GENETICAL STUDIES ON RICE PLANT, XXVI

Mode of Inheritance and Causal Genes for One Type of Anthocyanin Color Character in Foreign Rice Varieties[1)]

By

Seijin NAGAO, Man-emon TAKAHASHI and Toshiro KINOSHITA

Plant Breeding Institute, Faculty of Agriculture
Hokkaido University, Sapporo, Japan

Introduction

This is one of a series of reports on genic analysis of characters in foreign rice varieties based on a study of crosses with testers from Japanese varieties of which genic constitutions had been explored by the writers. In this paper are presented and discussed crossing works with a particular color character which is carried by two varieties introduced from the Philippines. These two varieties are characterized with purple leaves and purple pericarps, of which detailed color expressions are as mentioned in the following section.

According to the writers genic scheme previously reported, the occurrence of anthocyanin color in rice depends on the complementary effect of genes *C* and *A*; *C* is the basic gene for the production of chromogen, and *A* exerts its activation effect on *C* and turns the chromogen into anthocyanin. *C* and *A* comprises multiple allelic series of genes; five alleles have been found at *C*-locus and three at *A*-locus. They are arranged in the rank of dominancy as follows;

$$C^{B} > C^{Bp} > C^{Bt} > C^{Br} > C^{+} \quad \text{and} \quad A > A^{a} > A^{+}\ ^{2)}$$

1) Contribution from the Plant Breeding Institute, Faculty of Agriculture, Hokkaido University, Sapporo, Japan.

2) In the present paper the writers use the new gene symbols. They are based on the list of standard gene symbols and nomenclature which has been presented to the International Rice Commission Meeting on Rice Production and Protection held in Ceylon in 1959, through N. E. JODON of U.S.A., representing his co-workers in India and Japan, pending approval as "Recommended IRC Standard Symbols for Rice Genes." The gene which is designated as "A-A^{a}-A^{+}" in the present paper is the identical gene which the writers have designated as "Sp-Sp^{a}-Sp^{+}" in the previous papers, and a gene which is designated as P in the below is identical with A in the previous papers of the writers.

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The expression of anthocyanin color character of apiculus is essentially attributed to the complementary effect of *C* and *A*, however, with these genes alone, coloration is restricted and appears scatteringly at the apiculus. For distinct coloration in the apiculus it is necessary, in the presence of *C* and *A*, for another gene *P* to exist, which is concerned with spreading chromogenic substance over the entirety of the apiculus. The majority of varieties, as a matter of fact, however, possess *P* in common. It follows that principal color types on the apiculus color have been genetically explained as a result of a combination of any alleles of the *C* and *A* loci (NAGAO 1951, NAGAO & TAKAHASHI 1956, TAKAHASHI 1957).

With regard to the coloration in some parts other than apiculus, some distribution genes were proposed. The occurence and expression of color in these parts are closely related to the genic constitution of the apiculus color also; coloration occurs in these parts when the above distribution genes coexist with any gene combination at *C* and *A* loci. And in cases where the apiculus are colorless, no color develops in other part no matter whether these distribution genes are present or not. A gene *Pl* is estimated to be concerned with the color distribution over the entire surface of leaf blade, leaf sheath, collar, auricle, ligule, node, internode and also of pericarp when exposed to direct sun light. A gene *Pn* is responsible for the distribution of color in leaf apex, leaf margin and entire surface of node, collar, auricle and ligule. The most striking colored parts with *Pl* and *Pn* are the leaf blade and the node, respectively. The effect of *Pl* is diminished by the presence of a suppressor *I-Pl* that inhibits the coloration at the center of leaf blade (NAGAO & TAKAHASHI 1951-a, -b).

Before going further the writers wish to express their appreciation to Mr. Nelson E. JODON, Agronomist of U.S.D.A., Rice Experiment Station of Crowley, La., U.S.A., for giving one of the writers an opportunity to observe JODON's F_2 materials from which segregation modes furnished the writers with valuable information for discussing and advocating genic schemes on the color characters of their own materials dealt with in the present paper. Cost of the study was partly defrayed by a Grant in Aid for Fundamental Scientific Research from The Ministry of Education.

Materials and Methods

Two Philippine varieties of which color characters are the object of the present study are listed in Table 1, together with Japanese tester varieties used in the present cross experiment. As shown in the table and the figure, the expression of leaf color in these two varieties, E-44 and E-46, is similar to

TABLE 1. List of varieties and strains, and their color

stock No. / variety name		E-44 Pirurutong	E-46 Padi-palae beong	N-45
genes concerned	apiculus leaf & node pericarp			C^{Bp} A Pl
apiculus		purple	dark purple	purple
leaf	blade	purple color is confined to the tip and margins of the blade in seedling stage, but later the color slightly spreads down from the tip and also inside from the margins giving an appearance of scattered purple wash	same as in E-44	purple, all over the surface
	sheath	the entirety of innersurface is deeply colored, while outer-surface coloration is not so pronounced	same as in E-44, but in addition to this, dark purple lines are present in outer-surface	purple, all over the outer-surface
	ligule & auricle	purple; coloration is pronounced in auricle	same as in E-44	purple
	collar	purple streak on the sides	same as in E-44	purple, entire
stem	internode	dark purle, all over the inner and outer-surface	same as in E-44	purple, all over outer-surface exposed to direct sun light, but lighter than E-44 or E-46 in color intensity
	node	same as in collar	same as in E-44	purple, entire
pericarp		purple, all over the surface	same as in E-44	white, as far as it is enclosed with glumes

that of leaf color in such a genotypic plant as "C^{B} A Pl I-Pl" or "C^{Bp} A Pl I-Pl", where a suppressor I-Pl coexists with a purple-leaf gene Pl and basic color genes, C^{B} A or C^{Bp} A. These two color types, the "E-44 or E-46" type and the Japanese "suppressive" type, however, are distinctly different from each other in their color patterns on collars and stem nodes, and further in color intensity of internodes, also.

