop rotation, intercropping, different planting techniques and management of soil fertility. While each of these approaches has specific limitations, as outlined in Table 1, a common limitation observed with these kinds of approach is the seasonal and geographical variability in control achieved. It is understandable that farmers abandon methods or simply do not invest (time and money) in adoption if control cannot be 'guaranteed' in the current season with concomitant pay-offs in yield. This limitation in control efficacy is in part due to variation in application practices (extent and timing) and incorporation,

for example, of hand weeding (which impacts upon the density of *Striga* seed in the seed bank if weeding is achieved before seed set). In addition, efficacy of control is also governed through the action of abiotic and biotic factors (such as temperature and rainfall, soil flora and fauna) that directly influence the performance of the parasite and host themselves. Broad-brush technologies such as crop rotation and intercropping can make significant contributions to *Striga* control and farm productivity as a whole.<sup>15</sup> However, the way the approach fits into the farming system is critical to the adoption potential and success of continued

use. For example, soybean rotation or intercrop in *Striga*-infested fields lowers the density of *Striga* on the cereal host through elicitation of suicidal germination of *Striga* seed by the non-host intercrop, and potentially by improving soil fertility. This improved performance of the cereal crop and the added product of soybean add value to the farming system.<sup>15</sup> However, in order to realise the value addition, there must be a demand for soybean in the household/local community, or the farmer must have access to a market for the soybeans produced. Another intercropping species, *Desmodium*, gives high levels of *S. hermonthica* control owing to elicitation of suicidal germination stimulation and subsequent suppression of *Striga* radical elongation.<sup>16</sup> This intercrop species significantly lowers host losses due to *S. hermonthica* infection in farmers' fields. On farms where dairy or fodder production is an integrated component of the farming system, the benefits from *Desmodium* adoption are enhanced.<sup>17</sup> However, in those farms without an outlet for *Desmodium*, the willingness to invest in a non-food crop is smaller, as farmers have to adopt low-till practices (perhaps at a cost), buy *Desmodium* seed and wait one or more seasons for good *Desmodium* establishment (and *Striga* control) in the field. In a survey of adoption practices by farmers in Western Kenya, many farmers (18%) stated that they had not adopted control technologies as they did not have the available cash to buy the seed or inputs.<sup>18</sup> The utility of *Desmodium* for control of *S. hermonthica* in West and Central Africa and for the control of *S. asiatica* is still to be established, in spite of numerous years of research and technology dissemination.

Soil fertilisation through the use of organic and inorganic fertiliser has been demonstrated in some studies to alleviate the impact of *Striga* on cereal hosts, as illustrated in Table 1. Early experiments on *Striga* and fertilisation demonstrated that the role of nitrogen was the most important factor over other nutrients such as phosphorus and potassium (Parker C, private communication). Specifically, the action of elevated nitrogen availability has been shown to lower germination stimulant production of host roots, limiting potential attachment numbers, and to alleviate the impact of parasitism on host growth and photosynthesis.<sup>19,20</sup> However, in the field the impact of additional fertilisation on plant performance under *Striga*-infested conditions is often variable (Table 1). This may be due to the variability in soil fertility between and within locations, which confounds the impact of additional fertiliser. The form and concentration of nitrogen applied, in combination with soil type, could also influence the reliability of the control measure. More volatile/soluble forms of nitrogen could be more easily lost from the soil, and to a greater degree in those soils with lowered ability to retain nutrients.

Availability of fertiliser is a major obstacle to African farmers. Fertiliser is expensive, so cash constraints in conjunction with limited supply of inputs in many localities makes access to this as a control technology difficult for many farmers.<sup>18</sup>

Germplasm-based *Striga* resistance (the ability of a host to prevent/limit *Striga* attachment/growth) and tolerance (the ability of a host to maintain biomass and yield in spite of *Striga* infection) are the most widespread of the seed-based methods currently available. It is not surprising that there is a greater range and degree of tolerance/resistance found in those crop species that have coevolved with *Striga*, such as sorghum, as compared with introduced species such as maize. In sorghum there are numerous varieties that have been bred and deployed to help control *Striga*, such as Framida, Tiemarifing and N13.<sup>21–23</sup> These cultivars possess features such as lowered germination stimulant production and attachment stage resistance, which can contribute to improved

cereal yields compared with susceptible cultivars.<sup>23</sup> In addition, further understanding of tolerance/resistance and its genetic basis has been gained through classical study and through QTL-based approaches.<sup>24</sup> Some of this knowledge has been used to advance breeding gain in the development of *Striga*-tolerant sorghum varieties through marker-assisted breeding.<sup>25</sup> In the introduced species of maize the situation is more complex. Reports of field-level resistance/tolerance are seen, and many lines and varieties do display lowered *Striga* emergence and/or damage rating in some locations/seasons. However, the control afforded by many of these materials is erratic, and farmers often rate the effectiveness of control lower than their own traditional control practices, which can include weeding and burning newly emerged *Striga* plants and applying manure to fields.<sup>18</sup> Much of the control seen in the field and attributed to resistance/tolerance may in fact be avoidance (achieved by varying root architecture) or avoidance coupled with lowered germination stimulant production (a form of partial resistance). Architectural avoidance and/or lowered germination stimulant production will help limit the total number of *Striga* plants attached to a host and may alleviate the host response owing to a delay in infection.<sup>26</sup> However, crop varieties/lines adopting these as a control mechanism are only likely to be effective in conditions of low to moderate *Striga* seed densities where interaction between root and *Striga* seed is less frequent. Their effectiveness in soils with high density of viable *Striga* seed is highly questionable; the 'loss' of control in high-pressure situations is well documented.<sup>27</sup> While lowered germination stimulant production is a form of resistance, it is incomplete; stimulant is still produced, and, in conditions where contact between host root and parasite are more frequent (i.e. soils with high-density *Striga* seed banks), the resistance is of limited efficacy in the field. Failure to fully recognise this is in part due to the observed phenomenon of lowered emergence when there is high parasite attachment. In conditions where high numbers of *Striga* attach to host root systems, the emergence of these parasites can be delayed and is less abundant than emergence from root systems with fewer *Striga* attached. Prior to emergence, *Striga* are totally reliant on the host for nutrition, so when there are more sinks present (more parasites) the availability of nutrition to any one parasite may be more limited, resulting in slower growth and development than in a parasite with less resource competition. This is a reason why the use of emergence as a parameter for field evaluation of the performance of a line or variety may be fundamentally flawed.

Nonetheless, the situation is not all doom and gloom for maize. Some interesting and durable materials have been bred from wide crosses between maize and the maize wild progenitor teosinte (*Zea diploperennis* Iltis, Doebley & Guzman).<sup>28–30</sup> These resistant and tolerant materials have fewer attached *S. hermonthica* than susceptible lines and in addition show delayed parasitic post-attachment development and higher mortality of attached parasites.<sup>31</sup> In maize, tolerance/resistance has been introduced from both landraces and wild relatives (teosinte).<sup>28</sup> In the field, materials developed from maize–teosinte breeding have 31% lower yield as a result of *S. hermonthica* infection, compared with a 72% lowering seen in susceptible controls, so, in addition to resistance, some tolerance at the field level is also indicated.<sup>28</sup> In addition to teosinte, resistance to *Striga* has been identified in the tetraploid apomictic wild relative of maize *Tripsacum dactyloides* L. This displays post-attachment resistance to *S. hermonthica* and, in addition, extremely high levels of tolerance. Studies indicate that *T. dactyloides* produces a translocatable signal that inhibits haustorial development, resulting in arrested parasite development.<sup>32</sup>

