THE INHERITANCE OF SALMON SILK COLOR IN MAIZE

A THESIS

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CONTENTS

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At the Nebraska State Corn Show of 1908, a number of odd types of corn were gathered together to form a "freak" class. Among them was a "Bronze Pop Corn," so named became of a light bronze color in the pericarp. This ear was obtained by Professor R. A. Emerson, after the exhibit was over, in order to study the inheritance of that pericarp color. The plants grown therefrom were also characterized by brown or brownish silks (Plate LIII). An outcross gave green silks in the F_1. From brown-silked segregates in the progeny of this cross, a true-breeding stock was again obtained. This stock was used in crosses for a study of the inheritance of pericarp color. In one small F_2 of only five plants, there appeared three with green silks and one with brown. The fifth plant had very brilliant salmon or orange-colored silks (Plate LII). This plant was a dilute sun red with red pericarp. It was crossed with red, green, and brown silk colors, and with a purple plant having brown silks. F_1's were grown and selfed to obtain F_2 progenies. The crosses with red and with green silks gave in F_1 red and green silks, respectively. The cross with brown silks gave salmon.

In order to devote more time to studies on aleurone and plant colors and other problems, Dr. Emerson at this point requested the writer to take up the study of these silk colors and their relation to other characters in maize. In his further studies the writer has had the advantage of the hearty cooperation and ever-ready suggestions of Dr. Emerson, and he wishes to acknowledge his sincere gratitude for this help and encouragement.

NOMENCLATURE

The factors referred to in this paper, together with the factor symbols used, are given in the following list:

$A\ a$ — Anthocyanin pigment. A factor pair for pigmentation of aleurone, sheaths, leaves, anthers, and so forth. (Emerson, 1918, 1921.)

$B\ b$ — Brown plant color. A factor pair for leaf and sheath pigmentation. (Emerson, 1921.)

Pl pl — Purple anthers. A factor pair for pigmentation of anthers sheaths, pericarp, and so forth. (Emerson, 1921.)

These three factor pairs interact to give the following plant color types described by Emerson (1921):

$$
\begin{array}{lll}
A & B & Pl \text{— Purple} \\
A & B & pl \text{ — Sun red} \\
A & b & Pl \text{— Dilute purple} \\
A & b & pl \text{ — Dilute sun red} \\
a & B & Pl \text{— Brown} \\
a & B & pl \text{ — Green} \\
a & b & Pl \text{— Green} \\
a & b & pl \text{ — Green}
\end{array}
$$

$R^r \, R^g \, r^r \, r^g \, r^{ch}$ — Red aleurone. A series of allelomorphs affecting anthocyanin pigmentation in aleurone, sheaths, leaves, pericarp, anthers, and silks. (East and Hayes, 1911; Emerson, 1918, 1921.)

$P \, p$ — Pericarp color. Two of a series of allelomorphs for pericarp coloration. (Emerson, 1911.) The bronze type was so pale in color that it could not be satisfactorily distinguished from white (colorless). Only two symbols are used herein, P for red pericarp and p for white or bronze pericarp.

$Y \, y$ — Yellow endosperm. (East and Hayes, 1911; Emerson, 1921.)

Sm sm — Salmon silk color. Described in this paper.

<div align="center">DESCRIPTION OF SILK COLORS</div>

The colors of silk in maize may be described as follows:

1. Green (Plate L). Silks light green, paler below husks; varying from a pure pale green to yellowish green.

2. Red (Plate LI). Silks green, as above, with the addition of a red anthocyanin pigment where exposed to light. The amount of red pigment may vary from a slight trace in the hairs, to sufficient to obscure the green color, giving the silks a deep or dark red color. The darker red silks frequently have some red below the husks. Emerson (1921) has shown this color to be due to the R factor. Microscopic sections show anthocyanin pigment in peripheral parts of the silks.[2]

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[2] The microscopic sections are prepared as follows: Pigmented tissue is fixed for from twelve to twenty-four hours in a saturated solution of mercuric chloride in 95-per-cent alcohol, and washed with 95-per-cent alcohol without iodine. The usual paraffin method of embedding and sectioning is followed and the preparations are mounted in balsam without staining. Sections from 15 to 25 micra in thickness have proved satisfactory.

GREEN SILKS

Silks of this type may be associated with any plant-color type. Purple husks are shown
here for contrast

