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Major and Minor Genes for Stimulation of *Striga hermonthica* Seed Germination in Sorghum, and Interaction with Different Striga Populations

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ABSTRACT

The parasitic angiosperms *Striga hermonthica* (Del.) Benth. and *S. asiatica* (L.) Kuntze severely constrain cereal production in sub-Saharan Africa. A resistance mechanism to these root parasites in sorghum [*Sorghum bicolor* (L.) Moench] is low exudation of striga seed germination stimulants. The trait is controlled by a single recessive gene in the sorghum \times *S. asiatica* interaction, but information is lacking for *S. hermonthica*. Objectives of this investigation were to study the inheritance of stimulation of *S. hermonthica* seed germination in three F₂ and two F_{3,5} recombinant inbred populations of sorghum, and to determine the effects of striga populations from Mali, Niger, and Kenya on the effectiveness of the low-stimulant character. An agar-gel assay was employed for this purpose. In this laboratory assay, the maximal distance between sorghum rootlets and germinated striga seed ("maximal germination distance") reflects the magnitude of germination stimulation. Bimodal frequency distributions supported the hypothesis of one recessive gene with a major effect for low maximal germination distance in progenies from crosses of low-stimulant lines (Framida, IS 9830) with a high-stimulant line (E 36-1), tested with striga from Mali or Niger. However, low- versus high-stimulant classes were not always clearly distinct, indicating that additional minor genes modified maximal germination distance in the progenies. The Kenyan striga population led to higher maximal germination distances and larger overlap of low- and high-stimulant classes than striga from Mali or Niger. Minor genes seemed therefore more important with Kenyan striga seed. The general involvement of minor genes in stimulating *S. hermonthica* seed germination was also evident from the heritable, quantitative variation observed in F_{3,5} lines derived from a cross of the high-stimulant lines N 13 and E 36-1. Because of the higher sensitivity of Kenyan striga to germination stimulation, the low-stimulant character may be less effective in Kenyan fields.

PARASITIC FLOWERING WEEDS of the genus *Striga* (Scrophulariaceae) cause great losses to cereal production in sub-Saharan Africa. The economically most important species are *S. hermonthica* and *S. asiatica*. Two-thirds of the acreage used for cereal production in 17 sub-Saharan countries are estimated to be infested by the parasite (Kim et al., 1998). Most cultivars planted are highly susceptible to striga.

Resistant sorghum cultivars could become a major component of integrated striga control packages if effective host-plant resistance were incorporated into adapted, productive cultivars. The best-described mechanism of resistance in sorghum to the weed is low production of root exudates required by the striga seed to germinate. The major germination stimulant in sorghum is sorgo-lactone (Hauck et al., 1992), whereas sorgoleone and strigol seem to be of minor importance (Ejeta et al., 1992). Other putative mechanisms of resistance to striga include mechanical barriers, inhibition of germ tube exoenzymes by root exudates, phytoalexin synthesis, post-attachment hypersensitive reactions, antibiosis (e.g., unfavorable phytohormone supply by the host), insensitivity to a postulated striga toxin, and avoidance through root growth habit (Ejeta et al., 1992; Ejeta and Butler, 1993; Berner et al., 1995; Heller and Wegmann, 2000). Absence of a haustorial inducer in root exudate is an improbable resistance mechanism since the haustorial inducer 2,6-dimethoxy-parabenzoquinone is thought to be produced by all plants under striga attack (Frick et al., 1996).

The agar-gel assay developed by Hess et al. (1992) is an excellent tool for screening host genotypes in the laboratory for the low-stimulant character (Vogler et al., 1996). Low stimulation of *S. asiatica* seed germination was shown to be inherited as a single recessive gene in the sorghum cultivars Framida, 555, SRN 6496 (Ramaiah et al., 1990), and SRN 39 (Vogler et al., 1996). However, in the study of Vogler et al. (1996), distinction of low- and high-stimulant groups was not very clear. The authors suggested that the F₂ distributions reflected the presence of the three stimulant compounds, sorgo-lactone, sorgoleone, and strigol. Either the major stimulant, or the three separately or in combination, could induce germination in a 1 low: 3 high ratio in the tested F₂ populations.

