

## 6

# STRIGA: A SERIOUS PERSISTENT PROBLEM ON MILLETS

Boubacar A. Kountche<sup>1</sup>, Salim Al-Babili<sup>1</sup> and Bettina I. G.  
Haussmann<sup>2</sup>

<sup>1</sup>King Abdullah University of Science and Technology (KAUST), Center for Desert  
Agriculture (CDA), Thuwal 23955-6900, Saudi Arabia; <sup>2</sup>Institute of Plant Breeding, Seed  
Science and Population Genetics (350a), University of Hohenheim, Fruwirthstr, 21, D –  
70599 Stuttgart, Germany

E-mail ID: [boubacar.kountche@kaust.edu.sa](mailto:boubacar.kountche@kaust.edu.sa); [salim.babili@kaust.edu.sa](mailto:salim.babili@kaust.edu.sa);  
[bettina.haussmann@uni-hohenheim.de](mailto:bettina.haussmann@uni-hohenheim.de)

## Table of Contents

<b>6</b> .....	1
<b>1. INTRODUCTION</b> .....	2
<b>2. IMPORTANCE AND BIOLOGY</b> .....	3
2.1 Importance .....	3
2.2 Biology.....	4
<b>3. HOST PLANT RESISTANCE AND HEREDITY</b> .....	5
3.1 Host finding and orientation: the key role of strigolactones .....	5
3.2 Sources of resistance.....	7
3.3 Mechanisms of resistance .....	8
3.4 Nature and genetic basis of resistance .....	10
3.5 Development and use of <i>Striga</i> -resistant millet cultivars .....	11
3.5.1 Conventional breeding .....	11
3.5.2 Marker-assisted selection.....	13
3.5.3 Transgenics .....	15
3.6 Integrated <i>Striga</i> management .....	16
<b>4. CONCLUSIONS</b> .....	17
<b>5. FUTURE PERSPECTIVES AND PRIORITIES</b> .....	18
<b>6. ACKNOWLEDGEMENTS</b> .....	18
<b>REFERENCES</b> .....	18

## SUMMARY

*Striga* spp., *S. hermonthica* (Del.) Benth. and *S. asiatica* (L.) Kuntze, are obligate root-parasitic plants of the major agricultural cereal crops, including millets, in tropical and semi-arid regions of Africa, Middle East, Asia and Australia. Consequently, they cause severe to even complete losses in crop grain yield. Though limited in their efficiency, the control strategies available today represent major progress towards combating *Striga* when compared with the absence of any means some years ago. Hence, efforts have led to the development of

powerful approaches for understanding and exploiting the complex intricate host-parasitic plant interactions. It is widely agreed that genetic resistance is the most practical and economically feasible method for sustainable control of *Striga*. Hence, research efforts have been deployed over the past decades to identify resistance sources in certain millet crops, principally sorghum and pearl millet; to characterize the mechanisms underlying the resistance and to understand the genetic basis of the identified resistance phenotype. Furthermore, application of the modern breeding tools such molecular markers has revolutionized the field of search for *Striga* resistance. Information thus generated have been extensively used to identify several sources of resistance to *Striga* and individual genes conferring host plant resistance have been deployed for improving *Striga* resistance in sorghum varieties. More interestingly, we are facing an accelerated progress in the genomic and biotechnological research that should soon provide important understanding of some crucial developmental mechanisms in both the parasite and their host plants, thereby enhancing the efficiency of breeding for *Striga* resistance in millets. In the following, we provide a detailed state-of-the-art on the recent progress and perspectives for *Striga* research and management in millets.

**Key Words:** Millet, *Striga*, Production constraint, Host-plant resistance, Mechanism, Management

## 1. INTRODUCTION

*Striga* species, known as witchweeds, are one of the most troublesome and damaging weeds in the world (Parker, 2009). They belong to the *Orobanchaceae* family (ex *Scrophulariaceae*) and are obligate root hemi-parasitic plants (Olmstead et al., 2001; Tank et al., 2006). The genus '*Striga*' comprises of 42 species worldwide, out of which *S. hermonthica* (Del.) Benth. and *S. asiatica* (L.) Kuntze (henceforth denoted as *Striga*) are deemed to be the most economically important weeds parasitizing cereals (Berner et al., 1995; Cochrane and Press, 1997; Haussmann et al., 2000; Gressel et al., 2004; Gethi et al., 2005; Aly, 2007; Spallek et al., 2013). *Striga* infest millets, such as sorghum, pearl millet, finger millet, foxtail millet, little millet, proso millet, fonio, teff and barnyard millet (Chemisquy et al., 2010; Olivier, 1995; Parker, 2012; Atera et al., 2012), which represent the staple food and fodder crops of millions of poor rural families in the tropical and semi-arid regions of their cultivation, therefore are of utmost significance to subsistence farmers. Millets thus play a critical role in ensuring food security in these regions (Hash et al., 2000; Senthilvel et al., 2008). *Striga* also attack other crops including maize [*Zea mays* L.], upland rice [*Oryza sativa* (L.)], sugar cane [*Saccharum officinarum* L.] and wheat [*Triticum aestivum* L.] (Gurney et al., 2003, 2006; Elzein and Kroschel, 2004; Vasey et al., 2005; Amusan et al., 2008). Indeed, *Striga* are the major and persistent biotic threat to production of these crops mostly grown on the hottest and driest marginal regions of sub-Saharan Africa, Middle East and large part of Asia (Gurney et al., 2002; Gressel et al., 2004; Ejeta, 2007; Rispaill et al., 2007; Scholes and Press, 2008; Parker, 2012). At present, over 50 million ha of the arable farmland under cereals in sub-Saharan Africa are infested by *Striga*. Crop yield losses due to *Striga* attacks range from a few percent to complete crop failure and depend largely on the cereal host species and variety grown, rainfall distribution, soil fertility and the *Striga* seed density in soil (Haussmann et al., 2000; Parker and Riches, 1993). The annual yield loss has been estimated to exceed US\$10 billion (Gressel et al., 2004; Venne et al., 2009; Westwood et al., 2012; Pennisi, 2015). More recently, *S. hermonthica* has been identified as one of the seven most severe biological constraints to food production. Thus *Striga* present a worrying problem to subsistence farmers with small land holdings (Pennisi, 2010).

Deployment of several management strategies, including quarantine imposed on infested areas, control of movement of farm equipment between infected and uninfested areas, intensive herbicide application and depletion of *Striga* seed bank through injecting of ethylene gas, has resulted in the control of the witchweed, *S. asiatica*, in the United States, where the parasite was accidentally introduced (Berner et al., 1995; Berner et al., 1999; Van Mourik, 2007). However, these strategies are expensive methods and are not generally available to smallholder farmers in *Striga*-prone zones of Africa and Asia. In these regions, the *Striga* problem is, in general, associated with low economic resources, low soil fertility, marginal environments with continued cereal monoculture and newly infested areas regrettably due to various human and agricultural activities (Oswald, 2005; Rodenburg et al., 2005; Parker, 2009).

Over the years, efforts have been made to develop effective measures to combat *Striga*. A number of control strategies that aim at improving soil fertility or directly affecting the parasite life have been suggested to farmers (Hausmann et al., 2000; Rector, 2009). Genetic control of the witchweed through deployment of resistant-crops has been also extensively explored in millets, especially sorghum, and to a lesser extent in pearl millet (Ejeta, 2007; Kountche et al., 2013). However, the complexity of the host-parasite relationship, the life cycle of *Striga* and the ability of the parasite to adapt to diverse environments, and the diversity of millets farming systems and that of the parasite (case of *S. hermonthica*) have made the use of a single control approach ineffective. Considering this, there has been an increased effort to combine two or more methods to address the long-term management of the root parasitic weeds (Joel, 2000; Oswald, 2005). Although these efforts have helped in reducing the *Striga* damage on the host crops, they did not result in the complete control of the parasites, as this requires the destruction of *Striga* seed bank in infested fields.

In this chapter, we present the latest knowledge on *Striga* research and control in millet crops, highlighting the main gaps in our knowledge and suggesting how these gaps can be filled. We will split this chapter into three sections; the first section deals with the complex life cycle and *Striga* impact on millets. This section should provide a brief overview on the biology of *Striga* and how this relates to current and important future control strategies. The second section describes the host plant–*Striga* pathosystem, focusing on the events up to the recognition of the host by the parasite and the genetic basis of host resistance and defense mechanisms that have evolved as part of that interaction. The literature about *Striga* research in millet crops particularly in small millets is very limited. This makes it difficult to write this chapter exclusively about the sources and genetic resistance to *Striga*, and subsequent sections. In the third section, we discuss the deployment of genetically resistant cultivars as an important component of an integrated approach towards tackling the parasitic weeds *Striga* in millets.

## **2. IMPORTANCE AND BIOLOGY**

### **2.1 Importance**

*Striga* parasitize important food and forage grain grasses (*Poaceae*) and are therefore among the most agronomically destructive parasitic plants globally. Geographically, *Striga* are widely distributed in tropical and semi-arid regions of Africa, Middle East, Asia and Australia (Cochrane and Press, 1997; Teka, 2014), and have been reported in more than forty countries globally. Occurrence of the parasites in 25 African countries has been documented, the most severely affected being located in sub-Saharan Africa and India (Figure 6.1) (Vasey et al., 2005; Ejeta, 2007; De Groote et al., 2008; Parker, 2012). Mohamed et al. (2001) suggested *Striga* to be originated from the Nuba hills of Sudan and Semien Montains of

Ethiopia. This region has been also reported to be the native place of domesticated sorghum [*Sorghum bicolor* L.]. The distribution of *Striga* in relation to ecological zones in Africa and India indicates that sorghum and pearl millet are the most parasitized hosts (Ramaiah, 1984; Parker, 2009; 2012). Thus, over 50 million ha of the arable farmland under cereals in sub-Saharan Africa are reported to be infested with *Striga* (Westwood et al., 2010). In West Africa, *Striga* has been estimated to infest 17.2 million ha, covering about 64% of the total area of the major millets like sorghum and pearl millet (Gressel et al., 2004), and the parasites have been reported to expand their infection range (Ejeta, 2007; Parker, 2012). Crop yield loss due to *Striga* infection has been estimated to range from about 10 to 31% in pearl millet experimental trial (Ramaiah, 1984). Gressel et al. (2004) reported an estimated yield loss of 26% on average in pearl millet and sorghum in sub-Saharan Africa. In areas of heavy *Striga* infestation, yield loss may even reach 90 to 100% (total crop failure) in some years (Ramaiah, 1984; Wilson et al., 2000; Gressel et al., 2004). As a result, farmers have been reported to be eventually forced to abandon highly *Striga*-infested fields (Atera et al., 2011). For these poor farmers, millets are the major staple food providing them with carbohydrates and is the main source of vitamins and minerals including zinc and iron, (Andrews and Kumar, 1992; Rai et al., 2012; Bangoura et al., 2011; Mannuramath et al., 2015; Mishra et al., 2014). Hence, yield losses lead to significant negative socioeconomic problems: *Striga* affects the life of more than 300 million people in Africa and causes economic damage equivalent or even more than US\$10 billion annually (Obilana and Ramaiah, 1992; Gurney et al., 2002; Rodenburg et al., 2005; Ejeta, 2007; Scholes and Press, 2008; Westwood et al., 2012). More recently, as a consequence, sub-Saharan Africa has been reported to be the region with the highest prevalence of poverty and undernourishment, with one in four people (24.8%) estimated to be hungry (FAO, IFAD and WFP, 2013).

## 2.2 Biology

*Striga* are annual, chlorophyll-bearing, root-parasitic plants that need a host plant to complete their life cycle. The latter is complex, intimately associated with that of the host and to the climate, particularly during post-ripening (Hearne, 2009). *Striga* plants have a high reproductive capacity: a single plant can produce 100000 to 200000 very tiny (0.15 ~ 0.30 mm in diameter) seeds, which are easily dispersible (Parker and Riches, 1993; Gurney et al., 2006; Hearne, 2009). *Striga* seeds require a period of pre-treatment, conditioning in a moist warm environment (30°C in germination bioassays) for 2 to 16 days before they acquire potential to germinate (Longan and Stewart, 1991; Parker and Riches, 1993). After this phase, germination of *Striga* seeds will be initiated only upon induction by some specific chemicals, such as *strigolactones*, released by the host roots into the rhizosphere (Bouwmeester et al., 2003; Matusova et al., 2005; Shen et al., 2006; Zwanenburg et al., 2009; Yoneyama et al., 2010; Xie et al., 2010). The concentration of such chemicals is very low and ranges from  $10^{-10}$  to  $10^{-15}$  mole  $m^{-3}$  (Hearne, 2009). The root system in *Striga* is vestigial. Instead of a usual angiosperm root system, germinating seeds establish a sticky radical, which, in response to haustorial initiation factors derived from the host roots, develops to a haustorium. The haustorium connects the host and its parasite. Indeed, upon getting in contact with a host root, the haustorium develops a wedge-shaped group of cells that penetrates the host root cortex and endodermis to establish parasite-host xylem–xylem connections (Albrecht et al., 1999). This allows the direct uptake of water, assimilates and nutrients from the host plant to the parasite. Following the establishment of the host-parasite connection, *Striga* depend entirely on the host before emergence from the soil. During this holoparasitic stage of development, the parasite inflicts a severe damage to the host. Parker and Riches (1993) reported that *Striga* parasitism resulted in chlorosis, wilting, and, therefore, in drastic reduction of host plant growth and development and even in plant death under high infection.

Subsequently, the parasites grow towards the soil surface and emerge above the ground, develop chlorophyllous shoots (hemiparasitic stage) and produces flowers and seeds which will remain viable in the soil for 20 years or even more (Parker and Riches, 1993; Berner et al., 1997). However, albeit the capacity to perform photosynthesis, *Striga* are likely not able to survive independently of a host in the post-emergence stage. Joel et al. (2007) indicated that subsequent haustorial development, attachment and penetration, as well as further growth and development of the parasite also require signals or resource commitment from the host plant. A schematic version of the intricate *Striga* life cycle is provided in Figure 6.2.

