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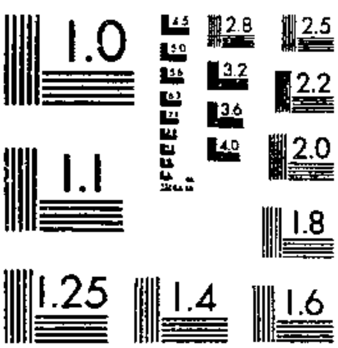

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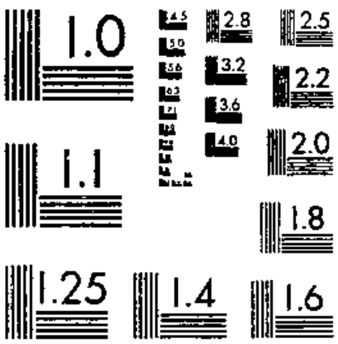

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THE INHERITANCE OF COLORED SCUTELLUMS IN MAIZE[1]

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CONTENTS

INTRODUCTION

In the genetic analysis of maize, genes determining endosperm and seedling characters have occupied a very prominent place. This is in part because of the greater ease of obtaining large numbers. These factors also seem to occur more frequently in the germ plasm of maize than do those affecting the mature plant. The list of reported genes is now well over 200, and of this number fully 150 show their effect in the endosperm or seedling. Genes producing a visible effect in the maize germ have been very few. The scarcity of such genes doubtless is due in part to the fact that they have not been sought.

In 1923 Mangelsdorf (*8*)[3] and Lindstrom (*7*) reported simultaneously on a condition in maize in which there is a failure of a definite proportion of the kernels to go through the normal rest period. The following year Eyster (*3*) reported a similar condition, which he designated "primitive sporophyte." In 1926 Mangelsdorf (*9, p. 607*) reported further on this same condition, designating it "premature

[1] Presented to the faculty of the Graduate School of Cornell University in partial fulfillment of the requirements for the degree of doctor of philosophy.

[2] The writer takes this opportunity to express his indebtedness to R. A. Emerson, under whose supervision these studies were conducted; to Mary Whitworth Sprague for assistance in making counts; to F. D. Richey for suggestions in the presentation of material; and to I. F. Phipps for the original stocks of the dominant white and orange scutellums.

[3] Italic numbers in parentheses refer to Literature Cited, p. 43.

germination" and presenting data from which he concluded that there were "nine Mendelian factors involved in the maintenance of a normal period of dormancy in maize seeds * * *." In 1930 he (*10*) presented additional data and concluded that 15 factor pairs were involved in the production of the nine different types of premature germination. There still remains the possibility, however, that certain of these factors may be genetically identical.

Jenkins (*6*) reported the factor pair *Pu pu* in 1926. The dominant member of this factor pair causes the development of purple color in the plumulary sheath. The writer (*12*) presented evidence that "colored scutellum" was a heritable character of maize and dependent upon the interaction of several factors. This bulletin gives the results of a continuation of the study of the genes concerned in the expression of various scutellum colors.

SOURCE AND DESCRIPTION OF MATERIAL

Data are presented on the inheritance and interaction of five different scutellum colors, namely, purple, red, orange, yellow, and white. The related colors purple and red are dominant to the absence of color, with the exception of one dominant white. The orange and yellow scutellums are recessive to white. In progenies segregating for orange and yellow and for purple or red, orange and yellow scutellums can be determined with accuracy only among the nonpurple and nonred classes.

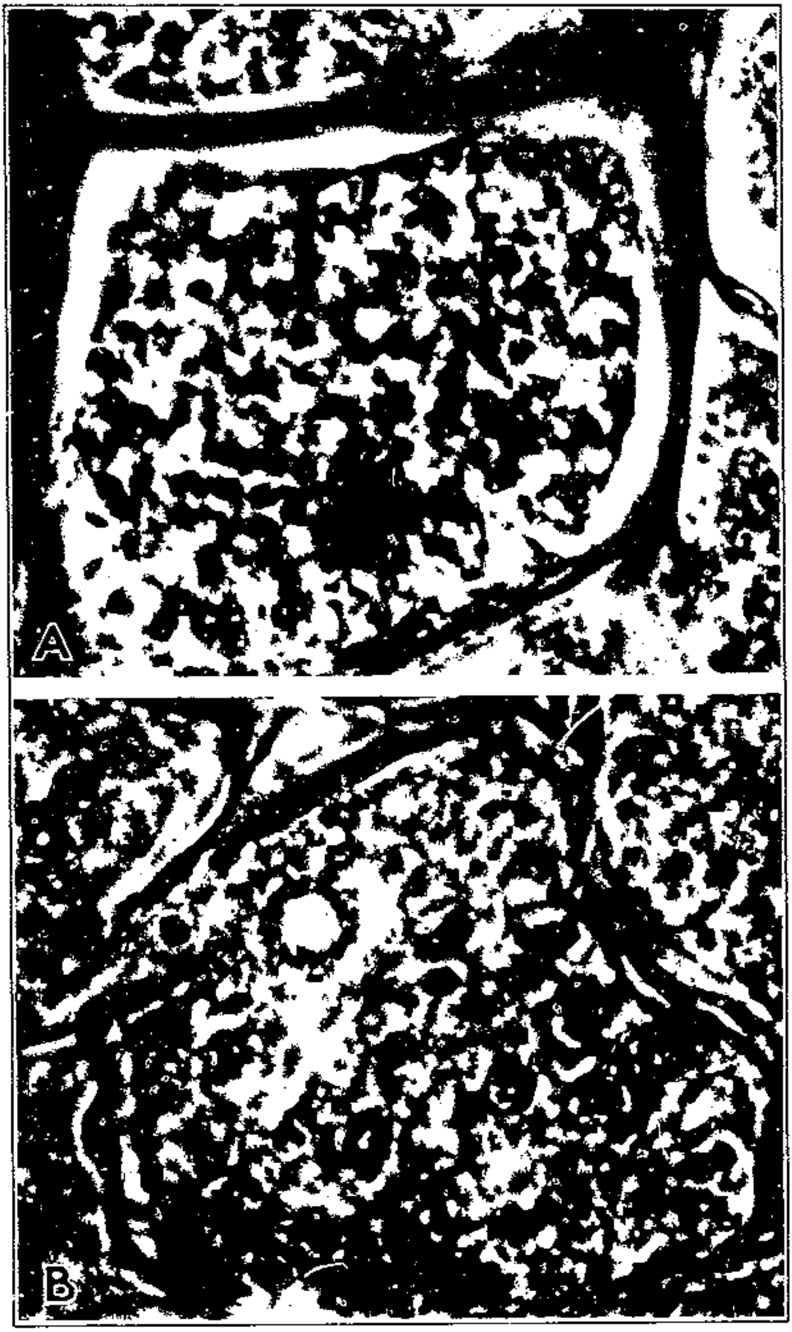
Purple scutellums were first noted at the North Platte (Nebr.) substation of the Nebraska Agricultural Experiment Station in 1923 on a single open-fertilized ear of a local variety known as Blue Flour. True-breeding colored scutellum strains, as well as testers for the purple and red series, were isolated from progeny of this original ear.

A selfed ear obtained from I. F. Phipps at Cornell University was segregating in a ratio of 9 colored to 55 white scutellums. A dominant white was isolated from the progeny of this ear. Scutellums most commonly are white, but with the exceptions of this one gene white has been recessive to purple and red.

Orange scutellums first were observed by Doctor Phipps in a single ear from one of his pedigrees. This ear was segregating in a ratio of 3 white to 1 orange. Other ears from the same pedigree exhibited similar ratios or ratios of 15 whites to 1 orange. Orange scutellums have not been observed by the writer in any material not tracing back to this original source.

Yellow scutellums were observed in the selfed progeny of the original Blue Flour ear. This color was found to be dependent on a single gene recessive to normal white. Several stocks involving South American parentage in Doctor Emerson's cultures were found to be segregating for yellow scutellums. These were tested with the writer's yellow and were found to be identical with it.

Cross sections of colored scutellum kernels through the germ show that the color is confined to the scutellum, the plumule and radicle being colorless. The intensity and distribution of color in the orange and yellow scutellums is fairly uniform. In the purples and reds the color may range from very pale to very dark in different kernels



ALEURONE GRAINS

A, In the aleurone layer; B, in the scutellum. × 2,500.

of the same ear. This difference in coloration is dependent in part upon the number of homozygous dominant scutellum factors present and may also be influenced by a concomitant variation in aleurone color. It follows that the segregating ears are subject to greater variation among the colored segregates than are homozygous ears.

In some kernels pigmentation is more intense immediately surrounding the embryo; in others it reaches its greatest intensity near the epithelial layer. The expression of color is fairly clear cut, and segregation is sufficiently sharp in most pedigrees so that no serious trouble has been experienced in classification. It has been found necessary, however, to cut into each scutellum to be certain of the correctness of its classification. This can be done in such a manner as to cause little decrease in germination and survival.

LOCATION OF SCUTELLUM PIGMENTS

Investigators who have studied the pigmentation in the aleurone of maize are agreed that the coloring matter is located in the aleurone grains. No mention could be found of the occurrence of aleurone grains in the maize scutellum.

Material for a study of the location of scutellum colors was fixed in formyl-alcohol at intervals of 5, 10, 14, 19, and 24 days after pollination. The material was then dehydrated, infiltrated with paraffin, and sectioned 10 to 12 microns thick. The most satisfactory stain combination of those tried was safranine and gentian violet in aniline oil.

The fixative was not suitable for studying the early development of aleurone grains. It was found, however, that aleurone grains were not recognizable in the material fixed 10 days after pollination but were present in the 14-day-old material. These periods undoubtedly will differ under other environmental conditions. Aleurone grains appeared in the scutellum at approximately the same time as in the aleurone layer.

In the material fixed 14 days after pollination aleurone grains were abundant in the scutellum. Near the plumule and radicle the grains apparently were fewer. This may have been more apparent than real. Cells in this region are densely protoplasmic, and aleurone grains might easily be obscured. The relatively undifferentiated parenchymatous cells in the scutellum are best suited for the study of aleurone grains.

In the aleurone layer these grains are easily distinguishable. The layers of cells underlying the aleurone layer also contain aleurone grains. The number of grains apparently decreases with each successive cell layer.

Material fixed 19 and 24 days after pollination looked very much alike. (Pl. 1.) The aleurone grains in the scutellum had increased greatly in size. In the aleurone layer the increase in size was not marked, but there was an increase in number. Aleurone grains in the scutellum were examined in free-hand sections, mounted in glycerin, observed under an oil-immersion lens. In purple, red, yellow, and orange scutellums the coloring matter appeared to be concentrated in the irregular envelope of the aleurone grain, with the remainder of the grain nearly colorless.

RELATION OF SCUTELLUM AND ALEURONE COLORS

Orange or yellow scutellums are not dependent upon the *A-C-R-Pr-i* aleurone genes or upon the genes for brown aleurone; that is, these colors may occur in kernels having purple, red, brown or colorless aleurone. Orange scutellums are dependent for their expression upon two recessive genes so_1 and so_2, while yellow scutellums are dependent upon only the single recessive gene *sy*.

The purple and red scutellums present an entirely different situation. These colors are dependent upon four dominant genes, S_1, S_2, S_3, and S_4, which may exhibit various types of interaction. In progenies segregating for both aleurone and scutellum color only those kernels having purple or red aleurone normally have colored scutellums.

The basic aleurone factors *A-C-R-pr* and *i* in the presence of the necessary scutellum factors will result in red scutellums. If recessive *pr* is replaced by its dominant allelomorph, *Pr*, the aleurone and scutellum color is purple. This relationship is illustrated by the data in Table 1.

It may be concluded from these data that the *Pr pr* factor pair differentiates purple and red scutellums.

With *I* in either a homozygous or heterozygous condition no purple or red develops in the scutellums. Similarly when *A*, *C*, or *R* is recessive, only colorless scutellums normally are produced. In progenies segregating for scutellum and aleurone genes, scutellar segregations can be observed only in the colored aleurone class. This relationship is illustrated for the *Ii*, *Rr*, *Aa*, and *Cc* factor pairs in Tables 2, 3, 4, and 5, respectively.

Among the progenies listed in Tables 3, 4, and 5 occur a few kernels having colorless aleurone and colored scutellums. This seems a direct contradiction of the interaction described above. When these kernels were planted, however, they produced progenies whose segregations for aleurone color were typical of those usually obtained from colored aleurone seeds that are heterozygous. Numerous tests have shown that the embryo and endosperm of such kernels are of different genetic constitutions and that the embryo always possesses the factors necessary for aleurone color. This condition has been reported by the writer (*13*) under the term "heterofertilization."