Quantitative variation with predominance of additive gene effects for maximal germination distance of *S. hermonthica* in the agar-gel assay was reported on the basis of a 9-by-9 diallel-cross study in sorghum (Haussmann et al., 2000). In the same experiment, different general combining ability effects of Framida and line 555 indicated that the low-stimulant genes (or alleles) may differ in these two lines.

While the genetics of stimulation of *S. asiatica* seed

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Table 1. Survey of the sorghum materials and *Striga hermonthica* populations used in the individual agar-gel assays.

| Generation | Cross | N† | Year | Striga population | | |
|----------------|---------------------------------|---------------|------|-------------------|-------|-------|
| | | | | Mali | Niger | Kenya |
| F ₂ | Framida × E 36-1 | 90 | 1996 | x‡ | | |
| | 555 × E 36-1 | 89 | 1996 | x | | |
| | IS 9830 × E 36-1 | 90 | 1996 | x | | |
| F ₅ | IS 9830 × E 36-1 (RIP 1, Set 1) | 696 (116 × 6) | 1997 | x | x | x |
| | IS 9830 × E 36-1 (RIP 1, Set 2) | 660 (110 × 6) | 1998 | x | x | x |
| | N 13 × E 36-1 (RIP 2, Set 1) | 696 (116 × 6) | 1997 | x | x | |

† Number of tested F₂ and F₅ seedlings, respectively. (Six F₅ plants were tested from each of the 116 or 110 F_{3.5} lines.)
 ‡ Each cross marks an individual experiment.

germination have been studied extensively (Ramaiah et al., 1990; Vogler et al., 1996), relatively little is known about the inheritance of stimulation of *S. hermonthica* seed germination and the effect of different striga populations on the expression of this character. Objectives of this investigation were to study the inheritance of stimulation of *S. hermonthica* seed germination in segregating populations of sorghum, and to determine the effects of striga populations from Mali, Niger, and Kenya on the effectiveness of the low-stimulant character.

MATERIALS AND METHODS

Genetic Materials

The genetic materials comprised three F₂ and two F_{3.5} recombinant inbred populations (RIPs) of sorghum (Table 1). The F₂ populations were derived from crosses of the low-stimulant cultivars Framida, 555, and IS 9830 with the high-stimulant line E 36-1. Each F₂ population was represented by

89 or 90 individual F₂ plants. The two recombinant inbred populations were produced from crosses between IS 9830 and E 36-1 (RIP 1), and N 13 and E 36-1 (RIP 2), respectively. Line N 13 is a high-stimulant line with “mechanical” resistance (e.g., lignification of cell walls) to striga under field conditions (Ramaiah, 1987). The crosses were selfed and 226 F₂ plants per population advanced by single-seed descent to the F₄ generation (Fig. 1). The F₄ lines were multiplied by selfing 40 panicles per line, and the resulting F₅ seed was bulked. These F₃-plant derived bulks in F₅ are called F_{3.5} lines here. Each recombinant inbred population was divided into Set 1 (116 F_{3.5} lines, tested in 1997) and Set 2 (110 F_{3.5} lines, tested in 1998), to allow for a verification of the first year’s results. However, for RIP 2, only Set 1 was tested for stimulation of striga seed germination.

Agar-Gel Assay

An agar-gel assay (Hess et al., 1992) was employed to test the various sorghum populations for stimulation of striga seed germination. For each lot of 10 Petri dishes (9-cm diam), 500 mg striga seed were surface-sterilized as described by Hess et al. (1992) and preconditioned for 12 d at 28°C in the dark. About 4500 conditioned striga seed (150Fl of settled seed) were pipetted into each plate. Twenty to 25 mL autoclaved 0.7% (w/v) water agar, cooled but not yet solidified, was poured into each plate in a manner such that a uniform distribution of striga seed throughout the agar was achieved. A 24-h old sorghum seedling was inserted with its rootlet (about 1.5 cm long) into the solidifying agar near one edge of the plate, with the root tip pointing across the plate. Because the sorghum root occasionally fails to grow or grows above the medium, a second seedling was placed opposite to the first, and the one less favorably oriented or less vigorously growing was removed within 12 h. After 5 d of incubation at 28°C in the dark, germination of striga seed was easily visible through the bottom of the plate with a dissecting microscope. The maximal germination distance 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.

