

Inheritance of Resistance to *Striga* in Sorghum Genotype SRN39

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With one figure and 5 tables

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Abstract

Striga hermonthica (Del.) Benth., a parasitic weed of grasses, causes major yield reductions in the principal cereal crops of semi-arid Africa. Cultivar resistance is the most economic control measure, since adapted, resistant cultivars can be grown without additional input from the subsistence farmer. Information on the genetics of resistance to *S. hermonthica* is scant. This is partially attributable to the rarity of germplasms which exhibit stable resistance across geographical regions. The objective of this study was to determine if the stable resistance observed in sorghum [*Sorghum bicolor* (L.) Moench] cultivar SRN39 is heritable. Crosses were made between SRN39 and a susceptible parent, P954063. Parental, F₁, F₂ and backcross generations were grown in infested pots and development of both host and parasite was monitored. Significant variation among genotypes was observed for both host traits and effects on parasite populations. The F₁ did not differ significantly in *Striga* resistance from the susceptible parent, suggesting recessive inheritance. However, hybrid vigor was exhibited by the F₁ which yielded and developed as well as the resistant parent. Broad sense heritability ranged from 0.23 to 0.55 for host traits and from 0.10 to 0.43 for effect of genotypes on the *Striga* population. Joint scaling tests showed that observed variation in each host or parasite trait consisted of additive and dominance components, suggesting possible progress could be made with appropriate selection schemes.

Key words: *Sorghum bicolor* — *Striga hermonthica* — parasitic weed — resistance — inheritance.

Striga hermonthica (Del.) Benth. is a serious agronomic pest in semi-arid regions of Africa. It is the most destructive weed occurring in

African sorghum [*Sorghum bicolor* (L.) Moench] fields and, excluding bird predation, may be the most important sorghum yield loss factor (MUSSELMAN et al. 1983). Because heavy infestations may lead in certain years to total crop failure, it is imperative that *Striga* populations be controlled so that they remain below the economic threshold.

Cultivar resistance may be the most economically promising *Striga* control measure, since adapted, resistant sorghum cultivars can be grown under conditions of erratic rainfall and low soil fertility and require no costly inputs from the subsistence farmer (KING and ZUMMO 1977, RAMAIAH and PARKER 1982). Sorghums resistant to *S. hermonthica* in Africa have been reported (DOGGETT 1965, EJETA and JAIN 1982, KAMBAL 1979, RAMAIAH 1987), but resistance in some cultivars does not hold up across geographical regions. The variable performance of a given host cultivar to *Striga* infestation in different areas may be due to the existence of intraspecific physiological variants of the parasite (BEBAWI 1981, KING and ZUMMO 1977, PARKER and REID 1979).

Published reports on the genetics of resistance to *Striga* spp. in sorghum are few. SAUNDERS (1933) reported that resistance to *S. asiatica* was recessive in two sorghum crosses and partially dominant in a third. KULKARNI and SHINDE (1985) found field tolerance to the same species to be governed by non-additive gene action. OBILANA (1984), defining resistance to *S. hermonthica* as “low total number of *Striga* per sorghum plant”, reported high (0.78)

broad sense heritability of this trait. He also found gene action to be non-additive with over-dominance of susceptibility and estimated that two to five genes control reaction to the weed. More recently, RAMAIAH et al. (1990) established that low *Striga* stimulant production in sorghum genotypes, Framida, 555, and SRN4846, is inherited as a single recessive gene. Progress on inheritance studies and breeding for resistance to *Striga* have been limited by variability in performance across geographical regions, lack of uniformity of field infestations and difficulty in evaluating individual segregating progenies for resistance when parasitism occurs below ground. The lack of a suitable laboratory assay that can predict field performance has also hampered progress.

The purpose of this study was to investigate the inheritance of resistance to *S. hermonthica* in sorghum cultivar SRN39. In field trials conducted in Niger, we observed superior field resistance and stability in this cultivar (HESS 1989), rendering it a suitable choice for the inheritance study. Resistance to *Striga* attack by this cultivar has also been reported in Burkina Faso, Ghana and the Sudan (KAMBAL 1979, RAMAIAH 1984). A unique aspect of this inheritance study was that infestation and evaluation were made on individual plants in pots.

Materials and Methods

Crosses were made between resistant (SRN39) and susceptible (P954063) sorghum cultivars in the greenhouse at Purdue University in the spring of 1985 using the susceptible cultivar as the male parent. For the production of F₂ seed, progeny were sown in the field at the Purdue Agronomy Farm in the spring of 1985. Backcrosses of the F₁ to both parents were made in the greenhouse in the spring of 1986.