TABLE 1.—*Records of scutellum color in 10 F_2 progenies of crosses of purple and red scutellums*

Pedigree No.	Purple aleurone		Red aleurone	
	Purple scutellum	Red scutellum	Purple scutellum	Red scutellum
336-8	100	0	0	34
381-1	179	0	0	75
381-2	201	0	0	58
381-4	172	0	0	71
381-5	175	0	0	54
381-8	123	0	0	36
381-9	143	0	0	62
381-12	208	0	0	82
381-15	179	0	0	75
381-16	65	0	0	29
Total	1,545	0	0	576

Table 2.—*Records of scutellum color in 10 F_3 progenies of crosses of dominant white aleurone × colored scutellums*

Pedigree No.	Colored aleurone		Colorless aleurone	
	Colored scutellum	Colorless scutellum	Colored scutellum	Colorless scutellum
198-2	34	13	0	198
198-4	19	7	0	116
198-5	75	20	0	423
198-6	86	28	0	496
198-8	45	18	0	286
198-10	32	9	0	181
198-12	36	10	0	190
198-14	56	19	0	331
198-15	28	11	0	169
198-17	15	7	0	87
Total	425	142	0	2,479

Table 3.—*Records of scutellum color in seven F_3 progenies of F_2 kernels having colorless aleurone (A C r) and colored scutellum*

Pedigree No.	Colored aleurone		Colorless aleurone	
	Colored scutellum	Colorless scutellum	Colored scutellum	Colorless scutellum
559-1	252	18	1	61
561-1	46	13	0	22
561-2	81	106	2	70
561-3	125	48	2	59
590-1	151	7	5	47
590-3	122	13	1	30
590-5	180	12	3	40

Table 4.—*Records of scutellum color in 10 F_3 progenies of F_2 kernels having colorless aleurone (a C R) and colored scutellum*

Pedigree No.	Colored aleurone		Colorless aleurone	
	Colored scutellum	Colorless scutellum	Colored scutellum	Colorless scutellum
580-1	127	31	0	57
583-2	148	59	1	61
583-3	156	50	0	65
585-1	56	67	1	24
586-1	294	16	3	93
586-2	122	20	3	33
588-1	264	2	1	72
596-1	119	81	0	48
598-1	67	8	0	26
598-2	155	29	1	53

TABLE 5.—*Records of scutellum color in 11 F_3 progenies of F_2 kernels having colorless aleurone (A c R) and colored scutellum*

Pedigree No.	Colored aleurone		Colorless aleurone	
	Colored scutellum	Colorless scutellum	Colored scutellum	Colorless scutellum
561-1	46	13	0	22
561-2	81	105	2	70
561-3	125	48	2	59
567-1	168	54	4	75
575-1	178	58	0	77
577-1	96	84	1	56
579-4	231	16	1	77
582-5	73	103	0	62
587-1	227	10	0	82
587-2	111	10	0	53
597-2	250	84	0	125

In progenies segregating for scutellum color and the aleurone pattern factor "Navaho," the segregations for scutellum color can be determined among both self-colored and Navaho classes. The data illustrating this behavior are presented in Table 6.

TABLE 6.—*Records of scutellum color in five F_3 progenies of F_2 colored scutellum kernels heterozygous for the Navaho pattern factor*

Pedigree No.	Number of individuals			
	Self-colored aleurone		Navaho aleurone	
	Colored scutellum	Colorless scutellum	Colored scutellum	Colorless scutellum
995-9	190	56	66	17
995-12	229	80	95	29
995-14	150	51	81	15
Total	569	187	242	61
995-3	194	10	70	3
995-10	134	10	55	4
Total	328	20	125	7

A similar situation exists with respect to the pattern factors "stipple" (Tables 7 and 8) and "blotch." (Table 9.) In the data of both Tables 7 and 8 the stippled aleurone class is deficient on the basis of a 3:1 segregation. This deficiency for the data in Table 7 may be due to a faulty classification. In Table 8 the percentage of stippled individuals suggests a duplicate gene relationship. Colored scutellums are exhibited in the presence of blotch, as shown by the data in Table 9.

TABLE 7.—*Records of scutellum color in five F_2 progenies of the cross self-colored aleurone, colored scutellum, × stipple aleurone, colorless scutellum*

Pedigree No.	Number of individuals			
	Self-colored aleurone		Stippled aleurone	
	Colored scutellum	Colorless scutellum	Colored scutellum	Colorless scutellum
838-1	187	14	53	4
838-2	245	17	42	3
838-3	174	13	52	4
838-4	276	12	72	5
838-5	175	12	67	6
Total	1,057	68	286	22

TABLE 8.—*Records of scutellum color in six F^3 progenies of the cross self-colored aleurone, colored scutellum, × stipple aleurone, colorless scutellum*

Pedigree No.	Number of individuals			
	Self-colored aleurone		Stippled aleurone	
	Colored scutellum	Colorless scutellum	Colored scutellum	Colorless scutellum
839-1	222	16	24	3
839-4	247	27	15	9
839-5	229	19	23	4
839-6	121	14	9	2
839-8	203	19	15	3
839-9	246	28	14	6
Total	1,268	123	100	27

TABLE 9.—*Records of scutellum color in six progenies segregating for blotch aleurone grown from heterofertilized kernels*

Pedigree No.	Number of individuals			
	Blotch aleurone		Colorless aleurone	
	Colored scutellum	Colorless scutellum	Colored scutellum	Colorless scutellum
990-1	138	12	3	61
990-3	180	11	25	76
990-5	127	12	9	83
990-6	71	6	16	72
990-7	173	15	8	65
990-13	65	6	0	22

The classification of scutellum color in stipple and blotch kernels is not so satisfactory as in self-colored or Navaho kernels. In the presence of the pattern factors stipple and blotch there is a strong tendency for the scutellum color to be restricted to a small area near the radicle.

NONALLELOMORPHISM OF SCUTELLUM AND ALEURONE FACTORS

The dependency of scutellum color upon aleurone color suggests that possibly the scutellum and aleurone factors are allelomorphic. Data do not bear out this suggested relationship. Let us, for the purpose of illustration, assume one of the complementary scutellum factors to be allelomorphic to C, designating it C^{sc}. A cross between a colored aleurone, colored scutellum strain, and a colorless aleurone, colorless scutellum strain, having the allelomorph c, should produce the following types and frequencies in F_2: 1 C^{sc} C^{sc} : 2 C^{sc} c : 1 c c. Only parental types should appear in F_2 or subsequent generations. Actually from every such cross studied a new type, colored aleurone, colorless scutellum, has appeared in F_2. This type can be extracted in a true breeding condition in F_3. This precludes the possibility of allelomorphism of scutellum and aleurone factors.

PURPLE AND RED SCUTELLUMS

For the sake of simplicity it is advisable to consider the inheritance of the related colors purple, red, and recessive white, apart from dominant white, orange, and yellow. The latter show a relatively simple mode of inheritance, whereas the behavior of the purples and reds is more complex.

Segregates from crosses of colored × colored, colored × colorless, and colorless × colorless scutellums have been studied. Some of the data on such progenies are presented in Table 10.

In addition to progenies exhibiting colored scutellums only and others segregating in the simple ratio of 3 colored scutellums to 1 colorless, other ratios were obtained indicative of a complex system of factor interaction.

The data in Groups 2 and 3 of Table 10 approximate 9 to 7 and 27 to 37 ratios, indicating complementary genes. Students of corn genetics are well acquainted with this type of interaction, exemplified by the well-known series of aleurone factors. The data in Group 4, on the other hand, suggest the action of duplicate genes. The ratios in Groups 5 and 6 of the same table suggest a combination of these two types of behavior.

THE SUGGESTED HYPOTHESIS

The following hypothesis has been formulated to account for these various ratios. Four factor pairs, S_1 s_1, S_2 s_2, S_3 s_3, and S_4 s_4, are postulated. Of this series, S_1 always must be present if purple or red scutellums are to result. In addition to S_1, the dominant allelomorphs of any two of the other three members of the series are required for the development of colored scutellums.

TABLE 10.—*Records of soutellum color in 108 segregating progenies of crosses of colored × colorless, colorless × colorless, and colored × colored parents*

Group and pedigree No.	Number of individuals			Percentage colorless	Dev./P. E.
	Colored	Colorless	Total		
Group 1 (3 : 1):					
100-1	326	101	427	23.7	1.0
100-2	233	84	317	26.5	.9
100-3	299	90	389	23.1	1.3
100-4	400	125	525	23.8	.9
100-7	373	110	483	22.8	1.7
100-8	348	127	475	26.7	1.3
100-10	407	140	547	25.6	.5
100-12	332	100	432	23.1	1.3
100-13	436	150	586	25.6	.5
100-16	340	110	450	24.4	.4
170-1	123	40	163	24.5	.2
170-2	125	36	161	22.4	1.1
170-4	81	24	105	22.9	.8
178-5	200	58	258	22.5	1.4
320-1	196	45	241	18.7	3.4
320-4	148	57	205	27.8	1.4
321-4	291	90	381	23.6	.9
321-5	320	91	411	22.1	2.0
322-1	159	37	196	18.9	2.9
322-2	66	15	81	18.5	2.0
322-3	251	62	313	19.8	3.1
322-6	217	80	297	26.9	1.1
323-2	227	72	299	24.1	.5
323-4	227	75	302	24.8	.1
323-5	183	58	241	24.1	.5
323-7	341	100	441	22.7	1.7
323-8	199	42	241	17.4	4.0
323-10	328	114	442	25.8	0.6
323-11	247	95	342	27.8	1.8
323-12	240	99	339	29.2	2.6
323-1	205	72	277	26.0	.6
324-1	182	41	223	18.4	3.4
324-7	224	55	279	19.7	3.0
325-1	160	59	219	26.9	1.0
325-8	179	65	244	26.6	.9
327-1	171	71	242	29.3	2.3
327-4	171	73	244	29.9	2.6
327-10	193	46	239	19.2	3.0
327-11	206	47	253	18.6	3.5
327-12	198	46	244	18.9	3.3
328-5	38	12	50	24.0	.2
329-1	205	55	260	21.2	2.1
329-5	217	55	272	20.2	2.7
Total	10,012	3,124	13,136	23.8	4.8
Group 2 (9 : 7):					
104-5	122	75	197	38.1	2.4
104-7	231	149	380	39.2	2.6
170-3	132	114	246	46.3	1.2
320-8	129	80	209	38.3	2.4
320-11	198	142	340	41.8	1.1
323-9	150	131	281	46.6	1.4
324-2	195	101	296	34.1	4.9
324-4	149	103	252	40.9	1.4
324-5	163	120	283	42.4	.7
324-7	132	127	259	49.0	2.5
324-10	186	124	310	40.0	2.0
325-5	153	124	277	44.8	.5
327-7	141	119	260	45.8	1.0
328-6	95	91	186	48.9	2.1
329-6	187	141	328	43.0	.4
Total	2,363	1,741	4,104	42.4	2.5
Group 3 (27 : 37):					
170-5	71	162	233	69.5	5.4
322-8	118	221	339	65.2	4.1
322-13	98	205	303	67.7	5.2
4-1	166	230	396	58.1	.1
102-6	259	366	625	58.6	.5
103-8	230	334	564	59.2	1.0
103-11	96	160	256	62.5	2.3
322-4	122	144	266	54.1	1.5
322-12	176	198	374	52.9	2.8
325-4	102	115	217	53.0	2.1
325-7	88	95	183	51.9	2.4

TABLE 10.—*Records of scutellum color in 108 segregating progenies of crosses of colored × colorless, colorless × colorless, and colored × colored parents*—Continued

Group and pedigree No.	Number of individuals			Percentage colorless	$\frac{\text{Dev.}}{\text{P. E.}}$
	Colored	Colorless	Total		
Group 3 (27 : 37)—Continued.					
325-6	67	85	152	55.9	0.7
327-2	107	162	269	60.2	1.2
327-5	84	122	206	59.2	.5
327-6	121	171	292	58.6	.4
327-8	118	124	242	51.2	3.1
327-9	99	120	219	54.8	1.3
328-1	121	134	255	52.5	2.6
328-2	104	124	228	54.4	1.5
328-4	86	105	191	55.0	.3
Total	2,433	3,377	5,810	58.1	.7
Group 4 (15 : 1):					
6-3	275	18	293	6.1	.1
4-4	163	13	176	7.4	.9
4-5	327	27	354	7.6	1.6
101-2	473	39	512	7.6	1.9
101-5	344	29	373	7.8	1.8
101-7	354	30	384	7.8	1.9
188-12	163	11	174	6.3	0
320-10	141	14	155	9.0	2.1
321-6	235	24	259	9.3	3.0
322-7	168	20	188	10.6	3.7
322-11	281	9	290	3.1	3.3
323-13	320	24	344	7.0	.8
323-14	276	11	287	3.8	2.5
323-3	160	8	168	4.8	1.2
328-3	211	16	227	7.0	.7
329-4	273	24	297	8.1	1.9
325-7	233	19	252	7.5	1.3
Total	4,397	386	4,783	7.1	3.6
Group 5 (54 : 10):					
320-2	256	33	289	11.4	2.9
320-3	246	33	279	11.8	2.6
320-9	262	45	307	14.7	.7
321-1	293	51	344	14.8	.6
324-6	155	26	181	14.4	.7
324-11	190	23	213	10.8	2.8
329-3	207	39	246	15.9	.1
322-7	168	20	188	10.6	2.8
Total	1,777	270	2,047	13.2	4.5
Group 6 (162 : 94):					
866-3	113	60	173	34.7	.9
866-4	75	39	114	34.2	1.0
866-8	136	68	204	33.3	1.6
867-2	86	57	143	39.9	1.1
867-7	101	58	159	36.5	.1
868-1	78	29	107	27.1	3.1
Total	589	311	900	34.6	2.0

Four wholly homozygous stocks of colored scutellums are then possible. These are:

$S_1 S_1,\ S_2 S_2,\ S_3 S_3,\ S_4 S_4$
$S_1 S_1,\ S_2 S_2,\ S_3 S_3,\ s_4 s_4$
$S_1 S_1,\ S_2 S_2,\ s_3 s_3,\ S_4 S_4$
$S_1 S_1,\ s_2 s_2,\ S_3 S_3,\ S_4 S_4$

Selfed parents giving rise to ratios of 3 colored to 1 colorless scutellum may be of 1 of 4 major classes of genotypes, namely:

A: $S_1 s_1,\ S_2 S_2,\ S_3 S_3,\ S_4 S_4$
B: $S_1 s_1\ (S_2 S_2,\ S_3 S_3,\ S_4 s_4)$
C: $S_1 s_1\ (S_2 S_2,\ S_3 S_3,\ s_4 s_4)$
D: $S_1 S_1\ (S_2 S_2,\ S_3 s_3,\ s_4 s_4)$

Classes A, B, and C are alike in having $S_1\ s_1$ heterozygous with at least two of the other members of the series homozygous dominant. It is immaterial which member of the series inclosed in parentheses is heterozygous in class B orhomozygous in class C, thus giving three subtypes within each of these two classes, all of which will segregate in the 3:1 ratio. The colorless scutellum segregates from classes A, B, and C will be specific testers for the $S_1\ s_1$ factor pair. If also recessive for one of the other members of the series, they will incidentally be testers for that member when used with certain genotypes.

