PERICARP STUDIES IN MAIZE. II. THE ALLELOMORPHISM
OF A SERIES OF FACTORS FOR PERICARP COLOR¹

E. G. ANDERSON

National Research Fellow in Biology, University of Michigan, Ann Arbor, Michigan

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INTRODUCTION

The majority of the pericarp colors found in North American varieties of maize are due to the presence of an orange or brick-red pigment rather insoluble in water. They differ from each other in the amount of pigment present and in its distribution. EMERSON (1911), studying several of these pericarp colors, found that they were not inherited independently; in fact they failed to give any recombinations. He interpreted his results on the basis of complete linkage (coupling and repulsion). The case has since been considered one of multiple allelomorphism of the *P* factor (ANDERSON and EMERSON 1923).

A survey of this series has been made to determine the extent of the series and also to see if any crossing over or recombination takes place between members of the series. The colors and color patterns belonging to this series are numerous and the intensity of color in each type varies with differences in stage of maturity and in rate of maturing. They have been grouped into relatively few classes according to the general color of the pericarp itself and of the cob.

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DESCRIPTIONS²

RR, red. Both pericarp and cob deep red.

OR, orange. Pericarp light red or orange; cob red or orange. This class includes several members differing in intensity of color.

WR, red-cob white. Pericarp white (colorless) in some varieties, pale orange in others; cob red. St. Charles White has colorless pericarp with red or light-red cob. Reid's Yellow Dent and Pride of the North sometimes have the basal part of the pericarp colored; ears with streaky coloration in the pericarp are frequent. Some other varieties show a pale orange color throughout the pericarp.

OW, light orange with white cob. Pericarp uniformly pale orange; cob white or pale. This class includes EMERSON's "Bronze Pop" (ANDERSON 1921) and "light brown" (EMERSON 1911), and HAYES's "Pattern" (HAYES 1917). These have not been used in the following tests because their heterozygous forms are so pale that their separation from white is difficult unless the plants are very well matured.

CW, white-cap. Pericarp red or orange at base and sides, gradually fading out to white at tip of grain; cob white. Northwestern Dent.

CR, Red-cob white-cap. Pericarp like the preceding; cob red.

WW, white. Pericarp and cob white (colorless).

VV, variegated. Variegated pericarp and cob. A series of types grading from almost entirely white to strongly variegated with red. They are highly mutable, throwing red, white and a series of light-, medium-, and strongly variegated types. This series has been described and figured by EMERSON (1914, 1917). Calico Dent.

MO, mosaic. Another series of mutable types resembling variegated in general appearance. Crown patch (at tip of grain) and cob light-colored or white. Mutable, throwing darker and lighter mosaics and white. Red occurs only rarely by mutation. This series has been described and figured by HAYES (1917). Brindle Flint.

DOMINANCE

In general, color in any portion of the pericarp or cob is dominant to white (colorless) and the deeper reds are dominant to the lighter ones. Dominance is, however, not complete. The less deeply-colored types (OR, OW, CR, CW), crossed with white, give F_1 hybrids lighter in color, but with the color distributed in the same pattern as in the colored parent.

² The symbols used in this paper refer to the color types or classes. In general, the first letter refers to the pericarp color, the second to the cob color. The factors responsible may be symbolized as allelomorphs of P by using the same letters as superscripts as P^{rr} P^{or} , P^{wr} P^{ow} , etc.

Red and variegated show but little reduction in color due to heterozygosis with white. In these types the amount of pigment is so great that a considerable decrease in quantity would have but little effect on the appearance.

When types showing color in different regions are crossed, both regions are colored in the hybrid. Thus, in the cross $WP \times VV$, the hybrid has a red cob and variegated pericarp. The hybrid $CW \times VV$ shows the CW pattern in light-red overlaid by deep-red variegation.

TESTS FOR ALLELOMORPHISM

The tests reported here were made by crossing two different types and out-crossing the hybrid with a white-pericarp strain. Independent inheritance should give four classes in equal numbers; the combination type (like the F_1), the two parental types, and white. Allelomorphism or complete linkage should give only two classes, the two parental types. Incomplete linkage should give mainly the two parental types, the cross-overs appearing as the combination type and white.

A small amount of error is expected due to accidental stray pollination. Such stray pollination may give plants resembling the pistillate parent but cannot give the alternative class. At most, the error should be only a very small fraction of one percent.