Although the parasitic plants exhibit a common life style (cycle), they show differences in reproductive phase. In a geneticist's point of view, these differences are expected to have some implications on the genetic diversity and the aggressiveness of the parasites, and, hence, on the breeding strategies towards resistant hosts. *S. asiatica* is an autogamous (self-pollinating) species and genetic diversity analyses have shown distinct races of that species across their ranges (Botanga et al., 2002). In contrast, *S. hermonthica* is a highly out-crossing species, thus it is expected to show greater diversity within a population than seen in related autogamous species (Hamrick, 1982; Koyama et al., 2000). This mode of pollination has contributed to the genetic variation in *S. hermonthica* plants and also made the restricted the geographical distribution of this species depending on the availability of pollinators (Berner et al., 1997; Mohamed et al., 2007). Genetic diversity in parasitic weed populations has been reported to impinge on host plant reaction (resistance/susceptibility) (Awad et al., 2006). More recently, Huang et al. (2011) reported the presence of genetic variation for host range specificity within *S. hermonthica* populations. This resulted in each *S. hermonthica* plant in a natural population having a different genotype and therefore carrying potentially different alleles for virulence (Kountche et al., 2013a). This intra-specific variation in the parasite implies that an acceptable level of resistance to one ecotype of *S. hermonthica*, for instance, may not hold when a cultivar is grown in the presence of different *S. hermonthica* populations. This nature of *Striga* is certainly one of the main reasons why the parasites cause significant damage on the host plant.

### **3. HOST PLANT RESISTANCE AND HEREDITY**

#### **3.1 Host finding and orientation: the key role of strigolactones**

In the course of evolution, many flowering plants have lost their autotrophic way of life and parasitized other plants in order to feed themselves directly from the host plants (Rubiales, 2003). Such parasitic plants pose a tremendous 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. So one can ask: which evolutionary conditions have favored the development of parasitism in plants? How a crop plant has become a host to the parasitic species? The evolutionary strategy of exchanging autotrophy for dependence on host plants (parasitism) may seem odd, but it has been proven to be evolutionarily successful for several plant species (Westwood et al., 2010). It has been hypothesized that during the evolution of parasitism, the parasitic plants have significantly reduced or even lost their capability for photosynthesis and, hence, cannot survive without a host plant (Xie et al., 2010). Depending on which host organ is infected, parasitic plants are grouped into stem or root parasites (Mayer, 2006).

Research on the roots parasitic plants, their interaction with the host and the environmental cues has started more than fifty years ago. One of the major questions to be answered was how the invasive root parasitic plants, including *Striga*, find and recognize their hosts. It has been reported that plants produce and release into the rhizosphere via their

roots, a multitude of compounds that play roles in plant-plant communication (Bertin et al., 2003; Hirsch et al., 2003; Steinkellner et al., 2007). Like other parasitic plants from the *Orobanchaceae* family, *Striga* seeds contain limited energy reserves, and, therefore, germinating seedlings must quickly locate and attach to suitable hosts upon germination in order to survive (Bouwmeester et al., 2003). Essentially, a bulk of work on host-parasite communication has focused on the parasitic partner and demonstrated that *Striga* recognize and invade the host via a series of developmental processes that depend on the presence of a host and are triggered by host signals: for example seed germination, haustorium formation, attachment to the host root, establishing vascular connections and penetration. Each of these complex processes has been reported to be stimulated independently by different specific host signals (Yoshida and Shirasu 2009; Estep et al., 2011). Thus, the high selection pressure associated with host co-evolution has prompted the parasite to employ efficient strategies for host recognition. To prevent the seeds from germinating too far from a host root, *Striga* have evolved a requirement for so-called 'germination stimulants' that are produced by the plant via their roots (Hirsch et al., 2003; Bouwmeester et al., 2003). Such strategy ensures the parasite seed to germinate when a host plant is within reach. Extensive work has been directed towards the characterization of these compounds, which are of economical and scientific importance for the biology and management of parasitic weeds. Cook et al. (1966) reported the first *Striga* germination stimulant, strigol, which was isolated from the roots of cotton (*Gossypium hirsutum* L.), a nonhost of *Striga*. Later, the same group discovered a new compound, strigyl acetate, from root exudates of cotton (Cook et al., 1972). The first *Striga* germination stimulant isolated from a host plant was sorgoleone, from sorghum (Chang et al., 1986). Hauck et al. (1992) reported the extraction and identification of a sorgolactone as the major *Striga* germination stimulant exuded by sorghum roots. These authors reported that strigol also occurs in root exudates of several host species of millets such as sorghum and proso millet, in addition to the related and more active sorgolactone (Hauck et al., 1992; Siame et al., 1993). After the discovery of the first root-derived germination stimulants, Butler (1995) coined the name strigolactones (SLs) for these strigol-related compounds. So far, a variety of different SLs have been isolated from a range of plant species, and it has been shown that exudates contain more than one strigolactone and differences in the composition exist even between varieties of one species (Awad et al., 2006; Xie et al., 2010; Cardoso et al., 2014).

The development of highly advanced analytical methods, for example the high performance liquid chromatography (HPLC) connected to tandem mass spectrometry (LC-MS/MS) (Sato et al., 2003), has allowed new SLs to be surveyed in the root exudates of many different plant species, including few millet species (Akiyama et al., 2005; Awad et al., 2006; Xie et al., 2007; Matsuura et al., 2008; Xie et al., 2008; Xie et al., 2009a; Xie et al., 2009b; Yoneyama et al., 2010; Kohlen et al., 2011; Ueno et al., 2011; Jamil et al., 2012).

More recently, several studies have provided evidence that SLs, which are carotenoid-derived signaling molecules, are the key cues towards first location of the host and also provide relevant directional cues (Al-Babili and Bouwmeester, 2015). The structure of these major SLs has been confirmed by total synthesis by Zwanenburg et al. (2009) and these structures (Figure 6.3) have been reviewed by Al-Babili and Al-Babili and Bouwmeester (2015).

In the meanwhile, around 20 known different SLs that have been isolated from the root exudates of different plants, all acting with varying efficiency as *Striga* and other parasitic seed germination stimulants (Muller et al., 1992; Yokata et al., 1998; Mori et al., 1999; Xie et al., 2008). Apparently, during the evolution of roots parasitic plants, SLs were selected to facilitate the process of host root recognition. This deleterious (negative) effect of SLs has led

to the question on why do plants produce SLs and why *Striga* and similar parasitic plants have selected such compounds as host finding signals? This mystery had remained unrevealed until much more recently when it was discovered that SLs are involved in establishing the beneficial arbuscular mycorrhizal symbiosis, by inducing hyphal branching in the fungal partner. , a critical step in host recognition by arbuscular mycorrhizal fungi (AMF), hence demonstrating that SLs play also a role in mediating ecologically significant interactions with the fungi (Akiyama et al., 2005). In addition, SLs are also produced in non-mycotrophic plants, suggesting that they exert other biological functions. Thus, SLs have been recognized as a new class of plant hormone that inhibits shoot branching (Umehara et al., 2008; Gomez-Roldan et al., 2008). In the meanwhile, SLs have been demonstrated to be involved in many other aspects of plant development and to coordinate plant growth and architecture in response to availability of nutrients, such as phosphate (Al-Babili and Bouwmeester, 2015). Accordingly, these findings have unveiled that parasitic plants utilized the communication cues, delivered by plants to attract their arbuscular mycorrhizal symbionts, by sensing the SLs that are released by the roots as signals for their symbiosis with AMF (Bouwmeester et al., 2007).

Though the perception of SLs induce seed germination of *Striga*, it is however not sufficient to establish the parasitic interaction: *strigol*, for example, was first identified from cotton, a non-host for *Striga* (Cook et al., 1972). That is evident by the fact that many non-host plants (such as cotton) also release. Thus, most stages of the parasite life showed a highly specific host-finding behavior and host specificity has been also determined at later stages following germination by other factors such as the haustorium-inducing factors, incompatibility reactions or the presence of toxic metabolites (Estabrook and Yoder, 1998; Goldwasser et al., 1999; Serghini et al., 2001).

The mechanisms that enable the recognition of the host by *Striga* are still elusive. However, it can be assumed that such strategies has also evolved to achieve maximal chance of parasitism under various ecological conditions. More recently, the usage of modern omics technologies is expected to shed light on the recent developments in molecular analysis and the need to study the biology of the parasitic plants at the molecular level which will provide insight into the genetic changes associated with parasitism throughout evolution (Westwood et al., 2012).

### **3.2 Sources of resistance**

The course from identification of good sources of resistance to exploitation of these sources by developing improved varieties is never straight forward. The development of improved varieties with *Striga* resistance depends on many factors. The most obvious one is the availability of resistance traits, the type of approach used to assess such trait and the power of detection. In the context of field experiments, the literature reported three types of response to *Striga*: resistance, tolerance and susceptibility. Resistance to *Striga* has been defined as the ability of the host genotype to hinder *Striga* attachment, growth and development when producing higher yield than the control susceptible genotype (Ramaiah, 1987; Ejeta and Butler 1993). While, tolerance was reported as the ability of a host plant to maintain biomass and yield compared to the susceptible genotype under the same level of *Striga* parasitism i.e., when supporting comparable numbers of *Striga* plants (Hausmann et al., 2000; Rodenburg et al., 2005; Hearne, 2009). The search for resistance or tolerance often begins by the recognition of plants around which fewer or less vigorous *Striga* plants are observed or the crop yield is less affected relative to other plants growing around them in fields deliberately infested with parasitic weed seeds. This was followed by the development of several screening, including both field and laboratory, methods that allow the assessment

of plant germplasm towards characterization for their reaction to *Striga* (Hess et al. 1992; Gurney et al. 2006; Mohamed et al., 2010; Amusan et al., 2011). The power and advantage of the laboratory-based approach is that it pushes the limit of what would traditionally (identified under field conditions) be considered good source for resistance to *Striga*.

Over the past decades, research efforts have led to the discovery of new sources of resistance to *Striga* in several host crops including millets and other cereals (Lane et al., 1997; Gurney et al., 2003; Karaya et al., 2012; Wilson et al., 2000, 2004; Gurney et al., 2006; Amusan et al., 2008; Cissoko et al., 2011). In sorghum, several cultivars and breeding lines have been reported to be resistant and/or tolerant to *Striga* (Hausmann et al., 2000; Rodenburg et al. 2006; Ejeta, 2007). Most of these donor sources have been summarized in Hausmann et al. (2000) and include Dobbs, Framida (SRN 4841), 555, N 13, SRN 6496, and SRN 39 (Ramaiah, 1987; Hess et al. 1992; Hess and Ejeta, 1992; Ezeaku and Gupta, 2004). Tesso et al. (2007) reported three sorghum cultivars (P-9401, P-9403 and PSL85061) to express resistance to *Striga*. More recently, new sorghum genotypes have been reported to be resistant to *Striga* (Robert, 2011). Resistance to *Striga* has been also documented to be present in wild accessions of *Sorghum versicolor*, *Sorghum drummondii* and *Sorghum arundinaceum* (Lane et al., 1995; Gurney et al., 2002).

In pearl millet, however, only a few reports have documented the presence of *Striga* resistance (Ramaiah, 1984; Ramaiah, 1987). Wilson et al. (2000) surveyed the presence of *Striga* resistance in wild accessions of *Pennisetum glaucum* subsp. *monodii*, a wild pearl millet relatives originating from Africa. Later, the same authors reported four accessions, PS 202 (also resistant to downy mildew), PS 637, PS 639, and PS 727, to be resistant to *Striga* (Wilson et al., 2004). Efforts to identify sources of resistance in cultivated pearl millet have followed and yielded in the identification of six resistant landraces (M141, M239, M029, M197, M017 and KBH), which show less sensitivity to the parasite and relatively higher yielding compared to susceptible controls (Kountche et al., 2013a).

Surprisingly, despite their importance as a source of nutrient-rich food grain for household farmers and the serious damage caused by *Striga* (Austin, 2006; Dida and Devos, 2006; Gigou et al., 2009; Bangoura et al., 2011; Rao et al., 2011; Mishra et al., 2014; Mannuramath et al., 2015; Muthamilarasan and Prasad, 2015), there are no similar examples of sources of resistance to *Striga* in small millets. However, because of their potential as smart crops meaning that they can provide alternative solution in the context of climate change, the small millets are now gradually being re-discovered and considered by scientists for various needs. In general, genetic resources across all millets species exist which remain highly unexplored and underused and might contain valuable additional sources of resistance to *Striga*. There is still a need for further research to characterize and identify new sources of resistance to *Striga* in millets for future exploitation.

### **3.3 Mechanisms of resistance**

At present, there is a strong consensus that resistance to parasitic plant is a multicomponent event, resulting from a battery of host plant defense acting at different levels of the host-parasite interaction (Hausmann et al., 2000; Rubiales, 2003; Ejeta, 2007). Where a potential host plant defense is expressed, it can be narrowed to a specific stage in the parasite life cycle. This has been made possible through the development and extensive exploitation of advanced laboratory- based bioassays, which have provided weed researchers with fine phenotyping tools (Hess et al., 1992; Ejeta, 2007; Omany et al. 2004). Based on the knowledge gained, it has been suggested that the overall expression of resistance to the parasites can be broken down into two major parts, pre-attachment and post-attachment, in the establishment of the parasitic association. The pre-attachment resistance mechanisms

involve host plant defense acting before the *Striga* seeds germinate to the formation of the haustorium, while post-attachment mechanisms start from the attachment of the haustorium to the host root to the subsequent parasite development (Scholes and Press, 2008; Irving and Cameron, 2009).

The first resistance mechanism observed in isolating genotypes with host plant resistance is at the level of parasitic seed germination. Some crop genotypes have been identified to produce relatively low amounts of germination stimulants, and, therefore, to induce germination of less parasitic seeds and preventing the host plant from parasitism. This resistance phenotype, which is called low germination stimulant production (*lgs*), has been commonly found in *Striga*-resistant sorghum genotypes (Hess et al., 1992; Ejeta and Butler, 1993; Jamil et al., 2011; Robert, 2011). Resistance associated with low production of germination stimulant may not be related to low production of total strigolactones, but rather to the types of strigolactones released. The sorghum-resistant cultivar SRN39 was found to produce lower amounts of 5-deoxystrigol but equal or even greater amounts of other strigolactones compared to a susceptible cultivar (Yoneyama et al., 2010). However, the low germination stimulant activity-based resistance phenotype has not been documented in pearl millet.

