INHERITANCE OF SPOTTED ALEURONE COLOR IN HYBRIDS OF CHINESE MAIZE¹

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The color in the aleurone cells of maize early attracted the attention of geneticists as affording ideal material for testing the segregation of characters in the second generation of hybrids.

The first cases that were investigated led to the idea of only one unit or factor being involved in the production of an aleurone color. With the progress of investigation, however, it became necessary to assume that two factors are involved. The occurrence of red and purple seeds on the same ear showed the need of recognizing a third factor, and the appearance of a pale color, or "dilute," necessitated the assumption of a fourth, modifying, factor.

A brief examination of the many varieties grown by the Indians of North and South America shows that there are still other aleurone colors not provided for in this scheme, such as clay (a light blue but very distinct from dilute) found in varieties grown by the Hopi Indians of Arizona; pink (a light red), isolated from the Chinese waxy type, and black (an exceedingly intense blue or purple) found in varieties grown by the Navajo Indians and brown found in a Bolivian variety. It is not absolutely certain as yet whether additional factors are concerned in the production of these variations, or whether we are dealing with one or more dilution factors similar to those found in guinea pigs (WRIGHT 1916).

Apart from the many shades of color there are several color patterns corresponding in a certain sense to those of animals. Not all of these patterns have been, as yet, thoroughly investigated, but they are so distinct in appearance that there can be little doubt that additional factors or heritable elements are involved in their expression.

While at least two color schemes found on maize seeds are undoubtedly

¹ Since this manuscript was prepared a paper by Professor R. A. EMERSON (1918) has appeared, in which a similar type of aleurone color has been analyzed and designated mottled. In general the conclusions reached are similar to those presented here, but there are some differences which it is believed will be of interest.

patterns, two others would be classed more properly perhaps as a color dilution. If this is true there are two types of color dilution in the aleurone layer. The first of these has color in each aleurone cell but of greatly reduced intensity. This type is found in both red and blue. Most of the seeds belonging to it are darker at the base, the color paling gradually toward the tip. This type may possibly correspond to that designated parti-colored by EAST and HAYS (1911).

The other type of color dilution found in maize is perhaps comparable to the blue roan color in horses and cattle, in that with respect to color, there are two kinds of cells, those with pigment and those without. Unlike the blue roans, where cells of a color do not occur in groups, the seeds of maize are flecked with spots of irregular size, scattered indiscriminately over the entire surface and seemingly showing no evidence of concentration either at the base or the tip.

Cells of a color occur in groups of varying sizes. In many cases the color, however, is intense, the seed appearing lighter in shade only when groups of colored cells alternating with groups of colorless cells are extremely small. Cases occur in which the two types of dilution are combined, the seeds being spotted with a faint color.

Chemically it is quite possible that the two types of color dilution found in the aleurone layer of maize seeds represent two conditions of a single enzyme which causes the development of anthocyanin through the oxidation of a chromogen, a suggestion already advanced by WRIGHT (1917) to account for a parallel case in the melanin pigment of mammals.

Where the intensity of the pigment itself is reduced, the entire seed being but faintly colored, it may be that the enzyme is weak and slow to react.

While in the spotted type of dilution in which the color is intense but does not extend over the entire seed, it would appear that the enzyme is sufficiently active, but the quantity may be reduced to such an extent that enough chromogen can not be oxidized to cover the entire seed.

The occurrence of spotted seeds in a cross between the Chinese white waxy corn and a colored Algerian pop corn has given the opportunity to study the inheritance of this spotted type of color distribution.

There are several peculiarities in the production of spotting which are not inharmonious with the supposition that this type of color distribution is in reality a color dilution, due perhaps to a reduced quantity of an enzyme concerned in the production of color.

The factors which influence the appearance and production of color

in the aleurone cells of maize, so far as investigated and reported, are listed below:

C, a factor for the production of any color, but inactive unless another factor (which has been designated *R*) is present.

R, a factor as necessary as *C* for the production of color. With *C* it will produce a red color. It may be distinguished from *C* because the latter factor is correlated with the texture of the endosperm.

A, a factor reported by Emerson (1918) as necessary for the production of any color.

P_r, a factor that in combination with the factors *C* and *R* changes the color of the aleurone from red to blue or purple.

I, a factor concerned with the inhibition of color. It is assumed to affect the production of both red and blue.

