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Quantitative-genetic parameters of sorghum growth under striga infestation in Mali and Kenya

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With 2 figures and 6 tables

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Abstract

To estimate quantitative-genetic parameters of sorghum for resistance to the hemi-parasitic weed striga [*Striga hermonthica* (Del.) Benth.] and for agronomic traits, 36 diallel F_2 populations and their nine parental lines were evaluated under severe striga infestation at two locations each in Mali and Kenya. Location means for grain yield ranged from 132 to 254 g/m^2. F_2 populations outyielded lines on average by 18%. For striga emergence traits, F_2 heterosis values ranged from −36% to 232% among populations. Genetic and genotype × environment interaction variances of lines and F_2s were highly significant for all traits. Broad-sense heritabilities for areas under striga severity progress curves and grain yield were 0.83 and 0.90 in lines, and 0.81 and 0.89 in F_2s, respectively. General and specific combining ability, and their interaction effects with locations were significant for most traits. F_2 superiority for grain yield under striga infestation demonstrates the potential merit of heterozygous cultivars in the target areas. Significant genotype × environment interaction entails multilocational testing to identify stable resistance. A combination of resistance with striga tolerance is recommended to breeders.

Key words: *Sorghum bicolor* — *Striga hermonthica* — diallel analysis — GCA — heritability — heterosis — resistance — SCA — tolerance

Sorghum is an important crop in traditional farming systems and in the diet of millions of people in the semi-arid tropics. In addition to abiotic stress factors such as drought and low soil fertility, parasitic weeds of the genus *Striga* (*Scrophulariaceae*) cause important losses in sorghum production in sub-Saharan Africa. Economically the most important species are *Striga hermonthica* (Del.) Benth. and *Striga asiatica* (L.) Kuntze. These parasites attach to the roots of their host and cause important damage even before plant emergence. Adapted, striga-resistant sorghum cultivars could be a major component of integrated striga control as their cultivation would not require costly inputs from the farmers. Investigation of striga resistance in sorghum began in the 1920s in South Africa (Saunders 1933). However, breeding progress has been slow owing to limited knowledge of the genetics of striga resistance and the difficulty of evaluating resistance in the field. Field screening for striga resistance is hampered by heterogeneity of natural infestations, high variability in African soils and concomitant large environmental effects on striga emergence. Improved field testing methodologies have been summarized recently (Haussmann et al. 2000a).

The best understood resistance mechanism to striga in sorghum is weak stimulation of striga seed germination. This character can easily be screened by determining the 'germination distance' in an agar-gel assay (Hess et al. 1992). Weak stimulation of *S. asiatica* seed germination by the sorghum cultivars 'Framida', '555', 'SRN 6496' and 'SRN 39' was reported to be due to a single recessive gene (Ramaiah et al. 1990, Vogler et al. 1996). One major and an unknown number of minor genes are involved in stimulation of *S. hermonthica* seed germination in progenies from crosses of 'Framida', '555', and 'IS 9830' with 'E 36-1' (B. I. G. Haussmann, unpubl. data). Estimates of broad-sense heritability were 0.91 and 0.97 for germination distance of F_1 diallel crosses and their parent lines, respectively, in the agar-gel assay in a combined analysis across striga populations from Mali and Niger (Haussmann et al. 2000b). Correlations between weak stimulation of striga seed germination and resistance under field conditions are mostly positive (Vasudeva Rao 1984) but are modified by the materials under investigation and the test environments (Omanya et al. 2000).

Other putative resistance mechanisms include: 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. unfavourable phytohormone supply by the host); insensitivity to a putative striga toxin (e.g. maintenance of photosynthetic efficiency); avoidance through root growth habit (e.g. fewer roots in the upper soil profile) (Ejeta et al. 1992, Ejeta and Butler 1993, Berner et al. 1995, K. Wegmann, personal communication). It would appear that the inheritance of these resistance mechanisms has not yet been studied.

Limited information is available on the genetics of striga emergence. Hess and Ejeta (1992) reported additive and dominance effects controlling the number of emerged *S. hermonthica* plants in sorghum progenies (F_1, F_2, BC_1) derived from the cross 'SRN 39' × 'P954063' grown in pots at Niamey (Niger). The significance of both general combining ability (GCA) and specific combining ability (SCA) effects, with predominance of additive-genetic effects, was reported for emerged-striga number in the evaluation of a 7 × 7 sorghum F_1 diallel in *S. hermonthica*-infested pots in Burkina Faso (Ramaiah 1984, 1987).