The inheritance study was conducted outdoors in pots at Niamey, Niger, during the 1987 growing season. Soil was prepared by thoroughly mixing clay, sand and cow manure (2 : 1 : 1, v/v/v). Each 27 cm diameter × 30 cm deep black polyethylene pot (E. C. Geiger, Box 285, Harleysville, PA 19438) was filled with 2.9 kg of the soil mix.

Pots were infested by thoroughly mixing 0.3 g (approximately 70,000) of *Striga* seed into the upper 5 cm of soil in each pot. Seed of *S. hermonthica* had been collected in sorghum fields at Birni N'Konni,

Niger at the end of the previous crop season. A series of sieves (0.25, 0.20, 0.16 and 0.125 mm mesh) was employed to separate seed from sand and plant debris. *Striga* seed were preconditioned by watering pots one week before sowing sorghum.

The infestation technique and viability of the *Striga* seed had been tested prior to beginning this experiment. On 21 February, 21 March and 18 April, 10 infested pots were sown with sorghum cultivar P954063. Cool temperatures in February and early March did not affect days to *Striga* emergence (average of 39.6 days) but retarded sorghum growth and development and were correlated with reduced levels of *Striga* infestation. At 70 days after sowing (DAS) average *Striga* number per pot were: 18, 52 and 125 plants for the 21 February, 21 March and 18 April sowings, respectively.

Thirty pots were sown with each parent and the F₁, 50 pots were sown with each backcross and 100 pots were sown with the F₂. Three seeds were sown in each pot on 13 May and thinned to 1 per pot 3 weeks later. A completely randomized design was used. The experiment was laid out in 5 double rows of 29 pots each. Spacing between plants within double rows was 33 cm and rows were 63 cm apart.

Data on the following variables were collected from each pot throughout the season: Seedling vigor (height [in cm] at 28 days after sowing); days to half bloom (number of days from planting until the sorghum plant had flowered to mid-panicle); plant height (in cm at 129 days after sowing); plant weight (in g after drying in the sun for 35 days); panicle weight (in g after drying in the sun for 28 days); yield (total weight [in g] of threshed grain from harvested panicles); 100-seed weight (weight [in g] of 100 whole kernels); *Striga* emergence (number of days from sowing sorghum until emergence of the first *Striga* plant); *Striga* counts (number of emerged *Striga* plants per pot, counted at 7-day intervals for 4 weeks beginning 1 week after emergence of the first *Striga* plant and at 28-day intervals thereafter); *Striga* flowering (number of days from *Striga* emergence to opening of the first flower).

Generation means were calculated and compared using Student-Newman-Keuls' test adapted for testing means with unequal replication (STEEL and TORRIE 1980). *Striga* counts were transformed with the base 10 logarithmic transformation since generation means and their variances were positively correlated. Correlations among the different traits were calculated for the F₂ generation. The broad sense heritability of each trait was calculated according to ALLARD (1960) as shown in Table 2. Two formulae proposed by SEWELL WRIGHT (1968) were employed to estimate the number of loci by which the F₁ differs from each parent for traits with a high broad sense heritability (Table 3). All loci were assumed to be plus factors with equal effect. If complete dominance at all loci is assumed, then the total number of loci

Table 1. Generation means of sorghum traits and effects of sorghum on *Striga* characters from a cross between resistant and susceptible parents grown outdoors in *Striga*-infested pots

Genotype ^a	Sorghum	Sorghum	Panicle	Yield	Days to <i>Striga</i> emergence	<i>Striga</i> number			
	Ht	Wt	Wt			30 DAS ^b	37 DAS	44 DAS	51 DAS
	(cm)	(g)	(g)	(g)					
P _R	127.1 ab ^c	88.8 a	41.9 a	30.9 ab	41.8 a	0.0 b	0.2 d	2.7 c	12.1 c
P _S	79.5 d	23.8 d	8.7 d	7.0 d	31.8 d	0.6 a	9.7 a	30.1 a	46.7 a
F ₁	127.5 ab	64.7 bc	36.7 abc	29.5 ab	33.3 cd	0.4 ab	6.3 ab	25.6 a	53.6 a
F ₂	116.4 bc	56.5 c	30.5 bc	23.6 ab	34.7 c	0.3 ab	3.9 b	17.3 a	40.6 a
BC _R	125.5 a	73.3 b	37.6 ab	28.8 a	37.0 b	0.2 ab	1.9 c	10.1 b	26.1 b
BC _S	108.1 c	53.1 c	26.5 c	20.8 bc	33.3 cd	0.4 ab	6.0 ab	22.8 a	46.7 a

^a P_R = resistant parent (SRN39); P_S = susceptible parent (P954063); BC_R = backcross to resistant parent; BC_S = backcross to susceptible parent.