The majority of F_1 hybrids from crosses between these Philippine varieties and the Japanese tester varieties showed a high fertility of more than 90% in their seed setting, but in a few cases where E-44 and E-46 were combined

characters conducted in the present examination

A-13 Chabo	H-69	A-31 Fukoku	A-43 Hokkai-mochi	A-58 Kokushoku-to	A-5 Akamuro	H-75	H-28
C^B +	C^{Bp} +	++	++	C^B *A* *Pn*	C^{Br} *A* *Rc Rd*	C^{Br} + *Rc* +	+ A^d
white, but turns into brown (Tawny)	same as in A-13	white	white	dark purple	pink	white	white
green	green	green	green	purple wash in tip and margins	green	green	green
green	green	green	green	purple lines in outer-surface	green	green	green
white	white	white	white	purple	white	white	white
white	white	white	white	purple, entire	white	white	white
green	green	green	green	purple lining	green	green	green
green	green	green	green	purple, entire	green	green	green
white	white	white	white	white	red	reddish brown with red speckles	white

with some tester varieties of relatively late maturity the fertility of their F_1s was low and variable, ranging from 80% to 30%. These low precentages may principally be due to unfavorable photo-thermal conditions under which the F_1 plants were grown. In order to examine the mode of inheritance, the writers conducted observations of the populations and strains up to F_3 generation, however, in the present paper, because of its brevity, the greater part of the discussion will be offered on F_1 and F_2. The plants were cultured both in frame beds placed in a green house and in an ordinary paddy field outdoors.

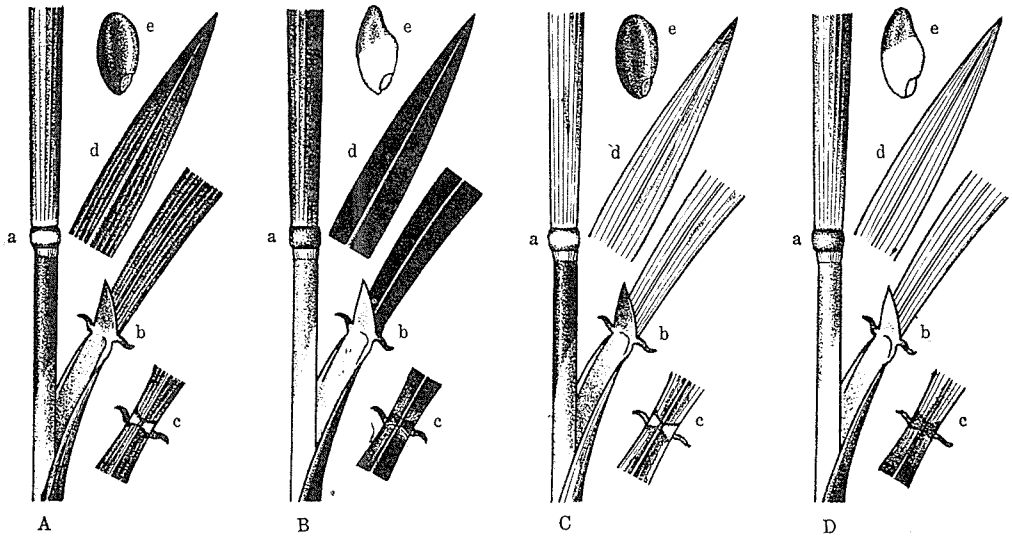

Fig. Expression of plant color due to *Pl*, Pl^W and their suppressors, in cooperation with basic genes C^{Bp} and *A*.

A. "Full purple type" obtained in segregants from crosses between the Philippine and the Japanese varieties. (C^{Bp} A^E Pl^W).

B. "Full purple type", so-called "Japanese purple rice." (C^{Bp} *A Pl*)

C. "Suppressive type" of the Philippine varieties examined. (C^{Bp} A^E $Pl^W I$–$Pl_{1\text{-}3}$)

D. "Suppressive type" in the "Japanese purple rice." (C^{Bp} *A Pl I*–*Pl*)

a: node, internode and leaf sheath. b: ligule, auricle and innersurface of leaf sheath. c: collar. d: leaf blade. e: pericarp.

Experimental Results

A. "White-tawny" × E–44, E–46

By the term "White-tawny" is meant a color type in which the apiculus is colorless at flowering but becomes brown or tawny in the ripening. This color type is considered to be due to an another effect of the potent chromogenic allele at the *C*-locus when this allele exists without the potent allele at the *A*-locus of activator (NAGAO 1951, TAKAHASHI 1957).

Three crosses, i) A–13 ($C^B A^+$) × E–44, ii) A–13 × E–46, and iii) H–69 ($C^{Bp} A^+$) × E–44, were made, and their F_1s, F_2s, and F_3s were produced. In i) and ii), F_1s are the same as E–46, in their color expression, and in iii) F_1 shows the same type of coloration as that of E–44, having no purple stripes in its outersurface of the leaf sheath.

These results give support to the view that, in the present crosses the apiculus color genes of the two varieties, E–44 and E–46, may possibly be

estimate as $C^{Bp}A$ and $C^{B}A$ respectively. It follows that the F_2s from these crosses should give segregation mode on their apiculus coloration as 3 purple vs. 1 white. In addition to this and with respect to purple stripes in the leaf sheath and the internode, which are considered to be the result of a pleiotropic effect of C^{B}, the most potent member of the *C*-locus, a cross of A-13×E-44 should give the following three color types in its F_2.[1] They are purple apiculus with purple striped sheath and internode, purple apiculus with no stripes of sheath and internode, and white apiculus with no stripes of sheath and internode. In this regard, the F_2 of this cross actually came up to the expectation, showing 9 : 3 : 4 segregation ratio (Table 2).

From the results in the Table 2, it is natural to say that, at least, a single distribution gene is responsible for the color expression of leaf blade since the segregation mode of blade coloration in the F_2 plants with colored apiculus is found to be 3 : 1 in ratio. In this table it is also pointed out that the majority of F_2 plants with colored leaves show the same type of coloration (color type Ib in the table) as that of their color leaved parent varieties, E-44 and E-46, but beside this, there appear F_2 plants with a new color type in which the entirety of the leaf blade is deeply colored with purple shade (color type Ia of the table). The type Ia is similar in appearance to the Japanese "purple rice" of which causal gene has been analyzed as *Pl* under the existance of $C^{B}A$ or $C^{Bp}A$. However, these two color types are different principally from each other in that the color in the new type almost fades out when plants mature, whereas the color in the Japanese purple rice does not show any noticeable change up to maturity. Regarding the segregation ratio between this new type (Ia) and parental type (Ib), it seems probable that F_2 ratios exhibit closely approximating 1 : 63 throughout the three crosses.

