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Striga Resistance in Cereal Crops: Recent Progress and Future Prospects. A Review

By Maryam A. Dawud
Lake Chad Research Institute

Abstract- Production of cereal crops such as sorghum, maize, rice and millet is threatened by Striga hermonthica (Del.) Benth and Striga asiatica (L.) Kuntze in sub-Saharan Africa and India. Varying levels of resistance have been identified and exploited in the breeding programmes of several crops. Considerable efforts have been invested in breeding for Striga resistance in cereals and significant progress has been made in the development of improved selection methods. However, the level of protection achieved to date is incomplete especially for orphan crops such as pearl millet. Resistance is mainly determined by the coexistence of several mechanisms controlled by multigenic and quantitative systems. Efficient control of the parasite requires a better understanding of the interaction and their associated resistance mechanisms at the histological, genetic and molecular levels. Application of postgenomic technologies and the use of model plants should improve the understanding of the plant–parasitic plant interaction and drive not only breeding programmes through either marker-assisted selection (MAS) or transgenesis but also the development of alternative methods to control the parasite.

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Abstract- Production of cereal crops such as sorghum, maize, rice and millet is threatened by Striga hermonthica (Del.) Benth and Striga asiatica (L.) Kuntze in sub-Saharan Africa and India. Varying levels of resistance have been identified and exploited in the breeding programmes of several crops. Considerable efforts have been invested in breeding for Striga resistance in cereals and significant progress has been made in the development of improved selection methods. However, the level of protection achieved to date is incomplete especially for orphan crops such as pearl millet. Resistance is mainly determined by the coexistence of several mechanisms controlled by multigenic and quantitative systems. Efficient control of the parasite requires a better understanding of the interaction and their associated resistance mechanisms at the histological, genetic and molecular levels. Application of postgenomic technologies and the use of model plants should improve the understanding of the plant–parasitic plant interaction and drive not only breeding programmes through either marker-assisted selection (MAS) or transgenesis but also the development of alternative methods to control the parasite. However, it is only a beginning that requires to be further exploited. This review presents an overview on recent advances in research on Striga in cereals and potential prospects using genomic tools as mentioned above with a final aim of crop improvement.

Keywords: striga spp., resistance, cereals, recent progress, potential prospects.

I. Introduction

Parasitic plants are a major threat to today's agriculture and provide an intriguing case of pathogenesis between species of relatively close evolutionary ancestry. Almost all crop species are potential hosts for parasitic plants, but severe disease outbreaks are usually restricted to certain host–pathogen combinations (Spallek et al., 2013). The evolutionary strategy of exchanging autotrophy for dependence on host plants (parasitism) may seem odd, but it has proven to be evolutionarily successful for several plant species. Plant parasitism has arisen at least 12 times independently, generating more than 4000 parasitic dicotyledonous plant species (Westwood et al., 2010). Although some parasitic plants are still photosynthetically active (hemiparasitic), others are not, and depend entirely on a host (holoparasitic). The establishment of parasitism is essential for holoparasites and several hemiparasites such as *Striga* spp., and therefore these species are called obligate parasites (Parker, 2009).

The genus *Striga* consists of obligate hemiparasitic root parasites, some of which are serious agricultural pests (Parker, 2009).They are a major biotic constraint and a serious threat to subsistence cereal crops (Pearl millet, finger millet, sorghum, maize and upland rice) grown in sub-Saharan Africa and India ((Rispail et al., 2007; Teka, 2014). In *Striga*-prone regions, *S. hermonthica* (Del.) Benth. and*S. asiatica*(L.) Kuntze are the most economically important weeds (Ejeta, 2007; Atera et al., 2011) that infect sorghum [*Sorghum bicolor* (L.)Moench], maize [*Zea mays* (L.)], upland rice [*Oryza sativa* (L.)] and pearl millet [*Cenchrus americanus* (L.) Morrone]. *Striga* spp. are now often identified as the greatest biological constraint to food production, and have been estimated to infest some 64% of the total cereal production area in West Africa (Figure 1) (Gressel et al., 2004; Ejeta, 2007; Parker, 2012), and are continuing to expand. Infection of crops can result in grain yield losses, of 20-80% in Africa but up to 100% in worst situations, and as consequence, have a significant negative impact on food security in these regions (Gurney, Press, & Scholes, 2002).