Class D differs basically from A, B, and C in having $S_1\ S_1$ homozygous dominant, with segregation due to the other members of the series. Here, it is immaterial which one of the three factor pairs, S_2, S_3, or S_4, is dominant, which one is heterozygous, and which one is recessive. The colorless scutellum segregates will be recessive for two of the factors within parentheses. They therefore will constitute testers for these two factors together or will determine that one of the two is concerned, but will not differentiate between them.

Ratios of 9 colored to 7 colorless scutellums are expected when any 2 factor pairs are heterozygous, and if in addition 1 of the factor pairs S_2, S_3, and S_4 is homozygous recessive.

Similarly, if one member of the series S_2, S_3, and S_4 is homozygous recessive, the two remaining members and S_1 being heterozygous, ratios of 27 colored to 37 colorless scutellums are expected. This and the preceding ratios comprise the complementary series.

Ratios of 15 colored to 1 colorless scutellum are to be expected when S_1 and 1 member of the series S_2, S_3, and S_4 are homozygous dominant and the other 2 members are heterozygous. White segregates from such ratios would be expected to constitute testers for the two genes recessive or will determine that one of the two is concerned, but will not differentiate between them. This ratio with its 3:1 components constitutes the duplicate series.

The remaining ratio types expected on the basis of the hypothesis are combinations of the complementary and duplicate series.

The ratio expected when 1 member of the series S_2, S_3, and S_4 is homozygous dominant and the remaining 3 factors are heterozygous is 45 colored to 19 colorless scutellums.

Ratios of 54 colored to 10 colorless scutellums are expected when S_1 is homozygous dominant and the factors $S_2\ s_2$, $S_3\ s_3$, and $S_4\ s_4$ are heterozygous.

The most complex ratio obtainable under the hypothesis is 162 colored to 94 colorless scutellums. This ratio would be expected if all four of the factors $S_1\ s_1$, $S_2\ s_2$, $S_3\ s_3$, and $S_4\ s_4$ were heterozygous.

The following diagram provides a detailed illustration of the various genotypes that may be involved in the production of each ratio type. All genotypes recessive for $s_1\ s_1$ are omitted, as colorless scutellums would result.

	$S_1\ S_1$	$S_1\ s_1$
$S_2\ S_2$, $S_3\ S_3$, $S_4\ S_4$	Colored	3 : 1
$S_2\ S_2$, $S_3\ S_3$, $S_4\ s_4$	Colored	3 : 1
$S_2\ S_2$, $S_3\ s_3$, $S_4\ S_4$	Colored	3 : 1
$S_2\ s_2$, $S_3\ S_3$, $S_4\ S_4$	Colored	3 : 1
$S_2\ S_2$, $S_3\ s_3$, $S_4\ s_4$	15 : 1	45 : 19
$S_2\ s_2$, $S_3\ S_3$, $S_4\ s_4$	15 : 1	45 : 19
$S_2\ s_2$, $S_3\ s_3$, $S_4\ S_4$	15 : 1	45 : 19

$S_2 s_2, S_3 s_3, S_4 s_4$	54 : 10	162 : 94
$s_2 s_2, S_3 S_3, S_4 S_4$	Colored	3 : 1
$s_2 s_2, S_3 s_3, S_4 S_4$	3 : 1	9 : 7
$s_2 s_2, S_3 S_3, S_4 s_4$	3 : 1	9 : 7
$s_2 s_2, S_3 s_3, S_4 s_4$	9 : 7	27 : 37
$S_2 S_2, s_3 s_3, S_4 S_4$	Colored	3 : 1
$S_2 s_2, s_3 s_3, S_4 S_4$	3 : 1	9 : 7
$S_2 S_2, s_3 s_3, S_4 s_4$	3 : 1	9 : 7
$S_2 s_2, s_3 s_3, S_4 s_4$	9 : 7	27 : 37
$S_2 S_2, S_3 S_3, s_4 s_4$	Colored	3 : 1
$S_2 s_2, S_3 S_3, s_4 s_4$	3 : 1	9 : 7
$S_2 S_2, S_3 s_3, s_4 s_4$	3 : 1	9 : 7
$S_2 s_2, S_3 s_3, s_4 s_4$	9 : 7	27 : 37

This hypothesis may be tested in a number of ways. In the first place, the system of interaction outlined accounts for all the ratios obtained and recorded in Table 10. In addition, a ratio of 45 colored to 19 colorless scutellums is permitted, which closely approximates the 48:16 of a 3:1 ratio. The F_3 breeding behavior, presented in a later section, shows that certain progenies listed in Group 1 (3:1) of Table 10 properly belonged in the 45:19 category.

The methods that have been employed to check the hypothesis in greater detail are the breeding behavior of colored and colorless F_2 segregates and the identification of colored and colorless genotypes by appropriate intercrosses.

BEHAVIOR OF COLORED SCUTELLUMS IN THE F_3 GENERATION

The system of factor interaction previously outlined requires the existence of eight different ratios. These have been obtained from various crosses, and the F_3 breeding behavior of the colored segregates is presented in the following sections.

RATIOS OF 162 TO 94

An F_2 ratio of 162 colored to 94 colorless scutellums is expected when the F_1 is of the constitution $S_1 s_1, S_2 s_2, S_3 s_3, S_4 s_4$.

Colored segregates from ratios approximating this were planted and the progeny classified to determine their F_3 behavior. The eight ratio types listed in the factor-interaction diagram (p. 11) were obtained. These data are presented in Groups A to G of Table 11. It was so obviously impossible to separate 3:1 and 45:19 ratios in the absence of data on breeding behavior that this was not attempted.

In Group A are listed six progenies that bred true for colored scutellums.

In Group B are listed 13 progenies whose ratios approximate 3:1 or 45:19. The total number of kernels in these progenies is 2,248. The mean percentage of colorless individuals in this group is 24.8. The percentage expectancy on the basis of a 3:1 ratio is 25.0, and that on a basis of 45:19 is 29.7.

Group C is composed of four progenies whose segregations approximate 9 colored to 7 colorless scutellums. The calculated percentage of colorless scutellums for this ratio is 43.8. The observed percentage is 41.3.

Progenies whose ratios approximate 27 colored to 37 colorless scutellums are listed in Group D. Only two such progenies were obtained, both of which have negative deviations. The mean deviation is only 1.3 times its probable error, and therefore well within the limits of chance fluctuations from expectancy.

TABLE 11.—*Records of scutellum colors in 35 F_3 progenies of F_2 colored segregates of a 162:94 ratio*

Group and ratio	Pedigree No.		Number of individuals			Percentage colorless	Dev. / P. E.
	F_1	F_2	Colored	Colorless	Total		
A (1 : 0)	639-5	853-2	157	0	157		
		853-3	133	0	133		
		853-10	58	0	58		
	639-15	852-8	108	0	108		
		852-9	175	0	175		
		852-18	191	0	191		
Total			822	0	822		
B (3 : 1; 45 : 10)	639-5	853-5	100	35	135	25.9	
		853-6	135	44	179	24.6	
		853-14	112	35	147	23.8	
		853-15	77	21	98	22.4	
		853-17	50	14	64	21.9	
		853-19	76	25	101	24.8	
		853-20	164	65	229	28.4	
	639-15	852-5	180	66	246	26.8	
		852-6	207	70	277	25.3	
		852-11	179	62	241	25.7	
		852-13	133	34	167	20.4	
		852-14	108	42	150	28.0	
		852-15	169	45	214	21.0	
Total			1,690	558	2,248	24.8	
C (9 : 7)	639-5	853-1	20	15	35	42.9	0.2
		853-13	91	63	154	40.9	1.1
		853-16	113	83	196	42.3	.6
	639-15	852-4	52	33	85	38.8	1.4
Total			276	194	470	41.3	1.6
D (27 : 37)	639-5	853-9	51	62	113	54.9	1.0
	639-15	852-17	105	132	237	55.7	1.0
Total			156	194	350	55.4	1.3
E (15 : 1)	639-5	853-4	145	8	153	5.2	.7
		853-18	115	7	122	5.7	.4
	639-15	852-1	194	18	212	8.5	2.0
		852-7	45	3	48	6.3	0
Total			499	36	535	6.7	.7
F (54 : 10)	639-5	853-7	190	30	220	13.6	.9
		853-11	155	33	188	17.6	1.1
	639-15	852-2	162	23	185	12.4	1.8
Total			507	86	593	14.5	1.1
G (162 : 94)	639-5	853-8	77	34	111	30.6	1.9
		853-12	129	65	194	33.5	1.4
	639-15	852-16	188	88	276	31.9	2.5
Total			394	187	581	32.2	3.4

Group E is composed of progenies approximating 15 colored to 1 colorless scutellum. Of the four progenies, two have negative and two have positive deviations. The group deviation is positive, the deviation divided by probable error being 0.7.

Progenies having approximately 54 colored to 10 colorless scutellums are listed in Group F. The observed percentage of colorless scutellums for this ratio is 14.5, the theoretical expectancy being 15.6 per cent.

Group G comprises the three progenies having ratios approximating 162 colored to 94 colorless scutellums. All three progenies have negative deviations. The deviation divided by probable error is 3.4.

Within each of the above groups the agreement between observation and theory is satisfactory, with the exception of the last group (G). The agreement between the observed and calculated number of progenies in each group is shown in Table 12. The value for χ^2 is 12.27, giving a probability of only 0.06. Half of the total χ^2 value is obtained from the Group A deviation. A possible explanation for the excess in this group may be differential germination. Kernels that are homozygous for colored scutellums or heterozygous for one or two factor pairs can be classified as colored with little injury to the germ. With an increase in the number of heterozygous factor pairs, the scutellums are lighter colored and must be cut more deeply to insure correct classification.

TABLE 12.—*Comparison of observed and calculated number of progenies in groups shown in Table 11*

Items	Group							Total
	A	B	C	D	E	F	G	
Observed	6	13	4	2	4	3	3	35
Calculated	2.2	12.1	7.8	5.2	2.6	1.7	3.5	35.1
Difference	+3.8	+.9	−3.8	−3.2	+1.4	+1.3	−.5	−.1

$\chi^2 = 12.27$. $P = 0.06$

The F_3 behavior of colored segregates from the 162 : 94 ratios gave all of the ratios called for by the hypothesis. The agreement between the observed and calculated distribution of progenies, however, is poor.

RATIOS OF 54 TO 10

Colored scutellum kernels of F_2 ratios approximating 54 colored to 10 colorless were tested in F_3. Ratios of this type are expected when the F_1 is of the constitution $S_1\ S_1$, $S_2\ s_2$, $S_3\ s_3$, $S_4\ s_4$. Thirty-eight F_3 progenies were classified, the number of individuals totaling 6,774. These progenies are divided into five groups on the basis of the percentage of colorless scutellum individuals. The data are listed in Table 13.

Group A includes 10 progenies. Among 1,853 kernels were 8 with colorless scutellums. These were not tested further, but are probably due to accidental pollination by stray pollen grains from the dominant white strain.

In Group B, whose progenies approximate ratios of 3 colored to 1 colorless scutellum, the percentages of colorless scutellums range from 18.8 to 30.4. The mean percentage of colorless individuals for the group is 24.7, which is close to the expected 25 per cent.

Group C, made up of progenies segregating in ratios of 9 colored to 7 colorless scutellums, has an average percentage of colorless individuals of 39.9. The expected percentage for this ratio is 43.8. Five of the six progenies have negative deviations. The total deficiency of colorless scutellums is 89 individuals, giving a deviation divided by probable error of 3.7.

