Trichomes in Segregating Generations of Sorghum Matings. II. Association with Shootfly Resistance[1]

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ABSTRACT

The shootfly (*Atherigona soccata* Rond.) is a major seedling pest of sorghum in Asia and Africa. To determine whether the presence of nonglandular trichomes on the leaf lamina was associated with resistance to shootfly, trichomed, segregating, and trichomeless F_2-derived lines in the F_3 and F_4 from four trichomed × trichomeless sorghum matings and their parents were studied at ICRISAT Center, Patancheru, India. Trichomed lines had significantly lower percentages of plants with shootfly eggs 18 days after emergence and of deadhearts (killed central shoot) at both 18 and 23 or more days after emergence. The ratio of the difference between the means of trichomed and trichomeless lines for the percentage of deadhearts to the corresponding difference between the parents ranged from 0.16 to 0.92 and exceeded 0.32 in seven of nine comparisons. Thus, trichomes were clearly a major factor, but not the only factor, involved in resistance. Means of the parents and trichomed, segregating, and trichomeless offspring were regressed on four possible genetic models. The results indicated that at least two additional loci that interact with each other were involved in resistance. Trichome density was examined as a possible factor in resistance, but correlation of deadheart percentage with the density of trichomes was low and nonsignificant.

Additional index words: Sorghum bicolor (L.) Moench, *Atherigona soccata* Rond., Trichome density, Oviposition nonpreference.

SHOOTFLY (*Atherigona soccata* Rond.) is a serious pest of sorghum [*Sorghum bicolor* (L.) Moench] in South Asia and in several parts of Africa (Young and Teetes, 1977). The female fly lays a single egg on the abaxial surface of the leaf blade, usually on the third to sixth leaves of the seedling (counting the coleoptile as the first). Two to 3 days later, the larva emerges, crawls between the leaf sheaths, and severs the growing point (Ponnaiya, 1951a, 1951b). Damage to the growing point usually induces tillering, but grain yield is considerably reduced even if the tillers escape shootfly attack.

Trichomes, found in some germplasm lines of sorghum (ICRISAT, 1978), confer resistance to a number of insect pests in various crop species (Webster, 1975; Norris and Kogan, 1980). Pubescence imparted resistance to the cereal leaf beetle (*Oulema melanopus* L.) in common wheat (*Triticum aestivum* L.) via both oviposition nonpreference and antibiosis (Gallun et al., 1973; Schillinger and Gallun, 1968). In sorghum, both Blum (1968) and Langham (1968) suggested that prickle hairs (short, pointed trichomes) on the leaf sheath confer shootfly resistance. Germplasm lines of sorghum with trichomes on the leaf lamina were significantly more resistant than glabrous lines (ICRISAT, 1978). Evidently, both oviposition nonpreference and interference with larval migration to the growing point were involved. Lines possessing both trichomes and the glossy-leaf seedling character were more resistant than lines with only one of these traits (Maiti and Bidinger, 1979). Most shootfly-resistant lines originated in central India where they have been selected during many generations for adaptation to local conditions and, consequently, may have several characteristics in common. Therefore, unselected lines of matings between trichomed and trichomeless parents were tested to isolate the effect to trichomes. The objectives of this study were to determine 1) if trichomed F_2-derived lines in the F_3 and the F_4 were more resistant to shootfly than the trichomeless lines originating from the same mating, 2) if a genetic model could be found which would adequately account for the differences in means of shootfly damage between the two parental lines and their trichomed, segregating and trichomeless progeny, and 3) if trichome density was correlated with shootfly resistance in the trichomed lines.

MATERIALS AND METHODS

Genetic Materials. The mating, generation, and number of F_2-derived lines in the F_3 and F_4 from four trichomed (+) × trichomeless (−) matings are shown in Table 1. F_3 lines were derived from random F_2 selfed plants and classified as homozygous trichomed, segregating, or homozygous trichomeless, based on leaf samples from 10 to 15 plants. The sampling procedure followed was as described by Gibson and Maiti (1982) and Maiti et al. (1980). F_4 lines were bulks of equal amounts of seed from 6 to 10 selfed F_3 plants. Seed was multipled when shootfly levels were low and with 1.2 kg carbofuran/ha applied to preclude shootfly attack.