Furthermore, since this resistance phenotype can be threatened by individual parasites within *Striga* populations able to germinate in response to other strigolactones, additional resistance characters have been identified to be involved in host plant defense system. These include strong resistant reactions which were found to be expressed through reduced number of parasitic attachments, failure of attached parasite seedlings to establish vascular connections with the host, and by diminished growth or eventual death of the few parasites (Amusan et al. 2008, 2011). Some potential resistant host plants have been reported to lack the capacity to stimulate haustorial initiation of *Striga* germinated seeds or to produce compounds that inhibits the formation of the haustorium, an important organ towards parasite connection to host root (Gurney et al., 2003; Rich et al., 2004; Robert, 2011). Several authors demonstrated also the establishment of mechanical barriers to protect the host root from parasite penetration and access to the host plant vascular system (Maiti et al., 1984; Gurney et al., 2006; Amusan et al., 2008; Yoshida and Shirasu, 2009). Another protecting mechanism is the recognition of the invasion as a threat and the rapid mobilization of defense response such as the hypersensitive response (HR). Two sorghum-resistant cultivars (Framida and Dobbs), four breeding lines (SAR 16, SAR 19 and SAR 33) and a wild sorghum accession (P47121) have been shown to exhibit a hypersensitive-like necrosis at the site of attachment of *S. asiatica* (Hausmann et al., 2000; Mohamed et al., 2003). Recently, hypersensitive response-based resistance phenotype has been observed in some breeding materials of cultivated pearl millet genotypes, SR-EC (for *Striga*-Resistant Epis Court), but this phenotype has not been confirmed yet. Alternatively, even if penetration of the host root is accomplished, some incompatibility response has been reported to prevent a parasite from thriving or surviving to growth and emerge above the soil. Amusan et al. (2011) demonstrated that SRN39, a *Striga*-resistant cultivar of sorghum, expresses an incompatible response, in addition to the low strigolactone production activity. Ejeta et al. (2000) reported other potential post-germination mechanisms of resistance that impede attachment and emergence of *Striga* in crops. It is possible that other host plant defense mechanisms may be overlooked. However, to our knowledge none of the described resistance mechanisms has been surveyed yet in any of the small millets. There is therefore an urgent need to put efforts in the identification of resistance donor sources, the detailed characterization and understanding of specific resistance mechanisms in small millets in particular. Improved and accurate laboratory-based co-culture approaches are now available, including the extended agar gel assay (EAGA) and

the paper roll assay (PRA), that allow the determination of germination stimulant production in host roots (Hess and Ejeta, 1992; Ejeta et al., 2000), in addition to the rhizotron (root observation chamber) and microscopy, which are used to investigate post-attachment resistance mechanisms (Gurney et al., 2006), and high-performance liquid chromatography coupled to tandem mass spectrometry analysis (HPLC, LC-MS/MS) used for quantifying and characterizing the production and the type of strigolactones (Sato et al., 2003; Yoneyama et al., 2010; Jamil et al., 2011). Hence, when available, the deployment of all these sources of resistance in a single millet cultivar should provide more durable resistance to the parasitic weed *Striga*.

### 3.4 Nature and genetic basis of resistance

From the previous section, it is evident that resistance to the parasitic weeds *Striga* appears to be complex, based on a chain of resistance mechanisms that are deployed by host plant either alone or in combination throughout the parasite infection process. In general, the nature of resistance to parasitic weeds has been reported to be qualitative, usually a strong acting character controlled by one or two major genes (monogenic), or quantitative described as partial resistance inheritance governed by several alleles at multiple loci (polygenic). Efforts to understand the inheritance of traits associated with resistance to *Striga* have yielded very mixed results, with relatively good success in sorghum, only ephemeral progress in pearl millet and with no efforts invested in small millets to date.

In sorghum, the low *Striga* germination stimulant activity (*lgs*), so far the best characterized resistance phenotype, has been reported to be under the control of a single nuclear recessive gene (Ramaiah et al., 1990; Hess and Ejeta, 1992; Vogler et al., 1996; Ezeaku and Gupta, 2004, Satish et al., 2012). Haussmann et al. (2001a) indicated that one major gene and several minor genes appear to be involved in the stimulation of *Striga* seed germination using sorghum recombinant inbred populations. Although the lines showing low germination-inducing activity have been reported to express good resistance in bioassays, resistance mediated by low strigolactone production has been, however, described to be less reliable when the *Striga* infestation pressure is high (Atera et al., 2011). In pearl millet, the heredity of host-plant resistance to *Striga* is not well described. Only few pearl millet cultivars have been reported to be partially resistant or tolerant to *Striga*, and resistance (or at least less susceptibility) in some pearl millet materials was shown to be dominant (Ramaiah, 1987). However, the very existence of *Striga* resistance in cultivated pearl millet has been questioned by others authors (Chisi and Esele, 1997). Recently, partial quantitative resistance to *S. hermonthica* has been reported in wild pearl millet relatives in Africa (Wilson et al., 2000; 2004). Field measure of *Striga* resistance, most commonly emergence counts of *Striga* plants, represents a sum total of the entire parasitic association and is therefore a quantitative trait with polygenic inheritance. More recently, Kountche et al. (2013a) reported the presence of quantitative resistance to *S. hermonthica* in a diversified genepool of cultivated pearl millet under field conditions.

In small millets, early studies towards germplasm characterization and breeding for crop improvement for agronomic traits have not been coupled with the investigation and assessment of the genetic variants for *Striga* resistance. Hence, characterization of the resistance mechanisms usually follows the identification of resistance sources (Rubiales et al., 2006).

Host plant resistance to *Striga* involves physiological and genetic mechanisms, and requires a thorough understanding of the biophysical processes of the host-parasite association. In many cases, *S. hermonthica* seeds collected from one cereal host can infect other cereal species, for instance, there is evidence for some relaxed interspecies specificity,

particularly with respect to the reciprocal infectivity of populations of *S. hermonthica* collected from sorghum and pearl millet (Vasudeva Rao and Musselman, 1987; Estep et al., 2011). A deeper understanding of the heredity of specific mechanism associated with resistance to *Striga* would facilitate the development of improved selection strategies to enhance *Striga* resistance in susceptible millet crops (Ejeta, 2007).

### **3.5 Development and use of *Striga*-resistant millet cultivars**

Research towards combating *Striga* has been going on for more than 60 years, however, the *Striga* control has remained a challenge. As a result of decades of intensive research and farmer experience, a wide range of *Striga* control strategies have been developed starting from those that relate to soil fertility improvement, as *Striga* are also good indicator of low soil fertility, to those that directly affect the parasite life (Oswald 2005; Rector, 2009; Teka, 2014). This has provided the smallholder farmers with a diversity of options to control the parasites. Several researchers have extensively documented these potential options to combat *Striga* which have been classified into the most commonly used terms: cultural and mechanical control options including hand-pulling, crop rotation, trap-cropping, intercropping, appropriate improvement of soil fertility, and planting methods (Berner et al., 1995; Kuchinda et al., 2003; Hess and Williams, 1994; Hess and Dodo, 2004; Samake et al., 2006; Gworgwor, 2007; Khan et al., 2002, 2006, 2008; Eltayb et al., 2013; Hooper et al., 2015); chemical control method such as application of chemical herbicides (Kanampiu et al., 2003; Kanampiu et al., 2007a; Kanampiu et al., 2007b) and biological control approaches using the pathogenic fungus *Fusarium oxysporum* as a mycoherbicide, or insects (Abbasher et al. 1995, 1998; Kroschel et al. 1996; Marley et al., 1999, 2005; Hess et al. 2002; Elzein and Kroschel, 2004; Yonli et al., 2006; Zahran, 2008; Venne et al., 2009; Zarafi et al., 2015; Watson, 2013). Recently, the potential of the plant growth promoting rhizobacteria (PGPR) of the genus *Bacillus* (*B. subtilis*, *B. amyloliquefaciens*) and *Burkholderia* (*B. phytofirmans*) as *Striga* biocontrol agent has been surveyed by Mounde (2014). Although, the potential of these control options has been demonstrated in various research centers across *Striga*-prone regions, they have had only limited or partial impact since they do not adequately and consistently address the long-term management, which requires a significant, if not complete, depletion of the parasitic seed reserve. In some cases, their adoption has been limited as the most affected small farmers cannot afford them.

*Striga* appear to be difficult to manage, as the parasites inflict most of their damage underground, produce numerous tiny seeds and continuously increasing the seed load in soil (Oswald 2005; Scholes and Press 2008). Certainly, huge seed reserves and long-term seed viability (more than 20 years) pose acute problem in *Striga* management. Any control method that affects directly the germination of parasitic seeds and their attachment to the host root have been accepted to be more effective than those that affect later stages of the parasites development. In this sense, host plant resistance has been widely recognized to be the most practical and sustainable method for the long-term control of the parasites that would be accessible to farmers (Ejeta, 2007; Hearne, 2009; Yoder and Scholes, 2010). The potential advantage of controlling *Striga* in subsistence agriculture via genetic resistance is high because, assuming that the resistant-varieties are locally adapted and adopted, they fit within the varied agricultural practices where these weeds occur (Hearne, 2009).

#### **3.5.1 Conventional breeding**

Keeping in view the persistent problem of *Striga*, the key role of genetic resistance to combat *Striga* must be emphasized, even though progress towards the development and release of *Striga*-resistant varieties has been small. Development of genetically-improved

varieties with resistance to *Striga* is often straightforward, given that reliable sources of resistance are available and efficient and easily controlled and practical screening methods to provide sufficient selection pressure exist (Rubiales, 2003). Unfortunately, this has been seldom the case. From the previous sections, it can be admitted that resistance against *Striga* is difficult to develop due to the complex nature of the parasites, scarcity of donor sources reported so far, and in some cases due to varying heritability (moderate to low) because of the numerous environmental effects and genetic variability of parasite populations (Rubiales, 2003; Aly, 2012). In spite of all these difficulties, significant success has been achieved. During the last few decades, research efforts have been devoted to identifying germplasm with resistance to *Striga*. Relatively few cultivars with good level of *Striga* resistance have been identified in millet crops, mainly sorghum and pearl millet (Hess and Ejeta, 1992; Kountche et al., 2013). Improved breeding approaches that promise good prospects for developing cultivars with resistance to *Striga* have been suggested to take advantage of the ever-growing knowledge of the complex nature of the host-parasite interactions (Ejeta and Butler 1993; Hausmann et al., 2000; Omany et al. 2004). Adoption of these strategies has resulted in the development of appropriate breeding populations, and deployment of deliberate selection for resistance to *Striga*. Although the effort for breeding for *Striga* resistance in millets has been very limited, the conventional breeding work has generally been successful with the development and release of crop varieties with relatively high levels of resistance to *Striga*. A number of lines and improved varieties with *Striga* resistance has been selected and documented by ICRISAT and Purdue University (US) (Ejeta et al., 2007; Adugna, 2007; Teka, 2014). Tesso et al. (2007) and Mbwaga et al. (2007) demonstrated that resistant sorghum cultivars, which have been developed based on the low production of germination stimulants, have shown good level of *Striga* resistance. Three *Striga*-resistant varieties, P9401 (locally called Gubiye), P9403 (called Abshir) and PSL5061 (named Birhan), have been reported to be officially released for wide cultivation in *Striga*-endemic regions of Ethiopia (Elzein and Kroschel, 2004; Adugna, 2007). The *Striga*-resistant sorghum variety (ICSV1112BF, locally named Hormat) has been developed and released in India by ICRISAT (Adugna, 2007). More recently, breeding for *Striga* resistance under field conditions using phenotypic recurrent selection resulted in significant improvement in *Striga* resistance in cultivated pearl millet and the development of the first pearl millet *Striga*-resistant experimental varieties (Kountche et al., 2013a). These experimental varieties are currently being validated under farmer's field conditions. Unfortunately, in other millet species no sources of resistance have been surveyed and yet reported, and consequently no resistant cultivars have been selected so far.

The outlook for long term stability of the released *Striga*-resistant varieties has been analyzed by many researchers and does not look bright. A high level of genetic variation has been reported to be maintained within populations from generation to generation, especially in *S. hermonthica* (Bharatha et al., 1990). Furthermore, the ability of this *Striga* species to quickly evolve new races and to overcome resistance has been documented (Rich and Ejeta, 2008). Thus, the use of genetically heterogeneous *Striga*-resistant open-pollinated cultivars, in which different plants carry different resistance alleles, has been reported to be a practical alternative for ensuring the stability of resistance to *Striga* over time (Kountche et al., 2013a). A key to long term stable resistance is more likely when both quantitative and qualitative resistance genes are deliberately stacked in the improved cultivars such that multiple mutations would have to accumulate in the parasite populations to overcome the multiple resistance genes in the host (Rich and Ejeta, 2008).

### 3.5.2 Marker-assisted selection

Although conventional breeding has made significant contributions to millet crops improvement for *Striga* resistance, particularly in sorghum and pearl millet, this approach has been in general slowed when targeting the complex quantitative trait of resistance to *Striga*. The development of molecular markers associated with resistance to *Striga* has offered a promising way to rapidly accumulate several resistance genes since conventional breeding has shown to be time-consuming, largely if not completely dependent on climatic and environmental conditions, and therefore less effective (Ejeta and Gressel, 2007; Rispaill et al., 2007). It is interesting to note that in the most studied millet crops, sorghum and pearl millet, potential resistance phenotypes have been identified in wild relatives. Hence, molecular markers may facilitate the transfer of resistance genes into cultivars and facilitate pyramiding of multiple resistance genes into agronomically desirable elite and locally-adapted *Striga*-susceptible varieties. Over the past decades, much progress has been made in the field of development of molecular markers to assist and boost the development of *Striga*-resistant varieties. However, their effective application in a marker-aided breeding requires a thorough understanding of the inheritance of *Striga* resistance, which in turn requires the development of tailor-made populations.

