

## Mini-Review

# Towards effective resistance to *Striga* in African maize

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**Abbreviations:** ABA, abscisic acid; AM, arbuscular mycorrhizal; IITA, International Institute for Tropical Agriculture; IR, imidazolinone resistant; RNAi, RNA interference

**Key words:** *Striga*, parasitic weed, maize, sorghum, resistance, integrated control

The fascinating biology of *Striga* parasitism is manifest through a series of signal exchanges between the parasite and its host. As an obligate root hemi-parasite, *Striga* development is cued to exudates and solutes of host roots but with negative ramifications on host plant health. *Striga* control in crops, via a variety of biotechnological approaches, needs to be based on increased understanding of this intricate biology. Maize has become the major cereal crop of Africa. However, this New World transplant has shown a paucity of *Striga* resistance characters relative to native sorghum. In this paper, we review growing evidence for maize genetic defenses against early pre-emergent phases of the *Striga* life cycle, when the tolls of parasitism are first manifest. Resistance characters first described in maize wild relatives have now been captured in *Zea mays*. The possible stacking of new and complementary sources of resistance in improved maize varieties targeted for *Striga* prone areas is discussed. An integrated approach combining genetic with other control measures is advocated with a more realistic view of the resource challenges prevalent in African agriculture.

## *Striga* Parasitism

Witchweeds, *Striga* spp., are menacing root parasites of significant importance in much of Africa and parts of Asia. The array of signal exchanges between *Striga* and its hosts leading to successful parasitism is a fascinating biological phenomenon. Specific chemical signals produced by host plants are required to induce germination of parasitic seeds and elicit attachment organ formation. Although capable of photosynthesis once it emerges, *Striga* relies on host plants for a significant portion of its carbon supply.<sup>1,2</sup> Beyond the burden of losing food and water to these parasites, host plants suffer from a characteristic malady resembling the symptoms of severe drought, including leaf scorching and increased root:shoot ratios.<sup>3,4</sup> The name *Striga* (Latin for “witch”), and its common names, both in English (witchweed) and in its various African local names, refer to these host symptoms which appear before the parasite emerges, as if a hex

had befallen the crop. The nature of this “hex” is not completely understood but is probably the result of hormonal perturbations (particularly in ABA)<sup>5,6</sup> or toxins produced by the parasite.<sup>4</sup> The *Striga* problem is particularly acute in Africa, where the native giant witchweed, *S. hermonthica*, is widespread and most damaging to many cereal crops, including sorghum, millet, rice and maize. Under extreme infestation, a single crop plant can support over a hundred parasitic weeds, each capable of producing tens of thousands of seeds. These seeds are long lived and spoil the fields against future cereal production.

*Striga* can be controlled through various cultural practices and through genetic manipulation of crop plants. Infestation is generally much less severe where water and soil fertility are optimal for crop growth. Growing conditions are, however, rarely optimal in much of Africa. While there are effective *Striga* control options such as the use of high levels of nitrogenous fertilizers, irrigation and herbicides,<sup>7</sup> these solutions are beyond the means of many African growers. Biocontrol options such as inoculation with *Fusarium* isolates,<sup>8</sup> arbuscular mycorrhizal (AM) fungi,<sup>9</sup> or via suppression by intercropping with allelopathic legumes<sup>10</sup> have also been proposed, though not widely deployed. In the short-run, improved crop varieties with resistance to *Striga* remain the more feasible technology for the resource poor. Integrating various control options with improved agronomic practices generally enhances the efficiency of control and cost.<sup>11</sup>

