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Inheritance of Striga seed-germination stimulant in sorghum

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Summary

Inheritance of *Striga* seed-germination stimulant in sorghum was investigated on three low-stimulant cultivars viz., 555, Framida, SNR 6496 and six high-stimulant cultivars viz., Swarna, NJ 2006, IS 508, 168, 148 and M 35-1 using seeds of *Striga asiatica* collected at ICRISAT Center. From a study of parents, F_1, F_2, and the backcross F_2 seedling progenies, it was concluded that low-stimulant production in all the three parents is under the control of a single recessive allele. Whether the allele is the same in all of them is yet to be determined. Implications of these findings in *Striga*-resistance breeding are discussed.

Introduction

The seeds of *Striga* remains viable in the soil for several years, and do not germinate unless they are stimulated to do so by the root exudates of certain crop species (see review by Pieterse & Pesch, 1983). All the subceptible host crops like sorghum, pearl millet, maize, etc. and trap crops like cotton, groundnuts, soybean, etc. possess stimulant substance(s) in their root exudates. Cook et al. (1972) identified one natural stimulant, strigol, in the root exudate of cotton. Visser & Botha (1974) identified a wide range of stimulant compounds exuded by different crop species. Johnson et al. (1976) synthesized several strigol analogs in the laboratory. Whether the stimulant substance present in sorghum root exudates is strigol is not yet confirmed. Subsequently, a laboratory technique was developed to identify low-stimulant cultivars which produce no or very low quantities of stimulant (Parker et al., 1977). Low or negligible production of this stimulant is one potential form of resistance. Cultivars resistant to *Striga* due to low stimulant production are known (Kumar, 1949; Rao, 1948; Williams, 1959; Parker et al., 1977; Ramaiah, 1978). The results of inheritance studies of this stimulant production are discussed in this paper. The term stimulant, as used herein refers to that component of the sorghum root exudate that germinates the strain of *Striga asiatica* that exists at ICRISAT Center.

Materials and methods

Three sorghum cultivars, Framida, SRN 6496, and 555 were used as low-stimulant and six cultivars, Swarna, NJ 2006, IS 508, M 35-1, 148, and 168 as high-stimulant parents for this study (Table 1). The *Stiga asiatica* seeds used in this study were collected from sorghum fields at ICRISAT Center, in March 1975.

Nine crosses were made between low- and high-stimulant parents (Table 2). Two of these crosses

(Swarna × Framida) and (Swarna × SRN 6496) were backcrossed to both parents. Since there was no simple laboratory technique to screen single plants in F_2 and backcross generations, the individual F_2 and backcross plants were advanced to obtain F_3 and backcross F_2 seed for progeny test using the double pot technique (Parker et al., 1977). Each such progeny traces back to one individual F_2 or backcross plant

The double-pot technique in which two pots are used one inside the other to score for stimulant production is briefly described below.

I. Pre-conditioning of *Striga* seeds. *Striga* seeds were surface sterilized with sodium hypochlorite (1% as available chlorine) for 5 min. The dried *Striga* seeds were sprinkled on moistened 8 mm diameter glass-fibre filter paper discs (20 to 30 seeds per disc) and preconditioned in an incubator at 25° C and at optimum moisture for 10 to 14 days.

II. Growing sorghum seedlings. Sorghum seeds were surface-sterilized with sodium hypochlorite (1% as available chlorine) for 25 min. and allowed to germinate in petri dishes. After 24 hr 15 seedlings were transferred to each pot filled with sand sterilized in boiling water for one hr and watered. Two replications were used for each progeny. The sorghum seedlings were allowed to grow for 7 to 10 days after which the root exudate was extracted using a suction pump.

III. Germinating *Striga* seeds. The root exudate (20 l) was added to the *Striga* seeds on each glass-fibre filter paper disc. Each replication had four discs.