^b Days after sowing.

^c Within each column, means followed by a common letter do not differ significantly, $P = 0.05$, according to Student-Newman-Keuls' test.

involved is given by $S_1 + S_2$, regardless of the distribution of plus factors, since each contributes to only one of the backcrosses.

MATHER and JINKS' (1982) scaling test was conducted to investigate the additive and dominance components of observed variation of these traits. The observed distributions of selected traits of parental and F₁ generations were tested for normality (STEEL and TORRIE 1980). Where these distributions were found to be normal, the expected F₂ and backcross distributions were calculated for segregation of 1 gene and the observed distributions were tested for goodness-of-fit to the expected distributions.

Results

Significant genotypic differences among generations were observed for all sorghum traits and effects of sorghum on the *Striga* population (Table 1). The resistant parent exhibited significantly superior plant productivity to the susceptible parent. Inheritance of plant height, plant weight, panicle weight and grain yield is dominant as the F₁ was not significantly different from the resistant parent.

Striga was observed on all plants in the experiment. Days to *Striga* emergence ranged from 23 to 81 days with delayed emergence in resistant sorghum genotypes. *Striga* number per pot, used as a measure of resistance, was significantly different among genotypes at all stages (Table 1). The F₁ did not differ signifi-

cantly from the susceptible parent, suggesting recessive inheritance of days to *Striga* emergence and *Striga* number. For both *Striga* and sorghum characters the means of the backcross generations were shifted towards the mean of their respective recurrent parent.

Tests for normality of frequency distributions of the sorghum and *Striga* characters in parental and F₁ generations showed that plant height, panicle weight, yield and effects of

Table 2. Broad sense heritability of sorghum traits and effects of *Striga* characters from a cross between a resistant parent (SRN39) and a susceptible parent (P954063) grown outdoors in *Striga*-infested pots

Character	Heritability ^a
Sorghum height	0.55
Sorghum weight	0.23
Panicle weight	0.52
Grain yield	0.50
Days to <i>Striga</i> emergence	0.19
<i>Striga</i> number, 30 DAS ^b	0.14
<i>Striga</i> number, 37 DAS	0.43
<i>Striga</i> number, 44 DAS	0.38
<i>Striga</i> number, 51 DAS	0.10

^a $H = \sigma^2 F_2 - \sigma^2 E / \sigma^2 F_2$ where $\sigma^2 E = \sigma^2 P_R + \sigma^2 P_S + \sigma^2 F_1 / 3$ and $\sigma^2 P_R$, $\sigma^2 P_S$, $\sigma^2 F_1$ and $\sigma^2 F_2$ are the variances of the resistant parent, susceptible parent, F₁ and F₂ generations, respectively.

^b Days after sowing.

Striga number at 44 DAS were normally distributed ($P = 0.01$). Fit was less good for the susceptible parent for panicle weight and yield ($P = 0.01$) and *Striga* number ($P = 0.04$) than for the resistant parent ($P = 0.48, 0.22$ and 0.31 for the same respective characters) and the F_1 ($P = 0.23, 0.14$ and 0.46 for the same respective characters). Goodness-of-fit tests in the segregating generation indicated acceptable fit for effects on *Striga* number (Fig. 1), yield and other plant characters (not shown). Because distributions for *Striga* count at 30, 37, 44 and 51 DAS were skewed, a log transformation was performed before computing variances for this trait.

Broad sense heritabilities were generally low (Table 2). They ranged from 0.23 to 0.55 for sorghum traits and from 0.10 to 0.43 for *Striga*

traits. Only for *Striga* number at the second and third counts (37 and 44 DAS) was heritability as high as 40 %, yet somewhat lower than estimated for sorghum height (0.55) and grain yield (0.50).

The number of loci controlling six traits were estimated using Sewell Wright's formulae (Table 3). Estimates for sorghum height, panicle weight, yield, effect on days to *Striga* emergence and *Striga* number at 37 and 44 DAS were: 3.66, 1.03, 1.14, 0.44, 1.74 and 2.78, respectively, assuming complete dominance at all loci. Joint scaling tests were also conducted on these traits. Results showed that observed variation in each trait consists of additive and dominance components (Table 4).

