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Utility of indirect and direct selection traits for improving Striga resistance in two sorghum recombinant inbred populations

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Abstract

Breeding of sorghum (*Sorghum bicolor* L. Moench) for resistance to the parasitic weed *Striga hermonthica* (Del.) Benth. has been hampered by the difficulty of evaluating host resistance in the field and lack of reliable screening techniques. Therefore, we investigated the value of various indirect and direct measures of Striga resistance as selection traits. Two sorghum recombinant inbred populations of 226 $F_{3:5}$ lines each were developed from the crosses (1) IS 9830 × E 36-1 and (2) N 13 × E 36-1. Striga-resistant line IS 9830 is characterized by low stimulation of Striga seed germination, whereas Striga-susceptible line E 36-1 produces germination stimulants in abundance. Line N 13 possesses "mechanical" resistance and probably also an antibiosis mechanism. Resistance was assessed in 1997 and 1998 using in vitro agar-gel assays with Striga seeds from Kenya, Mali, and Niger, pot trials in the respective three countries, and field experiments in Kenya and Mali. The agar-gel assay proved to be a useful, precise and fast indirect selection method to screen for sorghum entries with the low-stimulant character. However, correlation analysis showed that this resistance mechanism was ineffective in some environments, especially in Kenya, pointing to the necessity of field evaluation. Because of low heritability estimates and moderate to low correlations to Striga resistance under field conditions, pot screening appeared to be of limited use in breeding programs. The field trials confirmed the effectiveness of several direct measures of Striga resistance in sorghum: emerged Striga counts, Striga severity index, and area under the Striga number or severity progress curves. A two-row plot field layout with an empty row between plots, coupled with artificial infestation of test rows, lattice design and six replications offered an improved screening procedure that achieved high heritability. Significant genotype × environment interactions in the field experiments stress the importance of multi-locational trials to achieve stable Striga resistance.

Keywords: *Striga hermonthica*; *Sorghum bicolor*; Resistance breeding; Quantitative genetic parameters

1. Introduction

The parasitic weed *Striga hermonthica* (Del.) Benth. is a major constraint to sorghum (*Sorghum bicolor* L. Moench) production in semi-arid sub-Saharan Africa. Striga damage is particularly intense when it attacks sorghum crops that are already under moisture and

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nutrient stress. The ensuing grain yield reductions negatively impact resource-poor subsistence farmers (Doggett, 1965; Mumera, 1983; Sauerborn, 1991).

Host-plant resistance in adapted, productive cultivars is a central component of integrated Striga management. Previous research has shown that there is significant genetic variation for Striga resistance in sorghum (Mumera, 1983; Ramaiah, 1983, 1991; Obilana et al., 1991; Ejeta et al., 1997). Thus selection for this trait should be feasible. However, advances in breeding have been limited due to inadequate information on the genetics of Striga resistance and difficulty of evaluating resistance in the field.

The genetics of Striga resistance and methodologies for breeding Striga-resistant sorghums with special emphasis on direct field evaluation have recently been reviewed by Haussmann et al. (2000a,b). Among indirect selection methods, the agar-gel assay developed by Hess et al. (1992) is the most popular method to screen large numbers of entries for their capacity to stimulate Striga seed germination. It has been modified in order to evaluate stimulation of haustorium formation and to observe post-attachment interactions between host and parasite (Ejeta et al., 2000; Mohamed et al., 2003). A paper roll assay allows longer term observation of post-infection resistance mechanisms but requires refinement to be usable on a large scale (Ejeta et al., 2000).

Published experimental results on the utility and effectiveness of various indirect and direct selection methods for improving Striga resistance in sorghum are rare. We therefore undertook to (i) examine the genetic variance of two sorghum recombinant inbred populations (RIPs) and the estimated heritabilities for Striga resistance traits using agar-gel assays, pot experiments, and field trials with improved experimental layout; (ii) analyze the relationships between the various Striga resistance measures in both RIPs; and (iii) estimate the correlated selection gain for the most promising indirect selection trait as compared to direct selection under field conditions.

2. Materials and methods

2.1. Genetic materials and experimental design

Genetic materials consisted of two RIPs of sorghum, each comprising 226 $F_{3:5}$ recombinant inbred lines derived from the crosses (1) IS 9830 × E 36-1 and (2) N 13 × E 36-1. The Striga-resistant line IS 9830 produces low amounts of Striga germination stimulants, as opposed to the Striga-susceptible line E 36-1 (Haussmann et al., 2000b, 2001a,b). N 13 possesses ''mechanical'' resistance (Maiti et al., 1984) and probably an additional ''antibiosis'' mechanism since it was observed to support equal numbers of subterranean attached Striga but significantly fewer emerged Striga than susceptible line E 36-1 in a preliminary pot trial conducted at Samanko (Hess and Haussmann, unpublished). To develop the RIPs, F_1 plants from the two crosses were selfed and 226 F_2 plants per cross advanced by single-seed descent to the F_4 generation. The F_4 plants were multiplied by selfing 40 panicles per line, and the resulting F_5 seed was bulked. The F_3-derived bulks in F_5 are hereafter referred to as $F_{3:5}$ lines. The development of these materials has been described in detail by Haussmann et al. (2001b). To determine host resistance to Striga, each RIP was divided into two sets—Set 1: 116 $F_{3:5}$ lines tested in 1997; Set 2: 110 $F_{3:5}$ lines tested in 1998. Set 1 was evaluated together with the two parental lines and three checks. The latter were SRN 39 (Striga-resistant), Seredo (Striga-tolerant), CSM 335 or Tiémarifing (both Striga-susceptible) (Ramaiah, 1984, 1987; Sherif and Parker, 1990; Haussmann et al., 2000b). Set 2 was assessed together with the two parents and nine checks (Seredo, SRN 39, Tiémarifing) and the three most resistant and three most susceptible $F_{3:5}$ lines from Set 1). Hence, the agar-gel assay, pot, and field experiments each consisted of 121 entries arranged in an 11 × 11 lattice with six replications.

2.2. Agar-gel assay

The agar-gel assay developed by Hess et al. (1992) was used to evaluate RIP 1 for stimulation of Striga seed germination. Haussmann et al. (2001b) described our methodology in detail, so it is only summarized here. Striga seeds were harvested from parasites infesting sorghum in the 1996 and 1997 seasons from Kibos in Kenya, Samanko in Mali, and Bengou in Niger. Striga seeds were surface-sterilized and preconditioned for 10 to 12 days at 28 °C in the dark. About 4500 preconditioned Striga seeds were pipetted into each Petri dish. About 25 ml autoclaved 0.7% (w/v) water-agar, cooled but not yet solidified, was

poured into each dish such that a uniform distribution of Striga seed throughout the agar was achieved. The root (about 1.5 cm long) of a 24 h old sorghum seedling was inserted into the solidifying agar near one edge of the plate, with the root tip pointing across the plate. After 5 days of incubation at 28 °C in the dark, germination of Striga seed was easily visible through the bottom of the plate using a dissecting microscope. The maximal germination distance (GD5) was recorded, i.e., the distance between the host root and the most distantly germinated Striga seed. Plates with abnormal growth of the sorghum seedling were treated as missing observations.