In the laboratory, *T. dactyloides*–maize hybrids had intermediary tolerance between either parent. However, extensive screening of a wider range of maize–*Tripsacum* hybrids in pot trials in Kenya indicated that all apomictically derived materials with 15 or more *Tripsacum* chromosomes (*T. dactyloides*  $n = 18$ ) were tolerant to *S. hermonthica*. All sexually derived maize–*Tripsacum* with few or no *Tripsacum* chromosomes were susceptible (Hearne S and Kanampiu F, unpublished data). Preliminary analysis of maize–*Tripsacum* addition lines indicated that as few as three *Tripsacum* chromosomes contributed tolerance to *Striga* (unpublished data). Experience shows that the homeologous introgression between *Tripsacum* and maize genomes is limited, although it does occur.<sup>33</sup> Improved introgression of *Tripsacum* genome into that of maize may be achieved via the use of monosomic maize; alternatively, genes responsible for tolerance and resistance could be identified and transferred through targeted breeding and selection for specific genes or through transgenic approaches. It has been demonstrated in Nigeria that, out of a suite of cultural and germplasm-based *Striga* control technologies, the improved varieties with *Striga* tolerance are the most rapidly adopted by farmers.<sup>34</sup>

If farmers have access to improved varieties and have the funds to buy the initial seed, then adoption of tolerant/resistant varieties is simple, as the seed fits within their existing farm management framework, although in many cases access in the market to improved seed can be a significant barrier to adoption, as highlighted by farmer groups in western Kenya (some 22% of farmers).<sup>18</sup> Given the higher world market price for many staple cereal commodities and the knock-on impacts of lowered imports and higher local prices, the stimulus to buy improved seed may increase.

The third seed-based control technology is that of herbicide-coated maize seed. The germplasm used in this technology is resistant to the imidazolinone group of the acetolactate synthase (ALS) inhibiting family of herbicides. To date, no resistance to the ALS herbicides has been reported in *Striga*, making this approach an effective control option (Kanampiu F, private communication). Tolerant maize germplasm contains a double recessive natural mutation conferring resistance to the ALS inhibiting herbicides. Seeds of these materials are coated with a formulation of the imidazolinone herbicide imazapyr (registered as *StrigAway*<sup>™</sup> for seed treatment to control *Striga*; the seed treatment formulation), this control package being commonly termed IR (imazapyr resistant) in the literature. The seed can then be distributed to farmers for planting (following specific guidelines such as hand washing post-planting to prevent herbicide carryover to non-herbicide-resistant maize or other crop seed). The herbicide is taken up by the maize plant and also slowly moves through the soil, killing *Striga* and forming a localised protective zone around the growing maize roots.<sup>35</sup> The spread of herbicide is not extensive, so allowing intercropping of legumes 15 cm or more from the maize seed.<sup>35</sup> The technology package has been successfully commercialised in Kenya; the hybrid *Ua Kayango* ('*Striga* killer' in Kiswahili) has been adopted by the large local seed companies, and the full technology package (hybrid, herbicide seed treatment and farmer information) is available on the market to Kenyan farmers. In farmer participatory evaluation, the *Ua Kayango*–*StrigAway* package was consistently ranked the best technology for *Striga* control by all farmer groups.<sup>18</sup> Currently, hybrids and open pollinated varieties possessing imidazolinone resistance are in development or are being evaluated in national performance trials across Africa. A new wave of herbicide formulations has been

developed and is being tested in the field. These new formulations are slow release, ensuring longer duration of imazapyr herbicide release to the plant and soil, and the slower release lowers the initial transient phytotoxicity seen in IR germplasm treated with herbicide.<sup>36</sup> This may be of particular use during seasons with heavy rain, and with late maturing maize varieties.<sup>36,37</sup> An issue often raised with the use of low doses of single active ingredient pesticides is that of the evolution of resistance in the target pest species. Indeed, this has been suggested as an issue in the control of *Striga* by herbicides (Table 1).<sup>15</sup> Early modelling of the frequency of possible resistant *Striga* plants put a figure of five resistant plants  $\text{ha}^{-1} \text{year}^{-1}$ , a high figure. However, subsequent evaluation of model parameters and field data demonstrated that the initial model parameters were inaccurate. *Striga* imazapyr resistance (like the resistance seen in the maize germplasm) needs to be a double recessive mutation to give functional resistance in the field; initially, a heterozygote frequency was used in the resistance prediction model. When the double recessive frequency was factored into the modelling, a figure of five imazapyr-resistant *Striga* plants million  $\text{ha}^{-1} \text{year}^{-1}$  was estimated, a much lower figure than initially suggested.<sup>38</sup> While the occurrence of resistance is now estimated to be extremely rare, resistance prevention and management strategies still need to be implemented to prolong the effective life of the control technology. Strategies such as informing farmers to rogue any emerged *Striga* seen have already been put in place, although this would require farmers to weed their crops late in the season, sometimes after harvest, which in many areas is not common practice. The evolution of field level resistance to imazapyr in *Striga* (homozygous recessive) is more likely in systems cultivating late-maturing maize types. Herbicide concentration in the soil and plant will decrease over the growing season, and there is a greater risk of the herbicide concentration falling to a level that would not kill any single recessive plants in areas growing late-maturing maize. Crossing between two single recessive plants will give rise to the homozygous recessive imazapyr-resistant *Striga* materials that will be selected for in subsequent IR maize crops. Another classical approach to pesticide resistance management is to apply two (or more) pesticides of differing activity (different target sites) in one application. An individual of a target species possessing multiple resistance is by numerous orders of magnitude less likely to evolve than one possessing resistance to either pesticide alone. Following this argument, it has been suggested that resistance to the now generically manufactured, non-patent-controlled, inexpensive herbicide glyphosate (an enolpyruvylshikimate 3-phosphate synthase inhibitor) should be incorporated into IR-resistant maize germplasm. Foliar spray or spot treatment could be applied to the doubly resistant maize crop to control potentially imazapyr-resistant *Striga* as well as other weeds.<sup>36,37</sup> This application would fit particularly well with no or minimal till conservation agricultural practices where weed management through cultural practices can be difficult, and in systems where labour is expensive or in short supply. Another strategy being developed is to pyramid the IR resistance with biological resistance (like the resistance in *Z. diploperennis*-derived lines). Both IITA and CIMMYT are developing lines of maize that pyramid genes for both imazapyr and *Striga* resistance/tolerance.

One of the major pitfalls shared by all seed-based technologies is farmers' access to the seed. As stated earlier, farmers in Western Kenya raised access to improved *Striga*-tolerant/resistant varieties as a reason for non-adoption of *Striga* control.<sup>18</sup> In order to use an IR-based control package, farmers need to purchase treated

seed on an annual basis (farmers can save seed, but without herbicide treatment the varieties will be susceptible to *Striga*). If lack of access to improved *Striga*-tolerant/resistant varieties is an indicator of broader limitations in access to germplasm, this, coupled with cash constraints (18% of farmers stated cash flow limitations were the reason for non-adoption of *Striga* control technologies),<sup>18</sup> may limit adoption of IR technology and of tolerant/resistant varieties by farmers with poor market access, including resource-poor farmers.

Improvement of the germplasm–i package through reformulation or the addition of a different functional group resistance and the inclusion of a second herbicide need careful cost consideration. The cost borne by the farmer for development and deployment of any additional formulation/herbicide-tolerant germplasm needs to be factored, as does the availability of the second herbicide in the local area and the capacity of the farmers to use the herbicide (technical and knowledge based).