In addition to the above, correlations of colorations between leaf and other parts are worthy of note. As shown in the table, plants with colored leaves (type Ia and Ib) also have purple colors in their ligules, auricles, collars, nodes, internodes and pericarps, suggesting that the coloration in these parts is depend on a pleiotropic effect of a single distribution or localization gene or gene complex. Among them the most striking color expression is seen in the internode and the pericarp, though some variations in color intensities are recognizable. In this connection attention should be called to a fact that three quarters of the F_2 plants with white—which however turns into brown or tawny at ripening—apiculus also show brown ripening color in their internodes and pericarps, indicating that the same genic—distributing—effect as in the case of

1) C^{B} gives purple stripes in leaf sheath and internode when this gene coexists with *A* (NAGAO 1951, TAKAHASHI 1957).

TABLE 2. F_2 segregation of crosses between "White-tawny" and E-44 or E-46

phenotype			purple				white, but turns into Tawny at ripening		total	goodness of fit		
	apiculus		purple									
	internode		purple, entire		purple, striped	green	green but turns into Ty	green				
	node		purple		white	white	white	white				
	leaf blade		purple, entire	purple, partial	green	green	green	green				
	pericarp		purple	purple	white	white	reddish brown	white				
color type No.			*Ia*	*Ib*	*II*	III	IV	V		χ_2	d.f.	p
genotype	basic modifier suppressor for leaf color		$C^B(C^{Bp})A$ Pl^W triple recessive for I-Pl_1, I-Pl_2 and I-Pl_3	$C^B(C^{Bp})A$ Pl^W holds at least either one of dominant genes I-Pl_1, I-Pl_2 and IP-I_3	$C^B A$ + regardless of suppressors	$C^{Bp} A$ + do	$C^B(C^{Bp})$ + Pl^W do	$C^B(C^{Bp})$ + + do				
A-13 ($C^B A^+$) × E-44	paddy	O	2	295	77	30	106		510			
		C.R.	$36\times\frac{1}{64}$	$36\times\frac{63}{64}$	9	3	16					
		C	4.48	282.39	71.72	23.90	127.50		509.99	5.925	3	0.20~0.10
	green house	O	171		50		44	19	293			
		C.R.	36		12		12	4				
		C	164.81		54.94		54.94	18.31	293.00	2.736	3	0.50~0.30
H-69 ($C^{Bp}A^+$) × E-44	paddy	O	2	217		68	99		386			
		C.R.	$36\times\frac{1}{64}$	$2\times\frac{63}{64}$		3	4					
		C	4.39	213.73		72.38	96.50		386.00	0.346	2	0.90~0.80
	green house	O	45			24	19	12	100			
		C.R.	9			3	3	1				
		C	56.25			18.75	18.75	6.25	100.00	9.010	3	0.05~0.02
A-13 ($C^B A^+$) × E-46	paddy	O	5	223	83		89		400			
		C.R.	$9\times\frac{1}{64}$	$9\times\frac{63}{64}$	3		4					
		C	3.52	221.48	75.00		100.00		400.00	2.103	2	0.50~0.30

the anthocyanin coloration must exist in the case of the tawny coloration.

Considering the results of the examination presented in the table and the above descriptive notes, the following genic interpretation on the color characters of the two foreign varieties may be possibly considered.

As to genotypes of E-44 and E-46, regarding to basic—apiculus—genes for anthocyanin coloration, it is fairly certain that they possess such genes as C^{Bp} A and B^{B} A respectively. In addition to these genes, these two foreign varieties seem to have a single dominant gene of distribution or localization effect and three pairs of corresponding suppressors. This dominant gene, tentatively designated as Pl^{W}, gives its effect in leaf (leaf blade and leaf sheath), ligule, auricle, collar, node, internode and pericarp, giving appearance of full color in almost all of the said parts except in the middle portion of the collar and the node. In the actual color shade, this gene gives purple anthocyanin color in the said parts when it coexists with C^{B} A or C^{Bp} A, but when Pl^{W} coexists with C^{B} or C^{Bp} alone, viz. without A, it gives brown color in the said parts especially in the internode and the pericarp.

The three suppressors are multiple and only in the genotypic plants with the triple recessive suppressors the Pl^{W} can express its distribution effect in the respective parts, especially in the leaf blade. These three suppressors are designated as I-Pl_1, I-Pl_2 and I-Pl_3 respectively. As shown in Table 2, the observed results in the present cross combinations are in close accordance with the expectation based on these assumptions.

For further verification, however, 28 F_3 lines which were selected at random, from the F_2 of A-13 × E-44 were cultured. As regards the trigenic inheritance on C, A and Pl^{W}, in this cross, 27 genotypes in F_2, which is followed by 18 segregation types in F_3, should be expected. In the actual examination of the F_3, 14 segregation types out of 18 have appeared, showing the high propriety of the above genic interpretation (Table 3). And in reference with the effects of the suppressors, I-Pl_1, I-Pl_2 and I-Pl_3, the examined F_3 lines from F_2 plants with Ia-color type show no segregation with regard to the suppressors, and the segregation is limitted with A and Pl^{W}, indicating that this color type, Ia, resulted in such a genic constitution as triple recessive combination of the suppressors.

B. "White-straw white" × E-44

The term "white-straw white" represents a color type in which apiculus is colorless throughout the growing period, and no anthocyanin nor tawny colorations are expressed in any parts of the plant body, as a result of the absence of high potent allele at C-locus (NAGAO 1951, TAKAHASHI 1957).

