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Breeding Sorghum for Striga Resistance: A Review

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Abstract
Striga causes substantial losses in sorghum production in sub-Saharan Africa. Striga-resistant sorghum cultivars could be a major component of integrated striga management, if resistance was available in adapted, productive germplasm. In this paper I review activities of breeding sorghum for striga-resistant. The agar-gel assay is an excellent tool to screen host genotypes in the laboratory for low production of the striga seed germination stimulant. Further laboratory assays are needed which allow the non-destructive, rapid and inexpensive evaluation of individual plants for additional resistance mechanisms. Field screening for striga resistance is hampered by high micro variability in African soils, heterogeneity of natural infestations and concomitant large environmental effects on striga emergence. Due to the extreme variability of the parasite and significant genotype by environment interaction effects, multi-location screening is recommended to obtain materials with stable performance. characterization of crop germplasm and improvement of available sources of resistance for better agronomic performance; transfer and pyramiding of resistance genes into adapted, farmer-selected cultivars; development of striga-resistant parent lines for hybrid or synthetic cultivars; and development of random-mating populations with multiple sources of resistance. The development of marker assisted selection techniques for broad-based, polygenic striga resistance is underway. This approach is particularly promising because striga resistance tests are difficult, expensive, and sometimes unreliable; the parasite is quarantined; and some resistance genes are recessive. Transgenic, herbicide-tolerant sorghums could contribute to an immediate, cost-effective control of striga by herbicides, but such cultivars are not yet available. The selection of sorghum cultivars with specific adaptation to integrated striga management approaches could contribute to sustainable sorghum production in striga-infested areas.
Keywords: breeding strategies, striga, resistant, sorghum, integrated control

1. INTRODUCTION

Sorghum [*Sorghum bicolor* (L) Moench, 2*n* = 20] is one of the most important cereal crops and well adapted to harsh environments characterized by drought and high temperatures.Sorghum grows over a wide range of latitudes from 0 to 45° North and South of the equator (ICRISAT, 1991).It requires less water than most cereals; hence it offers great potential for supplementing food and feed resources (KARI Proceedings, 2000) especially in dry lands where rainfall is limited. Globally, sorghum is the fifth most important staple food crop after wheat, rice, maize and barley (FAO, 2012). The crop is produced for its grain which is used for food, and stalks for fodder and building materials in developing countries. It is the second most important cereal crop after maize (*Zea mays*L.) in sub-Saharan Africa. In developed countries, sorghum is used primarily as animal feed and in the sugar, syrup, and molasses industry (Dahlbert et al., 2004). Total sorghum production from all sorghum producing countries was 55.6 million tons in 2010. The world average annual yield for sorghum was 1.37 tons per hectare in 2010. FAO reported the United States of America as the top sorghum producer with a harvest of 9.7 million tons followed by India, Nigeria, Sudan, and Ethiopia (FAOSTAT, 2011).

The potential productivity of sorghum is reduced due to a number of abiotic and biotic stresses. Paramountamong the abiotic factors are low soil fertility (nutrient deficiency) and drought. Important biotic constraints include the parasitic weed; *Striga*(*Striga*species), foliar and panicle diseases, stem borers, and shoot fly (Wortmann et al., 2006). Among the major sorghum diseases anthracnose, smuts and rusts account for substantial yield losses in the country. Sorghum production constraints vary from region to region within Ethiopia. However, drought and *Striga* are the most important problems across regions.

Striga, is a parasitic weed belonging to the Orobanchaceae (formerly: Scrophulariaceae) family. It infests and significantly reduces yields of cereal crops including rice, pearl millet, maize and sorghum (Rich et al., 2004). The Orobanchaceae family includes 50 species, of these 11 are recognized as crop pests (Mohamed et al., 2007). *Striga* threatens the livelihoods of millions of smallholder farmers throughout the semi-arid Africa and parts of Asia. Continuous cropping and the extension of cultivation to marginal soils due to population pressure have resulted in the spread and intensification of the *Striga* problem (Parker, 1991). In Ethiopia, *Striga* is widely found in the lowland areas where sorghum is the dominant crop. Based on its infestation level sorghum yield loss due to *Striga* damage varies from place to place. On average sorghum yield losses of 65% were estimated in moderate to heavy infestations (Tesso et al., 2007), however, the continental average is 40% (Lagoke et al., 1991). Diagnostic surveys conducted in the past five years by Debrebirhan, Sirinka and Pawe agricultural research centers indicated that *Striga* is rapidly expanding in many parts of the country (unpublished survey

reports).