Striga Populations and Experimental Design

The three F₂ populations were tested in 1996 by means of *S. hermonthica* seed harvested at Samanko, Mali, in November 1994. Each population was handled as a separate experiment. The 89 or 90 F₂ seedlings per population (resulting in 89 or 90 petri plates), were completely randomized. The parent lines were evaluated in five replications, along with their progenies.

Sets 1 and 2 of RIP 1 (IS 9830 × E 36-1) were evaluated in 1997 and 1998, respectively, by means of *S. hermonthica* populations from Samanko, Mali, Bengou, Niger, and Kibos, Kenya. The respective striga seed had been harvested in 1995 and 1996. Set 1 of RIP 2 (N 13 × E 36-1) was tested in 1997

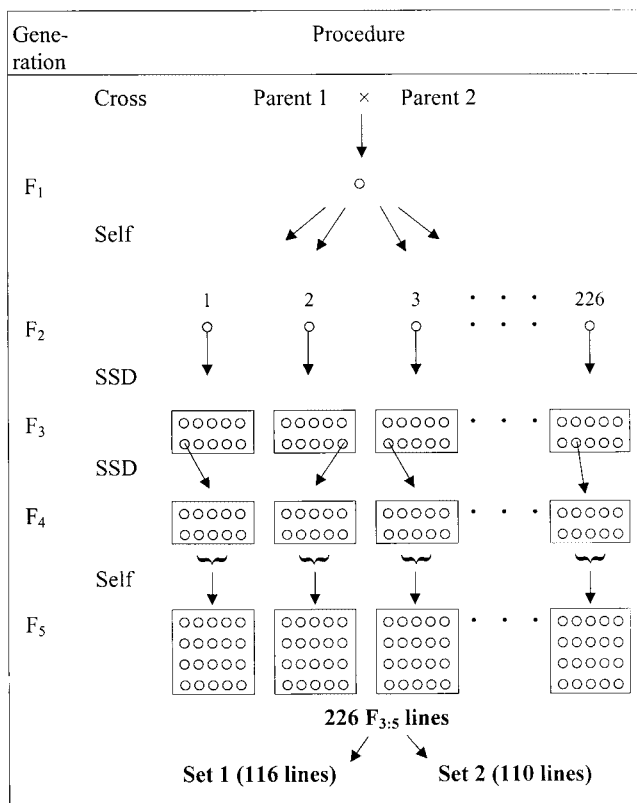


Fig. 1. Schematic representation of the development of the F_{3.5} lines forming the two recombinant inbred populations. SSD = single seed descent; circles = individual plants; rectangles = lines.

with the same two West African striga populations as Set 1 of RIP 1. Because of limited personnel and testing facilities, each genetic material \times striga population combination was analyzed in a separate 11-by-11 lattice design. The $F_{3.5}$ lines of each set were randomized together with the corresponding two parent lines and three (1997) or nine (1998) check cultivars, including the low-stimulant genotype SRN 39 and the Kenyan striga-tolerant cultivar Seredo. Six replications were employed in each experiment. Hence each original F_3 plant was represented by six random F_5 offspring, each in a separate Petri dish. Each experiment was conducted over 3 wk, with two out of the six replications being performed each week.

All tests were carried out in the laboratory at ICRISAT-Mali, except that for Set 1 of RIP 1 with the Kenyan striga seed, which was performed at the University of Hohenheim, Germany. All plates and remnant preconditioned striga seed were autoclaved before final disposal.

