



Diallel analysis of sooty stripe resistance in sorghum

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Summary

Sooty stripe [*Ramulispora sorghi* (Ellis and Everhart) Olive and Lefebvre] is a widespread foliar disease of sorghum [*Sorghum bicolor* (L.) Moench] in West Africa, responsible for grain yield losses up to 46%. We studied the inheritance of sooty stripe resistance in a 9 × 9 sorghum F₂-population diallel grown together with parent lines and checks in 1996 under natural disease pressure at two locations in Mali. The percentage of infected leaf area was determined twice over a two-week interval during the season. At the second evaluation, the mean sooty stripe severity amounted to 13% infected leaf area at Samanko and 12% at Cinzana. The frequency distribution of the entries was approximately normal for the mean disease severity, averaged across assessment dates and locations, pointing to the involvement of multiple genes. With the data combined across the two locations, genetic differences among lines and among F₂ populations were highly significant. Genotype × location interaction variances were also significant but much smaller than the genetic variances. Broad-sense heritability estimates were 0.92 for lines and 0.94 for the F₂ populations, for the mean percentage infected leaf area across the two assessment dates. General combining ability effects (GCA) determined most of the differences among the F₂ populations. Specific combining ability effects (SCA), and the interactions of GCA or SCA with locations were also significant but less important. Line performance *per se* was highly correlated with GCA. Because of the high heritability and predominance of additive effects, prospects are good for the genetic improvement of resistance to sooty stripe in sorghum in Mali, using simple pedigree or recurrent selection procedures.

Abbreviations: GCA – general combining ability; SCA – specific combining ability

Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] ranks fifth in importance among the world's cereals with 44.8 million ha cultivated area (FAO, 1999). It constitutes an important component of traditional farming systems and of the diets of millions of people in the semi-arid tropics.

Sooty stripe [*Ramulispora sorghi* (Ellis and Everhart) Olive and Lefebvre] is a common foliar disease of sorghum in many areas of the world. It occurs where

warm, humid conditions prevail during the growing season. The disease is particularly common in West Africa, including Mali, Senegal, Burkina Faso, and Nigeria (Bandyopadhyay, 1986; Thomas, 1992, 1993; Pande et al., 1993; Thakur et al., 1997). Severe sooty stripe epidemics were also observed in Tanzania, Zambia, and Zimbabwe (De Milliano, 1992). Results from Mali showed that in susceptible cultivars, the disease can cause as much as 46% reduction in grain weight (Thomas, 1993).

Young sooty stripe lesions have straw-colored centres of dead tissue and purplish to tan margins. Mature lesions are elliptical and can measure 5 to 14 cm in length and 1 to 2 cm in width. Lesions may coalesce to produce large areas of necrotic leaf tissue. As the lesions age, the centers darken and appear first greyish through conidia masses and then blackish or sooty with the production of numerous small black sclerotia (Williams et al., 1978; Bandyopadhyay, 1986). The pathogen survives as sclerotia in leaf residue on or below the soil surface. When conditions are favorable, sclerotia and sclerotial sporodochia produce abundant conidia that are disseminated by wind and rain to infect healthy foliar tissue (Bandyopadhyay, 1986).

Crop rotation and destruction of infected leaf debris are recommended as a means of reducing primary inoculum. Effective control is also achieved by the cultivation of sooty-stripe-resistant varieties, where available (Bandyopadhyay, 1986). To optimize the selection strategy in a breeding program, information is needed on resistance sources and the inheritance of resistance. The objective of this research was to study the gene action and mode of inheritance of sooty stripe resistance in diallel crosses of sorghum grown under natural infection pressure at two locations in Mali.

Materials and methods

Nine sorghum cultivars (Framida, Seredo, 555, N 13, IS 9830, M 35-1, E 36-1, DJS 1195, and IS 1037, all >S₇ inbreeding generation) with unknown reaction to sooty stripe were crossed in a diallel fashion. The F₁ hybrids were selfed to obtain enough seed for multi-location trials. The resulting 36 F₂ populations were grown in 1996 together with the parent lines and five checks under natural sooty stripe infection in Mali at Samanko (12°31'N, 08°04'W, 358 m altitude) and Cinzana (13°15'N, 05°57'W, 285 m altitude). The trials were sown on 17 June and 19 July at Samanko and Cinzana, respectively. The total rainfall amounted to 728 mm at Samanko and 569 mm at Cinzana. Mean minimum/maximum air temperatures during the first three months after planting were 20/38 °C at Samanko and 23/34 °C at Cinzana. Soil type was a tropical ferruginous soil with a sandy to loamy texture at both locations. The trials were fertilized with 30 kg ha⁻¹ N and 18 kg ha⁻¹ P₂O₅ at Samanko, and with 38 kg ha⁻¹ N and 44 kg ha⁻¹ P₂O₅ at Cinzana. Local checks were Wagita and Nakhadabo from East Africa;