S. This factor is here reported for the first time. It is concerned with the production of a certain type of minute spotting and seems to be associated or correlated with the factor *R*.

In 1910 crosses were made between a variety of maize received from Algeria, having colored aleurone and horny endosperm and a Chinese variety with white waxy endosperm. One cross was made with the Algerian variety as the male parent, the other with this variety as the female parent. Both of the resulting ears were uniform or self-colored, in this respect resembling the Algerian parent. The progeny of the ear having the Algerian plant as the male parent failed to show the usual association of endosperm texture and aleurone color.

This result seemed to afford ground for the belief that there might be a difference between reciprocal crosses with respect to the association of aleurone color and endosperm texture. To investigate this possibility, six crosses were made between these same two varieties in 1913. While no differences in the association of the characters were found between reciprocal crosses, the results showed conclusively that in these hybrids aleurone color may show different distributions in the seeds of reciprocal crosses.

Of the six hybrid ears three were borne on plants of the Algerian variety, the other three on plants of the Chinese variety. The former were self-colored and could not be distinguished from pure Algerian ears. The latter were also colored, but the color on two of these was in numerous small spots. Of these two, one had all the seeds spotted, the other approximately half of the seeds spotted, the actual ratio being 107 spotted to 97 self-colored. The relationship of the six ears is shown in figure 1.

It is to be noted that the Algerian plants, which bore the self-colored

FIGURE 1.—Diagram showing the relationship of the 6 hybrid ears.

ears Dh420 and Dh419, showed an incomplete dominance when used as male parents with some Chinese plants, but a complete dominance when these same Chinese plants were used as male parents. That the dominance of the Algerian color is not always incomplete when Algerian plants serve as male parents is demonstrated by the hybrid ear Dh416 which had self-colored kernels.

Plants from all six ears were grown in 1914, and a large number of hand-pollinated ears bearing seeds representing the second generation were secured. The progeny of all but one of the six ears produced ears with some spotted seeds. The one exception, ear Dh416, was borne on a Chinese plant and was pollinated from the same Algerian plant that served as the male parent of ear Dh417, which was spotted.

The progeny of the remaining 5 ears produced 60 hand-pollinated ears having some of the seeds spotted. Of these 35 showed a dihybrid ratio of white to colored seeds, and 2 had all the seeds colored. It must be borne in mind, however, that these 60 ears were the result of self-pollination, and crosses between plants grown from the other hybrid ears.

As both red and blue seeds were found on ears having a dihybrid ratio of white to colored seeds, it was necessary to assume that three factors are involved in the production of color: (1) A basic factor (C), which is essential for the production of any color, (2) a factor for red (R) which in conjunction with the factor C results in a red seed; and (3) a factor for blue (P_r), which, when present in the same zygote with the factors C and R , results in these seeds being blue. All com-

binations of these factors other than *C* and *R*, or *C*, *R*, and *P_r*, result in the production of white seeds. The suggestion has been advanced that the factor correlated with endosperm texture is the basic factor *C* (KEMPTON 1915, BREGGER 1918). This is mentioned here, as it affords a method of distinguishing between the factors *C* and *R*, which is of

TABLE I
Percentage of spotted seeds on ears with a dihybrid ratio of white to colored seeds.

Pedigree number	Total number	Number colored	Number spotted	Percentages of total spotted	Percentage of colored that are spotted	Percentage of white
2250	86	52	5	5.8	9.6	39.5
2251	648	369	104	16.1	28.2	43.0
2262	438	252	53	12.1	21.1	42.4
2263	251	153	36	14.3	23.5	39.0
2264	517	278	75	14.5	27.0	46.4
2265	345	199	49	14.2	24.6	42.3
2266	606	332	83	13.7	25.0	45.2
2301	218	124	35	16.1	28.2	43.2
2302	435	259	86	19.8	33.2	40.4
2311	178	110	28	15.7	25.4	38.2
2312	244	131	31	12.7	23.7	46.4
2315	508	288	100	19.7	34.7	43.3
2316	480	254	85	17.7	33.4	47.1
2324	283	168	61	21.5	36.3	40.6
2325	159	89	30	18.9	33.7	44.0
2326	309	177	55	17.8	31.1	42.7
2331	294	174	46	15.6	26.4	40.8
2332	526	286	104	19.8	36.4	45.6
2336	392	221	72	18.3	32.6	43.6
2339	595	358	129	21.7	36.1	39.8
2340	537	285	97	18.1	34.0	47.0
2342	357	208	70	19.6	33.6	41.7
2343	265	139	43	16.2	30.9	47.5
2347	395	226	80	20.3	35.4	42.8
2348	44	26	5	11.4	19.2	41.0
2350	311	165	64	20.6	38.8	47.0
2351	52	29	10	19.2	34.5	44.3
2352	565	320	89	15.8	27.8	43.4
2353	230	135	73	31.7	54.1	41.3
2356	454	268	80	17.6	29.8	41.0
2358	251	148	44	17.5	29.7	41.0
2359	512	309	105	20.5	34.0	39.6
2364	526	286	75	14.3	26.2	45.6
2365	34	13	3	8.8	23.1	61.7
2366	407	252	89	21.8	35.3	38.1
Total	12452	7083	2194	17.6	30.4	43.2