Correlation coefficients between indicators of *Striga* infestation and sorghum growth and

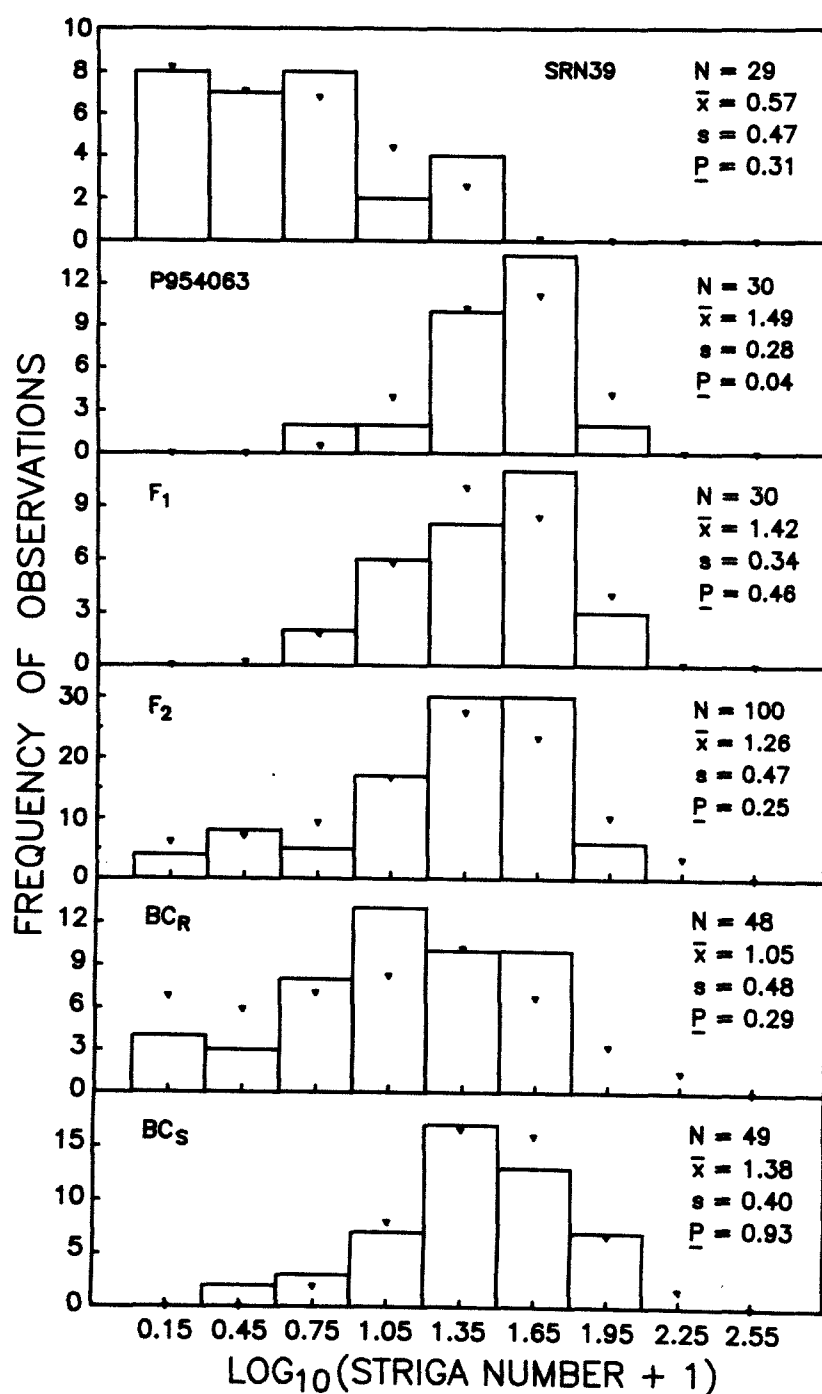


Fig. 1. Frequency distributions of *Striga* number at 44 days after sowing on sorghum cultivars SRN39 and P954063 and their F_1 , F_2 and backcross populations. \blacktriangledown = expected value of each class for a normal distribution of uniform genotypes and segregation of a single gene in the F_2 and backcross populations. P = probability of a larger value of χ^2 . (For SRN39, P954063, F_1 , F_2 , BC_R and BC_S populations, respectively: plant number = 29, 30, 30, 100, 48, 49; population mean = 0.57, 1.49, 1.42, 1.26, 1.05, 1.38; population standard deviation = 0.47, 0.28, 0.34, 0.47, 0.48, 0.40.)

yield characters in the F₂ generation are given in Table 5. Delayed *Striga* emergence correlated significantly with increased host plant height, panicle weight and yield. Correlation between early *Striga* emergence and delayed sorghum flowering was also highly significant. Increase in *Striga* number at 37, 44 and 51 DAS was highly correlated with reduction in sorghum height, dry weight, panicle weight, yield and delay in host plant maturity. *Striga* number at 30 DAS was significantly correlated only with reduction in sorghum dry weight.

