A SECOND RECESSIVE FACTOR FOR BROWN PERICARP IN MAIZE.*

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Seed of a strain of maize with a brown pericarp was obtained from eastern Ohio in 1922. Records of the existence of such corn in the Corn Belt go back some 50 or 75 years (Klippart 1860), it usually being referred to as "prehistoric" or by some term indicating that it was unusual. Seed having a similar brown pericarp was obtained in 1925 from a different variety of corn being grown in western Ohio. The determining factor for brown pericarp in this strain proved to be identical genetically with that in the strain obtained earlier from eastern Ohio.

Previously Reported Types of Brown Pericarp.

The genetics of two other types of brown pericarp in maize have been reported previously. The first and more complete study was made of the interaction of the *A a* factor pair either with the factor *P* or with the factors r^{ch} and *Pl*, as reported by Emerson (1921) and Anderson and Emerson (1923). The pericarp is pigmented when either the factor *P*, or the factors r^{ch} and *Pl* are present. With *A* and either *P*, or r^{ch} *Pl*, the pericarp is red or cherry, whereas with the homozygous recessive allelomorph *a*, the pericarp is brown or brownish. The pericarp pigment due to the *P* factor is insoluble in water, whereas the pigment developed due to the r^{ch} *Pl* factors is soluble in water, is an anthocyanin, and is similar to the anthocyanins conditioned in other parts of the plants by a system of interacting factors of which the pairs *A a*, *R r*, and *Pl pl*, are members.

Anderson (1925) has reported a factor for brown pericarp which is dominant to red, in corn from Ecuador. Unlike the *A a* factor pair which affects all pigments except green and yellow in all plant parts, this factor affects pigments in the pericarp only, so far as known.

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Genetic Relations of the New Brown Pericarp Factor.

The brown pericarp corn found in Ohio has been found to be distinct genetically from those previously reported, as shown in the following data from crossing experiments. The factor pair responsible accordingly has been designated *Bp bp*.

Interaction with the P p factor pair.

Several crosses were made between material homozygous for the new brown pericarp from Ohio and ordinary clear pericarp strains. All of the F_1 ears of this cross were red. The combined results from all the F_2 populations from such crosses are given in Table 1.

TABLE I.

Numbers of Ears with Red, Brown, and Clear Pericarp in F^2 Progenies from the Cross, Brown x Clear Pericarp, (*P bp* x *p Bp*).

	Red Pericarp	Brown Pericarp	Clear Pericarp
Observed frequencies..	199	67	88
Calculated frequencies on basis of 9:3:4 ratio.	199.12 ± 6.30	66.38 ± 4.95	88.50 ± 5.50
Deviation.....	.12	.62	.50

This clearly is a modified dihybrid ratio without linkage. The effect of the homozygous recessive factor for brown pericarp *bp bp* is to modify the pigment whose presence is determined by the *P* factor, from red to brown. Combining the red and brown classes in Table 1, there were 266 pigmented to 88 clear pericarp ears, obviously a 3 : 1 ratio. No pigment develops in the presence of homozygous recessive *p*, regardless of the condition of the *Bp bp* factor pair, hence the 3 : 1 ratio between the pigmented and non-pigmented ears.

The *P p* factors are members of an extensive series of multiple allelomorphs controlling the distribution and intensity of a water insoluble pigment in the pericarp and cob, (Emerson 1917, Hayes 1917, Anderson 1924 and Eyster 1925). One of this series determines variegation in pigmentation. A variegated brown ear was obtained from a selfed plant grown from an

open-pollinated brown seed. The plants grown from the seed of this ear produced mostly brown variegated ears and a few self-brown ears. A selfed plant from a related open-pollinated brown seed produced a red ear. The F_2 progeny from this ear consisted of 32 self-colored red, 10 variegated-red, and 9 self-colored brown ears, and 1 variegated-brown ear. Evidently the action of the *Bp bp* factor pair is the same with at least one additional member of this extensive *P p* series, modifying only the color and not the distribution of the pigment.

Relation to the A a factor pair.

The ears of this new brown type were indistinguishable phenotypically from the brown ears resulting from the interaction of homozygous recessive *a* with the *P* or r^{ch} *Pl* as noted

TABLE II.

NUMBERS OF EARS WITH RED, BROWN, AND CLEAR PERICARP, PRODUCED IN F^2 PROGENIES FROM CROSSES BETWEEN HOMOZYGOUS BROWN PERICARP AND RECESSIVE *a a* PLANTS (*P A bp* x *p a Bp*).