As the laboratory is equipped for screening only 20 progenies per day, the screening extended over several days. The differences in germination observed from batch to batch were adjusted by using a susceptible cultivar Swarna, which was included in each batch. The mean percent germination of each test entry has been expressed in terms of percent germination of Swarna, and is termed *Striga* seed-Germination Index (SGI).

Table 1. Mean *Striga* seed-germination index of parents

Parent	Origin	*Striga* seed-germination index (%) ± S.E.
Swarna	India	100 ± 10.7
NJ 2006	India	64 ± 2.6
IS 508	India	95 ± 11.8
168	India	86 ± 1.6
148	India	98 ± 0.4
M 35-1	India	95 ± 9.4
555	India	0
Framida	South Africa	1 ± 1.0
SRN 6496	Sudan	1 ± 0.8

Results

The SGIs of parents are presented in Table 1. The data clearly indicate large genotypic differences among the parents. The high stimulant parents showed large variation ranging from 64.06% for NJ 2006 to 100.00% for Swarna. In fact, when Swarna was tested in 24 different experiments a range of 58 to 154% with a mean of 100.00% and standard error of 25.5% was found. However, there is much less variability among low stimulant parents for SGI's less than 10%, and in most cases, less than 1%. In high-stimulant cultivars, the stimulant production varies depending upon environmental factors but they are never misclassified as low stimulant.

Swarna × SRN 6496. The frequency distribution of SGI of both parents, their F_1, F_2, and backcross F_2s are shown in Fig. 1. Swarna and SRN 6496 are clearly high- and low-stimulant producers, respectively. The mean SGI of F_1 was close to Swarna thus showing the dominance of high over low stimulant production. The distribution of SGIs of F_3s ranged from 0% to more than 100%. Clear differences were observed between low-stimulant types (0 to 10%) and the rest. Assuming a one-gene hypothesis, the F_3s are expected to have 25% of their progenies derived from homozygous recessive F_2 plants (low stimulant), 50% progenies from heterozygous F_2 plants and 25% from homozygous-dominant F_2 plants (high stimulant). Since the test was made on 30 seedlings from each progeny rather than on

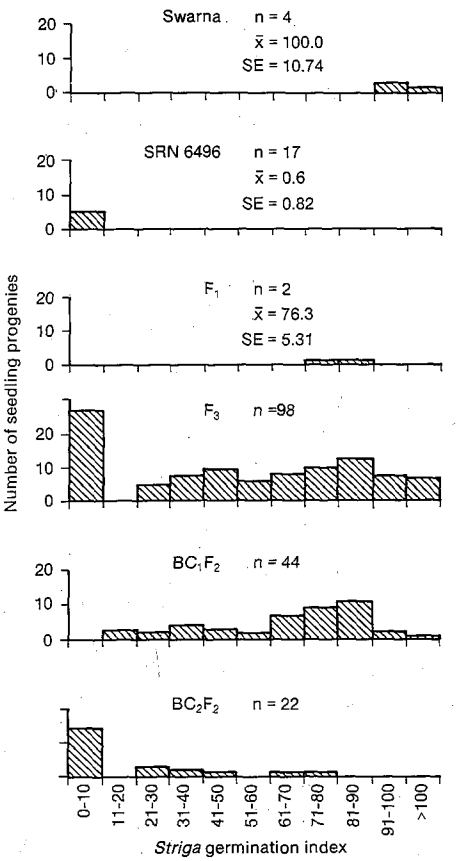

Fig. 1. Frequencies of number of plant progenies for *Striga* seed-germination index of parents (Swarna × SRN 6496), F_1, F_3, BC_1F_2, and BC_2F_2.