Discussion

Various environmental factors influence the growth and development of *Striga* (PATTERSON 1987). The inheritance study was carried out in pots to minimize environmental variation among plants. Growing sorghum in artificially-infested soil in pots gives the investigator more control over the experimental environment than is possible in the field (VASUDEVA RAO 1985).

Both sorghum and *Striga* grew well in this experiment, sown in early May. Significant

Table 3. Estimation of number of genes controlling sorghum and *Striga* characters from a cross between resistant and susceptible parents grown outdoors in *Striga*-infested pots

Character	Estimated number of genes ^a	
	Formula 1	Formula 2
Sorghum		
Plant height	0.00	3.66
Panicle weight	0.03	1.00
Grain yield	0.03	1.11
<i>Striga</i>		
Days to emergence	0.39	0.05
Number at 37 DAS	1.64	0.10
Number at 44 DAS	2.76	0.02

$$S_1 = \frac{(\bar{F}_1 - \bar{P}_R^2)}{4(\sigma_{BCR}^2 - \sigma_E^2)} \quad S_2 = \frac{(\bar{P}_S - \bar{F}_1^2)}{4(\sigma_{BCS}^2 - \sigma_E^2)}$$

^a \bar{P}_R , \bar{P}_S and \bar{F}_1 are, respectively, means of the resistant parent (SRN39), susceptible parent (P954063) and F₁ populations, and σ^2E , σ^2BC_R and σ^2BC_S are the environmental variance and variances of the backcross to resistant and backcross to susceptible populations, respectively.

Table 4. Joint scaling tests for sorghum traits and effects on *Striga* population from a cross between resistant and susceptible parents grown in *Striga*-infested pots

Genetic parameter ^b	Sorghum			Days to emergence	<i>Striga</i>	
	Plant height	Panicle weight	Grain yield		37 DAS ^a	44 DAS
<i>m</i>	103.75±2.19	26.43±1.51	18.86±1.20	36.71±0.51	0.55±0.04	1.04±0.04
[<i>d</i>]	22.56±2.20	14.84±1.50	11.48±1.19	4.77±0.53	-0.45±0.04	-0.43±0.04
[<i>b</i>]	24.99±3.93	9.98±3.28	10.71±7.02	-3.46±0.86	0.28±0.08	0.37±0.08
χ^2	1.83	1.15	1.44	1.98	1.07	2.57
<i>P</i>	0.61	0.76	0.70	0.58	0.78	0.46

^a Days after sowing.

^b *m* = estimate of mid-parent; [*d*] = estimate of the additive component; [*b*] = estimate of the dominance component.

Table 5. Correlation coefficients between sorghum traits and effects on *Striga* population from an F₂ of the SRN39 × P954063 cross grown outdoors in *Striga*-infested pots

	SDGHGT	PLNTHGT	HBLOOM	PLNTWT	PANICWT	YIELD	100SDWT
STRIEMER ^a	-0.1601 ^b	0.2970**	-0.2634**	0.3381**	0.4045**	0.3824**	0.1691
STEMTOFL	-0.1596	0.2103*	-0.1592	0.1623	0.2428**	0.2203*	0.0767
STR30DAS	-0.0510	-0.0893	0.0896	-0.2258*	-0.1714	-0.1723	-0.0366
STR37DAS	0.0819	-0.2913**	0.2756**	-0.3976**	-0.4161**	-0.3921**	-0.2008*
STR44DAS	0.1569	-0.3553**	0.3085**	-0.3671**	-0.5315**	-0.5190**	-0.1709
STR51DAS	0.2206*	-0.3479**	0.3065**	-0.2964**	-0.5612**	-0.5508**	-0.0592

^a STRIEMER = days to *Striga* emergence; STEMTOFL = days from *Striga* emergence to flowering; STR_nDAS = Log₁₀ (*Striga* no + 1) at n days after sowing, where n = 30, 37, 44 and 51; SDGHGT = seedling height (cm) at 28 days after sowing; PLNTHGT = plant height (cm) at 129 days after sowing; HBLOOM = days to sorghum flowering; PLNTWT = plant dry weight (g); PANICWT = panicle dry weight (g); YIELD = grain weight (g); 100SDWT = 100-seed weight (g).