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Table 1: Description of the cultivars used as parents of the F_2 diallel

Name	Origin	Race	Reported reaction to striga[1]
'N 13'	India	Durra	Resistant: mechanical barriers, antibiosis
'Framida'	Southern Africa	Caudatum	Resistant: low-stimulant, mechanical barriers
'555'	India	Durra	Resistant: low-stimulant
'IS 9830'	Sudan	Caudatum	Resistant: low-stimulant, thickened cell walls
'Seredo'	Uganda	Caudatum	Tolerant
'M 35–1'	India	Durra	Susceptible
'E 36–1'	Ethiopia	Guinea/caudatum	Susceptible
'DJ 1195'	India	Durra	Susceptible
'IS 1037'	India	Durra	Susceptible

[1] Shinde and Kulkarni (1982), Dixon and Parker (1984), Maiti et al. (1984), Ramaiah (1984, 1987), Vasudeva Rao (1984), Sherif and Parker (1990), D. E. Hess and B. I. G. Haussmann, unpubl. data.

Similar results were obtained from a 9 × 9 diallel experiment in *S. hermonthica*-infested pots conducted at Samanko (Mali) and Sadoré (Niger) (Haussmann et al. 2000b). In a field trial at Samaru (Nigeria), Obilana (1984) observed continuous variation and transgressive segregation in progenies from the cross 'ISNIB' (striga-susceptible) × 'L 187' (resistant) for the number of *S. hermonthica* plants emerged. He estimated two to five genes to be involved. A 7 × 7 sorghum F_1 diallel study at two fertility levels in a *S. asiatica*-infested field at Parbhani (India) revealed significant GCA and SCA effects for emerged-striga number and grain yield under striga infestation (Kulkarni and Shinde 1985a, 1985b, 1987). Sorghum hybrids derived from crosses between a resistant and a susceptible parent were reported to be susceptible (Rana et al. 1982, Shinde and Kulkarni 1982, Obilana 1984, Hess and Ejeta 1992), suggesting partial or complete dominance of genes for susceptibility.

The objective of the present study was to estimate quantitative-genetic parameters for striga resistance and agronomic traits in a 9 × 9 F_2 diallel of sorghum grown in striga-infested fields in Kenya and Mali.

Materials and Methods

Nine sorghum, *Sorghum bicolor* (L.) Moench, cultivars (all $> S_7$ inbreeding generation) differing in resistance to striga (Table 1) were crossed in all possible combinations. The complete F_1 diallel was evaluated in 1995 for stimulation of *S. hermonthica* seed germination, using the agar-gel assay (Hess et al. 1992) and striga seeds from Mali and Niger (Haussmann et al. 2000b). In addition, the half F_1 diallel was advanced to the F_2 generation to produce seed for multilocational field experiments. The resulting 36 F_2 populations were evaluated, together with their nine parents and five local controls ('Wagita' and 'Nakhadabo' from East Africa; 'CSM 335', 'CSM 228' and 'Bengou Local' from West Africa) in striga-infested fields at Samanko and Cinzana (both Mali) in 1996, and at Kibos and Alupe (both Kenya) in the short rainy season 1996–97 (Table 2). The experimental design was a randomized complete block with six replications at all four sites. Each plot consisted of two rows, 3 m long, separated from the two neighbouring entries by one empty row each. The advantages of this specific plot layout have been outlined recently (Haussmann et al. 2000a). The spacing between rows was 0.80 and 0.75 m, and the spacing between plants within rows 0.20 and 0.15 m in Mali and Kenya, respectively. All plots were hill-planted by hand and thinned to one plant per hill. The previous crop was sorghum at all four locations.

The following traits are reported: days after planting (d.a.p.) to striga emergence; d.a.p. to the appearance of the first striga flowers; number of emerged striga plants/m^2 at 59 and 85 d.a.p. (plus or minus 6 days, depending on the location); average striga vigour at 85 d.a.p.,

Table 2: Summary description of the four test locations

	Mali		Kenya	
	Samanko	Cinzana	Alupe	Kibos
Altitude (m)	358	285	1189	1214
Latitude	12°31′N	13°15′N	00°29′N	00°04S
Longitude	08°04′W	05°57′W	34°08′E	34°48′E
Soil type	Tropical ferruginous soil, leached; sandy loam	Tropical ferruginous soil, leached, rich in sesquioxids; sandy loam	Orthic ferrosol, part. petroferric phase with orthic acrisols	Retroentric planosol; sandy loam
Planting date (1996)	17 June	19 July	19 August	16 September
Total rainfall (mm)	728	569	622	469
Fertilization (kg/ha)	30 N, 18 P_2O_5	38 N, 44 P_2O_5	40 N, 40 P_2O_5	40 N, 40 P_2O_5
Striga infestation	77 700 viable seeds/m^2 plus natural	Natural	0.4 g Striga seeds/m^2 plus natural	Natural
Trait means[1]				
Emerged striga 85 d.a.p.	42	70	60	39
Striga vigour 85 d.a.p.	4.7	4.3	6.4	4.5
Sorghum anthesis (days)	83	75	62	60
Plant height (cm)	260	235	155	147
Grain yield (g/m^2)	132	252	148	132

[1] d.a.p. = days after planting.

rated on a scale from 0 to 9, with 0 = no emerged striga, 1 = average striga height ≤5 cm and striga plants without branches, . . . , and 9 = average striga height > 40 cm and average number of striga branches > 10 (Haussmann et al. 2000a); striga severity (i.e. striga count multiplied by striga vigour) at 85 d.a.p.; area under striga number progress curve, divided by 100, using the equation for area under the disease progress curve (AUDPC; Shaner and Finney 1977, see also Haussmann et al. 2000a); area under striga severity progress curve, divided by 100, using the striga severity values instead of striga counts in the formula; area under flowering-striga number progress curve, divided by 100; d.a.p. to 50% anthesis of sorghum; sorghum plant height from ground to the tip of the panicle; grain yield; number of panicles per plant; and grain weight per panicle.

