Review article

Improved methodologies for breeding striga-resistant sorghums

Bettina I.G. Haussmann[a], Dale E. Hess[b], H.-Günter Welz[a,1], Hartwig H. Geiger[a,*]

[a]*University of Hohenheim, Institute of Plant Breeding, Seed Science and Population Genetics, 70593 Stuttgart, Germany*
[b]*International Crops Research Institute for the Semi-Arid Tropics, BP 320, Bamako, Mali*

Abstract

Parasitic flowering weeds of the genus *Striga* (*Scrophulariaceae*) cause substantial losses in sorghum [*Sorghum bicolor* (L.) Moench] 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 we review methodologies for breeding striga-resistant sorghums. 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 microvariability in African soils, heterogeneity of natural infestations, and concomitant large environmental effects on striga emergence. An improved field testing methodology should include one or several of the following practices: field inoculation with striga seeds; appropriate experimental design including elevated replication number; specific plot layout; use of appropriate susceptible and resistant checks; evaluation in adjacent infested and uninfested plots; and the use of selection indices derived from emerged striga counts, striga vigor, and grain yield or a host plant damage score. Due to the extreme variability of the parasite and significant genotype×environment interaction effects, multi-locational screening is recommended to obtain materials with stable performance. Additional strategies include: careful definition of the target environments; determination of the most important selection traits in each target environment; 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 of sub-Saharan Africa. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Screening techniques; Striga vigor; Striga severity; Breeding strategies

[*] Corresponding author. Fax: +49-711-459-2343.
E-mail address: geigerhh@uni-hohenheim.de (H.H. Geiger).
[1] Present address: Hoechst Schering AgrEvo GmbH, Seeds/Crop Improvement, 65926 Frankfurt, Germany.

1. Introduction

Sorghum (*Sorghum bicolor*) is the second most important cereal crop after maize (*Zea mays* L.) in sub-Saharan Africa. The parasitic weeds *Striga hermonthica* (Del.) Benth. and *S. asiatica* (L.) Kuntze are major biotic constraints to sorghum production, especially in the infertile semi-arid areas of Africa. Of lesser economic importance are *S. aspera* (Willd.) Benth. and *S. forbesii* Benth. *Striga* spp. seem to be plants of the old world tropics and sub-tropics which have spread together with their host plants during the course of the history (Sauerborn, 1999). There is some evidence that *S. hermonthica* originated in the Nuba mountains of Sudan and in parts of Ethiopia (Musselman, 1987). The same regions are postulated as the place of origin of sorghum. It is therefore likely that *S. hermonthica* and sorghum co-evolved in sub-Saharan Africa. At present, two-thirds of fields used for cereal production in 17 sub-Saharan African countries are estimated to be infested by *Striga* spp. (Kim et al., 1998).

The parasitic lifestyle of striga plants and the adaptation to the semi-arid tropics are unique. Striga is heavily dependent on the host for its survival, and its life cycle is closely coordinated with that of the host plant (Fig. 1). Striga seeds are numerous (up to 500 000 are produced per plant) and can remain viable for as long as 20 years (Doggett, 1988). After dispersal, seeds may remain dormant for several months (after ripening), which may be an evolutionary adaptation to prevent germination during the last rains of the season, when there are no hosts present (Berner et al., 1997b). After this period, seeds will germinate only when exposed to favorable moisture and temperature for several days (preconditioning), and only in the presence of a germination stimulant, usually exuded by the roots of host; and some non-host plants. Subsequent developmental events of haustorial formation, attachment and penetration as well as further growth and development of the parasite also require signal or resource from the host plant (Ejeta et al., 1992, 2000). Physiological processes during striga infestation in sorghum are complex and have been summarized recently (Gurney et al., 2000). Initial host symptoms occur while the parasite is still subterranean; they may be evident in water soaked leaf lesions, chlorosis, severe stunting and drought-like symptoms
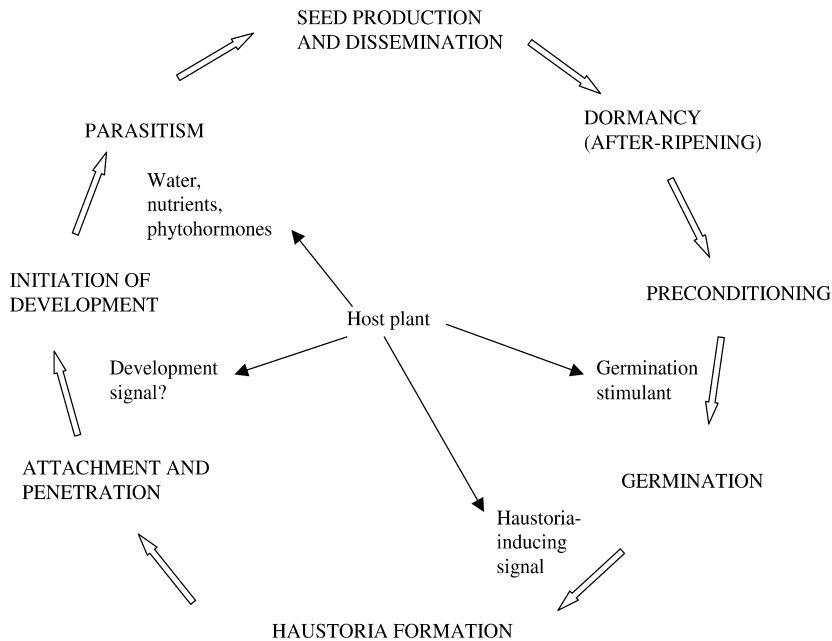