Statistical Analysis

The chi-square goodness-of-fit test (Gomez and Gomez, 1984) was used to check the hypothesis of a single recessive gene for low stimulant production in the F_2 populations. Since 25% of the $F_{3.5}$ lines of the RIPs were expected to segregate for the maximal germination distance under the single gene hypothesis, the frequency distributions and the chi-square test were not based on the line means but on the individual F_5 plant data observed in the six replications (696 and 660 in Sets 1 and 2). Ratios of low-stimulant to high-stimulant phenotypes were expected to be 1:3 and 15:17 in the F_2 and F_5 generations, respectively. In the literature, genotypes with a maximal germination distance below 10 mm are usually classified as low-stimulant types (Hess et al., 1992). However, in the present study with multiple populations and no clear border between the low- and high-stimulant types, F_2 or F_5 plants were classified as low-stimulant when their maximal germination distance was below the mean plus twice the standard deviation of the low-stimulant parent.

Analyses of variance combined across striga populations were performed with the lattice-adjusted $F_{3.5}$ -line means of each set of material from the RIPs by the statistical software PLABSTAT (Utz, 1998). The effects of the sorghum genotypes were considered as random and those of the striga populations as fixed. Since the distribution of the data was bimodal in most cases, mean squares were computed instead of variance components, and the F -tests applied are only approximate.

RESULTS

F_2 Populations

Low mean maximal germination distances confirmed the low-stimulant character of the parents Framida, 555, and IS 9830 (Fig. 2). Small standard errors of the parent lines indicated a high precision of the data. The frequency distributions of the three F_2 populations were bimodal, and the F_2 seedlings could be classified into a low-stimulant and a high-stimulant group. The corresponding chi-square test was in agreement with the single-gene hypothesis for low stimulant production (1:3 ratio of low-: high-stimulant seedlings) in the F_2 populations derived from the crosses Framida \times E 36-1 and IS 9830 \times E 36-1 (Table 2). However, there was an excess of low-stimulant plants in the F_2 population derived from the cross 555 \times E 36-1, because of the higher standard deviation of line 555 and, therefore, the higher

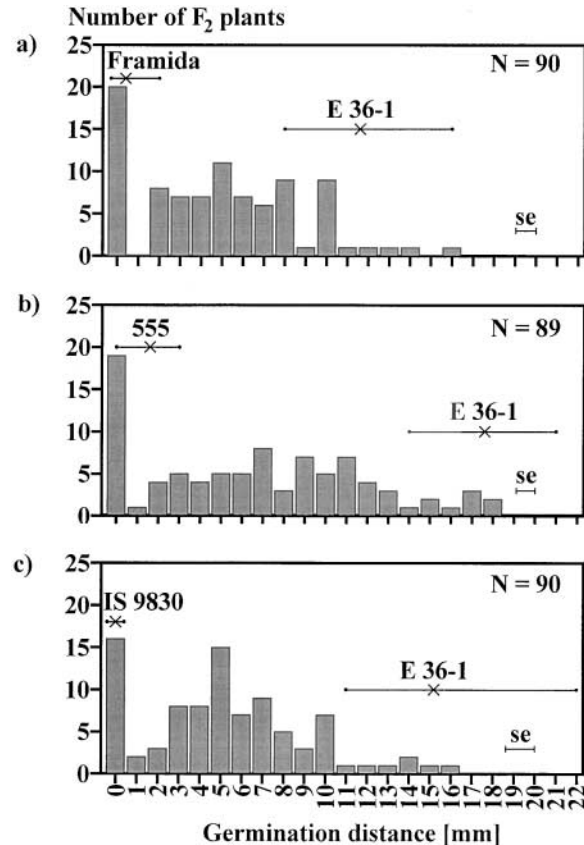


Fig. 2. Frequency distributions for maximal germination distance in the agar-gel assay of F_2 populations derived from the crosses (a) Framida \times E 36-1, (b) 555 \times E 36-1, and (c) IS 9830 \times E 36-1. — \times — indicates the mean and range of observations among seedlings of a given parent line; se = standard error of parent means.

limit for the low-stimulant class. In all three F_2 populations, there was extensive variation within the high-stimulant groups. Most seedlings in the high-stimulant groups had maximal germination distances lower than the high-stimulant parent E 36-1.

