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R. A. Emerson
University of Nebraska-Lincoln

E. G. Anderson
California Institute of Technology

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THE *A* SERIES OF ALLELOMORPHS IN RELATION TO PIGMENTATION IN MAIZE[1]

R. A. EMERSON

Cornell University, Ithaca, New York

AND

E. G. ANDERSON

California Institute of Technology, Pasadena, California

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INTRODUCTION

The inheritance of anthocyanin, flavonol, and related pigments in maize is dependent upon a number of genetic factors. Descriptions of characters and their factorial interrelations have been presented in previous publications on aleurone color (EMERSON 1918), general plant color (EMERSON 1921), silk color (ANDERSON 1921), and pericarp color (ANDERSON and EMERSON 1923, ANDERSON 1924, MEYERS 1927). Some of the more important factorial relations are shown in table 1.

TABLE 1

Factorial relations of plant, aleurone, pericarp, and silk colors.

GENES	PLANT COLOR	ALEURONE COLOR WITH CRP_r	PERICARP COLOR WITH		SILK COLOR WITH Ps_m
			P*	r^{ch}†	
ABP_l	Purple	Purple	Red	Cherry	Salmon
AbP_l	Dilute purple	Purple	Red	Cherry	Salmon
ABp_l	Sun red	Purple	Red	White	Salmon
Abp_l	Dilute sun red	Purple	Red	White	Salmon
aBP_l	Brown	White	Brown	Brown	Green
abP_l	Green	White	Brown	Brown	Green
aBp_l	Green	White	Brown	White	Green
abp_l	Green	White	Brown	White	Green

* These pericarp colors are absent with homozygous p. Other allelomorphs of P give variegated red or brown P^{vv}, red or brown cob with white (colorless) pericarp P^{wr}, etc.

† The cherry-brown pericarp colors do not appear even in the presence of P_l with any combination of the allelomorphs of R lacking r^{ch}.

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Other genetic factors also affect these pigments. The recessive gene b_p gives brown pericarp instead of red but does not affect aleurone or plant color (MEYERS 1927). A recessive gene found by Doctor M. T. JENKINS resembles a in its effect on aleurone and plant color but apparently does not affect red pericarp color. The P_r p_r factor pair differentiates bluish purple from reddish color of anthocyanin, most noticeable in the aleurone. These genes are all independent of A.

The pigments involved in chocolate pericarp (ANDERSON and EMERSON 1931) and in brown midrib (JORGENSON 1931, BURNHAM and BRINK 1932) seem to be unrelated to the anthocyanin, flavonol, and pericarp pigments dealt with in this paper.

THE ALLELOMORPH A^b

The source of the allelomorph A^b was a maize with brown pericarp from Ecuador. This brown was found to be dominant to red pericarp and a note on its inheritance has been published (ANDERSON 1925). At that time tests of its relation to a had not been completed. Since then tests have been made showing the absence of any recombination between Aa and the gene for dominant brown pericarp. The data are summarized in table 2.

TABLE 2

Summary of data on the relation of dominant brown pericarp to the a factor.

FORMULA	*A*			*a*		
	BROWN	WHITE	RED	BROWN	WHITE	RED
$a\times$(brown$\times a$)	93	70	0	58	75	0
$a\times$($a\times$brown)	60	56	0	62	49	0
($a\times$brown)$\times a$	37	9	0	31	13	0
(brown$\times a$)$\times a$	12	6	0	11	9	0
Total	202	141	0	162	146	0
$a\times$(brown$\times a$)	294	..	0	279	..	0

The classification for A and a was made on aleurone color but was checked by plant color. The white pericarp in these cultures was due to the segregation of p, and may be disregarded since p is independent of a (shown by the data itself and by other records) and of the factor for brown pericarp (ANDERSON 1925). The total absence of red pericarp color on plants from seeds with colored aleurone shows that there is no recombination between brown pericarp color and the A factor. The gene for dominant brown pericarp is apparently an allelomorph of a and is designated by the symbol A^b.

Homozygous A^b C R seeds have colored aleurone. Reciprocal crosses with recessive a also give colored aleurone, not distinguishable from the corresponding crosses of A with a. Homozygous A^b and heterozygous A^b a with the various combinations of B and P_l give typical purple, dilute purple, sun-red, and dilute sun-red plants. Thus A^b appears to be identical with A in its effect on aleurone and plant colors.