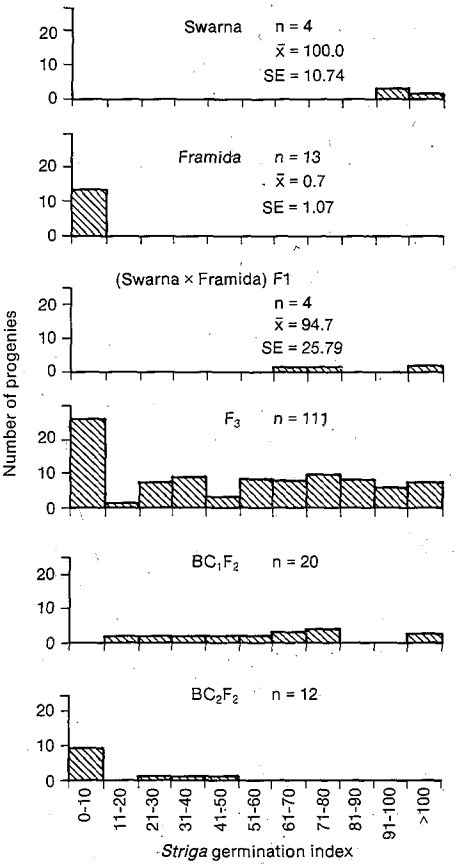

Fig. 2. Frequencies of number of plant progenies for *Striga* seed-germination index of parents (Swarna and Framida), F_1, F_3, BC_1F_2, and BC_2F_2.

individual plants and as the character is controlled by seedling genotype, the SGI of progenies from heterozygous F_2 plants would vary depending upon the proportion of high-stimulant seedlings. However, among the progenies of such heterozygous F_2 plants, 75% of the plants produce high stimulant thus bringing the whole progeny within the range of the high stimulant progenies. If we classify F_3 progenies with SGI ranging from 0 to 10% low-stimulant types and the rest as high-stimulant types, the ratio expected is 1 : 3. The X^2 test to fit this ratio was found nonsignificant (Table 2), thus indicating that this character is under one-gene control.

One-gene control of stimulant production in this cross was also confirmed from an evaluation of backcross progenies. Backcrosses with SRN 6496 segregated into 1 (high stimulant) : 1 (low stimulant) as per expectations (Table 2) thus confirming the segregation of a single gene.

Swarna × *Framida.* The progeny distribution of SGI of both parents, their F_1, F_2, and backcross F_2 progenies is shown in Fig. 2. In this cross also F_1 had high-stimulant production indicating the dominance of high over low-stimulant production. The frequency distribution of SGIs of F_3s and backcross progenies was similar to Swarna × SNR 6496 cross. The F_3 distribution fitted a 3 : 1 ratio. Backcross to Swarna produced all high-stimulant progenies while backcross to Framida segregated into 1 high stimilant : 1 low stimulant. In this cross also the parents differed by a single gene.

Table 2. Segregation pattern in F_3 and backcross (BCF_2) seedling progenies of two crosses

Cross	Number of			Ratio expected	X^2	Probability
	High stimulant	Low stimulant	Total			
Cross-I						
F_3 of Swarna × SRN 6496	71	27	98	3:1	0.217	0.50–0.70
Swarna (Swarna × SRN 6496)	44	0	44	1:0	–	–
SRN 6496 (Swarna × SRN 6496)	8	14	22	1:1	1.136	0.20–0.30
Cross II						
F_3 of Swarna × Framida	85	26	111	3:1	0.074	0.70–0.80
Swarna (Swarna × Framida)	20	0	20	1:0	–	–
Framida (Swarna × Framida	3	9	12	1:1	2.083	0.30–0.50

Other crosses. Several other crosses were made between low and high-stimulant parents (but field-resistant with some other mechanism of resistance) in order to combine both the resistance mechanisms. A few F_3 seedling progenies of seven such crosses were screened for stimulant production. The frequency distribution of SGIs are shown in Fig. 3. In all these crosses low-stimulant progenies were discrete and accounted for 25% of the total number of progenies. The progenies of homozygous-dominant and heterozygous F_2 plants were indistinguishable (all were high stimulant) as in the previous two crosses. The X^2 value (based on 3:1 ratio) was found significant for all the crosses (Table 3). The test for heterogeneity was nonsignificant and, hence, the crosses are in agreement with one another regarding the 3:1 ration of segregation.