RIP 1 (IS 9830 \times E 36-1)

Both sets of $F_{3.5}$ lines of RIP 1, the two parent lines, the low-stimulant standard line SRN 39 and the striga-tolerant cultivar Seredo generally revealed significantly higher mean maximal germination distances with the Kenyan striga than with the two West African striga populations (Table 3).

The frequency distributions of the F_5 plants were bimodal when tested with the two West African striga

Table 2. Chi-square test for deviations from a 1:3 low- (LS): high-stimulant (HS) ratio in the three F_2 populations for maximal germination distance (GD) in the agar-gel assay.

| Cross combination | Range of GD in the LS class† | Observed ratio LS:HS | χ^2 | P |
|-------------------------|------------------------------|----------------------|----------|-----------|
| | mm | | | |
| Framida \times E 36-1 | 0-2 | 28:62 | 1.48 | 0.10-0.25 |
| 555 \times E 36-1 | 0-5 | 38:51 | 13.93 | <0.01 |
| IS 9830 \times E 36-1 | 0 | 16:74 | 2.13 | 0.10-0.25 |

† Upper class limit: mean maximal germination distance + 2 standard deviations of the low-stimulant parent.

Table 3. Means of selected cultivars and the F_{3.5} lines of Sets 1 and 2 of RIP 1 (IS 9830 × E 36-1) for maximal germination distance in the agar-gel assays, using striga seed from Mali, Niger, and Kenya.

| Year | Striga | Mean maximal germination distance (mm)† | | | | |
|-----------------|--------|---|--------|--------|--------|------------------------|
| | | IS 9830 | E 36-1 | SRN 39 | Seredo | F _{3.5} lines |
| 1997 (Set 1) | Mali | 2.7ab | 18.8a | 1.3a | 15.0a | 8.7a |
| | Niger | 0.0a | 18.8a | 0.0a | 17.2a | 9.0a |
| | Kenya | 5.6b | 36.6b | 5.3b | 17.6a | 14.0b |
| 1998 (Set 2) | Mali | 0.8a | 21.8ab | 1.1a | 11.5a | 8.4a |
| | Niger | 0.8a | 20.7a | 0.0a | 13.8a | 8.5a |
| | Kenya | 5.6b | 24.7b | 6.7b | 18.7b | 13.3b |

† Means followed by the same letter within columns and years are not significantly different as determined by the least significant difference between striga populations at the 0.05 probability level.

populations (Fig. 3a and b, left and middle). The chi-square test led to acceptance of the single-gene hypothesis for low stimulant production (15:17 ratio of low:high-stimulant seedlings) in Set 1 with the striga seed from Mali and in Set 2 with both West African striga sources (Table 4). As observed with the F₂ populations, there was broad variation in the high-stimulant groups. No clear bimodality (though a strong negative kurtosis) resulted from the Kenyan striga population (Fig. 3c); therefore, the chi-square test was not applied to the Kenyan data sets.

In the combined analyses of variance across striga populations, the mean squares due to striga populations,

Table 4. Chi-square test for deviations from a 15:17 low- (LS): high-stimulant (HS) ratio in Sets 1 and 2 of RIP 1 (IS 9830 × E 36-1) for maximal germination distance (GD) in the agar-gel assay with striga populations from Mali and Niger†.

| Sorghum material | Striga population | GD range in the LS class‡ | Observed ratio LS:HS | χ ² | P |
|--------------------|-------------------|---------------------------|----------------------|----------------|-----------|
| | | | | | |
| Set 1 (N = 696) | Mali | 0–8 | 328:368 | 0.01 | 0.90–0.95 |
| | Niger | 0 | 268:428 | 19.24 | <0.01 |
| Set 2 (N = 660) | Mali | 0–5 | 300:360 | 0.48 | 0.25–0.50 |
| | Niger | 0–3 | 298:362 | 0.72 | 0.25–0.50 |

† The chi-square test was not applied to the data with the Kenyan striga, since the corresponding frequency distributions were not clearly bimodal.

