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Analysis of resistance to *Striga hermonthica* in diallel crosses of sorghum

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Summary

Parasitic flowering weeds of the genus *Striga* are major biotic constraints to sorghum (*Sorghum bicolor* (L.) Moench) production in sub-Saharan Africa. The agar-gel assay was used to evaluate stimulation of *Striga hermonthica* (Del.) Benth. seed germination by a complete F_1 diallel involving nine sorghum cultivars and inbred lines. Striga populations from Mali and Niger were employed. The same genetic materials were planted in pot trials in both countries to observe striga plant emergence. Variation in hybrid performance was determined by general (GCA) and specific combining ability (SCA) effects, with preponderance of GCA, for both germination distance in the agar-gel assay and number of emerged striga. Reciprocal effects were significant only in the agar-gel assay and were unstable across striga populations. For lines and hybrids, estimates of broad-sense heritabilities were 0.97 and 0.91 for germination distance, and 0.38 and 0.58 for emerged striga, respectively. Only a weak positive relationship existed between *in vitro* germination distance and emerged striga number in the pot trial. Although selection for low germination distance has merit, valuable material with resistance mechanisms other than low stimulant production may be lost if these traits are not additionally assessed. Laboratory assays which allow a non-destructive, quick and economical screening for resistance mechanisms other than the low stimulant character are likely to increase the efficiency of breeding programs for striga resistance. The significant contribution of SCA effects indicates that thorough screening of testcrosses is indispensable for selection in hybrid sorghum breeding programs.

Introduction

Parasitic angiosperms of the genus *Striga* (Scrophulariaceae) seriously limit cereal production in sub-Saharan Africa. Two out of three fields cropped in cereals are estimated to be infested by *Striga* spp. in 17 sub-Saharan African countries (Kim et al., 1998). Striga plants, although parasitic, produce normal green leaves and brightly colored flowers. Striga seeds are very tiny, some 0.30 mm long and 0.15 mm wide. Depending on the species and the environmental conditions for plant development, one striga plant may produce 40,000 to 90,000 seeds (Ejeta et al., 1997). Striga seeds require after-ripening, conditioning, and stimulation by chemical compounds exuded by hosts and pseudo-hosts before they can germinate to successfully parasitize a host plant (Doggett, 1988; Ejeta et al., 1992, 1997). The major germination stimulant in sorghum (*Sorghum bicolor*) is sorgolactone (Hauck et al., 1992) whereas sorgoleone and strigol seem to be of minor importance (Ejeta et al., 1992). The organ of parasitism, the haustorium, is also produced in response to a chemical signal from the host roots, probably 2-6-dimethoxy-parabenzoquinone (Lynn & Chang, 1990; Frick et al., 1996). The haustorium forms a morphological and physiological bridge between striga seedling and host roots. Numerous striga plants may penetrate and attach to a single individual host plant (Ejeta et al., 1997). Yield losses from damage by striga are often very significant, the range of estimates varying from 10–70% depending on crop cultivar and infestation level (Doggett, 1988).

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. Known sources of resistance to striga in sorghum are frequently low-yielding with poor agronomic background (Ramaiah, 1987). Transfer of resistance into varieties better adapted to target areas has been limited due to inadequate information on the genetics of striga resistance, and the difficulty of evaluating the trait in segregating progenies (Vasudeva Rao, 1985; Ejeta et al., 1992).

The presence of individual mechanisms conferring resistance to striga may be examined in the laboratory. One resistance mechanism to striga is low stimulation of striga seed germination. The trait can be easily assessed in an agar-gel assay developed by Hess et al. (1992). Complex resistance should be assessed under field conditions, but field screening is hampered by heterogeneity of infestation in naturally-infested fields, large environmental effects on striga emergence, and complex interactions between host, parasite and environment affecting the parasites' establishment and reproductive success. Screening in pots includes advantages of both laboratory and field experiments, providing some control over environmental conditions, but with the disadvantage of a rather artificial root environment.

The objective of this investigation was to estimate quantitative-genetic parameters for components of resistance to *Striga hermonthica* in sorghum, namely for stimulation of striga seed germination in the agar-gel assay and for number of emerged striga plants in pot experiments. These estimates will be useful in improving strategies for striga resistance breeding in sub-Saharan Africa.