Major advances in our understanding of the molecular genetic basis of mechanisms of *Striga* resistance have been achieved. Research effort invested to characterize the mechanisms behind and inheritance of resistance to *Striga* has been followed by the development of molecular markers. Recently, mapping of chromosomal regions affecting qualitative or quantitative traits has received growing attention in millets (Hess et al., 1992; Ejeta and Butler, 1993; Haussmann et al., 2001a; Omany et al., 2004; Rich et al., 2004; Mohamed et al., 2003; Kountche, 2013; Moumouni et al., 2015). In sorghum, several populations segregating for genes associated with low germination stimulant production (*lgs*), low haustorial initiation, mechanical barriers, hypersensitive response, and incompatible response mechanisms of *Striga* resistance have been developed using the source materials (Ejeta et al., 2000; Haussmann et al., 2000; Grenier et al., 2001, 2007; Rodenburg et al., 2006; Omany et al., 2004; Mutengwa et al., 2005). QTL mapping for *Striga* resistance has resulted in identification of many genes/QTLs spread across the genome. Haussmann et al. (2004) mapped several QTLs for *Striga* resistance in sorghum and reported 9 and 11 QTLs explaining respectively 77% and 82% of the phenotypic variation in a recombinant inbred line (RIL) population. The most significant QTL has been identified to correspond to the major gene locus *lgs*, which was recently fine-mapped on the chromosome 5 (Satish et al., 2012). More interestingly, validation of some of these QTLs has provided an opportunity to employ molecular marker-assisted breeding (MAB) for sorghum improvement for *Striga* resistance. MAB has been applied using the identified *Striga*-resistant QTLs for their introgression into elite farmer-preferred sorghum local varieties which lack *Striga* resistance (Grenier et al., 2007; Kapran et al., 2007). Four *Striga*-resistant sorghum lines developed through marker-assisted selection have been recently reported and released for cultivation in sub-Saharan Africa (Mohamed et al., 2014). Very recently, Yohannes et al. (2015) indicated that marker-assisted backcrossing (MABC) has been effective in introgressing five QTLs for *Striga* resistance from the donor source N13 to the genetic background of Hurgatay, a susceptible sorghum variety from Eritrea.

In pearl millet, although marker aided-selection (MAS) has not been practiced yet in breeding for *Striga* resistance, there have been extensive efforts towards development of DNA-based markers including simple sequence repeat (SSR) (Allouis et al., 2001; Budak et al., 2003; Mariac et al., 2006; Qi et al. 2001, 2004; Senthilvel et al., 2004, 2008; Jia et al., 2007; Yadav et al., 2007, 2008; Rajaram et al., 2013), diversity array technology (DArT)

(Mace et al., 2008, 2009; Supriya et al., 2011) and single nucleotide polymorphism (SNP) (Bertin et al., 2005; Feltus et al., 2006; Kountche, 2013; Moumouni et al., 2015). In most of these studies, a number of genetic maps have been constructed using different crosses, mostly with the aim of mapping specific traits. More recently, Moumouni et al., 2015 reported the development of a relatively high density SNP- based linkage map using a cross between the wild resistant PS202 and SOSAT-C88, a susceptible open-pollinated improved variety (OPV), segregating for *Striga* resistance. While the original aim was to conduct a classical QTL analysis in this population, a lack of reliable phenotypic data due to environmental factors has hampered the marker-trait association for mapping *Striga* resistance in pearl millet. Even when it is well established, marker-assisted backcrossing has certain limits for introgressing quantitative trait controlled by many genes/QTLs with minor effects. The markers to be used in MABC are usually identified in a biparental segregating population, which limits the exploitation of the potentially wide range of allelic diversity present in the crop species. In addition, markers may be valid only for the genetic background in which they were identified (Varshney and Dubey, 2009). Because of these limitations, marker-assisted recurrent selection (MARS) has emerged as an indispensable breeding strategy for developing germplasm with strong long lasting resistance (Bernardo and Charcosset, 2006). However, the key component and the great challenge towards an efficient system for molecular breeding for *Striga* resistance in pearl millet is the identification of significant associations between genetic markers and the genes that determine resistance to the parasites. Interestingly, a genome wide association studies (GWAS) has been recently surveyed in pearl millet for *Striga* resistance using a diversified *Striga*-resistant gene pool of full-sib populations derived from five cycles of phenotypic recurrent selection (Kountche et al., 2013a; Kountche, 2013). These authors reported three major and several minor SNPs which have been identified to be significantly associated with *Striga* resistance trait, each of which explaining 15%, 18% and 21% of the phenotypic variation respectively for the three major QTLs. From these preliminary results, they speculated that resistance to *Striga* in pearl millet is controlled by a small number of major loci which can easily be manipulated in a marker-assisted backcrossing program, as it was the case for sorghum. For this purpose, it is desirable to have molecular markers flanking the gene/QTL closely on both sites. Therefore, there is a need to map and validate these major QTLs across different genetic backgrounds and environments for their future deployment.

In the past decades, extensive efforts have been invested in small millets to develop genetic and genomic resources. Various DNA markers are routinely used to assess population structure, genetic diversity in small millets (Dwivedi et al., 2012; Barnaud et al., 2012). Interestingly, genetic maps of varying density level have been also documented for foxtail millet, finger millet, proso millet and tef (Dwivedi et al., 2012; Ref.?). However, to the best of our knowledge, no specific study has reported on *Striga* resistance, its molecular genetic basis and availability of molecular marker associated with resistance to *Striga* in small millets. The availability of these enormous genomic resources in small millets has now provided numerous scientific leads to proceed further towards crop improvement for *Striga* resistance in millets, particularly in small millets. National and international efforts need to be invested to assess and identify sources of *Striga* resistance, characterize and understand the specific resistance mechanisms underlying the resistance phenotype, and examine the inheritance of identified *Striga* resistance in small millet using phenomics and genomics resources. Notably, with the increased accessibility of low cost and high-throughput genotyping, genotyping-by-sequencing (NGS), and the availability of the whole genome sequence of some millet crops such as sorghum (Paterson et al., 2009), foxtail millet (Bennetzen et al., 2012) and pearl millet (which will be completed very soon), it can be speculated that targeting specific *Striga* resistance genes and employment of genomic tools to

tailor millets for *Striga* resistance will be less challenging (Kountche et al., 2013b). The combination of genetic mapping and gene expression studies should provide an integrated approach to pave the knowledge gap in millets, especially pearl millet and small millets. Moreover, comparative genomics can point to important resistance genes in the understudied millet crops as they are discovered in other millet crops like sorghum (Michelmore, 2000; Rispaïl et al., 2007).

### 3.5.3 Transgenics

To date, there is a consensus that genetic control of *Striga* through the use of resistant cultivars appears to be the central component of any concerted integrated *Striga* control approach (Ejeta, 2007). However, the deployment of host plant resistance even in the most studied millet crops, particularly sorghum and pearl millet, has been largely hampered by the scarcity of reliable resistance donor sources (Aly, 2012; Kountche, 2013a). This has prompted the researchers to explore new horizons for developing new strategies that allow extending the sources of resistance further (also known as artificial resistance) to the very limited number of natural resistance sources that have been identified so far. Genetic engineering for enhancing host plant resistance to *Striga* is a very promising approach and offers new opportunities for developing improved varieties. Thanks to the recent emergence of biotechnology techniques and genomic resources, the potential of artificial resistance in host plants makes the genetic engineering a viable strategy in this context. Indeed, studies aimed at 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, are the subject of increasing interest and offer weed researchers the opportunity for deploying genetic transformation tools to enhance the control of the parasitic plants (Rispaïl et al., 2007; Aly, 2012). With the great initiative of the parasitic plant genome project<sup>7</sup> (<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) and Runo et al. (2011) have investigated the use of RNA interference (RNAi) technology as a mean for enhancing host resistance against parasitic weeds. However, this approach has not been successful in controlling maize – *Striga* parasite interaction (Yoder and Scholes 2010). Nevertheless, understanding the biology of the early stages of parasitism by *Striga* will help identifying potential barriers towards success of this technology. Though significant progress has been achieved in genetic transformation, there have been very few reports on millet crops, which have trailed behind other cereals such as maize in the progress toward genetic transformation (Visarada and Kishore, 2015). To date, there are no transgenic *Striga*-resistant millets crops that have been reported and released for cultivation so far.

As an alternative approach to the control of parasitic weeds, Gressel (2009) suggested the development and use of herbicide-resistant crops. Green and Owen (2011) documented that herbicide-resistant sorghum varieties have been developed by the private sector in the USA using mutations. Interestingly, attempts are being made using the approach of the acetolactate synthase (ALS) to develop genetically engineered herbicide-resistant sorghum crops. However, the success of generating resistant cultivars by genetic engineering requires an efficient gene transfer, stable integration, and predictable expression of the transgene. Thus, with the genetic transformation techniques based on recombinant DNA technology, it is now possible to insert genes that confer resistance to a number of biotic stresses, including parasitic plants such as *Striga*, into the susceptible host plant genome (Rakshit and Patil, 2014). When identified and characterized, *Striga* resistance genes available across millet species can be deployed and incorporated into other species that lack resistance through gene transfer techniques along with reproducible tissue culture protocols to produce transgenic

millets varieties with enhanced agronomic performance. Recently, Kohlen et al. (2011) emphasized that the discovery of strigolactones, the major *Striga* germination stimulants, provides a potential way to enhance *Striga* resistance by reducing the production of strigolactones in the host plant roots using a transgenic approach. At least for the few millet crops such as sorghum, foxtail millet, pearl millet, for which a complete sequence of the genome is available.

Beside the potential advantages of these technologies, it appears that researchers have been reluctant towards development of engineered resistance through genetic engineering since the transgenic crops may not be easily adopted by farmers due to the current controversial debate on food safety issues. The approach provides genetically modified organisms (GMO), therefore the use of transgenic crops in the center of origin of most of millets crops may arise the concern regarding the possible gene flow from transgenic crops to cultivated plants and their wild relatives. In this regards, innovative genetic modifications have been developed to keep away from the classification of GMOs and biosafety concerns. These modifications such as zinc finger nuclease technology, cisgenesis, RdDM, and other technologies are dependent on transgenic technology for the introduction of DNA segments (Visarada and Kishore, 2015). Science and the arts of tissue culture, genetic transformation, and, more importantly, plant breeding has to be integrated to reach effective *Striga*-resistant millet cultivars.

### **3.6 Integrated *Striga* management**

The various *Striga* control methods reviewed above have offered varying levels of *Striga* control and have not proved to be as effective, economical, and applicable as desired (Joel, 2000). In the past decades, several control measures have been developed and extensively deployed for few crops, however, when applied individually the control method has been affected by the diversity of farming systems and environmental conditions, and has often shown only little success. In addition, although these methods have helped in reducing damage caused by the parasites to host crops, it has been observed that they did not adequately address the long term management of the root parasitic weeds, as this requires the destruction of *Striga* seed bank. It appears that there is no single control method that can effectively solve the *Striga* problem (Joel, 2000; Oswald, 2005). Thus, the most comprehensive and sustainable way to cope with the *Striga* is certainly through an integrated approach, incorporating a variety of measures in a concerted and smart manner (Oswald, 2005; Ejeta, 2007; Elzein et al., 2008). Haussmann et al. (2000) reported that an effective integrated control strategy must certainly include at least, if not all, one control method from each of the three major categories highlighted by the authors. Oswald (2005) suggested a combined action with containment and sanitation, using direct and indirect measures to prevent the damage caused by *Striga*, and with means to eradicate the *Striga* seed bank in infested soils. To ensure that the integrated *Striga* control technology is adopted by farmers, *Striga* control practices must improve crop yield, maintain soil fertility, and be practicable (Berner et al., 1995; Kroschel, 1998). To this end, adaptive and on-farm research has been invested, which must play an important role in identifying the most effective mix of component-practices. Berner et al. (1995) suggested crop rotation with highly effective trap crops as the key component of an integrated *Striga* control program. The combined use of the mycoherbicide, *Fusarium oxysporum*, and *Striga*-resistant sorghum cultivars has been demonstrated to be effective in controlling *Striga* and led to increased sorghum yield in the field (Marley et al., 2004; Venne et al., 2009). Hess and Dodo (2004) reported the potential use of sesame as a trap-crop in integrated control of *Striga* in pearl millet. Tesso and Ejeta (2011) suggested a promising integrated control strategy based on the use of sorghum

resistant variety, tied-ridge tillage and nitrogen fertilizer. More recently, ICRISAT and its collaborators embarked on participatory research on integrated *Striga* management through farmer field schools and came up with practical integrated *Striga* and soil fertility management practices for pearl millet and sorghum in West Africa.

Regardless of the global context of climate change, which will certainly have an impact on *Striga* infestation, the main obstacle in the long-term management of *Striga* in infested fields appears to be the persistent seed bank, with only very limited annual depletion percentage induced by the current integrated approach. As long as the *Striga* seed bank is not controlled effectively, the need to apply means to control the parasite will persist. An integrated approach that combine genetic resistance and suicidal germination components have been suggested to be the best approach for seedbank demise (Kgosi et al., 2012; Zwanenburg and Pospisil, 2013; Kannan and Zwanenburg, 2014). While several research efforts have been invested in the field of development and deployment of host plant resistance, the elimination of the *Striga* seed bank through suicidal germination approach using synthetic analogs of strigolactones has gained very little attention. This approach may be appropriate and even more efficient if suitable candidates of synthetic strigolactones are identified. Hence, the development of highly efficient synthetic germination stimulant analogs, economically affordable by smallholder farmers, and environmentally-friendly that can be used to induce suicidal germination of *Striga* seeds, when possible, will provide an important alternative component for the long term control of *Striga* (Zwanenburg et al., 2009; Zwanenburg et al., 2013).