^b The symbols * and ** indicate significant differences among treatment means at $P = 0.05$ and 0.01 , respectively.

delay in *Striga* emergence and flowering was observed in pots of resistant plants and at most counts significant differences were found among genotypes for number of emerged *Striga*. The highest number of emerged *Striga* were counted at eight weeks after initial emergence. In one pot sown with the backcross to the susceptible parent, 221 *Striga* plants were counted, equivalent to 38.6×10^6 plants ha⁻¹. In a field study (not reported here) the highest density of emerged *Striga* encountered was at the final *Striga* count and was equivalent to 1.75×10^6 plants ha⁻¹. The number of *Striga* seen in pots was 22 times higher, suggesting that the infestation level employed in these pots was very high.

The effect of the parasite on its host was dramatic. *Striga hermonthica* plantlets comprising less than 1 % of the total dry weight of the host may be associated with a 25 % reduction in host dry weight (RAMAIAH and PARKER 1982). Severe infestation of sorghum can result in a 60 % reduction in leaf and root weight and some plants may be prematurely killed (ANDREWS 1945, TARR 1962). We noted premature death of some of the most susceptible and severely stunted plants in the study. In general, delay in *Striga* emergence and flowering was significantly correlated with earlier flowering and increased yield of the host. We observed that shoot elongation of susceptible genotypes slowed or stopped at the time when the first

Striga shoots emerged. This was supported by the significant correlation (at $P = 0.01$) of reduction in emerged *Striga* at the different counts with earlier flowering and increased height and yield of host plants.

As older *Striga* plants died, new shoots frequently emerged, but the overall number declined. ANDREWS (1945) observed a decrease in emerged *Striga* plant number after five weeks on sorghum growing in pots 10 cm in diameter. He attributed the decline either to the roots of sorghum becoming pot bound or to the shedding of *Striga* seedlings as sorghum roots thickened. DOGGETT (1965) proposed that the number of *Striga* plants established on sorghum roots should follow the growth curve for the production of sorghum root tips. We observed that the decline may also be related to the development of the host canopy resulting in increased shading of the most stunted host plants. Reduction in photosynthesis of these severely stunted sorghum plants may have contributed to death of *Striga* attached to their root systems.

Striga is totally dependent on host carbon while unemerged. Even when the parasite is photosynthetically competent, high losses through respiration result in little net autotrophic carbon gain and 35 to 43 % of parasite carbon is estimated to be host-derived (GRAVES et al. 1989). Shading combined with reduction in photosynthesis of parasitized plants (PRESS et

al. 1987) may explain the observed die-back of *Striga* on the most susceptible genotypes. Since *Striga* can develop to maturity in complete darkness provided the host is maintained in the light (ROGERS and NELSON 1962), another factor must be responsible for *Striga* decline on more resistant genotypes which were not shaded. Daily watering was necessary to maintain the pot experiment. An increase in percent humidity within the host canopy may have occurred and adversely affected the parasite as resistant genotypes grew. The negative effect of abundant moisture on *Striga* infestation is recognized by subsistence farmers and has been demonstrated experimentally (ANDREWS 1945). The possibility that *Striga* die-back may be reduced or eliminated by increasing spacing between pots should be investigated.

Significant variation among genotypes was observed for both host traits and effects of the host on parasite populations. Genotypic variation in traits of interest (plant height, panicle weight, yield, days to *Striga* emergence and *Striga* number at 37 and 44 DAS) were attributable to both additive and dominance components, indicating opportunities for further improvement through selection.

Estimates of number of genes affecting *Striga* resistance (reduced infestation) suggested control by one or two genes. The magnitude of the shift in the backcrosses toward the respective recurrent parent also suggested simple inheritance of these characters, however, no distinct modes were present in the frequency distributions. This could have resulted from either the presence of plural segregating genes or from masking of the action of one or a few genes by effects of the environment. A single recessive gene controlling inheritance of low germination stimulant production in sorghum has recently been reported (RAMAIAH et al. 1990). Our estimates of minimum gene number for all traits measured were low (one to four genes). Although such estimates are only approximate, it is interesting to note that the formulae indicated that SRN39 and P954063 differ for four loci governing plant height. This is consistent with QUINBY'S (1974) classical report of four height loci in sorghum.