(Drawing by Carrie M. Preston)
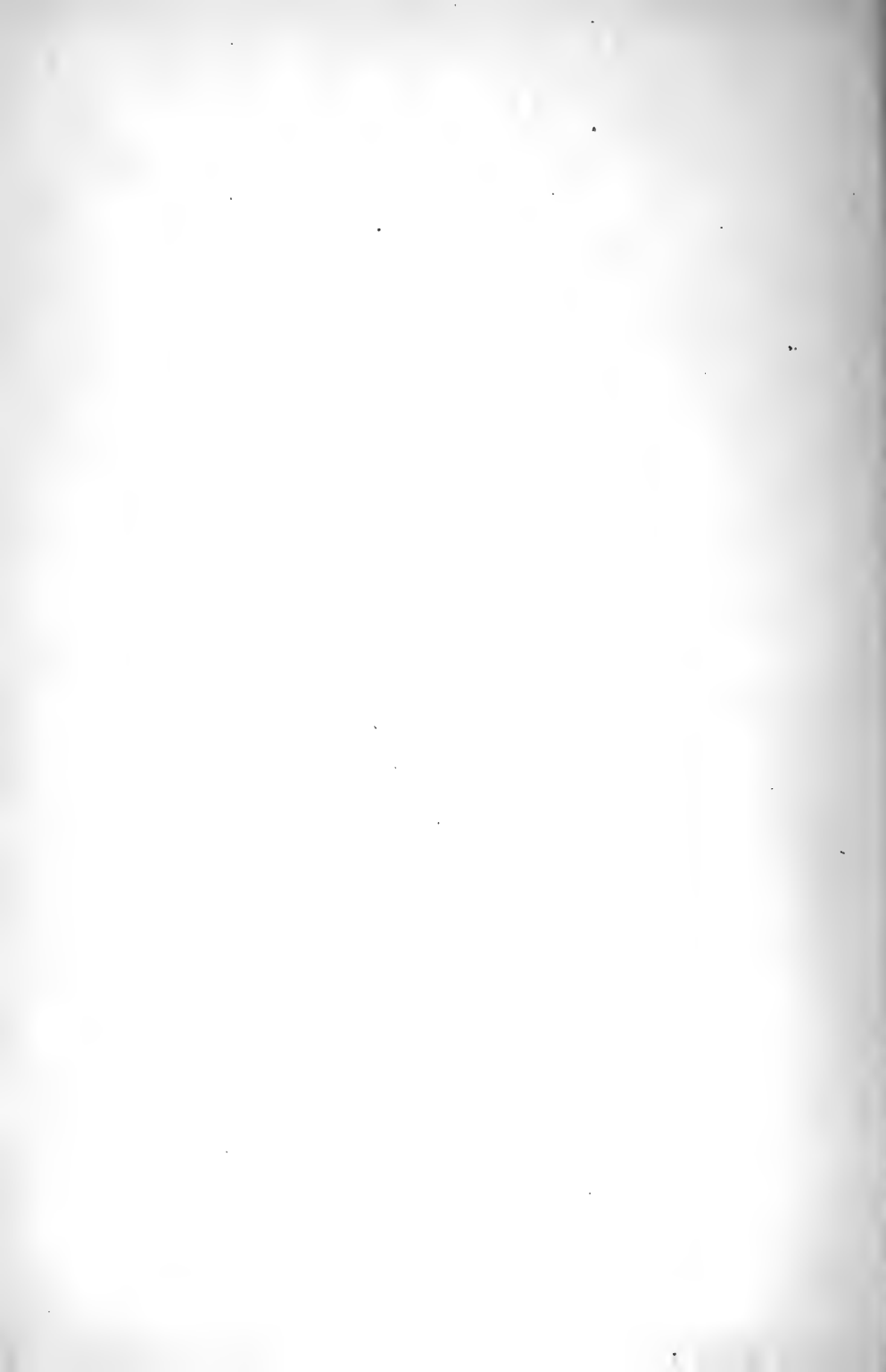
RED SILKS

The red pigment develops only in the parts of the silks exposed to the light
(Drawing by Carrie M. Preston)

SALMON SILKS

The color develops beneath the husks as well as in exposed parts of the silks
(Drawing by Bernice M. Branson)
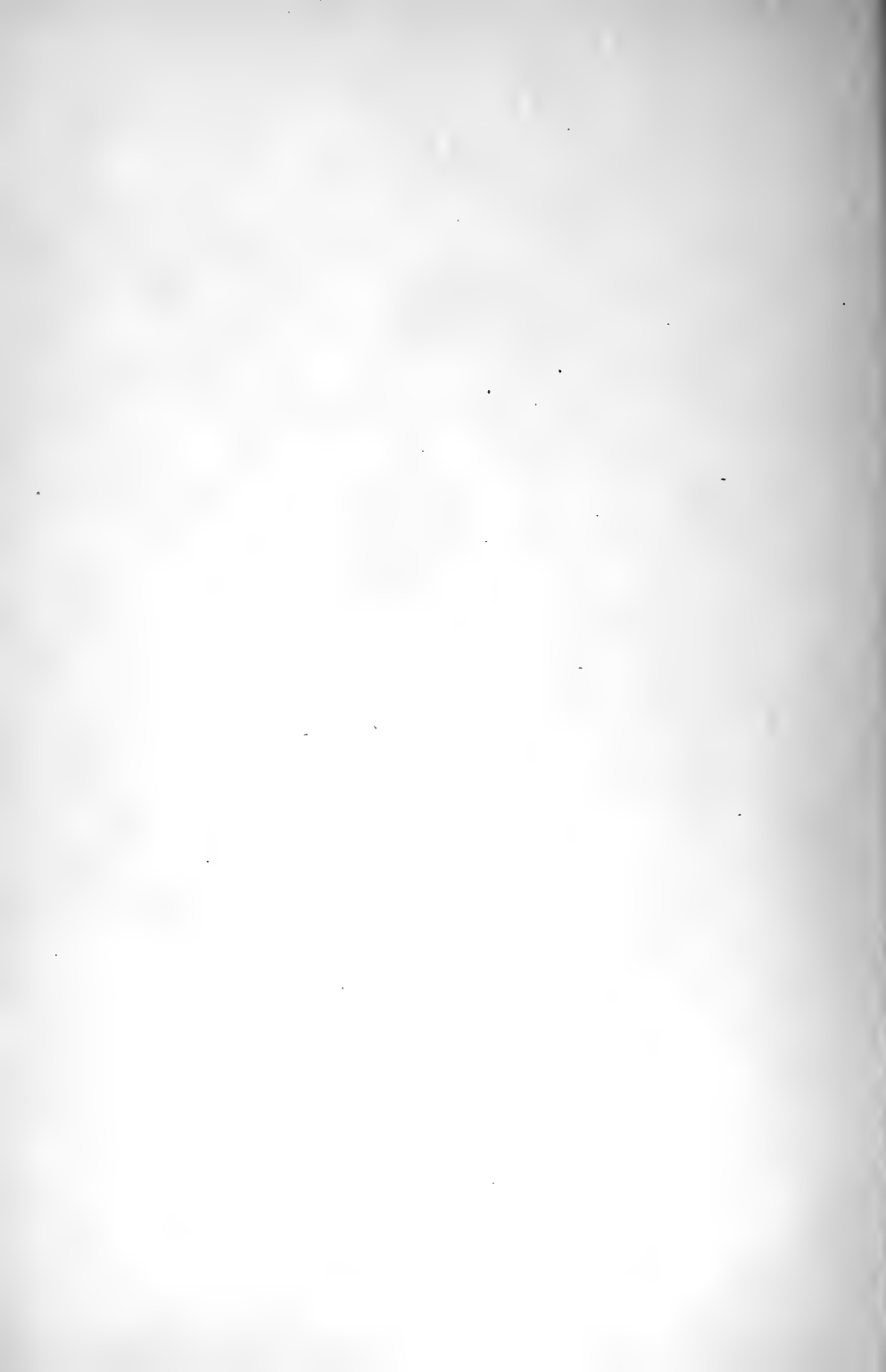
BROWN SILKS

The color develops in both exposed and protected parts of the silks
(Drawing by Carrie M. Preston)

3. Salmon (Plate LII). Silks light salmon-orange to salmon. The color below the husks is similar to that of exposed parts. Microscopic sections show only a faint brownish cast to the tissues thruout the silks.