Basic statistical analyses were performed with the computer program PLABSTAT (Utz 1998). The amount of relative heterosis shown by the F_2 populations (F_2 heterosis) was computed as the difference between the F_2 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 to allow an estimation of variance components. Details of the pattern of genotype × environment interaction will be published separately. Operative heritabilities were estimated on an entry-mean basis (Hallauer and Miranda 1981), with 90% confidence intervals (Knapp et al. 1985). In the diallel analysis, effects of the parents were considered as fixed. Genetic parameters were estimated following Method 4 of Griffing (1956) for fixed effects, using the computer programs PZ14 (Utz 1992) and DIALLEL (Burow and Coors 1994). Coefficients of genotypic correlation were computed as described by Mode and Robinson (1959).

Results

Location means

Striga emergence was high at all four locations (Table 2), with a maximum at Cinzana at 85 d.a.p. The average striga vigour and striga severity values were highest at Alupe. Overall, the sorghum plants grew taller and flowered later in Mali. The environmental mean for grain yield ranged from 132 to 252 g/m^2 and was highest at Cinzana.

F_2 heterosis

Averaged across the four locations, the F_2 populations outyielded their parental lines by 18% (Table 3). While the mean differences measured between lines and F_2s were rarely significant for striga emergence and developmental traits, the variation of individual heterosis estimates for these traits was mostly large and significant across the 36 F_2 populations tested. On average, the F_2s flowered earlier, grew taller, had more panicles per plant and a higher grain weight per panicle than their parents. The F_2 heterosis also varied among environments (Table 4). A significantly higher susceptibility to striga of the F_2s compared with the parents was observed at Cinzana and Kibos, while the differences were mostly nonsignificant at Samanko or Alupe. The F_2 heterosis for grain yield was significant at Cinzana and Alupe — sites with the highest striga emergence.

Comparison of F_2 populations with local cultivars

Combined across the four locations, a number of F_2s were superior to the local cultivars for lower area under the striga severity progress curve, higher grain yield, or both (Fig. 1). The overall best F_2 population ('Framida' × 'Seredo') significantly outyielded the highest-yielding local cultivar ('Wagita') by 35% at Samanko, 63% at Alupe and 33% at Kibos. Only at Cinzana did the West African cultivar 'Bengou Local' show specific adaptation and 18% superiority over the best F_2 population ('IS 9830' × 'Seredo'). The East African control 'Wagita' showed tolerance to striga infestation, as it maintained high grain yield while supporting above-average emerged striga. 'Nakhadabo' had the lowest area under the striga severity progress curve value among the local controls, but was low yielding. The most susceptible entry was the local cultivar 'CSM 228' from Mali.

Variance components and heritabilities

In the combined analysis of variance, genetic differences among parental lines and among F_2 populations, as well as

Table 3: Means of parents and F_2 populations, and means and genotypic ranges of F_2 population heterosis (%) for various traits, averaged across four locations

Trait[1]	Means Parents	F_2 populations	F_2 Heterosis (%) Mean	Range
Striga emergence (d)	39.9	38.7	−2.9*	(−9.3; 5.3)
Striga flowering (d)	73.6	72.8	−1.1*	(−5.4; 5.7)
Emerged striga 59 d.a.p.	13.0	15.8	21.2	(−36.2; 166.3)*
Emerged striga 85 d.a.p.	43.7	51.9	18.7	(−14.9; 232.4)**
Striga vigour 85 d.a.p.	4.8	5.0	3.7*	(−14.1; 14.2)*
Striga severity 85 d.a.p.	238.6	278.8	16.9	(−20.3; 241.1)**
Area under striga number progress curve	15.3	18.1	17.7	(−18.6; 213.8)**
Area under striga severity progress curve	72.1	83.3	15.5	(−20.7; 227.9)**
Area under flowering striga progress curve	11.9	13.8	16.0	(−37.7; 174.2)$^+$
Sorghum anthesis (d)	69.6	68.1	−2.2$^+$	(−9.7; 15.5)**
Plant height (cm)	178.6	201.3	12.7*	(−4.6; 37.8)**
Grain yield (g/m^2)	147.6	174.6	18.3*	(−28.8; 69.7)
Panicles/plant	0.98	1.02	4.1$^+$	(−7.2; 24.0)
Grain weight/panicle (g)	20.7	23.8	15.3*	(−19.1; 74.2)*

$^+$, *, ** Mean difference between parents and F_2 populations or variation of heterosis estimates significant at P = 0.1, P = 0.05, and P = 0.01, respectively.