2.3. Pot experiments

Twelve liter pots were arranged in serpentine order in single rows at Kibos and double rows at Samanko and Sadoré on raised beds with footpaths of 1 m between rows. Within rows, pots were placed 0.5 m apart. To facilitate drainage, three holes were drilled in the bottom of each pot and a layer of gravel was placed in each pot before filling it with soil mixtures and artificially infesting with viable Striga seeds (Table 1). Striga infestation in the 1998 trials was reduced following the observation in the first year that under high infestation level, highly susceptible sorghum entries supported low numbers of emerged Striga due to strongly reduced host vigor. To infest the pots, a mixture of Striga seeds collected in the preceding season and fine dry sand (250 g) was incorporated in the top 3 cm soil of each pot. Pots were filled to 2 cm below the top to facilitate watering. Pots were left to stand for 7 days with intermittent watering to precondition Striga seeds. To control shootfly (*Atherigona soccata* (Rondani)) and stemborers (*Chilo partellus* (Swinhoe), *Sesamia calamistis* Hmps.), carbofuran (Furadan) was applied at sowing of sorghum seeds. The non-infested control pots sown with Striga-susceptible cultivars were included at all sites to verify that the soils used were free of natural Striga infestation. After sowing, water was provided as needed (three times a week in Kenya and daily at Samanko and Sadoré). Thinning was performed to leave a stand of three plants in triangular arrangement or single plants. Three plants per pot were used to account for the genetic variation within the $F_{3:5}$ lines, and thereby to reduce the error variation. But it was found in 1997 that, especially in West Africa where sorghum plants grew taller and larger due to longer day length, too much competition resulted among the three plants in one pot and biased their reaction to Striga. The number of sorghum plants per pot was reduced to one in 1998. Diammonium phosphate and urea fertilizers were applied at sowing and after thinning, respectively, to provide the agronomic recommendation of 40 kg N ha^{-1} in Kibos, and 30 and 44 kg N ha^{-1} at Samanko and Sadoré, respectively.

2.4. Field experiments

Both RIPs were evaluated at Kibos and Alupe in Kenya, and at Samanko and Cinzana in Mali, during 1997 (Sets 1) and 1998 (Sets 2, Table 2). At Alupe, both long rains (LR) and short rains (SR) were used for the trials. Each field plot consisted of two rows separated from the neighboring entries by one empty row. On-station fields at Kibos, Alupe, and Samanko were artificially infested with Striga. Striga seed was harvested at each location in 1995 and 1996. Five sorghum seeds were placed into each sowing hole or "hill" at about 5 cm depth. Thinning was performed after 3 weeks to one plant per hill. Plants were spaced at 75 cm × 15 (or 20) cm in Kenya, and 80 cm × 20 cm in Mali. Diammonium phosphate was applied at sowing and urea fertilizers were applied after thinning as for pot trials.

Table 1
Details of pot experiments for both RIPs

Experimental detail	Kibos'97	Sadoré'97	Kibos'98	Samanko'98	Sadoré'98
Date of planting	21 May	2 May	18 April	12 June	29 June
Infestation (viable Striga seeds per pot)	16000	16000	6000	7000	7000
Media mixture	1/3 sand; 2/3 soil	3/6 sand; 2/6 clay; 1/6 organic manure	1/3 sand; 2/3 soil	3/8 soil;3/8 sand; 2/8 composition	Same as in Sadoré'97
Sorghum plants per pot	3	3	3	1	1

Table 2
Details of field experiments

Site characteristics and experimental details	Kenya			Mali	
	Kibos LR[a]	Alupe LR	Alupe SR[a]	Samanko R[a]	Cinzana R
Altitude (m)	1214	1189		358	285
Latitude	00°04′S	00°29′N		12°31′N	13°15′N
Longitude	34°48′E	34°08′E		08°04′W	05°57′W
Soil type	Retroentric planosol; sandy loam	Orthic ferrosol, part. Petroferric phase with orthic acrisols		Tropical ferruginous soil, leached; sandy loam	Ferruginous soil, leached, rich in sesquioxid; sandy loam
Set 1 of each RIP (1997)					
Planting dates	29 March	28 March	27 August	17 July	17 July
Infestation (viable Striga seeds per m^2)	40000	43000	43000	84000	Natural
Plot size/Striga counting area (m^2)	3.15	2.94	2.94	4.48	4.48
Total rainfall (mm)	541	671	1285	750	633
Set 2 of each RIP (1998)					
Planting dates	8 April	8 April	10/21 September[b]	1 July	16 July
Infestation (viable Striga seeds per m^2)	40000	40000	40000	43000	Natural
Striga counting area (m^2)	3.825	4.275	4.275	4.48	4.48
Total rainfall (mm)	657	784	584	982	683

[a] LR: long rains (March to July); SR: short rains (September to January); R: rains (June to September).
[b] Planting date for RIP 1/RIP 2.

2.5. Data assessment

Considering a macro-environment as a combination of one evaluation site and one season, data were assessed from a total of two pot (Kibos and Sadoré) and five field macro-environments (Kibos LR, Alupe LR and SR, Samanko, and Cinzana) for Sets 1 (evaluated in 1997) and three pot (Kibos, Sadoré, and Samanko) and similarly five field macro-environments in Sets 2 (evaluated in 1998) of both RIPs. The following traits are being reported from the pot and/or field trials:

- *Striga resistance traits*

Sn number of emerged Striga plants per pot or m^2 at *n* days after sowing (d.a.s.). Counts were performed at 2-week intervals starting 2–3 weeks after the first Striga plant emerged in the trials. A total of four counts at Cinzana and five counts at other sites were carried out in each experiment.

Vn mean Striga vigor score (1–9) in each pot or field plot at *n* d.a.s. The Striga vigor score is based on the visual assessment of mean Striga height and number of branches, and is scored at each counting date for each pot or field plot on a 1–9 scale (Haussmann et al., 2000a,b).

SVn Striga severity at *n* d.a.s. (emerged Striga count multiplied by its respective mean Striga vigor score) in each pot or field plot.

ASNPC area under Striga number progress curve in each pot or field plot (computed from emerged Striga counts by adapting the formula for area under the disease progress curve, AUDPC (Shaner and Finney, 1977); see Haussmann et al. (2000a,b)).

ASVPC area under Striga severity progress curve in each pot or field plot (for details, see Haussmann et al. (2000a,b)).

- *Sorghum characters*

DAN number of d.a.s. to 50% anthesis of the sorghum plants in the field.

GY grain yield (g m^{-2}), based on two-row field plots, assessed only in the field trials.

PHT average height (cm) of sorghum plants at physiological maturity in each field plot.

