INHERITANCE OF SOME BLOOMLESS AND SPARSE-BLOOM MUTANTS IN SORGHUM

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IN SORGHUM

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TABLE OF CONTENTS

LIST OF TABLES

CHAPTER I

INTRODUCTION

Grain sorghum, Sorghum bicolor (L.) Moench, is the fourth largest cereal crop in world production. In 1968 the greenbug, Schizaphis graminum (Rondani), mutated to a biotype capable of attacking sorghum. Greenbug infestation reduced sorghum grain yields up to 45%.

The bloom of sorghum is a grayish waxy plant exudate. The bloom condition exists in three forms: 1) heavy bloom - the plant having an ashy look from the waxy covering on the leaf sheath, boot, internode, and the leaf undersurface; 2) sparse bloom - the plant is covered only at critical points (the top of the leaf sheath and internode and the base of the undersurface of the lamina), and does not have an ashy look; 3) bloomless - no wax is present on the plant.

Greenbugs show nonpreference for bloomless plants as the plants increase in age, while with increasing age bloom plants remain susceptible to greenbug infestation. Sparse bloom plants should be intermediate in reaction. The purpose of this study was to determine the number of genes involved in the inheritance of the bloomless and sparse-bloom mutants in sorghum.

CHAPTER II

LITERATURE REVIEW

Sorghum [*Sorghum bicolor* (L.) Moench] is a member of the grass family Gramineae, subfamily Panicoideae, tribe Andropogoneae (27). Exceeded only by wheat, corn, and rice, sorghum ranks fourth in world acreage of the cereal crops. In the Western Hemisphere it is used as livestock feed while in Asia and Africa it is used as human food (39).

There are four main groups of sorghum: grain sorghum, the sorgos, broomcorn, and grass sorghums. The grain sorghums are further divided into seven groups. Of these groups kafir, milo, and feterita have contributed most of the germplasm used in the United States development of sorghum. Most new grain cultivars have come from crosses between kafirs and milos. At present there are over 17,000 entries in the world sorghum collection (27).

The Greenbug in General

The greenbug, *Schizaphis graminum* (Rondani), was first described in Italy in 1852. In the United States it was first identified in Virginia in 1882. Prior to 1968 two types, biotype A and biotype B, had been reported as serious pests of small grains. In 1969, Harvey and Hackerott (21) described a greenbug biotype injurious to sorghum designated as biotype C. Dickson and Laird (10) studied the sorghum greenbug biotype and concluded that it differed from previous biotypes

by its tolerance of high temperature, its use of sorghum as a host plant, and certain morphological details. Wood (44) reported several differences between the sorghum biotype and the small grain biotypes:

1) Biotype C feeds in the vascular bundles.
2) Biotype C has more antennal sensoria and a different placement of the lateral abdominal tubercles.
3) Biotype C has a paler green color, and its cornicles are not blacktipped.

This greenbug biotype reaches its greatest concentrations during the hot summer months.

The Greenbug on Other Crops

Hackerott and Harvey (15) conducted growth chamber tests to determine the effect of greenbug biotype C on 'Combine Kafir-60' grain sorghum, 'Gahi' pearl millet, 'White Wonder' foxtail millet, and 'Turghani' proso millet. On the basis of plant injury millet was more resistant than sorghum. Greenbugs also survived and reproduced better on sorghum than millet. The mature millet plants exhibited slightly less resistance than seedling plants. In a preference test seedling stage pearl millet was preferred over foxtail and proso millet.

Harvey and Hackerott (20) compared the effectiveness of resistance in wheat, barley, rye, and sudangrass to biotype B and C greenbugs. Genes for resistance in the plants to biotype B did not always confer resistance to biotype C. Harvey and Hackerott (21) conducted greenhouse tests with 30 species of grass to discover host plants that distinguished greenbugs originating from sorghum from those originating from wheat, and to establish biotypes by differential aphid-host

reactions. When offered a choice between five plant species biotype C preferred sorghum and sudangrass more than biotype B, which preferred wheat, barley, and rye.

Livers and Harvey (26) used the rye variety 'Caribou' as the source of resistance in a recurrent selection program to produce a rye population with homozygous resistance to the greenbug. Segregation studies with Caribou showed resistance to be controlled by a single dominant gene.

Gardenhire (11) crossed a resistant oat variety ('Russian 77') to two susceptible varieties ['New Nortex' and (Red Rustproof - Victoria x Richland) x Ranger, Texas Selection 2] to study the inheritance of resistance in oats. He concluded resistance in Russian 77 was conditioned by a single gene pair.

Gardenhire and Chada (13) studied the inheritance of greenbug resistance in barley. Utilizing 'Omugi' as the resistant parent, crosses were made to six susceptible lines ('Cordova', 'Mo. B538', 'Caucasus', 'Khayyam', 'Hokudo', and Cordova x Golaid). Resistance was completely dominant as F_1 and F_2 resistant plants were as resistant as the resistant parents. Reciprocal crosses between two parents showed no evidence of cytoplasmic inheritance. Gardenhire (12) examined the inheritance of greenbug resistance with segregating generations of four barley crosses using Omugi or a Cordova x Omugi selection as the resistant parent. The Omugi resistance was completely dominant. Gardenhire et al. (14) determined that chromosome one carried the single gene resistance in barley using the variety 'Will'. Resistance was carried in linkage group 1 and on the centromere-bearing segment of chromosome 1 in the T1-6a translocation.

Painter and Peters (29) on the basis of screening tests involving segregating wheat populations reported that a single genetic factor controlled greenbug resistance.