#### 4. CONCLUSIONS

In general, research efforts invested during the last decades have dramatically improved our understanding of host – parasite relationship in the *Orobanchaceae*, and more so, contributed to numerous methods for the control of the weed parasitic plants *Striga*. Albeit limited in efficacy in many cases, the control approaches developed so far represent today major progress in combating *Striga* in millet cropping systems. It is now evident that the cultivated millet crops can be protected by cultural methods, by biocontrol agents, and through genetic resistance. Moreover, it will be important to develop new strategies that can address the long-term control of the parasite. In this sense, fundamental research on key aspects of *Striga* parasitism should not only lead to a better understanding of this intricate pathosystem, but also provide new ideas for the development of novel methods for parasitic weed control, to increase millets productivity. From the above-cited knowledge on the millet – *Striga* pathosystem, it seems evident that multiple responses from specific host plant-dependent signals seem to be a part of a strategy to find and recognize host plants. Strigolactones (SLs) with their multifaceted biological roles can undeniably become a potent and valuable tool to develop new alternatives for breeding/managing for *Striga* resistance in millets. In this sense, it is important to understand some of the SLs interactions at the biosynthesis level and elucidation in SLs release/ pattern seems essential for understanding developmental and defense-related processes mediated by specific families of these phytohormones. Finally, it is crucial when dealing with *Striga* that several resistances, genetic and/or engineered, should be pyramided in susceptible millet cultivars, to avoid the development of more virulent parasite populations and to overcome the resistance. This is deliverable when only combined work at molecular, genetic, and physiological levels will be continuously invested in millet crops.

## 5. FUTURE PERSPECTIVES AND PRIORITIES

This review emphasizes the enormous efforts to understand the host – *Striga* interactions and the development of genetically *Striga*-resistant cultivars in millets. We firmly believe that an increased research effort in millet species will lead to significant progress. Indeed, a deeper understanding of parasite population dynamics and of the genetic changes associated with parasitism should improve our understanding of the virulence of the parasite and of host resistance mechanisms, and the transfer of the knowledge to breeders. With regard to *Striga* control, elucidation of the strigolactone biosynthesis pathway in millets will also offer possibilities for the development of chemical inhibitors of strigolactone production and allow to modulate the amounts and types of released SLs. Thus, a comprehensive effort should be made using all available tools to improve *Striga* resistance/tolerance in millets so that they can continue to play the indispensable role in the welfare of the poor in the semi-arid tropics of Africa and Asia.

Moreover, the many bioassays tools that have been developed for sorghum can be now used in other millets, to identify resistance source and to investigate the mechanisms underlying the resistance phenotype in the understudied millet crops. Conventional breeding can be supported, in addition to marker-aided selection and innovative genetic modification strategies, by a mutagenesis approach to produce new resistant variants to tackle the *Striga* problem in millets. In this concern, ethyl methane sulfonate (EMS), a commonly used chemical mutagen, has been largely used because of its high effectiveness in generating new and desired traits.

It is now clear that the main impediment of the long-term control of *Striga* in infested fields lies in the huge seedbank. As long as the *Striga* seed bank is not controlled, the need to apply means to control the parasite will persist. With regard to depletion of *Striga* seed reserve, the development and testing of efficient synthetic germination stimulant analogs is a promising approach towards eliminating the *Striga* seed bank. Therefore, it will be of interest to further explore this opportunity in order to provide farmers with new means for combating the parasitic weeds *Striga*.

## 6. ACKNOWLEDGEMENTS

Our grateful thanks are extended to the resource persons of the e-writeshop organized by the Collaborative Crop Research Program of the McKnight Foundation. This work was supported by funding from King Abdullah University of Science and Technology (KAUST).

## REFERENCES

- Abbasher, A.A., Kroschel, J., Sauerborn, J., 1995. Microorganisms of *Striga hermonthica* in Northern Ghana with potential as biocontrol agents. *Bio.Sci. Technol.* 5, 157–161.
- Abbasher, A.A., Hess, D.D., Sauerborn, J., 1998. Fungal pathogens for biocontrol of *Striga hermonthica* on sorghum and pearl millet in West Africa. *African Crop Sci. J.* 6, 179–188.
- Adugna, A., 2007. The role of introduced sorghum and millets in Ethiopian agriculture. *SAT e J.*3, (1).
- Akiyama, K., Matsuzaki, K., Hayashi, H., 2005. Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. *Nature* 435, 824–827.
- Al-Babili, S., Bouwmeester, H.J., 2015. Strigolactones, a novel Carotenoid-derived plant hormone. *Annu. Rev. Plant Biol.* 66, 161–186.
- Albrecht, H., Yoder, J.I., Phillips, D.A., 1999. Flavonoids promote haustoria formation in the root parasite *Triphysaria*. *Plant Physiol.* 119, 585–591.

- Allouis, S., Qi, X., Lindup, S., Gale, M.D., Devos, K.M., 2001. Construction of BAC library of pearl millet, *Pennisetum glaucum*. Theor. Appl. Genet. 102, 1200–1205.
- Aly, R., 2007. Conventional and biotechnological approaches for control of parasitic weeds. In Vitro Cellular & Developmental Biology-Plant 43, 304–317.
- Aly, R., 2012. Advanced technologies for parasitic weed control. Weed Sci. 60, 290–294.
- Amusan, I.O., Rich, P.J., Menkir, A., Housley, T., Ejeta, G., 2008. Resistance to *Striga hermonthica* in a maize inbred line derived from *Zea diploperennis*. New Phytologist 178, 157–166.
- Amusan, I., Rich, P., Housley, T., Ejeta, G., 2011. An in-vitro method for identifying post-attachment *Striga* resistance in maize and sorghum. Agron. J. 103, 1472–1478.
- Andrews, D.J., Kumar, K.A., 1992. Pearl millet for food, feed and forage. Adv. Agron. 48, 89–139.
- Atera, E.A., Itoh, K., Azuma, T., Ishii, T., 2012. Farmers' perspectives on the biotic constraint of *Striga hermonthica* and its control in western Kenya. Weed Biol. Manage. 12, 53–62.
- Atera, E., Itoh, K., Onyango, J.C., 2011. Evaluation of ecologies and severity of *Striga* weed on rice in sub-Saharan Africa. Agric. Biol. J. N. Am. 2, 752–760.
- Austin, D.F., 2006. Fox-tail millets (*Setaria*: Poaceae) – Abandoned food in two hemispheres. Econ. Bot. 60 (2), 143–158.
- Awad, A.A., Sato, D., Kusumoto, D., Kamioka, H., Takeuchi, Y. et al., 2006. Characterization of strigolactones, germination stimulants for the root parasitic plants *Striga* and *Orobanche*, produced by maize, millet and sorghum. Plant Growth Regul. 48, 221–227.
- Bangoura, M.L., Huiming, Z., Nsor-Atindana, J., Xue, Z.K., Tolno, M.B., Wei, P., 2011. Extraction and fractionation of insoluble fibres from foxtail millet (*Setaria italica* (L.) P. Beauv). Am. J. Food Technol. 6, 1034–1044.
- Barnaud, A., Vignes, H., Risterucci, A.M., Noyer, J.L., Pham, J.L., Blay, C., Buiron, M., Vigouroux, Y., Billot, C., 2012. Development of nuclear microsatellite markers for the fonio, *Digitaria exilis* (Poaceae), an understudied West African cereal. Am. J. Bot. 99, e105–e107.
- Bennetzen, J.L. et al., 2012. Reference genome sequence of the model plant *Setaria*. Nature Biotech. 30, 555–561.
- Bernardo, R., Charcosset, A., 2006. Usefulness of Gene Information in Marker-Assisted Recurrent Selection: A Simulation Appraisal. Crop Sci. 46, 614–621.
- Berner, D.K., Kling, J.G., Singh, B.B., 1995. *Striga* research and control: A perspective from Africa. Plant Dis. 79, 652–660.
- Berner, D.K., Schaad, N.W., Völksch, B., 1999. Use of ethylene-producing bacteria for stimulation of *Striga* spp. seed germination. Biol. Control 15(3), 274–282.
- Berner, D.K., Winslow, M.D., Awad, A.E., Cardwell, K.F., Mohan Raj, D.R., Kim, S.K., (Eds.), 1997. *Striga* Research Methods- A Manual, 2nd Edition. International Institute of Tropical Agriculture (IITA), PMB 5320, Ibadan, Nigeria, 1997 June. <http://www.cgiar.org/iita/inform/striga.pdf>.
- Bertin, I., Zhu, J.H., Gale, M.D., 2005. SSCP-SNP in pearl millet—a new marker system for comparative genetics. Theor. Appl. Genet. 110, 1467–1472.
- Bertin, C., Yang, X.H., Weston, L.A., 2003. The role of root exudates and allelochemicals in the rhizosphere. Plant Soil 256, 67–83.
- Bharatha, L., Werth, C.R., Musselman, L.J., 1990. A study of genetic diversity among host-specific populations of the witchweed *Striga hermonthica* (Scrophulariaceae) in Africa. Plant Syst. Evol. 172, 1–12.

- Botanga, C.J., Kling, J.G, Berner, D.K., Timko, M.P., 2002. Genetic variability of *Striga asiatica* (L.) Kuntz based on AFLP analysis and host-parasite interaction. *Euphytica* 128, 375–388.
- Bouwmeester, H.J., Matusova, R., Sun, Z., Beale, M.H., 2003. Secondary metabolite signalling in host–parasitic plant interactions. *Curr. Opin. Plant Biol.* 6, 358–364.
- Bouwmeester, H.J., Roux, C., Lopez-Raez, J.A., Becard, G., 2007. Rhizosphere communication of plants, parasitic plants and AM fungi. *Trends Plant Sci.* 12, 224–230.
- Budak, H., Pedraza, F., Cregan, P.B., Baenziger, P.S., Dweikat, I., 2003. Development and utilization of SSRs to estimate the degree of genetic relationships in a collection of pearl millet germplasm. *Crop Sci.* 43, 2284–2290.
- Butler, L.G., 1995. Chemical communication between the parasitic weed *Striga* and its crop host- a new dimension in allelochemistry. *ACS Symp. Ser. Am. Chem. Soc.* 582, 158–168.
- Cardoso, C., Zhang, Y., Jamil, M., Hepworth, J., Charnikhova, T., et al., 2014. Natural variation of rice strigolactone biosynthesis is associated with the deletion of two MAX1 orthologs. *Proc. Natl. Acad. Sci. USA* 111, 2379–84.
- Chang, M., Netzly, D.H., Butler, L.G., Lynn, D.G., 1986. Chemical regulation of distance: Characterization of the first natural host germination stimulant for *Striga asiatica*. *J. Am. Chem. Soc.* 108, 7858–7860.
- Chemisquy, M.A., Giussani, L.M., Scataglieni, M.A., Kellogg, E.A., Morrone, O., 2010. Phylogenetic studies favour the unification of Pennisetum, Cenchrus and Odontelytrum (Poaceae): a combined nuclear, plastid and morphological analysis, and nomenclatural combinations in Cenchrus. *Ann. Bot. (Oxford)* 106, 107–130.
- Chisi, M., Esole, P., 1997. Discussion for Session VII-Breeding for resistance to other abiotic stresses and Striga. In: *Proceeding International Conference: Genetic Improvement of Sorghum and Pearl Millet*. INTSORMIL, Lincoln, NE, pp. 525–528.
- Cissoko, M., Boissard, A., Rodenburg, J., Press, M.C., Scholes, J.D., 2011. New Rice for Africa (NERICA) cultivars exhibit different levels of post-attachment resistance against the parasitic weeds *Striga hermonthica* and *Striga asiatica*. *New Phytologist* 192, 952–963.
- Cochrane, V., Press, M.C., 1997. Geographical distribution and aspects of the ecology of the hemiparasitic angiosperm *Striga asiatica* (L.) Kuntze: a herbarium study. *J. Trop. Ecol.* 13 (3), 371–380.
- Cook, C.E., Whichard, L.P., Turner, B., Wall, M.E., Egley, G.H., 1966. Germination of witchweed (*Striga lutea* Lour.): Isolation and properties of a potent stimulant. *Sci.* 154, 1189–1190.
- Cook, C.E., Whichard, L.P., Wall, M., Egley, G.H., Coggon, P. et al., 1972. Germination stimulants. II. Structure of strigol, a potent seed germination stimulant for witchweed (*Striga lutea*). *J. Am. Chem. Soc.* 94, 6198–6199.
- De Groote, H., Wangare, L., Kanampiu, F., Odendo, M., Diallo, A., Karaya, H., Friesen, D., 2008. The potential of a herbicide resistant maize technology for Striga control in Africa. *Agric. Sys.* 97(1-2), 83–94.
- Dida, M.M., Devos, K.M., 2006. Finger millet. In: Kole, C., (Ed.), *Genome mapping and molecular breeding in plants, Vol. 1, cereals and millets*. Heidelberg: Springer, pp. 333–343.
- Dwivedi, S.L., Upadhyaya, H., Senthilvel, S., Hash, C.T., 2012. Millets: Genetic and Genomic Resources. In: Janick, J., (Ed.), *Plant Breeding Reviews*, Ch.5, Vol. 36, John Wiley & Sons, Inc., Hoboken, NJ, USA, pp. 247–375.
- Ejeta, G., 2007. Breeding for *Striga* Resistance in Sorghum: Exploitation of an Intricate Host–Parasite Biology. *Crop Sci.* 47, S216–S227.