2.6. Statistical analyses

Analysis of variance for raw data was done according to the lattice design, using PLABSTAT software (Utz, 1998). Extreme outliers, as defined by Anscombe and Tukey (1963), were declared as missing values only when there was an explanation in the field books. The latter were iteratively calculated according to Yates (1933) and Healey and Westmacott (1956), such that the error variance became minimal. Effective error variances were estimated as outlined by Cochran and Cox (1957). Operative repeatabilities for the 116/110 $F_{3:5}$ lines of Sets 1/2 of the RIPs were calculated with lattice-adjusted plot values as follows: $\text{rep}\,(\%) = (\sigma_g^2/(\sigma_g^2 + \sigma_e^2/R)) \times 100$, where σ_g^2 and σ_e^2 are the estimated genetic and error variances, respectively, and R is the number of replications.

Combined analyses across locations (or geographic sources of Striga in the agar-gel assay) but within years were computed with lattice-adjusted entry means from each individual environment or experiment. Experimental locations and Striga populations (sources) were regarded as fixed effects. All other effects were considered as random variables and assumed to be independently and normally distributed. The F-max test, outlined by Köhler et al. (1984), revealed heterogeneity of error variances for almost all traits. Thus a conservative F-test of the entry× environment (or Striga sources) interaction variance was made with $t - 1$ and n' degrees of freedom, where t designates the number of entries and n' the number of error degrees of freedom in the experiment with the highest error variance (Cochran and Cox, 1957). Broad-sense heritabilities were estimated on an entry mean basis (Hallauer and Miranda, 1981), with 90% confidence intervals (Knapp et al., 1985).

Coefficients of phenotypic correlation were calculated among the agar-gel assays, pot, and field experiments. Estimates of genetic correlation among traits were computed as outlined by Mode and Robinson (1959), based on lattice-adjusted entry mean values. The efficiency of indirect selection was determined by computing the correlated gain (CR_x) in the target trait x (i.e., Striga resistance under field conditions) that resulted from selection for the indirect trait y (i.e., germination distance in the agar-gel assay) according to the following formula (Falconer, 1989): $CR_x/R_x = r_g h_y/h_x$, where R_x is the gain in the target trait x if it is directly selected for, h_x and h_y the square roots of broad-sense heritability of the target and indirect trait, respectively, and r_g the coefficient of the genotypic correlation between target and indirect trait.

3. Results

3.1. Agar-gel assay

Detailed results from the agar-gel assays have been published by Haussmann et al. (2001b). They demonstrated that low stimulation of *S. hermonthica* seed germination in RIP 1 was due to one recessive major gene and several minor genes. In addition, the Kenyan Striga proved more sensitive to the stimulation by the tested sorghum entries, resulting in higher mean germination distances compared to Striga populations from Mali or Niger. In this paper, we will present the correlations between GD5 and Striga resistance traits under field conditions for RIP 1. In this context, it is important to note that the genetic variance among the entries for germination distance was highly significant in all individual experiments, and in the combined analysis across geographic Striga sources.

3.2. Pot experiments

3.2.1. Intensity of Striga infestation and accuracy of the experiments

Mean numbers of emerged Striga at around 80–90 d.a.s. were very high at Kibos, especially in the first year, moderate in Samanko, and comparatively low in Sadoré (Table 3). No Striga emerged in the control pots planted with Striga-susceptible sorghum varieties. Hence all the emerged Striga resulted from artificial infestation. Average Striga vigor, on the other hand, was highest at Sadoré. The $F_{3:5}$ lines differed significantly at each location ($P = 0.05$ or $P = 0.01$) for the majority of traits, with repeatabilities ranging between 44 and 76% for emerged Striga count, between 22 and 55% for the Striga vigor, between

Table 3
Environmental means, operative repeatabilities (rep (%)) and statistical significance of genotypic variance in the 121 entries of Sets 1 and 2 of RIPs 1 and 2 for selected Striga resistance traits during the pot experiments at Kibos (Kenya), Sadoré (Niger), Samanko (Mali) in 1997 and 1998

RIP[a]	Set (year)	Trait[b]	Kibos (Kenya)		Sadoré (Niger)		Samanko (Mali)	
			Mean	Rep (%)	Mean	Rep (%)	Mean	Rep (%)
1	1 (1997)	S89	91.8	49.3**	11.4	44.3**	–[c]	–
		V89	2.0	30.9*	5.8	54.6**	–	–
		SV89	205.8	43.2**	71.6	51.5**	–	–
		ASNPC[d]	20.0	47.3**	7.1	59.8**	–	–
	2 (1998)	S92	44.1	43.6**	13.5	32.8*	37.2	57.8**
		V92	3.1	24.3+	7.1	21.8 ns	3.9	53.4**
		SV92	148.0	49.4**	101.1	37.4*	154.5	61.1**
		ASNPC	17.1	47.2**	7.4	62.2**	12.6	58.6**
2	1 (1997)	S80	39.8	45.6**	10.8	59.5**	–	–
		V80	3.0	49.8**	6.8	54.3**	–	–
		SV80	171.0	57.3**	83.5	58.8**	–	–
		ASNPC[d]	19.0	51.1*	7.7	61.4**	–	–
	2 (1998)	S78	15.5	57.3**	12.6	59.0**	27.7	76.2**
		V78	1.9	33.3*	4.0	41.7**	3.2	36.3**
		SV78	37.3	49.8**	56.0	55.3**	102.9	79.5**
		ASNPC	9.3	61.3**	8.3	62.6**	13.4	84.9**

[a] RIP 1: derived from cross IS 9830 × E 36-1; RIP 2 derived from cross N 13 × E 36-1.
[b] Sn: emerged Striga number per m^2 at *n* days after sowing (d.a.s.); Vn: Striga vigor at *n* d.a.s.; SVn: Striga severity at *n* d.a.s.; ASNPC: area under Striga number progress curve.
[c] Not assessed.
[d] Means of ASNPC are divided by 10^2.
+ Genetic differences among the 121 sorghum entries significant at the 0.1 probability level.
* Genetic differences among the 121 sorghum entries significant at the 0.05 probability level.
** Genetic differences among the 121 sorghum entries significant at the 0.01 probability level.

37 and 80% for Striga severity, and between 47 and 85% for ASNPC. Overall, repeatabilities for Striga resistance traits in the pot trials were slightly higher in RIP 2 than in RIP 1.

3.2.2. Variance components and heritabilities

Despite moderate or high repeatabilities at the individual pot trial sites, genotypic differences among the $F_{3:5}$ lines of RIP 1 were not statistically significant in the combined analysis across locations for all Striga resistance traits in both sets, except for Striga vigor score at 80 d.a.s. in Set 2. On the other hand, the $F_{3:5}$ line × location interaction variances were much larger than the genotypic variances and highly significant for all traits (data not shown). Consequently, heritability estimates were very low, reaching a maximum of 0.26 for the Striga vigor score at 80 d.a.s. in Set 2 of RIP 1. In the combined analysis across locations for RIP 2, genotypic variances for Striga resistance traits were significant only in Set 2. As with RIP 1, the $F_{3:5}$ line × location interaction variances were much larger than the genotypic variances and highly significant for all traits. Heritability estimates for RIP 2 reached a maximum of 0.43 for the area under Striga number progress curve in Set 2 of RIP 2 (data not shown).