Author: Cereals Department, Lake Chad Research Institute, Maiduguri, Borno State, Nigeria. e-mail: maryamdawud6@gmail.com

Figure 1: *Striga* affects millions of smallholder farmers in sub-Saharan Africa(Mignouna et al., 2013)

Infested area and level are likely to increase in the near future because of continued increase in cereal monoculture in some parts of Africa that has led to reduced soil fertility coupled with high moisture stress, and the weed has consequently been described as an indicator of low soil fertility (Oswald, 2005;Teka, 2014). Agronomic control of *Striga* aimed at limiting *Striga* seed production, but as each *Striga* plant sets tens of thousands of seeds that can live for so many years, control appears very difficult (Kountche, 2013). Genetic control of *Striga*, where possible, is widely considered to be the most practical and economically feasible method for long-term control of *Striga* (Ejeta, 2007; Hearne, 2009; Yoder & Scholes, 2010).

Many scientists (Haussmann et al., 2001; Omanya et al., 2004; Gurney et al., 2003; Cissoko et al., 2011; Jamil et al., 2011) in the past have made intense investigation, to characterize the mechanisms and inheritance of resistance to *Striga* spp. in some major cereal crops such as sorghum, rice, and maize. This was followed by the development of molecular markers associated with *Striga* resistance and quantitative trait loci (QTL) in sorghum and their introgression into elite varieties (Haussmann et al., 2004;Gurney et al., 2006; Satish et al., 2012; Mutengwa et al., 2005; Rispail et al., 2007). However, despite these efforts, precise, validated information on the inheritance of resistance to *Striga* is still lacking in cultivated pearl millet (Kountche, 2013). Some scientists report the presence of resistance to *Striga* in cultivated pearl millet (Ramaiah, 1987), but these reports were questioned by other authors (Chisi & Esele, 1997). So far, Wilson et al. (2000, 2004) reported the presence of partial quantitative resistance to *S. hermonthica* in wild pearl millet relatives originating from Africa.. Kountche (2013) also stressed that, progress in genetic, genomic and physiological characterization of *Striga* resistance mechanisms is essential for the sustained improvement of pearl millet, which is the least studied major cereal crop cultivated in Africa.

This paper presents the latest information on breeding for resistance to *Striga* in cereal crops and future prospects.

II. Striga Biology and Life Cycle

'*Striga*' is the Latin word for 'witch'. Witchweed, Mukarram (Shuwa Arab), Maakasha or wuta wuta (Hausa) and other common names for *Striga* often refer to the word 'witch', fire or killer presumably because plants diseased by *Striga* display stunted growth and an overall drought-like phenotype long before *Striga* plants appear. *Striga* species are annual plants and most of their life cycle occurs underground (figure 2) (Spallek et al., 2013). *Striga* plants are highly reproductive (10 000 to 200 000 seeds) and can remain dormant in the soil for more than 20 years before germination (Parker & Riches, 1993). Germination is linked to the presence of a nearby host, because the endosperm of *Striga* seeds can sustain it survival only for the first 3–7 days (Berner et al., 1995). Within that time, *Striga* must successfully establish a parasitic relationship with the host plant or otherwise die. This aspect was successfully exploited during *S. asiatica* eradication programme in the USA, when 'suicide germination' was induced by fuming farmland with ethylene to trigger *Striga* germination in