- Ejeta, G., Butler, L.G., 1993. Host–parasite interactions throughout the *Striga* life cycle, and their contributions to *Striga* resistance. *Afr. Crop Sci. J.* 1, 75–80.
- Ejeta, G., Mohammed, A., Rich, P.J., Melake-Berhan, A., Housley, T.L., Hess, D.E., 2000. Selection for specific mechanisms of resistance to *Striga* in sorghum. In: Haussmann, B.I.G., et al. (Eds.), *Breeding for Striga resistance in cereals*. Proc. of a Workshop, IITA, Ibadan, Nigeria. 18–20. Aug. 1999. Margraf, Weikersheim, Germany, pp. 29–37.
- Ejeta, G., Gressel, J., 2007. *Integrating New Technologies for Striga Control: Towards Ending the Witch-hunt*. Singapore: World Sci. Publ. Co. Pte. Ltd., 345 p.
- Eltayb, M.T.A., Magid, T.D.A., Mohamed, A.G., Dirar, A.M.A., 2013. Effect of *Acacia seyal* (Del) Seeds Powder on Growth and Yield of Sorghum bicolor (L) in *Striga hermonthica* (Del.) Infested Area. *J. Forest Products & Industries* 2(6), 18–25.
- Elzein, A., Kroschel, J.K., 2004. *Fusarium oxysporum* Foxy 2 shows potential to control both *Striga hermonthica* and *S. asiatica*. *Weed Res.* 44, 433–438.
- Elzein, A., Kroschel, J., Cadisch, G., 2008. Efficacy of Pesta granular formulation of *Striga*-mycoherbicide *Fusarium oxysporum* f.sp. strigae Foxy 2 after 5-year of storage. *J. Plant Dis. Prot.* 115, 259–262.
- Estabrook, E.M., Yoder, J.I., 1998. Plant–plant communications: rhizosphere signalling between parasitic angiosperms and their hosts. *Plant Physiol.* 116, 1–7.
- Estep, M., Van Mourik, T., Muth, P., Guindo, D., Parzies, H., Koita, O., Weltzien, E., Bennetzen, J., 2011. Genetic diversity of a parasitic weed, *Striga hermonthica*, on sorghum and pearl millet in Mali. *Trop. Plant Biol.* 4, 91–98.
- Ezeaku, I.E., Gupta, S.C., 2004. Development of sorghum populations for resistance to *Striga hermonthica* in the Nigerian Sudan Savanna. *Afr. J. Biotech.* 3(6), 324–329.
- FAO, IFAD and WFP, 2013. *The State of Food Insecurity in the World 2013. The multiple dimensions of food security*. Rome, FAO.
- Feltus, F.A., Singh, H.P., Lohithaswa, H.C., Schulze, S.R., Silva, T.D., Paterson, A.H., 2006. A comparative genomics strategy for targeted discovery of single-nucleotide polymorphisms and conserved-monocoding sequences in orphan crops. *Plant Physiol.* 140, 1183–1191.
- Gethi, J.G., Smith, M.E., Mitchell, S.E., Kresovich, S., 2005. Genetic diversity of *Striga hermonthica* and *Striga asiatica* populations in Kenya. *Weed Res.* 45, 64–73.
- Gethi, J.G., Smith, M.E., 2004. Genetic responses of single crosses of maize to *Striga hermonthica* (Del.) Benth. and *Striga asiatica* (L.) Kuntze. *Crop Sci.* 44, 2068–2077.
- Gigou, J., Stilmant, D., Diallo, T.A., Cisse, N., Sanogo, M.D., Vaksman, M., Dupuis, B., 2009. Fonio millet (*Digitaria exilis*) response to N, P and K Fertilizers under varying climatic conditions in West Africa. *Expl. Agric.* 45, 401–15.
- Goldwasser, Y., Hershenhorn, J., Plakhine, D., Kleifeld, Y., Rubin, B., 1999. Biochemical factors involved in vetch resistance to *Orobanche aegyptiaca*. *Physiol. Mol. Plant Pathol.* 54, 87–96.
- Gomez-Roldan, V., Fermas, S., Brewer, P.B., Puech-Pages, V., Dun, E.A., et al., 2008. Strigolactone inhibition of shoot branching. *Nature* 455, 189–94.
- Green, J.M., Owen, M.D.K., 2011. Herbicide-resistant crops: utilities and limitations for herbicide-resistant weed management. *J. Agric. Food Chem.* 59, 5819–5829.
- Grenier, C., Haussmann, B.I.G., Kiambi, D., Ejeta, G., 2007. Marker-assisted selection for *Striga* resistance in sorghum. In: Ejeta G, Gressel J (eds) *Integrating new technologies for Striga control: Towards ending the witch-hunt*. World Scientific Publishing Company Pvt. Ltd., Singapore, pp. 159–172.
- Grenier, C., Rich, P.J., Mohamed, A., Ellicott, A., Shaner, C., Ejeta, G., 2001. Independent inheritance of *Igs* and *IR* genes in sorghum. In: 7<sup>th</sup> international parasitic weed symposium. Nantes, France, pp. 220–223.

- Gressel, J., 2009. Crops with target-site herbicide resistance for *Orobanche* and *Striga* control. *Pest Manage. Sci.* 65, 560–565.
- Gressel, J., Hanafi, A., Head, G., Marasas, W., Obilana, B., Ochanda, J., Souissi, T., Tzotzos, G., 2004. Major heretofore intractable biotic constraints to African food security that may be amenable to novel biotechnological solutions. *Crop Prot.* 23, 661–689.
- Gurney, A.L., Press, M.C., Scholes, J.D., 2002. Can wild relatives of sorghum provide new sources of resistance or tolerance against *Striga* species? *Weed Res.* 42, 317–324.
- Gurney, A.L., Grimanelli, D., Kanampiu, F., Hoisington, D., Scholes, J.D., Press, M.C., 2003. Novel sources of resistance to *Striga hermonthica* in *Tripsacum dactyloides*, a wild relative of maize. *New Phytologist* 160, 557–568.
- Gurney, A.L., Slate, J., Press, M.C., Scholes, J.D., 2006. A novel form of resistance in rice to the angiosperm parasite *Striga hermonthica*. *New Phytologist* 169, 199–208.
- Gworgwor, N., 2007. Trees to control weeds in pearl millet. *Agron. Sustain. Dev.* 27, 89–94.
- Hamrick, J., 1982. Plant population genetics and evolution. *Am. J. Bot.* 69(10), 1685–1693.
- Hash, C.T., Yadav, R.S., Cavan, G.P., Howarth, C.J., Liu, H., Qi, X., Sharma, A., Kolesnikova-Allen, M.A., Bidinger, F.R., Witcombe, J.R., 2000. Marker-assisted backcrossing to improve terminal drought tolerance in pearl millet. In: Ribaut, J.M., Poland, D., (Eds.), *Molecular Approaches for the Genetic Improvement of Cereals for Stable Production in Water-Limited Environments, A Strategic Planning Workshop held at CIMMYT, El Batan, Mexico, 21–25 June 1999*. Mexico, D.F., Mexico: International Maize and Wheat Improvement Center (CIMMYT), pp. 114–119.
- Hauck, C., Muller, S., Schildknecht, H., 1992. A germination stimulant for parasitic flowering plants from sorghum bicolor, a genuine host plant. *J. Plant Physiol.* 139, 474–478.
- Hausmann, B.I.G., Hess, D.E., Omany, G.O., Reddy, B.V.S., Welz, H.G., Geiger, H.H., 2001a. Major and minor genes for stimulation of *Striga hermonthica* seed germination in sorghum, interaction with different *Striga* populations. *Crop Sci.* 41, 1507–1512.
- Hausmann, B.I.G., Hess, D.E., Reddy, B.V.S., Mukuru, S.Z., Kayentao, M., Welz, H.G., Geiger, H.H., 2001b. Pattern analysis of genotype × environment interaction for *Striga* resistance and grain yield in African sorghum trials. *Euphytica* 122, 297–308.
- Hausmann, B.I.G., Hess, D.E., Welz, H.G., Geiger, H.H., 2000. Improved methodologies for breeding *Striga*-resistant sorghums. *Field Crops Res.* 66, 195–211.
- Hausmann, B.I.G., Hess, D.E., Omany, G. O., Folkertsma, R. T., Reddy, B. V. S., Kayentao, M., Welz, H.G., Geiger, H.H., 2004. Genomic regions influencing resistance to the parasitic weed *Striga hermonthica* in two recombinant inbred populations of sorghum. *Theor. App. Genet.* 109, 1005–1016.
- Hearne, S.J., 2009. Control – the *Striga* conundrum. *Pest Manage. Sci.* 65, 603–614.
- Hess, D.E., Dodo, H., 2004. Potential for sesame to contribute to integrated control of *Striga hermonthica* in the West African Sahel. *Crop Prot.* 23, 515–522.
- Hess, D.E., Ejeta, G., 1992. Inheritance of resistance to *Striga* in sorghum genotype SRN39. *Plant Breed.* 109, 233–241.
- Hess, D.E., Ejeta, G., Butler, L.G., 1992. Selecting sorghum genotypes expressing a quantitative biosynthetic trait that confers resistance to *Striga*. *Phytochem.* 31, 493–497.
- Hess, D.E., Thakur, R.P., Hash, C.T., Sérémé, P., Magill, C.W., 2002. Pearl millet downy mildew: Problems and control strategies for a new millennium. In: Leslie, J.F., (Ed.), *Sorghum and Millets Pathology 2000*. Iowa State Press, Ames, Iowa, USA., pp. 37–42.
- Hess, D.E., Williams, J.H., 1994. Influence of planting date on *Striga* infestation and yield of pearl millet. *Phytopath.* 84, 1104.

- Hirsch, A.M., Bauer, W.D., Bird, D.M., Cullimore, J., Tyler, B., Yoder, J.I., 2003. Molecular signals and receptors: controlling rhizosphere interactions between plants and other organisms. *Ecology* 84, 858–68.
- Hooper, A.M., Caulfield, J.C., Hao, B., Pickett, J.A., Midega, C.A.O., Khan, Z.R., 2015. Isolation and identification of *Desmodium* root exudates from drought tolerant species used as intercrops against *Striga hermonthica*. *Phytochem.* 117, 380–387.
- Huang, K., Whitlock, R., Press, M.C., Scholes, J.D., 2011. Variation for host range within and among populations of the parasitic plant *Striga hermonthica*. *Heredity*, 1–9.
- Irving, L.J., Cameron, D.D., 2009. You are What You Eat: Interactions Between Root Parasitic Plants and Their Hosts. In: *Adv.Bot. Res.* 50. 87–138.
- Jamil, M., Rodenburg, J., Charnikhova, T., Bouwmeester, H.J., 2011. Pre-attachment *Striga hermonthica* resistance of New Rice for Africa (NERICA) cultivars based on low strigolactone production. *New Phytologist* 192, 964–975.
- Jamil, M., Kanampiu, F.K., Karaya, H., Charnikhova, T., Bouwmeester, H.J., 2012. *Striga hermonthica* parasitism in maize in response to N and P fertilisers. *Field Crops Res.* 134, 1–10.
- Jia, X.P., Shi, Y.S., Song, Y.C., Wang, G.Y., Wang, T.Y., Li, Y., 2007. Development of EST-SSR in foxtail millet (*Setaria italica*). *Genet. Resour. Crop Evol.* 54, 233–236.
- Joel, D.M., 2000. The long-term approach to parasitic weeds control: manipulation of specific developmental mechanisms of the parasite. *Crop Prot.* 19, 753–758.
- Joel, D.M., Hershenson, J., Eizenberg, H., Aly, R., Ejeta, G., Rich, P.J., Ransom, J.K., Sauerborn, J., Rubiales, D., 2007. Biology and management of weedy root parasites. *Hort. Rev.* 33, 267–349.
- Kannan, C., Zwanenburg, B., 2014. A novel concept for the control of parasitic weeds by decomposing germination stimulants prior to action. *Crop Prot*, 61, 11–15.
- Kanampiu, F.K., Kabambe, V., Massawe, C., Jasi, L., Friesen, D., Ransom, J.K., Gressel, J., 2003. 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, 679–706.
- Kanampiu, F., Diallo, A., Karaya, H., 2007a. Herbicide-seed coating technology: A unique approach for *Striga* control in maize. *Afr. Crop Sci. Conf. Proc.* 8, 1095–1098.
- Kanampiu, F., Diallo, A., Burnet, M., Karaya, H., Gressel, J., 2007b. Success with the low biotech of seed-coated imidazolinone-resistant maize. In: Ejeta, G, Gressel, J., (Ed.), *Integrating New Technologies for Striga Control: Towards Ending the Witch-hunt*. World Scientific Publishing Company Pvt. Ltd. Singapore, pp. 145–158.
- Kapran, I., Grenier, C., Ejeta, G., 2007. Introgression of *Striga* resistance into African sorghum landraces. In: Ejeta, G., Gressel, J., (Eds.), *Integrating new technologies for Striga control: Towards ending the witch-hunt*. World Scientific Publishing Company Pvt. Ltd. Singapore, pp 129–142.
- Karaya, H., Kiarie, N., Mugo, S., Kanampiu, F., Ariga, E., Nderitu, J., 2012. Identification of new maize inbred lines with resistance to *Striga hermonthica* (Del.) Benth. *J. Crop Prot.* 1(2), 131–142.
- Kgosi, R.L., Zwanenburg, B., Mwakaboko, A.S., Murdoch, A.J., 2012. Strigolactone analogues induce suicidal germination of *Striga* spp. in soil. *Weed Res.* 52, 197–203.
- Khan, Z.R., Pickett, J.A., Hassanali, A., Hooper, A.M., Midega, C.A.O., 2008. *Desmodium* species and associated biochemical traits for controlling *Striga* species: present and future prospects. *Weed Res.* 48, 302–306.
- Khan, Z.R., Pickett, J.A., Wadhams, L.J., Hassanali, A., Midega, C.A.O., 2006. Combined control of *Striga hermonthica* and stemborers by maize-*Desmodium* spp. intercrops. *Crop Prot.* 25, 989–995.