importance in analyzing the inheritance of spotted seeds, as will appear later.

All the ears with a dihybrid ratio of white to colored seeds had some seeds that were spotted. The percentage of the total seeds that showed spotting was $17.6 \pm .236$, but since spotting can be detected only when the seeds are colored, it would seem that the percentage of spotted seeds on an ear should be determined by the percentage of colored seeds that are spotted. If this assumption is admitted the percentage of spotted seeds becomes $30.4 \pm .277$ for these hybrid ears.

The ears having a monohybrid ratio of white to colored seeds fell into two groups as regards spotted seeds—those having some of the seeds spotted and those without any spotted seeds.

Disregarding for the present those ears without spotted seeds, the percentage of spotted seeds on the others is $21.7 \pm .27$, but the per-

TABLE 2
Percentage of spotted seeds on ears with a monohybrid ratio of white to colored seeds.

Pedigree number	Total number	Number colored	Number spotted	Percentages of total spotted	Percentage of colored that are spotted	Percentage of white
2251	268	204	63	23.5	30.8	23.9
2252	39	29	8	20.5	27.6	25.6
2256	627	484	92	14.7	19.0	22.8
2257	574	436	138	24.0	31.7	24.0
2259	576	421	103	17.9	24.5	26.9
2260	518	397	87	16.8	21.9	23.4
2303	267	185	44	16.5	23.8	30.7
2308	600	440	145	24.2	33.0	26.6
2319	402	279	111	27.6	39.8	30.6
2333	579	403	155	26.8	38.5	30.4
2334	260	193	70	26.9	36.2	25.8
2335	399	293	93	23.3	31.7	26.5
2337	497	386	132	26.6	34.2	22.3
2338	400	292	83	20.8	28.4	27.0
2344	564	409	129	22.9	31.5	27.5
2346	588	452	145	24.7	32.1	23.1
2349	605	432	112	18.5	25.9	28.6
2355	202	156	48	23.7	30.8	22.7
2357	288	221	49	17.0	22.2	23.3
2360	618	466	142	23.0	30.5	24.6
2362	554	408	129	23.3	31.6	26.4
2363	225	161	52	23.1	32.3	28.4
2345	471	313	66	14.0	21.1	33.5
Total	10121	7460	2196	21.7	29.4	26.3

centage of colored seeds that are spotted is $29.4 \pm .30$, essentially the same percentage as was observed on the ears with a dihybrid ratio of white to colored seeds (see table 2). The percentage of spotted seeds based on the total can not, of course, be alike on ears with monohybrid and dihybrid ratios of white to colored seeds, since the latter class has a relatively larger percentage of the total seeds white.

A plant of the hybrid Dh420 when crossed with a plant of the hybrid Dh417 resulted in the production of an all-colored ear. A similar result was secured when a plant of the hybrid Dh415 was crossed with another plant of the hybrid Dh417. The assumption in these cases is that one of the plants is genotypically constituted *CCRr* and the other *CcRR*. These two all-colored ears had $29.1 \pm .82$ of the seeds spotted (table 3). They are represented diagrammatically in figures 2 and 3 (pp. 272, 273).

Thus it is seen that ears with a dihybrid and those with a hybrid ratio of white to colored seeds, as well as ears having all of the seeds colored, have essentially the same percentage of the colored seeds spotted, provided, of course, that they have spotted seeds at all.

Combining the three classes of ears, those with a monohybrid and dihybrid ratio of white to colored seeds as well as the two ears having all the seeds colored, the percentage of colored seeds that are spotted is found to be $29.9 \pm .19$. This percentage at first glance might be considered an approximation of the 25 percent expected for a simple monohybrid ratio, but the deviation is 23.8 times the probable error.