[1] d.a.p. = days after planting.

Table 4: Estimated average relative F_2 heterosis (%) at four locations for traits with significant (Parents vs. F_2 populations) × environment interaction

Trait[1]	Location Samanko	Cinzana	Alupe	Kibos
Emerged striga 59 d.a.p.	14.0^{+}	54.9**	0.5	37.1
Emerged striga 85 d.a.p.	19.4	37.3**	−4.4	29.1**
Striga severity 85 d.a.p.	17.5	38.2*	−3.6	35.2*
Area under striga number progress curve	14.9^{+}	42.1**	−6.5	32.1*
Area under striga severity progress curve	16.1	38.8*	−6.4	36.2*
Sorghum anthesis	−1.7	−0.7	−4.8**	−1.9*
Plant height	16.4**	13.8**	8.9**	8.7**
Grain yield	11.5	21.1**	23.2**	13.2
Panicles/plant	6.6^{+}	3.5**	5.9**	−1.2

$^{+}$, *, ** Mean difference between parents and F_2 populations significant at P = 0.1, P = 0.05 and P = 0.01, respectively.
[1] d.a.p. = days after planting.

genotype × environment interaction variances, were highly significant for all traits considered (Table 5). The ratio of genotype × environment interaction to genetic variance was high, i.e. above 0.7, for days to striga flowering and area under the striga number progress curve in both lines and F_2s, for days to striga emergence, area under the striga severity progress curve, and number of panicles per sorghum plant in lines, and for emerged-striga numbers at 59 and 85 d.a.p. and sorghum plant height in the F_2s. For sorghum grain yield, the importance of the genotype × environment interaction variance was moderate, with a ratio of genotype × environment interaction to genetic variance of 0.4 in both lines and F_2s. Heritability estimates were moderate or high for all traits considered, for both lines and F_2 populations.

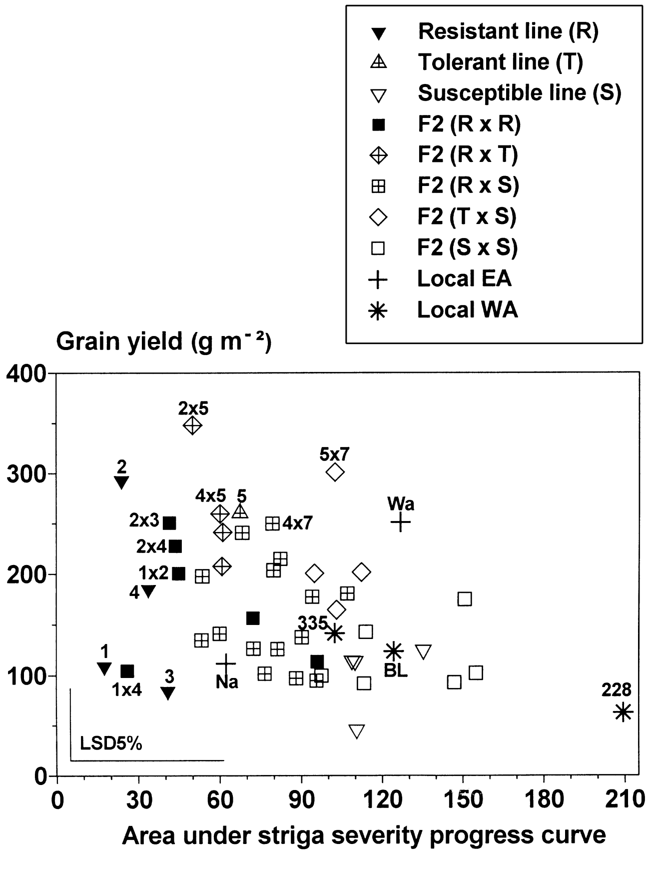

Fig. 1: Relationship between striga severity and grain yield

General and specific combining ability

The mean square due to GCA was significant (P ≤ 0.05) or highly significant (P ≤ 0.01) for all traits considered (data not shown). Variation among the F_2 populations was also due to significant SCA effects (P ≤ 0.05 or P ≤ 0.01) for all traits except days to striga emergence and days to striga flowering. The F-values of GCA were mostly larger than F-values of SCA. The interaction between GCA and environments was significant (P ≤ 0.05 or P ≤ 0.01) for all traits except striga vigour at 85 d.a.p. Significant SCA × environment interaction occurred for all traits (P ≤ 0.05 or P ≤ 0.01) except days to striga emergence, number of emerged striga at 59 d.a.p., striga severity at 85 d.a.p., and area under the flowering striga progress curve.