## *Striga* Resistance in Sorghum

With persistent effort in the identification of sources of resistance genes and development of improved selection schemes, we made significant gains in improving *Striga* resistance in sorghum. We devised an approach to systematically build effective resistance to *Striga* by developing increased understanding of the biology of host-parasite interactions.<sup>12</sup> Our premise has been to view the biology of *Striga* parasitism at its various stages as a series of signal exchanges between host and parasite that lead to successful establishment. Key to this approach is the ability to monitor *Striga*'s behavior around sorghum genotypes from its earliest stages, events normally hidden below ground. The laboratory co-culture methods we employ have helped us to identify sorghum mutants with low germination stimulant activity on *Striga*,<sup>13-16</sup> low haustorial (attachment organ) induction activity,<sup>16</sup> formation of necrotic lesions (hypersensitive

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reaction) when *Striga* first attaches<sup>17</sup> and incompatibility, whereby early post-attachment growth of the parasite is stopped or slowed.<sup>18</sup> The original germplasm in which these characters were identified often came from landrace improvement programs from *Striga* endemic areas in which field resistant cultivars were developed. Some also came from wild relatives of the crop. Sorghum and *Striga* share a common center of origin and, therefore, it is perhaps not surprising that the crop should have developed ways to overcome the pest over time. We have taken advantage of the natural resistance available in the primary sorghum gene pool and combined resistance characters into agronomically elite cultivars. Successful application of this approach resulting in deployment of sorghum genotypes with stacked genes and supplemented with agronomic options was recently detailed in a special supplement to *Crop Science*.<sup>19</sup>

## The Maize Crop in Africa

Unlike sorghum, maize is not native to Africa. Maize arrived in Africa through various introductions as long ago as 500 years.<sup>20</sup> Since then its range has expanded from lowlands to the highlands as well as from the marginal to optimal soil fertility environments with varying success. Maize has thus become the number one crop in the continent both in cultivated area and total grain production.<sup>21</sup> Some early names for maize like *yababar mashila*, meaning “sorghum from the sea,” in Ethiopia and *Piti*, “sorghum with a hat,” and *Mala*, “sorghum that carries a child,” in Nigeria attest to the alien nature of this New World crop in Africa and its resemblance to native sorghum.<sup>20</sup>

Perhaps owing to its exotic origin, maize shows greater susceptibility to abiotic and biotic stresses prevalent in the continent, including *Striga*. There has been an apparent paucity of *Striga* resistance genes among landraces of maize in Africa, although some tolerance was identified.<sup>22</sup> Some argued that a New World crop might not have any natural resistance to this Old World foe.

## *Striga* Resistance in *Zea* and *Tripsacum*

Encouraging reports of *Striga* resistance in maize or its wild relatives have emerged over the last decade. In a collection of perennial teosintes (*Zea diploperennis*) screened in a pot study, about 10% of the entries showed resistance relative to the other teosinte accessions and to maize. Resistant individuals had fewer attached *S. hermonthica* able to establish vascular connections. Among parasitic seedlings able to reach the vasculature of these resistant individuals, many died within a few days of penetration and those few parasites that eventually emerged in the resistant *Z. diploperennis* pots were smaller than those on the non-resistant types and on the *Zea mays* check.<sup>23</sup>

Another wild relative of maize, *Tripsacum dactyloides*, expressed resistance such that *S. hermonthica* attached at a frequency 25% that on *Z. mays*, and those attached *Striga* were much less likely to progress to the developmental stages reached by those on maize during the six weeks of observation. Although some parasites were able to tap the xylem of the *Tripsacum dactyloides* hosts, subsequent haustorial development was diminutive compared to the acquisition organ developed after vascular connection on the maize hosts. At the end of six weeks of laboratory co-culture, the average total dry weight of supported *Striga* shoots on the roots per *Tripsacum dactyloides* plant was 1000x less than that of *Striga* on maize.<sup>24</sup>

Tropical maize types occasionally show resistance reactions, but those are often associated with avoidance or escape mechanisms.