TABLE 13.—*Records of scutellum colors in 38 F_3 progenies of F_2 colored segregates of a 54:10 ratio*

Group and ratio	Pedigree No.		Number of individuals			Percentage colorless	$\frac{\text{Dev.}}{\text{P. E.}}$
	F_2	F_3	Colored	Colorless	Total		
A (1:0)	323-8	666- 2	235	2	237		
		666- 3	106	1	107		
		666- 7	326	0	326		
		666-11	165	2	167		
		666-14	207	1	208		
		666-17	166	0	166		
		666-19	194	0	194		
		666-21	129	0	129		
		666-24	106	2	108		
		666-26	151	0	151		
Total			1,845	8	1,853		
B (3:1)	323-8	666- 1	189	70	259	27.0	1.1
		666-10	138	39	177	22.0	1.2
		666-13	149	54	203	26.6	.8
		666-15	128	49	177	27.7	1.2
		666-18	147	34	181	18.8	2.9
		666-29	110	48	158	30.4	2.3
		666-31	126	33	159	20.8	1.8
		666-38	42	10	52	19.2	1.4
Total			1,029	337	1,366	24.7	.5
C (9:7)	323-8	666- 5	209	148	357	41.5	1.8
		666- 8	149	80	229	34.9	4.0
		666-25	148	112	260	43.1	.3
		666-27	54	41	95	43.2	.2
		666-34	65	34	99	34.3	2.8
		666-37	25	21	46	45.7	.4
Total			650	436	1,086	39.9	3.7
D (15:1)	323-8	666- 4	143	11	154	7.1	.7
		666- 6	197	9	206	4.4	1.7
		666-12	268	24	292	8.2	2.1
		666-16	249	22	271	8.1	1.9
		666-20	167	6	173	3.5	2.2
		666-22	236	7	243	2.9	3.2
		666-23	181	12	193	6.2	0
		666-29	81	4	85	4.7	.9
Total			1,522	95	1,617	5.9	.9
E (54:10)	323-8	666- 9	253	44	297	14.8	.6
		666-28	108	16	124	12.9	1.2
		666-30	143	21	164	12.8	1.5
		666-33	106	16	122	13.1	1.1
		666-35	61	9	70	12.9	.9
		666-36	64	11	75	14.7	.3
Total			735	117	852	13.7	2.3

Progenies whose segregations approximate 15 colored to 1 colorless scutellum comprise Group D. Five of the eight progenies in this group have negative deviations, the remaining three being positive. The cumulative deviation is very small, but negative, the deviation divided by probable error being 0.9.

Group E is made up of six progenies whose ratios approximate 54 colored to 10 colorless scutellums. There is a suggestion that deviations in this group are not random, as all are negative. The deviation divided by probable error, however, is 2.3, which is within the limits of random fluctuations.

It has been shown that the agreement between the theoretical and observed percentages of colorless scutellums within each group with one exception has been fair. A comparison of the number of progenies in each group with the calculated expectancy is shown in Table 14. The agreement is good, only one trial in four being expected to give a better fit.

TABLE 14.—*Comparison of observed and calculated number of progenies in groups shown in Table 13*

Items	Group					Total
	A	B	C	D	E	
Observed	10	8	6	8	6	38
Calculated	7	8.4	8.4	8.4	5.6	37.8
Difference	+3.0	−.4	−2.4	−.4	+.4	+.2

$\chi^2=2.05$. P=0.73

RATIOS OF 45 TO 19

The data from 13 F_3 progenies grown from colored scutellum kernels of 45:19 ratios are listed in Table 15. These progenies are divided into four groups on the basis of their breeding behavior.

Group A consists of the true-breeding colored scutellum progenies. These three progenies have a total of 324 kernels. In one progeny a single colorless scutellum kernel was observed.

TABLE 15.—*Records of scutellum colors in 13 F_3 progenies of F_2 colored segregates of a 45:19 ratio*

Group and ratio	Pedigree No.		Number of individuals			Percentage colorless	Dev./P. E.
	F_2	F_3	Colored	Colorless	Total		
A (1 : 0)	327-4	641-5	140	0	140		
		641-8	142	0	142		
		641-13	41	1	42		
Total			323	1	324		
B (3 : 1; 45 : 19)	327-4	641-1	190	63	253	24.9	
		641-2	189	36	225	16.0	
		641-3	170	63	233	27.0	
		641-4	181	25	206	12.1	
		641-9	137	32	169	18.9	
		641-10	102	18	120	15.0	
Total			969	237	1,206	19.6	
C (9 : 7)	327-4	641-7	85	87	172	50.6	2.8
D (15 : 1)	327-4	641-6	154	13	167	7.8	1.2
		641-11	112	10	122	8.2	1.4
		641-12	70	4	74	5.4	.4
Total			336	27	363	7.4	1.4

Group B comprises progenies approximating either 3:1 or 45:19 ratios. No attempt has been made to separate these progenies because of the obvious impossibility of doing so accurately except by breeding behavior.

A single progeny approximating a 9:7 ratio falls in Group C. In this progeny there is an excess of kernels belonging to the colorless scutellum class, the deviation divided by probable error being 2.8.

Group D includes those progenies having ratios of 15 colored to 1 colorless scutellum. Of the three progenies in this group, two have positive and one a negative deviation.

Considering all of the groups, the agreement between the number of progenies observed and expected on the basis of a 45:19 ratio is as shown in Table 16.

TABLE 16.—*Comparison of observed and calculated number of progenies in groups shown in Table 15*

Items	Group				Total
	A	B	C	D	
Observed	3	6	1	3	13
Calculated	2.0	7.5	2.3	1.2	13
Difference	+1.0	−1.5	−1.3	+1.8	0

$\chi^2=4.23$. $P=0.24$

A possible explanation of the large deviations occurring in certain of these F_3 progenies may be pollen-tube growth factors. Many of the progenies were segregating for sugary endosperm, and the deviations are greatest in these progenies. This suggests that the *Ga ga* factor pair (*11*) may be involved. Data were obtained on the linkage of S_1 s_1 and *Su su* in progenies homozygous for the gametophyte factor. The crossing over between these two factors was found to be about 37.6 per cent. The detailed data are presented in Table 17. If the S_1 locus is to the right of sugary, the gametophyte factor should have little influence on the colored to colorless segregations, as the map distance between the two genes would be approximately 60 units. However, if the S_1 locus is to the left of sugary, it would be only about 20 units from the gametophyte factor, with some 20 per cent of crossing over between S_1 and *Ga*.

In conformity with Mangelsdorf and Jones (*11*) it has been assumed that *Ga*-bearing gametes effect fertilization four times as often as gametes carrying *ga*. Linkage being in the coupling phase, the calculated percentage of colorless scutellums then would be 16.0. For the "low" progenies in group B of Table 15 the mean percentage of colorless scutellums is 15.4. Linkage being in the repulsion phase, the percentage of colorless scutellums would be 34.0. One progeny which might be classed as "high" had 27.0 per cent of colorless scutellums. The agreement is sufficiently close to suggest that the order of the genes may be S_1–*Ga*–*Su*, and that the action of *Ga ga* was a partial cause of the discrepancies.

TABLE 17.—*Records of scutellum color in five back-cross progenies of the cross* $(su\ S_1 \times Su\ s_1) \times su\ s_1$

Pedigree No.	*Su*		*su*		Percentage crossing over
	S_1	s_1	S_1	s_1	
1027-1 × 1026-1	40	57	58	26	36.5
1027-3 × 1026-1	27	41	49	26	37.1
1027-5 × 1026-1	38	61	56	35	38.4
1027-9 × 1026-1	26	43	47	31	38.8
1027-10 × 1026-1	10	19	19	12	36.7
Total	141	221	229	130	37.6

The situation is complicated further by the fact that some of the progenies in this group probably belonged in the 45:19 rather than in the 3:1 category.

RATIOS OF 27 TO 37

Seventeen F_3 progenies of colored segregates from 27:37 ratios were classified. The data are presented in Table 18. One of the 17 progenies bred true for colored scutellums.

Group B is made up of progenies having approximately 25 per cent of colorless scutellums, the mean percentage of colorless scutellums being 25.1.

In Group C half of the progenies have positive deviations on the basis of a 9:7 segregation, the remaining half being negative. The deviation for the group is negative, amounting to 12 individuals.

The three progenies in Group D approximate the 57.8 per cent of colorless scutellums expected with a 27:37 ratio. All the progenies have negative deviations. The deviation divided by probable error for the group is 2.4.

The agreement between the observed and calculated number of progenies for each group is shown in Table 19. The fit is reasonably good.

TABLE 18.—*Records of scutellum color in 17* F_3 *progenies of* F_2 *colored segregates of a 27:37 ratio*

Group and ratio	Pedigree No.		Number of individuals			Percentage colorless	$\frac{\text{Dev.}}{\text{P. E.}}$
	F_2	F_3	Colored	Colorless	Total		
A (1:0)	639-10	855-11	168	0	168		
B (3:1)	639-10	855-1	164	59	223	26.5	0.7
		855-2	148	48	196	24.5	.2
		855-5	210	76	286	26.6	.9
		855-15	60	18	78	23.1	.6
		855-16	140	41	181	22.7	1.1
Total			722	242	964	25.1	.1
C (9:7)	639-10	855-3	134	85	219	38.8	2.2
		855-4	116	70	186	37.6	2.5
		855-8	99	76	175	43.4	.1
		855-9	122	88	210	41.9	.8
		855-13	118	101	219	46.1	1.0
		855-14	120	97	217	44.7	.4
		855-17	80	67	147	45.6	.7
		855-19	141	118	259	45.6	.9
Total			930	702	1,632	43.0	.9
D (27:37)	639-10	855-7	79	97	176	55.1	1.1
		855-10	50	61	111	55.0	.9
		855-12	129	151	280	53.9	2.0
Total			258	309	567	54.5	2.4

TABLE 19.—*Comparison of observed and calculated number of progenies in groups shown in Table 18*

Items	Group				Total
	A	B	C	D	
Observed	1	5	8	3	17
Calculated	.6	3.8	7.6	5	17
Difference	+.4	+1.2	+.4	−2	0

$\chi^2=1.47$. P=0.69

RATIOS OF 9 TO 7

Colored scutellum kernels from 9:7 F_2 ratios were used in a test in which 28 F_3 progenies having a total of 5,379 individuals were classified. The detailed data are presented in Table 20. As expected, the progenies fall into three distinct groups. Group A contains all the true-breeding forms, Group B those progenies segregating in ratios of 3 colored scutellums to 1 colorless, and Group C the progenies approximating a ratio of 9:7.

Among the 662 individuals in Group A are 5 colorless scutellums. It is believed that these are due to foreign pollen.

The 11 progenies in Group B have percentages of colorless scutellums ranging from 21.7 to 29.1, the expected percentage being 25.0. Five of the 11 progenies have positive deviations, the cumulative deviation likewise being positive. The deviation divided by probable error is low, the value being 0.3.

Group C contains 13 progenies whose percentages of colorless individuals range from 38.5 to 47.3. The cumulative deviation is negative, the deviation divided by probable error being 3.2.

A comparison between the observed number of progenies in each group and the theoretical expectancy is shown in Table 21. The fit here is unusually close, χ^2 being less than 1.0.

TABLE 20.—*Records of scutellum colors in 28 F_3 progenies of F_2 colored segregates of a 9:7 ratio*

Group and ratio	Pedigree No.		Number of individuals			Percentage colorless	$\frac{\text{Dev.}}{\text{P. E.}}$
	F_2	F_3	Colored	Colorless	Total		
A (1:0)	327-7	640-3	188	0	188		
		640-5	143	5	148		
		640-19	208	0	208		
		640-22	118	0	118		
Total			657	5	662		
B (3:1)	327-7	640-2	176	62	238	26.1	0.6
		640-4	160	52	212	24.5	.2
		640-6	156	60	216	27.8	1.4
		640-7	155	50	205	24.4	.3
		640-8	181	57	238	23.9	.6
		640-9	186	68	254	26.8	1.0
		640-10	163	67	230	29.1	2.1
		640-11	185	52	237	21.9	1.6
		640-15	158	55	213	25.8	.4
		640-16	159	44	203	21.7	1.6
		640-27	28	8	36	22.2	.6
Total			1,707	575	2,282	25.2	.3

TABLE 20.—*Records of scutellum colors in 28 F_3 progenies of F_2 colored segregates of a 9:7 ratio*—Continued

Group and ratio	Pedigree No.		Number of individuals			Percentage colorless	$\frac{\text{Dev.}}{\text{P. E.}}$
	F_2	F_3	Colored	Colorless	Total		
C (9:7)	327-7	640-1	130	90	220	43.2	.2
		640-12	119	80	199	40.2	1.5
		640-13	116	89	205	43.4	.1
		640-14	151	95	246	38.6	2.4
		640-17	144	96	240	40.0	1.7
		640-18	126	84	210	40.0	1.6
		640-20	150	97	247	39.3	2.1
		640-21	101	82	183	44.8	.4
		640-23	83	58	141	41.1	.9
		640-24	87	69	156	44.2	.2
		640-25	60	41	101	40.6	.9
		640-26	67	42	109	38.5	1.6
		640-28	89	80	169	47.3	1.4
Total			1,423	1,012	2,435	41.6	3.2

TABLE 21.—*Comparison of observed and calculated number of progenies in groups shown in Table 20*

Items	Group			Total
	A	B	C	
Observed	4	11	13	28
Calculated	3.1	12.4	12.4	27.9
Difference	+.9	−1.4	+.6	+.1

$\chi^2=0.45$. P=0.80

The values for P when χ^2 is less than 1 have been taken from Fisher's table (*4*).

RATIOS OF 15 TO 1

Nineteen F_3 progenies were grown from colored scutellum segregates of ratios of 15 colored to 1 colorless. The detailed data are presented in Table 22. The data are divided into three groups on the basis of their F_3 segregations. Group A contains the true-breeding colored scutellum progenies. Among 1,258 individuals in nine progenies no colorless scutellums were observed.

Progenies whose segregations approximate 3 colored to 1 colorless scutellum are included in Group B. In this group the cumulative deviation is negative, the deviation divided by probable error being 1.3.

Group C contains six progenies whose segregations approximate 15 colored to 1 colorless scutellum. The total deviation is negative, the observed percentage of colorless individuals being 5.3, whereas 6.3 per cent were expected. The deviation divided by probable error is 1.7 for the group.

A comparison between the observed and calculated distribution of progenies is shown in Table 23.

