Trichomes in Segregating Generations of Sorghum Matings. I. Inheritance of Presence and Density[1]

P. T. Gibson and R. K. Maiti[2]

ABSTRACT

The presence of trichomes on the leaves of sorghum [*Sorghum bicolor* (L.) Moench] is associated with reduced susceptibility to shootfly (*Atherigona soccata* Rond.) attack. Segregation ratios in successive generations of five single-cross matings between trichomed and trichomeless parents indicated that the presence of leaf-blade trichomes is recessive and controlled by a single locus. Inheritance of the trichome trait in three matings among four trichomed parents involved the same locus. The symbol *tr* is proposed for the gene controlling trichome presence.

Trichome density on the abaxial leaf lamina varied among trichomed lines derived from single-cross matings. Standard unit heritability for F_4 on F_3, estimated only in the cross IS 1054 × B CK60, was 0.75 on a plot basis.

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

TRICHOMES on sorghum [*Sorghum bicolor* (L.) Moench] leaves are nonglandular hairs that are microscopic in size (approximately 50 μ long). They are of interest because they may be related to reduced insect damage, especially by the shootfly (*Atherigona soccata* Rond.). Langham (1968) and Blum (1968) noted that sorghum cultivars resistant to shootfly had trichomes on the leaf sheath, whereas susceptible cultivars did not. Recent studies (ICRISAT, 1978; Maiti et al., 1980; Gibson, 1981; Maiti and Gibson, 1982) have clearly established the association of trichomes on the leaf lamina with reduced shootfly damage in sorghum. Similarly, trichomes in wheat (*Triticum* spp.) reduce damage by the cereal leaf beetle (*Oulema melanopus* L.) (Gallun et al., 1966). The association between trichomes and pest resistance has been reviewed for numerous plant species by Webster (1975) and Norris and Kogan (1980).

Studies on trichome inheritance have been conducted in several grain crops. Ringlund and Everson (1968) reported that offspring from matings between densely and sparsely pubescent wheats (*Triticum aestivum* L.) ranged from moderately to densely pubescent and that the inheritance of density was complex with greater density being partially dominant. In the same species, Wallace et al. (1974) reported that two pubescent cultivars each had one gene that was dominant for pubescence and that a third cultivar may have carried more than one gene. Leisle (1974) found two, and perhaps three, dominant genes for pubescence in two durum wheat (*Triticum durum* L.) matings. In oats (*Avena sativa* L.), Sarkarung (1978) found two dominant genes that each gave both blade and sheath pubescence and a third dominant gene that gave only sheath pubescence. Fedak (1973), from studies on two sources of pubescence in barley (*Hordeum vulgare* L.), concluded that blade and sheath pubescence were separate characters, pubescence appeared to be dominant and density was complexly inherited. In pearl millet [*Pennisetum americanum* (L.) Leeke], trichome presence generally is recessive (Burton and Powell, 1968), but a recessive trichomeless mutant has been reported (Burton et al., 1977).

Ayyangar (1942) listed hairiness of the leaf tip and of midrib edges in sorghum as each being controlled by a single locus with hairiness dominant. Langham (1968) determined F_2 ratios of "prickle hairs" (pointed) and "microhairs" (short and blunt) on the edges of leaf sheaths in five sorghum matings. Approximately one-fourth of the progeny in two of the matings and slightly more than one-fourth of the progeny in the other three matings had prickle-hairs. He concluded that the segregations in all five matings fit a ratio of 11 microhairs to 5 prickle-hairs. Apparently, progeny testing to confirm this conclusion was not performed.

Oviposition nonpreference appears to be the prevalent mechanism of resistance to shootfly in sorghum, and trichomes on the leaf blade deter oviposition (ICRISAT, 1978; Maiti et al., 1980; Maiti and Gibson, 1982). Consequently, knowledge of the inheritance of trichomes on the leaf blade will enhance their utilization in breeding for resistance to shootfly.