4. Brown (Plate LIII). Silks orange-pink to pale salmon or salmon-buff in both exposed and covered parts. Salmon and brown silks intergrade, forming a continuous series. The lighter forms are difficult to distinguish from the yellowish green silks of No. 1. Both salmon and brown silks may have red anthocyanin pigment present, as in No. 2.
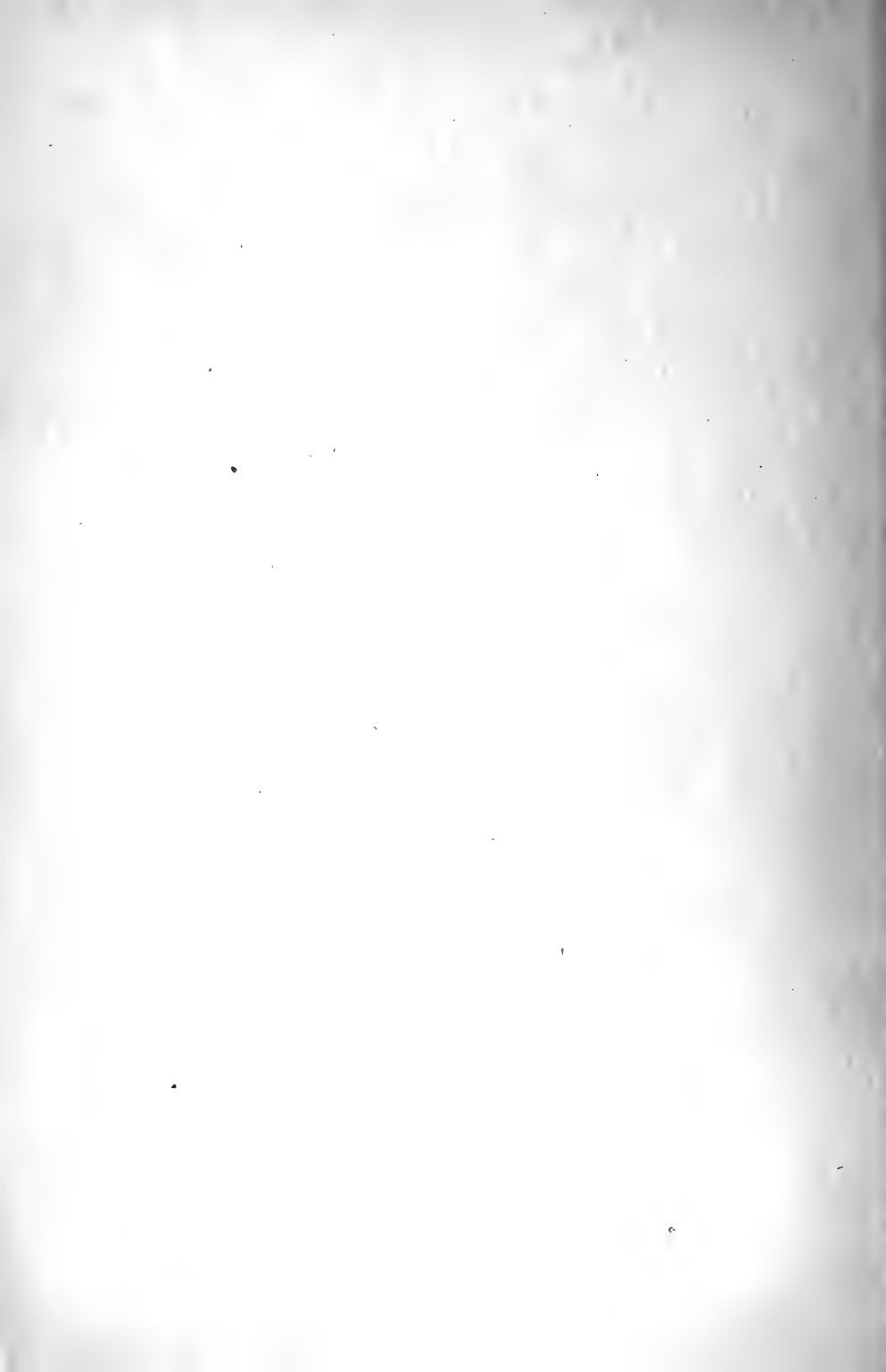
PRELIMINARY STUDIES AND INDICATIONS

Previous tests had shown salmon silk color to be recessive to green and at least partially dominant to brown. Crosses of salmon and brown did not give green color in the F_1. This was taken to indicate that these colors were recessive for a common factor. The anthocyanin pigment present in red silks was shown to be inherited separately by the occurrence of all combination classes (green-red, green, salmon-red, and salmon) in the F_2 of red x salmon.

From observation of cultures previously grown, both salmon and brown silks were known to occur on dilute sun red, on sun red, and on purple plants. Their occurrence on brown or green plants had not been recorded. Microscopic examination of the pigments of maize had shown the presence of a purple-red anthocyanin pigment in purple, sun red, dilute purple, and dilute sun red plants. When the A factor is recessive, no anthocyanin develops (except traces in the shank and the inner husks of brown plants). Instead, a yellow or brownish pigment may be formed. A similar relation holds with the pericarp pigments. Red pericarp color is due to an orange-red or brick-red pigment. Its homolog with recessive A is yellowish brown, similar in appearance to the brown plant-color pigment. The quantity of pigment in salmon silks is so small that microscopic sections gave little information. But the color of the salmon silks was so similar to the color of thin sections of red pericarp as to suggest the possible identity of the pigments. The brown silk might, it was thought, be only a dilute form of salmon. These suggestions were further strengthened by the fact that the original salmon-silked plant had red pericarp and that the brown silks had been obtained from a plant with bronze

pericarp. Sections of this bronze pericarp showed a small amount of orange pigment.