The parasite control is difficult, but it is not impossible. In the last few decades, efforts have been devoted to develop methods for *Striga* control. The most promising way for controlling the parasite resides on the development of resistant cultivars (Ejeta, 1991). Striga-resistant sorghums can be a major component of integrated striga control approaches if resistance is incorporated into adapted, productive cultivars. Resistant cultivars can reduce both new striga seed production and the striga seed bank in infested soils. A crop genotype which, when grown under conditions of striga infestation, supports significantly fewer striga plants and has a higher yield than a susceptible cultivar is called resistant (Doggett, 1988; Ejeta et al.,1992). In contrast, tolerant cultivars show smaller yield reductions than susceptible cultivars under the same level of infestation. Cultivation of tolerant cultivars can lead to an increased striga seed bank over time (Doggett, 1988).

Sorghum could be enhanced through effective breeding programs using locally adapted and well-characterized germplasm.In this paper, breeding for improved integrated striga control mechanisms, genetic control and breeding methods of striga resistance in sorghum have been reviewed.

2. LITERATURE REVIEW

2.1. Breeding for Durable Resistance to Striga in Sorghum

Progress from past efforts in breeding witch weed resistance in crops has been limited. Reasons for slow progress vary from complexity of the resistance trait to lack of research support and appropriate screening techniques and selection strategies (Ejeta *et al.,* 2001). However, resistant sorghum cultivars that have been developed so far have shown good level of resistance mainly based on low stimulant production (Ejeta *et al.,* 2000). Over the years, resistance has not been long-term or applicable over a wide geographical area. One of the main causes of failure of resistance is that breeding efforts have not been taking good account of both the interspecific variability among *Striga* species, and intraspecific variation for virulence.

Witch weed populations have an extraordinary elasticity and capacity to adapt to new host species through the gradual build-up of new “biological forms” (Koyama, 2000). The reported variability of witch weeds implies that using single resistance genes to manage infestations is inadequate. Stacking of resistance genes may be essential to manage witch weeds effectively. Various researchers have suggested a diversity of breeding strategies that could lead to the development of long-term polygenic resistance to witch weeds (Ejeta *et al.,* 1992; Ejeta and Butler, 1993; Haussman *et al.,* 2000a).

If sources of resistance have been identified, they can be incorporated for agronomic performance. Alternatively, the resistance gene in these sources can be incorporated for agronomic performance. Alternatively, the resistance genes in these sources can be obtained by pyramiding resistance genes. Crop genotypes that possess multiple genes for *Striga* resistance, based on distinct mechanisms, are likely to have genetic resistance that is durable across several environmental conditions as well as across ecological variants of the parasite. It has also been emphasized that breeding programs should target sources of resistance at different areas and understand the nature of resistance required (Koyama, 2000). Suggested breeding methods include: early generation selection for individual resistance mechanisms; use of recurrent selection procedures to develop breeding populations with multiple sources of resistance; lines with different resistance mechanisms are combined to form hybrids or synthetics, to increase durability of resistance and the use of marker-assisted selection techniques for the development of broad-based, quantitative resistance to witch weeds under field conditions (Haussman *et al.,* 2000b).

Progress has been made in breeding for single gene *Striga*resistance mechanisms in sorghum. The mechanisms have been extensively exploited. Diverse sorghum genotypes with little or no stimulant production capacity have been identified. A number of improved sorghum varieties with *Striga*resistance due to low germination stimulant production have been developed (Ejeta*et al.,* 2001). Screening of landraces and improved sorghum lines using different bioassays has shown that host variants with low germination stimulant production, hypersensitive response, and incompatible response are rare. Rather, a greater preponderance of genetic variation for these traits has been found among wild and related species of sorghum (Ejeta*et al.,* 2001).

2.2. Resistance Mechanisms

Striga is an obligate parasite the interaction between striga and its host plant play a crucial role in the survival of the parasite. The following resistance mechanisms have been proposed (Ejeta et al., 1992).

- ✓ Low production of germination stimulant;one of the better understood mechanisms of resistance against Striga by sorghum is low production of compounds by the host root that *Striga* seeds require as stimulants for germination.
- ✓ Mechanical barriers (e.g., lignification of cell walls); e.g. with this mechanism is N13 and Framida (Haussmann et al., 2000b, Ejeta, 2007).
- ✓ Inhibition of germ tube exoenzymes by root exudates;
- ✓ Phytoalexine synthesis; kill the attached Striga, hence does not penetrate host tissues or develop further.