TABLE 3
Percentage of spotted seeds on ears having all the seeds colored.

Pedigree number	Total number	Number colored	Number spotted	Percentages of total spotted	Percentage of colored that are spotted	Percentage of white
2254	699	699	191	27.3	27.3	0
2361	668	668	189	31.1	31.1	0
Total	1307	1307	380	29.1	29.1	0

As all of the ears having a dihybrid ratio of white to colored seeds had some of the seeds spotted and, further, as approximately one-half of the ears with a monohybrid ratio of white to colored seeds (the progeny of the hybrid Dh416 omitted) had some of the seeds spotted, it would appear that when a plant is heterozygous for one of the factors for aleurone color some of the seeds are spotted.

Confining the analysis to those ears which were the result of self-pollination it is found that when there is no correlation between aleurone color and endosperm texture all the ears have some spotted seeds, and conversely (if two ears having only slightly more than one percent of the seeds spotted are disregarded) when there is a correlation, none of the ears has spotted seeds. The distribution is then as follows:

	Some seeds spotted	No seeds spotted
Aleurone color and endosperm texture correlated.....	0	8
Aleurone color and endosperm texture not correlated.....	7	0

The factor for color correlated with endosperm texture has been designated *C*; therefore, when an ear is secured with a correlation between aleurone color and endosperm texture, the parents must have been heterozygous for the factor *C*, and if the ratio of colored to white seeds approximates 3 to 1, the parent must also have been homozygous for the factor *R*.

The above four-fold distribution establishes the fact that in the presence of a spotting factor, *S*, spotted seeds occur only when the factor uncorrelated with endosperm texture, *R*, is heterozygous. Since in these ears the factor *C* is homozygous, it remains to ascertain whether it is the homozygous *C* or the heterozygous *R* that determines the occurrence of spotting. This question is answered by the fact that spotted seeds are always found on ears with a dihybrid ratio of white to colored seeds. Since the parents of such ears were heterozygous for *C*, it follows that spotting is not dependent on *C* being heterozygous, and the alternative must be accepted, that spotting occurs only when the factor *R* is heterozygous.

A further refinement of this statement is necessary to account for spotted seeds on the two ears which were the result of crossing two plants, one genotypically constituted *CCRr*, the other *CcRR*. These ears were of course all colored but had 29.1 percent of the seeds spotted (table 2).

It is found that when the self-pollinated female parent produces some of the colored seeds spotted, and the male parent all the colored seeds self-colored, crossing these two will result in the production of an ear having some of the colored seeds spotted; but if this parentage is reversed

the female parent, when self-pollinated, producing all of the colored seeds self-colored, and the male parent producing some of the colored seeds spotted, a cross between them will have all the colored seeds self-colored. This harmonizes with the assumption that spotting can be detected only when the maternal parent is heterozygous for the factor R or homozygous for its allelomorph r . On this assumption the Chinese parent of the hybrids Dh417 and Dh418 must have been heterozygous for the factor R , and since both monohybrid and dihybrid ears were produced, all having correlations between aleurone color and endosperm texture, the genotypic composition must have been $ccRr_{ss}$, and the genotypic composition of the Algerian parent of these hybrids must have been $CCRRSS$.

The Chinese parent of Dh415 and Dh420 must have had the genotypic composition $Ccrr_{ss}$, the Algerian parent having the composition $CCRRSS$, since the progeny of these reciprocals had both monohybrid and dihybrid ratios, but the ears with a monohybrid ratio of white to colored had no correlation between aleurone color and endosperm texture. These ears were, therefore, homozygous for the factor C .

Since the hybrid Dh416 was not spotted and its progeny all had a monohybrid ratio of white to colored seeds, and since all of these ears had a correlation between aleurone color and endosperm texture, the Chinese parent must have been genotypically constituted $ccRR_{ss}$, and the Algerian parent must have been constituted $CCRRSS$, similar to the other Algerian plants. The progeny of this cross are all homozygous for the factor R ; no spotted are to be expected and none was observed.

The evidence therefore appears complete that spotted seeds occur only when the female parent is heterozygous for the factor uncorrelated with endosperm texture, this factor being designated R .