Fig. 1. Simplified life cycle of striga (modified from Ejeta et al., 1992).

such as leaf margin curling and reduced head exertion. After striga emergence, host symptom development intensifies. Grain yield losses due to striga parasitism can attain 100% in susceptible cultivars under high infestation levels, particularly under drought conditions.

Striga control methodologies can be grouped into three major categories with different effects on a striga population: (1) reduction of the soil seed bank; (2) limitation of striga seed production; and (3) reduction/prevention of striga seed dissemination to uninfested fields (Table 1). An effective control strategy should integrate at least one control method from each of the three major categories (Obilana, 1990). Although countless experiments over the decades have been conducted to investigate striga control approaches, few methods are having impact today in farmers' fields. In order to be adopted, striga control practices must improve crop yield per unit area, maintain soil fertility, and be acceptable to farmers even in the absence of striga infestation (Berner et al., 1996a; Kroschel, 1998). Due to the diversity of farming systems in Africa, research and extension of integrated striga control strategies should be tailored to local needs, i.e., ecological zone, ethnic group, population density, food preference, market accessibility, degree of farm modernization, etc. (Doggett, 1988; Bengaly and Defoer, 1997; Kroschel, 1998; Sallé, 1998). Farmer participatory research may be the most effective way of identifying the actual capacity of farmers to combat striga in sub-Saharan Africa. Information campaigns should be more frequently used for public awareness, and to increase knowledge of striga biology and control options (Obilana, 1990; Dembélé and Konaté, 1991; Berner et al., 1996a; Kroschel, 1998).

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. However, breeding progress has been limited due to the difficulty of evaluating resistance in the field and inadequate information on the genetics of striga resistance. This paper reviews aspects of breeding sorghum for striga resistance, emphasizing improved screening methods in the field.

2. Definition of resistance to striga

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).

3. Resistance mechanisms

Because striga is an obligate parasite, interactions 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; Ejeta and Butler, 1993; Berner et al., 1995; Wegmann, 1996):

- low production of germination stimulant;
- mechanical barriers (e.g., lignification of cell walls);
- inhibition of germ tube exoenzymes by root exudates;
- phytoalexine synthesis;
- post-attachment hypersensitive reactions or incompatibility;
- antibiosis, i.e., reduced striga development through unfavorable phytohormone supply by the host;
- 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-para-benzoquinone. 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.