Daniels and Porter (9) studied segregating wheat generations involving the resistant selection 'Dickinson' and five commercial varieties ('Vaughn Turkey', 'Westar', 'Blue Jacket', 'Kanred', 'Crockett'). A single factor pair controlled greenbug resistance, susceptibility being dominant to resistance, although modifying genes may be involved. Tests indicated that only if the most resistant plants were selected could substantial progress be made for greenbug resistance. Porter and Daniels (31) studied crosses between resistant and susceptible wheat varieties and backcrosses to both parents and concluded that the factor or factors controlling greenbug resistance were not dominant. If environmental factors are minimized by replication heritability estimates show greenbug resistance to be highly heritable.

Curtis et al. (8) working with two resistant wheat varieties (Dickinson Selection 28A and C.I. 9058) and three susceptible varieties ('Ponca' C.I. 12128, 'Concho' C.I. 12517, and Crockett C.I. 12702) concluded that greenbug resistance was governed by a single recessive gene pair (gbgb). Susceptibility was incompletely dominant in the F_1 of a resistant x susceptible cross. Reciprocal crosses showed no evidence of cytoplasmic influence on the inheritance of greenbug resistance.

Wood and Curtis (45), screening resistant x susceptible (Dickinson Selection 28A x Ponca) selections, concluded that infested and uninfested resistant selections produced no apparent significant yield differences. Some antibiosis was indicated as there were significantly fewer

greenbugs per linear row foot in infested resistant selections and checks compared with the infested susceptible check.

Starks et al. (36) conducted a nonpreference study with greenbug biotypes B and C on a broomcorn cultivar ('Deer') and 'RS610'. Biotype B had a noticeable nonpreference for Deer, but RS610 was dead at the end of the 30-day test. Biotype C indicated no preference for Deer over RS610 as both cultivars were killed. Results indicated that Deer can be used in the separation of biotypes B and C.

Bloom and Bloomless Sorghum

Ayyangar et al. (2) reported that bloom exists in several species of crops, and that the wax helps reduce transpiration by partly closing the stomata. The sorghum bloom exists as two types -- heavy and sparse. In the heavy-bloom condition there is a concentration of bloom on the leaf sheath, the boot, and the internode while the whole under leaf surface is bloomy. Plants in the sparse-bloom condition show bloom at the top of the leaf sheath, the top of the internode, and the base of the undersurface of the lamina. Inheritance of the character is controlled by one simply inherited gene, H and h, with H being dominant to h. Allele H is responsible for heavy bloom while allele h is responsible for sparse-bloom.

The first report of the bloomless condition was by Ayyangar and Ponnaiya (3). Crosses between bloom and bloomless were completely bloom in the F_1. The F_2 segregated in the ratio of 3 bloom:1 bloomless, indicating complete dominance of the bloom. When bloomless types were crossed with sparse-bloom types the F_1's were completely bloom, while the F_2 segregated in a 9 bloom:4 bloomless:3 sparse bloom ratio. They

concluded allele Bm was responsible for bloom, while allele bm was responsible for the bloomless condition where allele H was not expressed. Allele h governed the sparse-bloom condition.

Pieretti (30) studied the damage of greenbugs to plants of RWD3-Weskan (bloomless, seedling-susceptible), 'SA7536-1' (bloom, seedling-resistant), their F_1's, F_2's, and a susceptible check. He reported that bloomless plants were not "tolerant" to greenbugs, but they exhibited "nonpreference" with increasing age. SA7536-1 plants (bloom) were tolerant to greenbugs at all growth stages. Bloomlessness was a simply inherited recessive trait. The tolerance to greenbugs of SA7536-1 was regulated by a single pair of alleles with partial or no dominance. The similarity of the means for damage scores for bloom and bloomless groups of F_2 individuals suggested that the genetic factors responsible for the expression of bloom and bloomlessness were inherited independently from those regulating the expression of tolerance to damage.

Amini (1) studied the damage of greenbugs to plants of RWD3-Weskan (bloomless, seedling-susceptible), 'IS 809' (bloom, seedling-resistant), their F_1's, F_2's, and a susceptible check. He also concluded that bloomlessness was a simply inherited recessive trait. The tolerance to greenbugs of IS809 could not be explained on the basis of a single pair of alleles. He also concluded that bloom and bloomless groups of the F_2 individuals exhibited the same degree of tolerance to greenbugs, and therefore, the bloomless type of resistance (nonpreference) and the normal type of resistance (tolerance) were regulated by independent genetic factors, and there should be no apparent difficulty in combining them to improve resistance.

Weibel et al. (41) studied five pairs of adjacent bloom and bloomless plants in five F_3 segregating rows of four crosses at the heading stage. They concluded that less leaf damage in the bloomless plants was due to significantly fewer greenbugs. Weibel et al. (42) counted greenbugs on near isogenic lines three and four weeks after emergence. Fewer greenbugs were found on the bloomless plants for both counts, indicating greenbug nonpreference for this type. This difference was highly significant. A comparison of the two counts showed greenbugs to be increasing on the bloom plants but not on the bloomless plants.

Maunder et al. (28) using isogenic lines of Combine Kafir-60, Martin, and a Redbine showed bloomless plants to have 38.4% more stalk disease. Bloomless plants had greater resistance to water loss, indicating that under stress stomata on bloomless plants close quicker. Lambright and Maunder (25), using isogenic Redbine-60 B1 (bloom) and Redbine-60 b1 (bloomless) lines showed bloom lines to have a higher degree of resistance to stomatal diffusion than bloomless lines.