CSM 335 and CSM 228 from Mali, and Bengou Local from Niger. The experiment was laid out as randomized complete blocks with six replications. Each plot consisted of two rows, 3 m long, separated from the neighbouring entry by one empty row. The distance between rows was 0.8 m, and the spacing between plants within rows 0.2 m. All plots were sown by hand and thinned to one plant per hill. The previous crop had been sorghum at both locations. The experiments were conducted under striga infestation [*Striga hermonthica* (Del.) Benth., a parasitic weed] but striga did not noticeably affect the disease reaction of the entries. For more details of the locations, see Haussmann et al., 2001).

The percentage of the leaf area covered by sooty stripe lesions was estimated for five random plants within each plot at 46 and 57 days after planting at Samanko, and at 57 and 70 days after planting at Cinzana. Plot means were calculated for each of the two assessment dates, and are subsequently referred to as first and second score, respectively. Mean score, the third character considered here, is the average of the first and second score. Quantitative-genetic parameters estimated for other characters assessed in the trials are published elsewhere (Haussmann et al., 2001).

Basic statistical analyses were performed with the statistical software PLABSTAT (Utz, 1998). The relative heterosis shown by the F₂ populations (F₂ heterosis) was computed as the difference between the F₂ and midparent values, expressed as percentage of the midparent values. In the combined analysis of variance, the effects of entries, locations and replications were considered as random. Broad-sense heritabilities were estimated on an entry-mean basis (Hallauer & Miranda, 1981), with 90% confidence intervals (Knapp et al., 1985). In the diallel analysis, genetic parameters were estimated following Method 4 of Griffing (1956) for random effects, using the computer programs PZ14 (Utz, 1992) and DIALLEL (Burow & Coors, 1994). The importance of SCA effects was expressed as the ratio of SCA to the total genotypic variance (sum of twice the GCA variance plus SCA variance; Falconer, 1989).

Results

Sooty stripe symptoms appeared about two weeks later in Cinzana than in Samanko but reached similar severity as in Samanko at the second assessment date (Table 1). At Cinzana, the F₂ populations were slightly

Table 1. Mean percentage leaf area covered by sooty stripe lesions in parent lines and F₂ populations at two locations and two assessment dates in Mali in 1996

Location	Assessment date ^a	Mean infected leaf area [%]	
		Parent lines	F ₂ populations
Samanko	2 August (46 d.a.p.)	11.1	11.7
	13 August (57 d.a.p.)	13.4	13.1
Cinzana	13 September (56 d.a.p.)	7.3	7.6 ⁺
	27 September (70 d.a.p.)	13.3	12.2 ⁺

⁺ Difference between lines and F₂ populations significant at the 0.10 probability level.

^a d.a.p. = days after planting.

more susceptible than the parent lines for the first score, but slightly more resistant for the second score. In contrast, the F₂ mean did not differ significantly from the parental mean for either date at Samanko. Combined across the two locations, the mean difference between parents and F₂ populations was also not significant (data not shown).

The frequency distribution of the 50 test entries was approximately normal for the mean percentage of infected leaf area, averaged across assessment dates and locations (Figure 1). The distribution of solely the 36 F₂ populations was approximately normal as well, while the parent lines were evenly distributed across the range of observations. The local checks showed average susceptibility to sooty stripe.

Combined across the two locations, genetic differences among lines and among F₂ populations were highly significant (Table 2). Genotype × location interaction variances were also significant but of much lower importance than the genetic variances. The ratio of the genetic to the genotype × location interaction variance for the mean score was 1:0.13 in the parents, and 1:0.08 in the F₂ populations. Broad-sense heritability estimates were high for all three traits, but highest for the mean score across the two assessment dates.

Differences among the F₂ populations were caused by GCA as well as SCA effects (Table 3). However, the estimated SCA variances were much smaller than the GCA variances. The percentage of SCA relative to the total genotypic variance was 4.9% for the first score, 9.7% for the second score, and 7.5% for the mean score averaged across the two assessment dates. The GCA × location and SCA × location variances were also significant but of low importance.

Resistance of the lines *per se* was highly correlated with their GCA (Figure 2). Lines Seredo and IS 9830 were the best general combiners for sooty

stripe resistance in the present study, followed by Framida and E 36-1. The best F₂ populations resulted from the crosses Seredo × IS 9830 (2.6% infected leaf area), Seredo × E 36-1 (3.0%), and Seredo × Framida (4.5%). The coefficients of correlation between F₂ performance and SCA were not significant for the first and the mean scores, and rather low ($r = 0.35$) but significant ($p = 0.05$) for the second score.