Table 1
Summary of striga control methods in cereals[a]

Type of method	Category		
	Reduction of the soil seed bank	Reduction of striga seed production	Reduction in striga seed dissemination
Cultural	Trap crops: soybean, cotton, sunflower, groundnut	Resistant crops	Measures against soil erosion and flooding
	Catch crops: sudangrass, susceptible hosts	High plant density	Phytosanitary methods, including clean cultivation equipment
	Organic manure to promote biological soil suppressiveness	Delayed planting	
	Resistant crops (if resistance is based on	Transplanting	Clean seeds or planting material
	mechanisms other than the low stimulant character)	Mixed cropping of cereals and legumes	Management of livestock movement
Physical	Deep ploughing	Weeding (manual or mechanical)	Measures against soil erosion and flooding
	Soil solarization		
Chemical	Fertilization: N and P to promote biological soil suppressiveness	Fertilizer application at high rates	
		Herbicides: 2,4-D-Triclopyr, Dicamba,	
	Soil fumigation: methyl bromide	Chlorsulfuron, Paraquat, imazaquin,	
	Germination stimulants: ethylene, strigol,	glyphosate (in herbicide-tolerant crop)	
	strigol analogs	Antitranspirants	
Biological	Soil inundation with microbes that destroy striga seeds	*Fusarium* species	
		Smicronyx species	

[a] Source: Doggett (1988), Carson (1988), Obilana (1990), Dembélé and Konaté (1991), Babiker et al. (1993), Berner et al. (1994, 1996a, 1997a), Carsky et al. (1994), Odhiambo and Ransom (1994), Olivier (1995, 1996), Gressel et al. (1996), Hoffmann et al. (1997), Abayo et al. (1998), Kroschel (1998), Sallé (1998).

4. Screening techniques and selection traits

Precise and reliable screening techniques are indispensable prerequisites to breeding for resistance to any biotic or abiotic stress factor (Vasudeva Rao, 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. Having observed inconsistent genetic correlation between the reaction to striga in pot and field trials (Omanya et al., 2000), we discourage the use of pot trials in breeding programs.

4.1. 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. Preconditioned striga seeds are dispersed in agar in Petri dishes, a germinating sorghum seed is added to each dish, and the maximum distance between sorghum rootlets and germinated striga seeds (''germination distance'') is measured after 3–5 days. Entries with a germination distance below 10 mm are usually classified as low stimulant types. 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 of 2–3 weeks, 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 (Vasudeva Rao, 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 (Vasudeva Rao, 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 yet to be used in actual breeding programs, but since they are laborious, they are unsuited to selection programs with large numbers of entries to be screened.

4.2. Screening for complex resistance under field conditions

Field screening for striga resistance is hampered by the following: 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 one or more of the following measures:

- field inoculation with striga seeds;
- 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;
- use of selection indices combining striga counts, striga vigor, and grain yield or a host plant damage score.

Supplemental field inoculation with striga has been recommended for effective field screening by several authors (Kim, 1991; Efron, 1993; Kim and Adetimirin, 1994; Berner et al., 1996b). The site selected for inoculation should be on-station, well drained and absolutely level, as on sloped fields striga seed will be carried by run-off during heavy rains. Mulching the experimental field with mature striga plants (Efron, 1993) is a relatively easy but imprecise approach. For

more precision, sufficient striga seed must be collected in years before the field inoculation is supposed to take place. Three to four kilogram of clean, viable striga seed (with about 190 viable grains per mg) are sufficient to heavily infest an experimental area of 1 ha. To achieve uniform infestation, the field should be divided into plots of equal size or rows of equal length. Equal amounts of striga seeds are weighed, mixed with fine, dry sand, uniformly distributed in each plot (or row), and mixed with the top soil. Alternatively, the striga seed/sand mixture may be applied to individual planting holes (Kim, 1991; Kim and Adetimirin, 1994; Berner et al., 1996b). The latter method, however, is less representative to conditions in naturally-infested farmers' fields. Striga seeds may be preconditioned in the laboratory or directly in the field, if conditions are wet and a 7–14-day waiting period is provided between inoculation and planting (Berner et al., 1996b). However, preconditioning was not found to increase striga attack on sorghum and maize (Berner et al., 1996b). When dealing with supplemental field inoculation, quarantine regulations must be respected, and the spread of striga seeds to uninfested areas must be strictly avoided.

Despite careful field inoculation, variation in the number of emerged striga plants between plots of the same host cultivar can still be considerable (Vasudeva Rao, 1985; Efron, 1993; our own experience). This can be due to microvariability of soil fertility and variation in the natural base level of striga within the experimental area. Differences may also be caused by local occurrence of natural striga antagonists like *Fusarium oxysporum*. Forced striga germination using ethylene is a possibility to reduce the natural variability of striga infestation. However, although the actual cost of ethylene is small ($5 per acre), the logistic problem of its distribution has probably hindered its wider application not only in striga resistance screening but also as a striga control agent in Africa (Ransom, 1999).