Coefficients of correlation between performance of lines *per se* and their GCA were strong for most traits, ranging from 0.78 (P ≤ 0.05) to 0.98 (P ≤ 0.01; data not shown). However, the correlations between SCA and F_2 performance were also important (r ≥ 0.5, P < 0.01) for striga counts, striga severity, area under striga number or severity progress curves, area under flowering striga progress curve, days to anthesis, plant height, and panicles per plant, pointing to the significant contribution of non-additive effects to the expression of these traits. Heterosis for all characters was moderately correlated with SCA effects (correlation coefficients between 0.62 and 0.91, P < 0.01).

Among the parents, 'Framida' and 'IS 9830' were good general combiners for low area under striga number and severity progress curves, and grain yield (Fig. 2). Lines '555' and 'N 13' also revealed GCA for low striga emergence and severity, but negative GCA effects for grain yield. The striga-tolerant cultivar 'Seredo' had the highest positive GCA effect for grain yield, combined with GCA for increased area under the striga number progress curve but reduced striga vigour and therefore reduced area under the striga severity progress curve. Among the striga-susceptible parents, 'E 36-1' was unique in that it revealed positive GCA for grain yield. The largest GCA for early anthesis was shown by line 'IS 9830'. 'N 13' had the

Table 5: Estimated variance components (± standard error) and broad–sense heritabilities (h^2) of parents (P) and F_2 populations (F_2) for selected traits, combined across the four locations (E)

Trait[1]	Source of variation P	F_2	P × E	F_2 × E	Error	h^2 (90% confidence interval) Parents	F_2 populations
DSE	5.0** ± 3.0	1.4** ± 0.5	3.8** ± 1.8	0.7* ± 0.5	2.7 ± 0.1	*0.76* (0.05; 0.91)	*0.63* (0.33; 0.78)
DSF	10.2** ± 5.9	6.5** ± 2.0	7.3** ± 3.1	4.6** ± 1.2	4.0 ± 0.2	0.78 (0.14; 0.92)	0.75 (0.56; 0.85)
S59	32.8** ± 19.4	20.8** ± 7.0	21.1** ± 11.2	16.5** ± 4.9	19.1 ± 0.9	*0.77* (0.08; 0.92)	*0.70* (0.46; 0.82)
S85	532.2** ± 285.5	174.4** ± 58.6	302.4** ± 114.3	185.9** ± 40.7	109.3 ± 5.0	*0.84* (0.36; 0.94)	*0.70* (0.47; 0.82)
V85[2]	5.9** ± 2.9	3.1** ± 0.8	0.6+ ± 0.6	0.7** ± 0.3	1.5 ± 0.1	*0.92* (0.68; 0.97)	*0.85* (0.73; 0.91)
SV85[4]	185.7** ± 103.8	80.9** ± 25.2	124.9** ± 49.8	51.7** ± 14.7	54.4 ± 2.5	*0.81* (0.23; 0.93)	*0.75* (0.56; 0.85)
ASNPC	55.6** ± 31.2	21.8** ± 7.0	42.4** ± 15.1	19.8** ± 4.4	12.2 ± 0.6	*0.80* (0.22; 0.93)	*0.73* (0.52; 0.84)
ASVPC[5]	159.1** ± 90.4	72.3** ± 21.7	123.0** ± 46.0	38.6** ± 11.2	42.5 ± 1.9	*0.79* (0.19; 0.93)	*0.78* (0.61; 0.87)
AFSPC	33.8** ± 21.7	17.1** ± 5.8	31.9** ± 15.6	5.4+ ± 4.2	24.2 ± 1.1	*0.71* (0.00; 0.90)	*0.70* (0.46; 0.82)
DAN	45.5** ± 21.7	9.7** ± 2.7	10.3** ± 3.3	6.4** ± 1.1	1.6 ± 0.1	*0.94* (0.76; 0.98)	*0.83* (0.69; 0.90)
PHT	720.5** ± 378.9	169.0** ± 52.7	441.5** ± 136.8	169.8** ± 30.3	51.5 ± 2.3	*0.85* (0.42; 0.95)	*0.75* (0.56; 0.85)
GY[5]	597.5** ± 301.3	358.7** ± 95.4	246.7** ± 82.9	150.5** ± 27.8	52.1 ± 2.4	*0.89* (0.56; 0.96)	*0.88* (0.78; 0.93)
H/P[3]	0.6* ± 0.5	0.6** ± 0.2	1.4** ± 0.5	0.4** ± 0.1	0.3 ± 0.1	*0.58* (0.00; 0.85)	*0.78* (0.60; 0.87)
GW/H	81.3** ± 41.7	40.6** ± 11.5	38.7** ± 12.9	26.9** ± 4.8	7.9 ± 0.4	*0.88* (0.51; 0.96)	*0.82* (0.68; 0.89)

+, *, ** Significant at the P = 0.1, P = 0.05 and P = 0.01, respectively.