- ✓ Post-attachment hypersensitive reactions or incompatibility: characterized by the appearance of necrotic zones around the site of attempted infection (Agrios, 1988). Death of host cells results in unsuccessful establishment of the parasite hence its ultimate demise. Examples of sorghum genotypes with this mechanism are Framida, Dobbs, SAR 16, SAR 19, SAR 33, *Sorghum versicolor*and wild sorghum accession P47121 (Ejeta, 2007, Haussmann et al., 2000b).
- ✓ Antibiosis, i.e., reduced striga development through Unfavorable phytohormone supply by the host;This mechanism is present in SRN 39 and N13,
- ✓ Insensitivity to striga toxin (e.g., maintenance of stomatal aperture and photosynthetic efficiency);
- ✓ Avoidance through root growth habit (e.g., fewer roots in the upper 15±20 cm).

Absence of a haustorial induction compound in root exudates is unlikely to be a resistance mechanism in sorghum (Frick et al., 1996). Syringic acid was shown to be efficiently metabolized by horseradish peroxidase to the haustorial inducer 2,6-dimethoxy-parabenzoquinone.Since syringic acid is an ubiquitous metabolite of lignin biosynthesis and peroxidase reactions are involved in most pathogenic processes, a 2,6-dimethoxy-parabenzoquinone is probably produced by all host plants.

2.3. Screening Techniques

Precise and reliable screening techniques are indispensable prerequisites to breeding for resistance to any biotic or abiotic stress factor (VasudevaRao, 1985). The presence of individual mechanisms conferring resistance to striga may be examined in the laboratory, whereas complex resistance must be assessed under field conditions. Screening in pots may include advantages of both, providing some control over environmental conditions, but with the disadvantage of a largely artificial root environment (Omanya et al., 2000).

2.3.1. Screening for individual resistance mechanisms

In the laboratory the agar-gel assay developed by Hess et al. (1992) provides a simple means for screening host genotypes for low production of striga seed germination stimulant. The agar-gel assay may be extended in order to distinguish host genotypes on the basis of their ability to induce haustorial formation (Ejeta, 2000). The paper roll assay (Ejeta, 2000) allows observations of the early stages of striga infection. Sorghum seedlings are grown with their roots between rolled layers of germination paper. When seedlings are 1 week old, papers are unrolled and filter-paper strips containing artificially germinated striga seed are placed on sorghum roots. Papers are then rolled and placed in a glass container which allows light to reach growing sorghum shoots. After an interval of2±3weeks, papers are unrolled to reveal progressive invasion of the parasite on host roots. The paper roll assay can be an effective tool for identifying early post-infection resistance mechanisms, i.e., hypersensitivity reaction or incompatibility, but it still needs some modification to be employable on a large-scale (Ejeta, 2000).

Other laboratory tests have been developed including: various techniques to identify low stimulant producing genotypes (VasudevaRao, 1985); in vitro growth systems to study post-attachment reactions (Lane et al., 1991a, b); histological studies or analysis of lignin or silica content of host roots to elucidate mechanical barriers (VasudevaRao, 1985); in vitro culture of sorghum cells treated with extracts of striga plants to screen for resistance to the striga toxin (Ejeta et al., 1992); evaluation of extracts of host roots or other tissues for their ability to kill in vitro cultures of suspended striga cells (Ejeta et al., 1992). These tests have laborious; they are unsuited to selection programs with large numbers of entries to be screened.

2.3.2. Screening for complex resistance under field conditions

Field screening for striga resistance is hampered by the heterogeneity of natural field infestations, large environmental effects on striga emergence, and complex interactions between host, parasite and environment affecting the parasite's establishment and reproductive success. Improved field testing methodologies include: field inoculation with striga seeds and appropriate experimental design including a large number of replications, appropriate plot layout, Inclusion of susceptible and resistant checks at regular intervals, Evaluation in adjacent infested and uninfested plots and finally Use of selection indices combining striga counts, striga vigor, and grain yield or a host plant damage score (Haussman, 2000).