In large trials with many entries, the natural heterogeneity of the field should be compensated by an appropriate experimental design, i.e., incomplete block or lattice designs (Cochran and Cox, 1957). We experienced lattice efficiencies from 102% at the most uniform location to 167% at the most heterogeneous site for individual striga counts in our 1998 field experiments (unpublished data). The genetic

materials evaluated in these trials consisted of two sorghum recombinant inbred populations with 121 entries each, planted in 11×11 lattice designs with six replications at various locations in both East and West Africa. Spatial heterogeneity can also be detected and adjusted for by the techniques of spatial analysis (e.g., Ball et al., 1993; Brownie et al., 1993; Scharf and Alley, 1993; Stroup et al., 1994). These techniques should be used in conjunction with an appropriate experimental design.

When high experimental precision is required, the number of replications may be increased up to six. The relative merit of high numbers of replications is demonstrated here using data from field experiments including 50 sorghum entries (14 cultivars and 36 F_2 populations). The trials were conducted at Samanko, Mali, in 1996, and at Alupe, Kenya, in the Short Rains 1996–1997. The experiment was planted in a randomized complete block design with six replicates. Each plot consisted of two rows, 3 m long, separated from the neighboring entry by one empty row. Mean number of emerged striga plants per m^2 of the six individual replications were 22, 35, 41, 42, 47, and 64 at Samanko (82 days after planting, d.a.p.), and 33, 36, 40, 49, 56, and 70 at Alupe (85 d.a.p.). Therefore, both fields were rather heterogeneous, despite a field inoculation carried out before planting at Samanko. As a measure of the experimental accuracy, estimates of heritability in a replicated trial were calculated for all possible permutations of two, three, four, five and the actually available six replications, using the following formula:

$$\text{Heritability } (\%) = \frac{100\sigma_t^2}{(\sigma_t^2 + \sigma_e^2)/R}$$

where σ_t^2 and σ_e^2 are the estimated treatment and error components of variance, respectively, and R the number of replications (Allard, 1960). At both locations, the mean heritability estimates increased with increasing number of replications, as obvious from the formula (Fig. 2). By employing six replications, we obtained heritabilities of 80% at Samanko and 71% at Alupe. The range of heritability estimates was largest for the permutations of two out of the six available replications, demonstrating that in large field trials, the amount and/or distribution of error variation can be very heterogeneous over replications. If we had employed only two replications, the risk of experi-
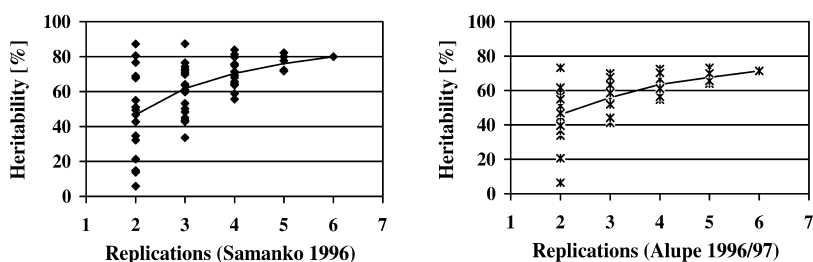
Fig. 2. Mean and individual estimates of the heritability in a replicated trial (%) across 50 sorghum entries for all possible permutations of two, three, four, five, and the actually available six replications, for the number of emerged striga plants per m^2 in field trials at Samanko, Mali, 1996 (82 d.a.p.) and Alupe, Kenya, in the Short Rainy Season 1996/1997 (85 d.a.p.).

mental failure would have been high. The range of heritability estimates decreased with increasing number of replications. With only four replications, the minimal estimated heritability was above 50% at both locations. We conclude that a minimum of four replications is essential for striga trials to reduce the risk of experimental failure due to the natural heterogeneity within experimental areas.