Materials and methods

Nine sorghum cultivars (Framida, Seredo, and inbred lines 555, N 13, IS 9830, DJ 1195, M 35-1, E 36-1, and IS 1037) were crossed in all possible combinations including reciprocals. The agar-gel assay developed by Hess et al. (1992) was employed to test the complete diallel (81 entries) for stimulation of striga seed germination. Surface-sterilized striga seeds are preconditioned for 12 days and then dispersed in water agar in petri dishes. A rootlet of a 24-hr old sorghum seedling is carefully inserted into the agar where it continues to grow. The maximal distance between the sorghum rootlet and germinated striga seed ('germination distance') is measured after five days of incubation at 28 °C in the dark. Entries with a germination distance below 10 mm were classified as low-stimulant types. For a more detailed description of the method see also Berner et al. (1997). It should be noted that the agar-gel technique is an assay for stimulation of striga seed germination rather than an assay for germination stimulant production. Although host production of germination stimulants is a prerequisite of striga seed germination, the assay integrates stimulant production with other aspects of interaction between host root and preconditioned striga seed. These aspects may include host root production of compounds that inhibit or stimulate striga seed germination, and different stability and mobility of these chemical signals in different host genotypes (Hess et al., 1992). The assay was performed twice with five replications using striga seeds harvested at both Samanko (Mali) and Bengou (Niger).

The same genetic materials were evaluated in pot trials in 1995 at Samanko, and in 1996 at Sadoré (Niger). At Samanko, three replications were employed. Each 12-l plastic pot was filled with natural, striga-free soil (tropical leached ferruginous soil; sandy loam). For each pot, approximately 34,000 viable seeds of *S. hermonthica* (harvested at Samanko in 1994) were carefully mixed with fine dry sand. Each pot was then infested by uniformly mixing the striga seed/sand mixture into the soil horizon 4–6 cm below the pot surface.

Table 1. Means and general combining ability (GCA) effects of the nine parent lines for the germination distance in the agar-gel assay, pooled across striga populations from Samanko (Mali) and Bengou (Niger)

Parent line	Mean	GCA
Framida	1.1	–4.5
555	4.6	0.3
N 13	15.4	3.5
IS 9830	0.4	–4.4
Seredo	9.8	–1.7
DJ 1195	11.7	–0.4
M 35-1	13.0	1.7
E 36-1	21.1	5.2
IS 1037	13.8	0.2
Standard error	1.3	0.5

Table 2. Analysis of variance in a complete 9 × 9 sorghum diallel evaluated for stimulation of striga seed germination using the agar-gel assay with populations of *S. hermonthica* from Samanko (Mali) and Bengou (Niger)

Source of variation	df	Mean square	F-value
Striga population	1	70.5	19.98 **
Sorghum genotypes	80	48.0	13.59 **
Parents	8	94.8	26.84 **
Parents vs. hybrids	1	6.4	6.37 *
Hybrids	71	43.0	12.19 **
GCA	8	292.0	82.73 **
SCA	27	16.6	4.69 **
Reciprocal differences	36	7.6	2.15 **
Sorghum genotype × striga population	80	6.2	1.76 **
Parents × striga population	8	5.2	1.46
(Parents vs. hybrids) × striga population	1	1.9	0.54
Hybrids × striga population	71	6.4	1.81 **
GCA × striga population	8	4.1	1.15
SCA × striga population	27	6.0	1.69 *
Recipr. diff. × striga population	36	7.3	2.05 **
Experimental error[1]	289	3.5	

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.
[1] Degrees of freedom reduced due to heterogeneity of error variances across striga populations and deductions for missing values.

At Sadoré, the experiment included five replications, and each pot was filled with a mixture of 3/6 sand, 2/6 clay, and 1/6 organic manure, and infested with approximately 16,000 viable striga seeds (harvested at Bengou in 1991). Pots were watered to allow preconditioning of the striga seed. After one week, four sorghum seeds were sown into each pot. Planting dates were 3rd August 1995 at Samanko and 14th May 1996 at Sadoré. Plants were thinned to one per pot at 14 days after planting (d.a.p.). Plants were watered as necessary, dependent on the natural rainfall. The total number of emerged striga plants pot^{-1} counted at 89 d.a.p. at Samanko, and at 62 d.a.p. at Sadoré are reported here. Entries were considered as resistant when they supported significantly fewer emerged striga plants pot^{-1} than the respective trial mean. Genetic parameters were estimated following Griffing's (1956) Method 3, using the computer programs PZ14 (Utz, 1992) and DIALLEL (Burow & Coors, 1993). The effects of genotypes and striga populations were regarded as fixed. Broad-sense heritabilities were calculated as described by Fehr (1987).