TABLE 22.—*Records of scutellum colors in 19 F_3 progenies of F_2 colored segregates of a 15:1 ratio*

Group and ratio	Pedigree No. F_2	Pedigree No. F_3	Number of individuals: Colored	Colorless	Total	Percentage colorless	Dev./P. E.
A (1:0)	328-3	643-1	217	0	217		
		643-2	192	0	192		
		643-3	147	0	147		
		643-5	157	0	157		
		643-7	167	0	167		
		643-10	172	0	172		
		643-15	123	0	123		
		643-17	49	0	49		
		643-19	34	0	34		
Total			1,258	0	1,258		
B (3:1)	328-3	643-8	129	49	178	27.5	1.2
		643-12	134	35	169	20.7	1.9
		643-16	107	32	139	23.0	.8
		643-18	56	14	70	20.0	1.4
Total			426	130	556	23.4	1.3
C (15:1)	328-3	643-4	161	6	167	3.6	2.1
		643-6	138	11	149	7.4	.8
		643-7	137	5	142	3.5	2.0
		643-11	116	7	123	5.7	.4
		643-13	128	8	136	5.9	.3
		643-14	108	7	115	6.1	.1
Total			788	44	832	5.3	1.7

TABLE 23.—*Comparison of observed and calculated number of progenies in groups shown in Table 22*

Items	Group A	Group B	Group C	Total
Observed	9	4	6	19
Calculated	8.9	5.1	5.1	19.1
Difference	+.1	−1.1	+.9	−.1

$\chi^2=0.40$. $P=0.82$

RATIOS OF 3 TO 1

The data on the five F_3 progenies grown from colored scutellum segregates of 3:1 F_2 ratios are given in Table 24. On the basis of monohybrid segregation, the F_3 population should consist of segregating and true-breeding progenies in the ratio of 2:1. With five progenies the calculated ratio becomes 3.3:1.7, whereas the observed ratio was 4:1. All the ratios in the segregating group have approximately 25 per cent of colorless scutellums.

TABLE 24.—*Records of scutellum color in five F_3 progenies of F_2 colored segregates of a 3:1 ratio*

Group and ratio	Pedigree No. F_2	Pedigree No. F_3	Number of individuals: Colored	Colorless	Total	Percentage colorless	Dev./P. E.
A (1:0)	781-1	859-2	112	0	112		
B (3:1)	781-1	859-1	85	30	115	26.1	0.4
		859-3	128	49	177	27.7	1.2
		859-4	68	19	87	21.8	1.0
		859-7	129	42	171	24.6	.2
Total			410	140	550	25.5	.4

The behavior of all the F_3 progenies grown from F_2 colored scutellum segregates has been in reasonable accord with the proposed hypothesis. In every case the expected ratio types have been obtained, and in most cases the agreement between observation and theory has been good. The results of other tests of the hypothesis are presented in the following sections.

BEHAVIOR OF COLORLESS SCUTELLUMS IN THE F_3 GENERATION

Colorless scutellum segregates of progenies representing each of the six groups in Table 10 were tested in F_3. The detailed data are given in Table 25.

The data presented in this table, totaling 8,054 individuals, are in accord with the hypothesis, as all colorless scutellum segregates breed true for this condition. In each group a few colored scutellum individuals were obtained. In every instance these exceptions represent a small percentage of the population and are believed to be due to accidental pollination. Again no attempt has been made to separate individuals from 3:1 and from 45:19 ratios.

TABLE 25.—*Records of scutellum color in 42 F_3 progenies of colorless F_2 segregates of groups 1 to 6 of Table 10*

Group and ratio of preceding generation	Pedigree No.		Number of individuals	
	F_2	F_3	Colored	Colorless
1 (3 : 1)	170-2	352-2	2	20
	178-5	355-10	0	191
	176-5	356-1	0	125
		356-6	0	61
	242-9	357-9	0	30
	196-6	361-2	0	109
		361-7	0	145
	242-13	365-3	2	300
	242-9	429-1	4	238
Total			8	1,216
2 (9 : 7)	327-7	649-1	8	270
		649-2	1	238
		649-3	0	239
		649-4	0	216
		649-5	1	99
		649-6	0	203
		649-7	2	215
Total			12	1,480
3 (27 : 37)	327-6	648-1	3	87
		648-2	0	192
		648-3	0	283
		648-4	6	250
		648-5	3	311
		648-6	0	312
		648-7	1	231
		648-8	1	261
		648-9	0	285
Total			14	2,212
4 (15 : 1)	320-10	655-1	0	187
		655-2	0	132
		655-3	2	211
		655-4	1	198
		655-6	0	158
		655-7	0	101
		655-8	0	83
Total			3	1,068

TABLE 25.—*Records of scutellum color in 42 F_3 progenies of colorless F_2 segregates of groups 1 to 6 of Table 10*—Continued

Group and ratio of preceding generation	Pedigree No.		Number of individuals	
	F_2	F_3	Colored	Colorless
5 (54 : 10)	320-9	651-1	0	171
		651-2	0	50
		651-3	7	118
		651-4	1	213
		651-5	0	137
		651-6	0	164
		651-9	1	198
Total			9	1,051
6 (162 : 94)	322-13	647-3	0	350
		647-4	0	275
		647-5	0	356
Total			0	981

The hypothesis under test requires that colorless scutellum segregates from 3 : 1 and 15 : 1 ratios should be of four types. These can be used as scutellum testers to determine the genotypic constitution of unknown whites. These theoretical types are given below prior to the proof of their existence.

s_1 tester .... $s_1\ S_2\ S_3\ S_4$
s_2, s_3 tester .... $S_1\ s_2\ s_3\ S_4$
s_3, s_4 tester .... $S_1\ S_2\ s_3\ s_4$
s_2, s_4 tester .... $S_1\ s_2\ S_3\ s_4$

Each of these testers should produce only colorless scutellums when self-pollinated or when crossed with strains having a similar genetic constitution. In addition, the F_1 cross between any two different testers should produce only colored scutellums.

Evidence that four testers exist, and that their behavior is as outlined above, is presented in Table 26. Selfed progenies of each of the testers bred true for colorless scutellums, the few colored scutellum kernels presumably being outcrosses. F_1 crosses of one tester by any different tester have all colored scuttelums. The numbers are not large, but they are consistent and in accord with the hypothesis.

TABLE 26.—*Records of scutellum colors in F_1 of selfed and intercrossed scutellum testers*

Pedigree No.	Testers and crosses	Number of individuals		
		Colored	Colorless	Total
822-5	s_1	3	207	210
821-4	do	0	264	264
824-14	do	14	230	244
Total		17	701	718
820-2	s_1	0	180	180
820-11 × 2	do	0	253	253
Total		0	433	433
823-2	s_1	0	195	195
823-6	do	1	113	114
831-9	do	2	81	83
Total		3	389	392

TABLE 26.—*Record of scutellum colors in F_2 of selfed and intercrossed scutellum testers*—Continued

Pedigree No.	Testers and crosses	Number of individuals		
		Colored	Colorless	Total
832-13	s_4	4	187	191
821-7 × 820-2	$s_1 \times s_2$	17	0	17
822-11 × 820-2		46	0	46
822-9 × 820-2		247	0	247
834-3 × 820-2		29	0	29
Total		339	0	339
822-8 × 823-4	$s_1 \times s_3$	3	0	3
831-11 × 822-5	do	2	0	2
822-15 × 819-2	do	62	0	62
822-1 × 819-2	do	108	13	121
Total		175	13	188
822-4 × 832-11	$s_1 \times s_4$	88	5	93
833-9 × 822-5	do	22	0	22
Total		110	5	115
823-3 × 820-2	$s_2 \times s_3$	2	0	2
831-7 × 820-2	do	7	0	7
819-2 × 820-1	do	59	4	63
Total		68	4	72
832-1 × 820-2	$s_2 \times s_4$	27	0	27
820-7 × 832-11	do	83	0	83
Total		110	0	110
831-10 × 832-11	$s_3 \times s_4$	219	1	220
832-6 × 823-4		158	2	160
Total		377	3	380

Crosses between the various testers would be expected to show two types of breeding behavior in the F_2 generation. Crosses involving s_1 and any two factors of the series s_2, s_3, and s_4 will exhibit F_2 ratios of 45 colored to 19 colorless scutellums. Crosses of testers involving only members of the s_2, s_3, and s_4 series should give an F_2 ratio of 9 colored to 7 colorless scutellums. The data for such F_2 crosses are presented in Table 27 and are in close accord with expectations.

In the early attempts to isolate testers, success was only partial. Colorless scutellum kernels from supposedly 3:1 ratios behaved very erratically in crosses. This unexpected behavior was easily explained after proper distinction had been made between 3:1 and 45:19 ratios. The nonconforming whites had been obtained from 45:19 ratios and were actually recessive for 1, 2, or 3 factor pairs.

No attempt has been made to prove the existence of all the expected genotypes of colorless scutellums from any single cross or group of crosses.

HOMOZYGOUS COLORED × MULTIPLE RECESSIVE COLORLESS SCUTELLUMS

Colored scutellum strains homozygous for all four factors, S_1, S_2, S_3, and S_4, when crossed with the multiple recessive colorless stocks should produce F_2 ratios of approximately 162 colored to 94 colorless scutellums. On the other hand, colored scutellum strains homozygous for S_1 S_1 and two of the other three factor pairs should produce 27 : 37 ratios in F_2 when crossed with multiple recessive colorless stocks. Both of these ratios were obtained, as shown by the data in Table 28, proving the existence of true-breeding colored scutellums of at least two genotypes.

TABLE 27.—*Records of scutellum color in 18 F_2 progenies of crosses of colorless scutellum testers*

Tester and pedigree No.	Number of individuals			Percentage colorless	$\frac{\text{Dev.}}{\text{P.E.}}$
	Colored	Colorless	Total		
$s_1 \times s_2$:					
6696-2	110	40	150	26.7	1.2
6697-3	39	18	57	31.6	.5
Total	149	58	207	28.0	.8
$s_1 \times s_3$:					
6700-1	308	131	439	29.8	1.0
6700-3	162	35	197	17.8	5.4
6700-4	104	37	141	26.2	1.3
6700-5	159	60	219	27.4	1.1
6701-2	75	32	107	29.9	.1
6701-4	134	59	193	30.6	.4
Total	942	354	1,296	27.3	2.8
$s_2 \times s_3$:					
6702-2	62	41	103	39.8	1.2
$s_2 \times s_4$:					
6704-2	74	51	125	40.8	1.0
6704-3	219	160	379	42.2	.9
6704-5	80	62	142	43.7	0
Total	373	273	646	42.3	1.1
$s_3 \times s_4$:					
6705-1	49	29	78	37.2	1.7
6705-2	85	76	161	47.2	1.3
6705-3	72	58	130	44.6	.3
6705-4	74	56	130	43.1	.2
6706-1	65	48	113	42.5	.4
6706-5	26	20	46	43.5	.1
Total	371	287	658	43.6	.1

TABLE 28.—*Records of scutellum colors in 11 F_2 progenies of crosses of homozygous colored × multiple recessive colorless scutellum strains*

Group and ratio	Pedigree No.	Number of individuals			Percentage colorless	$\frac{\text{Dev.}}{\text{P.E.}}$
		Colored	Colorless	Total		
A (162:94)	866-3	113	60	173	34.7	0.9
	866-4	75	39	114	34.2	1.0
	866-8	136	68	204	33.3	1.6
	867-2	86	57	143	39.9	1.1
	867-7	101	58	159	36.5	.1
	868-1	78	29	107	27.1	3.1
Total		589	311	900	34.6	2.0
B (27:37)	862-5	114	126	240	52.5	2.5
	862-4	81	98	179	54.7	1.3
	863-3	79	100	179	55.9	.8
	870-1	101	120	221	54.3	1.5
	870-5	124	148	272	54.4	1.7
Total		499	592	1,091	54.3	3.5

INTERCROSSES OF HOMOZYGOUS COLORED SCUTELLUM STRAINS

Colored scutellum strains of the constitution $S_1 S_1$, $S_2 S_2$, $S_3 S_3$, $S_4 S_4$, when crossed with any other true-breeding colored scutellum genotype, should produce only colored scutellums in subsequent generations. Data from one such cross are presented in Table 29.

Crosses between colored scutellum strains homozygous for three factors but unlike in genotype should give ratios of 15 colored to 1 colorless scutellum in F_2. Data from one cross of this kind are presented in Table 30. The data prove the existence of two different genotypes of colored scutellum strains, each homozygous for three factor pairs. The hypothesis calls for three such genotypes. The occurrence of the third has not been demonstrated. The data which have been presented, however, give sufficiently conclusive proof of the existence of three of the four required types of homozygous colored scutellum strains.