TABLE 3. Segregation types of pedigree in F_3 progenies from the cross, A-13×E-44, mentioned in Table 2

F_2 genotype	F_3 gegregation observed						estimated genotype in F_2								estimated ratio in F_3				
	Ia	Ib	II	III	IV	V	C^B	C^B	C^{Bp}	C^{Bp}	A	A	Pl^W	Pl^W	I-Pl_1, I-Pl_2, I-Pl_3	I	II	III	IV	V
Ia	12		2				C^B	C^B			A	A	Pl^W	+	n. d. h.[1]	3	1			
	10		8			5	〃	〃			〃	+	〃	〃	do	9	3		3	1
	16		4			5	〃	〃			〃	〃	〃	〃	do	9	3		3	1
Ib		8					〃	〃			〃	A	〃	Pl^W	o. d. h.[2]	1				
	3	31			18		〃	〃			〃	+	〃	〃	n. d h.	3			1	
		9			1		〃	〃			〃	〃	〃	〃	o. d. h.	3			1	
		45	17				〃	〃			〃	A	〃	+	do	3	1			
		13	4				〃	〃			〃	〃	〃	〃	do	3	1			
		38	8				〃	〃			〃	〃	〃	〃	do	3	1			
		18		13					C^{Bp}	C^{Bp}	〃	〃	〃	〃	do	3		1		
	2	33	9		14	2	C^B	C^B			〃	+	〃	〃	n. d. h.	9	3		3	1
		14	4		4	3	〃	〃			〃	〃	〃	〃	o. d. h.	9	3		3	1
	2	30	5	2	7	5		〃	C^{Bp}		〃	〃	〃	〃	n. d. h.	36	9	3	12	4
		13	2	1	3			〃	〃		〃	〃	〃	〃	o. d. h.	36	9	3	12	4

II			54				C^B	"		"	A	+	"	1			
			32				"	"		"	"	"	"	1			
			38			16	"	"		"	+	"	"	3			1
			6			1	"	"		"	"	"	"	3			1
			4	3		7		"	C^{Bp}	"	"	"	"	9	3		4
			18	6		7		"	"	"	"	"	"	9	3		4
			28	6		10		"	"	"	"	"	"	9	3		4
III				42				"	C^{Bp}	"	A	"	"		1		
IV					9		any C-allele will do			+	+	Pl^W	Pl^W			1	
					7	5	do			"	"	"	+			3	1
					4	2	do			"	"	"	"			3	1
V						39	do			"	"	+	"				1
						27	do			"	"	"	"				1
						42	do			"	"	"	"				1

1) n. d. h.: no dominant homozygous.

2) o. d. h.: at least one pair of dominant homozygous.

Two testers, A-13 ($C^+ A^+ Pl^+$) and A-43 ($C^+ A^+ Pl^+$), of which color types are "White- straw white", were crossed with E-44, which was, in the preceeding section, estimated to be $C^{Bp} A\ Pl^W$ in its related genotype. F_1s from these two crosses show the same type of coloration as their colored parent E-44. And in F_2s, regards to apiculus colors, in addition to the parental types, purple and straw white, a "white-tawny" and a new type which shows an appearance of very faint red dots on the very tip of apiculus or on the bases of awnes appear (Table 4). The color of this new type fades out when plants begin to ripen, without any increase of color intensity due to ripening tawny color.[1] The segregation ratio is 9 purple : 3 faint red : 3 white-tawny : 1 white-white straw, indicating the existence of a digenic difference between the parental varieties.

Regarding the anthocyanin and the tawny coloration in leaf and stem, among F_2 populations of the present crosses, F_2 plants with purple or tawny apiculus, show the same type of color expression and of segregation mode as in the F_2s with purple or tawny apiculus colors in the preceeding cross, H-69 × E-44. This is as shown in the table and this indicates the existence of the three suppressors for leaf color in the present cross likewise. The F_2 plants with faint red or "white-straw white" apiculus, however, give no coloration in their leaves and stems.

As to the pericarp color, three types, purple, red and white are recognized, and the segregation mode is completely related to the apiculus coloration; that is to say, the plants with purple or faint red apiculus are assorted into purple and white in their pericarp colors, while the plants with tawny or "white-white straw" apiculus are assorted into reddish brown and white pericarp colors.

In discussing the genes appearing in the present crosses, the genic interpretation of the new color type, the faint red apiculus, must be considered at the beginning. The appearance of this type may not readily be explained under the above mentioned assumption that the parental varieties may have such genotypes of the apiculus coloration as $C^{Bp} A$ (E-44) and $C^+ A^+$ (A-13 and A-43), without adding some other genes or proposing new allele at the C and the A loci. In this respect, it must be pointed out that the F_1s of the present crosses show the same type of coloration in their apiculus as their parental variety E-44 and consequently it is impossible to presume that their colorless parents,

1) It has been reported by the writers that when high potent C-allele, such as C^B or C^{Bp}, coexists with less potent A-allele, such as A^a, only a fraction of the chromogenic substance produced by C can be utilized in the formation of anthocyanin pigment, and therefore a plant with $C^B A^a$ or $C^{Bp} A^a$ shows red or pink color in its apiculus instead of purple or reddish purple. The remaining quantity of unchanged chromogenic substance is turned into tawny pigment at ripening (NAGAO 1951, TAKAHASHI 1957).