With these suggestions in mind as a working basis, experiments were planned to test them.

ANALYSIS OF INHERITANCE

Interrelations of green, salmon, and brown silks

The indications just mentioned, regarding the relationships of these silk colors, were all checked and corroborated by further tests. Crosses of green with salmon gave green in the first generation, segregating green and salmon, or green, salmon, and brown, in the second. The distinction between salmon and brown was not sharp. With the small numbers used in these tests, the numbers approach a simple ratio of 3 greens to 1 salmon or to 1 salmon and brown.

Crosses between green and brown likewise gave green, segregating in the F_2 into green and brown or in some cases into green, salmon, and brown. In either case there was about 75 per cent of greens.

Crosses of salmon with brown gave salmon. The F_2 ranged from salmon to brown, with salmon predominating.

These results show that there is a common factor pair which differentiates between green on the one hand and salmon and brown on the other. This pair is herein referred to as the salmon-silk factor pair and is designated by the symbols *Sm sm*.

The difference between salmon and brown silks is not explained by these simple tests, tho the occurrence of brown silks in the progenies of outcrosses of salmon, and vice versa, is at least a strong indication of one or more modifying factors.

Relation of salmon silks to pericarp color

In order to test the relationship of the salmon factor to the factor for pericarp color, two series of crosses were made. In the first, a colored-pericarp, green-silked plant (*P Sm*) was crossed with a light-bronze-pericarp, brown-silked plant (*p sm*). In the second, two white-pericarp green-silked plants (*p Sm*) were crossed with the original salmon-silked plant, which had red pericarp (*P sm*). The F_1's were crossed with the double recessive. The results are given in table 1:

TABLE 1. Relation of Salmon Silks to Pericarp Color

I. Backcrosses of P Sm x p sm with p sm

Pedigree no.	P Sm	P sm	p Sm	p sm	Total
253–4......................	9	6	11	20	
255........................	5	11	12	10	
256........................	9	6	15	7	
777–8.....................	41	32	41	39	
Totals...................	64	55	79	76	274

Observed per cent of recombinations........................48.9
Per cent expected with independent segregation..............50.0±2.0

II. Backcrosses of p Sm x P sm with p sm

Pedigree no.	P Sm	P sm	p Sm	p sm	Total
238–9......................	43	61	51	53	
241–2......................	31	28	31	38	
779–80.....................	23	25	25	28	
781–2......................	43	40	50	40	
Totals................	140	154	157	159	610

Observed per cent of recombinations........................48.9
Per cent expected with independent segregation..............50.0±1.4

The observed per cent of recombinations is 48.9 in both series, which is in very close agreement with the expectancy for independent segregation of P and Sm.

In order to determine the possible relation of pericarp color to the difference between salmon and brown silks, a light-pericarp, brown-silked plant was crossed with a red-pericarp salmon. This was backcrossed

with a light-pericarp, brown-silked plant similar to the one parent.   The
silk colors were noted during the summer.   It was impossible to make
any sharp separations, for the colors varied from a deep salmon to a typical
or even light brown.   The presence of red anthocyanin pigment added to
the difficulty, as did also the fact that the silks could not be noted at the
same stage.   So they were only roughly classified, the classifications
from time to time not being entirely comparable.   The notes were under-
scored for a number of good salmons and browns.   The pericarp colors
were determined in the fall.   The results are given in table 2:

TABLE 2.   BACKCROSSES OF p, sm x P sm WITH p sm

Silk color	Red pericarp	White or light bronze
Salmon, underscored.............................	17	0
Salmon..	167	19
Salmon —......................................	25	10
Salmon-brown..................................	33	11
Brown-salmon..................................	10	24
Brown +.......................................	24	65
Brown...	11	172
Brown, underscored.............................	0	44

It will be seen from this table that most of the red-pericarp plants had
been noted as having salmon silks, while the light-pericarp ones were
mostly noted as having brown silks.   It is also significant that, of those
cases in which salmon was underscored, all had red pericarp.   Like-
wise, of the cases in which brown was underscored, all had light pericarp.
Since the salmon factor pair Sm sm has been shown to segregate inde-
pendently of the factor pair P p for pericarp color, this variation can-
not be due to the Sm sm pair.   The conclusion is drawn that the intensity
of pigmentation of silks recessive for sm is largely a function of the inten-
sity of pigmentation of the pericarp or of some factor closely associated
with the factor for pericarp color.   The former view is substantiated

by the fact that no selfed progenies from light-pericarp plants have ever given any good salmon silks, while progenies from red-pericarp plants have always given some salmon silks even tho the parents had been noted otherwise. No brown silks have been found in families breeding true for red pericarp.

Relation of salmon silks to the B and Pl factors for plant color

Several crosses made with salmon silks involved the B factor. Both F_1 combinations, B Sm x b sm and B sm x b Sm, were backcrossed with the double recessive. The results (table 3) show independent segregation of these factors.