Various authors [Cummins and Dobson (6); Hanna et al. (19); and Cummins and Sudweeks (7)] have reported that in modified in vitro dry matter tests using isogenic or near-isogenic bloom and bloomless sorghum lines the bloomless lines are more digestible. They reported the superior performance of the bloomless lines was due to the absence of bloom, which acted as a barrier and slowed the penetration of microorganisms. Cummins (5) reported small yield differences between isogenic bloom and bloomless sorghum lines and he suggested that bloomless types could be grown in humid areas to improve forage quality. Ross (32) used near-isogenic Combine Kafir-60 lines to test yield in

relation to the bloom and bloomless characteristic and concluded that bloom plants outyielded bloomless plants, the difference being highly significant. Chatterton et al. (4) measured net carbon dioxide and water vapor exchanges in isogenic lines of bloom and bloomless sorghums. He concluded that in arid and semi-arid regions the yield increase associated with bloom plants may result in more digestible forage per hectare than the bloomless plants, although in humid areas bloomless types may provide more digestible dry matter.

Greenbug Resistance in Sorghum

Starks et al. (35) found greenbug resistance to be dominant and present in most plant growth stages. Effective at a range of temperatures, it is most effective at high temperatures. The three types of resistance (antibiosis, tolerance, and nonpreference) were present, the most common being antibiosis. Starks et al. (34) studied 15 grain, forage, grassy, semi-grassy or broomcorn lines and reported the level of resistance to vary with the cultivar. The three types of resistance were found. Levels and types of resistance should combine. Resistance in a single source was thought to be controlled by single gene action.

Hackerott et al. (18) rated 648 cultivars and breeding lines for reaction to a natural infestation of greenbugs, and surveyed for greenbug resistance 157 entries in the greenhouse. All sources of resistance seemed to trace to S. virgatum (one of the parents in Sudan Grain), and the genes conditioning resistance appeared to be at the same loci. However, F_2 segregation ratios indicated that dominant genes at more than one locus controlled resistance. Tolerance appeared to be the major component of resistance.

Teetes et al. (37) studied greenbug nonpreference and antibiosis with six sorghum lines (resistant lines SA 7536-1, 'KS 30', IS 809, and 'PI 264453' and susceptible line 'TX 2536') in comparison to the susceptible line 'TX 7000'. The resistant lines exhibited nonpreference over susceptible TX 7000, with PI 264453 being the most preferred resistant line. Sorghum hybrids utilizing the resistant lines as parents had a lower level of nonpreference than the resistant sorghum lines. For antibiosis, the resistant lines had a longer prereproductive period than either susceptible line, although the mortality rate of nymphs did not vary with resistance or susceptibility. Greenbugs reared on resistant sorghum secreted less honey dew than those reared on susceptible sorghums.

Teetes (38), studied five sorghum lines (resistant lines IS 809, KS 30, and SA 7536-1 and susceptible lines TX 7000 and 'SD 100') and certain F_1 hybrids in the field to determine differences in resistance. Resistance levels varied with the line. Tolerance appeared to be the primary mechanism in resistance, although nonpreference and antibiosis mechanisms were present to a lesser degree.

Johnson et al. (23) studied the effects of a natural infestation of greenbugs feeding on selected resistant lines and their F_1 hybrids in the adult plant stage. Experimental materials consisted of three susceptible commercial hybrids, a susceptible line, two resistant lines, and three resistant hybrids. Resistant lines had significantly less leaf tissue damage than susceptible entries, and fewer greenbugs than the susceptible lines and the two late-blooming susceptible hybrids but not the two early-blooming susceptible entries.

Wood (44) screened 1761 varieties and hybrids for resistance and found eight resistant lines. While all of the resistant lines showed a high degree of nonpreference, biotype C adapted easier to the resistant lines. A test for fecundity showed biotypes A and B to survive poorly on resistant species, while biotype C had about the same survival rate on resistant and susceptible species.

Schuster and Starks (33) evaluated eleven sorghum selections in greenhouse and growth chamber studies to determine the components of host plant resistance. Apterate and alate forms of the greenbug were used. Eight entries showed low preference by both the apterate and alate forms. Antibiosis was a resistance factor in some selections, and in all resistant selections. Plant height differences between infested and uninfested plants of each entry and by individual plant-injury ratings indicated that tolerance may be the main component of PI 264453. Five of the selections: 'PI 229828', IS 809, Shallu Grain, 'PI 302178', and 'PI 226096', indicated comparatively high degrees of all three resistance components.

Weibel et al. (43) studied the F_1 and F_2 progeny of Shallu Grain, PI 264453, and IS 809 for greenbug resistance. Reaction of F_1 plants, although closer to the resistant parent, seemed intermediate between the parents. They concluded that the resistance gene could readily be transferred to adapted lines, and that one resistant parent in a cross should confer sufficient resistance.

Weibel et al. (40) compared crosses among resistant SA 7536-1, IS 809, and PI 264453 for greenbug resistance and concluded that PI 264453 had a different source of resistance, possibly not from a single

factor pair. However, the forms of resistance were somewhat similar and differences appeared to be of degree and not of number.

Harvey and Hackerott (22) studied the effect of a seedling infestation of greenbugs on susceptible Combine Kafir-60, resistant 'H39' and their F_1 hybrid. The greenbug preferred the susceptible more than the F_1 and both more than the resistant line. Significantly more greenbugs were found on the susceptible Combine Kafir-60 than on the resistant H39, the F_1 not differing from either parent. Injury scores and delayed maturity followed the pattern of susceptible parent, F_1, and resistant parent. The yield reduction of susceptible plants infested in the seedling stage appeared to be due primarily to a reduction in the number of secondary culms.

Hackerott and Harvey (16) studied the effect of C-biotype greenbugs on resistant (KS 30) and susceptible (Combine Kafir-60) cultivars in the field. The reduction in grain yield of susceptible cultivars was caused by smaller seed size and number of seeds per head as a result of leaf damage. Seed quantity rather than quality was more severely damaged. Hackerott and Harvey (17) reported that heterozygous resistant hybrids will tolerate fewer greenbugs than homozygous resistant hybrids.