Sampling F_4 lines of 'IS 1054' × 'B CK60' confirmed that they corresponded to their F_3 ancestors for trichome presence or absence. This correspondence was assumed for the F_4 lines of IS 5604 × B CK60 because trichome presence is controlled by a single locus in this and other crosses (Gibson and Maiti, 1982).

Experiments 1 to 5 contain the same F_2-derived lines of IS 1054 × CK60B in the F_3 or F_4, except for a few lines omitted from some experiments because of lack of seed. The F_2-derived lines of IS 5604 × B CK60 correspond exactly in Exp. 6 to 8, except that two lines were omitted in Exp. 6.

The two matings (Exp. 9 and 10) with A-line female parents (cytoplasmic-genic male steriles) produced some male-sterile F_2 plants, but there was no significant departure from the segregation ratios expected for single-gene inheritance in the F_3 lines of either 'A Kaffinum' or 'A 3659' × 'En 3332-2' (Gibson and Maiti, 1982). Therefore, we included these matings, recognizing that the number of lines sampled was not sufficient to exclude the possibility of linkage between the trichome and male-sterile loci.

Evaluation of Shootfly Resistance. Of the 10 experiments listed in Table 1, all but Exp. 5 and 6 (described later) were conducted with similar techniques during December of 1978 to March 1979 (late post-rainy season) at ICRISAT Center on heavy black soils (Vertisols). These eight experiments each were planted in a simple lattice design, with 5 to 13 repetitions of each parent and various numbers of other checks to complete the lattice. In each experiment, results were analyzed as a randomized complete block (RCB) including only parents and derived lines because the lattice analysis failed to give a lesser error mean square. Plots were single rows

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Table 1. Means of percentage of plants with shootfly eggs (E) and of plants with deadhearts (DH) of trichomed, segregating, and trichomeless sorghum lines and their parents.

Group	Entries	E	DH	Entries	E	DH	Entries	E	DH	Entries	E	DH
	No.	—— %‡ ——		no.	—— % ——		no.	—— % ——		no.	—— % ——	
	Exp. 1-IS 1054 (+) × B CK60 (−), F_3†			Exp. 2-IS 1054 (+) × B CK60 (−), F_3			Exp. 3-IS 1054 (+) × B CK60 (−), F_4					
Trichomed parent	9	20.6 a	32.4 a	13	19.8 a	43.2 a	10	18.4 a	23.8 a			
Trichomed lines	33	24.2 a	45.1 b	29	19.5 a	45.6 a	40	23.4 a	42.9 b			
Segregating lines	57	35.2 b	56.8 c	--	--	--	69	31.6 b	54.4 c			
Trichomeless lines	32	37.9 b	60.9 c	28	25.0 a	64.8 b	34	36.4 bc	58.9 d			
Trichomeless parent	10	51.4 c	68.6 d	13	42.0 b	70.3 b	9	41.8 c	59.9 cd			
Ratio§	--	0.25	0.43	--	0.25	0.71	--	0.56	0.44			
	Exp. 4-IS 1054 (+) × B CK60 (−), F_4			Exp. 5-IS 1054 (+) × B CK60 (−), F_4			Exp. 6-IS 5604 (+) × B CK60 (−), F_4					
Trichomed parent	10	30.1 ab	29.7 a	--	--	--	5	86.9 a	68.9 a			
Trichomed lines	41	26.1 a	39.1 b	40	89.1 a	50.7 a	26	89.1 a	83.7 b			
Segregating lines	--	--	--	--	--	--	--	--	--			
Trichomeless lines	37	35.2 b	58.2 c	37	90.8 a	69.4 b	28	91.5 a	87.6 b			
Trichomeless parent	10	38.4 b	54.0 c	--	--	--	5	96.3 b	93.6 c			
Ratio	--	1.10	0.79	--	--	--	--	0.26	0.16			
	Exp. 7-IS 5604 (+) × B CK60 (−), F_3			Exp. 8-IS 5604 (+) × B CK60 (−), F_4			Exp. 9-A Kaffinum (−) × IS 1082 (+), F_3			Exp. 10-A 3659 (−) × EN 3332-2 (+), F_3		
Trichomed parent	10	--	13.7 a	10	--	24.1 a	5	--	28.9 a	5	--	42.0 a
Trichomed lines	26	--	35.5 b	26	--	48.4 b	7	--	48.8 b	14	--	48.4 a
Segregating lines	40	--	52.6 c	40	--	60.4 c	28	--	57.5 bc	21	--	61.9 b
Trichomeless lines	30	--	55.9 cd	30	--	64.8 c	13	--	59.0 c	12	--	68.7 c
Trichomeless parent	10	--	59.2 d	10	--	63.8 c	5	--	81.2 d	5	--	64.1 bc
Ratio	--	--	0.45	--	--	0.41	--	--	0.20	--	--	0.92

† Trichomed and trichomeless parents indicated by (+) and (−), respectively.