TABLE 3, RELATION OF SALMON SILKS TO THE B AND Pl FACTORS FOR PLANT COLOR

I. Backcrosses of B Sm x b sm with b sm

Pedigree no.	B Sm	B sm	b Sm	b sm	Total
241–2	25	24	39	41	
779–80	21	19	28	35	
Totals	46	43	67	76	232

Observed per cent of recombinations 47.4
Per cent expected with independent segregation . . . . 50.0±2.2

II. Backcrosses of B sm x b Sm with b sm

Pedigree no.	B Sm	B sm	b Sm	b sm	Total
774–6	78	62	80	53	273

Observed per cent of recombinations 47.6
Per cent expected with independent segregation . . . . 50.0±2.0

One of the crosses of the original salmon-silked plant, A b pl sm, was with a purple plant with green silks, A B Pl Sm, related to the bronze stock. The progeny consisted of purple and sun red plants with green and salmon silks, showing the parent to have been heterozygous for both Pl and Sm. Two small plantings gave the following distributions; Pl Sm, 26; Pl sm, 7; pl Sm, 4; pl sm, 23; whereas equality of the four classes would be expected if the factors were independent. This was obviously a linkage relation. The factor Pl was known to be linked with a factor Y for yellow endosperm (Emerson, 1921). Tests of the linkage relations within this group are given in a later section of this paper.

Relation of salmon silks to the A factor

From an outcross of the original salmon-silked plant with one heterozygous for brown silks and for the A factor, several plants were selfed. One sun red plant was homozygous recessive for the salmon silk factor and heterozygous for A and B. Thirty-four sun red and dilute sun red plants had salmon or brown silks. Two others were first noted as green but were presumably a light brown, both having white pericarp. Eleven green plants appeared, all having green silks. Later observations on green and brown plants of other families segregating for both a and sm have likewise failed to reveal any green plants with other than green silks. That this is not due to linkage is shown by the linkage of Sm with the Pl factor, which is known to be independent of A, and by the fact that the green plants have green silks in families that are homozygous recessive sm.

Relation of salmon silks to the R factor

Two questions of interest arose regarding the relation of salmon silk color to the R series of allelomorphs. The first was the relation of cherry pericarp color to the intensity of color in salmon or brown silks; the second was the possibility of the occurrence of salmon silks on green plants of the constitution R^g A b Pl or R^g A b pl.

To test the effect of cherry pericarp, a sun red with brown silks, A B pl sm r^r, was crossed with a dilute purple with cherry pericarp and green silks, A b Pl Sm r^{ch}. Backcrosses gave a few plants with cherry pericarp and brown silks. They were not noticeably different in silk color from the white-pericarp plants of the same families.

. To test for the occurrence of salmon silks on green plants of the constitution R^g *A b Pl* or R^g *A b pl*, a dilute purple plant with salmon silks was crossed with a green plant of the constitution R^g *A b pl*. Two of the F_1 plants were selfed. Purple seeds only were planted. These gave 44 dilute purples and dilute sun reds, of which 32 had green silks and 12 had salmon. There were 25 green plants, R^g *A b*, 18 of which had green silks; the other 7 had typical salmon and brown silks.

From these two tests, it may be concluded that salmon silk color is not dependent on the *R* factor nor is it noticeably influenced thereby. This is similar to the relation between red pericarp color and R^g (Emerson, 1921).

Summary of inheritance

Salmon and brown silks are recessive to green silks by a single factor pair, *Sm sm*.

This factor, *Sm*, is independent in inheritance from *P* (pericarp), *A* (aleurone and plant color), *B* (plant color), and *R* (aleurone, plant color, cherry pericarp, and red silk color).

It is linked with the factor *Pl* (plant color), and consequently also with *Y* (yellow endosperm).

Dominant *A* is necessary for the production of salmon or brown silk color; that is, the combination *a a sm sm* is green.

The intensity of pigmentation of salmon-brown silks is directly related to the intensity of pigmentation of the pericarp.

The relation of the factors *A*, *Sm*, and *P* to silk color may be represented schematically as follows:

A Sm P = Green	***a** Sm P* = Green		
A Sm p = Green	***a** Sm p* = Green		
A sm P = Salmon	***a** sm P* = Green		
A sm p = Brown	***a** sm p* = Green		

LINKAGE RELATIONS OF *Y*, *Pl*, AND *Sm*

Preliminary tests of linkage of Pl and Sm

The first indication of the linkage of the *Sm* and *Pl* factors was observed in the progeny of an outcross of the original salmon with a purple plant having green silks. This plant proved to be heterozygous for both *Sm*

and *Pl*. To the distribution given on page 546 may be added the data from a duplicate planting by Dr. Emerson:

	Pl Sm	*Pi sm*	*pl Sm*	*pl sm*	Per cent of crossing-over
111–2.	26	7	4	23	
From Emerson.	25	9	4	38	
	51	16	8	61	17.6

Two other backcrosses were then made, which the following year gave the results:

	Pl Sm	*Pl sm*	*pl Sm*	*pl sm*	Per cent of crossing-over
238–9	76	24	20	93	20.3
241	60	4	4	66	6.3

Construction and results of three-point tests

In the meantime, crosses were made to involve the *Y* factor for yellow endosperm in addition to *Pl* and *Sm*, since *Y* and *Pl* were known to be linked. To get a satisfactory three-point backcross test involved several difficulties, as follows:

1. Yellow endosperm is not easily distinguished from white if brought in only by the pollen. This is assumed to be due to the dominant *Y*'s being represented only once in the triple-fusion endosperm nucleus. It is therefore desirable that the F_1 plants should be used as female parents in the backcrosses.

2. Brown silks are not readily separated from green. This difficulty can be avoided only by having red pericarp in each plant. But the presence of red pericarp obscures the color of the endosperm. So in order to make endosperm separations possible, the female parent of the backcross must be free from red pericarp.

3. Purple and dilute purple plants usually have some purplish pigment in the pericarp, which in some cases interferes with the classification of yellow endosperm.

4. The dominant A factor must be present in every individual where silk color separations are to be made.

5. Aleurone color must be avoided.

6. Presence of the dominant B factor, while not affecting accuracy, would nevertheless facilitate note-taking by making all the plants of two sharply differentiated classes, purple and sun red.

To avoid as many as possible of these difficulties and accomplish the results within the shortest period of years, the following procedure was put into effect: Crosses were made involving the factors Y, Pl, and Sm in different combinations. In all of these crosses, pericarp color and also the R factor for aleurone color were kept recessive. At the same time, an attempt was made to find or isolate a stock of the triple recessive of the desired composition. Tests of all available salmon-silk material revealed two closely related families breeding true for red pericarp, white endosperm, and recessive r. Both families consisted of sun red and dilute sun red plants showing the B factor to have been heterozygous. These were used the following year in the backcrosses. Their composition was y y pl pl sm sm r r P P A A, some plants being homozygous and some heterozygous for dominant B. Pollen of these plants was used on silks of the F_1 crosses.