## 2.2 What are the best approaches for *Striga* control with current technologies and strategies?

The farmers impacted by *Striga* occupy a very heterogeneous biophysical, cultural, social, economic and political landscape. Failure to recognise, understand and take into account this heterogeneity will invariably hinder the adoption of control approaches. To lessen the impact of variable efficacy of individual control practices, many advocate integrated *Striga* control approaches – combinations of cultural and, where available and applicable, seed-based technologies.<sup>15,39,40</sup> When demonstrated to farmers through farmer field schools, this approach has proven to be successful, with the more resource-poor farmers being the keenest to adopt new technologies.<sup>40</sup> Nonetheless, just as there is no magic bullet for *Striga* control, there is no magic shotgun cartridge either. Technologies need to be packaged in such a way as to suit the abiotic, biotic and market access constraints experienced by farmers. It is perhaps common sense that technologies that fit in with the farming system are more likely to be rapidly adopted by the majority of farmers than those that demand significant modification to farming practices. The technology needs to be readily available, and, if necessary, a market or demand has to be in place for the byproducts of the technology in order to promote adoption and improve overall productivity of the system. Information dissemination is key to adoption of *Striga* control technologies. This is underlined by a Kenyan adoption study in which the majority of non-adopters, some 44%, indicated they had not adopted any *Striga* control methods as they were 'gathering more information about the technology'.<sup>18</sup> This information should include a simple explanation to farmers as to how control measures work; to explain, for example, that IR maize is a combination of variety and herbicide, that both are needed to control the *Striga* and that farmers should wash their hands after handling imazapyr-treated maize seed before planting other seed. Information should also be provided on complementary control technologies to increase awareness of integrated *Striga* control (ISC) options and value for *Striga* control and for wider yield improvement (e.g. fertilisation). When demonstrating ISC technologies to farmers, including at least one method in all packages that gives rapid *Striga* control would facilitate sustained interest in ISC, allowing the sustained adoption of longer impact technologies such as tools to improve soil fertility to continue.<sup>40,41</sup> Information dissemination for ISC has been formulated in many ways, in part depending on the actors involved in spreading information, be they NGOs, national systems, farmers, etc. A

number of interesting examples of approaches to introducing ISC methods to farmers in *Striga*-infected regions have been formulated.<sup>15,18,39,40</sup> One interesting point to note and perhaps highlight is the economic returns on farmer investment, an area for which little work has been conducted.<sup>42</sup> This is not from lack of interest, but from experience, from lack of funding by donors and/or from lack of inclusion and of expertise within projects. The little comparative economic analysis that has been conducted indicated that the marginal rate of return for IR technology was 135:1. The farmer received \$135 of benefit for every \$1 invested, while that for inorganic fertiliser as a control option was essentially zero; the farmer invested \$125 ha<sup>-1</sup> and in return made an additional \$133 ha<sup>-1</sup>.<sup>42</sup> Given this analysis, it is interesting to note that 'simple' cultural control technologies such as fertiliser application may not be as financially rewarding for *Striga* control as a more 'hi-tech' approach such as IR, although the prior soil fertility and the forms of fertiliser added all need to be considered. Certainly, more work is needed in this area to gain an understanding not only of what works at the biological level but also of what works and is sustainable at the farming system level, and where the significant bottlenecks are. Essentially, the natural and social sciences need to work together closely to provide more effective and sustainable *Striga* control implementation strategies based on current technologies. This harmonisation is achieved in the agricultural arena of many developed countries. For example, *S. asiatica* control in the USA was not achieved by chemical control alone, but along with policy, quarantine, public awareness and media campaigns in combination with many things enjoyed by North American farmers that are often out of the reach of African farmers, such as access to agrochemical inputs and credit.<sup>43</sup>

## 3 WHAT POTENTIAL TECHNOLOGIES MAY BE ON THE HORIZON?

There are many exciting suggestions for new and improved *Striga* control technologies; a selection is listed in Table 1.

Some of the new technologies expand on existing control approaches, and bundling packages together is one approach suggested. For example, approaches that could be tested include the following: incorporation of glyphosate resistance with IR germplasm to extend the existing control technology (discussed above) and continuation of germplasm development; looking for new forms of tolerance/resistance within cultivated crop species; and wild relatives (Table 1) to pyramid in order to make more durable germplasm.

Other potential control technologies suggested can largely be grouped into three categories: biological control, control using competitors and transformation-mediated *Striga* control.

Biological control is an old but increasingly re-employed approach to pest management. It has been used successfully to control many pests, largely arthropods, although it is also used commercially to control other organisms such as pathogenic fungi, e.g. the fungus *Trichoderma harzianum* Rifai (sold as BioTrek™ 22G; Wilbur Ellis Company, USA) is used to control fungi that cause damping off, such as *Pythium*, *Rhizoctonia* and *Fusarium*.<sup>44</sup> Biocontrol of weeds also exists commercially; there are good examples from the USA of weed control programmes that use biocontrol with commercial suppliers cultivating and selling the agents (e.g. see Texas A&M University's biological control of weeds website: bc4weeds.tamu.edu).

Inundative biological control of *Striga* has been suggested and demonstrated to be biologically feasible using agents such as

*Fusarium oxysporum* Schlecht. (Table 1).<sup>45</sup> In inundative biological control, large quantities of a control agent, in this case *F. oxysporum*, are applied to the system each season, as a herbicide would be. A *Striga*-specific *forma specialis* of *F. oxysporum* (*F. oxysporum* f. sp. *strigae*, also called f. sp. *striga*) has been identified that, importantly for biocontrol agents, has specific activity against *Striga*. A strain of *F. oxysporum* f. sp. *strigae*, isolated from Ghana, termed Foxy 2, has been shown to be an effective *Striga* control agent.<sup>46</sup> Different formulations of *F. oxysporum* control agent have been tested for control efficacy, including sodium alginate pellets, vermiculite, Pesta granules and coated crop seeds.<sup>47,48</sup> Both application of granulated formulations of Pesta and coated crop seeds have been demonstrated to give significant *Striga* control in field trials.<sup>45</sup> Nonetheless, the major obstacle to such 'bioherbicides' is the large-scale commercialised production and delivery of the technology to farmers, be it Pesta or coated seed. National or private enterprise must see a market demand for this technology. It has been suggested that *F. oxysporum* f. sp. *strigae* isolates resistant to the herbicide imazapyr could be used in combination with the IR technology package to deliver IR–Foxy 2-treated seed.<sup>45</sup> Resistance to imazapyr would be necessary, as fungi have ALS; hence, imazapyr has fungicidal activity in addition to herbicidal activity. Fungal biological control agents without imazapyr resistance would not be effective in combination with IR technology. The bundling of IR and imazapyr-resistant *F. oxysporum* f. sp. *strigae* is at face value a noteworthy idea, although consideration would have to be given to the fact that seed companies usually include fungicides in seed dressings to protect maize from seed rotting and the carryover of pathogens including pathogenic *Fusarium* spp.,<sup>49–51</sup> although it could be possible that imazapyr itself may be able to replace the current fungicide entirely given the fungicidal activity of the agent.

It has been suggested, and in some cases demonstrated, that genetic transformation can be used to enhance biological control – to generate improved control agents of pests including parasitic weeds.<sup>52</sup> Specific and more virulent agents would boost the benefits of biological control of *Striga*, although any such products would face the same delivery issues as highlighted above, and would face additional regulatory issues surrounding use and deployment of transgenes (discussed later).

Another potential control option is the use of competitive/antagonistic arbuscular mycorrhizae species to limit growth of and parasitism by *Striga*.<sup>53,54</sup> Arbuscular mycorrhizae limit *Striga* seed germination, attachment and emergence, and in addition delay emergence time. This, coupled with improved host performance under arbuscular mycorrhizae colonisation, gives higher yields than controls. The mechanistic basis of this phenomenon is unclear, although it may be linked to strigolactone biosynthesis/release from the plant root, as the hormone has dual roles in *Striga* seed germination and arbuscular mycorrhizae colonisation of plant roots.<sup>55–57</sup> Low soil fertility, specifically low nitrogen and phosphorus availability, promotes the production and release of the strigolactone 5-deoxystrigol from sorghum roots.<sup>58</sup> This release of strigolactones will encourage the symbioses of both beneficial mycorrhizae and parasitic *Striga*. This may help explain the high incidence of *Striga* infestation in areas of low nitrogen and phosphorus. Competition for strigolactones or limited/no strigolactone production from host roots colonised with mycorrhizae may be responsible for lowered germination, attachment and emergence of *Striga* in plants with effective mycorrhizal symbioses. While promising, this technology has not, however, been tested to see whether it can be developed into

a practical and transferable control technology. If a technology package could be developed, it would likely face the same distribution issues that biocontrol options face, coupled with the potential difficulty in inoculum (spore) generation. These issues are not insurmountable but need careful consideration for both arbuscular mycorrhizae and the biocontrol options.