MATERIALS AND METHODS

Matings of Trichomed and Trichomeless Parents. Segregation ratios were studied in several filial generations of five single-cross matings of sorghum each involving a trichomed and a trichomeless parent (Table 1). The matings were 'IS 1054' × 'B CK60', 'IS 5604' × B CK60, 'A Kaffinum' × 'IS 1082', 'A 3659' × 'EN 3332-2', and 'A 2219' × 'IS 2312'. In each mating, F_3 lines were developed by selfing random F_2 plants. For Is 1054 × B CK60 the parents, F_1, F_2, F_3, and several backcross generations were evaluated. Two sets containing different F_3 lines were observed as were two samples of the same BC_3F_2 lines. In IS 5604 × B

Table 1. Genotypes of sorghum parents.†

Parent	Genotype	Comments
B CK60	*Tr Tr*	Texas line B Tx 3197
A Kaffinum	*Tr Tr*	Developed at Serere, Uganda
A 2219	*Tr Tr*	Parent of a commercial hybrid in India
A 3659	*Tr Tr*	Parent of a commercial hybrid in India
IS 1054	*tr tr*	Selected cultivar (M 35-1) from an Indian 'Maldandi' landrace cultivar
IS 1082	*tr tr*	Collection from an Indian landrace
IS 2312	*tr tr*	Collected in Sudan
IS 5604	*tr tr*	Collection from an Indian landrace
EN 3332-2	*tr tr*	Stem borer resistant

† A and B designate a cytoplasmic-genic male-sterile line and a sterility maintenance line, respectively. IS indicates Indian Sorghum, the accession number in the world sorghum collection. A 2219, A 3659, and EN 3332-2 were developed by the All-India Coordnated Sorghum Improvement Project. *Tr Tr* = trichomeless and *tr tr* = trichomed.

---

[1] Journal Article No. 205 of the Int. Crops Res. Inst. for the Semi-Arid Tropics, ICRISAT Patancheru P.O., Andhra Pradesh 502324, India, and Journal Paper No. J-10422 of the Iowa Agric. and Home Econ. Exp. Stn., Ames, IA 50011, Project No. 2447. Part of the dissertation submitted by the senior author to Iowa State Univ. in partial fulfillment of the requirements for the Ph.D. degree. Received 22 Feb. 1982.

[2] Formerly research scholar, ICRISAT (currently assistant professor, Plant and Soil Science Dep., Southern Illinois Univ., Carbondale, IL 62901) and sorghum physiologist, ICRISAT, respectively.

CK60, the parents, F_2, and F_3 were studied. F_3 lines of A Kaffinum × IS 1082, A 3659 × EN 3332-2, and A 2219 × IS 2312 had been developed for other purposes. Because A Kaffinum, A 3659, and A 2219 are male sterile, some F_2 plants from these matings also were male sterile and, when selfed, did not produce F_3 seed. Therefore, in these three matings, any linkage between male sterility and the absence of trichomes would cause the proportion of progeny with trichomes to be higher than if linkage were not present.

Matings of Trichomed with Trichomed Parents. Twenty F_2 plants from each of three single-cross matings involving four trichomed parents were evaluated. The matings were IS 1054 × IS 5604, IS 1082 × IS 5604, and IS 1082 × IS 2312.

Determination of Trichome Presence. Trichome evaluations were conducted between 1977 and 1979 in field experiments at ICRISAT Center, Patancheru, India. Almost all materials were grown with 1.2 kg carbofuran (2,3 dihydro-2,2-dimethyl-7-benzofuranyl methylcarbamate) (AI)/ha applied in the seed furrow to preclude shootfly infestation. The exceptions were the F_3 (1st set), BC_1F_2 and BC_3F_2 (1st set) of IS 1054 × B CK60, and the F_3 of IS 5604 × B CK60. These last three groups were grown in wooden boxes with soil during the offseason (January-May). All plots in the field were slightly overseeded and subsequently thinned to one seedling every 10 cm. No thinning was done in the soil box experiments.