[1] DSE = Days after planting (d.a.p.) to striga emergence; DSF = days to striga flowering; Sn = emerged striga plants/m^2 at *n* d.a.p.; Vn = striga vigour at *n* d.a.p.; SVn = striga severity at *n* d.a.p.; ASNPC = area under striga number progress curve; ASVPC = area under striga severity progress curve; AFSPC = area under flowering striga progress curve; DAN = days to sorghum anthesis; PHT = sorghum plant height; GY = sorghum grain yield; H/P = panicles per sorghum plant; GW/H = grain weight per sorghum panicle;

[2, 3] Variance components multiplied by 10 and 100, respectively.

[4, 5] Variance components divided by 100 and 10, respectively.

largest positive GCA, and line '555' the largest negative GCA for plant height (data not shown).

SCA for both low striga emergence and increased grain yield were displayed in the F_2s derived from 'Framida' × '555', 'Framida' × 'Seredo', 'Framida' × 'M 35–1', '555' × 'Seredo', 'N 13' × 'IS 1037', and 'IS 9830' × 'E 36–1' (data not shown).

Relationships among traits

High grain yield was associated with late striga emergence (coefficients of genetic correlation $r_G = 0.76$ and 0.65 in lines and F_2s, respectively), late striga flowering ($r_G = 0.84$ and 0.81) and low striga vigour ($r_G = -0.77$ and -0.76; all coefficients exceeding their standard errors twice). Correlations were moderate between grain yield and striga severity at 85 d.a.p. ($r_G = -0.49$ and -0.46 in lines and F_2s, respectively), area under the striga severity progress curve ($r_G = -0.55$ and -0.44), and area under the flowering striga progress curve ($r_G = -0.55$ and -0.49; all coefficients exceeding their standard errors at least once). The correlations between grain yield and emerged-striga numbers or area under the striga number progress curve were rather low. High grain yield was not related to sorghum plant height, and only weakly associated with early anthesis in the F_2 populations ($r_G = -0.33$). There was no significant relationship between days to sorghum anthesis and number of striga plants, striga vigour or striga severity.

Relationship between striga resistance under field conditions and *in vitro* stimulation of striga seed germination

High *in vitro* stimulation of striga seed germination by the F_1 hybrids (averaged over reciprocal crosses and striga populations from Mali and Niger) was associated with early striga emergence and flowering, and high emerged-striga numbers and vigour in the corresponding F_2s in the Kenyan environments (Table 6). The correlations were lower and even partly non-significant for the Malian compared with the Kenyan sites.

Discussion

The experimental series presented here shows that satisfactory accuracy can be obtained in striga resistance screening when experimental fields are artificially infested or carefully selected for uniformity of striga infestation, and if using a large number of replications, the specific plot layout and appropriate resistance measures such as area under striga severity progress curves.

The superior yield of the F_2 populations over the corresponding homozygous parents points to the potential merit of heterozygous cultivars for striga-infested areas in Mali and Kenya. Earlier anthesis and increased plant height compared with the parents are other characteristic effects of heterozygosity in sorghum (Bartel 1949, Kirby and Atkins 1968, Blum et al. 1990, Haussmann et al. 1998, 1999). The reaction to striga of the F_2 populations relative to their parents varied with the parental combination. Ramaiah (1984) also reported heterosis for striga resistance in sorghum to be positive or negative, depending on the cross. Further generation means analyses of selected parental combinations are necessary to elucidate the mode of gene action in these materials. The level of the F_2 heterosis also depended on the test location. With regard to grain yield, higher F_2 heterosis estimates were obtained at Cinzana and Alupe, the two sites with the highest striga emergence. The F_2 populations were therefore relatively more tolerant to high striga infestation than the parents. Similarly, Hess and Ejeta (1992) and Kling et al. (2000) reported that hybrid vigour can provide a degree of tolerance to striga in sorghum and maize (*Zea mays* L.), which is reflected in reduced yield depression under conditions of severe striga infestation.

Significant and exploitable quantitative-genetic variation existed among parental lines and among F_2 populations for striga resistance and grain yield. In contrast to sorghum, Berner et al. (1995) reported only limited genetic variation in maize and low heritabilities for striga emergence traits under field conditions. However, resistance (low striga emergence) to