A high number of replications may require a reduction in plot size, due to limited availability of large and uniformly infested fields and insufficient seed quantities of the test entries. To achieve high precision in field tests, we developed a novel plot layout. Each plot consists of two rows, separated from the neighboring entry by one empty row. The distance between rows should be between 0.7 and 0.8 m for sorghum. The row length depends on the size of the experimental area, the number of plots to be accommodated, and seed availability of the test entries. As a minimum, we recommend that each row contain about 10 host plants (e.g., 2.0 m row length with 0.2 m distance between plants within rows). The specific arrangement has distinct advantages. For each entry, traits can be assessed in both rows, and no land is lost to border rows. Neighbor effects are reduced due to the empty row, and more light reaches the ground, reducing shading which is deleterious to striga emergence and development. Non-destructive striga counts are facilitated by increased space between plots. When using the new plot layout, one should be aware that grain yield data may be overestimated due to the empty row between plots.

Susceptible check cultivars should be included at regular intervals as they give a good indication of the homogeneity and severity of infestation in the experi-

mental area. A simple way of including checks is to randomize them together with the test entries. If included at a higher frequency, as in augmented designs (Federer, 1961; Kempton, 1984), local checks offer the possibility to express all observations as percentage values relative to the nearest susceptible check. Carried to an extreme, this results in the checkerboard layout, where each test entry is surrounded by the susceptible cultivar (Vasudeva Rao, 1985). This layout requires considerable space, reducing either the number of entries which can be evaluated or the number of replications. Further, converting measured plot values to a percentage of the nearest check does not always improve experimental accuracy (Ransom et al., 1990). The method can only be effective if the check cultivars show the same general response to variable striga infestation levels and trends in soil fertility as the test material (Kempton, 1984). The inclusion of common resistant checks like Framida or SRN 39 offers the possibility to further compare infestation levels and aggressiveness of striga across various experiments.

Entries may be evaluated simultaneously under infested and non-infested conditions in adjacent strips of land (Berner et al., 1995). This technique allows accurate quantification of yield reduction and convenient assessment of stress symptoms relative to the control and is being used in breeding maize for tolerance to striga at the International Institute for Tropical Agriculture (IITA). After each experiment, the area is planted with a highly efficient trap crop for two seasons and then treated with ethylene to eliminate any germinable striga seed (Berner, pers. comm.). Subsequently the field can be reinfested and reused for striga resistance screening. For the trap

crop, legumes selected for high stimulation of striga seed germination are a good choice, as their cultivation also enhances soil fertility.

Data collection in field trials should include striga development traits and quantification of host plant reaction. The following striga traits are frequently assessed: days to striga emergence and days to onset of striga flowering in each plot; total number of emerged striga plants; number of flowering striga plants; and number of striga plants with seed capsules (i.e., to measure the reproductive success of striga). Counts are often made at 2-week intervals during the season, generally beginning 2 or 3 weeks after striga emerges in the experiment. However, when resources are limited, the number of striga counts may be limited to two, performed at around 70 and 90 d.a.p., i.e., around sorghum flowering. The counts should be accompanied by a visual estimation of striga vigor, as the effect of striga plants of 5 cm height may differ significantly from that of fully-developed 40 cm striga plants with numerous branches, flowers and seed capsules. The striga vigor score can be based on the average striga height and the extent of branching, as shown in Fig. 3 and Table 2. Multiplying the striga count by the average striga vigor in each plot results in a new measure of the entries' reaction to striga which we call "striga severity". Successive striga counts can be used to calculate the "area under the striga number progress curve" (ASNPC), using the formula for "area under the disease progress curve" (AUDPC; Shaner and Finney, 1977):

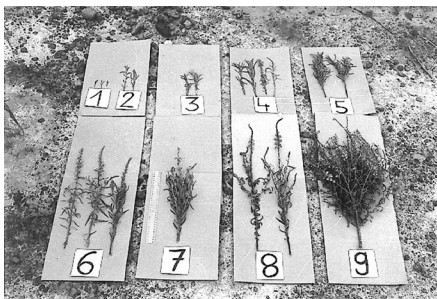$$\text{ASNPC} = \sum_{i=0}^{n-1} \left[\frac{Y_i + Y_{(i+1)}}{2} \right] (t_{(i+1)} - t_i)$$

Table 2
Description of nine striga vigor classes

Score	Striga height (cm)	Number of striga branches
1	≤5	No
2	6–20	No
3	6–20	≥1
4	21–30	≤5
5	21–30	>5
6	31–40	≤10
7	31–40	>10
8	>40	≤10
9	>40	>10
0	No emerged striga plants	

where n is the number of striga assessment dates, Y_i the striga count at the ith assessment date, t_i the d.a.p. at the ith assessment date, t_0 the d.a.p. to striga emergence minus 1, and Y_0 is 0. Similarly an "area under the striga severity progress curve" (ASVPC) can be computed by using the striga severity values as Y_i.