The possibility of single gene control of resistance in SRN39 was suggested by fitting observed and expected distributions for segregation of one recessive gene controlling re-

duced *Striga* number at 44 DAS (Fig. 1). At present we are unable to explain how this putative resistance gene(s) may affect *Striga* infestation and/or host response to infestation. Although average emerged *Striga* number in pots of SRN39 eventually reached a high level (66 plants per pot at 79 DAS) the effect on its productivity was insignificant. The F₁ plants supported more emerged *Striga* than the susceptible parent (123 vs. 77 plants per pot at 65 DAS), yet hybrid vigor was evident in this cross and growth and yield of the F₁ paralleled that of the resistant parent.

The ability of host cultivars to maintain photosynthetic capacity in spite of *Striga* attack may help to alleviate the effects of *Striga* infestation on crop productivity (GRAVES et al. 1989). Adapted hybrid cultivars with one or both parental sources possessing resistance to *Striga* should contribute to increased sorghum yields in *Striga*-infested fields.

Zusammenfassung

Vererbung der Resistenz des Sorghum-Genotyps SRN39 gegen *Striga*

Striga hermonthica (Del.) Benth. ist ein auf Gräsern parasitär lebendes Unkraut, das im semi-ariden Afrika bei den Hauptgetreidearten große Ertragseinbußen verursacht. Der Einsatz resistenter Sorten ist die wirtschaftlichste Maßnahme, da solche Sorten von den Bauern, die für den Eigenbedarf produzieren, ohne zusätzliche Aufwendungen angebaut werden können. Es liegen nur wenige Kenntnisse über die Genetik der Resistenz gegen *S. hermonthica* vor. Das ist zum Teil darauf zurückzuführen, daß es nur wenig Ausgangsmaterial gibt, das sich über alle geographischen Regionen hinweg als stabil resistent erweist. Ziel dieser Untersuchung war es festzustellen, ob die bei der Sorghumsorte SRN39 (*Sorghum bicolor* [L.] Moench) beobachtete stabile Resistenz erblich ist. Dazu wurden Kreuzungen zwischen SRN39 und dem anfälligen Elter P954063 durchgeführt. Eltern, F₁, F₂- und Rückkreuzungsnachkommenschaften wurden in infizierten Töpfen angezogen und die Entwicklung von Wirt und Parasit verfolgt. Zwischen den Genotypen wurde eine signifikante Variation sowohl für die Merkmale des Wirts

als auch im Hinblick auf dessen Einflüsse auf die Parasiten-Population festgestellt. Die F_1 unterschied sich nicht signifikant vom anfälligen Partner, so daß angenommen werden kann, daß die Resistenz rezessiv vererbt wird. Sie zeichnete sich aber durch Hybridwüchsigkeit aus; sie entwickelte sich so gut wie der resistente Elter und entsprach diesem im Ertrag. Die Werte für die Heritabilität im weiteren Sinn bewegten sich für Merkmale des Wirts zwischen 0,23 und 0,55 und für genotypische Einflußfaktoren des Wirts auf die *Striga*-Population zwischen 0,10 und 0,43. Tests zum Vergleich der Generationsmittel machten deutlich, daß sich die beobachtete Variation aller Wirts- und Parasiten-Merkmale aus additiven und Dominanz-Komponenten zusammensetzt, was darauf hinweist, daß unter Anwendung geeigneter Selektionsverfahren Fortschritte erzielt werden können.