Kofoid et al. (24) studied the relationship of greenbug resistance to various sorghum agronomic traits by evaluating 100 resistant and 100 susceptible S_2 progenies from a random mating population in the presence and absence of greenbugs. With no greenbugs present the populations differed in none of the traits studied, while in the presence of greenbugs the resistant population had better agronomic characters.

CHAPTER III

MATERIALS AND METHODS

Parents

Five bloomless and four sparse-bloom sorghum lines were used to study the number of genes involved in the inheritance of the bloomless and sparse-bloom mutants in sorghum.

Bloomless lines used were RWD 3 X Weskan-4-3-1-1-2, Redbine-60, Restorer Combine Kafir-60, Brooks, and Cyto 13 X Tan Sugar Drip-1-3-1-1 (Table I). Bloomless RWD 3 X Weskan-4-3-1-1-2 and Cyto 13 X Tan Sugar Drip-1-3-1-1 appeared as mutants in early generation breeding rows in the Oklahoma breeding program. Bloomless Redbine-60 originated in the DeKalb breeding program at Lubbock, Texas. Bloomless R Combine Kafir-60 was developed in the Kansas breeding program at Hays, Kansas. Bloomless Brooks was developed or discovered by the late J. S. Brooks as a genetic stock. Lines were assigned the genetic designation for the bloomless trait, bm, plus a number to indicate the gene.

Sparse-bloom lines were a Redlan derivative, Redlan X Wiley-1221122, Martin, and Redlan X Y10-Calico-1-1 (Table II). Sparse-bloom Redland derivative and Redlan X Y10-Calico-1-1 appeared as mutants in segregating rows in the Oklahoma breeding program. Sparse-bloom Redlan X Wiley 1221122 originated from the sparse-bloom Wiley parent in the Oklahoma program. Sparse-bloom Martin was developed in the Kansas

TABLE I

BLOOMLESS SORGHUM PARENTAL LINES WITH APPROPRIATE GENETIC DESIGNATION

Parent	Genetic Designation
RWD 3 X Weskan-4-3-1-1-2	bm_1
Redbine-60	bm_2
R Combine Kafir-60	bm_3
Brooks	bm_4
Cyto-13 X Tan Sugar Drip-1-3-1-1	bm_5

TABLE II

SPARSE-BLOOM SORGHUM PARENTAL LINES WITH APPROPRIATE GENETIC DESIGNATION

Parent	Genetic Designation
Redlan Deriv	h_1
Redlan X Wiley-1221122	h_2
Martin	h_3
Redlan X Y10-Calico-1-1	h_4

program at Hays, Kansas. Lines were assigned the genetic designation for the sparse-bloom trait, h, plus a number to indicate the gene.

The number assigned to the bloomless and sparse-bloom parental lines was an arbitrary, temporary designation until determination was made as to the number of genes involved.

Crosses and Backcrosses

A diallel set of crosses among the five bloomless and four sparse-bloom parental lines was attempted during the summer of 1976 in the field at the Perkins Agronomy Research Station. Twenty-four of the cross combinations were grown in the winter nursery in Puerto Rico, or in the greenhouse in Oklahoma during the winter of 1976-1977. Because of the use of cytoplasmic male-sterile female parents in making some of the crosses, some of the resulting F_1 plants in some of the combinations were all completely male sterile. This necessitated backcrossing the sterile F_1 plants to one or both parents to obtain seed. For convenience in the analysis of data the crosses were grouped into four types of crosses: bloomless parent X bloomless parent (Table III), sparse-bloom parent X sparse-bloom parent (Table IV), bloomless parent X sparse-bloom parent (Table V), and backcrosses (Table VI). The F_1 and parental plants were classified for the presence or absence of bloom (See Tables III, IV, V, and VI).

Growing of the F_2 and BC_1 Generations

The 20 F_2 and 11 BC_1 populations were planted at the Perkins Agronomy Research Station, Perkins, Oklahoma, on 13 June 1977. The soil was Teller loam, a member of the fine-loamy, mixed, thermic

TABLE III

SUMMARY OF BLOOMLESS X BLOOMLESS CROSSES

Cross	F_1 Bloom[1/]	Cross	F_1 Bloom[1/]
$msbm_1$ X bm_2	+	$msbm_1$ X bm_5	+
$msbm_1$ X bm_3	+	bm_5 X bm_2	-
$msbm_1$ X bm_4	+		

1/ + = bloom
- = bloomless

TABLE IV

SUMMARY OF SPARSE-BLOOM X SPARSE-BLOOM CROSSES

Cross	F_1 Bloom [1/]	Cross	F_1 Bloom[1/]
h_2 X h_1	+	h_3 X h_1	+
h_2 X h_4	+	h_3 X h_4	+

1/ + = bloom
- = bloomless

TABLE V

SUMMARY OF BLOOMLESS X SPARSE-BLOOM CROSSES

Cross	F_1 Bloom[1/]	Cross	F_1 Bloom[1/]
h_1 X bm_3	+	h_3 X bm_2	+
h_1 X bm_5	+	h_3 X bm_3	+
h_2 x bm_2	+	h_3 X bm_4	+
h_2 X bm_3	+	$msbm_1$ X h_1	+
h_2 X bm_4	+	$msbm_1$ X h_4	+
h_2 X bm_5	+		

[1/] + = bloom
- = bloomless

TABLE VI

SUMMARY OF BACKCROSSES

Cross	F_1 Bloom[1/]	Cross	F_1 Bloom[1/]
($msbm_1$ X bm_2) X bm_1	+	(h_2 X bm_1) X h_2	+
($msbm_1$ X bm_2) X bm_2	+	(h_2 X bm_1) X bm_1	+
($msbm_1$ X bm_5) X bm_1	+	(h_2 X bm_5) X h_2	+
(h_3 X h_2) X h_2	+	(h_3 X bm_1) X h_3	+
(h_3 X h_2) X h_3	+	(h_3 X bm_1) X bm_1	+
		(h_3 X bm_5) X h_3	+