TABLE 4. F_2 segregation of crosses between "White-straw white" and E-44

phenotype														goodness of fit		
	apiculus		purple			white, but turns into Tawny		faintly colored with anthocyanin		white		total			
	internode		purple, entire		green	green, but turns into brown	green	green		green			χ^2	d.f.	p
	node		purple		green	green		green		green					
	leaf blade		purple, entire	purple, partial	green	green		green		green					
	pericarp		purple	purple	white	reddish brown	white	purple	white	reddish brown	white				
color typd No.			I a	I b	II	IIIa	IIIb	IVa	IVb	Va	Vb				
genotype	basic		C^{Bp} A^{E}	C^{Bp} A^{E}	C^{Bp} A^{E}	C^{Bp}+	C^{Bp}+	C^{Bm} A^{E}	C^{Bm} A^{E}	C^{Bm}+	C^{Bm}+				
	modifier		Pl^{W}	Pl^{W}	+	Pl^{W}	+	Pl^{W}	+	Pl^{W}	+				
	suppressor		triple recessive for I-Pl_1, I-Pl_2 & I-Pl_3	holds at least one pair of the dominant suppressors	regardless of the suppressors	do	do	do	do	do	do				
A-43 ($C^{Bm}A^{+}$) × E-44	paddy	O	2	160	58	37	20	37	17	23	7	361			
		C.R.	$27\times\frac{1}{64}$	$27\times\frac{63}{64}$	9	9	3	9	3	3	1				0.10～
		C	2.38	149.91	50.77	50.77	16.92	50.77	16.92	16.92	5.64	361.00	12.186	7	0.05
E-44 × A-31 ($C^{Bm}A^{+}$)	paddy	O	1	129	48	29	15	50	13	21	8	314			
		C.R.	$27\times\frac{1}{64}$	$27\times\frac{63}{64}$	9	9	3	9	3	3	1				0.20～
		C	2.07	130.40	44.16	44.16	14.72	44.16	14.72	14.22	4.91	314.02	11.194	7	0.10

TABLE 5. Segregation types of pedigree in F_3 progenies from the cross A-43 × E-44 mentioned in Table 4

F_2 genotype	F_3 segregation observed						F_3 pericarp color			estimated genotype in F_2							estimated ratio in F_3				
	I a	I b	II	III	IV	V	purple	red	white	C^{Bp}	C^{Bp}	A	A	Pl^W	Pl^W	I-Pl_1, I-Pl_2, I-Pl_3	I	II	III	IV	V
I b		32		7			○	○		C^{Bp}	C^{Bp}	A^E	+	Pl^W	Pl^W	o. d. h.	3		1		
		35	11				○		○	〃	〃	〃	A^E	〃	+	do	3	1			
		17	6		11		○		○	〃	C^{Bm}	〃	〃	〃	〃	do	9	3		4	
		27	5	8			○	○	○	〃	C^{Bp}	〃	+	〃	〃	do	9		3	4	
	1	10		4	5	1	○			〃	C^{Bm}	〃	〃	〃	Pl^W	n. d. h.	9		3	3	1
	1	10		3	2	1	○	○		〃	〃	〃	〃	〃	〃	do	9		3	3	1
	1	28	9	6			○	○	○	〃	C^{Bp}	〃	〃	〃	+	do	9		3	4	
		16	10	5	2	3	○	○	○	〃	C^{Bm}	〃	+	〃	〃	o. d. h.	27	9	12	12	4
	2	9	4	6	4	4	○	○	○	〃	〃	〃	〃	〃	〃	n. d. h.	27	9	12	12	4
		17	1	3	2	4	○	○		〃	〃	〃	〃	〃	〃	o. d. h.	27	9	12	12	4
	1	23	11	3	11	3	○	○	○	〃	〃	〃	〃	〃	〃	n. d. h.	27	9	12	12	4
II			52						○	〃	C^{Bp}	〃	A^E	+	+			1			
			21	5					○	〃	〃	〃	+	〃	〃			3	1		
			8	3					○	〃	〃	〃	〃	〃	〃			3	1		
			27	5					○	〃	〃	〃	〃	〃	〃			3	1		
			22	7	3	3			○	〃	C^{Bm}	〃	〃	〃	〃			9	3	3	1

IIIa					38						„	C^{Bp}	+	„	unknown		1		
IIIb					28		13			○	„	C^{Bm}	„	„	+	+	3		1
					48		16				„	„	„	„	unknown		3		1
IVa						8		○			C^{Bm}	„	A^E	A^E	Pl^W	Pl^W		1	
						29		○		○	„	„	„	„	„	+		1	
						30					„	„	„	„	unknown			1	
						30		○	○	○	„	„	„	+	Pl^W	+		3	1
						19		○	○	○	„	„	„	„	„	„		3	1
						19		○	○		„	„	„	„	„	„		3	1
						30					„	„	„	„	unknown			3	1
						46		○	○		„	„	„	„	Pl^W	+		3	1
IVb						39					„	„	„	„	+	„		3	1
						8					„	„	„	„	„	„		3	1
Va							51				„	„	+	„	unknown				1
							49		○	○	„	„	„	„	Pl^W	+			1
							22		○	○	„	„	„	„	„	„			1
							22		○	○	„	„	„	„	„	„			1

A-31 and A-43, possess a dominant suppressor for apiculus coloration. Another assumption that the colorless parents may have an enhancer which exerts its effect on the color intensity of the apiculus when it coexists with *C* seems to be acceptable as far as the present crosses are concerned. However, this is inconsistant—the details are abridged here—with the previously estimated genic constitution of some colorless tester varieties, involving A-31 and A-43, when they are crossed with other varieties with colored apiculus (TAKAHASHI 1957).

Thus at present, it may be more natural to consider that the appearance of the new type may depend on the presence of another alleles at the *C* and *A* loci. They are temporarily designated as C^{Bm} and A^{E} respectively, and may be arranged as $C^{B}>C^{Bp}>C^{Bt}>C^{Br}>C^{Bm}>C^{+}$ and $A^{E}>A>A^{d}>A^{+}$ according to their dominancies. As to the action of C^{Bm} and A^{E}, C^{Bm} may be less potent than C^{Br} and give no sign of anthocyanin coloration in the apiculus even when coexisting with *A*. However, when C^{Bm} coexists with A^{E} the highest potent allele at the *A*-locus—also A^{E} is estimated to have more activation effect than *A*—a faint red color is produced in the apiculus. The basic genotypes of the parental varieties are considered to be $C^{B}A^{E}$ in E-46, $C^{Bp}A^{E}$ in E-44 and $C^{Bm}A^{+}$ in A-31 and A-43 instead of $C^{+}A^{+}$. The leaf color gene Pl^{W} is effective under the basic genotype of $C^{Bm}A^{E}$ and exerts its pleiotropic effect of localizing purple color into the pericarp. Pl^{W} is also effective when it coexists with C^{Bm} alone, viz. without A^{E}, and renders the pericarp brown.