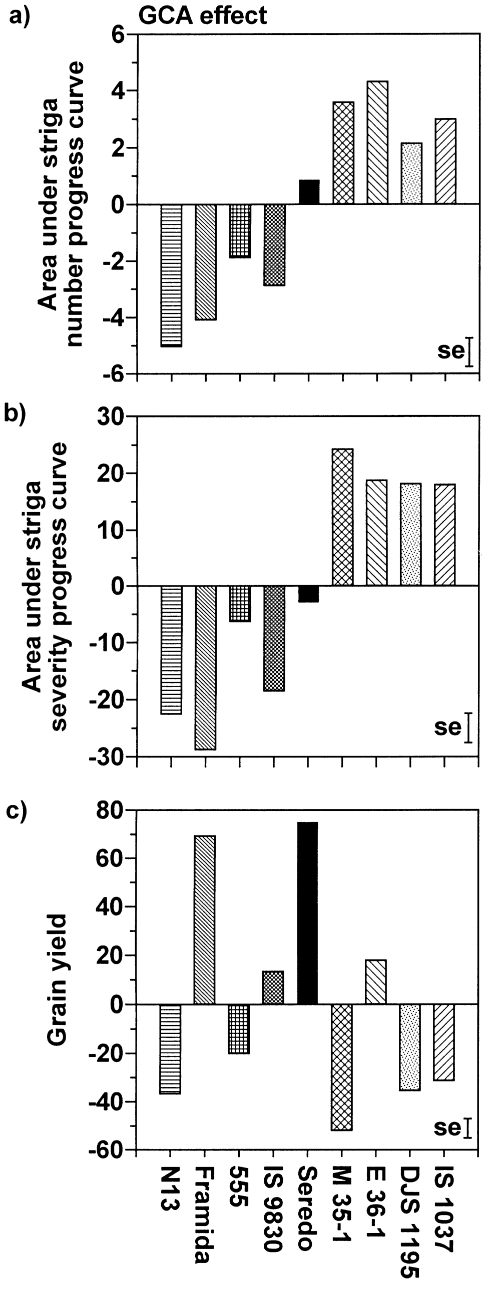

Fig. 2: GCA of nine sorghum lines for striga number, striga severity and grain yield

striga in maize has recently been improved by introgressing resistance genes from teosinte (*Zea diploperennis*), a wild relative of cultivated maize (Kling et al. 2000).

The genotype × environment interaction was another important source of variation for most striga emergence and development traits and for sorghum grain yield. Resistance identified at one location must therefore be verified at other sites to assess its utility for a wide use in breeding programmes. Significant genotype × environment interactions for striga resistance traits have previously been described in sorghum (Ramaiah 1987, Omanya et al. 2000) and maize (Kim 1994).

Both GCA and SCA effects contributed significantly to the genetic variation for the striga resistance traits examined, as was reported earlier by Hess and Ejeta (1992), Ramaiah (1984, 1987) and Kulkarni and Shinde (1985a, 1985b, 1987). Rather strong correlations between line performance *per se* and GCA indicate a preponderance of additive genetic effects and the potential efficiency of early selection among breeding lines to improve their utility for hybrid or synthetic breeding. However, owing to significant SCA effects, evaluation of test crosses would be important in later stages of a hybrid breeding programme. In the present study, SCA effects were more important for striga resistance traits than for grain yield. In contrast, Shinde and Kulkarni (1982) reported additive genetic effects to be more important for emerged-striga number, while dominance effects contributed most to the variation in grain yield under *S. asiatica* infestation at two fertility levels in India. Kim (1994) conducted a 10 × 10 diallel study with maize over 5 years at Mokwa (Nigeria). Despite significant SCA effects the author found a preponderance of additive-genetic effects for the '*S. hermonthica* tolerance rating' (= a host plant damage rating). Non-additive gene action played a major role in the inheritance of striga emergence counts.

Line 'N 13' proved to be an outstanding source of resistance, especially in terms of low emerged-striga numbers, but it is low-yielding, and its durra grains do not fulfil the quality requirements of African farmers. When incorporating the resistance of 'N 13' into adapted materials, mapping of quantitative trait loci (QTL) for striga resistance followed by marker-assisted backcrossing could aid the breeder to select simultaneously for striga resistance genes (foreground selection) and against the otherwise undesirable genetic background of 'N 13' (background selection; Hospital and Charcosset 1997).

One shortcoming of the present study is the lack of information on the entries' performance under striga-free conditions at the four locations. This deficiency may have caused a bias in the observed relationships among traits. For example, low

Table 6: Phenotypic correlations between the *in vitro* germination distance of striga in F_1 hybrids and field data for striga resistance of the corresponding F_2 populations in Mali, Kenya, and across the four locations

Country	Coefficient of correlation between *in vitro* germination distance and[1] DSE	DSF	S59	S85	V85	SV85	ASNPC	ASVPC	AFSPC
Mali	−0.56**	−0.43**	−0.08	−0.07	0.42*	0.07	−0.06	0.08	0.09
Kenya	−0.38*	−0.53**	0.32	0.57**	0.48**	0.55**	0.54**	0.54**	0.55**
Combined	−0.61**	−0.51**	0.08	0.25	0.48**	0.35*	0.23	0.35*	0.35*

*, ** Significant at P = 0.05 and P = 0.01, respectively.