[1/] + = bloom
- = bloomless

family of Udic Argiustolls. Fertilizer was applied at the rate of 133 kg N/ha of 45-0-0 and 114 kg K_2O/ha broadcast preplant. The experimental area was irrigated on 20 July 1977, with approximately 5 cm of water being applied. Experimental rows were 10.4 m long and 91.4 cm apart. Plants were thinned after emergence to one plant every 15.2 cm. Each population consisted of seed from at least two F_1 generation plants. Two rows were seeded with each source. The total number of plants in each population ranged from 38 to 383, with most having at least 175 plants.

Approximately 6 weeks after planting, during the early heading stage, plants were classified as bloom, bloomless, or sparse bloom. This was done by visual observation of the plants and corresponded to the time when the bloom reached its highest concentration.

Statistical Analysis

The chi-square (X^2) goodness of fit test was used as the statistical test of segregation ratios. The .05 level was used as the significance level.

CHAPTER IV

RESULTS AND DISCUSSION

F_1 Generation

A bloom F_1 was produced in all crosses except one. The bloom F_1 was apparently the result of heterozygosity at the loci in question. A bloom F_1 in a bloomless X bloomless cross resulted from a dominant Bm gene and a recessive bm gene at each of two separate loci ($Bm_i bm_i$ $Bm_j bm_j$). A bloom F_1 in a sparse-bloom X sparse-bloom cross had a dominant H gene and a recessive h gene at each of two separate loci ($H_i h_i H_j h_j$). The bloom F_1 in a bloomless X sparse-bloom cross had a dominant Bm allele and a recessive bm allele at one locus, with a dominant H allele and recessive h allele at the second locus (BmbmHh).

Bloomless X Bloomless Crosses

The classification of F_2 plant types of bloomless X bloomless crosses are given in Table VII with chi-square and probability values. Observed numbers were obtained by assigning each plant to the bloom or bloomless classification on the basis of presence or absence of bloom. Expected numbers were obtained under the assumption of a 9 bloom:7 bloomless two-gene segregation ratio with epistasis in the F_2. The .05 level was the significance level under which the hypothesis was accepted or rejected. At least one dominant Bm allele is required at each locus for expression of bloom in the F_2. Bloomless plants in the

TABLE VII

CLASSIFICATION OF F_2 PLANT TYPES OF BLOOMLESS X BLOOMLESS CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Cross		Number of Plants in Classes[1]				Values	
		Bm	bm	h	Total	X^2	P
Expected Ratio 9:7							
$msbm_1$ X bm_2	(O)[2]	84	53		137	1.43	.25-.10
	(E)[3]	77.1	59.9				
$msbm_1$ X bm_3	(O)	162	131		293	0.11	.75-.50
	(E)	164.8	128.2				
$msbm_1$ X bm_4	(O)	199	147		346	0.22	.75-.50
	(E)	194.6	151.4				
$msbm_1$ X bm_5	(O)	73	59		132	0.05	.90-.75
	(E)	74.3	57.7				
bm_5 X bm_2	(O)		141				

[1]Bm = bloom; bm = bloomless; h = sparse-bloom
[2]Observed values
[3]Expected values

F_2 result from at least one locus with the homozygous recessive bm allele ($bm_i bm_i$-- or --$bm_j bm_j$), plus the double recessive homozygote. Of the seven bloomless individuals three resemble one parent, three resemble the other parent, and one is the double recessive homozygote. When the bm allele is homozygous at one locus the bloom (Bm) allele at another locus is not expressed--single recessive epistasis.

An F_2 population of 84 bloom and 53 bloomless individuals was produced in the $msbm_1$ (RWD 3-Weskan) X bm_2 (Redbine-60) cross. The probability level of .25-.10 indicated a reasonable fit to the hypothesis. Genes bm_1 and bm_2 appeared to be different. A probability level of .75-.50 was indicated from F_2 data of the $msbm_1$ X bm_3 (Restorer Combine Kafir-60) cross. Based on the population of 162 bloom and 131 bloomless individuals the bm_1 and bm_3 genes appeared to be not identical.

The cross of $msbm_1$ X bm_4 (Brooks) also produced a probability level of .75-.50. Size of the F_2 population was quite large, 346 individuals, with 199 bloom and 147 bloomless individuals. The fit of the data with the expected values indicated that genes bm_1 and bm_4 were different. A very strong fit of the data was apparent in the $msbm_1$ X bm_5 (Cyto-13 X Tan Sugar Drip) cross. Observed and expected numbers were almost equal (73 bloom and 59 bloomless individuals observed versus 74.3 bloom and 57.7 bloomless individuals expected). The .90-.75 probability level indicated that the bm_1 and bm_5 genes were not the same.

In the cross of bm_5 X bm_2 a bloomless F_1 was found. When F_2 progeny were observed in the field no bloom and 141 bloomless individuals were identified. Segregation for height was apparent. It appears

that proposed genes bm_5 and bm_2 are the same. This conclusion is drawn based on the segregation for height, and a bloomless F_1.