These backcrosses were made in 1918 and the progenies were grown in 1919. The results are given in table 4 (page 550). The percentages of crossing-over are: Y-Pl, 28.9; Pl-Sm, 9.1; Y-Sm, 36.6; showing their relative order to be Y-Pl-Sm.

While material for these tests was being built up, some much less satisfactory backcrosses were made by pollinating white-endosperm, brown-silked, dilute sun red plants with pollen from crosses involving Y, Pl, and Sm. These were grown in 1918. The results are given in table 5 (page 551).

A summary of the percentages of crossing-over is given in table 6 (page 552).

The chromosome map

From the totals of all the data obtained on these linkage relations, the observed percentages of crossing-over are found to be 29.70 for Y-Pl, 10.01 for Pl-Sm, and 36.79 for Y-Sm. This shows their relative map order to be Y-Pl-Sm. The distance from Y to Pl as observed is 29.7,

TABLE 4. BACKCROSSES INVOLVING Y. *Pl*, AND *Sm*, 1919

Pedigree no.	Character of F₁	Non-crossovers		Crossovers y-pl		Crossovers pl-sm		Double crossovers	
		Y Pl Sm	*y pl sm*	*Y pl sm*	*y Pl Sm*	*Y Pl sm*	*y pl Sm*	*Y pl Sm*	*y Pl sm*
1451–3	*y pl sm* x *Y Pl Sm*	79	74	57	48	7	19	0	3
1454–6	*y pl sm* x *Y Pl Sm*	32	24	20	16	1	4	0	1
		Y pl Sm	*y Pl sm*	*Y Pl sm*	*y pl Sm*	*Y pl sm*	*y Pl Sm*	*Y Pl Sm*	*y pl sm*
1457–9	*Y pl Sm* x *y Pl sm*	160	145	75	79	13	24	0	0
1460–2	*Y pl Sm* x *y Pl sm*	144	113	49	71	14	18	3	1
1463–6	*Y pl Sm* x *y Pl sm*	132	119	41	56	18	8	2	0
		Y Pl sm	*y pl Sm*	*Y pl Sm*	*y Pl sm*	*Y Pl Sm*	*y pl sm*	*Y pl sm*	*y Pl Sm*
1467–8	*y pl Sm* x *Y Pl sm*	72	67	16	20	2	10	0	0
1469–70	*y pl Sm* x *Y Pl sm*	124	99	39	36	10	10	0	0
1471–3	*y pl Sm* x *Y Pl sm*	109	99	52	68	16	10	0	1
		Y pl sm	*y Pl sm*	*Y Pl Sm*	*y pl sm*	*Y pl Sm*	*y Pl sm*	*Y Pl sm*	*y pl Sm*
1476–7	*Y pl sm* x *y Pl Sm*	43	45	23	13	13	5	1	0
1478–80	*Y pl sm* x *y Pl Sm*	69	83	25	26	11	21	1	0
1481–2	*Y pl sm* x *y Pl Sm*	58	50	18	24	15	11	4	4
Totals		1,940		872		260		21	

TABLE 5. BACKCROSSES INVOLVING Y, Pl, AND Sm, 1918

Pedigree no.	Character of F₁	Non-crossovers		Crossovers Y–Pl		Crossovers Pl–Sm		Double crossovers	
		Y pl sm	*y Pl Sm*	*Y Pl Sm*	*y pl sm*	*Y pl Sm*	*y Pl sm*	*Y Pl sm*	*y pl Sm*
772–3.........	Y pl sm x y Pl Sm	51	73	43	29	9	7	2	5
774–6.........	Y pl sm x y Pl Sm	63	94	50	40	13	8	4	1
781–2.........	Y pl sm x y Pl Sm	49	66	24	20	5	7	4	2
		Y Pl Sm	*y pl sm*	*Y pl sm*	*y Pl Sm*	*Y Pl sm*	*y pl Sm*	*Y pl Sm*	*y Pl sm*
777–8.........	y pl sm x Y Pl Sm	51	51	14	28	9	4	1	0
779–80.........	Y Pl Sm x y pl sm	29	31	18	12	4	4	4	1
Totals........		558		278		70		24	

TABLE 6. SUMMARY OF LINKAGE DATA

Pedigree no.	Total number of plants	Percentage of crossing-over		
		Y-Pl	Pl-Sm	Y-Sm
111–2.................................	136	....	17.5	....
238–9.................................	213	....	20.7	....
241...................................	134	....	6.0	....
Totals	483	....	15.73	....
772–3.................................	219	36.1	10.5	40.2
774–6.................................	273	34.8	9.5	40.7
781–2.................................	177	28.2	10.2	31.6
777–8.................................	158	27.2	8.9	34.8
779–80................................	103	34.0	12.6	36.9
Totals 1918	930	32.47	10.11	37.42
1451–3................................	287	37.7	10.1	45.6
1454–6................................	98	37.8	6.1	41.8
1457–9................................	496	31.0	7.5	38.5
1460–2................................	413	30.0	8.7	36.8
1463–6................................	376	26.3	7.4	32.7
1467–8................................	187	19.3	6.4	25.7
1469–70...............................	318	23.6	6.3	29.9
1471–3................................	355	34.1	7.6	41.1
1476–7................................	143	25.9	13.3	37.8
1478–80...............................	236	22.0	14.0	35.2
1481–2................................	184	27.2	18.5	37.0
Totals 1919	3,093	28.87	9.09	36.60
Totals 1918–1919	4,023	29.70	9.32	36.79
Totals of all data	4,506	....	10.01	....

or approximately 30 units. Since in such long distances double crossing-over may be expected, a corrected map distance should be 30 plus twice the per cent of unobserved double crossovers between the two points. But with the high amount of interference indicated by the small number of observed coincident crossovers in the two regions Y-Pl and Pl-Sm, the corrected value for these data is probably not much above 30 or 35. The value 10 for the map distance between Pl and Sm is probably correct for these data.