3.3. Field trials

3.3.1. Environmental means and accuracy

Striga infestation was intense at all sites in both RIPs (Table 4). The highest infestation level was observed in Set 1 of RIP 1 at Alupe, with a mean of 91 emerged Striga plants per m^2 at 95 d.a.s. The average Striga vigor ranged from 1.2 (RIP 1, Set 1,

Table 4
Means, operative repeatabilities (rep (%)), and statistical significance of genotypic variance among the 121 entries of each set for selected traits in the field experiments

RIP[a]	Set (year)	Trait[b]	Kibos LR		Alupe LR		Alupe SR		Samanko R		Cinzana R	
			Mean	Rep (%)	Mean	Rep (%)	Mean	Rep (%)	Mean	Rep (%)	Mean	Rep (%)
1	1 (1997)	S95	21.5	63.9**	18.3	70.7**	91.1	36.1**	21.1	58.3**	31.5	82.6**
		V95	3.8	41.9**	2.5	32.0 +	1.2	27.1 ns[c]	2.5	41.9**	3.5	46.2**
		SV95	89.9	60.5**	53.3	62.7**	107.7	29.0 ns	62.3	54.7**	120.9	78.1**
		ASNPC[d]	7.8	61.2**	10.0	65.3**	32.1	45.1**	7.3	63.2**	7.2	81.7**
		GY (g m^{-2})	291.0	62.6**	250.8	79.4**	39.5	82.5**	246.7	89.7**	254.9	87.5**
	2 (1998)	S89	39.1	67.6**	57.1	63.0**	30.5	74.5**	16.0	22.1**	48.6	76.4**
		V89	3.5	30.1*	4.1	52.2**	1.7	4.5 ns	2.9	45.8**	3.5	53.4**
		SV89	141.4	63.5**	263.8	52.9**	52.4	68.5**	48.3	66.7**	194.5	74.1**
		ASNPC[d]	13.8	66.6**	23.3	62.2**	10.2	75.2**	5.2	76.3**	16.4	74.8**
		GY (g m^{-2})	353.1	73.3**	199.7	77.5**	177.5	74.8**	256.4	90.6**	221.7	90.0**
2	1 (1997)	S81	14.7	76.7**	49.4	77.6**	48.3	65.7**	22.1	66.8**	28.8	91.5**
		V81	3.7	63.0**	2.0	22.6 ns	1.8	43.3**	2.4	60.9**	2.6	71.7**
		SV81	69.6	75.4**	108.9	68.9**	90.7	63.6**	61.7	64.8**	86.5	90.7**
		ASNPC[d]	8.9	82.3**	21.7	79.1**	22.1	71.7**	10.0	72.4**	9.0	92.7**
		GY (g m^{-2})	149.0	69.2**	163.6	84.8**	19.9	85.2**	74.3	93.3**	125.5	97.0**
	2 (1998)	S88	51.3	74.0**	56.0	74.0**	19.4	85.2**	16.3	83.7**	48.7	88.3**
		V88	3.7	48.5**	3.6	36.6**	2.0	21.4 ns	2.9	52.5**	3.5	71.3**
		SV88	198.3	69.5**	198.6	69.0**	39.8	79.1**	51.0	81.3**	200.5	88.3**
		ASNPC[d]	18.1	75.8**	21.2	77.7**	6.6	82.3**	5.7	71.6**	16.6	88.5**
		GY (g m^{-2})	256.1	78.5**	154.2	82.4**	111.5	76.5**	104.1	94.3**	114.4	92.4**

[a] RIP 1: derived from cross IS 9830 × E 36-1; RIP 2 derived from cross N 13 × E 36-1.
[b] Sn: emerged Striga number per m^2 at *n* days after sowing (d.a.s.); Vn: Striga vigor at *n* d.a.s.; SVn: Striga severity at *n* d.a.s.; ASNPC: area under Striga number progress curve; GY: grain yield (g m^{-2}).
[c] Not significant.
[d] Means of ASNPC are divided by 10^2.
+ Genetic differences among the 121 entries significant at the 0.10 probability level.
* Genetic differences among the 121 entries significant at the 0.05 probability level.
** Genetic differences among the 121 entries significant at the 0.01 probability level.

Alupe SR) to 3.8 (RIP 1, Set 1, Kibos LR). The low Striga vigor in the Alupe short rainy season in both sets of both RIPs was due to the presence of fungal antagonists, probably *Fusarium* species, in the soil that attacked Striga plants and lead to blackening and premature death of the parasite. The experimental means for grain yield ranged from 19.9 g m^{-2} (RIP 2, Set 1, Alupe SR) to 353 g m^{-2} (RIP 1, Set 2, Kibos LR). These grain yield differences reflected different climatic and soil conditions, different levels of Striga infestation, and different grain yield potentials under Striga infestation of the two RIPs. RIP 1 revealed a higher average grain yield performance level than RIP 2 at all sites and in both years. Repeatabilities were moderate to high and highly significant for most traits considered in both RIPs. As with the pot trials, RIP 2 revealed slightly higher repeatabilities than RIP 1 for the majority of traits. The Striga vigor score had the largest range of repeatabilities (4.5–72%), pointing to the fact that the genetic variation among the entries for Striga vigor score was not expressed in all instances. The overall high repeatabilities for grain yield (63–97%) point to the high experimental accuracy in all individual trials.

3.3.2. Variance components and heritabilities

The combined analyses of variance across locations within years revealed highly significant genetic variances ($P = 0.01$) among the tested $F_{3:5}$ lines for all traits in both RIPs, except for the Striga vigor score in

Table 5
Estimated variance components due to $F_{3:5}$ lines (G), $F_{3:5}$ line × location interaction (G × E) and error, and corresponding operative heritabilities (h^2) with their 95% confidence intervals (95% CI) of Sets 1 and 2 of RIPs 1 and 2 for various traits, combined across five field experiments in Kenya and Mali