Transgenics that address the host–parasite interaction have also been suggested as a way of developing technologies that can contribute to *Striga* control (Table 1). The suggestions are split into transformation of the host to induce resistance and transformation of the parasite to prevent parasitic behaviour.

Taking the first into consideration, there are many potential sources of genes for *Striga* resistance or tolerance, ranging from non-host-resistant species such as marigold to tolerant host species such as sorghum respectively.<sup>59</sup> In addition, an understanding of the gene regulation in host roots before and during *Striga* parasitism can be utilised to identify promoters for a barnase–barstar system designed to induce a hypersensitive resistance response in host roots on parasitism.<sup>60</sup> Many studies have been conducted on changes in gene expression of host and non-host species in response to *Striga* parasitism, and some have identified candidate resistance genes.<sup>59–61</sup> In the *Striga*-tolerant rice cultivar Nipponbare, of the many genes up- and downregulated in response to *Striga* infection, three differentially expressed genes were colocalised with a QTL, explaining 7.4% of the overall variance in post-attachment resistance. The genes underpinning this QTL may serve as potential candidate genes for *Striga* resistance.<sup>61</sup> Where physical maps are available, in species such as rice, the potential to identify candidate tolerance/resistance genes underpinning QTL via comparative mapping is a possibility.<sup>62</sup> This effort will be enhanced if fine mapping of the relevant QTL regions is employed to narrow down the area on the physical map that corresponds to the QTL location. Identification of genes involved in tolerant/resistant reactions of close relatives of crop species such as *Tripsacum* may provide an additional source of genes or promoters for transgenics or targeted breeding using genic markers. However, only one study has been published that documents tests of transformation to control *Striga*. RNAi has been utilised to silence genes involved in *Striga* development on maize. Eleven different events were tested in maize for the impact of the event on *Striga* parasitism.<sup>63</sup> These events comprised single *Striga* RNAi targets of  $\alpha$ CTase, needed for *Striga* fatty acid biosynthesis in the plastid (two events), VCL1, a gene essential for vacuole formation and morphogenesis (two events), and adenylo-succinate synthase, a key enzyme in adenosine monophosphate synthesis (three events). Four further chimeric events containing portions of the above sequences and additional portions of 5-enoylpyruvylshikimate 3-phosphate synthase, required for aromatic amino acid synthesis in plants, and enoyl-ACP reductase, essential for fatty acid biosynthesis in plants, were included in the set of 11 events tested. None of the 11 events tested displayed any *Striga* resistance, although slower *Striga* growth was observed in some events relative to non-transformed maize.<sup>63</sup> One possible reason for this lack of control may be limited translocation of RNA through the host plant to the parasite, as demonstrated in other parasitic plant–host interactions.<sup>64</sup> Proof of the concept of the use of RNAi for parasitic weed control has been demonstrated in laboratory tests investigating the engineering of resistance to the model parasitic plant *Triphysaria*.<sup>65</sup> The use of RNAi to control *Striga* and the reasons for the lack of control of early RNAi attempts warrant further investigation.

Transformation to revert the parasitic nature of *Striga* has been suggested.<sup>66</sup> It was proposed that the transposons with armed cassettes for targeted insect control (TAC-TIC) strategy based on work on insects could be used to prevent the parasitic nature of *Striga* using transposon-carried antisense constructs of key genes, termed kev genes.<sup>66,67</sup> The transgenic *Striga* would either die or their growth would be severely restricted on contact with the suitable elicitor driving production of the antisense transcript. Once introduced into a population (via 'inoculation' of fields with transformed *Striga* seed), the spread of the kev gene(s) would occur via pollination of wild-type plants and would be accelerated through the activity of transposons.<sup>68</sup> Given the need for a specific inducer to facilitate kev gene expression, careful consideration would have to be paid to the nature and mode of application of any elicitor to enable application in the African smallholder context.<sup>68</sup> A modification of this approach has been suggested that is designed to spread a suicidal gene construct through a population without the need for induction for activation. The proposed system is based on the creation of transformed *Striga* plants carrying female-tissue-specific lethal gene constructs that would result in female sterility.<sup>68,69</sup> The dissemination of the transgene through the weed population would be facilitated by pollen which would transmit the trait from the female-sterile plants to wild-type plants, rendering the successive generations female sterile. Populations of the transgenic plant could only be maintained in the presence of wild-type plants.<sup>68,69</sup> Introduction of the female-sterile trait into a wild-type population would, as with TAC-TIC, be achieved through the introduction of transgenic seed into each locality.

Although the initial TAC-TIC strategy for *Striga* control was suggested over 8 years ago, no group has taken up the gamble to test the biological feasibility of this or modified approaches for *Striga* control.

The lack of progress on the transformation front of *Striga* control may be due to a lack of gene resources; in addition, it is likely that scientists are waiting for a more favourable regulatory and perceptory climate, and some funding, to conduct such transgenic work.

The stance towards transgenics may be shifting slowly. At the recent African Green Revolution meeting in Oslo, Rhoda Peace Tumusiime, the African Union Commissioner for Rural Economy, stated that 'GM is extremely important. Unfortunately there is little appreciation of what it is and how it can improve food production. There is a need for advocacy' (www.scidev.net).

#### 4 WHAT CAN BE DONE TO ACCELERATE THE DEVELOPMENT, IMPROVE THE EFFICACY, ENSURE DELIVERY AND DISSEMINATION AND IMPROVE THE ADOPTION POTENTIAL OF CONTROL TECHNOLOGIES?

In order to accelerate the development of technologies and test their efficacy in on-station trials in a more informative way, technologies must be evaluated in a more robust and systematic manner. There is a need to document and take into account many variables that are often unrecorded during *Striga* field trials, such as soil fertility, soil water status, soil type, climatic data, etc. Improved *Striga* screening methodologies and/or standard operating procedures would enable screening of larger germplasm collections for resistance/tolerance to *Striga* and evaluation of different technologies, old and new, alone and in combination,

for efficacy. Potential issues that may limit adoption could be identified and strategies evaluated to mediate them prior to on-farm evaluation: take something that works out for the farmer. This screening/evaluation needs to be underpinned by a better understanding of the parasite in order to develop technologies that are more robust and reliable in farmers' hands. The issue of *Striga* genetic diversity, for example, has been largely overlooked, certainly for the *Striga* species that parasitise the grasses. For example, materials screened in West Africa under *Striga* population X may show very good levels of field resistance while the same materials screened in East Africa under *Striga* population Y may show much lower resistance, if any, compared with local controls. This has been observed in practice in the exchange of *Striga*-tolerant/resistant germplasm between the maize breeding programmes of IITA and CIMMYT (unpublished data). While the specific adaptation of the materials screened to a different agroecology may influence overall performance, this would not be expected to alter the general response to *Striga*. There is growing evidence from field studies and from molecular analysis that there is host specificity and adaptation in *S. asiatica* and *S. hermonthica* populations (Scholes J, private communication).<sup>5</sup> Different *Striga* populations show specific genetic adaptation to host and host genotypes displaying variable virulence. In addition to variation in the genetic diversity between populations of a species of *Striga*, there is likely to be a difference between the species in within-population diversity. *Striga hermonthica* is a self-incompatible outbreeder, while *S. asiatica* is autogamous, self-pollinating prior to floral opening, and, as such, it is highly inbred.<sup>70,71</sup> The difference in reproductive biology is likely to have a significant impact on the within-population diversity of these species, *S. hermonthica* having a higher within-population genetic diversity than *S. asiatica*. What implication this has for plasticity of populations regarding host specificity needs to be determined. Work is currently being conducted at IITA and the University of Sheffield to try to evaluate the genetic diversity of *Striga* populations and determine the influence of parasite genotype on virulence in differing hosts. This knowledge will better enable *Striga* researchers to ensure that potential control products are fully evaluated. This knowledge is key to the generation of more durable technologies and will enable better targeting of dissemination of control technologies to specific localities.