It should be understood that the chromosome map is primarily a graphic representation of the data on linkage relationships. Its correspondence with actual positions on the chromosome itself is not implied, tho the work of Morgan and his coworkers has given much evidence of at least a correspondence between relative map order and the actual relative position of the genes in the chromosome.

The variability of the percentages of crossing-over shown in table 6 is not greater than would be expected of heterogeneous data. Gowen (1919) has shown crossing-over in Drosophila to be an extremely variable phenomenon. Plough (1917) has shown it to be modified by temperature, and Bridges (1915) by age of the individual. The subject of variation of crossing-over in maize must remain for study with less difficult characters than those involved in these experiments.

The distributions when the F_1's were used as pistillate and as staminate parents give nearly the same averages, but the data are inadequate for any conclusion except that the crossing-over is not widely different in the two cases.

Coincidence of crossing-over

Coincidence of crossing-over in two regions of a chromosome is the ratio of observed coincident (simultaneous) crossing-over to the calculated expectancy. The expectancy is the product of the percentages of crossing-over of the two regions. The actual calculation may be simplified, as shown by Weinstein (1918). The derived formula is

$$\text{Coincidence} = \frac{xn}{ab}$$

in which n = the total number of individuals,

   x = the number of coincident crossovers,

 a and b = the total number of crossovers in the respective regions.

The coincidence of crossing-over in the two regions Y-Pl and Pl-Sm, calculated from tables 4 and 5, is as follows:

From table 4:

$$\text{Coincidence} = \frac{21 \times 3093}{893 \times 281} = 0.26$$

From table 5:

$$\text{Coincidence} = \frac{24 \times 930}{302 \times 94} = 0.79$$

From combined data of tables 4 and 5:

$$\text{Coincidence} = \frac{45 \times 4023}{1195 \times 375} = 0.40$$

These values are entirely comparable with those listed by Weinstein (1918) for Drosophila. From this and the similarity of all phases of linkage and crossing-over, it is evident that the mechanism of crossing-over in maize is not strikingly different from that in Drosophila except in one respect. In Drosophila, crossing-over occurs in oogenesis only, in spermatogenesis not at all. In maize the phenomena of crossing-over are at least of the same order in both megasporogenesis and microsporogenesis.

Summary of linkage studies

The factor Sm for salmon silk color is shown to be linked with the factor Y for yellow endosperm and the factor Pl for plant and anther color.

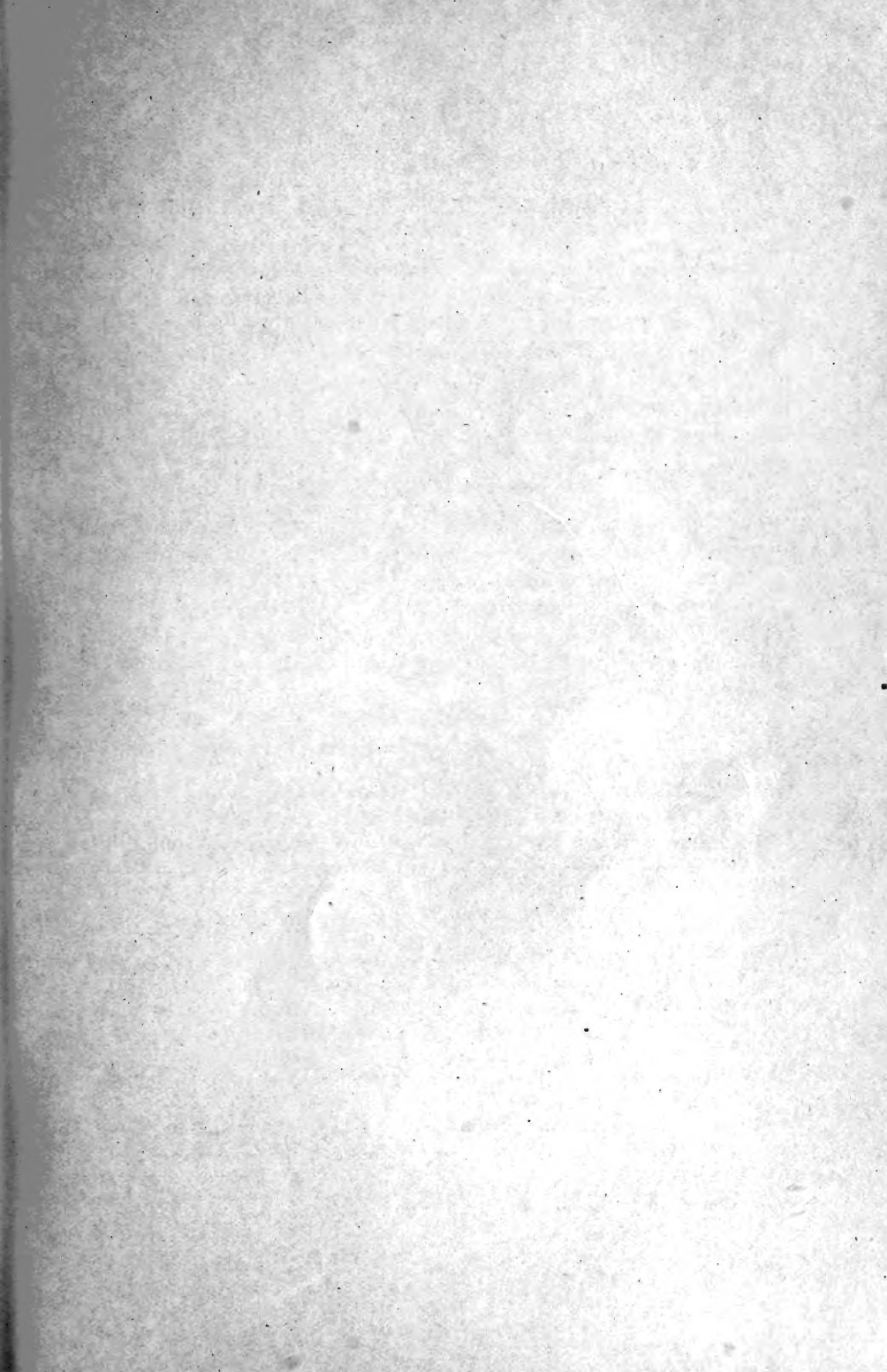The relative order of these three factors is Y-Pl-Sm.