Set (year)	Trait[a]	RIP 1 (IS 9830 × E 36-1)					RIP 2 (N 13 × E 36-1)				
		Variance component[b] due to			h^2	95% C.I.	Variance component[b] due to			h^2	95% C.I.
		G	G × E	Error			G	G × E	Error		
1 (1997)	S81	25.3**	25.0**	75.7	0.56	[0.40, 0.66]	156.6**	120.2**	100.1	0.78	[0.70, 0.83]
	S95	41.3**	31.6**	103.0	0.61	[0.47, 0.70]	254.7**	159.7**	152.8	0.80	[0.73, 0.85]
	V81	8.2**	9.0*	72.9	0.33	[0.10, 0.50]	56.5**	43.4**	86.8	0.68	[0.57, 0.76]
	V95	13.0**	17.5**	89.0	0.38	[0.16, 0.53]	78.7**	85.5**	121.8	0.66	[0.53, 0.74]
	SV81	191.4**	185.0**	557.0	0.56	[0.41, 0.67]	1480.6**	785.7**	814.7	0.82	[0.76, 0.87]
	SV95	406.3**	450.7**	810.5	0.62	[0.48, 0.71]	3246.6**	2799.7**	1942.6	0.77	[0.69, 0.83]
	ASNPC	4.4**	2.4**	9.1	0.65	[0.53, 0.74]	28.7**	15.6**	15.1	0.82	[0.76, 0.87]
	ASVPC	22.6**	19.3**	47.5	0.62	[0.50, 0.72]	241.3**	151.7**	138.0	0.81	[0.74, 0.85]
	GY	195.7**	1191.2**	479.8	0.37	[0.15, 0.52]	747.7**	637.1**	333.3	0.79	[0.72, 0.84]
	DAN	10.1**	4.2**	1.4	0.90	[0.87, 0.92]	20.9**	10.7**	4.4	0.87	[0.83, 0.90]
	PHT	607.9**	237.4**	32.8	0.92	[0.89, 0.94]	261.5**	192.13**	43.7	0.85	[0.79, 0.88]
2 (1998)	S75/74[c]	45.5**	29.3**	61.5	0.71	[0.61, 0.79]	96.7**	46.6**	77.1	0.80	[0.72, 0.85]
	S89/88	99.3**	76.7**	97.3	0.74	[0.65, 0.80]	171.6**	70.2**	117.8	0.82	[0.75, 0.86]
	V75/74	2.0+	13.8**	29.1	0.19	[0.00, 0.39]	9.2**	14.7**	35.2	0.48	[0.28, 0.61]
	V89/88	2.0 ns[d]	29.3**	68.8	0.09	[0.00, 0.32]	15.5**	28.3**	57.3	0.48	[0.28, 0.61]
	SV75/74	287.7**	370.3**	636.7	0.59	[0.44, 0.69]	686.6**	683.5**	779.5	0.70	[0.59, 0.78]
	SV89/88	1201.0**	1717.4**	2054.2	0.61	[0.47, 0.71]	2273.5**	1820.3**	2028.2	0.75	[0.65, 0.81]
	ASNPC	11.6**	8.3**	11.9	0.74	[0.65, 0.81]	22.7**	9.5**	14.9	0.82	[0.76, 0.87]
	ASVPC	120.5**	160.9**	190.9	0.63	[0.50, 0.72]	264.0**	222.1**	221.0	0.75	[0.66, 0.81]
	GY	663.8**	1229.0**	581.3	0.65	[0.52, 0.73]	562.1**	852.0**	445.7	0.68	[0.57, 0.76]
	DAN	11.3**	2.7**	0.8	0.94	[0.92, 0.96]	12.5**	4.1**	1.0	0.93	[0.90, 0.94]
	PHT	614.7**	196.9**	30.6	0.93	[0.91, 0.95]	366.1**	172.8**	37.7	0.90	[0.86, 0.92]

[a] Sn: emerged Striga number per m^2 at n days after sowing (d.a.s.); Vn: Striga vigor at n d.a.s.; SVn: Striga severity at n d.a.s.; ASNPC: area under Striga number progress curve; GY: grain yield (g m^{-2}); DAN: days to anthesis; PHT: plant height.
[b] Variance components for V78 and V92 are multiplied by 10^3.
[c] d.a.s. for RIP1/RIP2.
[d] Not significant.
+ F-test significant at the 0.10 probability level.
* F-test significant at the 0.05 probability level.
** F-test significant at the 0.01 probability level.

Set 2 of RIP 1 (Table 5). $F_{3:5}$ line × location interaction variances were also significant ($P = 0.05$) or highly significant ($P = 0.01$) for all traits in both RIPs and years. Estimated heritabilities were generally moderate to high, except for the Striga vigor score in both sets of RIP 1 and for grain yield in Set 1 of RIP 1. RIP 2 generally revealed higher heritability estimates than RIP 1. The combination of several Striga counts or Striga severity indices into ASNPC or ASVPC generally led to slightly higher heritability estimates compared to Striga counts or severity indices at individual dates.

3.3.3. Relationships among traits

In both RIPs, higher grain yield was genetically correlated with lower Striga infestation, Striga vigor, severity indices and ASNPC (Table 6). While grain yield was not correlated to days to anthesis in RIP 1, higher grain yield was associated with earlier anthesis in RIP 2 (the later maturing population of the two RIPs). On the other hand, high grain yield was not associated with plant height in RIP 2, but linked to taller plants in RIP 1. High ASNPC was correlated with later sorghum anthesis, especially in RIP 1. The correlation between ASNPC and plant height was

Table 6
Coefficients of genotypic correlation among selected traits in Sets 1 and 2 of RIPs 1 and 2, combined across five field environments

Correlated traits[a]	Genotypic correlation coefficients			
	RIP 1		RIP 2	
	Set 1 (1997)	Set 2 (1998)	Set 1 (1997)	Set 2 (1998)
GY × S88-96	−0.37[b]	−0.30[c]	−0.37[c]	−0.40[c]
GY × V88-96	−0.18	−0.84[b]	−0.17	−0.22[b]
GY × ASNPC	−0.27[b]	−0.31[c]	−0.37[c]	−0.38[c]
GY × ASVPC	−0.24[b]	−0.35[c]	−0.35[c]	−0.39[c]
GY × DAN	0.02	0.16[b]	−0.71[c]	−0.53[c]
GY × PHT	0.36[c]	0.59[c]	−0.18[b]	0.03
ASNPC × DAN	0.52[c]	0.63[c]	0.28[c]	0.20[b]
ASNPC × PHT	−0.47[c]	−0.16[b]	0.29[c]	0.13[b]

[a] GY: grain yield; S88-96, V88-96: Striga count and vigor between 88 and 96 d.a.s., respectively; ASNPC, ASVPC: area under Striga number or severity progress curves, respectively; DAN: days to anthesis; PHT: plant height.
[b] Estimate exceeds its standard error once.
[c] Estimate exceeds its standard error twice.

negative in RIP 1, but positive in RIP 2. The relationship between ASNPC and grain yield in the combined analysis across five locations is further illustrated for both sets of both RIPs in Fig. 1. The figure shows the relatively higher mean grain yield level of RIP 1 on one hand, and the relatively larger genetic variation for ASNPC in RIP 2. In all four series of experiments (2 sets × 2 RIPs), the Kenyan check cultivar Seredo was the overall highest yielding entry, thereby maintaining moderate ASNPC. It may therefore be considered as Striga-tolerant. The Striga-resistant check SRN 39 revealed stable resistance in all four experimental series, with mostly below-average grain yield performance. In terms of mean ASNPC, our resistant parent line IS 9830 was slightly less resistant and N 13 slightly more resistant than SRN 39.

3.4. Relationship between pot and field experiments

Since the genetic variance among the tested $F_{3:5}$ lines was significant only in the individual pot experiments but not in the combined analysis across pot trial locations, the relationship between pot and field trials was studied only for individual experimental pairs within Kenya or Mali/Niger. Coefficients of phenotypic correlation between ASNPC in pot versus field experiments were moderate and highly significant ($P = 0.01$) for RIP 2 in Kenya, but low for the same RIP in Niger/Mali, and also low for RIP 1 in both Kenya and Niger/Mali (Table 7). ASNPC assessed in the pot trials at Samanko in 1998 did also not correlate to those at Samanko or Cinzana fields (data not shown).