2.4. Sources of Resistance

Numerous sorghum cultivars or breeding lines have been reported as resistant to striga. Examples are Dobbs, Radar, Framida (SRN 4841), Seguetana sorghums from Mali, 555, N 13, IS 9830, Najjad, ICSV 1002 BF (from a cross between Framida and E 35-1), ICSV 1007 BF, CS 54, CS 95, KSV 4, SSV 6, SRN 6838, SAR (Striga asiatica resistant)-lines developed by ICRISAT (including SAR 16, SAR 19, SAR 33), IS 1005, IS 1006, IS 7777, IS 7739, IS 6961, IS 1260, IS 8140, IS 9934, 14825, IS 14829, IS 14907, IS 14928, IS 15401 and SRN 39 (Ramaiah, 1986; Carson, 1988). Among wild relatives, resistance has been expressed by accessions of Sorghum versicolor (Lane et al., 1995) and Sorghum drummondii (Ejeta, 2000). Different resistance mechanisms have been described by the above-named authors from different sources of resistance, i.e., low production of the germination stimulant (SRN 39, IS 9830, Framida, 555, SAR lines, IS 15401) low haustorial initiation stimulant (accession P-78 of Sorghum drummondii) mechanical barriers (N 13, Framida) antibiosis (SRN 39, N 13) and

hypersensitivity (SAR 16, SAR 19, SAR 33, Sorghum versicolor).

2.5. Genetics of Resistance

The low stimulation of Striga seed germination by the sorghum cultivars Framida, 555, and SRN 39 has been reported to be under the control of a single recessive gene (Ramaiah et al., 1990; Vogler et al., 1996). However, agar-gel assays conducted with a recombinant inbred population derived from the cross IS 9830_E 36-1 and F2 populations from crosses of Framida, 555, and IS 9830 with E 36-1 indicated that one major gene and several minor genes are involved in the stimulation of S. hermonthica seed germination (Haussmann, unpublished data). **It was also related by gene diversity in different plant species (Dutkuner et al., 2008; Yazici and Bilir, 2017).**

Diverging general combining ability (GCA) effects for germination distance in the agar-gel assay (using S. hermonthica) indicated that different sets of alleles or genes are responsible for low stimulant production in 555 and Framida (Haussmann et al., 1996, 2000a). Diallel studies and line tester analyses with sorghum clearly indicated the presence of quantitative genetic variation with preponderance of additive effects for stimulation of S. hermonthica seed germination in the agar-gel assay, the number of aboveground striga plants supported in pots, and the number of emerged striga under field conditions (Shinde and B.I.G. Haussmann et al. / Field Crops Research 66 (2000).

Estimates of broad-sense heritability were 0.91 and 0.97 for germination distances in a diallel cross and its parental lines, respectively, in the agar-gel assay (Haussmann et al., 1996). In field trials combined across two locations each in Mali and Kenya, estimated broad-sense heritability in two sorghum recombinant inbred populations ranged between 0.70 and 0.81 for striga (Omanya et al., 2000). In the same study, the genotype environment interaction variance was highly significant. Heterosis for striga resistance is genotype-dependent, and may be positive or negative (Ramaiah, 1984; Haussmann et al., 2000b). Sorghum hybrids derived from crosses between a resistant and a susceptible parent were reported to be susceptible (Rana et al., 1982; Obilana, 1984), suggesting partial or complete dominance of genes for susceptibility. It was concluded that both parents of a hybrid should be selected for striga resistance.

2.6. Variability Within and Among Striga Species, and Stability of Resistance

In field trials across diverse geographic regions, the total genotype environment interaction variance contains both interaction effects between genotypes and locations, and interaction effects between genotypes and putative striga races or biotypes. The two types of interaction, however, cannot be separated. Striga is a highly variable parasite and appears to have extraordinary plasticity and capacity to adapt to new hosts (Ejeta et al., 1992; Koyama, 1998, 2000a, b).

Resistance to striga is partially species-specific, i.e., resistance to S. asiatica does not necessarily hold against S. hermonthica and vice versa. Ramaiah (1987) reported some sorghum cultivars to be resistant in certain locations and susceptible in others. This may be due to the presence of site-specific striga races or biotypes. Striga hermonthica populations specific for sorghum and millet have been reported, whereas other populations attack both host species (VasudevaRao and Musselman, 1987). Koyama (1998, 2000a, b), using isozyme and RAPD (random amplified polymorphic DNA) marker techniques, reported low selection pressure on striga populations growing on susceptible sorghum cultivars, and increasing selection pressure (reducing the genetic variability of striga) on tolerant and resistant cultivars. Precise information on the genetics of the parasite's virulence is lacking. A better understanding of the variation for virulence among striga populations is required to direct the effective deployment of resistance genes against these parasites (Lane et al., 1997). There is a need to resolve the origin and relatedness of parasitic races, and to elucidate the observed genotype race interactions. The fact that S. hermonthica plants are extremely difficult to self-renders the topic the more difficult to study. However, genetic stocks of various striga biotypes could also be created by the development of full-sib families grown on uniform host plants, i.e., by caging two striga plants and a pollinator.