Discussion

Inheritance of resistance to *Striga* in sorghum has not been well understood. Saunders (1933) reported that field resistance to *Striga asiatica* of South Africa in two of the three crosses studied was recessive and in the third was partially dominant. Chandrasekharan & Parthasarathy (1953) reported the dominant nature of resistance to *S. asiatica* of India, whereas Narasimhamurty & Sivaramakrishnaiah (1963) reported it to be recessive. Ramaiah & Chidley (1977) screened a wide range of sorghum

Table 3. Segregation pattern in F_3 seedling progenies

Cross	Number of			X^2 (based on 3:1 ratio)	Probability
	High stimulant	Low stimulant	Total		
NJ 2006 × Framida	35	9	44	0.273	0.50–0.70
555 × IS 508	24	5	29	0.563	0.30–0.50
555 × 168	30	8	38	0.140	0.70–0.80
148 × 555	27	6	33	0.495	0.30–0.50
Framida × 168	19	5	24	0.056	0.80–0.90
148 × Framida	26	8	34	0	0.99
M 35-1 × 555	16	3	19	0.439	0.50–0.70
Total	177	44	221	2.789	0.05–0.10
Heterogeneity				1.618	0.95–0.98

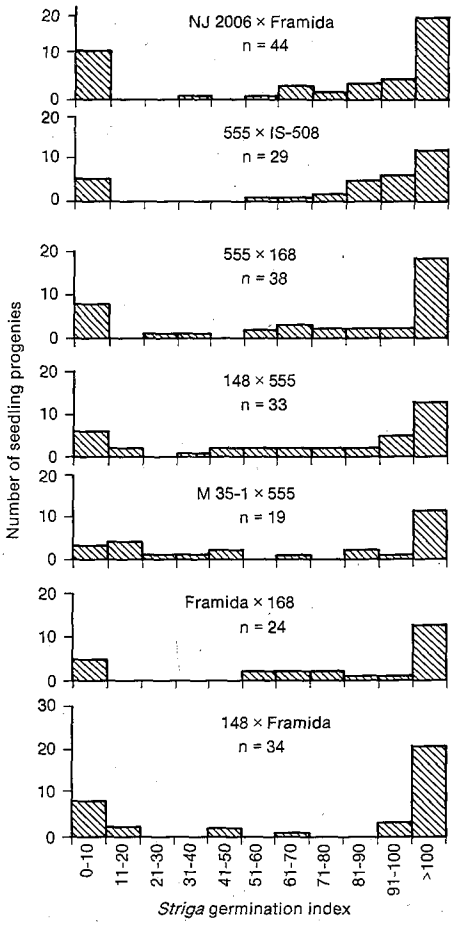

Fig. 3. Frequencies of number of plant progenies for SGI of F_3 seedling progenies of several crosses between low- and high-stimulant parents.

cultivars for stimulant production in the laboratory and observed two groups – low- and high-stimulant types – with very few intermediates. The present study clearly demonstrates one recessive gene for low-stimulant production. The allelism for low-stimulant production needs further investigation.

The single gene control of stimulant production and the availability of double pot technique to screen F_3 seedling progenies to identify the low-stimulant ones are very helpful in a breeding program aimed at transferring the low-stimulant trait into elite agronomic background. The laboratory screening of advanced generation lines of crosses between low and high stimulant parents by Vasudeva Rao et al. (1983) revealed a higher proportion of low stimulant lines showing field resistance supporting the usefulness of low stimulant form of resistance. Our present results of single gene control of stimulant production open up possibilities for detailed genetic investigation involving over 600 low-stimulant sorghum cultivars that are now available at the ICRISAT Center to determine if there are different genes controlling this trait. Identification of different genes for low-stimulant production and their use in gene pyramiding to reinforce resistance to *Striga* will be of great value in breeding improved resistant sorghum cultivars.

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