‡ Values presented are the percentages obtained from means of arcsin × (transformed data)$^{-1/2}$. Means followed by the same letter did not differ significantly at P = 0.05 when tested by pairwise two-tailed t-tests (tests performed on transformed data). The pairwise t-test was used because each mean had a different standard error (obtainable using the mean square of Table 2, the number of reps given in text, and the number of lines involved in that mean).

§ Ratio = (trichomeless-trichomed lines)/(trichomeless-trichomed parent).

of 4 m, with 75 cm between rows. Twenty kg each of N and P_2O_5/ha were applied at sowing, and irrigation was supplied as needed. The number of seeds planted was about twice the desired number of seedlings. Thinning to 10 cm between plants at 7 to 10 days after emergence preceded the appearance of deadhearts (desiccation and browning of the central leaf or two in the whorl is the characteristic symptom of shootfly damage). Just after thinning, the total number of plants per plot was recorded. Plots were allowed to grow with natural shootfly infestation. In Exp. 1 to 6, the number of main culms with eggs was recorded approximately 18 days after emergence. By 40 days after emergence, no new shootfly deadhearts appeared, and the number of main culms without deadhearts due to shootfly was counted in all experiments. Occasional main culms (usually none, but infrequently as many as five per plot) were found with deadhearts due to stem borers [*Chilo partellus* (Swinhoe) and *Sesamia* spp.]. Differences in the appearance of the deadheart symptom, the presence of the characteristic exit hole of the borer at the base of the stem, and where necessary, examination of the inside of the stem for borer feeding was used to differentiate deadhearts due to borer from those due to shootfly. Borer infestation appeared usually after shootfly attack subsided, so plants with borer deadhearts were counted as unaffected by shootfly. All percentages underwent arcsin square-root transformation to equalize variances. Plots with 0 or 100% deadhearts were adjusted according to Snedecor and Cochran (1967).

Four genetic models were fitted by weighted linear regression to the means of parents and of trichomed, segregating, and trichomeless lines. The inverse of the squared standard error of each group mean was used as the weighting factor (Mather and Jinks, 1971). The models fitted were 1, trichomes only; 2, trichomes plus genes operating additively; 3, trichomes plus genes dominant for susceptibility; and 4, trichomes plus genes having duplicate dominant type of digenic epistasis for susceptibility. These genetic models were selected to represent the simplest possibilites consistent with the authors experience with the inheritance of shootfly resistance. Each model included an intercept, and the coefficient for each term was the expected frequency of genotypes exhibiting a resistance effect (Table 2). The concepts of components of means (Mather and Jinks, 1971) and the partitioning methods of genetic analysis (Powers et al., 1950) were used to develop the regression models. These models are dependent only on the type of gene action and not on the number of genes involved and are independent of linkage except in model 4, in which tightly linked pairs of interacting loci would affect the means similarly to dominant single loci of model 3 and less tightly linked loci would affect the means intermediate to model 3 and 4. The adequacy of each model was tested by assuming the deviations from the model were distributed as Chi^2 (Cavalli, 1952).

Table 2. Coefficients used in regression of percentage of shootfly deadhearts of F_2-derived F_3 and F_4 lines on four genetic models. Coefficients for the F_4 are in parentheses if different from those for the F_3.

	Term in model†			
Group	T	A	D	I
Resistant parent	1	1	1	1
Trichomed lines	1	1/2	3/8 (7/16)	9/64 (49/256)
Segregating lines	1/4 (3/8)	1/2	3/8 (7/16)	9/64 (49/256)
Trichomeless lines	0	1/2	3/8 (7/16)	9/64 (49/256)
Susceptible parent	0	0	0	0

† T = trichomes, A = genes additive for resistance, D = genes dominant for susceptibility, and I = pairs of genes exhibiting duplicate dominant epistasis for susceptibility. See text for additional description of the models tested.