It is obvious from the genotypic composition necessary for the appearance of this type of spotted seeds that a strain having all of the colored seeds spotted can not be obtained, although it is possible to secure strains that will always have some of the colored seeds spotted.

Thus, spotting can be observed when the female gamete is of the class CrS , and the male gamete cRS , CRS , cRs , or CRs , or the female gamete of the class Crs and the male gamete either cRS or CRS , or the female gamete crS and the male gamete CRs or the female gamete crs and the male gamete CRS . A plant which will produce these gametic classes must be heterozygous for the factor R , and since this is true some of the female gametes will be of the class CRS . And though the zygote will be colored regardless of the composition of the male gamete, it will not be spotted.

Since in this type of spotting the zygotes are heterozygous for the factor R , no ears bearing all the seeds colored should be obtained from self-pollinating plants grown from spotted seeds, while if the spotted seeds were not heterozygous for the factor R , self-pollinating plants grown from spotted seeds, secured from ears with a ratio of 3 colored to 1 white, should give one third of the ears with all the seeds colored. At the present time 90 plants have been grown from spotted seeds of these hybrids, but none of the ears from these plants has had all of the colored seeds spotted or all of the seeds colored.

As a further test several plants grown from spotted seeds were crossed with a strain called " R tester" secured from R. A. EMERSON and all proved to be heterozygous for R . It is known that varieties of maize having all of the seeds minutely spotted are grown by the North American Indians. These varieties breed true for spotting, and it is hoped that by the end of another season it will be possible to determine the relationship of this type of spotting to that represented by the hybrids under discussion.

ASSOCIATION OF SPOTTING AND ALEURONE FACTORS

Having satisfied ourselves that spotting appears only when the female parent is heterozygous for the factor for aleurone color, R , attention may be turned to the rather unusual percentage of spotted seeds. The percentage of colored seeds that are spotted prevents any very simple explanation on the basis of multiple factors.

A satisfactory approximation of the observed percentage may be obtained by assuming a coupling or linkage between the factor for aleurone color, R , and a dominant spotting factor, S .

The best fit is secured by assuming the gametic ratio to be 7:1:1:7, the combination RS and rs being 7 times as numerous in the gametes as the combinations rS and Rs . This ratio may be the result of the two factors being located on the same chromosome and separated by 12.5 units, or the cells bearing the associated factors may divide or reduplicate 7 times as fast as the cells bearing the odd combinations.

On this assumption a plant which, when self-pollinated, produces an ear with a monohybrid ratio of white to colored seeds, with no correlation between aleurone color and endosperm texture, and having some spotted seeds, would be making the gametic classes shown in diagram 1.

Such a series will give 135 self-colored to 57 spotted seeds or 29.68 percent of the colored seeds spotted, which is a very close approximation to the observed percentage $29.4 \pm .30$.

	7 CRS	1 CRs	1 CrS	7 Crs
7 CRS	Self	Self	Self	Self
1 CRs	Self	Self	Self	Self
1 CrS	Spot	Spot	White	White
7 Crs	Spot	Self	White	White

DIAGRAM 1.

Continuing with the assumption that the factor for color, *R*, and the factor for spotting, *S*, are correlated in the gametes in a ratio of 7:1:1:7, self-pollinating a plant heterozygous for both color factors, *C* and *R*, as well as the spotting factor, *S*, would give an ear with the following zygotic classes (Diagram 2):

	7 CRS	1 CRs	1 CrS	7 Crs	7 cRS	1 cRs	1 crS	7 crs
7 CRS	⁴⁹ Self	⁷ Self	⁷ Self	⁴⁹ Self	⁴⁹ Self	⁷ Self	⁷ Self	⁴⁹ Self
1 CRs	⁷ Self	¹ Self	¹ Self	⁷ Self	⁷ Self	¹ Self	¹ Self	⁷ Self
1 CrS	⁷ Spot	¹ Spot	¹ White	⁷ White	⁷ Spot	¹ Spot	¹ White	⁷ White
7 Crs	⁴⁹ Spot	⁷ Self	⁷ White	⁴⁹ White	⁴⁹ Spot	⁷ Self	⁷ White	⁴⁹ White
7 cRS	⁴⁹ Self	⁷ Self	⁷ Self	⁴⁹ Self	⁴⁹ White	⁷ White	⁷ White	⁴⁹ White
1 cRs	⁷ Self	¹ Self	¹ Self	⁷ Self	⁷ White	¹ White	¹ White	⁷ White
1 crS	⁷ Spot	¹ Spot	¹ White	⁷ White	⁷ White	¹ White	¹ White	⁷ White
7 crs	⁴⁹ Spot	⁷ Self	⁷ White	⁴⁹ White	⁴⁹ White	⁷ White	⁷ White	⁴⁹ White

DIAGRAM 2.