Most of the white-pericarp plants used in the out-crosses were derived from intercrosses of Sanford's White (flint), a medium-early white dent and two early pop-like strains from Doctor EMERSON's cultures.

Crosses between stable types

$WR \times CW$. Table 1 gives the results of tests for allelomorphism of the factors for red-cob white and white-cap. Only the two parental types were obtained. There were 1751 red-cob white plants, 1684 white-cap. This cross is not wholly satisfactory, since heterozygous CW is light-colored, making immature ears difficult to separate from white. No red-cobbed ears showed the CW pattern, whereas all well-matured white-cobbed ears showed this pattern distinctly.

$WR \times RR$. Similar tests involving red-cob white and red gave 1001 red-cob white, 993 red and 1 variegated. Occasional variegated ears are expected as mutations from red. This test does not give evidence on the combination class, due to the dominance of red. White ears would have been detected if present.

TABLE 1

Progeny of the hybrid WR×CW out-crossed to WW.

PEDIGREE NUMBERS	WR	CW
542	112	105
543	42	44
544	31	38
545	66	71
546	77	79
548	150	152
550	35	37
551	177	149
554	139	145
555	122	109
1702	179	158
1703	208	188
1704	117	118
1735	219	210
1767	77	81
Total	1751	1684

TABLE 2

Progeny of the hybrid WR×RR out-crossed to WW.

PEDIGREE NUMBERS	WR	RR	VV
533	155	170	..
534	134	125	..
535	21	22	..
536	70	78	..
537	146	122	..
538	130	114	..
539	150	158	1
1501	106	112	..
1502	89	92	..
Total	1001	993	1

CW×RR. In tests involving the white-cap and red types, 1149 plants were white-cap and 1227 were red. Many plants were immature, making white-cap difficult to distinguish from white. If cob color and pericarp color were due to separate but closely linked factors, crossovers would be detected in this test.

TABLE 3
Progeny of the hybrid CW×RR out-crossed to WW.

PEDIGREE NUMBERS	CW	RR
566	206	221
1503	85	83
1504	78	87
1505	50	52
1522	147	162
1523	95	131
1524	137	137
1525	148	172
1526	89	85
1527	114	97
Total	1149	1227

Crosses involving variegated

For tests involving variegated, red-cob white is of greatest value, as it is easily separated from the mutation products of variegated. Red-cob white-cap is second in value. In all tests with variegated a small number of reds and whites are expected by mutation.

WR×VV. Tests for allelomorphism of the factors for red-cob white and variegated have given 2374 red-cob white, 2246 variegated, 70 red

TABLE 4
Progeny of the hybrid WR×VV out-crossed to WW.

PEDIGREE NUMBER	WR	VV	RR	WW
454	243	229	25	1
501	192	179	12	1
502	152	154	1	..
503	270	263	..	1
579	146	167	5	1
1686	185	168	5	..
1691	107	104	..	..
508	186	193	5	..
509	157	124	1	3
510	92	76	3	..
512	76	51	1	1
513	133	126	7	3
514	62	56	2	1
515	120	117	1	1
1770	138	118	1	..
1772	115	121	1	2
Total	2374	2246	70	15

and 15 white (table 4). No combination-type ears (red-cob variegated) were obtained. The presence of white ears by mutation would prevent the detection of whites by crossing over if any such occurred.

OR×VV. For this test a medium-orange with red cob was used. When heterozygous the cob was red and the pericarp frequently very pale. There were obtained 773 red-cob light-orange ears, 712 variegated, 26 red and 4 white (table 5). Again no combination-type ears appeared. Tests with deep-orange were carried out with smaller numbers, but the difficulty of making separations makes the data of much less value.

TABLE 5
Progeny of the hybrid OR×VV out-crossed to WW.

PEDIGREE NUMBER	OR	VV	RR	WW
517	132	121	4	1
518	142	119	12	..
520	101	74	1	1
522	137	137	2	..
523	124	126	5	..
516	137	135	2	2
Total	773	712	26	4

CR×VV. Tests involving red-cob white-cap and variegated gave 714 CR, 683 VV and 14RR (table 6). In addition one combination-type (CR+VV) ear appeared, which may have been due to crossing over or to stray pollination, the F₁ having been used as pistillate parent. The seeds had been killed by freezing before maturity, so no progeny tests could be made.