In accordance with these interpretations and with consideration to the mode of coloration in F_1s and F_2s, the theoretical ratios of F_2 segregations are as shown in Table 4, where the observed results are in fairly close accordance with the above scheme of genes.

For further verification of this scheme, 25 F_3 lines from F_2 plants of A-43 × E-44 were cultured, and 8 F_3 lines from F_2s of E-44 × A-31 were added for examining segregation on color types. Including the phenotypic expression due to Pl^{W} and I-Pl_{1-3} the segregation types of the F_3 lines and their numerical relationships are presented in Table 5. The details of the results are omitted —however, as given in the table, in every instance more than half of segregation types expected in F_3 generation have appeared in spite of growing relatively few F_3 lines. With respect to leaf blade coloration it is noticed that some F_3 lines from the F_2 plants with Ib-color type (partially colored due to the coexistence of Pl^{W} and I-Pl_{1-3}) show three types of segregation ratios, 1 : 3, 1 : 15 and 1 : 63, regarding fully colored vs. partially colored. This indicates that in the partially colored type, at least three dominant suppressors exert their effect in addition to Pl^{W}, a gene for leaf color disribution.

C. "Purple leaf" × E-44

In order to investigate the possible genic inter-relationship between *Pl* and Pl^W, a purple leaved tester variety, N-45, of which genotype is C^{Bp} *A Pl*, was crossed with E-44 which is estimated to be C^{Bp} A^E Pl^W *I-*Pl_{1-3} or C^{Bp} A^E Pl^W *I-Pl* in its genotype refered to. Coloration in apiculus and leaf of the F_1 is the same as that of a plant of which genic constitution is C^{Bp} *A Pl I-Pl*, showing purple wash in the leaf blade. However, the pericarp color of the F_1 is purple and is different from that of the genotypic plants C^{Bp} *A Pl* and C^{Bp} *A Pl I-Pl*, in which pericarps are white so far as they are enclosed with floral glumes and unexposed to the direct sun light during their development.

In F_2, no segregation on the apiculus color is observed, giving purple apiculus in all plants. In connection with leaf and internode coloration, throughout whole F_2 seedlings, the leaf sheaths are distinctly colored and there appears some sign of color in the leaves, though noticeable variations in pattern and intensity of color existed. As a result of a close observation on the matured F_2 plants, however, two color types are distinguished, with respect to the coloration in the collar, node and internode. They are;

i) E-44 type ··· Color spreads along the entire surface of internode, but in collar and node coloration is restricted only to the both fringes (upper and lower margin) of these parts.

ii) N-45 type ··· The entire surface of internode, collar and node are colored, but color expression in the internode is not so intense when compared with the E-44 type.

These types can be further divided into two groups of leaf blade coloration. In one, the coloration is confined to the margin or is scatteringly located in the whole surface as purple wash, and in the second color type spreads over the entire leaf blade. On the whole therefore, four color types, which are presented in Table 6 under the name of color type I, II, III and IV, are distinguised. As shown in the table they segregate in the digenic scheme of 9 : 3 : 3 : 1. In this connection it may be worthy to note that there is an intimate correlation between pericarp color and leaf or stem colors, that is to say, no plant with white pericarp is given in the type III and IV, while in the type I and II, two kinds of plants, viz. with colored (purple) and colorless (white) pericarps, exist.

Considering the genic interpretation of the present cross, as already noted, E-44 was assumed to have the genotype of C^{Bp} A^E, in which color expression on the apiculus is similar to that of C^{Bp} A, even though three is a slight difference in color intensity between them. The difference may mostly be due to the differential activation effect of A and A^E to C^{Bp}. If these differences

TABLE 6. F_2 segregation of a cross between "Purple leaf" and E-44

phenotype	apiculus		purple						total	goodness of fit		
	internode		purple, entire				dark purple, entire					
	node		purple, entire				purple streak on the sides					
	leaf blade		purple, partial		purple, entire		purple, partial	purple, entire [1]		χ^2	d. f.	p
	pericarp		purple	white[2]	purple	white[2]	purple	purple				
color type No.			I a	I b	II a	II b	III	IV				
genotype	basic		$C^{Bp}A(A^E)$	$C^{Bp}A(A^E)$	$C^{Bp}A(A^E)$	$C^{Bp}A(A^E)$	$C^{Bp}A(A^E)$	$C^{Bp}A(A^E)$				
	modifier		$Pl\ Pl^W$	$Pl\ Pl^W$	$Pl\ Pl^W$	$Pl\ Pl$	$Pl^W\ Pl^W$	$Pl^W\ Pl^W$				
	suppressor		I-Pl_1	I-Pl_1	+	+	I-Pl_1	+				
N-45 ($C^{Bp}A\ Pl$) × E-44	paddy	O	73	26	27	18	31	10	185			
		C. R.	6	3	2	1	3	1				
		C	69.38	34.69	23.13	11.56	34.69	11.56	185.01	7.202	5	0.30～0.20
	paddy	O	161		55		63	17	296			
		C. R.	9		3		3	1				
		C	166.50		55.50		55.50	18.50	296.00	1.321	3	0.80～0.70

1) Purple color fades out at the later part of growing stage.

2) When pericarp is exposed to the sun, purple color appears on its surface.

are not included in the consideration and genotypes of the parental varieties in the present cross is considered to be the same, no noticeable segregation in apiculus color is observed in the F_2 of this cross.