While the difference between the means of parents and F₂ populations was not significant for the mean score across the two locations (see above), there was significant ($p = 0.01$) variation for F₂ heterosis among the progenies. Individual F₂ heterosis estimates ranged from -43% to 30% for the mean score (data not shown). Heterosis for resistance was displayed by F₂ populations derived from crosses of either two resistant, one resistant and one susceptible, or two susceptible parent lines. Estimates of relative heterosis in the individual F₂ populations were moderately correlated to SCA effects ($r = 0.48$, $p = 0.01$ for the mean score).

Discussion

Sooty stripe of sorghum has been listed as a major production constraint in Western Africa (Thakur et al., 1997). The development and cultivation of varieties that are resistant to important pathogens is the most effective means of disease management for resource-poor farmers.

In the present study, the natural infection level at Samanko and Cinzana (Mali) was high and uniform so artificial inoculation was not required. But if natural infection is unreliable at a certain location, the artificial inoculation technique developed by Thomas

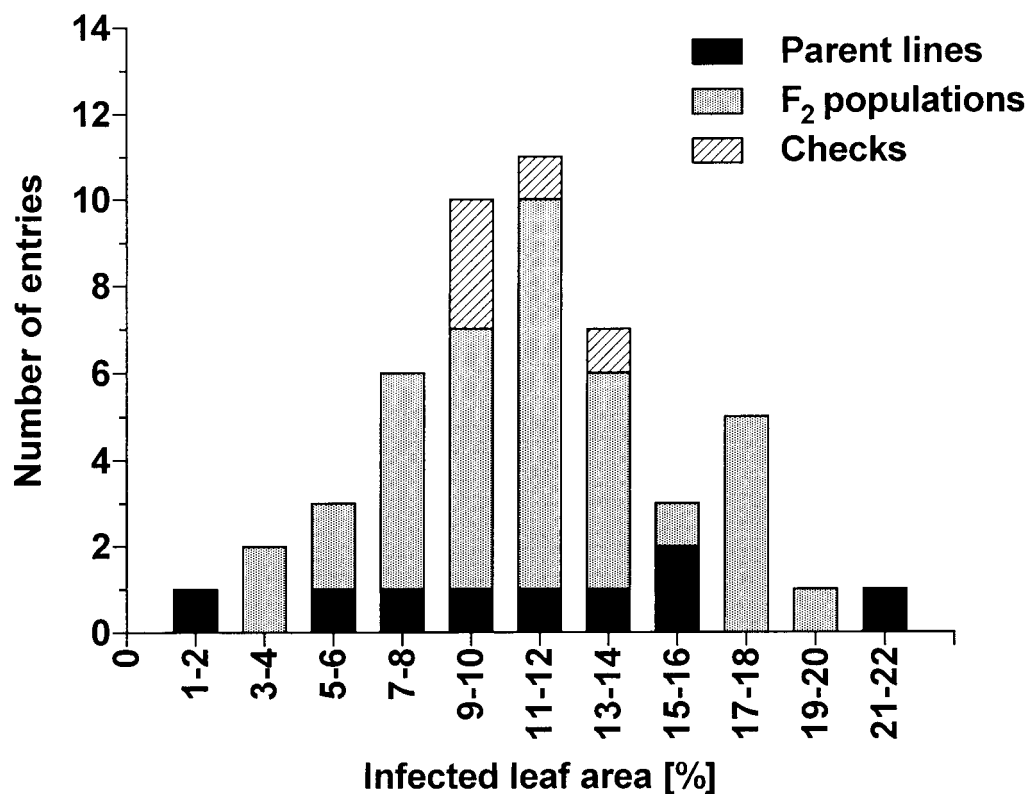


Figure 1. Frequency distribution of the 50 entries for the mean percentage of infected leaf area, averaged across two assessment dates and two locations (Cinzana & Samanko, Mali) in 1996; least significant difference between entry means = 3.7%.

Table 2. Estimated variance components (\pm standard error) and broad-sense heritabilities (h^2) of lines and F₂ populations for percentage leaf area covered by sooty stripe lesions determined at two assessment dates and for the mean score; ANOVA combined across two locations (Cinzana & Samanko, Mali) in 1996

Trait	Source of variation					h^2 [90% confidence interval]	
	Parent lines	F ₂ populations	Parent \times location	F ₂ \times location	Error	Parent lines	F ₂ populations
Score 1	20.7** \pm 10.6	11.1** \pm 2.9	4.4** \pm 2.5	1.2* \pm 0.6	1.1 \pm 0.1	0.88 [0.48; 0.97]	0.91 [0.81; 0.95]
Score 2	42.9** \pm 21.9	22.3** \pm 6.0	9.9** \pm 5.2	4.4** \pm 1.4	1.7 \pm 0.1	0.88 [0.47; 0.97]	0.88 [0.76; 0.94]
Mean score	31.3** \pm 15.2	16.6** \pm 4.1	4.2** \pm 2.3	1.4** \pm 0.5	0.9 \pm 0.1	0.92 [0.66; 0.98]	0.94 [0.87; 0.97]