Just as benchmark sites are being developed/identified in Africa for drought phenotyping across many crops, the same could be envisaged being done for *Striga* phenotyping, at least for the graminaceous *Striga* species where multiple crops can be screened in one location. This would allow greater standardisation across on-station trials (allowing better meta-analysis) and would lower phenotyping costs, as equipment and field-based expertise could be condensed and shared across projects. Under such a system, *Striga* seed bank densities and genotypes could be determined and the information used to help understand their role in variability of performance of *Striga* control technologies and approaches.

From the host side of the parasitic symbiosis, understanding of the biology and chemistry of the problem has grown exponentially over the past few years. However, only one or two approaches have harnessed this understanding to develop something tangible in the farmer's field. More tolerant sorghum germplasm produced using marker-assisted breeding and IR maize are two notable exceptions. This begs the question, why are there not more control measures resulting from this work?

The first answer would be that not enough is known still. There remain fundamental questions that need to be addressed



fully. What is the genetic basis of susceptibility, for example? Many researchers view resistance/tolerance without looking at susceptibility. As remarked in one study, 'one of the most striking differences between the susceptible and resistant reaction (of rice) is the extent of the downregulation of gene expression that takes place as *Striga* develops on the roots of the susceptible cultivar'.<sup>72</sup> In a separate study looking at susceptible interaction in maize it was noted that a putative pectin acetyltransferase was upregulated in the stem of infected maize plants, which has direct implications for cell elongation and plant height.<sup>73</sup> Understanding why a plant is susceptible may provide novel approaches to the development of tolerance or resistance to *Striga*. The current research approaches try to identify or select for resistance/tolerance genes in host and non-host plants. Instead of focusing upon how to make a plant resistant/tolerant, the problem of how to stop a plant being susceptible can be addressed. There may be novel genetic approaches that could be developed to prevent or lower susceptibility that are not present in nature. For example, it may be possible to block the expression of a gene or genes in a host that underpin some of the debilitating responses to *Striga* infection such as stomatal closure or lowered internode elongation. The end-result would be a functionally tolerant/resistant plant, but the approach and thinking underpinning the work are different from that currently employed. This approach may yield more outputs in species that have limited tolerance/resistance to *Striga*, such as maize. In addition, a greater understanding of the fundamental interactions between host and parasite in susceptible interactions may help to develop other strategies or tools that could be adopted in the development of better control methods.

A second reason for the lack of control measures is that there is little variation in many cultivated crops to make adequate breeding gain for *Striga*. As one senior maize breeder in East Africa once said, 'after 30 years of trying, I am no nearer to developing durable *Striga*-tolerant varieties with my germplasm, the trait just is not there'. Wild relatives have been demonstrated to be a potential source of alleles for resistance/tolerance to *Striga* and should be investigated/utilised further. There has been a tendency to focus on either resistance or tolerance to *Striga*, and the interplay and value of combining both have not been considered fully. A maize plant with one successfully attached *Striga* parasite is as detrimentally impacted, in terms of growth, as a maize plant supporting 20 *Striga* parasites (given similar timing of attachment).<sup>73</sup> Unless resistance is complete or crops are being cultivated under low/moderate *Striga* pressures, the usefulness of resistance without tolerance, in terms of limiting crop yield losses, is questionable.

A third reason for the limited uptake and adoption of control methods by farmers relates to the inability of many researchers accurately to assess a farmer's own priorities. As outlined in documentation generated by the system-wide programme of integrated pest management, surveys tend to highlight production constraints such as low soil fertility and parasitic weeds rather than the farmer's concerns of poor market access, etc.<sup>74</sup> The use of participatory research and capacity building better enables researchers to gauge farmers' priorities and problems in a holistic manner, and better enables the generation of suitable technologies. For example, with respect to seed-based technologies, in addition to achieving higher yields, farmers also want specific colour, cooking traits, tolerance to diseases, resistance to storage pests, maturity, etc., of their crops.<sup>18</sup> In many cases, lines and varieties that possess one

or two desirable traits have not been adopted by farmers, as they do not match other important criteria. Increasing importance is being placed on the use of farmer participatory breeding/variety selection to ensure that farmers receive improved varieties that match their requirements in the field, home and market.<sup>75</sup> In addition, participatory evaluation of technologies and ISM packages such as the farmer field school approach and pilot site approach to technology evaluation have enabled a greater feedback from farmers on the strengths and weaknesses of technologies than would otherwise have been gained.<sup>18,74</sup> Another pro of participatory approaches is that they often facilitate greater collaboration between researchers from across the research and development spectrum.<sup>74</sup> They create a platform for dialogue between stakeholders in the agricultural sector, including members of the private sector agribusinesses, national agricultural research systems, international centres, universities, extension workers, processors/buyers, NGOs, policy makers and farming communities. This can be a great advantage when evaluating broader issues such as bottlenecks to farmer market access, as many and varied actors may be involved in addressing the issues in different localities.

A more general bottleneck to the development and deployment of more effective control technologies and strategies is more reflective of the form and interaction within the *Striga* research community. There are many people doing interesting and exciting work on *Striga*, but this tends to be done in fragmented ways. As a community, the communication and dissemination of ideas and findings to one another and to wider stakeholders are very poor. This is not unique to *Striga* or parasitic plant research, and is in part due to the competitive funding environment in which researchers find themselves entrenched. Nonetheless, this fragmentation and lack of coordinated group effort does not help the resource-poor farmer spoken of in proposals. Technologies and ideas are often thrust forward as 'magic bullets', when it should be reasoned from experience that each technology invariably has its limitations and there is no stand-alone approach that will provide farmers with adequate sustainable *Striga* control (Table 1). Only in conjunction with other technologies and integration with other disciplines can a technology have an impact in the field.

Given the greater insights now available into the fundamental interactions between host and parasite, it is perhaps time to consider focusing on the issue of *Striga* in a more generic way rather than by the commodity-based approach typically adopted. The cultivation of cereals in farmers' fields is not demarked by maize-, rice- or sorghum-only signs. Farmers do mix cultivation of cereals with non-cereal crops, and sometimes cereals are mixed, as is the case of sorghum/maize rotation in Western Kenya. Somewhere down the line of control measure development and ISC, more thought needs to be given to the farmers' viewpoint rather than to the host species' perspective. Advances in comparative genomics enable linkages and synergies to be made between many crop species. This facilitates advances in one crop to be investigated in detail as a potential option in another species. An example of this approach is the comparative work led by the University of Sheffield, which aims to utilise knowledge of the molecular genetic basis of resistance in rice to *Striga* species to identify and confirm the existence of homologous QTL and resistance genes in sorghum (Scholes J, private communication).

Finally, the lack of grounding of many ideas in the African farming system context is also an issue. This is highlighted with existing control options. As this article has shown, there are many barriers to farmer adoption that need to be encapsulated and

considered when any novel control method is suggested or when there is a wider attempted deployment of existing methods. Failure to do so is a disservice to the farmers, researchers and donors; no one wants a technology to sit on the shelf.