2.7. Breeding Strategies

Both interspecific variability among Striga species and intraspecific variation for aggressiveness must be taken into account when breeding for striga resistance (Ramaiah, 1987; Ejeta et al., 1992). In order to obtain stable, polygenic resistance, breeding materials should be evaluated at various locations with different striga populations or host-specific races (Ramaiah, 1987). In doing so, quarantine regulations must be strictly respected, and striga species or strains should not be introduced into regions where they do not already occur. If seed shortage imposes a constraint on progeny evaluation, a reduction in plot size should be preferred over reduction of the number of test locations, since there is always the danger of losing data from one location due to ``non-striga years'' or other obstacles. The breeder may also consider a trade-off between numbers of replications versus number of sites; however, the number of replications should not fall below four. To avoid seed shortage and therefore a trade-off between replications and sites, breeders could use inbred generations as test entries

(Kling et al., 2000).

In addition to multi-locational testing, the following breeding measures have been put forward by groups active in the field (Ramaiah, 1987; Kim, 1991, 1994, 1998; Ejeta et al., 1992. Characterize crop germplasm, search for sources of resistance and tolerance in elite material, and improve currently available sources of resistance for agronomic performance;

- ✓ include wild relatives with superior resistance in the breeding program;
- ✓ Transfer resistance genes into productive, well adapted genotypes;
- ✓ pyramid resistance genes to obtain more durable and stable, polygenic resistance;
- ✓ combine lines with different resistance mechanisms to form hybrids or synthetics, to increase durability of resistance;
- ✓ develop breeding populations with multiple sources of resistance using recurrent selection procedures;
- ✓ Develop and employ marker-assisted selection techniques for broad-based, quantitative striga resistance under field conditions.

Sorghum, due to the availability of nuclear and cytoplasmic-genic male sterility, offers a wide range of possible genetic structures to the breeder, including homozygous lines, homogeneous or heterogeneous hybrids, as well as homo or heterozygous, heterogeneous population or synthetic varieties. The potential merit of heterozygous sorghum cultivars was demonstrated by the average superiority of F2 populations over their parental lines of 18% for grain yield under striga infestation, averaged across four locations in Mali and Kenya (Haussmann et al., 2000a). In addition, Hess and Ejeta (1992) and Kling et al. (2000) reported that hybrid vigor can provide a degree of tolerance to striga in sorghum and maize, which is reflected in reduced yield depression under conditions of striga infestation.

Sorghum hybrids were reported to out yield parental lines or local varieties under variable drought stress in semi-arid, striga-free areas of East and West Africa (Doggett and Jowett, 1966). Instead of hybrids, other types of cultivars could be produced which capitalize on heterozygosity, e.g., synthetics built up from components with high out crossing rates and superior combining ability for striga resistance and grain yield. A synthetic cultivar can be regrown for a few seasons without serious changes in its genetic composition, which is convenient for the small-scale farmers (Haussmann et al., 2000c). The lack of reliable single-plant screening techniques in the field generally causes selection for striga resistance to be deferred until true-breeding progenies are available. This means that large numbers of progeny have to be advanced before the trait of interest can be assessed, a time- and cost-intensive procedure.

The agar-gel assay (Hess et al., 1992) is an excellent tool to transfer the low stimulant character to locally adapted cultivars using classical back-cross procedures. The fact that the low stimulant gene(s) were reported to be recessive renders the back-cross program more complicated and time-consuming. With its high heritability and the possibility to screen large numbers of entries, the in vitro germination distance fulfills two major prerequisites for an indirect selection trait. Coefficients of correlation between germination distance and striga resistance under field conditions are generally positive but vary among genetic materials and test locations (VasudevaRao, 1985; Omanya et al., 2000). In trials involving a recombinant inbred population derived from the cross of line IS 9830 (low stimulant) with line E 36-1 (high-stimulant), coefficients of correlation between germination distance in the agar-gel assay and striga emergence in the field ranged between 0 and 0.32 (significant at P.0.01) in Kenya, and between 0.29 and 0.64 (both significant at P.0.01) in Mali, (Omanya et al., 2000).