the absence of host plants (Parker, 2009).These *Striga* seeds germinates only in response to specific chemicals, most commonly strigolactones, which are apocarotenoid signaling molecules (Matusova et al., 2005). The germination of *Striga* depends on the perception of germination stimulants released by host roots. In order to be responsive to germination stimulants, *Striga* seeds must go through a phase of moisture and high temperatures for 7–14 days, called 'conditioning'. If, during that time, no germination stimulant is perceived, *Striga* seeds fall into a secondary dormancy. Strigolactones are certainly the best studied and extremely potent inducers of *Striga* germination (Spallek et al., 2013). The signals are then released by the host plant roots into the rhizosphere (Bouwmeester et al., 2003;Yoneyama et al., 2010; Xie et al., 2010). The concentration of stimulant required to initiate *Striga* seed germination ranges from 10-10 to 10-16 mole m^{-3} (Hearne, 2009). When the appropriate concentration is achieved, each *Striga* seedling establishes a sticky radicle which, in response to haustorial initiation factors derived from the host roots (such as quinone), forms the haustorium. In contact with a host root, the haustorial cells undergo a remarkable differentiation processes to form a wedge-shaped group of cells that penetrates the host root cortex and endodermis to establish parasite-host xylem–xylem connections (Figure 2) (Albrecht et al., 1999; Dorr, 1997). This allows the direct transfer of water, carbohydrates and nutrients from the host plant to the parasite, drastically reducing host plant growth and yield (Parker & Riches, 1993; Van, 2006). Subsequently, *Striga* grows upwards and adventitious roots are produced, emerges above the ground and flowers to produce seeds (Spallek et al., 2013).

In many cases, *S. hermonthica* seeds collected from one cereal host can infect other cereal species, although there is evidence for some interspecies specificity, particularly with respect to the reciprocal infectivity of populations of *S. hermonthica* collected from sorghum and pearl millet (Vasudeva & Musselman, 1987). Perhaps, genetic variation is likely to be maintained within populations (ecotypes) from generation to generation, especially in *S. hermonthica* (Bharatha et al., 1990). More recently, the presence of genetic variation for host range specificity within *S. hermonthica* populations have been reported by Huang et al.(2011). The dual phase life-cycle of parasitic weed and its mode of action make it difficult to control (Kountche, 2013). Furthermore, host plant resistance to *Striga* involves physiological and genetic mechanisms and requires a thorough understanding of the biophysical processes of the host-parasite interaction (Figure 2).