From intercrosses of dominant brown pericarp with salmon silk red pericarp, backcrossed to salmon silk red pericarp plants, only three classes are obtained, as follows:

Brown pericarp green silks
Red pericarp green silks
Red pericarp salmon silks

Some of the brown pericarp plants when selfed give 25 percent of salmon silks; when crossed to salmon they give 50 percent of salmon. In these cultures all salmon silk plants have red pericarp, and all green silk plants have brown pericarp. These are homozygous s_m s_m, the salmon silk color being suppressed by A^b. This is to be expected if the salmon silk color is due to an extension of the red pericarp pigment into the silks. A small amount of brown pigment in the silks would be entirely masked by the chlorophyll and carotinoid pigments present.

Thus A^b may be described as the equivalent of the normal A in its effect on the anthocyanin pigmentation of the plant; but it converts the red pericarp pigment into a corresponding brown pigment. In the latter effect it is dominant to A.

A dominant brown pericarp similar to that discussed here has been isolated from maize (C. I. 501) collected by RICHEY and EMERSON at Huancayo, Peru, in 1924.

THE ALLELOMORPH a^p

Another dominant brown pericarp came from the maize collection made in 1924 by RICHEY and EMERSON. An ear with cherry pericarp and purple aleurone (C. I. 499–2) was obtained at Huancayo, Peru. An individual grown at Ithaca, New York in 1925 from seed of this ear had purple plant color (apparently A B P_l) but produced no ear. Pollen from this plant crossed onto an individual of an inbred strain of Onondaga White Dent, a type with dilute sun-red plant color and white pericarp, A b p_l p, produced an F_1 progeny of 25 purple plants with cherry pericarp (apparently A B P_l r^{ch}) and 28 sun-red plants (like A B p_l). But all plants of both color types had brown mosaic pericarp (in addition to cherry in case of $A\ B\ P_l$ plants) as if the genotype were $a\ P^{mo}$. Moreover, in F_2 and later generations of this cross, brown and green plants appeared as if the genotype were $a\ B\ P_l$ or $a\ b\ p_l$. When such green plants, however, were crossed with A-testers, $a\ C\ R$, the resulting aleurone color was pale purple rather than white as expected from $a\ a$ or strong purple as expected from $A\ a$ or $A^b\ a$.

Evidently the Peruvian plant used in this cross carried some gene like a with respect to plant color, like A^b with respect to pericarp color, and intermediate between A or A^b and a with respect to aleurone color. A gene a^p allelomorphic to A, A^b and a with characteristics noted above provides a ready interpretation of all the results obtained with this material.

That P^{mo} was present in the original Peruvian plant is sufficiently indicated by the appearance of brown mosaic pericarp in F_1 of crosses with white pericarp, and only mosaic and white segregates in F_2. Crosses of brown mosaic with red self-colored pericarp gave brown self color in F_1 and brown and red self and brown and red mosaic in F_2.

Peruvian type green plants with brown pericarp a^pP crossed with green, white pericarp A-testers $a\ b\ p_l\ p$, and with brown plants with or without pericarp color, $a\ B\ P_l\ P$ or p, the F_1's being recrossed with $a\ C\ R\ p$ or with $A\ p$, gave the results summarized in table 3. These data show that $a\ C\ R\ p$

TABLE 3

Summary of data from ap and $aP \times a^pP$.

F_1 CROSSED WITH	ALEURONE COLOR			PLANT COLOR		PERICARP COLOR		
	STRONG PURPLE	PALE PURPLE	WHITE	RED OR PURPLE	GREEN OR BROWN	BROWN	RED	WHITE
$aCRp$	..	883	..	..	74	39	..	35
$aCRp$	..	..	892	..	79	47	..	32
Ap	121	..	..	121	..	41	30	50
Ap	282	..	..	282	..	125	157	..

$\times(a\ p \times$green plant brown pericarp) gave approximately equal numbers of pale purple and of white and no strong purple aleurone, and that both aleurone color types produced only green plants with approximately equal numbers of brown and of white and no red pericarp. Also $A\ p \times (a\ p$ $\times$green plant brown pericarp) gave only strong purple aleurone, only red plants and approximately equal numbers of brown and red pericarp. These results indicate the independence of brown and P and show no recombination of brown and a.

Green plants with brown pericarp of the Peruvian stock, a^p P crossed with A p and A P gave the results shown in table 4. As shown in this table, selfed F_1's gave approximately the expected frequency of strong purple and pale purple but no white aleurone. The pale purple seeds produced only green plants with brown (or brown and white) pericarp while the strong purple seeds gave only red plants some with brown and some with red pericarp (and some white when P p). The F_1's$\times a$ C R p gave some strong purple aleurone, red plants, and red or white pericarp, and about an equal number of pale purple aleurone, green plants, and brown or white pericarp. These results establish the independence of brown and P and the allelomorphism of brown and A.