3.5. Relationship between agar-gel assays and field experiments in RIP 1

In both sets of RIP 1, moderate phenotypic correlations existed between germination distance in vitro and ASNPC in Mali, especially at Cinzana (Table 8). For Kenya, the correlations were lower and partly non-significant, indicating that the reaction of the tested $F_{3:5}$ lines in the Kenyan fields was not associated with their capacity to stimulate Kenyan Striga seed germination in the agar-gel assay.

3.6. Expected correlated response to selection for in vitro germination distance in RIP 1

Assuming equal selection intensities, indirect selection for mean maximal germination distance in the agar-gel assays (with Striga from Samanko and Bengou) was estimated to be only 7% less effective as direct field selection for ASNPC at Samanko and Cinzana (both Mali) for Set 1 of RIP 1, and even 58% more effective than direct field selection in Set 2 (Table 9). In Kenya on the other hand, using in vitro germination distance (with Striga from Kibos) as the

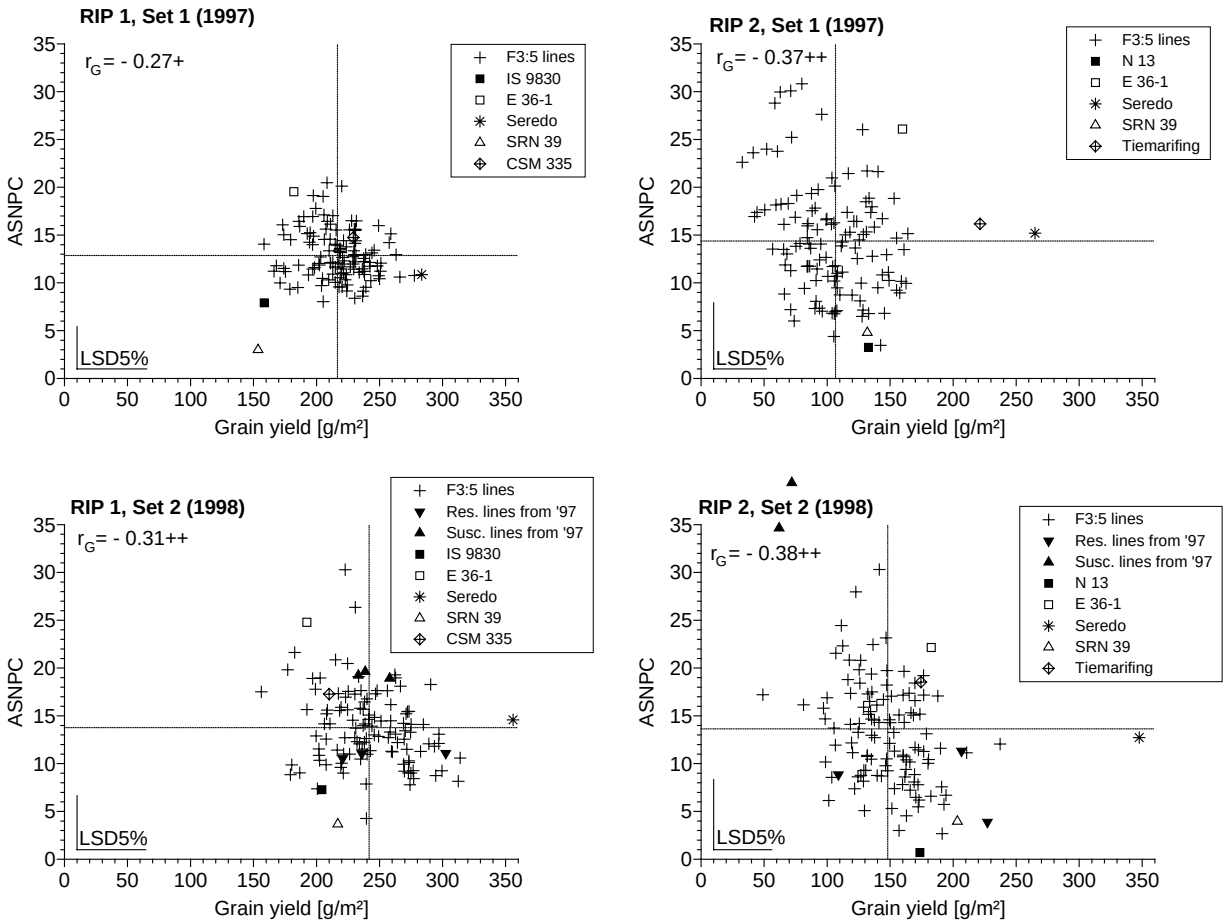

Fig. 1. Relationship between the entry means across five test sites in Kenya and Mali for grain yield and area under Striga number progress curve (ASNPC) in Set 1 (top) and Set 2 (bottom) of RIP 1 (left) and RIP 2 (right). r_G: coefficient of genetic correlation; $^{+}$, $^{++}$: estimate exceeds its standard error once or twice, respectively; LSD5%: least significant difference at $P = 0.05$. Dotted lines indicate the overall mean values across all entries.

Table 7
Coefficients of phenotypic correlation between area under Striga number progress curve (ASNPC) in the pot versus field experiments conducted for Sets 1 and 2 of RIPs 1 and 2

Country	Pot trial	Field trial	Correlated traits[a]	RIP 1		RIP 2	
				Set 1	Set 2	Set 1	Set 2
Kenya	Kibos	Kibos LR	ASNPC	0.23*	0.21**	0.50**	0.49**
	Kibos	Alupe LR	ASNPC	0.16 ns[b]	0.29**	0.40**	0.47**
	Kibos	Alupe SR	ASNPC	0.14 ns	0.32**	0.46**	0.53**
Niger/Mali	Sadoré	Samanko	ASNPC	0.29**	0.26**	0.15 ns	0.31**
	Sadoré	Cinzana	ASNPC	0.36**	0.45**	−0.02 ns	0.29**

[a] Same trait in pot and field trials.
[b] Not significant.
* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.

Table 8
Coefficients of phenotypic correlation between area under Striga number progress curve in field experiments and maximal germination distance in the agar-gel assays with the corresponding *Striga* population from the same country for the $F_{3:5}$ lines in Sets 1 and 2 of RIP 1

Country	Correlated traits[a]		Set 1 (RIP 1)	Set 2 (RIP 1)
	ASNPC in field experiment at	GD5 using Striga seeds from		
Kenya	Kibos LR	Kibos	0.24**	0.21*
	Alupe LR	Kibos	0.19*	0.32**
	Alupe SR	Kibos	0.04 ns[b]	0.13 ns
Mali	Samanko	Samanko	0.45**	0.29**
	Cinzana	Samanko	0.63**	0.51**

[a] ASNPC: area under Striga number progress curve; GD5: germination distance after 5 days in the agar-gel assay.
[b] Not significant.
* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.