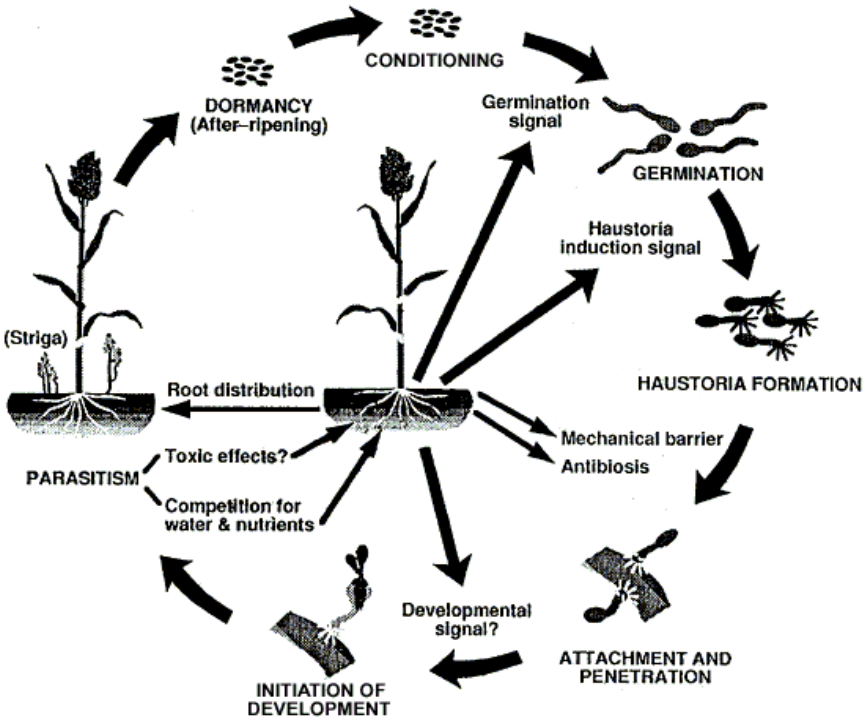

Figure 2: Stages in *Striga*life-cycle and its interaction with the host plant(Ejeta & Butler, 1993)

III. Striga Control Methods

Research aimed at *Striga* control has been carried for a long time and a wide range of technologies have been developed (Atera et al., 2011). Despite efforts made to control the *Striga* problem, it has persisted and increased in magnitude prompting to research aimed at preventing infestation. Many potential *Striga* control

methods have been applied, ranging from agricultural practices to biological control (Joel, 2000). According to Haussmann et al.(2000) *Striga* control strategies can be broadly classified into three major categories that have different impacts on a *Striga* population: (1) reduction of the *Striga* seed bank; (2) limitation of *Striga* seed production; and (3) reduction/prevention of *Striga* seed dissemination to uninfested fields. Also, Strategies may be directed to the alternative management options of *Striga* control, containment, or eradication (Ejeta & Gressel, 2007). Although, control of *Striga* could be slow but is feasible. The severity of *Striga* damage and infestation can be reduced with well-managed practices and measures that fit the local knowledge, economy, as well as labor capacities, and practiced for several seasons. Four independent *Striga* control approaches that have been widely investigated and developed have been outlined by Ejeta and Gressel (2007); cultural, chemical, genetic, and biological options. Some of these control options aim to improve soil fertility, through the use of organic and inorganic fertilizers, while others directly affect the parasite (Rector, 2009). So far the various control options available to farmers include; the use of cultural and mechanical practices such as hand-pulling, crop rotation, trap-cropping, intercropping, appropriate improvement of soil fertility, soil and water management, tillage and planting methods (Hess & Dodo, 2004; Jamil et al., 2011) biological control using the insect *Smicronix* spp or pathogenic fungus *Fusarium oxysporum* as a mycoherbicide (Marley et al., 2005; Zahran et al., 2008; Rebeka et al., 2013) application of chemicals using pre-emergence and post emergence herbicides (Kanampiu et al., 2003) and host plant resistance (sorghum, rice and maize) (Parker & Riches, 1993; Haussmann et al., 2000; Gurney et al., 2006;Hearne, 2009; Teka, 2014). The fact that symptoms of *Striga* damage on the host appears before *Striga* emerge above the ground illustrates how ineffective the control of the parasite by hand weeding or application of herbicide is likely to be. Therefore, control methods that affect *Striga* germination and attachment to the host are expected to be more effective because they prevent the host from *Striga* parasitism. Nevertheless, former techniques are important because they could avoid the reproduction of *Striga* thereby reducing the seed bank. Elzein et al. (2010) reported *Fusarium oxysporum* is highly effective in hindering germination, growth and development of *Striga*. Also, the fodder crop legume, *Desmodium uncinatum* is highly effective in controlling *Striga* as reported by Khan et al.