As to the leaf color, no plant with colorless feaf is segregated. This indicates that the locus of Pl^w may be identical with that of Pl and therefore so-called "Pl-locus" consists of multiple allelomorphic series of genes, Pl^w, Pl and Pl^+. Through the mode of coloration on leaves and stems in the F_1 and the F_2 of this cross—and the others—the dominancy of these alleles is considered to be $Pl > Pl^w > Pl^+$. But in a case where emphasis is placed on the pericarp

TABLE 7. Segregation types of pedigree in F_3 progenies from the cross N-45 × E-44 mentioned in Table 6

F_2 phenotype	F_3 segregation observed				estimated genotype in F_2				estimated ratio in F_3			
	I	II	III	IV	*Pl*	*Pl*	*I-Pl*$_1$	*I-Pl*$_1$	I	II	III	IV
Ia	5		3		*Pl*	Pl^w	*I-Pl*$_1$	*I-Pl*$_1$	3		1	
	16		4		〃	〃	〃	〃	3		1	
	41		7		〃	〃	〃	〃	3		1	
	5		6		〃	〃	〃	〃	3		1	
	11	5	6	2	〃	〃	〃	+	9	3	3	1
	14	9	9	1	〃	〃	〃	〃	9	3	3	1
	22	5	16	4	〃	〃	〃	〃	9	3	3	1
	18	7	13	3	〃	〃	〃	〃	9	3	3	1
	54	4	24	2	〃	〃	〃	〃	9	3	3	1
Ib	17	6			〃	*Pl*	〃	〃	3	1		
IIa		40		10	〃	Pl^w	+	〃		3		1
		21		4	〃	〃	〃	〃		3		1
		46		15	〃	〃	〃	〃		3		1
		41		9	〃	〃	〃	〃		3		1
IIb		36			〃	*Pl*	〃	〃		1		
		17			〃	〃	〃	〃		1		
		13			〃	〃	〃	〃		1		
III			32	15	Pl^w	Pl^w	*I-Pl*$_1$	〃			3	1
			31	7	〃	〃	〃	〃			3	1
			29	11	〃	〃	〃	〃			3	1
IV				43	〃	〃	+	〃				1
				54	〃	〃	〃	〃				1

color by *Pl* and Pl^W, another order of $Pl^W > Pl > Pl^+$ is also possible. Leaf blades of the F_1 plants show an appearance of somewhat deppressed coloration, and thus it is probable that a suppressor from E-44 may, at the same time, extend its suppression effect on the *Pl* from N-45. In the present cross, therefore, it is possible to consider that genic constitutions of both parents are *Pl* $I\text{-}Pl_1^+$ $I\text{-}Pl_2^+$ $I\text{-}Pl_3^+$ (N-45) and Pl^W $I\text{-}Pl_1$ $I\text{-}Pl_2^+$ $I\text{-}Pl_3^+$ (E-44) respectively.

The reasonableness of these interpretations is readily comprehensible through Table 6, however, for further confirmation, 22 F_2 plants were selected, at random, for pedigree culture and segregation modes of their F_3 lines were examined. The results are presented in Table 7. In this table, F_3 lines from the F_2 plants with two color types, the tyep II and IV, bred true regarding color expression of Pl^W, giving support to the above assumption that there exists a multiple allelic relationship between *Pl* and Pl^W. And further, in this examination, it is ascertained that one of $I\text{-}Pl_{1-3}$ extends its effect on *Pl* as well as on Pl^W. The problem whether one of these three suppressors is identical with the Japanese *I-Pl* previously reported by the writers or not is yet unsolved in the present cross examination.

D. "Purple node" × E-44

As mentioned in the introduction of the present paper, a gene *Pn* which is responsible for coloration node and collar extends its pleiotropic effect on leaf, and consequently *Pn* gives rise to purple wash in the tip and the margin of the leaf as a result of interaction between *Pn* and higher alleles at *C* and *A* loci. In order to ascertain the genetic interrelationship between *Pn* and Pl^W, E-44 was crossed with a tester A-58, which carries *Pn* together with basic genes, C^B and *A*.

The F_1 has dark purple apiculus (due to $C^B A$), purple striped leaf sheath (due to $C^B A$), fully colored purple node and collar (due to *Pn*), fully colored purple internode (due to Pl^W), and purple pericarp (due to Pl^W). In F_2, no segregation on the apiculus and leaf sheath colors are recognized, though, with respect to color intensity, two types which are expectd to appear as a result of differential effect between C^B (in A-58) and C^{Bp} (in E-44) may be distinguished. Coloration in internode, segregates into three types; fully colored (the same as in E-44), colored with purple stripes (the same as in A-58) and colorless. This segregation is reasonably explained on an assumption that Pl^W and C^B extend their pleiotropic effects on these parts.[1] As to coloration in leaf, four types have been observed. They are i) fully colored, ii) partially colored—scatteringly, iii) partially colored—confined to tip and margin, and iv)

1) Refer to the footnotes on page 25.

TABLE 8. F_2 segregation of a cross between "Purple node" and E-44

phenotype			apiculus	purple				total	goodness of fit		
			internode	purple, entire		pulple lining or green					
			node	purple		purple	green				
			leaf blade	purple, partial	purple, entire	purple wash, confined to margin	green		χ^2	d. f.	p
			pericarp	purple	purple	white	white				
color type No.				I	II	III	IV				
genotype			basic	$C^B(C^{Bp})\ A(A^E)$	$C^B(C^{Bp})\ A(A^E)$	$C^B(C^{Bp})\ A(A^E)$	$C^B(C^{Bp})\ A(A^E)$				
			modifier	$Pl^W Pn$, Pl^W+	$Pl^W Pn$, Pl^W+	+Pn	++				
			suppressor	I-Pl_1	+	I-Pl_1, +	I-Pl_1,+				
A-58 ($C^B A\ Pn$) × E-44	paddy	O		148	44	51	22	265			
		C. R.		$12\times\frac{3}{4}$	$12\times\frac{1}{4}$	3	1				
		C		149.06	49.69	49.69	16.56	265.00	2.478	3	0.50~0.30
	paddy	O		247	66	72	38	423			
		C. R.		$12\times\frac{3}{4}$	$12\times\frac{1}{4}$	3	1				
		C		237.94	79.31	79.31	26.44	423.00	8.310	3	0.05~0.02

colorless. Of these four types, i may be due to the presence of Pl^W, ii may be due to the co-existence with Pl^W and I–Pl_1, iii may be due to Pn, and iv may have resulted from the absence of Pl^W and Pn. Regarding the coloration in pericarp, purple pericarps are given only in plants with purple internodes which are assumed to be caused by a pleiotropic effect of Pl^W.