Table 9
Relative effectiveness of using the germination distance measured in the agar-gel assay (GD5) as indirect selection criterion (trait y) versus direct selection for area under Striga number progress curve (ASNPC, trait x) in the field, measured as the ratio, $CR_x/R_x = r_g h_y/h_x$[a], and estimated from the data of Sets 1 and 2 of RIP 1 separately for Kenya and Mali

Country	Trait x	Trait y	Set	h_x	h_y	r_g	CR_x/R_x
Mali	ASNPC, combined across Samanko and Cinzana	GD5, combined across Striga populations from Samanko and Bengou	1	0.81	0.97	0.78^{++}	0.93
			2	0.56	0.97	0.91^{++}	1.58
Kenya	ASNPC, combined across Kibos and Alupe	GD5, combined across two Striga populations from Kibos	1	0.62	0.92	0.25^{++}	0.37
			2	0.70	0.95	0.41^{++}	0.55

[a] CR_x is the correlated gain in the target trait x resulting from selection for the trait y; R_x is the gain in the target trait x if it is directly selected for; h_x, h_y are the square roots of broad sense heritability of the target and indirect trait, respectively; r_g is the coefficient of the genotypic correlation between target trait and indirect trait.

selection criterion appeared 63 and 45% less effective than field selection for area ASNPC at Kibos and Alupe in Sets 1 and 2, respectively, of RIP 1.

4. Discussion

4.1. Utility of the agar-gel assay in breeding for Striga resistance

The usefulness of an indirect selection trait is determined primarily by its heritability and genetic correlation to the actual target trait, but also by economic parameters which may lead to increased selection intensity through indirect as compared to direct selection. In this study, it was possible to screen a set of 121 sorghum entries for stimulation of Striga seed germination (from a single Striga population) in the laboratory in 3 weeks. Two replicates of 242 Petri dishes were examined weekly. This provided a relatively easy and quick way of obtaining reliable results with high heritability. The agar-gel assay is therefore a useful selection method for determination of the genotype's capacity to stimulate Striga seed germination. The present results with Set 2 of RIP 1 showed that indirect selection for Striga resistance based on the in vitro germination distance can be up to 58% more effective than direct selection for reduced field Striga infestation, if the heritability for resistance under field conditions is only moderate and if the genetic correlation between in vitro germination distance and field resistance is sufficiently high. The relative efficiency of indirect selection in the agar-gel assay was lower in the other data sets, but it should be remembered that

computations were based on the assumption of equal selection intensities for evaluation in the agar-gel assay versus field conditions which is unrealistic. With a given budget, many more entries could be evaluated in the agar-gel assay than in field trials. Therefore, given the much lower cost and time investments for agar-gel assays compared to field trials, it is definitely worthwhile to perform the agar-gel assay to identify low-stimulant materials, which could subsequently be tested in the field to screen for other Striga resistance mechanisms. In addition, the agar-gel assay could facilitate transfer of the low-stimulant gene(s) into adapted local cultivars using classical backcross procedures. Due to the recessive nature of the major gene governing low stimulation of Striga seed germination (Ramaiah et al., 1990; Vogler et al., 1996; Haussmann et al., 2001b), selfing generations must be included in the backcrossing schemes.

Haussmann et al. (2001b) emphasized the importance of regional differences in *S. hermonthica* populations. This observation was supported in the present study by the lower correlations between in vitro germination distance and ASNPC in Kenya as compared to Mali. Ramaiah (1987) also noted that there is variability in Striga species for germination stimulant requirements. Netzly and Butler (1986) and Hauck et al. (1992) have documented the production of the sorgolactones and sorgoleones by sorghum roots. It remains unclear whether Striga seeds from Kenya are more sensitive to lower concentrations of the major germination stimulant sorgolactone, or to sorgoleone and strigol stimulants thought to be of lesser importance (Haussmann et al., 2001b). In any case, the lower correlations among the in vitro germination distance and Striga resistance in field experiments in Kenya suggest that low stimulant production is a less effective resistance mechanism in Kenya than in Mali. At the same time, not being linked to the in vitro germination distance, the highly significant genetic variation in RIP 1 for ASNPC at the Kenyan locations suggests the presence of additional Striga resistance mechanisms in RIP 1 and its Striga-resistant parent line IS 9830.

4.2. Measures of resistance to Striga using pot experiments

Despite the careful use of controlled Striga infestation and optimal agronomic conditions, it proved difficult to substantially reduce the genotype × location interaction and error components of variation associated with the pot trials. Coefficients of correlation between Striga resistance measures in the pot versus field resistance were mostly weak or inconsistent, though slightly higher in RIP 2 compared to RIP 1. The non-significance of the genotypic variance and large genotype × location interactions resulted in low heritability estimates in the pot studies, hence eliminating pot screening as a reliable indirect evaluation method. Possible aspects which may be responsible for the inconsistent performance in pot trials include: cracking of soil media, which may lead to washing away of Striga seeds and hence alter infestation levels; cracks in soil can also interfere with soil moisture in pots, which may in turn influence Striga germination and emergence; subterranean Striga may cause significant host stress but are not included in emerged Striga counts, a particular problem in highly susceptible hosts; restricted pot volume confounds entries with a Striga avoidance mechanism since root growth patterns are altered and germinated Striga seeds nearby the roots will have a higher likelihood of attaching to host roots; accumulation of Striga seed germination stimulants, obscuring separation of low- and high-stimulant hosts, due to cumulative amounts of germination stimulants in the vicinity of Striga seeds. All these aspects, in interaction with different Striga populations, soil, and climatic factors, may have increased genotype × environment interactions, obscuring detection of genetic variation, and resulting in low heritabilities. In addition, the residual genetic heterogeneity of our $F_{3:5}$ lines may have contributed to increased error variances in the individual pot trials, since only 1–3 plants per line were evaluated in each replication (pot).

4.3. Direct selection for Striga resistance under field conditions

4.3.1. Artificial infestation

Heterogeneity of field Striga infestation on-station was reduced through artificial infestation with Striga seeds. These fields were well drained and efforts were made to level them so as to minimize loss of Striga seeds through run-off during rains. The on-farm field at Cinzana in Mali had been managed for a number of years and its Striga infestation was highly

homogenous as indicated by the high repeatabilities achieved at this site. For on-station field screening where artificial infestation can be done, sufficient Striga seed must be collected in seasons preceding the testing season. Experience from this study indicates that collection of 3–4 kg of clean, viable Striga seed is sufficient to heavily infest an experimental area of one hectare. An aspect to consider is that freshly produced mature Striga seeds are dormant and require a period of after-ripening under dry conditions to lower seed moisture content and break dormancy. Hence Striga seeds used for infestation should be preferably at least 6 months old to avoid the effects of dormancy. Uniformity of infestation was achieved by first dividing the field into plots of two rows of equal length. Equal amounts of Striga seeds were weighed, mixed with fine dry sand, and uniformly distributed in each test row. Alternatively, the Striga seed/sand mixture may be uniformly distributed to individual sowing holes (Berner et al., 1996), although this method is less true to conditions in naturally infested farmers' fields (Haussmann et al., 2000a,b).