(2008), as it attract the parasite thereby preventing the host from *Striga* attack. In general, only a few of these control measures have been widely adopted or commercialized. Low adoption of the control practices are as a result of limited knowledge of the problem, its biology, the lack of labor or resources to make the needed investment, an uncertainty of potential control, and a return to investment, and an unwillingness to make the long-term investments (Joel et al., 2007). Considering the challenges to a successful control of the parasitic weed so far, it is generally believed that no single method of control can provide an effective and economically feasible solution. Therefore, the most practicable, comprehensive and sustainable way to deal with this parasitic weed is integrated control approach which is essential, ideal and useful to small-scale farmers, in order to achieve sustainable crop production (Teka, 2014; Ejeta, 2007)). Therefore, control strategies should be geared towards individual cropping systems, local needs and preferences to help adapt and optimize control strategies to different agro-ecosystems. Oswald (2005) suggested first containment, sanitation as a measure to prevent Striga damage and finally eradication, as a means to eradicate the soil *Striga* seed bank. According to FAO(2016) and Khan et al.(2008) the "push pull" system of integrated pest management inhibit *Striga* growth and does not need high levels of external inputs. Also, farmers have adapted "push pull" to allow intercropping with beans and report that their maize yields have increased three to four times. In northern Nigeria, some farmers control *Striga* by applying organic and inorganic fertilizer and crop rotation (Dugje et al., 2006). Ibrahim et al. (2014) also suggested the use of cover crops such as *Mucuna* spp. as an intercrop to reduce *Striga* infestation. The potential use of sesame as a trap-crop in integrated control of *Striga* in pearl millet was reported by Hess & Dodo (2004). Also, Midega et al. (2013) reported significant decrease in *Striga* count when *desmodium* was used as an intercrop to control *Striga* in maize. Integrated *Striga* management package combining a mycoherbicide based on *F. oxysporum* isolate and host plant resistance has been demonstrated on farmers' fields as effective *Striga* control approach (Yonli et al., 2012; Teshome, 2013; Teka, 2014). All these facts demonstrate the need for integrated *Striga* control as an effective tool in addition, reduce the environmental impact of individual control strategy. It has generally been accepted that, *Striga* can be controlled if a wide range of individual control methods are brought together as a program of integrated *Striga* control (ISC), to serve a range of bio-physical and socio-economic environments (Ellis-Jones et al., 2004; Douthwaite et al., 2007; Harker & O'Donovan, 2013). According to Atera et al. (2011) the major objective of ISC is to reduce *Striga* densities in the soil thereby avoiding new *Striga* plants from emerging in the subsequent seasons. Moreover, integrating genetic resistance with other technologies is the smartest option possible both for effectiveness of control as well as for increasing durability of resistance genes (Ejeta, 2007; Cissoko et al., 2011). In recent years, efforts have been undertaken to elucidate the molecular characterization of the host plant – parasite interaction and host resistance through expression analysis of the genes,