Evaluations for trichome presence or absence were done on leaf samples from 10 or more plants per progeny taken 15 to 21 days after seedling emergence. A section taken from the center of the abaxial surface of the fourth or fifth leaf (counting the coleoptile as the first leaf) was cleared of cell contents by using ethanol and lactic acid and mounted on a slide following the technique of Maiti et al. (1980). Presence or absence of trichomes on these cleared samples was determined with the aid of a microscope.

Heritability of Trichome Density. Thirty-seven F_3 lines from the mating IS 1054 × B CK60 were developed by selfing random F_2 plants and retaining the lines in which all F_3 plants were trichomed. These lines in F_4 were bulks made by compositing equal quantities of selfed seed from each of 6 to 10 F_3 plants. The lines were evaluated for trichome density in an unreplicated experiment with the F_3 generation in one block and the F_4 in an adjacent one. Plots were single rows 4 m long and 75 cm apart. Spacing between plants was 10 cm. Samples for analysis obtained from the fourth leaf of 10 plants and from the fifth leaf of 10 other plants were cleared as previously described. Trichomes were counted in two microscope fields of 0.8 mm^2 per leaf, and density was expressed as trichomes/mm^2. Standard unit heritability was calculated by regressing trichome density of F_4 on F_3 (Frey and Horner, 1957).

RESULTS AND DISCUSSION

Matings of Trichomed and Trichomeless Parents. Segregation ratios for various generations from IS 1054 × B CK60 indicated that trichome presence was recessive and controlled by a single locus (Table 2, 3). Progeny tests confirmed this result. Evaluation of 85 F_3 lines derived from the BC_1F_1 of (IS 1054 × B CK60) × B CK60 showed that those derived from trichomed plants were always trichomed and that some derived from trichomeless plants were trichomeless while others segregated. Additionally, homogeneous trichomed F_2 derived F_3 lines from IS 1054 × B CK60 produced homogeneous trichomed lines in F_4. The matings of IS 5604 × B CK60, A Kaffinum × IS 1082, and A 3659 × EN 3332-2 (Table 4), produced segregation ratios mainly consistent with a single-locus inheritance.

Table 2. Ratio of trichomeless (*Tr-*), segregating, and trichomed (*tr tr*) sorghum lines in various generations from the mating IS 1054 (*tr tr*) × B CK60 (*Tr Tr*) and X^2 tests.

Generation	Lines			Ratio tested	X^2	P
	Tr-	Seg.	*tr tr*			
	no.					
F_1	40	--	--	--	--	--
F_2	49	--	20	3:1	0.44	0.51
F_3	39	77	42	1:2:1	0.21	0.90
F_1 × IS 1054	36	--	29	1:1	0.38	0.54
F_1 × B CK60	58	--	--	--	--	--
(F_1 × B CK60) F_2 lines	8	12	--	1:1	0.80	0.37

Table 3. Pooled numbers of trichomeless (*Tr-*) and trichomed (*tr tr*) plants in segregating sorghum lines of various generations from the mating IS 1054 (*tr tr*) × B CK60 (*Tr Tr*) and X^2 tests for a 3:1 ratio.

Generation	Seg. lines	Plants		X^2	P
		Tr-	*tr tr*		
	no.				
F_3 (1st set)	22	340	107	0.27	0.60
F_3 (2nd set)	77	493	210	8.90	<0.01
BC_1F_2	12	130	37	0.72	0.40
BC_2F_2	4	96	31	0.14	0.71
BC_2F_3	41	432	129	1.20	0.27
BC_3F_2 (1st set)	21	234	81	0.09	0.76
BC_3F_2 (2nd set)	21	567	230	6.33	0.01
BC_3F_1 × BC_3F_1	9	511	119	0.80	0.37

Generally, evidence from our study supported single-locus control of trichome presence or absence, although in certain cases the observed ratios were different from expected. The most extreme departure occurred in A 2219 × IS 2312 (Table 4). Since the trichomes of IS 1082 were transmitted via a recessive allele at a single locus in the cross with A Kaffinium, and the progeny of IS 1082 × IS 2312 were all trichomed, it appears that trichome presence in IS 2312 is controlled at the same locus. No explanation has been determined for the absence of homogeneous trichomeless F_3 lines in A 2219 × IS 2312.