Breeders should bear in mind that screening for individual resistance mechanisms in the laboratory could result in a loss of valuable materials possessing resistance mechanisms other than those evaluated. The risk increases with increasing selection intensity, i.e., with a reduced effective population size. One strategy could be to use laboratory assays for individual resistance mechanisms as an initial screening of a larger number of breeding materials, followed by the more resource-demanding field screening. This would offer the possibility to identify resistance sources with multiple resistance mechanisms (Rattunde, H.F.W.,pers. comm.). Networking and exchange of useful materials are also important steps towards more efficient breeding programs for resistance to striga in sorghum.

2.8. Use of Molecular Markers

Molecular marker techniques are a powerful new tool in plant breeding. They permit identification and mapping of genes for individual, monogenic resistance mechanisms (like the low stimulant locus) and of quantitative trait loci (QTL) involved in polygenic, quantitative resistance under field conditions. The utility of DNA markers in resistance breeding depends on the existence of tight linkage between these markers and the resistance genes or QTL of interest.

In marker-assisted breeding programs, such linkage allows the breeder to select for resistance by identifying the DNA marker instead of evaluating the materials directly for resistance traits (Tanksley et al., 1989; Melchinger, 1990; Paterson et al., 1991). The integration of molecular marker selection techniques into plant

breeding promises a more rapid incorporation of desirable genes into improved cultivars, and facilitates the transfer of novel genes from related wild species (Tanksley et al., 1989). Detecting resistance genes by their linkage to DNA markers makes it possible to screen for many different resistance genes simultaneously, without the need to inoculate with pathogens. Pyramiding of resistance genes to provide durable resistance is therefore greatly facilitated. When resistance genes are transferred from wild relatives into a cultivated crop, molecular markers can assist in selecting against the undesired genetic background of the donor parent (Frisch et al., 1999). According to Melchinger (1990), the application of marker-assisted selection is particularly advantageous when:

- ✓ Resistance tests are difficult, complex, expensive or unreliable;
- ✓ The pathogen is quarantined;
- ✓ Breeding materials are advanced in off-season nurseries where the disease does not occur;
- ✓ Resistance genes are recessive, restricting the effectiveness of back-cross schemes.

Striga resistance breeding in cereals is one case in point. Efforts are currently underway to identify and map genes for qualitative and quantitative resistance to striga in three sorghum mapping populations. These were derived from three crosses: SRN 39_Shanqui Red (Ejeta, 2000; Bennetzen et al., 2000); IS 9830_E 36-1; and N 13_E 36-1 (Haussmann et al., 2000d). The identification of individual genes or QTL for striga resistance and their transfer into adapted cultivars will also allow to evaluate whether there are ``costs of striga resistance'', i.e., whether resistance is associated with any yield drag. Such costs of resistance might have been another reason for the slow breeding process in the past.

2.9. Genetic Engineering

Genetic engineering permits the transfer of resistance genes from any organism into a chosen crop. In the case of striga resistance, the main limitation at present is the lack of well-defined resistance genes. However, there is an alternative means by which genetic engineering can be brought to bear on the striga problem. To achieve immediate, cost-effective selective control of parasitic weeds by herbicides, Gressel et al. (1994, 1996) and Joel et al. (1995) proposed the introduction of transgenic, herbicide tolerant crops. According to the above-cited authors, herbicide tolerance in crops affected by parasitic weeds has several positive properties: (1) it allows the control of the parasitic weeds at a very low dosage; (2) it is effective against all major species or strains of the parasite; and (3) it supports or even replaces cultivation methods for control of other weeds. Furthermore, herbicide tolerance should only be used in crops which do not crossbreed with related weeds in the same locality. The transfer of the XA-17 gene into sorghum could therefore be recommended only for regions, where the crop does not have feral or weedy relatives, i.e., in Asia, but not in Africa. Even if this condition is respected, there exists the strong possibility of evolution of herbicide resistance in parasitic weeds. The high natural frequency of such mutations and the huge seed output of striga only serve to exacerbate this risk (Gressel et al., 1994). Another consideration involving herbicide-tolerant crops as components of integrated striga control strategies is the ability of farmers to purchase improved seed and the herbicide.