- Khan, Z.R., Hassanali, A., Overholt, W., Khamis, T.M., Hooper, A.M., Pickett, J.A., Wadhams, L. J., Woodcock, C.M., 2002. Control of witchweed *Striga hermonthica* by intercropping with *Desmodium* spp., and the mechanism defined as allelopathic. *J. Chem. Ecol.* 28, 1871–1885.
- Kohlen, W., Charnikhova, T., Liu, Q., Bours, R., Domagalska, M.A., Beguerie, S., Verstappen, F., Leyser, O., Bouwmeester, H., Ruyter-Spira, C., 2011. Strigolactones are transported through the xylem and play a key role in shoot architectural response to phosphate deficiency in nonarbuscular mycorrhizal host *Arabidopsis*. *Plant Physiol.* 155, 974–987.
- Kountche, B.A., 2013. Resistance to *Striga hermonthica* (Del.) Benth.: From development of resistant populations towards understanding the molecular genetic basis in pearl millet [*Cenchrus americanus* (L.) Morrone]. Ph.D thesis, Montpellier SupAgro, Montpellier, France, 143 p.
- Kountche, B.A., Hash, C.T., Dodo, H., Oumarou, L., Sanogo, M.D., Amadou, T., Vigouroux, Y., This, D., Nijkamp, R., Haussmann, B.I.G., 2013a. Development of a pearl millet *Striga*-resistant genepool: Response to five cycles of recurrent selection under *Striga*-infested field conditions in West Africa. *Field Crops Res.* 154, 82–90.
- Kountche, B.A., Kane, N., Ousseini, I.S., Vigouroux, Y., 2013b. Crop Adaptation to Biotic and Abiotic Conditions: Going Wild with Next Generation Sequencing Technologies. *Agrotechnol* 2: <http://dx.doi.org/10.4172/2168-9881.1000e103>.
- Koyama, M.L., 2000. Molecular markers for studying pathogen variability: Implications for breeding for resistance to *Striga hermonthica*. In: Haussmann, B.I.G., Hess, D.E., Koyama, M.L., Grivet, L., Rattunde, H.F.W., Geiger, H.H., (Eds.), *Breeding for Striga Resistance in Cereals*, Margraf Verlag, Weikersheim, Germany, pp. 227–245.
- Kroschel, J., 1998. *Striga* – How will it affect African agriculture in the future? – An ecological perspective. In: Martin, K., Müther, J., Auffarth, A. (Eds.), *Agroecological, Plant Protection and the Human Environment: Views and Concepts*. *Plits* 16 (2), Verlag W. and S Koch, Am Eichenhain, Germany, pp. 137–158.
- Kroschel, J., Hundt, A., Abbasher, A.A., Sauerborm, J., 1996. Pathogenicity of fungi collected in northern Ghana to *Striga hermonthica*. *Weed Res.* 36, 515–520.
- Kuchinda, N.C., Kureh, I., Tarfa, B.D., Shinggu, C., Omolehin, R., 2003. On-farm evaluation of improved maize varieties intercropped with some legumes in the control of *Striga* in the Northern Guinea savanna of Nigeria. *Crop Prot.* 22, 533–538.
- Lane, J.A., Child, D.V., Reiss, G.C., Entcheva, V., Bailey, J.A., 1997. Crop resistance to parasitic plants. In: Crute, I.R., Holub, E.B., Burdon, J.J. (Eds.), *the Gene-for-Gene Relationship in Plant Parasite Interactions*. CAB International, Oxfordshire, UK, pp. 81–97.
- Lane, J.A., Child, D.V., Moore, T.H.M., Bailey, J.A., 1995. Wild relatives of cereals as new sources of resistance to *Striga*. In: *Parasitic Plants: Biology and Resistance*. International Workshop, IACR-Long Ashton Research Station, Bristol, UK, 30 May–2 June 1995, p. 13.
- Logan, D.C., Stewart, G.R., 1991. Role of ethylene in the germination of the hemiparasite, *Striga hermonthica*. *Plant Physiol.* 97, 1435–1438
- Mbwaga, A.M., Riches, C., Ejeta, G., 2007. Integrated *Striga* management to meet sorghum demand in Tanzania. In Ejeta, G., Gressel, J., (Eds.), *Integrating new technologies for Striga control: Towards ending the witch-hunt*. World Scientific Publ. Co. Pvt. Ltd., Singapore. p. 253–264.
- Mace, E.S., Ling Xia, Jordan, D.R., Halloran, K., Parh, D.K., Huttner, E., Wenzl, P., Kilian, A., 2008. DArT markers: diversity analyses and mapping in *Sorghum bicolor*. *BMC Genomics* 9, 26. DOI:10.1186/1471-2164-9-26.

- Mace, E.S., Rami, J.F., Bouchet, S., Klein, P.E., Klein, R.R., Kilian, A., Wenzl, P., Ling Xia, Halloran, K., Jordan, D.R., 2009. A consensus genetic map of sorghum that integrates multiple component maps and high-throughput Diversity Array Technology (DArT) markers. *BMC Plant Biology* 9, 13. DOI:10.1186/1471-2229-9-13.
- Maiti, R.K., Ramaiah, K.V., Bisen, S.S., Chidley, V.L., 1984. A comparative study of the haustorial development of *Striga asiatica* (L.) Kuntze on sorghum cultivars. *Ann. Bot. (Lond.)* 54, 447–457.
- Mannuramath, M., Yenagi, N., Orsat, V., 2015. Quality evaluation of little millet (*Panicum miliare*) incorporated functional bread. *J. Food Sci. Technol.* 52(12), 8357–8363.
- Mariac, C., Luong, V., Kapran, I., Mamadou, A., Sagnard, F., Deu, M., Chantereau, J., Gerard, B., Ndjeunga, J., Bezançon, G., Pham, J., Vigouroux, Y., 2006. Diversity of wild and cultivated pearl millet accessions [*Pennisetum glaucum* (L.) R. Br.] in Niger assessed by microsatellite markers. *Theor. Appl. Genet.* 114, 49–58.
- Marley, P.S., Ahmed, S.M., Shebayan, J.A.Y., Lagoke, S.T.O., 1999. Isolation of *Fusarium oxysporum* with potential for biocontrol of the witchweed (*Striga hermonthica*) in the Nigerian Savanna. *Bio. Sci. Technol.* 9, 159–163.
- Marley, P.S., Aba, D.A., Shebayan, J.A.Y., Musa, R., Sanni, A., 2004. Integrated management of *Striga hermonthica* in sorghum using a mycoherbicide and host plant resistance in the Nigerian Sudano-Sahelian savanna. *Weed Res.* 44, 157–162.
- Marley P.S., Kroschel, J., Elzein, A., 2005. Host specificity of *Fusarium oxysporum* Schlecht (isolate PSM 197), a potential mycoherbicide for controlling *Striga* spp. in West Africa. *Weed Res.* 45, 407–412.
- Matsuura, H., Ohashi, K., Sasako, H., Tagawa, N., Takano, Y. et al., 2008. Germination stimulant from root exudates of *Vigna unguiculata*. *Plant Growth Regul.* 54, 31–36.
- Matusova, R.K., Rani, F.W., Verstaen, A., Franssen, M.C.R., Beale, M.H., Bouwmeester, H.J., 2005. The strigolactone germination stimulants of the plant-parasitic *Striga* and *Orobanches* are derived from the carotenoid pathway. *Plant Physiol.* 139, 920–934.
- Mayer, A.M, 2006. Pathogenesis by Fungi and by Parasitic Plants: Similarities and Differences. *Phytoparasitica* 34(1), 3–16.
- Michelmore, R., 2000. Genomic approaches to plant diseases resistance. *Curr. Opin. Plant Biol.* 3, 125–131.
- Mishra, V., Yadav, N., Pandey, S., Puranik, V., 2014. Bioactive components and nutritional evaluation of underutilized cereals. *Ann. Phytomed.* 3(2), 46–49.
- Mohamed, A., Ellicott, A., Housley, T.L., Ejeta, G., 2003. Hypersensitive Response to *Striga* Infection in *Sorghum*. *Crop Sci.* 43, 1320–1324.
- Mohamed, K.I., Musselman, L.J., Riches, C.R., 2001. The genus *Striga* (*Scrophulariaceae*) in Africa. *Ann. Missouri Bot. Garden.* 88, 60–103.
- Mohamed, K., Bolin, J., Musselman, L., Peterson, A., 2007. Genetic diversity of *Striga* and implications for control and modeling future distributions. In: Ejeta, G., Gressel, J., (Eds.), *Integrating new technologies for striga control: towards ending the witch-hunt*, pp. 71–84.
- Mohamed, A.H., Housley, T.L., Ejeta, G., 2010. An *in vitro* technique for studying specific *Striga* resistance mechanisms in sorghum. *Afr. J. Agric. Res.* 5, 1868–1875.
- Mohamed, A., Ali, R., Elhassan, O., Suliman, E., Mugoya, C., Masiga, C.W., Elhusien, A., Hash, C.T., 2014. First products of DNA marker-assisted selection in sorghum released for cultivation by farmers in sub-saharan Africa. *J. Plant Sci. Mol. Breed.* 3, 3. <http://dx.doi.org/10.7243/2050-2389-3-3>
- Mori, K., Matsui, J., Yokota, T., Sakai, H., Bando, M. et al., 1999. Structure and synthesis of orobanchol, the germination stimulant for *Orobanche minor*. *Tetrahedron Lett.* 40, 943–946.

- Moumouni, K.H., Kountche, B.A., Jean, M., Hash, C.T., Vigouroux, Y., Haussmann, B.I.G., Belzile, F., 2015. Construction of a genetic map for pearl millet, *Pennisetum glaucum* (L.) R. Br., using a genotyping-by-sequencing (GBS) approach. *Mol. Breed.* 35, 5. DOI 10.1007/s11032-015-0212-x
- Mounde. L.G., 2014. Understanding the role of plant growth promoting bacteria on sorghum growth and biotic suppression of *Striga* infestation. PhD thesis, University of Hohenheim, Stuttgart, Germany, pp. 113.
- Muller, S., Hauck, C., Schildknecht, H., 1992. Germination stimulants produced by *Vigna unguiculata* Walp cv Saunders Upright. *J. Plant Growth Regul.* 11, 77–84.
- Mutengwa, C.S., Tongoona, P.B., Sithole-Niang, I., 2005. Genetic studies and a search for molecular markers that are linked to *Striga asiatica* resistance in sorghum. *Afr. J. Biotechnol.* 4, 1355–1361.
- Muthamilarasan, M., Prasad, M., 2015. Advances in *Setaria* genomics for genetic improvement of cereals and bioenergy grasses. *Theor. Appl. Genet.* 128, 1–14.
- Obilana, A.T., Ramaiah, K.V., 1992. *Striga* (witchweeds) in sorghum and millet: knowledge and future research needs. In: de Milliano, W.A.J., Frederiksen, R.A., Bengston, G.D., (Eds.), *Sorghum and millets diseases: a second world review*. International Crops Research Institute for the Semi-Arid Tropics Patancheru, India, pp. 187-201.
- Olivier, A., 1995. *Le striga*, mauvaise herbe parasite des céréales africaines: biologie et méthodes de lutte. *Agron.* 15, 517–525.
- Olmstead, R.G., DePamphilis, C.W., Wolfe, A.D., Young, N.D., Elisons, W., Reeves, P.A., 2001. Disintegration of the Scrophulariaceae. *Am. J. Bot.* 88, 348–361.
- Omanya, G.O., Haussmann, B.I G, Hess, D.E., Reddy, B.V.S., Kayentao, M., Welz, H.G., Geiger, H.H., 2004. Utility of indirect and direct selection traits for improving striga resistance in two sorghum recombinant inbred populations. *Field Crops Res.* 89, 237–252.
- Oswald, A., 2005. *Striga* control – technologies and their dissemination. *Crop Prot.* 24, 333–342.
- Parker, C., 2012. Parasitic Weeds: A World Challenge. *Weed Sci.* 60, 269–276.
- Parker, C., Riches, C. R., 1993. *Parasitic Weeds of the World: Biology and Control*. Wallingford, UK: CAB International, 332 p.
- Parker, C., 2009. Observations on the current status of *Orobache* and *Striga* problems worldwide. *Pest Manage. Sci.* 65, 453–459.
- Paterson, A. H. et al., 2009. The *Sorghum bicolor* genome and the diversification of grasses. *Nature* 457, 551–556.
- Pennisi, E., 2015. How crop-killing witchweed senses its victims. *Science* 350,146–147.
- Pennisi, E., 2010. Armed and dangerous. *Science* 327, 804–805.
- Qi, X., Lindup, S., Pittaway, T.S., Allouis, S., Gale, M.D., Devos, K.M., 2001. Development of simple sequence repeat markers from bacterial artificial chromosomes without subcloning. *Bio.Techniques* 31, 355–362.
- Qi, X., Pittaway, T.S., Lindup, S., Liu, H., Waterman, E., Padi, F K., Hash, C.T., Zhu, J., Gale, M.D., Devos, K.M., 2004. An integrated genetic map and a new set of simple sequence repeat markers for pearl millet, *Pennisetum glaucum*. *Theor. Appl. Genet.* 109, 1485–1493.
- Rai, K.N., Govindaraj, M., Rao, A.S., 2012. Genetic enhancement of grain iron and zinc content in pearl millet. *Quality Assurance and Safety of Crops and Foods* Vol. 4, Issue 3: 119–125. DOI: 10.1111/j.1757-837X.2012.00135.x
- Rajaram, V., Nepolean, T., Senthilvel, S., Varshney, R.K., Vadez, V., Srivastava, R.K., Shah, T.M., Supriya, A., Kumar, S., Kumari, B.R., Bhanuprakash, A., Narasu, M.L., Riera-Lizarazu, O., Hash, C.T., 2013. Pearl millet [*Pennisetum glaucum* (L.) R. Br.] consensus