‡ Upper class limit: mean maximal germination distance + 2 standard deviations of the low-stimulant parent.

F_{3.5} lines, and interaction between F_{3.5} lines and striga populations were highly significant in both sets of material (Table 5). Maximal germination distance was more highly correlated between the two West African striga populations (coefficient of correlation *r* = 0.92 and 0.91 in Sets 1 and 2, respectively, significant at *P* ≤ 0.01) than between either of the West African and the Kenyan striga population (correlation coefficient ranging from 0.74 to 0.87, *P* ≤ 0.01, data not shown).

RIP 2 (N 13 × E 36-1)

Although both parental lines of RIP 2 were high-stimulant types, there was significant genetic variation

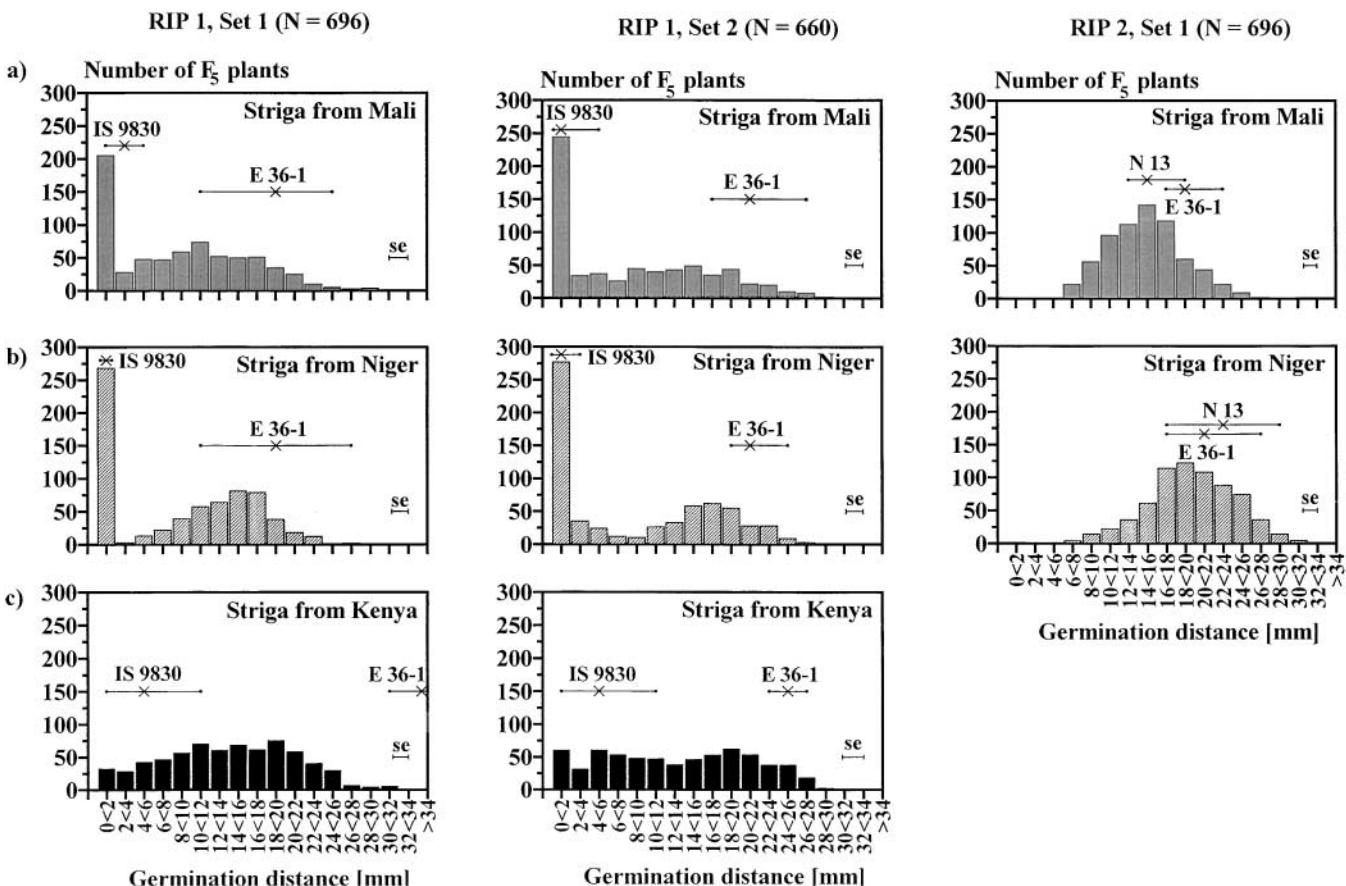


Fig. 3. Frequency distributions of the individual F₅ plants in Sets 1 and 2 of recombinant inbred population (RIP) 1 (IS 9830 × E 36-1) and in Set 1 of RIP 2 (N 13 × E 36-1), for maximal germination distance in the agar-gel assay with striga populations from (a) Mali, (b) Niger, and (c) Kenya. —x— indicates the mean and range of observations among seedlings of a given parent line; se = standard error of parent means.

Table 5. Mean squares of striga populations, F_{3.5} lines, and their interaction in RIP 1 (IS 9830 × E 36-1) and RIP 2 (N 13 × 36-1) for maximal germination distance in the agar-gel assay, combined across striga populations from Mali, Niger and Kenya for RIP 1, and Mali and Niger for RIP 2.

| Source of variation | RIP 1† | | RIP 2 |
|----------------------------|--------------|---------------|--------------|
| | Set 1 | Set 2 | |
| Striga population (S) | (2) 1031.7** | (2) 846.1** | (1) 1405.5** |
| F _{3.5} lines (G) | (115) 99.4** | (109) 121.4** | (115) 9.1** |
| S × G | (230) 7.9** | (218) 5.9** | (115) 3.3** |
| Error | (1596) 3.1 | (1620) 3.7 | (1004) 2.1 |

** Significant at the 0.01 probability level.

† Degrees of freedom for RIP 1, Sets 1 and 2, and RIP 2, respectively, are numbers in parentheses preceding mean squares.