The *Striga* research community is strong and full of good ideas, knowledge and research tools. Given a more direct focus, involving a more robust partnership, from gene to field-molecular biologist to sociologist and anthropologist, the dogmatic issue of *Striga* control can be more decisively addressed.

## REFERENCES

- Bouwmeester HJ, Matusova R, Sun Zhongkui and Beale MH, Secondary metabolite signalling in host-parasitic plant interactions. *Curr Opin Plant Biol* **6**:358–364 (2003).
- Botanga CJ, Kling JG, Berner DK and Timko MP, Genetic variability of *Striga asiatica* (L.) Kuntz based on AFLP analysis and host-parasite interaction. *Euphytica* **128**:375–388 (2002).
- Parker C and Riches CR, *Parasitic Weeds of the World. Biology and Control*. CAB International, Wallingford, UK (1993).
- Matusova RK, Rani FW, Verstaen A, Franssen MCR, Beale MH and Bouwmeester HJ, The strigolactone germination stimulants of the plant-parasitic *Striga* and *Orobanches* are derived from the carotenoid pathway. *Plant Physiol* **139**:920–934 (2005).
- Riopel JL and Timko MP, Haustorial initiation and differentiation, in *Parasitic Plants*, ed. by Press MC and Graves JD. Chapman and Hall, London, UK, pp. 39–79 (1995).
- Chang M and Lynn DG, Haustoria and the chemistry of host recognition in parasitic angiosperms. *J Chem Ecol* **12**:561–579 (1986).
- Fate GD, Chang M and Lynn DG, Control of germination in *Striga asiatica*: chemistry of spatial definition. *Plant Physiol* **93**:201–207 (1990).
- Stewart GR and Press MC, The physiology and biochemistry of parasitic angiosperms. *Ann Rev Plant Phys Biochem Mol Biol* **41**:127–151 (1990).
- Boone LS, Fate G, Chang M and Lynn DG, Seed germination, in *Parasitic Plants*, ed. by Press MC and Graves JD. Chapman and Hall, London, UK, pp. 14–38 (1995).
- Gbehounou Gand Adango E, Trap crops of *Striga hermonthica*: *in vitro* identification and effectiveness *in situ*. *Crop Prot* **22**:395–404 (2003).
- Oswald A, *Striga* control – technologies and their dissemination. *Crop Prot* **24**:333–342 (2005).
- Kroschel J, Analysis of the *Striga* problem, the first step towards joint action, in *Advances in Parasitic Weed Control at On-Farm Level, Vol. 1*, ed. by Kroschel J, Mercer-Quarshie H and Sauerborn J. Margraf Verlag, Weikersheim, Germany, pp. 3–25 (1999).
- Joel DM, Hershenhorn Y, Eizenberg H, Aly R, Ejeta G, Rich PJ, *et al*, Biology and management of weedy root parasites. *Hort Revs* **38**:267–349 (2007).
- De Groote H, Wangare L, Kanampiu F, Odendo M, Diallo A, Karaya H, *et al*, The potential of a herbicide resistant maize technology for *Striga* control in Africa. *Ag Syst* **97**:83–94 (2008).
- Schulz S, Hussaini MA, Kling JG, Berner DK and Ikie FO, Evaluation of integrated *Striga hermonthica* control technologies under farmer management. *Exp Ag* **39**:99–108 (2003).
- Tsanuo MK, Hassanali A, Hooper AM, Khan Z, Kaberia F, Pickett JA, *et al*, Isoflavonones from the allelopathic aqueous root exudate of *Desmodium uncinatum*. *Phytochemistry* **64**:265–273 (2003).
- Khan ZR, Midega CAO, Amudavi DM, Hassanali A and Pickett JA, On-farm evaluation of the 'push-pull' technology for the control of stem borers and *Striga* weed on maize in western Kenya. *Field Crop Res* **106**:224–233 (2008).
- Manyong VM, Nindi SJ, Alene AD, Odhiambo GD, Omanyua G, Mignouna HD and Bokanga M, *Farmer Perceptions of Imazapyr-Resistant (IR) Maize Technology on the Control of Striga in Western Kenya*. African Agricultural Technology Foundation (www.aatf-africa.org), Nairobi, Kenya (2008).
- Cechin I and Press MC, Nitrogen relations of the sorghum–*Striga hermonthica* host–parasite association – germination, attachment and early growth. *New Phytol* **124**:681–687 (1993).
- Cechin I and Press MC, Nitrogen relations of the sorghum–*Striga hermonthica* host–parasite association – growth and photosynthesis. *Plant Cell Env* **16**:237–247 (1993).
- Rodenburg J, Bastiaans L, Kropff MJ and Hermonthica A, Effects of host plant genotype and seedbank density on *Striga* reproduction. *Weed Res* **46**:251–263 (2006).
- Bastiaans L and Katile S, Cultural control measures to diminish sorghum yield loss and parasite success under *Striga hermonthica* infestation. *Crop Prot* **24**:1023–1034 (2005).
- Rodenburg J, Bastiaans L, Weltzien E and Hess D, How can field selection for *Striga* resistance and tolerance in sorghum be improved? *Field Crop Res* **93**:34–50 (2005).
- Grenier C, Ibrahim Y, Haussmann BIG, Kiambi D and Ejeta G, Marker assisted selection for *Striga* resistance in sorghum, in *Integrating New Technologies for Striga Control: Towards Ending the Witch-hunt*, ed. by Ejeta G and Gressel J. World Scientific, Singapore, pp. 159–171 (2007).
- Folkertsma RT, Haussmann BIG, Parzies HK, Hoffmann V and Geiger HH, Arresting the scourge of *Striga* on sorghum in Africa by combining the strengths of marker-assisted backcrossing and farmer-participatory selection. Presented at Deutscher Tropentag, Hohenheim, Germany, 11–13 October 2005, (www.tropentag.de/2005/abstracts/links/Parzies\_NfQBcDqx.php), *The Global Food and Product Chain – Dynamics, Innovations, Conflicts, Strategies* (2005).
- Gurney AL, Press MC and Scholes JD, Infection time and density influence the response of sorghum to the parasitic angiosperm *Striga hermonthica*. *New Phytol* **143**:573–580 (1999).
- Oswald A and Ransom JK, *Striga* control and improved farm productivity using crop rotation. *Crop Prot* **20**:113–120 (2001).
- Kling JG, Fajemisin JM, Badu-Apraku B, Diallo A, Menkire A and Melake-Berhan A, *Striga* resistance breeding in maize, in *Breeding for Striga Resistance in Cereals*, ed. by Haussman BIG, Hess DE, Koyama ML, Grivet L, Rattunde HFW and Geiger HH. Megraf Verlag, Weikersheim, Germany, pp. 103–118 (2000).
- Menkir A, Assessment of reactions of diverse maize inbred lines to *Striga hermonthica* (Del.) Benth. *Plant Breed* **125**:131–139 (2006).
- Gethi JG and Smith ME, Genetic responses of single crosses of maize to *Striga hermonthica* (Del.) Benth. and *Striga asiatica* (L.) Kuntze. *Crop Sci* **44**:2068–2077 (2004).
- Amusan IO, Richi PJ, Menkir A, Housley T and Ejeta G, Resistance to *Striga hermonthica* in a maize inbred line derived from *Zea diploperennis*. *New Phytol* **178**:157–166 (2008).
- Gurney AL, Grimanelli D, Kanampiu F, Housington D, Scholes JD and Press MC, Novel sources of resistance to *Striga hermonthica* in *Tripsacum dactyloides*, a wild relative of maize. *New Phytol* **160**:557–568 (2003).
- de Wet JM, Engle LM, Grant CA and Tanaka ST, Cytology of maize–*Tripsacum* introgression. *Am J Bot* **59**:1026–1029 (1972).
- Franke AC, Ellis-Jones J, Tarawali G, Schulz S, Hussaini MA, Kureh I, *et al*, Evaluating and scaling-up integrated *Striga hermonthica* control technologies among farmers in northern Nigeria. *Crop Prot* **25**:868–878 (2006).
- Kanampiu F, Ransom J, Friesen D and Gressel J, Imazapyr and pyriothobac movement in soil and from maize seed coats to control *Striga* in legume intercropping. *Crop Prot* **21**:611–619 (2002).
- Gressel J, Crops with target-site herbicide resistance for *Orobanche* and *Striga* control. *Pest Manag Sci* **this issue** (2009).
- Kanampiu F, Diallo A, Burnet M, Karaya H and Gressel J, Success with the low biotech of seed-coated imidazolinone-resistant maize, in *Integrating New Technologies for Striga Control: Towards Ending the Witch-hunt*, ed. by Ejeta G and Gressel J. World Scientific, Singapore, pp. 145–158 (2007).
- Gressel J, Problems in qualifying and quantifying assumptions in plant protection models: resistant simulations can be mistaken by a factor of million. *Crop Prot* **24**:1007–1015 (2005).
- Kamara AY, Menkir A, Chikoye D, Omoigui LO and Ekeleme F, Cultivar and nitrogen fertilization effects on *Striga* infestation and grain yield of early maturing tropical maize. *Maydica* **52**:415–423 (2007).
- Douthwite B, Schulz S, Olanrewaju AS and Ellis-Jones J, Impact pathway evaluation of an integrated *Striga hermonthica* control project in Northern Nigeria. *Ag Syst* **92**:201–222 (2007).
- Stringer LC, Twyman C and Thomas DSG, Learning to reduce degradation on Swaziland's arable land: enhancing understanding of *Striga asiatica*. *Land Des Devel* **18**:163–177 (2007).