	Red Pericarp	Brown Pericarp	Clear Pericarp
Observed frequency...	365	286	230
Calculated frequency on basis of 27:21:16 ratio.....	371.67 ± 9.89	289.08 ± 9.40	220.25 ± 8.67
Deviation.....	6.67	3.08	9.75

above. The *A a* factor pair, however, influences pigments in other parts of the plant than the pericarp. When the production of brown is the result of segregation of the *A a* factor pair, seeds with red or blue aleurone, and plants that are purple, dilute purple, sun red or dilute sun red always produce ears with either red or clear pericarp, but never ears with brown pericarp. A cross between two plants homozygous for recessive *a* would result in seeds with colorless aleurone and in either brown or green plants in the F_1 generation. Plants of the new brown pericarp type were crossed repeatedly with *a*-tester and brown plants grown from seed obtained from Dr. R. A. Emerson of Cornell University. In every case the F_1 endosperm had colored aleurone or the F_1 plants were purple and the pericarp red,

establishing the fact that a factor other than the *A a* allelomorphs was responsible for the brown in the new material. Moreover, brown pericarp ears occurred on F_2 plants carrying anthocyanin pigment as well as on brown and on green plants. The F_2 populations from such tri-hybrid crosses produced ears with red, brown and clear pericarp, as shown in Table 2.

The 27 : 21 : 16 ratio is expected if the three factors *A*, *P*, and *Bp* are not linked, if the *A a* and the *Bp bp* factor pairs are complementary in their interaction with the *P* factor, and if ears of the constitution *P a bp* are brown. The fit between the observed and the calculated frequencies for this ratio is very good, the highest value for $\frac{\text{Dev.}}{\text{P. E.}}$ being only 1.12.

The plants homozygous for both *a* and *bp* in the F_2 populations from this cross constitute a new combination. The recessive condition of either factor alone is sufficient to condition brown pigment in the presence of dominant *P*. If different steps in the physiology of the development of the pigment were disrupted by the two factors it is conceivable that the whole process might fail to come to visible completion or might give an end result different from either red or brown in the double recessive. If the ears from *P a bp* plants had clear pericarps the expected ratio in Table 2 would be 27 red; 18 brown; 19 clear, with a calculated frequency of 371.67 ±9.89 red; 247.78 ±9.00 brown; 261.54 ±9.15 clear. This gives a poorer fit than before, the deviations of the calculated from the observed frequencies being increased from 0.33 times to 4.25 times the P. E. in the brown class, and from 1.12 times to 3.45 times the P. E. in the clear class, the two classes affected by this change. Apparently the effect of the combination of the two factors in the homozygous recessive condition is not different from the effect of either alone.

Linkage with the Wx wx factor pair.

Eight linkage groups have been recognized up to the present time in corn. The factor pair for waxy endosperm *Wx wx* is in Group I. Crosses were made between plants homozygous for brown pericarp and *wx wx* plants. The F_1 plants from this cross were backcrossed to *bp bp* plants. The plants segregating for the waxy factor in the resulting population were determined by testing the pollen of each plant with chloral-hydrate iodine.

The polysaccharide reserve of pollen grains bearing the *wx* factor stains red with iodine while the polysaccharide reserve of pollen grains bearing the *Wx* factor stains blue, (Demerec 1924, and Brink and MacGillivray 1924). The ears then were classified at harvest to obtain data on the segregation for the factor for brown pericarp. The distribution obtained in the classification of these backcross populations is given in Table 3.

TABLE III.

NUMBERS OF EARS WITH RED AND WITH BROWN PERICARP ON *Wx wx* AND *Wx* PLANTS FROM THE BACKCROSS $\frac{P\ Wx\ bp}{p\ wx\ Bp}$ x *P Wx bp*.

	EARS WITH	
	Red Pericarp	Brown Pericarp
Plants segregating for *Wx wx*.....	49	9
Plants homozygous for *Wx*.....	9	56

The 18 cross-overs in a total of 123 plants indicate a crossing-over percentage of 14.63 ±3.19 per cent.

SUMMARY.

The genetic relationships of a second recessive factor for brown pericarp in maize are reported.

The new factor, designated *bp*, is recessive to its normal allelomorph *Bp* for red, and is expressed only in interaction with the dominant *P* factor for pericarp color.

The factor *bp* is distinct from the *A a* factor pair and, although complementary with the *A a* factor pair in its behavior in interaction with large *P* factor, there is no interaction between *Bp bp* and *A a*.

The *Bp bp* factor pair is linked with the factor pair for waxy, *Wx wx*, with 14.63 ± 3.19 per cent crossing over, as determined from a back-cross population of 123 plants.

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