TABLE 29.—*Records of scutellum color in 10 F_2 progenies of crosses of colored × colored scutellum strains*

Pedigree No.	Number of individuals			Pedigree No.	Number of individuals		
	Colored	Colorless	Total		Colored	Colorless	Total
349-1	203	0	203	349-7	209	0	209
349-2	179	5	184	349-8	197	0	197
349-3	106	0	106	349-9	154	2	156
349-4 × 349-2	70	0	70	349-10	222	5	227
349-5	250	0	250				
349-6	242	8	250	Total	1,832	20	1,852

TABLE 30.—*Records of scutellum colors in five F_2 progenies of crosses of colored × colored scutellum strains*

Pedigree No.	Number of individuals			Percentage colorless	$\frac{\text{Dev.}}{\text{P. E.}}$
	Colored	Colorless	Total		
348-1	227	14	241	5.8	0.4
348-2	225	13	248	5.2	1.0
348-6	246	15	261	5.7	.5
348-7	264	10	274	3.6	2.6
348-9	236	13	249	5.2	1.0
Total	1,208	65	1,273	5.1	2.5

AGREEMENT WITH HYPOTHESIS

The data for the purple and red scutellum series have been in agreement with the proposed hypothesis in each of the several ways that it was tested. The behavior of colored segregates from the different ratios was in accord with expectancy. Colorless segregates bred true for this condition. Intercrosses between colorless scutellum strain from 3:1 and 15:1 ratios furnished evidence for the existence of four different colorless testers. Colored scutellum strains crossed with a multiple recessive colorless strain produced the expected F_2 results. Appropriate intercrosses demonstrated the existence of three of the four different homozygous colored scutellum strains required by the hypothesis. There is close agreement between expectations under the hypothesis and all the observed facts. This seems to prove conclusively the assumption of at least four factors interacting as described, determining the purple-red coloration of the scutellum.

DOMINANT WHITE SCUTELLUMS

Through the kindness of I. F. Phipps, many of his cultures were examined for possible scutellum color segregation. In his culture 1561–A an ear was found which segregated in a ratio of approximately 9 colored to 55 colorless scutellums. Such a ratio would be expected from the interaction of a dominant white scutellum factor with factors of the purple and red series which otherwise would have resulted in a 9 : 7 ratio.

A dominant white scutellum strain was isolated from the progeny of this ear. Repeated tests have shown this scutellum factor, S_5 s_5, to be completely dominant in either the homozygous or the heterozygous condition. Unlike the *I i* factor pair, it has no effect on aleurone coloration.

Colorless scutellum seeds from this original ear were tested in the next generation. The results of this test are presented in Table 31. The 15 progenies can be divided into four groups.

TABLE 31.—*Records of scutellum color in 15 F_3 progenies of F_2 colorless segregates of a 9 : 55 ratio*

Group and ratio	Pedigree No.		Number of individuals			Percentage colorless	Dev./P. E.
	F_2	F_3	Colored	Colorless	Total		
A (0 : 1)	P1561A–1	380–3	0	[illegible]	196		
		380–4	0	117	117		
		380–7	0	329	329		
		380–13	0	328	328		
		380–14	0	215	215		
		380–10	0	98	98		
		672–2	0	291	291		
		672–3	0	170	170		
Total			0	1,744	1,744		
B (1 : 3)	P1561A–1	380–11	46	156	202	77.2	1.1
		380–15	59	185	244	75.8	.4
Total			105	341	446	76.5	1.1
C (3 : 13)	P1561A–1	380–5	17	75	92	81.5	.1
		380–9	31	174	205	84.9	2.0
Total			48	249	297	83.8	1.7
D (9 : 55)	P1561A–1	380–8	18	141	159	88.7	1.5
		380–12	19	189	208	90.9	3.0
		672–1	21	118	139	84.9	.5
Total			58	448	506	88.5	2.5

Group A, totaling eight progenies, bred true for colorless scutellums. This group is composed of different types of whites. Some are white due to the action of the dominant scutellum factor; others are white because of the recessive condition of one or more of the necessary factors of the purple and red series. To identify these different whites, all plants that were selfed were also used as pollen parents on colored scutellum strains. This will differentiate three sorts of whites, namely, homozygous dominant, heterozygous, and recessive. The results of these crosses are shown in Table 32. The three types of whites mentioned above should occur in the ratio of 16:32:7, or, for eight individuals, 2.3:4.7:1.0. The observed ratio was 2:5:1, an excellent fit in spite of the small number of progenies.

Group B (Table 31) contains two progenies approximating 1:3 ratios. In both progenies the deviations are small and positive.

The two progenies of Group C approximated ratios of 3 colored to 13 colorless scutellums. The fit is fair, the deviation divided by probable error being 1.7.

Group D consists of three progenies whose segregations approximate a 9:55 ratio. In two of the three progenies there is a deficiency of colored scutellums. For the three progenies the deviation divided by probable error is 2.5. This is a poor fit, but values of this magnitude are to be expected occasionally.

TABLE 32.—*Records of scutellum color in crosses of individuals of group A of Table 31 × colored scutellum strains*

Tester and pedigree No.	Number of individuals		
	Colored	Colorless	Total
$S_3 S_3$:			
B26-6 × 380-14	0	80	80
678-4 × 672-2	0	134	134
$S_3 s_3$:			
459-4 × 380-3	126	132	258
459-7 × 380-4	88	76	164
459-8 × 380-10	109	115	224
459-11 × 380-13	28	31	59
678-6 × 672-3	142	137	279
$s_3 s_3$:			
459-2 × 380-7	213	0	213

A comparison of the observed number of progenies in each group and the calculated expectancy is given in Table 33. When the small number of progenies is taken into consideration, the fit is fair.

TABLE 33.—*Comparison of observed and calculated number of progenies in groups shown in Table 31*

Items	Group				Total
	A	B	C	D	
Observed	8	2	2	3	15
Calculated	10.1	0.5	2.2	2.2	15
Difference	−2.1	+1.5	−.2	+.8	0

$\chi^2 = 5.26$, $P = 0.16$

Table 34 presents the detailed records of 20 F_4 progenies grown from colorless scutellum kernels from an F_3 ear segregating in the ratio of 3 colored to 13 colorless scutellums. In each group the individual progeny records accord well with expectations. The comparison between the observed and expected number of progenies in each group is given in Table 35.

TABLE 34.—*Records of scutellum color in 20 F_4 progenies of F_3 colorless segregates of a 3:13 ratio*

Group and ratio	Pedigree No.		Number of individuals			Percentage colorless	Dev. / P. E.
	F_2	F_4	Colored	Colorless	Total		
A (0:1)	380-5	645-1	0	450	450		
		645-2	0	529	529		
		645-3	0	182	182		
		645-9	0	256	256		
		645-10	0	249	249		
		645-12	0	207	207		
		645-13	0	165	165		
		645-15	0	208	208		
		645-19	0	68	68		
		645-22	0	90	90		
		645-23	0	70	70		
Total			0	2,474	2,474		
B (1:3)	380-5	645-5	74	249	323	77.1	1.3
		645-6	49	143	192	74.5	.2
		645-7	85	232	317	73.2	1.1
		645-17	51	175	226	77.4	1.3
Total			259	799	1,058	75.5	.6
C (3:13)	380-5	645-1	64	259	323	80.2	.7
		645-3	58	265	323	82.0	.5
		645-11	55	226	281	80.4	.5
		645-14	79	292	371	78.7	1.9
		645-18	16	89	105	84.8	1.4
Total			272	1,131	1,403	80.6	.9

TABLE 35.—*Comparison of observed and calculated number of progenies in groups shown in Table 34*

Items	Group			Total
	A	B	C	
Observed	11	4	5	20
Calculated	10.8	3.1	6.2	20.1
Difference	+.2	+.9	−1.2	−.1

$\chi^2=0.49$. $P=0.78$

Records of scutellum color for 13 F_4 progenies, grown from F_3 colorless scutellum kernels from ears segregating in a 1:3 ratio, are shown in Table 36. The first group contains those progenies breeding true for colorless scutellums. The second group includes all progenies approximating a 1:3 segregation. The observed ratio of homozygous to heterozygous forms is 4:9. The calculated ratio for this number of progenies is 4.3:8.7. The fit is as nearly perfect as possible with this number of progenies.

Progenies heterozygous for dominant white and for duplicate factors of the purple and red scutellum series were obtained by appropriate crosses. The calculated F_2 ratio for such crosses is 15:49. This is a close approximation to the 1:3 ratio expected when only the dominant white factor is involved. In the latter case the calculated percentage of colored scutellum kernels is 25.0, whereas for a 15:49 ratio it is 23.4. Random deviations from these theoretical expectancies would overlap to such a degree that separation on the basis of F_2 counts would be impossible. For this reason F_3 behavior has been used as proof for the existence of this type of ratio.

Table 37 contains the records for 11 F_3 progenies grown from colorless scutellum seeds from a 15:49 F_2 ratio. The data are listed in three groups on the basis of their percentages of colorless scutellums. Group A contains those progenies having all colorless scutellums. Group B is made up of progenies approximating a 3:13 ratio. Each of the three progenies in this group shows an excess of colorless scutellums. The cumulative excess amounts to 17 individuals. The deviation divided by probable error is 2.4, which is not a close fit.

TABLE 36.—*Records of scutellum colors in 13 F_4 progenies of F_3 colorless segregates of a 1:3 ratio*

Group and ratio	Pedigree No.		Number of individuals			Percentage colorless	Dev./P.E.
	F_3	F_4	Colored	Colorless	Total		
A (0:1)	380-11	659-5	0	126	126		
		659-8	0	108	108		
		659-11	0	183	183		
		659-12	0	52	52		
Total			0	469	469		
B (1:3)	380-11	659-1	78	218	296	73.6	0.8
		659-2	135	388	523	74.2	.6
		659-3	88	290	378	76.7	1.1
		659-4	38	133	171	77.8	1.2
		659-6	62	160	222	72.1	1.5
		659-7	36	108	144	75.0	.0
		659-9	44	129	173	74.6	.2
		659-10	56	138	194	71.1	1.8
		659-12	10	26	36	72.2	.6
Total			547	1,590	2,137	74.4	1.0

Group C is made up of progenies having approximately 75 per cent of colorless scutellums. No attempt has been made to separate the 1:3 and 15:49 ratios. The percentage of colorless individuals for this group is intermediate between the theoretical expectancies for these ratios. In view of the small numbers, however, this point should not be stressed.

The agreement between the observed distribution of progenies and the theoretical expectancies on the basis of a 15:49 F_2 ratio is given in Table 38.

TABLE 37.—*Records of scutellum color in 11 F_3 progenies of F_2 colorless segregates of a 15:49 ratio*

Group and ratio	Pedigree No.		Number of individuals			Percentage colorless	$\frac{\text{Dev.}}{\text{P. E.}}$
	F_2	F_3	Colored	Colorless	Total		
A (0:1)	P2804-2	722-1	0	148	148		
		722-4	0	197	197		
		722-5	0	126	126		
		722-9	0	109	109		
		722-11	0	54	54		
Total			0	634	634		
B (3:13)	P2804-2	722-2	50	235	285	82.5	0.8
		722-7	33	180	213	84.5	1.8
		722-8	30	165	195	84.6	1.8
Total			113	580	693	83.7	2.4
C (1:3; 15:49)	P2804-2	722-3	57	166	222	74.8	
		722-6	58	157	215	73.0	
		722-10	24	78	102	76.5	
Total			139	400	539	74.2	

TABLE 38.—*Comparison of observed and calculated number of progenies in groups shown in Table 37*

Items	Group			Total
	A	B	C	
Observed	5	3	3	11
Calculated	4.3	4.9	1.8	11
Difference	+.7	−1.9	+1.2	0

$\chi^2 = 1.65$. $P = 0.45$

Additional proof for the existence of factors that interact with the S_5 s_5 factor pair to produce F_2 ratios of 15 colored to 49 colorless scutellums is given in Table 39. Colored scutellum kernels from 15:49 F_2 ratios were planted to determine the breeding behavior of their progeny. On the basis of a 15:49 F_2 ratio the colored segregates should show three types of behavior in the following generation, namely, true breeding and segregating in ratios of 3:1 and 15:1. In accordance with theory, observation revealed these three types. In the two segregating groups the percentages of colorless individuals are in close accord with expectancy. The comparison between the observed number of progenies in each group and the theoretical expectancy is given in Table 40.

TABLE 39.—*Records of scutellum color in eight F_3 progenies of F_2 colored segregates of a 15:49 ratio*

Group and ratio	Pedigree No.		Number of individuals			Percentage colorless	Dev./P. E.
	F_2	F_3	Colored	Colorless	Total		
A (1:0)	P2804-2	721-1	304	0	304		
		721-5	287	0	287		
		721-6	193	0	193		
		721-7	176	0	176		
Total			960	0	960		
B (3:1)	P2804-2	721-2	194	53	247	21.5	1.9
		721-8	132	49	181	27.1	1.0
Total			326	102	428	23.8	.8
C (15:1)	P2804-2	721-3	214	17	231	7.4	1.0
		721-4	164	9	173	5.2	.8
Total			378	26	404	6.4	.2

TABLE 40.—*Comparison of observed and calculated number of progenies in groups shown in Table 39*

Items	Group			Total
	A	B	C	
Observed	4	2	2	8
Expected	3.7	2.1	2.1	7.9
Difference	+.3	-.1	-.1	.1

$\chi^2=0.03$. P=0.98

Data to be presented later indicate that the dominant action of the S_5 gene is specific for members of the S_1, S_2, S_3, and S_4 series, having no influence on orange (so_1 so_2) or yellow (sy) segregations.

ORANGE SCUTELLUMS

Orange scutellums were first observed by I. F. Phipps among his cultures in 1927. These were turned over to the writer for further study. All the data dealing with this color type were obtained from progenies tracing back to this original source.

Orange scutellum color develops only in the presence of the recessive allelomorphs of the factor pairs So_1 so_1 and So_2 so_2. Orange scutellum kernels produce progeny breeding true for this condition, as evidenced by the data in Table 41. Among 2,689 kernels, all except 5 have orange scutellums. These 5 probably were due to stray pollen, though this was not proved.