- 42 De Groote H, *Striga* economics, in *Integrating New Technologies for Striga Control: Towards Ending the Witch-hunt*, ed. Ejeta G and Gressel J. World Scientific, Singapore, pp. 253–264 (2007).
- 43 Eplee RE, Witchweed (*Striga asiatica*) – an overview of management strategies in the USA. *Crop Prot* **11**:3–7 (1992).
- 44 Bale JS, Lenteren JC and van Bigler F, Biological control and sustainable food production. *Phil Trans R Soc Lond Biol Sci* **363**:761–776 (2008).
- 45 Beed FD, Hallet SG, Venne J and Watson AK, Biocontrol using *Fusarium oxysporum*; a critical component of integrated *Striga* management, in *Integrating New Technologies for Striga Control: Towards Ending the Witch-hunt*, ed. by Ejeta G and Gressel J. World Scientific, Singapore, pp. 283–300 (2007).
- 46 Elzein A and Kroschel J, *Fusarium oxysporum* Foxy2 shows potential to control both *Striga hermonthica* and *S. asiatica*. *Weed Res* **44**:433–438 (2004).
- 47 Elzein A and Kroschel J, Development and efficacy of granular formulations of *Fusarium oxysporum* Foxy 2 for *Striga* control: an essential step towards practical field application in Africa. *J Plant Dis Prot* **SXX**:889–905 (2006).
- 48 Venne J, Beed F, Avocanh A and Watson A, Integrating *Fusarium oxysporum* f. sp. *strigae* into cereal cropping systems in Africa. *Pest Manag Sci this issue* (2009).
- 49 Goulart ACP and Fialho WFB, Corn seed treatment with fungicides for pathogen control. *Summa Phytopath* **27**:414–420 (2001).
- 50 Galperin M, Graf S and Kenigsbuch D, Seed treatment prevents vertical transmission of *Fusarium moniliforme*, making a significant contribution to disease control. *Phytoparasitica* **31**:344–352 (2003).
- 51 Yates IE, Arnold JW, Hinton DM, Basinger W and Walcott RR, *Fusarium verticillioides* induction of maize seed rot and its control. *Can J Bot* **81**:422–428 (2003).
- 52 Gressel J, Meir S, Herschkovitz Y, Al-Ahmad H, Babalola O and Amsellem Z, Transgenic biocontrol agents to overcome evolutionary barriers, in *Integrating New Technologies for Striga Control: Towards Ending the Witch-hunt*, ed. by Ejeta G and Gressel J. World Scientific, Singapore, pp. 313–323 (2007).
- 53 Lenzemo VW, van Ast A and Kuyper TW, Can arbuscular mycorrhizal fungi contribute to *Striga* management on cereals in Africa? *Outlook Ag* **35**:307–311 (2006).
- 54 Gworgwor NA and Weber HC, Arbuscular mycorrhizal fungi–parasite–host interaction for the control of *Striga hermonthica* (Del.) Benth. in sorghum (*Sorghum bicolor* (L.) Moench). *Mycorrhiza* **13**:277–281 (2003).
- 55 Yoneyama K, Xie X, Yoneyama K and Takeuchi Y, Strigolactones: structure, activity and regulation of production. *Pest Manag Sci this issue* (2009).
- 56 López-Ráez JA, Matusova R, Cardoso C, Jamil M, Charnikova T, Kohlen W, et al, Strigolactones: ecological significance and use as a target for parasitic plant control. *Pest Manag Sci this issue* (2009).
- 57 Gomez SK and Harrison MJ, Laser microdissection and its application to analyze gene expression in the arbuscular mycorrhizal symbiosis. *Pest Manag Sci this issue* (2009).
- 58 Yoneyama K, Xie XN and Kusumoto D, Nitrogen deficiency as well as phosphorus deficiency in sorghum promotes the production and exudation of 5-deoxystriol, the host recognition signal for arbuscular mycorrhizal fungi and root parasites. *Planta* **227**:125–132 (2007).
- 59 Gowda BS, Riopel JL and Timko MP, NRSA-1: a resistance gene homolog expressed in roots of non-host plants following parasitism by *Striga asiatica* (witchweed). *The Plant J* **20**:217–230 (1999).
- 60 Bennetzen JL, Gong F, Xu J, Newton C and de Olivera AC, The study and engineering of resistance to the parasitic weed *Striga* in rice, sorghum and maize, in *Breeding for Striga Resistance in Cereals*, ed. by Haussman BIG, Hess DE, Koyama ML, Grivet L, Rattunde HFW and Geiger HH. Megraf Verlag, Weikersheim, Germany, pp. 197–205 (2000).
- 61 Swarbrick PJ, Huang K, Liu G, Slate J, Press MC and Scholes JD, Global patterns of gene expression in rice cultivars undergoing a susceptible or resistant interaction with the parasitic plant *Striga hermonthica*. *New Phytol* **179**:515–529 (2008).
- 62 Swarbrick PJ, Scholes JD, Press MC and Slate J, A major QTL for resistance of rice to the parasitic plant *Striga hermonthica* is not dependent on genetic background. *Pest Manag Sci this issue* (2009).
- 63 de Framond A, Rich PJ, McMillan J and Ejeta G, Effects on *Striga* parasitism of transgenic maize armed with RNAi constructs targeting essential *S. asiatica* genes, in *Integrating New Technologies for Striga Control: Towards Ending the Witch-hunt*, ed. Ejeta G and Gressel J. World Scientific, Singapore, pp. 185–196 (2007).
- 64 Westwood JH, RNA translocation between parasitic plants and their hosts. *Pest Manag Sci this issue* (2009).
- 65 Yoder JI, Gunathilake P, Wu B, Tomilova N and Tomilov AA, Engineering host resistance against parasitic weeds with RNA interference. *Pest Manag Sci this issue* (2009).
- 66 Gressel J and Levy A, Giving *Striga hermonthica* the DTs, in *Breeding for Striga Resistance in Cereals*, ed. by Haussman BIG, Hess DE, Koyama ML, Grivet L, Rattunde HFW and Geiger HH. Megraf Verlag, Weikersheim, Germany, pp. 207–224 (2000).
- 67 Pfeifer TA and Grigliatti TA, Future perspectives on insect pest management: engineering the pest. *J Inv Path* **67**:109–119 (1996).
- 68 Rector BG, Molecular biology approaches to control of intractable weeds: new strategies and complements to existing biological practices. *Plant Sci* **175**:437–448 (2008).
- 69 Rector BG, A sterile-female technique proposed for control of certain parasitic and intractable weeds: advantages, shortcomings and risk management. *Pest Manag Sci this issue* (2009).
- 70 Nickrent DL and Musselman LJ, Autogamy in the American strain of witchweed, *Striga asiatica* (Scrophulariaceae). *Brittonia* **31**:253–256 (1979).
- 71 Safa SB, Jones BMG and Musselman LJ, Mechanisms favoring outbreeding in *Striga hermonthica* (Scrophulariaceae) *New Phytol* **96**:299–305.
- 72 Scholes JD, Swarbrick PJ, Slate J and Press MC, The molecular genetic basis of host resistance to *Striga* species: a way forward, in *Integrating New Technologies for Striga Control: Towards Ending the Witch-hunt*, ed. by Ejeta G and Gressel J. World Scientific, Singapore, pp. 173–184 (2007).
- 73 Hearne SJ, Morphological, physiological and molecular interactions between maize and the parasitic angiosperm *Striga hermonthica*. *PhD Thesis*, University of Sheffield, UK (2001).
- 74 SP-IPM, Tackling the scourge of parasitic weeds in Africa. IPM brief no. 1. IITA, Cotonou, Benin () (2003).
- 75 Banziger M and Cooper M, Breeding for low input conditions and consequences for participatory plant breeding: examples from tropical maize and wheat. *Euphytica* **122**:503–519 (2001).
- 76 Kureh I, Kamara AY and Tarfa BD, Influence of cereal–legume rotation on *Striga* control and maize grain yield in farmers' fields in the northern Guinea savanna of Nigeria. *J Ag Rural Devel Trop Subtrop* **107**:41–54 (2006).
- 77 Samake O, Stomph TJ, Kropff MJ and Smaling EMA, Integrated pearl millet management in the sahel: effects of legume rotation and fallow management on productivity and *Striga hermonthica* infestation. *Plant Soil* **286**:245–257 (2006).
- 78 Gacheru E and Rao MR, The potential of planted shrub fallows to combat *Striga* infestation on maize. *Internat J Pest Manag* **51**:91–100 (2005).
- 79 Gworgwor NA, Trees to control weeds in pearl millet. *Agron Sustain Dev* **27**:89–94 (2007).
- 80 Khan ZR, Midega CAO, Hassanali A, Pickett JA and Wadhams LJ, Assessment of different legumes for the control of *Striga hermonthica* in maize and sorghum. *Crop Sci* **47**:730–736 (2007).
- 81 Reda F and Verkleij JAC, Cultural and cropping systems approach for *Striga* management – a low cost alternative option in subsistence farming, in *Integrating New Technologies for Striga Control: Towards Ending the Witch-hunt*, ed. by Ejeta G and Gressel J. World Scientific, Singapore, pp. 229–239 (2007).
- 82 Gbehounou G, Adango E, Hinvi JC and Nonfon R, Sowing date or transplanting as components for integrated *Striga hermonthica* control in grain-cereal crops? *Crop Prot* **23**:379–386 (2004).
- 83 Oswald A, Ransom JK, Kroschel J and Sauerborn J, Transplanting maize and sorghum reduces *Striga hermonthica* damage. *Weed Sci* **49**:346–353 (2001).
- 84 van Delft GJ, Graves JD, Fitter AH and van Ast A, *Striga* seed avoidance by deep planting and no-tillage in sorghum and maize. *Internat J Pest Manag* **46**:251–256 (2000).