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References

- ALLARD, R. W., 1960: Principles of Plant Breeding, 75—108. John Wiley and Sons, New York.
- ANDREWS, F. W., 1945: The parasitism of *Striga hermonthica* Benth. on *Sorghum* ssp. under irrigation. I. Preliminary results and the effect of heavy and light irrigation on *Striga* attack. Ann. Appl. Biol. 32, 193—200.
- BEBAWI, F. F., 1981: Intraspecific physiological variants of *Striga hermonthica*. Expl. Agric. 17, 419—423.
- DOGGETT, H., 1965: *Striga hermonthica* on sorghum in East Africa. J. Agric. Sci. 65, 183—194.
- EJETA, G., and R. P. JAIN, 1982: Annual Report of the ICRISAT-Sudan Cooperative Sorghum and Millet Improvement Program. Report No. 5. Agric. Res. Corp., P.O. Box 126, Wad Medani, Sudan.
- GRAVES, J. D., M. C. PRESS, and G. R. STEWART, 1989: A carbon balance model of the sorghum-*Striga hermonthica* host-parasite association. Plant, Cell, and Environment 12, 101—107.
- HESS, D. E., 1989: Resistance to *Striga hermonthica* (Del.) Benth. in sorghum. Ph.D Thesis. Purdue Univ., Indiana.
- KAMBAL, A. E., 1979: *Striga* Research in the Sudan. Technical Progress Report No. 1. Agric. Res. Corp., Wad Medani and Fac. of Agric., Khartoum.
- KING, S. B., and N. ZUMMO, 1977: Physiological specialization in *Striga hermonthica* in West Africa. Plant Dis. Repr. 61, 770—773.
- KULKARNI, N., and V. K. SHINDE, 1985: Genetics of grain yield in sorghum under *Striga* stress. Ind. J. Genet. 45, 21—24.
- MATHER, K., and J. L. JINKS, 1982: Biometrical Genetics, 65—81. 3rd Ed. Chapman and Hall. London.
- MUSSELMAN, L. J., P. C. MATTESON, and S. FORTUNE, 1983: Potential pollen vectors of *Striga hermonthica* (Scrophulariaceae) in West Africa. Ann. Bot. 51, 859—862.
- OBILANA, A. T., 1984: Inheritance of resistance to *Striga* (*Striga hermonthica* Benth.) in sorghum. Prot. Ecol. 7, 305—311.
- PARKER, C., and D. C. REID, 1979: Host specificity in *Striga* species — some preliminary observations. In: L. J. MUSSELMAN, A. D. WORSHAM, and R. E. EPLEE (eds.), Proc. Second Int. Symp. on Parasitic Weeds, 79—90. North Carolina State Univ., Raleigh, North Carolina, USA.
- PATTERSON, D. T., 1987: Environmental factors affecting witchweed growth and development. In: L. J. MUSSELMAN (ed.), Parasitic Weeds in Agriculture. *Striga*, Vol. 1, 27—41. CRC Press, Inc. Boca Raton, Florida.
- PRESS, M. C., J. M. TUOHY, and G. R. STEWART, 1987: Gas exchange characteristics of the sorghum-*Striga* host-parasite association. Plant Phys. 84, 814—819.
- QUINBY, J. R., 1974: Sorghum Improvement and the Genetics of Growth. Texas A&M Univ. Press, College Sta., TX 77843. 108 pp.
- RAMAIAH, K. V., 1984: Patterns of *Striga* resistance in sorghum and millets with special emphasis on Africa. In: E. S. AYENSU, H. DOGGETT, R. D. KEYNES, J. MARTON-LEFEVRE, L. J. MUSSELMAN, C. PARKER, and A. PICKERING (eds.), *Striga: Biology and Control*, 71—92. ICSU Press, Paris.
- —, 1987: Breeding cereal grain for resistance to witchweed. In: L. J. MUSSELMAN (ed.), Parasitic Weeds in Agriculture. *Striga*, Vol. 1, 227—242. CRC Press, Inc. Boca Raton, Florida.
- —, V. L. CHIDLEY, and L. R. HOUSE, 1990: Inheritance of *Striga* seed-germination stimulant in sorghum. Euphytica 45, 33—38.
- —, and C. PARKER, 1982: *Striga* and other weeds in sorghum. In: Sorghum in the Eighties. Vol. 1, 291—302. Proc. Int. Symp. on Sorghum. 2—7 November 1981, Patancheru, India. ICRISAT, Patancheru, A.P. 502 324, India.
- ROGERS, W. E., and R. R. NELSON, 1962: Penetration and nutrition of *Striga asiatica*. Phytopath. 52, 1064—1070.

- SAUNDERS, A. R., 1933: Studies in phanerogamic parasitism with particular reference to *Striga lutea* Lour. S. Afr. Dep. Agric. Sci. Bull. 128.
- STEEL, R. G. D., and J. H. TORRIE, 1980: Principles and Procedures of Statistics, 2nd Ed. McGraw-Hill, New York.
- TARR, S. A. J., 1962: Diseases of Sorghum, Sudan Grass and Brown Corn. The Commonwealth Mycological Institute, Kew, Surrey, England.
- VASUDEVA RAO, M. J., 1985: Techniques for screening sorghums for resistance to *Striga*. Information Bull. No. 20. ICRISAT, Patancheru, A.P. 502 324, India.
- WRIGHT, S., 1968: Evolution and Genetics of Populations, Vol. 1, 391—403. Genetic and Biometric Foundations, Univ. Chicago Press.

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