TABLE 41.—*Records of scutellum color in nine F_3 progenies of F_2 orange scutellum segregates*

Pedigree No. F_2	Pedigree No. F_3	White	Orange	Total
P2286-B-5	727-1	0	287	287
	727-7	0	254	254
	727-12	0	313	313
	727-14	0	418	418
	727-15	2	379	381
P2641-2	652A-1	0	177	177
	652A-3	1	211	212
	652A-5	2	389	391
	652A-6	0	256	256
Total		5	2,684	2,689

The records for scutellum color segregation for the original ears from Doctor Phipps's cultures are presented in Table 42. The first group includes the progenies whose ratios approximate 3:1. The fit is good, the deviation divided by probable error being only 0.4. The second group is made up of the progenies segregating in 15:1 ratios. The fit is reasonably good.

White scutellum segregates from 15 : 1 F_2 ratios were planted to serve as the basis for a study of F_3 breeding behavior. The detailed data of the 22 progenies obtained are presented in Table 43. These progenies fall into three groups as expected. Group A contains the true-breeding whites. The nine progenies in this group have a total of 1,813 colorless scutellum kernels. Group B is made up of the progenies segregating in 3:1 ratios. Positive and negative deviations occur with equal frequency. The deviation for the group, however, is negative, the observed percentage of recessives being 23.5. Group C is composed of the progenies segregating in ratios of 15 colorless to 1 orange scutellum. The deviation divided by probable error for the group is 1.4. The agreement between the observed and expected number of progenies in each group is given in Table 44.

TABLE 42.—*Records of scutellum color in seven progenies segregating orange and white scutellums.*

Group and ratio	Pedigree No.	Number of individuals: White	Orange	Total	Percentage orange	Dev./P. E.
A (3 : 1)	P2644-1-A	27	8	35	22.9	0.4
	P2286-A-2	111	40	151	26.5	.5
	P2286-B-5	103	35	138	25.4	.1
Total		241	83	324	25.6	.4
B (15 : 1)	P2640-1	40	4	44	9.1	1.2
	P2641-2	62	3	65	4.6	.8
	P2645-7	84	6	90	6.7	.2
	P2645-5x6	72	3	75	4.0	1.2
Total		258	16	274	5.8	.4

TABLE 43.—*Records of scutellum color in 22 F_3 progenies of F_2 white segregates of a 15:1 ratio*

Group and ratio	Pedigree No.		Number of individuals			Percentage orange	$\frac{\text{Dev.}}{\text{P. E.}}$
	F_2	F_3	White	Orange	Total		
A (1:0)	P2641-2	652-2	247	0	247		
		652-3	255	0	255		
		652-4	323	0	323		
		652-9	290	0	290		
		652-11	162	0	162		
		652-15	227	0	227		
		652-17	112	0	112		
		652-18	160	0	160		
		652-21	37	0	37		
Total			1,813	0	1,813		
B (3:1)	P2641-2	652-7	230	88	318	27.7	1.6
		652-10	261	58	319	18.2	4.2
		652-16	62	16	78	20.5	1.4
		652-19	132	54	186	29.0	1.9
		652-20	88	19	107	17.8	2.6
		652-22	25	10	35	28.6	.7
Total			798	245	1,043	23.5	1.7
C (15:1)	P2641-2	652-1	307	18	325	5.5	.8
		652-5	299	14	313	4.5	1.9
		652-6	320	19	339	5.6	.7
		652-8	317	26	343	7.6	1.8
		652-12	189	9	198	4.5	1.5
		652-13	67	6	73	8.2	1.0
		652-14	56	2	58	3.4	1.3
Total			1,555	94	1,649	5.7	1.4

TABLE 44.—*Comparison of observed and calculated number of progenies in groups shown in Table 43*

Items	Group			Total
	A	B	C	
Observed	9	6	7	22
Calculated	10.3	5.9	5.9	22.1
Difference	−1.3	+.1	+1.1	−.1

$\chi^2=0.37$. $P=0.83$

Table 45 lists the records of scutellum color in 37 F_3 progenies grown from colorless scutellum segregates of a 3:1 ratio. The two expected groups were obtained. Group A contains 2,990 individuals with no recessive types appearing. Group B contains the segregating progenies. All are reasonably close to the expected 3:1 except 673–8. For this progeny the deviation divided by probable error is 2.9. The observed segregation more nearly approximates a 15:1 ratio. The numbers in this progeny are small, however, and deviations of this magnitude are to be expected occasionally. The ratio of homozygous to heterozygous progenies is 13:24, very close to the expected 1:2.

The relation between the factors causing orange and the factors of the purple and red scutellum series has not been determined. This relation has been obscured by the linkage of one of the *So so* factor pairs with one of the aleurone factors. This linkage distorted the colorless to orange scutellum ratio in the colored aleurone class, the only class in which segregation for the S factors could be detected. This difficulty can be overcome by using a homozygous colored aleurone, orange scutellum strain. Such a strain is now available, but the crosses have not been made. The data on the linkage of the aleurone factor and the So_1 so_1 factor are presented in Table 46. The percentage of crossing over was calculated by the product method to be 10.9. The aleurone factor involved is believed to be either A or R, since there is no indication of linkage between the orange scutellum factors and shrunken endosperm.

TABLE 45.—*Records of scutellum colors in 37 F_3 progenies of F_2 white segregates of a 3:1 ratio*

Group and ratio	Pedigree No.		Number of individuals			Percentage orange	Dev. P. E.
	F_2	F_3	White	Orange	Total		
A (1:0)	P2286A-2	653-2	221	0	221		
		653-3	207	0	207		
		653-7	189	0	189		
		653-9	100	0	100		
		653-14	350	0	350		
		653-15	325	0	325		
	P2286B-5	653-16	206	0	206		
		673-1	310	0	310		
		673-6	67	0	67		
		673-10	318	0	318		
		673-16	119	0	110		
		673-17	218	0	218		
		673-20	360	0	360		
Total			2,990	0	2,990		
B (3:1)	P2286A-2	653-1	66	20	86	23.3	0.6
		653-4	35	11	46	23.9	.3
		653-5	57	22	79	27.8	.9
		653-6	154	55	209	26.3	.7
		653-8	31	18	49	36.7	2.8
		653-10	251	57	308	18.5	3.9
		653-11	167	51	218	23.4	.8
		653-12	104	36	140	25.7	.3
		653-13	190	56	246	22.8	1.2
		653-17	271	79	350	22.6	1.6
	P2286B-5	673-2	117	48	165	29.1	1.8
		673-3	317	102	419	24.3	.5
		673-4	214	75	289	26.0	.6
		673-5	202	69	271	25.5	.3
		673-7	199	65	264	24.6	.2
		673-8	28	3	31	9.7	2.9
		673-9	150	65	215	30.2	2.4
		673-11	183	59	242	24.4	.3
		673-12	310	123	433	28.4	2.4
		673-14	280	84	364	23.1	1.3
		673-15	48	19	67	28.4	.9
		673-18	216	56	272	20.6	2.5
		673-19	115	33	148	22.3	1.1
		673-21	298	88	386	22.8	1.5
Total			4,003	1,294	5,297	24.4	1.4

TABLE 46.—*Records of scutellum color in five F_2 progenies exhibiting linkage between colored aleurone and orange scutellum (So_1 so_1)*

Pedigree No.	Number of individuals				Percentage of crossing over
	Colored aleurone		Colorless aleurone		
	So_1	so_1	So_1	so_1	
843-1	214	6	49	20	10.7
843-2	135	5	34	14	13.0
843-3	256	1	72	25	2.1
843-4	289	5	70	13	13.4
843-5	384	14	63	34	13.0
Total	1,278	31	308	106	10.9

The records for scutellum color for four F_2 progenies from the cross $S_s S_s, So_1 So_1, So_2 So_2 \times s_s s_s, so_1 so_1, so_2 so_2$ are shown in Table 47. The dominant white factor S_s has no influence on the white to orange segregations, as the deviation from a 15:1 ratio is only 1.3 times its probable error.

One F_2 progeny was segregating for the So_1 So_2 and *Sh* factor pairs. The observed ratio was 222 *So Sh*:68 *So sh*:16 *so Sh*:3 *so sh*. This is a very close approximation to the 45:15:3:1 ratio expected with independent inheritance, the value for *P* being 0.75. A second progeny segregating for one of the *So* factors and *Sh* exhibited a ratio of 76 *So Sh*:26 *So sh*:30 *so Sh*:8 *so sh*. This again is a close approximation to the expected 9:3:3:1 ratio, the value for χ^2 being 1.06. Thus, only 11 out of 100 repetitions would be expected to give a closer approximation to the theoretical distribution. There is, then, no evidence of linkage of the So_1 or So_2 factors with the *Sh* factor.

Certain of the progenies listed in Table 46 were segregating for brown aleurone and others for yellow endosperm. Separations for these characters were made among only the nonpurple aleurone class. Owing to the distortion of the ratios of colorless to orange scutellum, indications of linkage were sought by comparing the observed segregations of brown aleurone and yellow endosperm with the calculated 3:1 among the nonpurple aleurone class. These comparisons indicate random assortment for the So_1 So_2, *Bn*, *bn, and Yy* factor pairs.

TABLE 47.—*Records of scutellum color in four F_2 progenies of a cross between dominant white ($S_s S_s$) and orange ($so_1 so_1 so_2 so_2$)*

Pedigree No.	Number of individuals			Percentage orange	Dev./P. E.
	White	Orange	Total		
842-1	174	9	183	4.9	1.1
842-4	36	3	39	7.7	.5
842-6	396	23	419	5.5	1.0
842-10	195	12	207	5.8	.4
Total	801	47	848	5.5	1.3

YELLOW SCUTELLUMS

Yellow scutellum color is inherited as a simple recessive to the normal colorless scutellum. It has been designated by the symbol *sy*, normal white having the dominant allelomorph *Sy*.

The first yellow scutellums were observed in a selfed ear of the Blue Flour variety. Later, similar colored scutellums were observed in some of Doctor Emerson's cultures, tracing back to North American-South American maize crosses. Intercrosses between these yellows and the Blue Flour yellows indicated that all were of the same constitution.

In crosses of yellow × white scutellums the F_2 progenies show a close approximation to the expected 25 per cent of yellow scutellums. (Table 48.) The observed percentage of yellows in progenies totaling 5,014 kernels is 24.9. The range in percentages of yellow scutellums is from 21.6 to 30.9. Yellow scutellums from F_2 ears breed true for this condition, as evidenced by the data in Table 49.

The F_3 breeding behavior of F_2 whites agreed satisfactorily with the monohybrid interpretation. Of the 10 F_3 ears, 7 segregated in ratios approximating 3 whites to 1 yellow. Three ears bred true for colorless scutellums. This is a close approximation to the expected 2:1 ratio of heterozygous to homozygous forms. The detailed data are presented in Table 50.

TABLE 48.—*Records of scutellum colors in 19 F_2 progenies of a cross of white × yellow scutellums*

Pedigree No.	Number of individuals			Percentage yellow	Dev./P. E.
	White	Yellow	Total		
740-1	181	69	250	27.6	1.4
740-2	229	63	292	21.6	2.0
740-3	270	86	356	24.2	.5
740-4	223	66	289	22.8	1.3
740-5	163	57	220	25.9	.5
740-6	103	46	149	30.9	2.6
740-7	204	70	274	25.5	.3
740-8	207	67	274	24.5	.3
740-9	254	91	345	26.4	.9
740-10	267	83	350	23.7	.8
740-11	162	53	215	24.7	.2
740-12	239	85	324	26.2	.8
740-13	202	59	261	22.6	1.3
740-14	146	59	205	28.8	1.9
740-15	219	61	280	21.8	1.6
740-16	141	42	183	23.0	.9
740-17	253	83	336	24.7	.2
740-18	142	54	196	27.6	1.2
740-19	163	52	215	24.2	.4
Total	3,768	1,246	5,014	24.9	.4

TABLE 49.—*Records of scutellum colors in eight F_3 progenies of yellow scutellum F_2 segregates*

Pedigree No.		Number of individuals		
F_2	F_3	White	Yellow	Total
176-5	358-1	0	125	125
242-9	357-9	0	30	30
	420-1	4	238	242
328-4	531-4	0	210	210
321-5	540-13	0	261	261
356-1	1021-5	0	219	219
	1021-8	0	132	132
326-1	1048-1	0	6	6
Total		4	1,221	1,225

TABLE 50.—*Records of scutellum color in 10 F_3 progenies of F_2 white segregates of a 3:1 ratio*

Group and ratio	Pedigree No.		Number of individuals			Percentage yellow	Dev./P. E.
	F_2	F_3	White	Yellow	Total		
A (1:0)	322-8	654-3	357	0	357		
		654-7	235	0	235		
		654-10	234	0	234		
Total			826	0	826		
B (3:1)	322-8	654-1	214	64	278	23.0	1.1
		654-2	295	90	385	23.4	1.1
		654-4	245	70	315	22.2	1.7
		654-5	184	56	240	23.3	.9
		654-6	240	67	307	21.8	1.9
		654-8	156	52	208	25.0	0
		654-9	178	62	240	25.8	.4
Total			1,512	461	1,973	23.4	2.5

A few ears showing the relation between purple and yellow scutellum color are available. The F_1 seeds from such a cross have purple scutellums. In F_2 the yellow segregation can be detected with certainty among only the nonpurple segregates. For a single *S* factor, then, the calculated ratio becomes 12 purples to 3 whites to 1 yellow. Four such progenies are listed in Table 51. The value for *P* for these progenies is 0.87. In the interaction of the *Sy* factor pair with two of the *S* factors, which would normally have a 9:7 F_2 ratio, the ratio becomes modified to 36 purples to 21 whites to 7 yellows. The value for *P* for progenies falling in this group is only 0.22. With the interaction of three *S s* factor pairs, normally exhibiting a 27:37 F_2 ratio, and the *Sy sy* factor a modified F_2 ratio of 108 purples to 111 whites to 37 yellows is expected. The value for *P* for this group of progenies is 0.56. These data indicate that there is no close linkage between the *Sy sy* factor and three of the four factors of the purple and red scutellum series.