among the F_{3.5} lines for the maximal germination distance (Table 5). The mean squares due to striga populations and interaction effects between F_{3.5} lines and striga populations were also highly significant. The frequency distributions were unimodal and normal for the F₅ seedlings tested with the striga population from Mali (Fig. 3a, right). With the striga population from Niger, the frequency distribution had a slight negative skewness (Fig. 3b, right). Transgressive segregation towards lower maximal germination distances was observed with both striga populations.

DISCUSSION

The observed bimodal frequency distributions for maximal in vitro germination distance of F₂ and F₅ plants from crosses of low- × high-stimulant parent lines tested with West African striga demonstrate the presence of one recessive gene for low stimulation of *S. hermonthica* seed germination. However, in none of the experiments were low- and high-stimulant plants clearly distinct. Because of this fact, it proved difficult to differentiate between the two groups for an unbiased application of the chi-square test. In the present study, the upper limit for the low-stimulant group was defined as the mean plus twice the standard deviation of the low-stimulant parent. About 95.4% of a random sample of homozygous low-stimulant genotypes would be expected to lie within that range (Athen and Bruhn, 1980). The fact that the single-gene hypothesis could not be accepted in all instances, and the large variation observed in the high-stimulant groups suggest that minor genes modify maximal germination distance, possibly by influencing the quantity and/or composition of striga germination stimulants. The involvement of minor genes in stimulation of striga seed germination was also evident from the heritable, quantitative variation observed in progenies derived from a cross between the two high-stimulant lines N 13 and E 36-1. The reported presence of at least three germination stimulants in sorghum root exudates (Ejeta et al., 1992; Siame et al., 1993; Vogler et al., 1996) provides a physiological explanation of multiple genes controlling the stimulation of *S. hermonthica* seed germination.