- linkage map constructed using four RIL mapping populations and newly developed EST-SSRs. *BMC Genomics* 14, 159. <http://www.biomedcentral.com/1471-2164/14/159>
- Rakshit, S., Patil, J.V., 2014. Sorghum. In: Chopra, V.L., (Ed.), *Breeding field crops II: advances*. Studium Press (LLC), Houston, pp 79–96.
- Ramaiah, K.V., 1987. Breeding cereal grains for resistance to witchweed. In: Musselman, L.J., (Ed.), *Parasitic Weeds in Agriculture, Vol I, Striga*. CRC Press, Boca Raton, FL, pp. 227–242.
- Ramaiah, K.V., 1984. Patterns of *Striga* resistance in sorghum and millets with special emphasis on Africa. In: *Striga: Biology and Control, Proceedings Workshop on the biology and control of Striga*, 14-17 Nov 1983, Dakar, Senegal. ICSU Press/IDRC, pp. 71–92.
- Ramaiah, K.V., Chidley, V.L., House, L.R., 1990. Inheritance of *Striga* seed-germination stimulant in sorghum. *Euphytica* 45, 33–38.
- Rao, P.S., Reddy, P.S., Rathore, A., Reddy, B.V.S., Panwar, S., 2011. Application GGE biplot and AMMI model to evaluate sweet sorghum (*Sorghum bicolor*) hybrids for genotype × environment interaction and seasonal adaptation. *Indian J. Agric. Sci.* 81, 438–444.
- Rector, B.G., 2009. Molecular biology approaches to control of intractable weeds: new strategies and complements to existing biological practices. *Plant Sci.* 175, 437–448.
- Rich, P.J., Ejeta, G., 2008. Towards effective resistance to *Striga* in African maize. *Plant Signaling & Behavior* 3, 618–621.
- Rich, P.J., Grenier, C., Ejeta, G., 2004. *Striga* resistance in the wild relatives of sorghum. *Crop Sci.* 44, 2221–2229.
- Rispail, N., Dita, M.A., González-Verdejo, C., Pérez-de-Luque, A., Castillejo, M.A., Prats, E., Román, B., Jorrín, J., Rubiales D., 2007. Plant resistance to parasitic plants: molecular approaches to an old foe. *New Phytologist* 173, 703–712.
- Robert, O.J., 2011. Genetic Analysis of *Striga hermonthica* Resistance in Sorghum (*Sorghum bicolor*) Genotypes in Eastern Uganda. Ph.D thesis, University of KwaZulu-Natal, Pietermaritzburg, South Africa.
- Rodenburg, J., Bastiaans, L., Weltzien, E. Hess, D.E., 2005. How can field selection for *Striga* resistance and tolerance in sorghum be improved? *Field Crops Res.* 93, 34–50.
- Rodenburg, J., Bastiaans, L., Kropff, M.J., Van Ast, A., 2006. Effects of host plant genotype and seedbank density on *Striga* reproduction. *Weed Res.* 46, 251–263.
- Rubiales, D., 2003. Parasitic plants, wild relatives and the nature of resistance. *New Phytol.* 160, 459–461.
- Rubiales, D., Pérez-de-Luque, A., Fernandez-Aparico, M., Sillero, J.C., Roman, B., Kharrat, M., Khalil, S., Joel, D.M., Riches, C., 2006. Screening techniques and sources of resistance against parasitic weeds in grain legumes. *Euphytica* 147, 187–199.
- Runo, S., Alakonya, A., Machuka, J., Sinha, N., 2011. RNA interference as a resistance mechanism against crop parasites in Africa: a ‘Trojan horse’ approach. *Pest Manage. Sci.* 67, 129–136.
- Samake, O., Stomph, T.J., Kropff, M.J. and Smaling, E.M.A., 2006. 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.
- Satish, K., Gutema, Z., Grenier, C., Rich, P.J., Ejeta, G., 2012. Tagging and validation of microsatellite markers linked to the low germination stimulant gene (*lgs*) for *Striga* resistance in sorghum [*Sorghum bicolor* (L.) Moench]. *Theor. App. Genet.* 124, 989–1003.
- Sato, D., Awad, A.A., Chae, S.H., Yokota, T., Sugimoto, Y., Takeuchi Y, Yoneyama K., 2003. Analysis of strigolactones, germination stimulants for *Striga* and *Orobanche*, by

- high-performance liquid chromatography/tandem mass spectrometry. *J. Agric. Food Chem.* 51, 1162–1168.
- Scholes, J.D., Press, M.C., 2008. *Striga* infestation of cereal crops—an unsolved problem in resource-limited agriculture. *Curr. Opin. Plant Biol.* 11, 180–186.
- Senthilvel, S., Jayashree, B., Mahalakshmi, V., Sathish, K.P., Nakka, S., Nepolean, T., Hash, C.T., 2008. Development and mapping of Simple Sequence Repeat markers for pearl millet from data mining of Expressed Sequence Tags. *BMC Plant Biol.* 8, 119  
doi:10.1186/1471-2229-8-119.
- Senthilvel, S., Mahalakshmi, V., Sathish, K.P., Reddy, A.R., Markandeya, G., Reddy, M.K., Misra, R., Hash, C.T., 2004. New SSRs markers for pearl millet from data mining of Expressed Sequence Tags. 4th International Crop Science Congress, Brisbane-Australia, 26 Sep–1 Oct 2004. [www.cropscience.org.au](http://www.cropscience.org.au)
- Shen, H., Ye, W., Hong, L., Huang, H., Wang, Z., Deng, X., Yang, Q., Xu, Z., 2006. Progress in Parasitic Plant Biology: Host Selection and Nutrient Transfer. *Plant Biol.* 8, 175–185.
- Serghini, K., Perez-de-Luque, A., Castejon-Munoz, M., Garcia-Torres, L., Jorrin, J.V., 2001. Sunflower (*Helianthus annuus* L.) response to broomrape (*Orobanche cernua* Loefl.) parasitism: induced synthesis and excretion of 7-hydroxylated simple coumarins. *J. Exp. Bot.* 52, 2227–2234.
- Siame, B.A., Weerasuriya, Y., Wood, K., Ejeta, G., Butler, L.G., 1993. Isolation of strigol, a germination stimulant for *Striga asiatica*, from host plants. *J. Agric. Food Chem.* 41, 1486–1491.
- Spallek, T., Mutuku, J.M., Shirasu, K., 2013. The genus *Striga*: a witch profile. *Mol. Plant Pathol.* 14, 861–869.
- Steinkellner, S., Lenzemo, V., Langer, I., Schweiger, P., Khaosaad, T., Toussaint, J.P., Vierheilig, H., 2007. Flavonoids and strigolactones in root exudates as signals in symbiotic and pathogenic plant-fungus interactions. *Molecules* 12, 1290–1306.
- Supriya, S., Senthilvel, S., Nepolean, T., Eshwar, K., Rajaram, V., Shaw, R., Hash, C.T., Kilian, A., Yadav, R.C., Narasu, M.L., 2011. Development of a molecular linkage map of pearl millet integrating DArT and SSR markers. *Theor. Appl. Genet.* 123, 239–250.
- Tank, D.C., Beardsley, P.M., Kelchner, S.A., Olmstead, R.G., 2006. Review of the systematics of Scrophulariaceae and their current disposition. *Aust. System. Bot.* 19, 289–307.
- Teka, H.B., 2014. Advance research on *Striga* control: A review. *Afr. J. Plant Sci.* 8(11), 492–506.
- Tesso, T., Gutema, Z., Deressa, A., Ejeta, G., 2007. An integrated *Striga* management option offers effective control of *Striga* in Ethiopia. In: Ejeta, G., Gressel, J., (Eds.), *Integrating new technologies for Striga control: Towards ending the witch-hunt*. World Scientific Pub. Co. Pvt. Ltd., Singapore, pp. 199–212.
- Tesso, T.T., Ejeta, G., 2011. Integrating Multiple Control Options Enhances *Striga* Management and Sorghum Yield on Heavily Infested Soils. *Agron. J.* 103, 1464–1471.
- Ueno, K., Nomura, S., Muranaka, S., Mizutani, M., Takikawa, H. et al., 2011. Ent-2'-epi-orobanchol and its acetate, as germination stimulants for *Striga gesnerioides* seeds isolated from cowpea and red clover. *J. Agric. Food Chem.* 59, 10485–10490.
- Umehara, M., Hanada, A., Yoshida, S., Akiyama, K., Arite, T., et al., 2008. Inhibition of shoot branching by new terpenoid plant hormones. *Nature* 455, 195–200.
- Van Mourik, T.A., 2007. *Striga hermonthica* seed bank dynamics: process quantification and modelling. PhD thesis, Wageningen University, Wageningen, The Netherlands, 123 pp.
- Varshney, R.K., Dubey, A., 2009. Novel genomic tools and modern genetic and breeding approaches for crop improvement. *J. Plant Biochem. Biotechnol.* 18, 127–138.

- Vasey, R.A., Scholes, J.D., Press, M.C., 2005. Wheat (*Triticum aestivum*) Is Susceptible to the Parasitic Angiosperm *Striga hermonthica*, a Major Cereal Pathogen in Africa. *Phytopath.* 95, 1294–1300.
- Vasudeva, R.M.J., Musselman, L.J., 1987. Host specificity in *Striga* spp. and physiological strains. In: Musselman, L.J. (Ed.), *Parasitic Weeds in Agriculture, Vol. I, Striga*. CRC Press, Boca Raton, FL, pp. 13–25.
- Venne, J., Beed, F., Watson, A., 2009. Integrating *Fusarium oxysporum* f. sp. *strigae* into cereal cropping systems in Africa. *Pest Manage. Sci.* 65, 572–580.
- Visarada, K.B.R.S., Saikishore, 2015. Advances in Genetic Transformation. In: Madhusudhana, R. et al., (Eds.), *Sorghum Molecular Breeding*, Springer (India) Pvt. Ltd., pp. 199–215.
- Vogler, R.K., Ejeta, G., Butler, L.G., 1996. Inheritance of low production of *Striga* germination stimulant in sorghum. *Crop Sci.* 36, 1185–1191.
- Watson, A.K., 2013. Biocontrol. In: Joel, D.M., Gressel, J., Musselman, L.J., (Eds.), *Parasitic Orobanchaceae*. Springer Verlag, Berlin Heidelberg, pp. 469–497.
- Westwood, J.H., dePamphilis, C.W., Das, M., Fernandez-Aparicio, M., Honaas, L.A., Timko, M.P., Wafula, E.K., Wickett, N.J., Yoder, J.I., 2012. The Parasitic Plant Genome Project: New Tools for Understanding the Biology of *Orobanche* and *Striga*. *Weed Sci.* 60, 295–306.
- Westwood, J.H., Yoder, J.I., Timko, M.P., Pamphilis, C.W., 2010. The evolution of parasitism in plants. *Trend. Plant Sci.* 15(4), 227–235.
- Wilson, J.P., Hess, D.E., Hanna, W.W., 2000. Resistance to *Striga hermonthica* in wild accessions of the primary gene pool of *Pennisetum glaucum*. *Phytopath.* 90, 1169–1172.
- Wilson, J.P., Hess, D.E., Hanna, W.W., Kumar, K.A., Gupta, S.C., 2004. *Pennisetum glaucum* subsp. *monodii* accessions with *Striga* resistance in West Africa. *Crop Prot.* 23, 865–870.
- Xie, X., Yoneyama, K., Yoneyama, K., 2010. The Strigolactone Story. *Annu. Rev. Phytopathol.* 48, 93–117.
- Xie, X., Yoneyama, K., Kusumoto, D., Yamada, Y., Yokota, T., et al., 2008. Isolation and identification of alectrol as (+)-orobanchyl acetate, a germination stimulant for root parasitic plants. *Phytochem.* 69, 427–431.
- Xie, X., Kusumoto, D., Takeuchi, Y., Yoneyama, K., Yamada, Y., 2007. 2'-epi-Orobanchol and solanacol, two unique strigolactones, germination stimulants for root parasitic weeds, produced by tobacco. *J. Agric. Food Chem.* 55, 8067–8072.
- Xie, X.N., Yoneyama, K., Harada, Y., Fusegi, N., Yamada, Y. et al., 2009a. Fabacyl acetate, a germination stimulant for root parasitic plants from *Pisum sativum*. *Phytochem.* 70, 211–215.
- Xie, X.N., Yoneyama, K., Kurita, J.Y., Harada, Y., Yamada, Y. et al., 2009b. 7-Oxoorobanchyl acetate and 7-oxoorobanchol as germination stimulants for root parasitic plants from Flax (*Linum usitatissimum*). *Biosci. Biotechnol. Biochem.* 73, 1367–1370.
- Yadav, O.P., Mitchell, S.E., Zamora, A., Fulton, T.M., Kresovich, S., 2007. Development of new simple sequence repeat markers for pearl millet. *SAT eJ.* 3(1).
- Yadav O.P., Mitchell, S.E., Fulton, T.M., Kresovich, S., 2008. Transferring molecular markers from sorghum, rice and other cereals to pearl millet. *SAT eJ.* 6.
- Yoder, J.I., Gunathilake, P., Wu, B., Tomilova, N., Tomilov, A.A., 2009. Engineering host resistance against parasitic weeds with RNA interference. *Pest Manage. Sci.* 65, 460–466.
- Yoder, J.I., Scholes, J.D., 2010. Host plant resistance to parasitic weeds; recent progress and bottlenecks. *Curr. Opin. Plant Biol.* 13, 478–484.
- Yohannes, T., Abraha, T., Kiambi, D., Folkertsma, R., Hash, C.T., Ngugi, F., Mutitu, E., Abraha, N., Weldetsion, M., Mugoya, C., Masigag, C.W., de Villiers, S., 2015. Marker-

- assisted introgression improves *Striga* resistance in an Eritrean Farmer-Preferred Sorghum Variety. *Field Crops Res.* 173, 22–29.
- Yokota, T., Sakai, H., Okuno, K., Yoneyama, K., Takeuchi, Y., 1998. Alectrol and orobanchol, germination stimulants for *Orobancha minor*, from its host red clover. *Phytochem.* 49, 1967–1973.
- Yoneyama, K., Awad, A.A., Xie, X., Yoneyama, K., Takeuchi, Y., 2010. Strigolactones as germination stimulants for root parasitic plants. *Plant Cell Physiol.* 51, 1095–1103.
- Yonli, D., Traoré H., Hess, D.E., Sankara, P., Sérémé, P., 2006. 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.
- Yoshida, S., Shirasu, K., 2009. Multiple layers of incompatibility to the parasitic witchweed, *Striga hermonthica*. *New Phytologist* 183, 180–189.
- Zahran, E., Kohlschmid, E., Sauerborn, J., Abbasher, A.A., Muller-Stover, D., 2008. Does an alication as seed coating stabilize the efficacy of biological control agents of *Striga hermonthica* under field conditions? *J. Plant Dis. Prot.* S21, 467–471.
- Zarafi, A.B., Elzein, A., Abdulkadir, D.I., Beed, F., Akinola, O.M., 2015. Host range studies of *Fusarium oxysporum* f.sp. strigae meant for the biological control of *Striga hermonthica* on maize and sorghum. *Arch. Phytopathol. Plant Prot.* 48, 1, 1–9, DOI:10.1080/03235408.2014.880580
- Zwanenburg, B., Mwakaboko, A.S., Reizelman, A., Anilkumar, G., Sethumadhavan D., 2009. Structure and function of natural and synthetic signalling molecules in parasitic weed germination. *Pest Manage. Sci.* 65, 478–491.
- Zwanenburg, B., Pospisil, T., 2013. Structure and activity of strigolactones: new plant hormones with a rich future. *Mol. Plant* 6, 38–62.
- Zwanenburg, B., Mwakaboko, A.S., Reizelman, A., Anilkumar, G., Sethumadhavan D., 2009. Structure and function of natural and synthetic signaling molecules in parasitic weed germination. *Pest Manage. Sci.* 65, 478–491.
- Zwanenburg, B., Nayak, S.K., Charnikhova, T.V., Bouwmeester, H.J., 2013. New strigolactone mimics: Structure–activity relationship and mode of action as germinating stimulants for parasitic weeds. *Bioorg. Med. Chem. Lett.* 23, 5182–5186.