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 3. Estimated components of combining ability variance for percentage leaf area covered by sooty stripe lesions determined at two assessment dates and for the mean score; ANOVA combined across two locations (Cinzana & Samanko, Mali) in 1996

Sooty stripe severity	Source of variation ^a			
	GCA	SCA	GCA \times location	SCA \times location
Score 1	6.49**	0.66**	0.14	0.96**
Score 2	12.32**	2.66**	2.19**	0.89*
Mean score	9.47**	1.54**	0.49**	0.61*

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

^a GCA = general combining ability; SCA = specific combining ability.

et al. (1993) may be employed in a breeding program to increase accuracy and heritability.

The wide range of genetic variation for sooty stripe resistance in current sorghum breeding materials and the high heritability estimates observed in the present study indicate good prospects for genetic improvement of sooty stripe resistance in sorghum. The continuous distribution of the resistance parameters, the different GCA effects of resistant lines, and the variable expression of F_2 -heterosis in different cross combinations indicate that several genes control the disease reaction. Predominance of additive-genetic effects was reflected by the large variance components due to GCA, the low relative importance of SCA, and the close correlation between line performance *per se* and GCA. Therefore, the degree of resistance in progenies appears to be largely predictable from the parent's performance, and preselection of lines for use in a crossing program or in population improvement should be highly effective.

The high heritability estimate obtained in the present study was to some extent due to the high number of replicates (which had been chosen to additionally test the entries for resistance to the root parasite *Striga hermonthica*). However, even when analyzing only two randomly chosen replicates at each site, genetic differences among entries were highly significant ($p = 0.01$) with repeatability estimates (= genetic variance divided by the sum of genetic and error variance) above 0.79 for the mean score across the two assessment dates. Therefore, two replicates should be sufficient for screening when sooty stripe resistance is the major objective of the trial.

The importance of genotype \times location interaction was low, another reason for the high heritability estimate obtained in the present study. But as the experiment was performed at just two locations in Mali, the heritability may be overestimated and more trials are needed before final conclusions about the stability and the heritability of resistance in the present materials can be made.

Our results revealed that both GCA and SCA effects contribute to resistance, with a predominance of GCA variance. None of the entries tested in the present study was completely resistant to sooty stripe. Even the most resistant parent line, Seredo, showed 2.4% infected leaf area, i.e., the infection was not completely stopped but the build-up of the disease was delayed. Other resistance sources include IS 9830 (identified in this study), Tegemeo, MR 841, and MR 904.3 (Thomas, 1993). In a combining ability study, Tege-

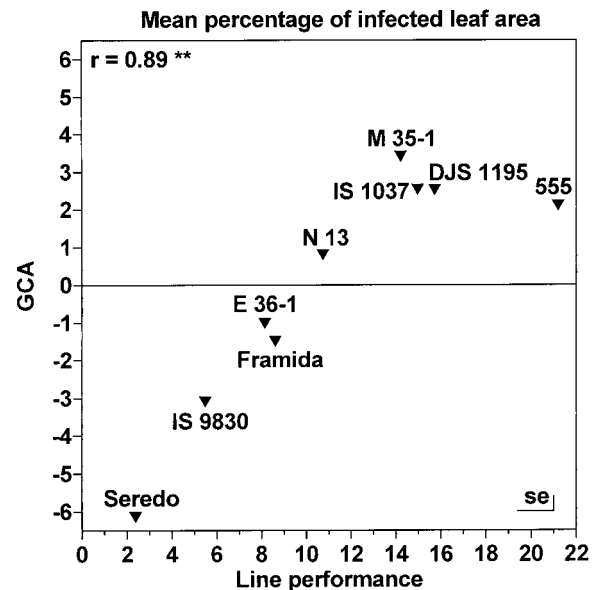


Figure 2. Relationship between line *per se* performance and GCA for the mean percentage of infected leaf area, averaged across two assessment dates and two locations (Cinzana & Samanko, Mali) in 1996; r = coefficient of phenotypic correlation; se = standard error.

meo had the largest GCA for sooty stripe resistance and showed, similar to Seredo, partial resistance (D.S. Murty, pers. comm.). In resistance breeding, such partial resistance, if inherited polygenically, should be preferred over complete monogenic resistance, since it is less likely to be overcome by new virulent races in the pathogen population.

The identification of different resistance genes and their pyramiding in sorghum cultivars by means of pedigree or recurrent selection can be expected to enhance the degree and durability of resistance to the sooty stripe pathogen in Mali.

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