TABLE 4

Summary of data from $A p$ and $AP\times a^pP$.

F_1	ALEURONE COLOR		PLANT COLOR		PERICARP COLOR		
	STRONG PURPLE	PALE PURPLE	RED	GREEN	BROWN	RED	WHITE
Selfed	76	..	76	..	28	15	..
	..	28	..	28	10	0	..
Selfed	161	..	161	..	42	18	23
	..	36	..	36	17	0	7
$\times aCRp$	1816	..	272	..	0	107	143
	..	1787	..	267	112	0	127

The relation of a^p to salmon silk colors, P s_m, has not been determined. Its relation to the cherry-brown pericarp colors is apparently the same as that of a. Some of the plants of the cross of the original Peruvian plant, a^p B P_l P^{mo} R, with Onondaga White Dent, A b p_l p r^{ch}, were purple and the pericarp of all these was brown mosaic on a background of cherry. This indicates that a^p either has the same effect as A or is recessive to it as regards cherry pericarp. A reddish brown plant, a^p B P_l, which appeared in a later generation of this cross, crossed with a purple plant having cherry pericarp and known to be A a B P_l r^{ch}, produced a small F_1 culture consisting of purple and of reddish brown plants. All the purple plants had cherry pericarp, A a^p B P_l r^{ch}, and the brown plants had brown pericarp, a^p a B P_l r^{ch}. It is certain, therefore, that, with P_l and r^{ch}, A a^p gives cherry and a^p a gives brown pericarp. Since the allelomorphs A and a are related to cherry brown pericarp colors exactly as they are to plant colors, A giving purple plants and cherry pericarp and a a green or brown plants and brown pericarp and since a^p a^p gives green or brown plants, it is presumable that it would also give brown pericarp with P_l r^{ch}.

The allelomorph a^p resembles A^b only in its effect on the pericarp pigment. Like A^b it produces brown pericarp color and is dominant to the red pericarp color produced by A. With C and R it gives a pale purple aleurone color instead of the deep color of A and A^b or the absence of color with a. In its effect on plant color it resembles the recessive a except that the brown color in combination with B and P_l is a reddish brown.

DOMINANCE

These four allelomorphs of A do not form a simple series in their dominance relationships. The sequences from dominant to recessive are as follows:

For aleurone color with C and R

A and A^b	strong purple
a^p	pale purple
a	colorless

For plant color with B and P_l

A and A^b	purple
a^p	reddish brown
a	brown

For pericarp color

A^b and a^p	brown (dominant)
A	red
a	brown (recessive).

The interactions of the several allelomorphs of A with various other aleurone, plant, pericarp and silk color genes are summarized in table 5. Combinations which have not been tested directly are given in parentheses.

SUMMARY

Two new allelomorphs of the A factor for aleurone, plant and pericarp color are described.

A^b resembles the normal A in its effect on the anthocyanin pigmentation of the plant; but it converts the red pericarp pigment into a corresponding brown pigment. It is dominant to A in this respect.

The allelomorph a^p resembles A^b in its dominant effect on pericarp color. But it gives pale aleurone color with C and R and it is almost like the recessive a in its effect on plant color.

Table 5 gives a summary of the effects of these four allelomorphs in combination with the factors C, R, B, P_l, P, and s_m.

TABLE 5

Relations of the A allelomorphs to aleurone, plant, pericarp and silk color.

ALLELOMORPHS OF A	ALEURONE COLOR WITH CRP_r	PLANT COLOR		PERICARP COLOR		SILK COLOR WITH Ps_m
		WITH BPl	WITH Bpl	WITH Pl_r^{ch}	WITH P	
AA	Strong purple	Purple	Sun red	Cherry	Red	Salmon
Aa	Strong purple	Purple	Sun red	Cherry	Red	Salmon
AA^b	Strong purple	Purple	Sun red	(Cherry)	Brown	Green
Aa^p	Strong purple	Purple	Sun red	Cherry	Brown	(Green)
A^bA^b	Strong purple	Purple	Sun red	(Cherry)	Brown	Green
A^ba^p	(Strong purple)	(Purple)	(Sun red)	(Cherry)	(Brown)	(Green?)
A^ba	Strong purple	Purple	Sun red	(Cherry)	Brown	(Green?)
a^pa^p	Pale	Reddish brown	Green	Brown	Brown	(Green?)
a^pa	Pale purple	Reddish brown	Green	Brown	Brown	(Green?)
aa	White	Brown	Green	Brown	Brown	Green

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