proteins and metabolites involved in these processes (Rispail et al., 2007; Aly, 2012). Recent discovery of a new class of plant hormones, strigolactones by Yoneyama et al. (2010) not only controlled branching but also play a role in attracting *Arbuscular mycorrhizal fungi* (AMF).Strigolactones are certainly the best studied and extremely potent inducers of *Striga* germination (Xie et al., 2010; Kohlen et al., 2011).

An RNA interference (RNAi) technology was recently investigated as a genetic tool for enhancing host resistance against parasitic weeds (Yoder et al., 2009). The development of herbicide-resistant crops is an alternative approach to the control of parasitic weeds (Gressel, 2009). However, these approaches use genetically modified organisms and may thus not be easily adopted by farmers and (Kountche, 2013), in addition, may be associated with problems in the field (gene flow, coexistence with local varieties). The foregoing shows that *Striga* is not a new problem on cereals in Africa; some early work was done and much is now being done to understand biology of the interaction and its control.

IV. Approaches used for Striga Resistance Breeding

Considerable efforts have been invested in breeding for *Striga* resistance in cereals and significant progress has been made in the development of improved selection methods. Haussmann et al., (2000) reported an improved field testing method for *Striga* resistance. More recently, Kountche et al. (2013) used phenotypic recurrent selection to breed for *Striga* resistance under field conditions and this resulted in significant improvement in *Striga* resistance in cultivated pearl millet and the development of the first pearl millet *Striga*-resistant experimental varieties. However, multi-location field screening for *Striga* resistance resulted in significant genotype ×environment (G×E) interactions for *Striga* resistance traits in sorghum, maize and pearl millet trials (Haussmann et al., 2001; Badu-Apraku et al., 2010). These results suggest that there is need to select for specific adaptation in *Striga* resistance breeding, particularly in the case of contrasting environments where different putative *Striga* ecotypes may exist. The use of laboratory-based assays, on the other hand, has enabled further insights into the interactive biological processes between *Striga* and the roots of host plants during each individual stage of the parasitic process (Ejeta, 2007). The power of the physiology-based breeding approach is that it pushes the limit of what would traditionally be considered good source material for resistance to the parasitic weed (Kountche, 2013). Physiology-based approaches have also threw more light on the specific mechanisms of resistance associated with each source of host genotype (Ejeta & Butler, 1993; Gurney et al., 2006). However, laboratory experiments need to be tested in the field, because laboratory environment is different from field environment. Recently, a number of genes or chromosomal regions that control quantitative traits, quantitative trait loci (QTL), associated with resistance to *Striga* spp. in sorghum (Haussmann et al., 2004; Satish et al., 2012), and rice have been reported (Gurney et al., 2006; Kaewchumnong & Price, 2008). As a result, QTLs have been refined to introgress *Striga* resistance into farmer-preferred sorghum varieties in most parts of African countries (Grenier et al., 2007). Marker assisted-selection techniques for parasitic plant resistance can be used to rapidly accumulate several resistance genes (Rispail et al., 2007). However, marker-assisted backcrossing (MABC) has certain limits for introgressing a quantitative trait (Kountche, 2013). Since markers to be used in MABC are usually identified in biparental mapping populations, this becomes a limitation in exploiting potentially wider range of allelic diversity present in the crop species, and markers may be valid only for the genetic background in which they were identified (Varshney & Dubey, 2009). The limitation of pyramiding quantitative traits with minor effect brought about the use of marker-assisted recurrent selection (MARS) as an indispensable breeding strategy for developing germplasm with durable resistance(Bernardo & Charcosset, 2006). However, the most important point to note in molecular breeding for resistance to *Striga* is the identification of strong associations between genetic markers and the genes that determine resistance to the parasite.

Because of the ability of *Striga* spp., particularly *S. hermonthica*, to break down resistance (Rich & Ejeta, 2008), deliberate stacking of quantitative (polygenic) resistance in addition to the qualitative (monogenic) resistance in the cultivars to be used reduces the likelihood of resistance breakdown. Gene stacking is of upmost importance for durability because multiple mutations would have to accumulate in the parasite population to overcome resistance genes in the host (Rich & Ejeta, 2008). Kountche et al. (2013) reports that, the use of genetically different *Striga*-resistant open-pollinated cultivars, with different resistance alleles, could be a practical alternative to stability of resistance over time.

V. Research Achievements

Significant advances have been made on *Striga* control research in Africa from 1940s onwards (Andrews, 1947; Ejeta, 2007) and, in the last 20 years these efforts have been increased and considerable resources have been invested in developing control options (Oswald, 2005; Khan et al., 2010; Midega et al., 2013). Several organizations have been involved in conducting *Striga* control research in Africa. These includes; International Maize and Wheat Improvement