The ratio of self-colored to spotted seeds is 405 to 171, the same ratio as in the monohybrid ears and in accord with the observed ratios. From this evidence it would not seem unreasonable to assume that the spotting

on these seeds is due to a dominant partial-inhibiting factor which is linked or coupled with the factor for color, *R*, in a ratio closely approximating 7:1:1:7.

For the two ears with all seeds colored obtained by crossing two first-generation plants, both of which when self-pollinated produce ears with a monohybrid ratio of white to colored seeds, the percentage of spotted seeds should be reduced from 29.68 to 28.1.

These two ears are represented in figures 2 and 3.

FIGURE 2.—Showing the relationship of ear 2254 which had all the seeds colored. The female parent of this ear when used as the male parent of 2256 produced 19.3 percent of the colored seeds spotted and produced no spotted seeds when used as the male parent of ear number 2305. The coefficients of association indicated on the ears 2256 and 2305 refer to the correlation between endosperm texture and aleurone color.

It is seen from this diagram that the male parent was making gametes *CRS*, *CRs*, *cRS*, *cRs*, and the female parent *CRS*, *CRs*, *CrS*, *Crs*. It is observed that no reduplication can occur in the gametes of the male parent between the factors *R* and *S*, as all of the gametes possess the factor *R*. In the female gametes, however, a 7:1:1:7 reduplication can be obtained. The gametic composition of the parents and the resulting zygotic classes are shown in diagram 3.

Were it not for the peculiar fact that spotting can appear only when the female gametes do not possess the factor *R*, the result of the gametic reduplication in the female gametes would not be apparent in the zygotes, and 37.5 percent of the seeds would be expected to be spotted.

FIGURE 3.—Showing the relationship of ear 2361, an all-colored ear, with 31.1 percent of the seeds spotted. This ear was borne on the same plant, which when self-pollinated produced ear 2360. This ear (2360) had approximately 25 percent of the seeds white. The coefficients of association indicated on the ears 2360, 2357 and 2356 refer to the correlation between endosperm texture and aleurone color.

♀	♂ CRS	CRs	cRS	cRs
7 CRS	7 Self	7 Self	7 Self	7 Self
I CRs	I Self	I Self	I Self	I Self
I CrS	I Spot	I Spot	I Spot	I Spot
7 Crs	7 Spot	7 Self	7 Spot	7 Self

DIAGRAM 3.

The present assumption, however, gives a ratio of 46 self-colored to 18 spotted, or 28.1 percent spotted. The observed percentage for the two ears was $29.1 \pm .82$. The numbers are not sufficient to discriminate between the percentages 29.1 and 28.1, but the facts do not violate the assumption and the observed percentage of spotted seeds is actually lower in the ears with all the seeds colored.

CONCLUSIONS

Reciprocal crosses between maize plants having white and colored seeds sometimes differ in the distribution of the aleurone color.

The seeds of some of the ears borne on white-seeded plants, if pollinated from colored plants, have the aleurone color distributed in numerous small spots, while the reciprocal crosses are self-colored.

The spotting is assumed to be due to a dominant spotting factor, *S*, which is in the nature of a partial inhibitor.

From the results of this investigation it would seem that the factor which causes spotting can operate only when the factor *R* is heterozygous and furthermore is not present in the female gamete but is introduced into the zygote by the male gamete.

As the male gamete contributes but one nucleus while the female gamete contributes two, the difference between reciprocals may be ascribed to the fact that the female parent contributes twice as much chromatin material as the male parent.

It would appear, therefore, that a single nucleus does not contain enough of the factor *R* to produce a self-colored seed in the presence of the dilution factor *S*.

The percentage of spotted seeds and the fact that spotted seeds are found only on those self-pollinated ears which have no correlation between aleurone color and endosperm texture, has led to the conclusion that there is a coupling or linkage between the factor for aleurone color, *R*, and the factor for spotting, *S*.

It is to be noted further that the gametic ratio in these hybrids is an approximation to a 7:1:1:7 series, equivalent to the location of the two factors on the same chromosome, 12.5 units apart.

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