In four other mating-generation cases, there was a slight, but significant, excess of trichomed plants. These cases were the pooled ratios of plants from segregating lines in the F_3 (2nd set) and the BC_3F_2 (2nd set) of IS 1054 × B CK60 (30 and 29% trichomed plants, respectively) (Table 3), the F_3 of IS 5604 × B CK60, and the F_3 of A 3659 × EN 3332-2 (30 and 33% trichomed plants) (Table 4). Usually 10 plants/line were sampled, so there was about a 1 in 20 chance of misclassifying a segregating line as trichomeless. To compensate for misclassified lines, one was added to the number of segregating lines for each 19 lines identified as segregating, and the number of trichomeless lines was decreased by the same number. The total of trichomeless plants in segregating lines was increased 10 plants times the estimated number of misclassified lines. These adjustments reduced the difference between the observed and expected ratios, but did not eliminate it. The discrepancy could have resulted from differential emergence between trichomed and trichomeless plants or from gametic selection that favored pollen and/or ovules that carried the allele for trichomes, but neither

Table 4. Ratios of trichomeless (*Tr-*), segregating, and trichomed (*tr tr*) sorghum plants and lines from the matings IS 5604 (*tr tr*) × B CK60 (*Tr Tr*), A Kaffinum (*Tr Tr*) × IS 1082 (*tr tr*), A 3659 (*Tr Tr*) × EN 3332-2 (*tr tr*), and A 2219 (*Tr Tr*) × IS 2312 (*tr tr*), and X^2 tests.

Description	Plants or lines			Ratio tested	X^2	P
	Tr-	Seg.	*tr tr*			
		no.				
IS 5604 × B CK60						
F_2 plants	60	--	14	3:1	1.46	0.23
F_3 plants	38	50	32	1:2:1	3.93	0.14
Plants from 50 F_3 seg. lines	349	--	150	3:1	6.81	<0.01
A Kaffinum × IS 1082						
F_3 lines	13	28	8	1:2:1	2.02	0.36
F_3 plants from 28 seg. lines	243	--	95	3:1	1.57	0.21
A 3659 × EN 3332-2						
F_3 lines	12	21	14	1:2:1	0.70	0.70
F_3 plants from 21 seg. lines	164	--	79	3:1	7.31	0.01
A 2219 × IS 2312						
F_3 lines	0	26	15	1:2:1 0:2:1 0:1:1	17.58 0.18 3.27	<0.01 0.70 0.07
F_3 plants from 26 seg. lines	133	--	138	3:1 2:1 1:1	97.12 37.73 0.09	<0.01 <0.01 0.77

of these possibilities has been verified.

Matings of Trichomed with Trichomed Parents. The 20 F_2 plants from each mating between trichomed parents were trichomed, indicating that the same locus was involved in controlling trichome presence in the parents IS 1054, IS 1082, IS 2312, and IS 5604.

Heritability of Trichome Density in IS 1054 × B CK60. Trichome densities for the average of leaves 4 and 5 ranged from 1.5/mm^2 to 7.3/mm^2 ($\pm$1.0/mm^2), with a mean of 4.63 ($\pm$0.48/mm^2). Standard unit heritability (Frey and Horner, 1957) of trichome density between F_3 and F_4 was 0.75 (significantly different from 0 at 0.01 probability level) on a plot basis. This high heritability shows that much of the variation for density is genetically controlled.

CONCLUSIONS

Trichome presence on sorghum leaves is controlled by a recessive gene at one locus in the cultivars we studied. The symbol *tr* is proposed for this gene, with *Tr-* being trichomeless and *tr tr* genotypes being trichomed. The Nomenclature Committee for Sorghum Gene Symbols concurred with our proposal (Schertz, 1979).

If trichome presence is controlled by an allele at a single locus in other sorghum cultivars, trichomed segregates could be selected easily in a breeding program. This would be an effective way to recover resistance to shootfly in segregating generations from matings involving one trichomed parent. By backcrossing, trichomes could be easily transferred to shootfly-susceptible genotypes having other desirable characteristics. To test the effectiveness of this procedure, trichomes are being added by backcrossing to A and B CK60. The recovered lines with trichomes added will be tested for resistance.