Experiment 5. This experiment was conducted during the postrainy season of 1978. Only homozygous trichomed and trichomeless F_4 lines of IS 1054 × B CK60 were grown in a randomized complete block design with three replicates. Plots were single rows, 2 m long with 45 cm between rows and 10 cm between plants. Fishmeal attractant was applied 10 days after emergence to increase shootfly attack. The final number of deadhearts was counted

Table 3. Mean squares for percentage of plants with shootfly deadhearts (transformed to angles) within sorghum parent and within trichomed, segregating, and trichomeless derived lines.

	Within group mean square for experiment†									
Group	1	2	3	4	5	6	7	8	9	10
Resistant parent	77.0	70.0	155.5*	39.9	--	69.2	41.5	20.1	39.6	53.0
Susceptible parent	55.8	38.6	95.7	55.9	--	14.4	58.4	85.0	52.2	61.6
Trichomed lines	127.0**	86.0**	69.4	74.7	128.8	147.3*	139.4**	135.0**	52.4	136.2**
Segregating lines	50.3	--	80.8	--	--	--	148.6**	82.2**	52.4	69.0
Trichomeless lines	100.2	64.9	64.9	56.1	178.6**	135.6**	134.6**	90.6	57.7	39.4
Experimental error	66.5	48.4	62.6	75.9	107.7	58.8	68.1	43.6	48.8	40.4

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

† Degrees of freedom for each value can be obtained from the number of lines given in Tables 2 and 3 and the number of replications given in text. Mean squares are reported on a individual-plot basis.

Table 4. Total and residual sums of squares for the percentage of sorghum plants with shootfly deadhearts (transformed to angles) regressed on genetic models including trichomes and other genes for resistance, along with Chi² probabilities of obtaining a larger residual sum of squares if the model is adequate.†

			Model‡							
	Total		T		T + A		T + D		T + I	
Experiment	df	SS (weighted)	Residual SS	P	Residual SS	P	Residual SS	P	Residual SS	P
1	4	89.34	14.45**	0.002	0.86	0.651	0.04	0.980	3.58	0.167
2	3	110.18	4.90	0.086	0.62	0.431	1.63	0.202	3.73	0.053
3	4	93.02	17.36**	0.001	10.50**	0.005	8.37*	0.015	1.80	0.407
4	3	147.97	13.18**	0.001	10.42**	0.001	9.01**	0.003	3.86	0.049
6	3	50.32	24.07**	<0.001	2.44	0.118	0.95	0.330	1.09	0.296
7	4	326.07	50.00**	<0.001	31.85**	<0.001	18.14**	<0.001	0.93	0.628
8	4	347.09	76.91**	<0.001	42.84**	<0.001	32.32**	<0.001	5.85	0.054
9	4	119.72	45.76**	<0.001	0.39	0.823	5.31	0.070	22.15**	0.001
10	4	47.35	2.37	0.499	2.37	0.306	2.24	0.326	1.57	0.456

*,** Significant at the 0.05 and 0.01 levels of probability, respectively.

† The residual sums of squares are expected to be distributed as Chi² with n-t degrees of freedom if the model is adequate, where n = the number of group means in the experiment and t = the number of terms in the model, including the intercept.

‡ T = trichomes, A = genes additive for resistance, D = genes dominant for susceptibility, I = pairs of genes exhibiting duplicate dominant epistasis for susceptibility.

23 days after emergence because plant growth was rapid and deadheart formation had ceased by then. Data were analyzed as described for the other experiments.

Experiment 6. This experiment was grown during July-August 1979 (rainy season) in a quadruple lattice design analyzed as an RCB. One hundred kg N/ha and 40 kg P_2O_5/ha were applied. Otherwise, management practices and data analysis were as in the other experiments.

Trichome Density. Density of Trichomes/mm² was determined from the central portion of the abaxial leaf surface for the trichomed F_3 and F_4 lines of IS 1054 × B CK60 and the trichomed F_3 lines of IS 5604 × B CK60. Most shootfly egg laying occurs between the third and sixth leaves. Consequently, in each plot, the fourth leaf was sampled on 10 plants, and the fifth leaf on 10 additional plants. Each sampled leaf section was cleared following the methods described by Maiti et al. (1980), and the number of trichomes was counted in two 0.8 mm² microscope fields. The average density for leaves 4 and 5 was then correlated with deadheart data from infested plots of the same lines in a different field. Means of the percentage deadhearts (angular transformation) from Exp. 1 and 2 were averaged for each trichomed line, as were those from Exp. 3 and 4, and were correlated with trichome density in the F_3 and F_4, respectively, of IS 1054 × B CK60. Trichome density of F_3 lines of IS 5604 × B CK60 was correlated with F_3 and F_4 deadheart data from Exp. 7 and 8, respectively.