4.3.2. Experimental design

In this study, sorghum entries were accommodated in a hexa-lattice design. As Cochran and Cox (1957) noted, with large trials including many entries, the natural heterogeneity of the field can at least partially be taken into account by an appropriate experimental design, i.e., incomplete block or lattice designs. This enables increased precision to the extent that the experimental units within an incomplete block are more uniform than the incomplete blocks within a replication. Using an appropriate design is of great importance so as to derive useful information with minimum error from the trials. However, the increased replicates (six in these trials) required reduction in plot size, due to the limited availability of uniformly infested fields. The two-row field plot layout described by Haussmann et al. (2000a,b) was employed in this study. Each field plot consisted of two rows, separated from the neighboring entry by one empty row. This arrangement had several distinct advantages: for each entry, traits could be assessed in both rows, and no space was lost to border rows; due to the empty row, neighbor effects were reduced and more light reached the ground, reducing shading which is deleterious to Striga emergence and development; Striga counts were facilitated as there was more space between plots. In addition, field plots were laid out in serpentine order to ease data collection and permit quick plot identification in case of fallen plot tags. The described layout and modifications offered a significant improvement to field screening.

4.3.3. Striga vigor score

The visual Striga vigor score developed by Haussmann et al. (2000a,b) was employed in this study. This score takes into account morphological features of the Striga plants, i.e., Striga height and branching. It offers a quick, effective, non-destructive approximation of Striga development and average Striga biomass in each field plot. In the present study, heritability estimates for the Striga vigor score were higher in RIP 2 (48–68%) than in RIP 1 (9–38%). This could possibly reflect the presence of a larger genetic variation for antibiosis in N 13-derived materials, thereby confirming earlier observations on antibiosis in N 13 by Hess and Haussmann (unpublished data). But also in RIP 2, repeatabilities for the Striga vigor score showed a large range at individual locations (21–72%). One reason for the lack of genetic variation for the Striga vigor score at some locations in both RIPs (i.e., at Alupe in the short rains, Table 4) was a severe infection of Striga plants by Striga antagonists, like *Fusarium* species, that reduced Striga vigor and led to the death of many newly emerged Striga plants. While efforts are underway to exploit these natural antagonists for biological control of Striga (e.g., Hess et al., 2002), the unwanted presence of these hyperparasites in a field interferes with screening for Striga resistance. Experimental areas in which Striga antagonist populations are well established should therefore be avoided for this work.

4.3.4. Striga severity index

In the field experiments, multiplying the emerged Striga counts with their respective Striga vigor score provided an index, termed "Striga severity index", that is highly heritable, and provided another reliable screening trait. Obviously, it should make a difference whether a sorghum plot bears five Striga plantlets of less than 5 cm height with no branches (Striga vigor = 1, Striga severity = 5) or five Striga plants of 45 cm height with more than 10 branches (vigor = 9, severity = 45). The actual idea behind

the Striga severity index is to have a proportional estimate of the total Striga biomass in a plot, since the assessment of Striga biomass is laborious, destructive, and usually has a high error variance.

4.3.5. Area under Striga number and severity progress curves

Using the equation for calculating AUDPC (Shaner and Finney, 1977), the individual emerged Striga counts and Striga severity indices were transformed into ASNPC and ASVPC, respectively. Both measures were found to be mostly under stronger genetic control than traits from individual assessment dates and offered useful measures of progressive Striga emergence in the field. Pooled data across the five field environments illustrated the tight correlation between ASNPC and ASVPC, which is partly an autocorrelation. It is important to note that the present results were obtained with up to five Striga assessment dates and six replications at each experimental site. This improved the reliability of data and gave high heritabilities, which enhanced the accuracy of the search for quantitative trait loci for Striga resistance, a further project objective. If time and funds are limiting, a single Striga count at 70–85 d.a.s. may be sufficient. At this stage, genetic differences in reaction to Striga are greatest as indicated by the higher heritability coefficients, and hence screening large numbers of sorghum entries would be more cost-efficient.

4.3.6. Grain yield under Striga infestation

Both RIPs revealed highly significant variation for grain yield under Striga infestation. The consistently negative (though rather low) coefficients of genetic correlation between grain yield and area under Striga number progress curve in all four experimental series (2 sets $\times$ 2 RIPs) suggest that it should be possible to have selection gains in both traits. On the other hand, the highest yielding entries (local checks and $F_{3:5}$ lines) had about average ASNPC and the most resistant entries in terms of this trait were not the highest yielding ones in all four experimental series (Fig. 1). Also in a previous sorghum diallel study of Haussmann et al. (2001a), the highest yielding entry, an F_2 population derived from a cross of Striga-resistant Framida with Striga-tolerant Seredo, did not have the lowest ASVPC value, i.e., was not outstandingly resistant. This could be an indication that there are some costs of Striga resistance to sorghum, i.e., that outstanding suppression of Striga requires assimilates that are consequently lost to grain yield performance. But this hypothesis needs further confirmation through transfer of Striga resistance genes into locally adapted materials. Mechanisms of Striga tolerance are still unclear, but studies of Gurney et al. (2000) have revealed that when attachment is delayed, the effect on the host grain yield is significantly reduced compared with early attachment even at a similar level of Striga biomass production. This is the idea behind experiments investigating transplanting of cereals to reduce *S. hermonthica* damage (Oswald et al., 2001; Hess unpublished data). But in the long term, cultivating tolerant cultivars may not be advisable as this can lead to an increased Striga soil seed bank that can culminate in the abandonment of arable land. Practically, subsistence farmers cannot consistently perform labor-intensive hand weeding in large, highly Striga-infested fields. Striga-tolerant cultivars with superior yield under Striga infestation such as Seredo or Tiémarifing would be suitable candidates to be included in backcross breeding programs so as to introgress into them low-stimulant and/or other Striga resistance genes. In such efforts, either conventional or marker-assisted backcrossing could be employed to transfer the resistance gene(s).

5. Conclusions

The present study showed that field screening for Striga resistance in sorghum can achieve high heritabilities if appropriate measures like experimental design and specific resistance traits are taken into account. Both RIPs revealed highly significant genetic variation for the Striga resistance traits under investigation and the usefulness of the Striga-resistant parent lines IS 9830 (RIP 1) and N 13 (RIP 2) was hereby confirmed. The data showed that line IS 9830 possesses the low stimulant character and additional resistance mechanism(s). Line N 13, though lower yielding than IS 9830, proved to be outstandingly resistant compared to other resistant checks in terms of low ASNPC. In addition, RIP 2 revealed an outstandingly large genetic variation for Striga resistance traits, an important requirement for selection response. In Striga resistance breeding, it is important

to simultaneously consider Striga resistance traits and grain yield, using selection indices, in order to avoid selecting high-yielding entries that support numerous emerged Striga, or highly resistant entries that are low yielding. Significant genotype × environment interactions in the field experiments stress the importance of multi-locational trials to achieve stable Striga resistance. They also point to the need of investigations into putative Striga variability and other reasons for the observed interactions, as well as to the need to determine the most suitable selection environments for breeders.

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