- 85 Sauerborn J, Kranz B and Mercer-Qviarshie H, Organic amendments mitigate heterotrophic weed infestation in savannah agriculture. *Appl Soil Ecol* **23**:181–186 (2003).
- 86 Ahonsi MO, Berner DK, Emechebe AM and Lagoke ST, Effects of soil pasteurisation and soil N status on severity of *Striga hermonthica* (Del.) Benth. in maize. *Soil Biol Biochem* **34**:1675–1681 (2002).
- 87 Showemimo FA, Kimbeng CA and Alabi SO, Genotypic response of sorghum cultivars to nitrogen fertilization in the control of *Striga hermonthica*. *Crop Prot* **21**:867–870 (2002).
- 88 Ahonsi MO, Berner DK, Emechebe AM and Lagoke ST, Effects of ALS-inhibitor herbicides, crop sequence, and fertilization on natural soil suppressiveness to *Striga hermonthica*. *Ag Ecosys Env* **104**:453–463 (2004).
- 89 Kanampiu FK, Kabambe V, Massawe C, Jasi L, Friesen D, Ransom JK, *et al*, Multi-site, multi-season field tests demonstrate that herbicide seed-coating herbicide-resistance maize controls *Striga* spp. and increases yields in several African countries. *Crop Prot* **22**:697–706 (2003).
- 90 Westerman PR, van Ast A, Stomph TJ and van der Werf W, Long-term management of the parasitic weed *Striga hermonthica*: strategy evaluation with a population model. *Crop Prot* **26**:219–227 (2007).
- 91 Menkir A, Kling JG, Badu-Apraku B and Ibikunle O, Registration of 26 tropical maize germplasm lines with resistance to *Striga hermonthica*. *Crop Sci* **46**:1007–1009 (2006).
- 92 Gurney AL, Slate J, Press MC and Scholes JD, A novel form of resistance to the parasitic angiosperm *Striga hermonthica*. *New Phytol* **169**:199–208 (2006).
- 93 Rich PJ, Grenier C and Ejeta G, *Striga* resistance in the wild relatives of sorghum. *Crop Sci* **44**:2221–2229 (2004).
- 94 Wilson JP, Hess DE, Hanna WW, Kumar KA and Gupta SC, Identification of *Pennisetum glaucum* subsp. *monodii* with *Striga* resistance. *Phytopathology* **93**:S90 (2003).
- 95 Zahran E, Kohlschmid E, Sauerborn J, Abbasher AA and Muller-Stover D, Does an alication as seed coating stabilize the efficacy of biological control agents of *Striga hermonthica* under field conditions? *J Plant Dis Prot* **521**:467–471 (2008).
- 96 Schaub B, Marley P, Elzein A and Kroschel J, Field evaluation of an integrated *Striga hermonthica* management in sub-Saharan Africa: synergy between *Striga*-mycoherbicides (biocontrol) and sorghum and maize resistant varieties. *J Plant Dis Prot* **20**:691–699 (2006).
- 97 Yonli D, Traore H, Hess DE, Sankara P and Sereme P, Effect of growth medium, *Striga* seed burial distance and depth on efficacy of Fusarium isolates to control *Striga hermonthica* in Burkina Faso. *Weed Res* **46**:73–81 (2006).
- 98 Marley PS and Shebayan JAY, Field assessment of *Fusarium oxysporum* based mycoherbicide for control of *Striga hermonthica* in Nigeria. *Biocontrol* **50**:389–399 (2005).
- 99 Vurro M, Gressel J, Butts T, Harman G, Pilgeram A, St-Leger R, *et al* (eds), *Enhancing Biocontrol Agents and Handling Risks*. NATO Science Series No. 339. IOS Press, Amsterdam, The Netherlands, p. 295 (2001).
- 100 Rispaill N, Dita MA, Gonzalez-Verdejo C, Perez-de-Luque A, Castillejo MA, Prats E, *et al*, Plant resistance to parasitic plants: molecular approaches to an old foe. *New Phytol* **173**:703–711 (2007).