RESULTS AND DISCUSSION

The mean of the trichomed lines for the percentage of main culms with shootfly deadhearts was significantly less than those of the trichomeless lines in every experiment, except in Exp. 6, in which the difference approached significance at P = 0.05 (Table 1). The trichomed lines had a significantly smaller percentage of plants with eggs in three of six instances. High levels of egg laying may have obscured differences between trichomed and trichomeless lines in Exp. 5 and 6. Differences between trichomed and trichomeless percentage of deadhearts ranged from 4 to 20% (3.2 to 11.9° transformed). The ratio of the difference between trichomed and trichomeless lines to the difference between the parent ranged from 0.32 to 0.92, except in Exp. 6 and 9, in which the ratio was 0.16 and 0.20, respectively. These ratios indicate roughly the proportion of shootfly resistance that can be ascribed to the presence of trichomes.

It is clear that trichomes (including possible pleiotropic effects of the same genetic locus and/or effects of closely linked genes) are responsible for a significant portion of the resistance observed in the resistant parents used here. The effects of trichomes varies in magnitude among crosses, and Exp. 6 and unpublished data of the authors suggest that trichomes may be less effective during the rainy season than during the post-rainy season, possibly because of physiological factors or a more severe shootfly attack during late rainy-season plantings.

Genetic factors other than trichomes seem to contribute to resistance, as is shown by the difference of the trichomed parent and the mean of the trichomed lines derived from it, which was statistically significant in seven of nine instances (Table 3). A significant difference between the trichomeless parent and the trichomeless derived lines in Exp. 9, and differences that approach significance in Exp. 2 and 8, gave further evidence of these additional factors.

Within-group variances also indicate the presence of resistance factors other than trichomes (Table 4). In Exp. 1 through 5 involving lines from IS 1054 × B CK60 three of 12 groups of lines showed significant within-group variances, in contrast to only one of eight groups of parental repetitions. Every group of lines from IS 5604 × B CK60 in three experiments (6 to 8) had significant variances within the group, but none of the parental groups did. Significant within-group variance also occurred in the trichomed lines of A 3659 × EN 3332-2.

Results of fitting a regression to the group means for percentage of deadhearts were consistent with the presence of additional genes for resistance (Table 4). The genetic model involving only trichomes was inadequate in seven of nine experiments ($P<0.05$). Trichomes plus genes additive for resistance and trichomes plus genes dominant for susceptibility each gave an adequate fit to the data in five experiments. Trichomes plus pairs of genes having duplicate dominant epistasis for susceptibility adequately fit the data in eight of nine experiments, and a simpler model is adequate for the ninth. Only the model including epistasis conforms to data from all experiments involving IS 1054 × B CK60 and IS 5604 × B CK60. The lack of significant deviations of the data from the model that includes digenic epistasis does not rule out a more complex model. Conversely, the presence of significant deviations from simpler models indicates that at least two resistance factors besides trichomes and epistatsis of the duplicate dominant type may be present. The glossy-leaf trait was not recorded in this experiment, so its relationship to these results is unknown.

It was presumed that the density of trichomes might affect the degree of resistance shown by a line, as has been documented earlier in wheat (Schillinger and Gallun, 1968). However, correlations between trichome density and percentage of main culms with deadhearts (transformed to angles) ranged from −0.29 to 0.24 (all nonsignificant at $P=0.10$) in the four experiments that tested such a relationship. More detailed results of this experiment are reported by Gibson (1981). Although trichome density did not affect resistance levels in this study, further investigation is needed to determine conclusively the effect of density on resistance.

The knowledge that trichome presence on sorghum leaf lamina confers resistance to shootfly and the finding that the glossy-leaf trait imparts additional resistance (Maiti and Bidinger, 1979) should simplify detection of other factors involved in reistance by allowing investigators to isolate the effects of these two factors. Sorghum breeders also can use these two traits as selection criteria in conjunction with initial field screening for shootfly resistance and, thereby, reduce the number of lines retained for further use.

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