Hybrid maize selections from resistant x resistant inbreds, supported fewer emerged parasites and these emerged *Striga* plants on the resistant hybrids were less likely to flower and set seed.<sup>25</sup> Short cycle maize entries tested in Kenya generally were less attacked by *Striga* than long cycle varieties.<sup>26</sup>

## Evidence of *Striga* Resistance in Improved Maize

We recently reported resistance reactions manifested in laboratory co-culture in a cultivated maize inbred line, ZD05, developed through a longterm breeding effort at the International Institute for Tropical Agriculture (IITA).<sup>27</sup> This inbred was selected for its field resistance to *S. hermonthica* and has in its pedigree *Zea diploperennis* as well as tropical maize germplasm.<sup>28</sup> In the field it had reduced numbers of emerged *Striga* but the underlying mechanism of this resistance was uncharacterized. Laboratory observations of the early interactions with *S. hermonthica* revealed that ZD05 had fewer thin root branches than the susceptible maize to which it was compared. Furthermore, it had fewer attachments than the susceptible inbred, even though equal amounts of pre-germinated *Striga* were placed on the roots of both. The *Striga* that did attach usually died on the resistant roots, rarely developing to the growth stages attained on the susceptible maize. Microscopic investigation of dissected parasitic attachments showed retarded haustorial development on ZD05 relative to that on susceptible maize. These manifestations of resistance echo what was reported in similar investigations of wild maize, *Zea diploperennis*<sup>23</sup> and *Tripsacum dactyloides*,<sup>24</sup> except that these reactions occurred in an improved *Zea mays* inbred. Both of the resistant wild maize reports looked at early generations of progeny from the resistant accessions finding weaker expression of resistant reactions relative to the donor parent. Our report shows that the strong resistance manifest in these progenitors can be successfully transferred to cultivars. This points to potential gains to be made through plant breeding using careful selection protocols.

With these reports of true resistance reactions captured in cultivated *Z. mays*, building durable *Striga* resistance in the crop appears likely. *Striga* resistance is most effective when expressed early in the parasitic life cycle since *Striga* causes much damage during establishment.<sup>6</sup> Like our approach in sorghum,<sup>19</sup> and similar efforts in grain legumes against *Orobanche*,<sup>29</sup> sustainable resistance could be attained in maize by pyramiding multiple characters against the parasite in varieties intended for *Striga* endemic environments. It appears that ZD05 already has three defenses: avoidance through a less branched root architecture, some ability to resist attachments of nearby germinated *Striga* and a kind of incompatibility that does not support normal growth of attached parasites.

Although we found resistant inbred ZD05 shows no difference from susceptible inbreds in its ability to stimulate *Striga* seed germination or haustorial initiation (unpublished results), these pre-attachment defenses are not completely unknown in the maize gene pool. In the study with *Tripsacum dactyloides*, Gurney et al.,<sup>24</sup> reported an approximate 2/3 reduced ability of *T. dactyloides* root exudate to stimulate germination of warm stratified *S. hermonthica* seed relative to the *Z. mays* exudate they tested. This group also reported some lower stimulant types against *S. asiatica* germination among improved maize inbreds.<sup>30</sup>

In recent years, much has been learned about the nature of host produced signals needed for parasitic weed seed germination, the

strigolactones, since the discovery of their alternate role as hyphal branching factors for AM fungi.<sup>31</sup> Maize produces at least two strigolactones with *Striga* germination stimulant activity.<sup>32</sup> Evidence from inhibitor and mutant studies suggests that these are synthesized from cleavage of carotenoids in maize.<sup>33</sup> Mutations that specifically alter or eliminate strigolactone production in maize may exist naturally or could be induced through targeted mutagenesis resulting in low *Striga* germination stimulant activity as we have exploited in sorghum.<sup>19</sup> Such mutagenesis may have already occurred in sodium azide treated maize in Kenya.<sup>34</sup> Some progeny of these mutagenized seeds produced root exudates with very low or no germination stimulant activity on *S. hermonthica* seeds.