Actual striga biomass may be another trait of interest, but it is difficult to measure and usually has a large error variance. It is correlated to striga counts, vigor score, and striga severity (unpublished data) and could be estimated visually if the latter traits cannot be assessed. Assessment of the number of subterranean attached striga plants, i.e., striga plants which are attached to the roots but have not emerged above ground, is very laborious and is only practical in small trials or with selected entries in a large trial.

Considering data on emerged striga plants as the sole resistance measure can lead to problems when extremely susceptible cultivars are evaluated, especially in maize (e.g., Kim, 1998), but also in sorghum. Very susceptible plants frequently support fewer emerged striga plants due to strongly reduced host vigor and underground competition among young, newly attached striga plants. Selection for striga resistance should therefore always take into account both acceptable grain yield and reduced number of emerged or flowering striga plants (Doggett, 1988). Either in addition or as an alternative to measuring grain yield, visual host plant damage or "striga syndrome" ratings have been recommended (Kim, 1991, 1994; Efron, 1993; Berner et al., 1997b). The rating on a 1–9 scale reflects host plant damage by striga in the form of leaf chlorosis or firing (scorching), poor ear or

Fig. 3. Illustration of nine striga vigor classes.

panicle development, and stunting. Assessment could be done weekly, but at least once about 2 weeks after anthesis. The rating is reportedly useful to assess tolerance to striga in maize. In sorghum however, striga-induced symptoms are infrequent and may only occur under conditions of extremely high infestation or in poor, shallow soils.

Adjusting striga emergence and development data for a variable host plant stand is a difficult, if not impossible task. According to our experience, there is no simple relationship between host plant stand and striga count or vigor score. Various environmental factors may contribute to uniform infestation by vigorous striga plants under conditions of either uniform or variable host plant stand. In order to avoid an uncontrolled bias in the data, we would recommend not to adjust striga traits according to host plant stand. It is better to do everything possible during the first 2 or 3 weeks after planting to obtain a good host plant stand. Excessively variable plots should be excluded from data analysis, to avoid false data interpretation.

A final point to be considered here is the appropriate fertility level in a screening nursery. On one hand, high nitrogen is a control technique. On the other hand, weak host plants with low vigor are undesirable as attached striga would tend to remain underground. We recommend that local recommendations for fertilization be followed, but that late top dressing with urea (N) be avoided, as it could have a negative effect on striga attachment/emergence. The ''optimum'' fertility will provide for good host plant growth without reducing striga emergence. In this respect, the specific plot layout described above has an advantage in that the empty row provides for sunlight and aeration, both of which contribute to avoid striga death due to shading.

5. 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; Anaso, 1990; Obilana, 1990; Dembélé and Konaté, 1991; Olivier et al., 1991; Carsky et al., 1996; Chantereau, pers. comm.). 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*). However, more information is needed about individual resistance mechanisms in different sources of resistance so that they can be pyramided in productive, adapted genotypes.

6. Genetics of resistance

The low stimulation of *S. asiatica* 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 F_2 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).

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

Kulkarni, 1982; Ramaiah, 1984, 1987; Haussmann et al., 1996, 2000a,b).

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 heritabilities in two sorghum recombinant inbred populations ranged between 0.70 and 0.81 for striga counts at 95 d.a.p., striga severity, and ASNPC (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.

7. 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 (Vasudeva Rao and Musselman, 1987; Hess, 1994; Freitag et al., 1996). 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. She also found striga samples from West African sites to be more closely related to each other than to an East African population.

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.

8. Breeding strategies

Both interspecific variability among *Striga* spp. 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 loosing data from one location due to "non-striga years" or other obstacles. The breeder may also consider a trade-off between number of replications versus number of sites; however, the number of replications should not fall below four, as illustrated above (Section 4.2). 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; Ejeta and Butler, 1993; Efron, 1993; Berner et al., 1995):

- 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.