TABLE 6
Progeny of the hybrid CR×VV out-crossed to WW.

PEDIGREE NUMBER	CR	VV	RR
1740*	92	97	1
1743	103	106	2
1746	113	109	5
1747	74	71	..
1751	120	111	3
1754	111	105	1
1760	101	84	2
Total	714	683	14

*Also one combination type (CR+VV).

CW×VV. Tests with white-cap proved unsatisfactory, due to immaturity and the paleness of the pericarp color in heterozygous white-cap ears. One ear was obtained which was apparently of the combination type, CW+VV. Like the one in the preceding test, it may have been due either to crossing over or to stray pollination, the F₁ having been used as pistillate parent. It also was frozen before maturity.

RR×VV. This test gave 1399 red, 1308 variegated and 2 white (table 7). The red class includes the red mutations from variegated. As neither recombination class could be separated from other types present, a small amount of crossing over would not have been detected.

TABLE 7
Progeny of the hybrid RR×VV out-crossed to WW.

PEDIGREE NUMBER	RR	VV	WW
567	98	87	..
568	79	81	..
1506	98	94	..
1507	46	41	..
1509	133	112	2
1510	131	112	..
1511	72	83	..
1512	54	58	..
1514	66	59	..
1516	120	104	..
1517	78	70	..
1518	92	86	..
1519	87	86	..
1520	119	109	..
1521	126	126	..
Total	1399	1308	2

Crosses involving mosaic

HAYES (1917) concluded from studies on mosaic pericarp color that mosaic, self-red, "pattern," and colorless form a series of allelomorphic types. Through the kindness of Professor HAYES, the writer has been enabled to compare both his mosaic and his self-red with other types. "Pattern" proved so light-colored in heterozygous combination with white, especially in immature ears, that no significant results were obtained with it. The self-red appears to be identical with reds obtained from other sources and has been used interchangeably with them. The results with mosaic are in accord with those obtained by HAYES, except

that crosses between mosaic and self-red have given self-red instead of intermediates when grown under field conditions at Ithaca, New York.

The data in the following tables show that mosaic is included in the same series as the other types presented in this paper. A few reds occur, which are presumably mutations from mosaic. Some of the light mutations from mosaic were nearly white, a few perhaps entirely white, so that white crossovers if present would not have been detected. Table 8 gives the results of tests for allelomorphism of red-cob white and mosaic. Table 9 gives similar data on tests of orange and mosaic. No combination-type ears were present in either lot. Table 10 gives the results of tests with white-cap and mosaic. These data are not very satisfactory, since

TABLE 8

Progeny of the hybrid WR×MO out-crossed to WW.

PEDIGREE NUMBER	WR	MO	RR
1551	116	119	..
1556	143	135	1
1562	138	144	..
1597	163	139	1
1601	23	26	..
1603	128	142	..
1607	159	170	..
1644	106	106	..
1648	129	125	1
1653	74	85	..
1658	118	120	..
1663	73	73	..
1668	139	124	..
Total	1509	1508	3

TABLE 9

Progeny of the hybrid OR×MO out-crossed to WW.

PEDIGREE NUMBER	OR	MO	RR
1581	48	45	..
1592	106	98	..
1593	62	49	..
1594	98	87	..
1638	128	106	..
1640	146	166	1
Total	588	551	1

the combination type is not easily detected except on well-matured ears. No combination-type ears were observed. Table 11 gives the results of tests with red and mosaic, giving, as expected, only red and mosaic ears.

TABLE 10
Progeny of the hybrids CW×MO out-crossed to WW.

PEDIGREE NUMBER	CW	MO	RR
1565	139	138	..
1569	70	53	1
1570	79	81	..
1572	124	131	..
1574	118	118	..
1579	30	25	..
1583	77	77	..
1584	63	47	..
1586	127	123	..
1588	148	149	..
1615	114	94	1
1617	40	45	..
1618	51	53	..
1621	60	55	..
1624	32	32	3
1626	99	109	..
1630	72	68	..
1633	154	132	..
1635	66	42	..
Total	1663	1572	5

TABLE 11
Progeny of the hybrid RR×MO out-crossed to WW.