Density of trichomes per unit area of leaf lamina surface also is genetically controlled, but the presence of trichomes probably is more important for increasing resistance to shootfly than is density (Maiti and Gibson, 1982). However, if density is shown to be important, its high heritability would facilitate selection.

REFERENCE

1. Ayyangar, G.N.R. 1942. The description of crop plant characters and their ranges of variation. The variability of Indian sorghum (Jowar). Indian J. Agric. Sci. 12:528-563.
2. Blum, A. 1968. Anatomical phenomena in seedlings of sorghum varieties resistent to the sorghum shootfly (*Atherigona varia soccata*). Crop Sci. 8:388-391.
3. Burton, G.W., W.W. Hanna, J.C. Johnson, Jr., D.B. Leuck, W.G. Monson, J.B. Powell, H.D. Wells, and N.W. Widstrom. 1977. Pleiotropic effects on the *tr* trichomeless gene in pearl millet on transpiration, forage quantity, and pest resistance. Crop Sci. 17:613-616.
4. ----, and J.B. Powell. 1968. Pearl millet breeding and cytogenetics. Adv. Agron. 2:49-89.
5. Fedak, G. 1973. Leaf pubescence in barley. Barley Genet. Newsl. 3:14.
6. Frey, K.J., and T. Horner. 1957. Heritability in standard units. Agron. J. 49:59-62.
7. Gallun, R.L., R. Ruppel, and E.H. Everson. 1966. Resistance of small grains to the cereal leaf beetle. J. Econ. Entomol. 59:827-829.
8. Gibson, P.T. 1981. Inheritance of resistance to shootfly in sorghum. Ph.D. Dissertation, Iowa State Univ., Ames. Diss. Abst. 42/07B:2639.
9. International Crops Research Institute for the Semi-Arid Tropics. 1978. ICRISAT Ann. Rep. 1977-78, Hyderabad, India.
10. Langham, R.M. 1968. Inheritance and nature of shootfly resistance. M.S. Thesis, Ahmadu Bello Univ., Samaru, Nigeria.
11. Leisle, D. 1974. Genetics of leaf pubescence in durum wheat. Crop Sci. 14:173-174.
12. Maiti, R.K., F.R. Bidinger, K.V. Seshu Reddy, Paul Gibson, and J.C. Davies. 1980. Nature and occurrence of trichomes in sorghum lines with resistance to shootfly. Joint Progress Report, Sorghum Physiology-3/Sorghum Entomology-3, International Crops Research Institute for the Semi-Arid Tropics, Hyderabad, India.
13. ----, and P.T. Gibson. 1982. Trichomes in segregating generations of sorghum matings: II. Association with shootfly resistance. Crop Sci. 23:76–79.
14. Norris, D.M., and M. Kogan. 1980. Biochemical and morphological bases of resistance. p. 22-61. *In* F.G. Maxwell and F.R. Jennings (ed.). Breeding plants resistant to insects. John Wiley and Sons, New York.
15. Ringlund, K., and Everson, E.H. 1968. Leaf pubescence in common wheat, *Triticum aestivum* L., and resistance to the cereal leaf beetle, *Oulema melanopus* (L.). Crop Sci. 8:705-710.
16. Sarkarung, Surapon. 1978. Influence of heredity and environment on leaf pubescence in oats. Ph.D. Dissertation, Univ. of Arkansas, Fayetteville. Diss. Abst. 39/06B:2603.
17. Schertz, K.F. 1979. Personal communication.
18. Wallace, L.E., F.H. McNeal, and M.A. Berg. 1974. Resistance to both *Oulema melanopus* and *Cephus cintus* in pubescent leaved and solid stemmed wheat selections. J. Econ. Entomol. 67:105-107.
19. Webster, J.A. 1975. Association of plant hairs and insect resistance, an annotated bibliography. USDA Misc. Publ. 1297.