Further important aspects include a careful definition of the target environments; farmer participation in identification of adapted parents for use in a back-cross program; and determination of the most important selection traits for each target environment (Rattunde et al., 2000). Due to the diversity of farming systems in Africa, priority selection traits besides striga resistance and grain yield may vary among target environments, and must therefore be tailored to local needs. Grain color and quality, plant height, maturity, photoperiod sensitivity, and disease resistance are examples for region-specific selection traits. Standard methods of multi-trait improvement are needed to combine striga resistance with grain yield and other specific traits. Important requisites in this context are existence of base materials with the desired genes, adequate recombination, sufficiently large population sizes to obtain recombinants, and use of index selection to select for multiple traits (total genetic worth; Rattunde, H.F.W., pers. comm.).

Also the optimal genetic structure of the cultivar, (i.e., degree of heterozygosity and heterogeneity) will depend on the target environment. 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 F_2 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 also reported to outyield parental lines or local varieties under variable drought stress in semi-arid, striga-free areas of East and West Africa (Doggett and Jowett, 1966; Kapran et al., 1997; Haussmann et al., 1998, 1999, 2000c). However, hybrid production and successful marketing requires skilled labor, an effective seed industry, a good infrastructure, and a sufficient income of the farmers to be able to afford the costly hybrid seed. These prepositions are not ubiquitous. Instead of hybrids, other types of cultivars could be produced which capitalize on heterozygosity, e.g., synthetics built up from components with high outcrossing 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 development of laboratory assays which allow the non-destructive, rapid and inexpensive evaluation of individual plants would greatly facilitate early generation testing and increase selection efficiency. 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 (Vasudeva Rao, 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). The paper roll assay is another potentially very useful assay to screen for hypersensitivity or incompatibility. Data on the correlation between results from the paper roll assay and striga resistance under field conditions are not yet available. 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.

9. 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.

10. 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. In maize, the single recessive gene *XA*-17 confers resistance to acetolactate synthase (ALS)-inhibiting herbicides like the sulfonylurea herbicide ''nicosulfuron'' or the imidazolinone herbicide ''imazaquin''. Seed treatment of herbicide-resistant maize with imazaquin has been shown to be an effective, inexpensive, practical measure to control striga, with immediate benefit to farmers (Berner et al., 1996a, 1997a; Abayo et al., 1998). Glyphosate resistance has been transferred to a number of crops, utilizing a modified enolphosphate–shikimate phosphate (EPSP) synthase gene. Glyphosate controls not only striga but also *Cyperus* spp., which can be very troublesome perennial weeds in southern Africa (Gressel et al., 1994).

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. The great efficacy and low labor and energy requirements of herbicide treatments are important prerequisites for high cost effectiveness. However, it should not be forgotten that herbicides may have negative impact on the environment. 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.

11. 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. There is a need for national programs in Africa to screen legume cultivars at the local level, to identify those that effectively stimulate germination of local striga strains. The selected cultivars must also have the desired agronomic and quality characteristics to meet the needs of farmers and consumers (Berner et al., 1995, 1996a; Dashiell et al., 2000).

12. Conclusions and outlook

Several methods are now available to increase the accuracy of screening sorghum for resistance to striga. An increased accuracy in the resistance tests will result in better heritabilities for striga resistance traits, and therefore, into enhanced gains from selection. The efficiency of striga resistance breeding in sorghum

could be further increased by combining laboratory assays with the field evaluation, and by the development of marker-assisted selection techniques. For effective striga control, resistant cultivars must be integrated with other control methods such as crop rotation. The outputs of research on striga resistance breeding can only have impact if:

- there are effective mechanisms in place for exchange of germplasm with the national agricultural research systems (NARS),
- there are active links between the NARS and farmers, and
- an adequate seed supply infrastructure is in place.

There must also be extensive feedback between farmers and breeders at the national and international levels to ensure that the cultivars developed are adapted to farmer circumstances and satisfy end-user preferences (Kling et al., 2000; Rattunde et al., 2000). A joint development of integrated striga management strategies by breeders, agronomists, pathologists, and farmers could contribute to more sustainable sorghum production in striga-infested areas of sub-Saharan Africa.

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