[1] DSE = days to striga emergence; DSF = days to striga flowering; Sn = emerged striga plants/m^2 at *n* days after planting (d.a.p.); Vn = striga vigour at *n* d.a.p.; SVn = striga severity at *n* d.a.p.; ASNPC = area under striga number progress curve; ASVPC = area under striga severity progress curve; AFSPC = area under flowering striga progress curve.

grain yield might have been due to susceptibility to striga, lack of adaptation, and/or low yield potential. The three factors could only have been separated with substantial additional experimental effort. Therefore, the following interpretations of the genetic correlations should be treated with caution. The observed association between high grain yield and late striga emergence may confirm the recent results of Gurney et al. (1999) that late striga attachment alleviates the impact of the parasite on the host. It may also reflect antibiosis. Press et al. (1999) suggested that not only the time of attachment *per se* is important but also the proportion of the life cycle that the cereal has completed prior to attachment. The authors concluded that a combination of delayed attachment and the use of early cultivars may hold promise as part of an integrated control programme. In our study, high grain yield under striga infestation was only weakly associated with early sorghum anthesis in the F_2s, and there was no relationship between the two traits in the parents. Sorghum anthesis date was not related to any striga character. The relationship between sorghum anthesis and striga resistance or tolerance seems, therefore, to depend on the materials under study.

Low grain yield was more strongly associated with a high striga vigour, striga severity, areas under striga severity and flowering striga progress curves than with striga counts. Because of their close relationship to the actual grain yield performance, these characters must be considered as important selection traits. Conveniently, the striga vigour can be scored very quickly. However, more data involving other genetic materials are required to prove the relation between grain yield and striga vigour or severity.

Gurney et al. (1999, 2000) reported a non-linear relationship between sorghum grain production and striga biomass. In their studies, a very large reduction in striga biomass was needed before there was any significant improvement in host grain yield. The authors suggested that the metabolic perturbations caused by the parasite outweigh the direct loss of resources to the parasite. It was concluded that mechanisms that lower the numbers of emerged striga can contribute to a reduction of the density of the soil seed bank in the medium or long-term, but that they are unlikely to have any short-term impact on crop yield (Press et al. 1999). In contrast, our results show very clearly that the relationship between sorghum grain yield and area under the striga severity progress curve (a parameter which is closely related to striga biomass) is largely affected by the striga resistance or tolerance level and the yield potential of the entries tested. For example, 'Framida' and 'N 13' both had low area under striga severity progress curve values, but 'Framida' yielded much better owing to its better adaptation to the test environments and a higher yield potential (Fig. 1). 'Framida', 'Seredo', the local cultivar 'Wagita' and the F_2s derived from the crosses 'Framida' × '555', 'IS 9830' × 'Seredo', 'IS 9830' × 'E 36-1' and 'Seredo' × 'E 36-1' all yielded at a similar level while having different area under striga severity progress curve values. The superior entry for both grain yield and striga resistance was the F_2 population derived from a cross of the striga-resistant line 'Framida' with the striga-tolerant cultivar 'Seredo', pointing to the importance of combining resistance with tolerance in breeding programmes. Such a strategy is also being followed in breeding striga-resistant maize (DeVries 2000, Kling et al. 2000). Since it is unlikely that cultivars can be developed which are totally striga free under conditions of high striga infestation, tolerance is needed to minimize grain yield reduction. In contrast to Press et al. (1999), it is therefore concluded that a combination of resistance (or any other mechanism that lowers the number of emerged striga) with striga tolerance is likely to be effective in reducing the striga seed bank in the long term and to achieve short-term impact through improved crop yield.

The positive relationship between low *in vitro* stimulation of striga seed germination and striga resistance under field conditions confirms that the agar-gel assay can be a useful indirect test for striga resistance in breeding. In trials with 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 opposite was observed in the present study. The relationship between germination distance in the agar-gel assay and resistance under field conditions therefore depends on the genetic materials and climatic factors in different years. In addition, specific conditions, such as an environmental-stress-induced ethylene production by microorganisms or the cultivated crop could render the low-stimulant character less effective in certain site/season combinations (K. Wegmann, pers. comm.).

In conclusion, the yielding superiority of selected F_2 populations over parents and local cultivars underlines the potential impact of heterozygous sorghum cultivars for striga-infested areas in Kenya and Mali. In a hybrid breeding programme, the choice of suitable parent lines for experimental hybrids would be crucial, since the performance of the F_2 populations depends on the parental combination for both reaction to striga and grain yield. In traditional sorghum-growing areas, where the prerequisites for successful hybrid marketing are not fulfilled, synthetics could be produced from components with superior combining ability and high outcrossing rates. While taking advantage of heterotic effects, such cultivars can be regrown by the farmers for a few seasons. Significant genotype × environment interaction variances underline the necessity to evaluate breeding materials under a broad range of environments in order to identify stable, resistant cultivars. Tight correlations between performance of lines *per se* and their GCA confirmed the preponderance of additive genetic effects for striga emergence, vigour and severity, and sorghum grain yield and morphological traits. The significant contribution of SCA effects to the performance of the F_2 populations for the majority of traits indicates that extensive test-cross evaluation would be essential in later stages of hybrid breeding. The two low-stimulant-producing lines 'Framida' and 'IS 9830' excelled in the best GCA effects for both low striga emergence and development, and high grain yield. 'Seredo' is an excellent source of striga tolerance under high striga infestation. A combination of resistance with striga tolerance is recommended to achieve short-term impact in terms of low striga emergence and high grain yield in striga-infested areas in Kenya and Mali.

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