The amount of crossing-over between Y and Pl is about 30 per cent; between Pl and Sm it is about 10 per cent.

The observed coincidence of crossing-over in the two regions Y-Pl and Pl-Sm was about 0.4.
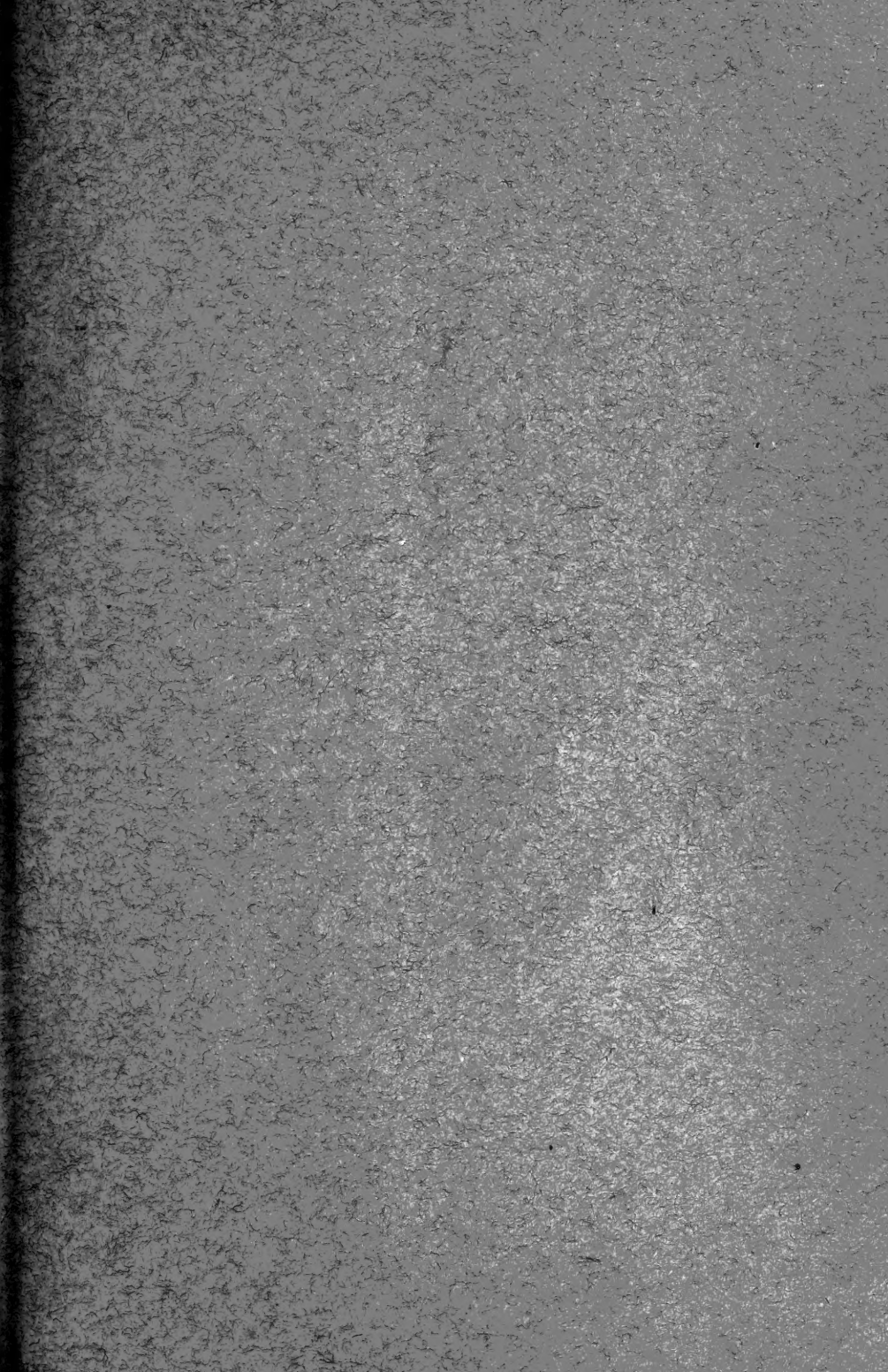
LITERATURE CITED

BRIDGES, CALVIN B.   A linkage variation in Drosophila.   Journ. exp. zool. 19:1–21.   1915.

EAST, E. M., AND HAYES, H. K.   Inheritance in maize.   Connecticut Agr. Exp. Sta.   Bul. 167:1–142.   1911.

EMERSON, R. A.   Genetic correlation and spurious allelomorphism in maize.   Nebraska Agr. Exp. Sta.   Ann. rept. 24:58–90.   1911.

————   A fifth pair of factors, A a, for aleurone color in maize, and its relation to the C c and R r pairs.   Cornell Univ. Agr. Exp. Sta. Memoir 16:225–289.   1918.

————   The genetic relations of plant colors in maize.   Cornell Univ. Agr. Exp. Sta.   Memoir 39:1–156.   1921.

GOWEN, JOHN WHITTEMORE.   A biometrical study of crossing over.   On the mechanism of crossing over in the third chromosome of Drosophila melanogaster.   Genetics 4:205–250.   1919.

PLOUGH, HAROLD H.   The effect of temperature on crossingover in Drosophila.   Journ. exp. zool. 24:147–209.   1917.

WEINSTEIN, ALEXANDER.   Coincidence of crossing over in Drosophila melanogaster (ampelophila).   Genetics 3:135–172.   1918.