Results

Germination distance in the agar-gel assay

The mean germination distance in the agar-gel assay was 11.8 and 10.5 mm for striga populations from Mali and Niger, respectively. The effect of striga population was highly significant (p =0.01). Individual entry means ranged from zero (IS 9830 × 555) to 21.6 mm (E 36-1 × N 13). Framida, 555, and IS 9830 revealed low-stimulant characteristics (Table 1). Differences among parents and among hybrids were both highly significant (p =0.01; Table 2). On the average, hybrids differed from the respective midparent values by +11.7% (p =0.05) for the germination distance, i.e., they tended towards high stimulant character. The interaction between sorghum genotypes and striga populations was highly significant (p =0.01) but with a relatively small F-value suggesting that, across all entries, the genotype × striga population interaction was less important than the genotypic effects. A lower importance of the genotype × striga population interaction was also reflected by the high coefficient of correlation between germination distances of the two striga populations from Mali and Niger (r = 0.86, significant at p =0.01). The hybrids contributed most to the interaction while the parent lines did not differ

Table 3. Phenotypic correlations among line performance and GCA, hybrid performance and SCA, and between striga populations[1] for GCA, SCA and reciprocal effects for the germination distance in the agar-gel assay, and the number of emerged striga plants pot^{-1}

Correlated variables	Phenotypic correlation coefficient	
	Germination distance	Striga plants pot^{-1}
Line performance – GCA	0.93**	0.77*
Hybrid performance – SCA	0.40*	0.59**
Mali striga – Niger striga for GCA	0.98**	0.48
for SCA	0.49**	0.46**
for reciprocal effects	0.02	0.31

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.
[1] In the pot trials, the effects of striga populations and test locations are confounded.

significantly in their reaction to the two striga populations. Estimates of broad-sense heritabilities were 0.97 and 0.91 for the germination distances of lines and hybrids, respectively.

The variation in hybrid performance was largely determined by general combining ability (GCA) effects. The high F-value of GCA and the close correlation between line performance *per se* and GCA (Table 3) reflect the predominance of additive gene action. However, specific combining ability (SCA), reciprocal effects, and their interactions with the striga populations were also significant (p =0.05 or 0.01). The correlations between striga populations were tight for GCA, moderate for SCA, and non-significant for the reciprocal effects, indicating instability of SCA and reciprocal effects across the striga populations.

Negative GCA effects reduce the germination distance while positive effects increase the germination distance in the progenies. Among the parent lines, the weakest stimulant producers, Framida and IS 9830, also had the largest negative GCA effects while for line 555, the estimated GCA effect did not differ significantly from zero (Table 1). Germination distances in crosses among the three low-stimulant lines were 0.5 mm for Framida × IS 9830, 6.7 mm for Framida × 555, and 1.2 mm for 555 × IS 9830. The lower value in the third cross was due to a significant, large SCA effect towards low germination distance (–6 mm). The parent line N 13, known to possess resistance to striga under field conditions (Ramaiah, 1984), had high-stimulant characteristics and a positive GCA effect for the germination distance in the agar-gel assay.

Table 4. Means and general combining ability (GCA) effects of the nine parent lines for the number of emerged striga plants pot^{-1} at Samanko (Mali) and Sadoré (Niger) with populations of *S. hermonthica* from Samanko and Bengou (Niger), respectively, and pooled across the two locations/striga populations

Parent line	Samanko		Sadoré		Pooled	
	Mean	GCA	Mean	GCA	Mean	GCA
Framida	3.0	3.5	2.6	2.3	2.8	2.9
555	7.3	–1.0	4.6	–5.3	6.0	–3.1
N 13	4.0	–3.2	2.4	–4.5	3.2	–3.8
IS 9830	2.7	–8.1	9.6	–3.3	6.1	–5.7
Seredo	12.3	1.5	4.0	–2.3	8.2	–0.4
DJ 1195	4.0	1.7	30.6	16.0	17.3	8.9
M 35-1	3.0	–5.6	11.8	–5.0	7.4	–5.3
E 36-1	12.3	7.6	24.0	10.6	18.2	9.1
IS 1037	13.0	3.6	5.4	–8.5	9.2	–2.4
Standard error	1.0	2.1	0.9	1.8	5.5	1.7