Sparse-Bloom X Sparse-Bloom Crosses

The classification of F_2 plant types of sparse-bloom X sparse-bloom crosses with calculated chi-square and probability values are given in Table VIII. Classification of each plant into either the bloom or sparse-bloom group was done by visual observation of the amount of bloom produced. Expected segregation ratio in the F_2 was 9 bloom:7 sparse-bloom with the assumption of two gene involvement. The .05 level was used as the acceptance level. The F_2 bloom plants have at least one dominant H allele at each locus. Sparse-bloom F_2 plants contain two recessive sparse-bloom h alleles at one locus (h_ih_i-- or --h_jh_j), which are expressed regardless of alleles at the other locus--single recessive epistasis. Three of the seven sparse-bloom types resemble one parent, three resemble the other parent, and one is the double recessive homozygote. Expression of sparse bloom ranges from a very light wax covering to a heavier wax covering intermediate to the heavy bloom condition. In the parental lines of this study the h_2 (Redlan-Wiley) type produced the most bloom, the h_1 (Redlan deriv) and h_3 (Martin) types intermediate amounts, and the h_4 (Redlan x Y10-Calico) type the least bloom.

An F_2 population of 202 bloom and 160 sparse-bloom individuals were found in the h_2 (Redlan-Wiley) X h_1 (Redlan deriv) cross. This was in close agreement with 203.6 bloom and 158.4 sparse bloom expected individuals. The probability of .90-.75 gives a strong fit of the data. Genes h_2 and h_1 appeared to be different.

TABLE VIII

CLASSIFICATION OF F_2 PLANT TYPES OF SPARSE-BLOOM x SPARSE-BLOOM CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Crosses		Number of Plants in Classes[1]				Values	
		Bm	bm	h	Total	X^2	P
Expected Ratio 9:7							
h_2 X h_1	(O)[2]	202		160	362	0.03	.90-.75
	(E)[3]	203.6		158.4			
h_2 X h_4	(O)	197		119	316	4.76	.05-.025
	(E)	177.8		138.2			
h_3 X h_1	(O)	196		125	321	3.02	.10-.05
	(E)	180.6		140.4			
h_3 X h_4	(O)	181		130	311	0.48	.50-.25
	(E)	174.9		136.1			

[1]Bm = bloom; bm = bloomless; h = sparse-bloom
[2]Observed values
[3]Expected values

The cross of h_2 with h_4 (Redlan x Y10-Calico) produced an F_2 population of 197 bloom and 119 sparse-bloom individuals. Based on expected numbers of 177.8 bloom and 138.2 sparse-bloom individuals, a significantly larger number of bloom individuals were observed. As a result the probability, .05-.025, exceeds the .05 significance level. Yet genes h_2 and h_4 appeared to be different. Several reasons for this discrepancy are possible. The sparse-bloom gene series, the h alleles, caused production of varying amounts of bloom. Of the alleles in question h_2 produced the most. This heavier covering of bloom in the F_2 could have been mistaken for full bloom and individual plants misclassified. Misclassification of 5% of the population in this manner would indicate significance. Penetrance is also a possible explanation. Some plants with the bloom phenotype may actually have a sparse-bloom genotype, yet for some unexplained reason this was not expressed. Random chance could also play a role. For some unknown reason the ratios did not fit. Although a seemingly adequate population, 316 individuals, was grown a larger population may be needed.

A low probability level, .10-.05, was found from analysis of the h_3 (Martin) X h_1 cross. While more bloom types were observed than expected (196 and 180.6, respectively) sufficient fit of the data was indicated with the .05 significance level. The genes h_3 and h_1 are not the same genes. Reasonable fit of the data was found from examining the F_2 population of the h_3 X h_4 cross. A probability level of .50-.25 indicated the presence of two separate genes.

Bloomless X Sparse-Bloom Crosses

Classification of the F_2 plant types of bloomless X sparse-bloom

TABLE IX

CLASSIFICATION OF F_2 PLANT TYPES OF BLOOMLESS X SPARSE-BLOOM CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Cross		Number of Plants in Classes[1]				Values	
		Bm	bm	h	Total	X^2	P
Expected Ratio 9:4:3							
h_1 X bm_3	(O)[2]	20	10	10	40	1.11	.75-.50
	(E)[3]	22.5	10	7.5			
h_1 X bm_5	(O)	67	32	19	118	0.66	.75-.50
	(E)	66.4	29.5	22.1			
h_2 X bm_2	(O)	208	79	63	350	1.56	.50-.25
	(E)	196.9	87.5	65.6			
h_2 X bm_3	(O)	217	85	46	348	8.03	.025-.01
	(E)	195.8	87	65.2			
h_2 X bm_4	(O)	186	97	41	324	9.66	.01-.005
	(E)	182.2	81	60.8			
h_2 X bm_5	(O)	19	10	9	38	0.78	.75-.50
	(E)	21.4	9.5	7.1			
h_3 X bm_2	(O)	204	86	78	368	1.60	.50-.25
	(E)	207	92	69			
h_3 X bm_3	(O)	212	101	70	383	0.39	.90-.75
	(E)	215.4	95.8	71.8			
h_3 X bm_4	(O)	158	57	54	269	2.11	.50-.25
	(E)	151.3	67.2	50.5			
$msbm_1$ X h_1	(O)	196	111	57	364	6.62	.05-.025
	(E)	204.8	91	68.2			
$msbm_1$ X h_4	(O)	178	87	67	332	0.96	.75-.50
	(E)	186.8	83	62.2			

[1] Bm = bloom; bm = bloomless; h = sparse-bloom
[2] Observed values
[3] Expected values

crosses with the chi-square analysis and associated probability levels are given in Table IX. Observed numbers were obtained by assigning plants to the proper classification--bloom, bloomless, or sparse-bloom. Expected ratios and statistical analysis was done on the basis of a 9 bloom:4 bloomless:3 sparse bloom ratio. The .05 level was used as the significance level. Two distinct genes were involved: Bm, causing bloom, and bm, causing bloomlessness; H, causing heavy bloom but not expressed with bm, and h, causing sparse-bloom. For F_2 expression of bloom one locus must contain at least one dominant Bm allele and the other locus must contain at least one dominant H allele (Bm_H_). The plants are heavily bloomed. Expression of the bloomless characteristic requires one locus to be homozygous recessive for the bm allele, regardless of the alleles at the second locus. The double homozygous recessive (bmbmhh) genotype is also bloomless. Double recessive epistasis is responsible for expression of the bloomless trait as each recessive allele is normally expressed in the homozygous condition. The bloomless plant genotypes can be bmbmHH, bmbmHh, or bmbmhh. The allele h in the homozygous recessive condition (hh) and at least one dominant Bm gene at the second locus induces the expression of sparse bloom. Genotypes of these plants are BmBmhh or Bmbmhh.