Centre (CIMMYT) (Odhiambo & Ransom, 1993)); International Centre of Insect Physiology and Ecology (ICIPE) (Khan et al., 2008); International Crops Research Institute for the Semi-Arid-Tropics (ICRISAT) (Haussmann et al., 2001); Integrated soil fertility management program in sub-Saharan Arica by IITA, IFDC and IPNI (Vanlauwe et al., 2015); African Agricultural Technology Foundation (AATF) and International Institute of Tropical Agriculture (IITA) (Manyong, 2008). Other institutions from advanced countries mostly from Europe (The UK and The Netherlands), USA and Canada have also been involved in conducting research on *Striga* (Andersson & Halvarsson, 2011). Recently, a four-year project *Achieving sustainable Striga control for poor farmers in Africa* (April 2011-March 2015) reported by Oluoch et al.(2014), also known as the Integrated *Striga* Management Project (ISMA), was conducted to improve the livelihoods of over 25 million small-holder farmers in northern Nigeria (15 million) and western Kenya (10 million) in the long term. Sustainability, which is one of the key aspects of the project, focuses on stakeholder involvement and feedback mechanisms. Project activities have been positioned within national programs (IITA, CIMMYT, ICIPE, Institute of Agricultural Research, Ahmadu Bello University, Nigeria, Bauchi State Agriculture Development Programme (BSADP), AATF) and local project sites to assure end users' access to technical information, technologies, and experience. More than 10 herbicide and *Striga* resistant maize hybrids and OPVs have been developed and promising materials have been identified for further testing and potential release in the two countries. These institutions have recommended control options to farmers in Nigeria geared towards reducing infestation and damage. The options include: the use of resistant crop varieties, intercropping of cereals and legumes, crop rotation, use of trap crops that stimulate suicidal germination such as *desmodium*, and application of manure and nitrogenous fertilizer.

Research on the parasitic weed, have been going on for so long that it would be wrong to suggest that there has been little progress in their control. From the aforementioned studies, dedicated work leading to useful *Striga* control strategies have been done on at least local basis.

VI. Next Generation *Striga* Research

A thorough knowledge of the molecular bases of resistance to *Striga* is essential to provide the fundamental information necessary to drive not only crop improvement but also the development of alternative control methods.

In recent years, efforts have been undertaken to elucidate the molecular events underlying *Striga* infections using next generation and conventional sequencing technology (Yoshida et al., 2010). For example, comparative studies on repetitive regions in five *Striga* species generated a total of about 2200 Sanger sequence reads and about 10 000 454 reads (Estep et al., 2012). Partially assembled and identified repeats were most similar to the most closely related plant species. Overall, the authors came to the conclusion that the analysed *Striga* genomes have a rather typically complex angiosperm genome. Estimated haploid genome sizes range from 615 Mb for *S. asiatica* and 1425 Mb for *S. hermonthica* suggesting several polyploidization events.

No evidence of large transfers of repetitive DNA regions from the hostgenomes was observed, which is in contrast with the observed HGT events between monocot genes and *S. hermonthica* (Yoshida,et al., 2010), and favours the hypothesis that HGT events originate from mRNA species rather than from large pieces of genomic DNA.

Until recently, genomic resources associated with resistance to parasitic weeds due to RNA interference were rare. This new strategy has great potential for the control of parasitic plants (Jennifer, 2012). Thanks to the great progress made in the Parasitic Plant Genome Project' (http://ppgp.huck.psu.edu/) (Westwood et al., 2012), genetic resistance based on silencing of a target gene in the host plant is now feasible (Yoder et al., 2009).

Nevertheless, there is still a need for further research into the mechanisms involved in the translocation and regulation of the macromolecules involved in host- parasite interactions (Aly, 2012).

Moreover, comparative genomics can point to important resistance genes and signaling pathways in pearl millet as they were discovered in other *Striga*- host cereal crops (Michelmore, 2000; Rispail et al., 2007). Alignment of the high-density pearl millet genetic map currently under development will thus enable exploitation of comparable grass resources for the identification of potential *Striga* resistance genes in pearl millet (Devos & Gale, 2000; Kountche, 2013).

Next-generation sequencing technology has led to an increase in available transcriptional data for *S. hermonthica* and related species. For example, Wickett et al.(2011) analysed sequence data obtained from Illumina short reads of mRNA isolated from above-ground tissue of three Orobanchaceae species: the facultative hemiparasite *T. versicolor*, *S. hermonthica* and *Phelipanche aegyptiaca* (pers.) Pomel. The expression of photosynthesis-related genes was much lower in *S. hermonthica* than in *Triphysaria*, and no expression of these genes was detected in *Phelipanche*. The study also revealed that chlorophyll *a* synthesis gene expression was conserved and detectable in all three species, even in the non photosynthetically active *Ph. aegyptiaca*.