Striga emergence in the pot trials

The mean number of emerged striga plants pot^{-1} was 19.6 and 16.6 in Mali and Niger, respectively. Individual entry means, averaged across the two locations, ranged from 2.8 (Framida) to 56.1 (DJ 1195 × Framida). In addition to Framida, the parent lines N 13, 555, and IS 9830 exhibited reduced striga emergence (Table 4). Effects of test locations and striga populations are confounded in the pot trials. The joint effect was non-significant (Table 5). Differences among parent lines and among hybrids were significant (p =0.05 and 0.01, respectively). Hybrids supported on average 18.6 striga plants pot^{-1} while the mean of the parent lines was 8.7 striga plants pot^{-1}, resulting into an average relative midparent heterosis for susceptibility

Table 5. Analysis of variance in a complete 9 × 9 sorghum diallel evaluated for the number of emerged striga plants pot^{-1} at Samanko (Mali) and Sadoré (Niger) with populations of *S. hermonthica* from Samanko and Bengou (Niger), respectively

Source of variation	df	Mean square	F-value
Location/striga population (confounded)	1	97.8	1.24
Sorghum genotypes	80	205.2	2.66**
Parents	8	61.2	2.68*
Parents vs. hybrids	1	1557.9	20.22**
Hybrids	71	202.3	2.43**
GCA	8	913.9	10.99**
SCA	27	144.1	1.73*
Reciprocal differences	36	87.6	1.05
Sorghum genotype × location/striga population	80	85.4	1.11
Parents × location/striga population	8	61.4	2.69*
(Parents vs. hybrids) × location/striga population	1	138.0	1.79
Hybrids × location/striga population	71	87.4	1.05
GCA × location/striga population	8	368.4	4.43**
SCA × location/striga population	27	53.8	0.65
Recipr. diff. × location/striga population	36	50.2	0.60
Pooled experimental error[1]	468	77.1	
Pooled error lines[2]	48	22.8	
Pooled error hybrids[2]	414	83.1	

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.
[1] Degrees of freedom reduced due to deductions for missing values.
[2] Error term split due to heterogeneity of error variances for lines and hybrids.

of 114%. The interaction between sorghum genotypes and striga populations was non-significant across all entries, but significant (p =0.05) for the parent lines. Estimates of broad-sense heritabilities for the number of emerged striga plants pot^{-1} were 0.38 and 0.58 for lines and hybrids, respectively.

The variation in hybrid performance was caused by GCA (p =0.01) and SCA (p =0.05) effects (Table 5). The larger F-value of GCA compared to SCA effects reflects preponderance of additive-genetic effects. However, the correlation between line performance and GCA was only slightly higher than the one between hybrid performance and SCA (Table 3), pointing to the additional contribution of non-additive effects. The interaction between GCA effects and striga populations was highly significant (p =0.01, Table 5). The instability of GCA effects in some lines is also reflected in the moderate correlation between the two striga populations for GCA effects (Table 3). However, the parent lines 555, N 13, IS 9830, and M 35-1 revealed negative GCA at both locations (Table 4). Large SCA effects for low striga emergence in the pots were detected in the crosses Framida × IS 9830 (–9.0), Framida × E 36-1 (–9.5), and DJ 1195 × M 35-1 (–8.2).

Relationship between agar-gel assay and pot trials

The relationship between germination distance (from the agar-gel assay) and emerged striga number (in the pot trial) was moderate but non-significant for the parent lines (r = 0.59), weak for the hybrids (r = 0.26, non-significant), and also weak pooled across all entries (r = 0.26, significant at p =0.05).

Discussion

Our results clearly reveal the presence of genetic variation in sorghum for stimulation of *S. hermonthica* seed germination in the agar-gel assay and for the number of emerged striga plants in pots. Both, GCA (additive) and SCA (non-additive) effects were significant for the two traits considered with the GCA effects being overall more important than SCA effects. These findings corroborate earlier reports on the genetics of resistance to *S. asiatica* (Shinde & Kulkarni, 1982; Vasudeva Rao, 1984; Kulkarni & Shinde, 1987)

and *S. hermonthica* (Obilana, 1984; Ramaiah, 1984, 1987; Hess & Ejeta, 1992) in sorghum. Partial recessiveness of the genes for resistance is suggested by the inferior performance of hybrids in the agar-gel assay as well as in the pot trials.