The records for scutellum color for four F_2 progenies from the cross $S_5\ S_5,\ Sy\ Sy \times s_5\ s_5,\ sy\ sy$ are listed in Table 52. Positive and negative deviations occur with equal frequency, the cumulative deviation being negative and 1.9 times its probable error. The close approximation to the expected 3 white to 1 yellow indicates that the S_5 gene has no inhibiting influence on yellow scutellums.

TABLE 51.—*Records of scutellum color in 10 progenies segregating for purple and yellow scutellums*

Group, ratio, and pedigree No.	Number of individuals			
	Purple	White	Yellow	Total
Group 1 (12:3:1):				
324-7	224	42	13	279
325-1	160	41	18	219
325-8	179	49	16	244
327-1	171	55	16	242
Total	734	187	63	984 (P=0.87)
Group 2 (36:21:7):				
324-9	132	91	36	259
324-10	186	91	33	310
325-4	102	88	27	217
325-5	153	90	34	277
Total	573	360	130	1,063 (P=0.22)
Group 3 (108:111:37):				
325-6	67	64	21	152
328-4	86	75	30	191
Total	153	139	51	343 (P=0.56)

TABLE 52.—*Records of scutellum color in four F_2 progenies of a cross of dominant white ($S_5\ S_5$) × yellow scutellums (sy sy)*

Pedigree No.	Number of individuals			Percentage yellow	Dev./P. E.
	White	Yellow	Total		
1047-1	227	63	290	21.7	1.9
1047-2	95	34	129	26.4	.5
1047-8	134	32	166	19.3	2.5
1047-14	225	76	301	25.2	.1
Total	681	205	886	23.1	1.9

Crosses between orange and yellow scutellum strains may exhibit four kinds of ratios in F_2. In crosses heterozygous for all three factors the expected F_2 ratio is 45 white to 15 yellow to 4 orange scutellums. When the recessive gene *sy* is common to both parents, the F_1 scutellums will be yellow and the F_2 ratio will be 15 yellow to 1 orange or 3 yellow to 1 orange, depending on whether two or one of the *So* factors are segregating. When one of the recessive *so* genes is common to both parents, the other two factors being heterozygous, the expected F_2 ratio is 9 white to 3 yellow to 4 orange scutellums.

The scutellum-color segregations for F_2 progenies approximating ratios of 45:15:4 are presented in Table 53. The χ^2 value is 3.99, and P is only 0.14. Both the yellow and orange classes are in excess. Such a condition would be expected if there were linkage between the factor causing yellow and one of the factors causing orange scutellums. If linkage does occur, however, it must be fairly loose, as the departure from the 45:15:4 ratios is not excessive.

Data from a single cross segregating for only yellow and orange scutellums are presented in Table 54. The genotypic constitution of the orange parent was $so_1\ so_1\ so_2\ so_2\ sy\ sy$, so the constitution of the yellow parent must have been $So_1\ so_1\ So_2\ So_2\ sy\ sy$ or $So_1\ So_1\ So_2\ so_2\ sy\ sy$, since both 15:1 and 3:1 ratios were obtained.

TABLE 54.—*Records of scutellum color in five F_2 progenies of a cross of yellow × orange scutellums*

Pedigree No.	Number of individuals			
	White	Yellow	Orange	Total
841-1	289	79	23	391
841-2	206	83	24	313
841-3	213	77	22	312
841-6	285	120	36	441
Total	993	359	105	1,457
Calculated 45:15:4	1,024.7	341.6	91.1	1,457.4

TABLE 54.—*Records of scutellum color in five F_2 progenies of a cross of yellow × orange scutellums*

Pedigree No.	Number of individuals			Percentage orange	$\frac{\text{Dev.}}{\text{P. E.}}$
	Yellow	Orange	Total		
6857-7	56	13	69	18.8	1.7
6857-15	190	63	253	24.9	.1
Total	246	76	322	23.6	.9
6857-4	234	17	251	6.8	.5
6857-8	215	9	224	4.0	2.0
6857-13	233	15	248	6.0	.2
Total	682	41	723	5.7	1.0

The fourth possible ratio, 9:3:4, has not been obtained. Such a ratio would be expected when one of the *so* factors is recessive in both parents, the remaining two factors being heterozygous.

The data for a cross involving the *Pr pr* and *Sy sy* factor pairs are presented in Table 55. The cross was made so that linkage, if present, would be in the repulsion series. There is an excess of individuals in both the double dominant and double recessive classes. The deviation is not great and may be due to chance or to crossing over in excess of 50 per cent.

Two progenies involving the *Sh* and *Sy* factors exhibited the following F_2 distributions: 225 *Sh Sy*: 77 *Sh sy* : 67 *sh Sy*: 20 *sh sy*. When allowance is made for the deficiency of shrunken seeds, the approximation to the expected 9:3:3:1 ratio is well within the limits of chance fluctuations.

A single progeny segregating for the *Su* and *Sy* factor pairs gave no indication of linkage. The F_2 distribution is as follows: 138 *Sy Su* : 37 *Sy su* : 48 *sy Su* : 20 *sy su*. The F_2 distribution for four progenies segregating for the *Y* and *Sy* factors was 545 *Y Sy* : 187 *Y sy* : 160 *y Sy* : 46 *y sy*. The fit is poor, but there is no indication of linkage. Available data, then, indicate random assortment between the *Sy sy* factor pairs and the *Pr pr*, *Sh sh*, *Su su*, and *Y y* factor pairs.

TABLE 55.—*Records of scutellum color in 11 F_2 progenies of the cross A C R Pr sy × A C R pr Sy*

Pedigree No.	Number of individuals				Pedigree No.	Number of individuals			
	Pr		*pr*			*Pr*		*pr*	
	Sy	*sy*	*Sy*	*sy*		*Sy*	*sy*	*Sy*	*sy*
742-2	259	50	61	18	742-11	144	62	42	12
742-5	144	44	64	21	742-12	90	40	43	12
742-6	165	58	65	22	742-14	183	52	46	18
742-7	154	61	36	12	742-15	167	48	55	21
742-8	134	43	52	17					
742-9	154	38	52	23	Total	1,747	525	550	191
742-10	153	39	34	15					

DISCUSSION

In the purple and red series the interaction may be such as to give rise to complementary or duplicate gene ratios. The same factor pair may show one type of behavior in one factor complex and a different behavior when operating in a different factor complex. This is of special interest in connection with certain views relative to the origin and properties of duplicate genes.

In 10 instances in maize duplicate gene ratios have been obtained. Ratios indicative of triplicate genes have been observed less frequently. The reported cases are listed in Table 56.

TABLE 56.—*Reported instances of duplicate and triplicate gene ratios in maize*

Character	Symbol	Investigator
Duplicate gene ratios:		
White seedling	w_4 w_8	Demerec (*2*).
Do	w_b w_e	Do.
Piebald seedling	pb_2 pb_3	Do.
Lineate leaf	li_1 li_1	Collins (*1*), Hutchison (*5*).
Premature germination	ge_6 ge_7	Mangelsdorf (*9*).
Do	ge_8 ge_9	Do.
Purple or red scutellum	s_1 s_2	Described here.
Do	s_2 s_3	Do.
Do	s_3 s_4	Do.
Orange scutellum	so_1 so_2	Do.
Triplicate gene ratios:		
White seedlings	$w?$ $w?$ $w?$	Demerec (*2*).
Germless seeds	$gm?$ $gm?$ $gm?$	Do.
Premature germination	ge_{12} ge_{13} ge_{11}	Mangelsdorf (*9*).

In the small grains the presence of duplicate and triplicate gene ratios has been offered as evidence in support of the hypothesis that those species with higher chromosome numbers have arisen by the duplication of chromosome sets. That the taxonomic relationships bear out this supposed origin is a general belief. Cytologists seem agreed that cytological studies of species representing the different chromosome groups and of species crosses are in support of this supposed origin.

If genetic evidence for the presence of duplicate and triplicate genes can be taken as indicative of chromosome duplication, then maize may be considered as hexaploid for a portion of its chromosome complement. Chromosome morphology in maize has not been studied sufficiently to throw much light on this problem. Chromosome doubling is, without question, a possible mode of origin of duplicate factors. However, it does not seem necessary that this must be the only method of origin. Neither does it seem necessary to believe that genes, interacting to give complementary and duplicate ratios, must have fundamentally different physical or chemical properties.

The aleurone factors C and R normally interact to produce a 9:7 ratio in F_2. Interaction between C and R results in aleurone color. The interactions between C and r, c and R, and c and r, while possibly giving a different end product in each case, are not distinguishable, and all are included in the colorless class. In a 15:1 ratio the interaction of two dominants or of one dominant and one recessive produces, visibly, the same end product. The apparent difference between the 9:7 and 15:1 ratios is merely one of dominance.

If the possible physiological processes engendered by genetic factors are considered, the fundamentality of different types of interaction largely disappears. In the 9:7 ratio for aleurone color, the R and C factors, in conjunction with other genes, initiate two chains of physiological processes. These processes are complementary in that both are necessary for the end product, aleurone color. In a 15:1 ratio the processes initiated by each dominant, in conjunction with other genes, are identical, or at least are so in terms of the end product.

Certain of the ratios in the purple and red scutellum series may be used to emphasize the importance of the residual genetic mass. A plant of the constitution S_1 S_1, S_2 S_2, S_3 s_3, S_4 s_4 will exhibit ratios of approximately 15 colored to 1 colorless scutellum in F_2. If 15:1 ratios are caused by a duplication of chromosomes, then $S_3\ s_3$ and $S_4\ s_4$ must be located on the duplicate chromosomes. Now, if the $S_2\ S_2$ pair is replaced by its recessive allelomorph $s_2\ s_2$, the constitution will be $S_1\ S_1$, $s_2\ s_2$, $S_3\ s_3$, $S_4\ s_4$. The F_2 ratio now will be approximately 9 colored to 7 colorless scutellums. In this case $S_3\ s_3$ and $S_4\ s_4$ must be on nonduplicated chromosomes, since a 15:1 ratio is not obtained. Obviously these factors are on the same chromosomes in both instances. The difference between these two F_2 ratios is due entirely to the residual genetic mass and not to the factor pairs that were heterozygous.

Similar results may be obtained with other combinations of these factors, as indicated in the following comparison:

Genotypes producing ratios of—

15:1	9:7
$S_1\ S_1$, $S_2\ s_2$, $S_3\ s_3$, $S_4\ S_4$	$S_1\ S_1$, $S_2\ s_2$, $S_3\ s_3$, $s_4\ s_4$
$S_1\ S_1$, $S_2\ s_2$; $S_3\ S_3$, $S_4\ s_4$	$S_1\ S_1$, $S_2\ s_2$, $s_3\ s_3$, $S_4\ s_4$

When any two of the factor pairs $S_2\ s_2$, $S_3\ s_3$, and $S_4\ s_4$ are heterozygous, the third factor being homozygous dominant, the ratio is approximately 15:1. Conversely, if any two of these same factor pairs are heterozygous, the third factor being homozygous recessive, the ratio is approximately 9:7. In either event the $S_1\ s_1$ factor pair must be homozygous dominant.

The unusualness of this case lies, possibly, in the reactions involved in the development of scutellum color. Genetic evidence indicates that purple or red scutellum coloration is a resultant of two main reactions or series of reactions. One of these reactions is initiated by the $S_1\ s_1$ factor pair. The second main reaction is conditioned by the other factor pairs, $S_2\ s_2$, $S_3\ s_3$, and $S_4\ s_4$. Indications are that these genes produce a very similar physiological response. The combined action of the dominant allelomorphs of any two of these factor pairs, however, is required to pass a certain threshold concentration necessary for the manifestation of the end result—purple or red scutellum color.

SUMMARY

The pigments of colored scutellums are found most abundantly in the envelope of the scutellar aleurone grains.

Purple and red scutellums normally are exhibited only in the presence of purple and red aleurone. These scutellum colors are shown to be dependent upon the interaction of four factor pairs, $S_1\ s_1$. $S_2\ s_2$, $S_3\ s_3$, and $S_4\ s_4$. Of this series of factors S_1 is indispensable. The interaction is such that S_1 in combination with any two other members of the series will result in colored scutellums. Colorless scutellums must have the dominant member of the factor pairs Ii or $S_5\ s_5$, or recessive s_1, or at least two of the factor pairs $S_2\ s_2$, $S_3\ s_3$, and $S_4\ s_4$ in a recessive condition.

Some evidence is presented indicating that S_1 is linked with Su.

Dominant white scutellums are shown to be due to the action of the $S_5\ s_5$ or $I\ i$ factor pairs.

Orange scutellums develop in the presence of $so_1\ so_1$, $so_2\ so_2$. One of these factors for orange scutellums, so_1, is linked either with the A or R aleurone factor.

Yellow scutellums were inherited as a simple Mendelian recessive. The symbol [illegible] *sy* [illegible] used to designate this factor pair.

The residual genetic mass was [illegible] the factor determining whether [illegible] were [illegible] from crosses involving [illegible] two segregating factor pairs.

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