PEDIGREE NUMBER	RR	MO
1531	29	35
1533	19	15
1534	81	54
1536	3	5
1537	32	52
1540	9	13
Total	173	174

ALLELOMORPHISM *versus* LINKAGE

The more obvious lines of evidence bearing on this question may be summarized as follows:

1. Data from the tests reported. No case of crossing over or recombination was found where the tests were critical and not subject to other interpretations. Two combination-type ears appeared which may have been due to crossing over or more probably to stray pollination. Unfortunately these exceptional ears could not be tested as they were frozen before reaching maturity. The evidence is strongly in favor of complete linkage or allelomorphism. The other genes in the same linkage group, those for tassel seed, brachytic culms and fine striping, give about one, thirty-seven, and thirty-five percent of crossing over, respectively, with genes for pericarp color (ANDERSON and EMERSON 1923).

2. New types such as might occur from crossing over have not been observed in progenies resulting from crosses of different pericarp types. The only new types found are those which are known to occur by mutation in the variegated and mosaic series. Red-cob variegated, such as is obtained in the F_1 of $WR \times VV$, has never bred true and no varieties of this type have been found.

The evidence here also favors allelomorphism or complete linkage. But the evidence does not contribute to the distinction between allelomorphism and complete linkage of non-allelomorphic genes. By allelomorphism is meant the actual homology of genes; by complete linkage, the failure of non-homologous genes to show crossing over.

3. New types occurring repeatedly in the variegated and mosaic series behave as allelomorphs of the genes from which they were derived. Crossing over is here out of the question, as the mutations may occur in any somatic cell. Synchronous mutation of a group of genes is far less probable than mutation of a single gene. This evidence is strongly in favor of allelomorphism as opposed to linkage, either complete or incomplete.

NUMBER OF ALLELOMORPHS AND THEIR ARRANGEMENT IN SERIES

The total number of distinct genes included in this allelomorphic series is much greater than the number of classes given on page 443. Most of the classes include several heritably different colors or color patterns. All red-cob types were included in the class WR if the pericarp was so light-colored when heterozygous with white, that it could not readily be separated from a standard red-cob white. All that were fully red in both homozygous and heterozygous condition were designated as red. All that were distinctly intermediate in pericarp color and either red or intermediate in cob color were classified as orange. Only strains which appeared to be free from pericarp color were classified as white. All white-

cob strains showing color in the pericarp were classified as OW if the color was uniformly distributed over the pericarp or as CW if the pericarp was white-capped. Only the type CR was represented by a single strain. No attempt was made to establish the allelomorphism of the different grades included in the same class. It was observed, however, that in general the type recovered from a cross resembled closely the parental type.

These allelomorphic genes can be arranged in several series. A series can be formed from the deepest red through orange and light-orange to white. A similar series can be formed from red through orange with red cob (included in OR) and red-cob with pale-orange pericarp (included in WR) to a red-cob white which has no color in its pericarp. The existence of different intensities of cob color in such red-cob white varieties as St. Charles White suggests a series grading from a deep-red cob to pure white. However, no data are available on this point. Several other series may also be formed, but no one simple series can be formed to include all types.

The variegated and mosaic classes are even more complex, and each can be separated into a series based on the amount of color in the pericarp or on the frequency of mutation. EMERSON (1913, 1917) has shown for variegated (VV) that a series of allelomorphs can be formed to include white, light-variegated, medium-variegated, dark-variegated and red. These divisions are arbitrary, for as many grades can be selected as one chooses to work with. HAYES (1917) has shown a somewhat similar series for mosaic. These mutable types are unique in that they can generate very quickly a complete graded series of allelomorphs.

Since the known varieties of maize are numerous and the pericarp and cob colors are capable of such diverse modifications, it is not surprising to find a very large number of allelomorphs. The varieties and strains as yet unknown or untested are even more numerous. Doubtless this series will be greatly enriched by future acquisitions.

SUMMARY

A large series of pericarp color types in maize has been shown to be allelomorphic or closely linked in inheritance.

The evidence is believed to be in favor of allelomorphism because:

1. Tests have given no clear evidence of crossing over.
2. In progenies of crosses of different pericarp types, parental types only have been observed to breed true.

3. Inherited somatic mutation is more easily interpreted as resulting from modifications of single genes.

An undetermined but large number of genes are involved in this series. Two series of highly mutable genes are included

The genes in this allelomorphic series can not be arranged in any simple graded series. Rather, they group themselves into several diverse series.

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