The cross of h_1 (Redlan deriv) X bm_3 (Restorer Combine Kafir-60) produced an F_2 population which when compared to the expected ratio resulted in a chi-square value and probability level of .75-.50. This indicated the presence of two genes, h_1 and bm_3. However, this prediction was based on a small F_2 population of 40 plants. If possible a larger population should be grown to provide greater assurance of this conclusion. When the h_1 type was crossed with bm_5 (Cyto 13 X Tan

Sugar Drip) the results fit the expected ratio of 9 bloom:4 bloomless: 3 sparse-bloom. Observed and expected results are nearly equal and a strong fit is indicated by the .75-.50 probability level. This indicates the presence of two genes. Acceptance of the hypothesis of two genes is also possible when examining results of the F_2 of the h_2 (Redlan-Wiley) X bm_2 (Redbine-60) cross. Although observed plant types deviate from expected types, particularly with the bloom and bloomless types, an adequate fit is indicated by the .50-.25 probability level.

In two crosses involving h_2 (h_2 X bm_3 and h_2 X bm_4) the probability level falls below the .05 acceptance level. In the first cross significantly fewer sparse-bloom types were observed than expected, and in the second cross more bloomless individuals were observed than expected yet the genes in question are different. Several plausible explanations for this discrepancy exist. Since the h_2 allele induces production of heavy sparse bloom these plants could have been misclassified as bloom. Misclassification of 5% of such types would show significance. Penetrance is also a possible explanation, particularly when more bloomless individuals occur. This is possible as bloomless types cannot be misclassified. Random chance and a population level too small to fit the ratio are also possible explanations.

A small population of 38 F_2 individuals was produced in the h_2 X bm_5 cross. The probability level of .75-.50 indicates a good fit of the data, and the presence of different genes. Larger populations of this cross should be grown to confirm this result. The cross of h_3 (Martin) X bm_2 produced a reasonable fit of the data with the expected. A probability level of .50-.25 indicates the presence of different genes.

A large number of individuals, 383, were produced in the cross of h_3 X bm_3. Observed numbers agreed closely with expected values. The probability level of .90-.75 indicated a strong fit of the data to a 9 bloom:4 bloomless:3 sparse bloom ratio and the presence of two genes- h_3 and bm_3. When h_3 was crossed to bm_4 a fairly large population was produced. Based on the probability level of .50-.25 it appears that the h_3 and bm_4 genes are different.

The cross of $msbm_1$ (RWD 3-Weskan) X h_1 (Redland deriv) produced a probability level of .05-.025, below the .05 significance level. Fewer bloom and sparse-bloom individuals and more bloomless individuals were observed than expected. There appear to be two possible explanations. Penetrance, when a phenotype is not expressed yet the gene is present, appears to be the primary explanation. Such action would allow the expression of more bloomless individuals. Additionally, although a large population was grown it might not have been large enough to allow the observed number to equal expected numbers. The alleles $msbm_1$ and h_1 appeared to be different.

When $msbm_1$ is crossed to h_4 (Redlan X Y10-Calico) good agreement is shown between observed and expected results. The probability level was shown to be .75-.50. Genes $msbm_1$ and h_4 appear to be different.

Backcrosses

The classification of $backcross_1$ plant types with the chi-square and probability levels are given in Table X. Expected numbers were obtained by assigning plants to the bloom and bloomless classes in a backcross to the bloomless parent or the bloom and sparse-bloom classes in a backcross to the sparse-bloom parent. Expected numbers

TABLE X

CLASSIFICATION OF BC_1 PLANT TYPES WITH CHI-SQUARE AND PROBABILITY VALUES

Backcross		Number of Plants in Classes[1] Bm	bm	h	Total	Values X^2	P
Expected Ratio 1:1							
$(msbm_1 \times bm_2) \times bm_1$	(O)[2]	37	46		83	0.98	.50-.25
	(E)[3]	41.5	41.5				
$(msbm_1 \times bm_2) \times bm_2$	(O)	59	50		109	0.74	.50-.25
	(E)	54.5	54.5				
$(msbm_1 \times bm_5) \times bm_1$	(O)	54	73		127	2.84	.10-.05
	(E)	63.5	63.5				
$(h_3 \times h_2) \times h_2$	(O)	45		32	77	2.20	.25-.10
	(E)	38.5		38.5			
$(h_3 \times h_2) \times h_3$	(O)	98		76	174	2.78	.10-.05
	(E)	87		87			
$(h_2 \times bm_1) \times h_2$	(O)	146		105	251	6.70	.01-.005
	(E)	125.5		125.5			
$(h_2 \times bm_1) \times bm_1$	(O)	126	127		253	0.004	.95-.90
	(E)	126.5	126.5				
$(h_2 \times bm_5) \times h_2$	(O)	151		119	270	3.80	.10-.05
	(E)	135		135			
$(h_3 \times bm_1) \times h_3$	(O)	160		130	290	3.10	.10-.05
	(E)	145		145			
$(h_3 \times bm_1) \times bm_1$	(O)	118	146		264	2.96	.10-.05
	(E)	132	132				
$(h_3 \times bm_5) \times h_3$	(O)	142		152	294	0.34	.75-.50
	(E)	147		147			

[1] Bm = bloom; bm = bloomless; h = sparse bloom
[2] Observed values
[3] Expected values

were obtained and statistical analysis done on the basis of a 1 bloom: 1 bloomless or 1 bloom:1 sparse-bloom ratio, depending on the recurrent parent. The .05 level was the significance level.