2.10. Breeding for Improved Integrated Striga Control

In addition to selection for host plant resistance, sorghum breeders could consider selecting cultivars for specific adaptation to integrated striga management regimes. For example, the interaction between local sorghum cultivars and fertilizer application or intercropping with legumes could be studied with the aim of selecting cultivars with the highest positive interaction with these measures for grain yield and striga suppression. Another possibility would be to select legume cultivars that effectively induce suicidal germination of S. hermonthica (Berner et al., 1995, 1996a; Dashiell et al., 2000).

Rotations with legumes increase soil nitrogen and organic matter, and hence enhance the biological control of striga (soil suppressiveness). The mentioned authors identified substantial variation in striga stimulant production among soybean cultivars using a simple laboratory assay. Field trials validated results from laboratory assays, showing reduced parasite emergence and increased cereal yields following rotations with high-stimulant producing legume cultivars (Berner et al., 1995, 1996a; Dashiell et al., 2000).

2.11. Heritability and Genetics of Resistance to *Striga*in Sorghum

The heritability of a character measures the extent to which it is transmitted from one generation to the next. Thus it is a valuable tool when used in conjunction with other parameters in predicting the magnitude of genetic gain that follows selection for the character (Katata*et al.,* 1976a). Sorghum resistant to *S. hermonthica*in Africa have been reported (Ramaiah, 1987), but resistance in some cultivars does not hold up across geographical regions. The variable performance of a given host cultivar under *Striga*infestation in different areas may be due to the existence of intraspecific physiological variants of the parasite (Bebawi, 1981). Published reports on the genetics of resistance to *Striga*spp. in sorghum are few.

Saunders (1933) reported that resistance to *S. asiatica*was recessive in two sorghum crosses and partially dominant in the third. Kulkarni and Shinde (1985) found field tolerance to the same species to be governed by

non-additive gene action. Obilana (1984), defining resistance to *S. hermonthica*as "low total number of *Striga*per sorghum plant", reported high (0.78) broad sense heritability of this trait. He also found gene action to be non-additive with over-dominance of susceptibility and estimated that two to five genes control reaction to the weed. More recently, Ramaiah et al. (1990) established that low *Striga*stimulant production in sorghum genotypes, Framida, 555, and SRN4846 is inherited as a single recessive gene. Progress on inheritance studies and breeding for resistance to *Striga*have been limited by variability in performance across geographical regions, lack of uniformity of field infestations and difficulty in evaluating individual segregating progenies for resistance when parasitism occurs below ground (Ramaiah et al. 1990).

3. SUMMARY AND CONCLUSION

Striga-resistant cultivars should be a major component of integrated striga control packages, since they effectively reduce striga emergence, enhancing the efficiency of other control measures. It is generally not possible to select single plants for striga resistance in the field, as there are no appropriate techniques. Selection for resistance is therefore usually deferred until true breeding progenies are available. This means that large numbers of progeny have to be advanced before *Striga*resistance is assessed, a time- and cost-intensive procedure. On the other hand, screening for individual resistance mechanisms in the laboratory could result in a loss of valuable materials possessing resistance mechanisms other than those evaluated. One strategy could be to use laboratory assays for individual resistance mechanisms as an initial screening of a large number of breeding materials, followed by field screening. This would offer the possibility of identifying resistance source with multiple resistance mechanisms (Haussman*et al.,* 2000a). All prospective resistant cultivars should be evaluated at various locations with different *Striga*populations or host-specific races (Ramaiah, 1997; Koyama, 2000).

Molecular marker techniques are a powerful new tool in plant breeding. They permit identification and mapping of genes for individual, monogenic resistance mechanisms (like the low stimulant locus) and of quantitative trait loci (QTL) involved in polygenic, quantitative resistance under field conditions. The utility of DNA markers in resistance breeding depends on the existence of tight linkage between these markers and the resistance genes or QTL of interest.

In addition to selection for host plant resistance, sorghum breeders could consider selecting cultivars for specific adaptation to integrated striga management regimes. For example, the interaction between local sorghum cultivars and fertilizer application or intercropping with legumes could be studied with the aim of selecting cultivars with the highest positive interaction with these measures for grain yield and striga suppression. Another possibility would be to select legume cultivars that effectively induce suicidal germination of S. hermonthica.

Conflict of Interest

The author has not declared any conflict of interest.

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