The Kenyan striga population caused larger maximal germination distances in the parent lines, checks, and the F_{3.5} lines of RIP 1 than the striga populations from Mali and Niger. The observations from the first year

were confirmed in the second year with independent striga seed samples. However, these results need further confirmation with a larger set of sorghum genotypes. It also remains unclear whether Kenyan striga reacts stronger to sorgolactone, the major germination stimulant exuded by sorghum roots, or to sorgoleone and strigol, stimulants thought to be of minor importance (Ejeta et al., 1992). The overlap of low- and high-stimulant groups was so strong, that the frequency distributions of the F_{3.5} lines of RIP 1 challenged with Kenyan striga could not be considered as bimodal or qualitative. This points to the increasing importance of minor genes.

The correlations among the striga populations for maximal germination distance in RIP 1 suggest greatest similarity between the two West-African striga populations. Similarly, Koyama (2000a), using isozyme and random amplified polymorphic DNA (RAPD) marker techniques, found striga samples from West African sites to be more closely related to each other than to an East African population.

Because of the apparently higher sensitivity of the Kenyan striga seed to germination stimulants, the low-stimulant character might be a less effective resistance mechanism in Kenyan than in West African fields. In fact, Omany (2000) found correlations between maximal germination distance and resistance of RIP 1 under field conditions to be stronger in Mali than in Kenya. On the other hand, in diallel crosses of sorghum, Haussmann et al. (2001) observed stronger correlations between maximal germination distance and resistance under field conditions in Kenya than in Mali. According to Vasudeva Rao (1984), correlations between weak stimulation of striga seed germination and resistance in the field are mostly positive, but depend on the materials under investigation and the test environments. Wegmann (personal communication, 1997) suggests that specific conditions like ethylene production by microorganisms caused by abiotic stress could render the low-stimulant character less effective in certain site × season combinations.

Significant genotype × environment interactions for striga resistance in sorghum have been reported by several authors (e.g., Ramaiah, 1987; Haussmann et al., 2001; Omany et al., 2000). In field trials across diverse geographic regions, the total genotype × environment interaction variance comprises interaction effects between genotypes and locations (soil, temperature, precipitation, etc.), between genotypes and putative striga races or biotypes, and the corresponding three-way interaction. The three types of interaction, however, could only be separated by evaluating the sorghum materials at each location against striga populations of different geographic origin. For reasons of quarantine, this cannot be done in Africa. In the present agar-gel assays with the two RIPs, the importance of F_{3.5}-line × striga population interaction was relatively small, as indicated by the rather high correlations among the various striga populations. However, these results concern just one resistance mechanism to striga, i.e., stimulation of striga seed germination. Other host-parasite interaction mechanisms such as penetration of striga into the host roots and subsequent growth of the parasite need to be stud-

ied as well. *Striga* was reported to be a genetically highly variable parasite, and to have an extraordinary capacity to adapt to new hosts (Ejeta et al., 1992; Koyama, 2000b). Resistance to *striga* is partially species-specific, i.e., resistance to *S. asiatica* does not necessarily hold against *S. hermonthica* and vice versa (Ramaiah, 1984). *Striga hermonthica* populations with specific adaptation to sorghum and millet [*Pennisetum glaucum* (L.) R. Br.] have been reported, whereas other *striga* sources attack both host species (Vasudeva Rao and Musselman, 1987; Hess, 1994; Freitag et al., 1996). Koyama (2000b) found evidence for low selection pressure on *S. hermonthica* populations parasitizing susceptible sorghum varieties, and increasing selection pressure—reducing the genetic variability of the *striga* population—on tolerant and resistant varieties.

There is a lack of information about the population genetics of *striga* virulence. A better understanding of the variation for virulence among and within *striga* populations would facilitate the effective deployment of resistance genes against these parasites (Lane et al., 1997). There is need to resolve the origin and relatedness of parasitic races, and to elucidate the observed race \times variety interactions. However, the high degree of self-incompatibility of *S. hermonthica* would render this endeavor very difficult.

Variability among *Striga* spp. as well as intraspecific variation must be taken into account when breeding for *striga* resistance (Ramaiah, 1987; Ejeta et al., 1992). In order to obtain stable resistance, breeding materials should be evaluated against multiple *striga* populations differing in host-specificity and across environmentally diverse testing sites.

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