Each original cross produced a bloom F_1 which was sterile. The sterile F_1's were then backcrossed to one parent, or to both parents if possible. Expression of bloom in any backcross population requires the presence of a dominant Bm gene at one locus and heterozygosity at the second locus. The expression of the bloomless character in a backcross genotype requires one locus to be homozygous for the recessive bm allele (Bm_bmbm). Expression of the sparse bloom character requires one locus to be homozygous for the recessive h allele (Bm_hh).

The F_1 of the $msbm_1$ (RWD 3-Weskan) X bm_2 (Redbine-60) cross was backcrossed to both parents. Both backcross populations were of moderate size. In both cases the probability level was .50-.25. This indicates a good fit of the data, and substantiates data in Table VII on this cross indicating that genes or loci bm_1 and bm_2 appear to be different or independent.

The F_1 of the $msbm_1$ X bm_5 (Cyto-13 X Tan Sugar Drip) was backcrossed to bm_1. More bloomless individuals were observed than expected yet the probability level was nonsignificant -.10-.05. It appears that genes $msbm_1$ and bm_5 are not identical. This supports data in Table VII on this cross.

Backcrosses to both parents were obtained from the sterile h_3 (Martin) X h_2 (Redlan-Wiley) F_1. In both backcrosses more bloom and fewer sparse-bloom individuals were observed than expected. Probabilities were .25-.10 for the h_2 backcross and .10-.05 for the h_3 back-

cross. While the probabilities are low they are not significant. Genes h_3 and h_2 appear to be different.

While results of the backcross of h_2 X bm_1 to both parents conflict, the genes are different. When backcrossed to bm_1 a very strong fit was indicated, the probability of .95-.90 indicating close agreement. Yet when the F_1 was backcrossed to the sparse-bloom h_2 parent a highly significant probability level of .01-.005 was obtained. There are several possible explanations. Penetrance, when the sparse genotype does not express itself is most probable. Misclassification of sparse-bloom types as bloom types, could cause significance. Random chance and too small a population are also possible explanations.

A low probability, .10-.05, was obtained in the (h_2 X bm_5) X h_2 backcross. More bloom types than expected caused the deviation. However, this level was not significant. Therefore, h_2 and bm_5 are different independent genes. This substantiates data in Table IX.

The sterile h_3 X bm_1 F_1 was backcrossed to both parents. In the sparse-bloom backcross more sparse-bloom progeny were observed than expected, while in the bloomless backcross more bloomless progeny were observed than expected. These deviations were not significant. Although the probability level was low in both cases, .10-.05, the presence of two genes is indicated.

A good fit of the data was apparent in the (h_3 X bm_5) X h_3 backcross. The closeness of observed and expected numbers gave a probability level of .75-.50. Genes h_3 and bm_5 appear to be different.

CHAPTER V

SUMMARY AND CONCLUSIONS

The purpose of the study was to determine the number of genes involved in the inheritance of the bloomless and sparse-bloom mutants in sorghum [Sorghum bicolor (L.) Moench]. Inheritance studies were conducted with five bloomless and four sparse-bloom parental lines. Twenty-four of thirty-six possible crosses among the nine lines were studied. For purposes of discussion the crosses were grouped into four categories: bloomless X bloomless, sparse-bloom X sparse-bloom, bloomless X sparse-bloom and backcrosses which were made to male sterile F_1 plants of the original crosses. All studies were conducted in the field using segregating F_2 and BC_1 populations. Statistical analysis was done using the chi-square test for goodness of fit.

Among the five bloomless X bloomless crosses examined four had F_1's with bloom and their F_2's segregated in a ratio of 9 bloom to 7 bloomless. This indicated different loci were involved. In the fifth cross the F_1 was bloomless and the F_2 was all bloomless, although the population segregated for other characters.

Among the four sparse-bloom X sparse-bloom crosses examined all had F_1's with bloom and their F_2's segregated in a ratio of 9 bloom to 7 sparse-bloom. This indicated different loci were involved. One cross (h_2 X h_4) did not quite fit the 9:7 ratio statistically, but the observed ratio did indicate two different loci were involved.

Among the eleven bloomless X sparse-bloom crosses examined all had F_1's with bloom and F_2's that segregated in a ratio of 9 bloom to 4 bloomless to 3 sparse-bloom, indicating that different loci were involved. Three crosses (h_2 X bm_3, h_2 X bm_4, and bm_1 X h_1) did not satisfy the test, but the observed ratio did indicate two different loci were segregating.

The backcross data showed segregation in a ratio of 1 to 1 and provided supportive information on two of the bloomless X bloomless crosses, and on one of the bloomless X sparse-bloom combinations. Data on the h_3 X h_2 cross indicated two different loci, and the data on h_2 X bm_1, h_3 X bm_1, and h_3 X bm_5 indicated independent inheritance.

It was concluded that among the cross combinations of bloomless and sparse-bloom parental lines tested, only those designated as bm_2 and bm_5 appeared to be the same. All others were inherited independently of each other. Further study is needed to determine:

a) why the h_2 allele does not consistently segregate in accordance with the two gene hypothesis

b) the range of expression of the sparse bloom character

c) the inheritance of crosses from the diallel not included here.

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VITA 2

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