Next-generation sequencing technology will almost certainly provide detailed transcriptional information for *Striga* at different stages of infection and on different hosts, and will allow the simultaneous detection of host and pathogen transcriptomes. So far, host transcriptome data are mainly based on microarray studies or similar methods. Hiraoka et al. (2009) used a suppression subtractive hybridization strategy of mRNA isolated from *Lotus japonicus* to investigate differences when infected with *S. hermonthica* (resistant) or *Ph. aegyptiaca*.

The accumulation of cytotoxic material is also probably the cause of nonhost resistance to *S. hermonthica* in *Tripsacum dactyloides*, a wild relative of maize. In contrast with *Z. mays*, haustoria formation is impaired on *T. dactyloides* plants by an unknown factor. This factor is also able to suppress haustoria formation on *Z. mays*, when *Striga* plants are attached to *T. dactyloides* at the same time (Gurney et al., 2003).In rice, when one susceptible rice variety (IAC 45) and one resistant variety (Nipponbare) were infected with *S. hermonthica* and analysed 2, 4 and 11 days after infection using whole-genome microarrays (Swarbrick et al., 2008), the incompatible interaction between *S. hermonthica* and Nipponbare showed enhanced expression of defence-related genes, such as genes encoding pathogenesis-related (PR) proteins, WRKY transcription factors and pleiotropic ABC transporters, whereas the compatible (susceptible) interaction was characterized by large-scale down-regulation of genes associated with growth regulation, metabolism, biogenesis of cellular components and cell division. Several genes coding for nutrient transporters, enzymes involved in amino acid metabolism, were up-regulated at the same time in the susceptible rice cultivar.

Overall, these data, although sometimes very difficult to compare, draw a common picture, in which *Striga* is actively recognized by resistant plants and triggers a defence-like response. This response appears to be very similar to that observed for other nonhost or race-specific resistance responses to other plant pathogens. It also shows that *Striga* actively manipulates host transcription to foster parasitism by either up-regulating host genes associated with nutrient supply or by down-regulating defence-related genes. It is not known how *Striga* manipulates transcription in host plants. Avirulence gene products are interesting candidates, but difficult to isolate as a result of limited genetic resources in parasitic plants.

VII. Conclusion

Over the years, many researchers have tackled the problems caused by parasitic plants in infested regions. Although advances have been made in the understanding of the interaction, complete solutions remain to be found. The lack of efficient control methods is rooted in the high complexity of the interaction and the nature of the parasite. The detection of partial resistance within genotypes of some crop oriented further development of control methods toward genetic crop improvement. However, the multigenic and quantitative system generally controlling the resistance dramatically slows down breeding. It is now evident that efficient control of the parasite requires a more comprehensive understanding of the molecular bases of the interaction and its transfer to breeders. The few studies targeting the analysis of gene expression and accumulation of proteins and metabolites start to reveal the molecular dialogue involved in resistance. However, it is only a beginning that requires to be further exploited. Application of some of these biotechnological tools has already been initiated to tackle plant parasite problems such as MAS or the 'omic' technology, but to develop resistant crops the inclusion of other tools such as genetic transformation and functional genomics will be needed. The most efficient approach to crop improvement would be the integration of these different tools from fundamental to applied biology. Indeed, a comprehensive understanding of the interaction obtained from molecular studies of the host responses to parasite in model plants – including transcriptomic, proteomic and metabolomic – should provide candidate genes to improve resistance in crops, which will need to be validated through functional analysis. In addition, the better understanding of the interaction and the parasite biology gained by these molecular methods may also allow the development of new methods of control. Although much work remains to be done, the different approaches presented in this review should, in the near future, provide solutions to the problems caused by parasitic plants.

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