There is also some evidence, again in *T. dactyloides*, that low haustorial initiation activity may exist in the maize gene pool. Gurney et al.,<sup>24</sup> found that the frequency of *S. hermonthica* attachments on *T. dactyloides* was much improved by the addition of syringic acid, a compound with high haustorial initiation capacity.<sup>35</sup> Like the low haustorial initiation activity noted in some wild sorghums,<sup>16</sup> this trait could be a useful early defense against *Striga* attachment.

As in sorghum, it may now be possible to counter *Striga* parasitism in maize at its earliest stages, before its notorious bewitching effects on the crop occur. Based on observations to date, there is evidence that *Striga* resistance genes have been placed in maize that can intervene at several points in the pre-emergent stages of the *Striga* life cycle. Maize resistance can be expressed through low stimulation of *Striga* seed germination,<sup>24,30,34</sup> low haustorial induction,<sup>24</sup> avoidance through root architecture (fewer thin branches),<sup>27</sup> escape by early maturity,<sup>26</sup> resistance to attachment (as expressed by ZD05—seemingly *not* the result of low haustorial initiation)<sup>27</sup> and failure to support attached parasites (incompatibility).<sup>23,24,27</sup>

## Gene Stacking for Effective Control

The ability of *Striga*, particularly *S. hermonthica*, to overcome resistance is known.<sup>36</sup> Deliberate stacking of resistance characters into deployed cultivars decreases likelihood of resistance breakdown. Virulent *Striga* races would be less likely to emerge if multiple mutations were required to overcome host resistance genes.<sup>29</sup> *Striga* resistance in maize, reported to date, appears to be qualitative and recessive in nature,<sup>23-26,37</sup> qualities that may further ensure its stability.<sup>38</sup>

For national and regional deployment, integrating genetic resistance with other control measures is the smartest option possible both for effectiveness of control as well as for increasing durability of resistance genes.<sup>11</sup> One such technology currently being deployed as a complement to *Striga* resistance in maize involves use of herbicide as a seed coating. A mutation for herbicide resistance in maize was recently exploited as a *Striga* control technology in East Africa.<sup>39</sup> Seed treatment of imidazolinone resistant (IR) maize with herbicide, combining low doses of imazapyr (<30 g/ha) to maize gave effective control of *Striga* in the early stages of parasitic attachment to maize seedlings. The technology was field tested successfully for multiple seasons before it was trademarked by BASF as “Strigaway” and deployed in a hybrid maize distributed by a private seed company. A second generation maize hybrid is expected to possess an introgressed stack of herbicide resistance from IR maize with native *Striga* resistance genes from *Zea diploperennis*. Maize breeders at IITA are currently engaged in developing such maize hybrids for deployment in West Africa.

Pyramiding multiple resistance characters into maize cultivars for *Striga* prone areas would be greatly aided by the ability to phenotype breeding materials for the component traits and ultimately taking this to the genotypic level by robust molecular markers. Developing these markers may be easier in maize for which powerful genomic resources exist. Moreover, comparative genomics can provide new discoveries of important resistance genes as they are discovered in other crops against weedy root parasites.<sup>38</sup> Maize is also amenable to new technologies such as RNAi<sup>40</sup> to supplement natural resistance since it can be efficiently transformed. Transgenic approaches, however, are likely to meet obstacles to deployment unless we remain cognizant of the delivery schemes available to the end users of *Striga* control technologies. African seed delivery mechanisms need to be built up to ensure reliable availability of good seed on a timely basis. Stacking resistance genes in an open pollinated landrace for communal seed production is not wise, for example, as the genes are likely to segregate in open pollination during seed propagation. Delivering such a technology via commercial hybrid seeds produced by an organized private seed sector would guarantee timely supply of quality seed in sufficient quantity each year. With organized plant breeding and improved seed production capacity, new and replacement resistance genes can be continually bred in and deployed. As in the case of the native American sunflower against the Mediterranean root parasitic weed *Orobanche*,<sup>41,42</sup> sustained resistance to *Striga* is likely possible even for the transplanted “sorghum of the sea”.

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