A single recessive gene was shown to control low-level stimulation of *S. asiatica* seed germination by Framida and line 555 (Ramaiah et al., 1990), and line SRN 39 (Vogler et al., 1996). Differing GCA effects for the germination distance in the agar-gel assay and the divergent performance of their crossing progenies indicate that the alleles (or genes) for low stimulant production may differ among 555, Framida and IS 9830. Further agar-gel assays conducted with three F_2 – and two recombinant inbred populations (B.I.G. Haussmann, unpublished data) indicate that one major and several minor genes are involved in the stimulation of *S. hermonthica* seed germination. The identification of different genes controlling low stimulation of striga seed germination and their combination in sorghum cultivars can be expected to enhance degree and durability of resistance to striga (Ramaiah et al., 1990).

The large relative midparent heterosis (114%) for the number of emerged striga plants pot^{-1} may be overestimated since very susceptible lines (e.g., E 36-1) exhibit striga stress symptoms despite low numbers of emerged striga. The number of emerged striga may only present a small portion of the actual subterranean attached striga numbers. Doggett (1965) determined that on badly infested land in Tanzania only 10 to 30% of attached striga appeared above ground. Extreme susceptibility may result in such severe host damage that emergence of striga is strongly reduced. Therefore, low numbers of emerged striga do not necessarily reflect striga resistance (e.g., Kim, 1994, 1998) and this could have been the case for some of the parent lines in the present pot experiment.

Difficulties in screening for striga resistance under field conditions (Vasudeva Rao, 1984) render indirect selection traits desirable. Germination distance in the agar-gel assay can be measured easily, quickly, and cheaply, and has a high heritability. It therefore meets some of the requirements for the usefulness of indirect selection traits. Correlations between stimulant production and striga counts in the field were reported as positive and sometimes very high (Vasudeva Rao, 1984). However, it should be noted that these correlations depend on the genetic material evaluated. In the present study, the weak relationship between the germination distance in the agar-gel assay and the number of striga plants in the pot trials confirmed Bapat's (1982) report that low-stimulant sorghum genotypes are not necessarily highly striga resistant and, conversely, that the high-stimulant characteristic does not necessarily confer high susceptibility to striga. Parent line N 13 is an example of a high-stimulant genotype with superior resistance to striga in pot trials and under field conditions and a negative GCA for the number of emerged striga plants in pots (this study) and field experiments (Shinde & Kulkarni, 1982; Ramaiah, 1984, 1987). Line N 13 was characterized as 'mechanically resistant' (Shinde & Kulkarni, 1982) with a highly thickened endodermis and pericycle tissue (Ramaiah, 1987), and fewer lateral roots in the upper 10 cm soil (Dixon & Parker, 1984). Following a preliminary pot experiment where we investigated subterranean attached and emerged striga plants (D.E. Hess & B.I.G. Haussmann, unpublished data), we suggest antibiosis as a likely additional resistance mechanism in N 13. Obviously, resistance to striga is not attributable to a single mechanism and interactions among different mechanisms may influence field reactions to striga infestation (Bapat, 1982).

Conclusions

Among the parent lines under study, IS 9830, M 35-1, N 13, and 555 were the most promising sources of resistance and can be recommended for future use in breeding programs. Due to the predominance of additive-genetic effects for germination distance in the agar-gel assay, preselection of parent lines for a crossing program should be very effective with regard to the low-stimulant character. However, the exclusive selection for low germination distances could result in loss of valuable materials possessing resistance mechanisms other than low-stimulant production. The development of further laboratory or controlled environment assays which allow the non-destructive, quick and inexpensive evaluation of individual plants for resistance mechanisms other than the low stimulant character is essential, and could facilitate early generation testing and increase the efficiency of breeding programs for striga resistance. Until such assays become available, breeders need to continue to test their materials in pot trials and especially under field conditions to identify complex and stable resistance. As GCA effects of some lines turned out to be unstable across locations/striga populations for the number of emerged striga plants pot^{-1}, experiments should be

conducted at various locations using the corresponding different geographic sources of striga. If available, screenhouse or field inoculation techniques (e.g., Kim, 1994; Berner et al., 1995, 1996) can be used to increase homogeneity of striga infestation and reduce the error variation. Finally, the significant contribution of SCA effects to the studied components of striga resistance indicates that thorough screening of individual testcrosses is indispensable for selection in hybrid sorghum breeding programs.

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