The expectation of the coloration mode based on the above mentioned genic scheme was in good accordance with the observation results given in Table 8. Here it is noteworthy that I–Pl_1 extends no suppression effect on the expression of the leaf color caused by Pn.

E. "Pink apiculus with red pericarp" × E–44

In examining color expression by Pl^W, when it co-existed with C^{Br} A— which, as a result of producing a small amout of the chromogen, gives rise to pink apiculus—E–44 was crossed with a tester A–5, of which genotype of the basic genes is C^{Br} A. F_1 shows the same coloration mode as E–44, with respect to colors in apiculus, leaf, stem and pericarp; and in F_2, six color types presented in Table 9 are distinguished. These segregation, except on pericarp color, are naturally explained as a result of independent assortment between C^B and C^{Br}, and, Pl^W and Pl^+, under the supposition that Pl^W may be able to express its effect on leaf and internode and turns color of the said parts into red, when this gene coexists with a less potent chromogen gene, such as C^{Br}, together with high potent activator, A.

As previously reported by the writers (NAGAO 1951), A–5 has a red pericarp of which causal genes are Rc Rd, and it is natural to expect, in the present cross, that, besides purple and white, another colors viz. red and/or brown pericarp, of which genotypes are Rc Rd and Rc Rd^+ respectively, will appear. As shown in the table, three types, purple, red and white, appeared in a ratio of 12 : 3 : 1, suggesting that two genes, Pl^W and Rc, cause this segregation and that A–5 and E–44 possess Rd in common. Here it is noteworthy that Pl^W causes purple pericarp, even if Pl^W coexists with less potent chromogenic allele C^{Br}.

As a whole, the constitutions of the involved genes in the present cross are estimated as, C^{Br} A Pl^+ Rc Rd in A–5 and C^{Bp} A^E Pl^W Rc^+ Rd in E–44.

F. "$C^{Br}A^+$" × E–44

As mentioned in the previous section of the present paper, Pl^W is estimated to have an effect of distributing brownish red color, which is a product of high potent chromogenic alleles C^B and C^{Bp}, into pericarp, when Pl^W coexists with them. Further, in the preceeding section it was estimated that Pl^W causes pericarp color purple, even if it coexists with such a basic gene combination

TABLE 9. F_2 segregation of a cross between "Pink apiculus with red pericarp" and E-44

phenotype			purple			pink			total	goodness of fit		
	apiculus		purple, entire	green		light red	green					
	internode		purple	green		nearly green	green					
	leaf blade		purple	red	white	nearly purple	red	white		χ^2	d. f.	p
	pericarp											
color type No.			I	II	III	IV	V	VI				
genotype	basic		$C^{Bp}A(A^E)$	$C^{Bp}A(A^E)$	$C^{Bp}A(A^E)$	$C^{Br}A(A^E)$	$C^{Br}A(A^E)$	$C^{Br}A(A^E)$				
	modifier		Pl^W	+	+	Pl^W	+	+				
	pericarp color gene		$Rc\,Rd$,+Rd	$Rc\,Rd$	+Rd	$Rc\,Rd$,+Rd	$Rc\,Rd$	+Rd				
A-5 ($C^{Br}A\,Rc\,Rd$) × E-44	paddy	O	64	26	8	27	5	2	132			
		C.R.	36	9	3	12	3	1				
		C	74.25	18.56	6.19	24.75	6.19	2.06	132.00	5.320	4	0.30~0.20

as $C^{Br}A$, which gives rise to pink apiculus color. It is, however not yet ascertained whether this kind of effect of Pl^{W} holds true in a case where Pl^{W} coexists with $C^{Br}A^{+}$, the genotype for light tawny apiculus color, and turns pericarp color into brown, or not. In order to clarify this point, a cross was made between E-44 and H-75, which has the genotype of $C^{Br}A^{+}RcRd^{+}$ and shows light tawny apiculus and brown (exactly speckled with red color) pericarp.

F_1 has purple apiculus and purple pericarp, which are the expected coloration from the coexistence of genes, C^{Bp}, A^{E}, and Pl^{W}. In F_2, apiculus colorations are assorted into four types, purple ($C^{Bp}A^{E}$), pink ($C^{Br}A^{E}$), white-tawny ($C^{Bp}A^{+}$) and white-light tawny ($C^{Br}A^{+}$), as expected apriori (Table 10). As to pericarp color, four types as purple, red, brown and white appear in an approximate ratio of 36 : 21 : 3 : 4 (in total 254 plants. p=0.2–0.1). Here it can be pointed out that all the plants which are suppossed to have $Pl^{W}A^{E}$ show purple color in their pericarps irrespective of color intensities in their apiculus, and that all the plants which have $Pl^{W}A^{+}$—viz. Pl^{W} alone—show red color in their pericarps without exception.

This follows that the expression of pericarp color in the present cross is said to be governed by the genes presented in the following diagram and that Pl^{W} exerts its effect and turns pericarp into red even if a coexisting chromogenic gene is less in its potency for producing the tawny color in the apiculus.

Basic genes		Distribution gene		Proper genes for pericarp color	Phenotypic expression in pericarp
3	($C^{Bp}A^{E}$, $C^{Br}A^{E}$) ···	3 (Pl^{W})·····	16	(*Rc Rd*, *Rc*+, +*Rd*, ++)·····	144 purple
		1 (+) ·····	9	(*Rc Rd*)·····	27 red
			3	(*Rc* +) ·····	9 brown
			4	(+ *Rd*. ++) ·····	12 white
1	(C^{Bp} +, C^{Br} +) ···	3 (Pl^{W})·····	16	(*Rc Rd*, *Rc*+, +*Rd*, ++)·····	48 red
		1 (+) ·····	9	(*Rc Rd*)·····	9 red
			3	(*Rc* +) ·····	3 brown
			4	(+ *Rd*, ++) ·····	4 white

Thus, on the whole, a segregation ratio of "purple : red : brown : white =144 : 84 : 12 : 16 (=36 : 21 : 3 : 4)" is given in this diagram.

G. Linkage

Since Pl^{W} is assumed to be one of the allele at the *Pl*-locus, it is natural to expect the existence of linkages between Pl^{W} and other genes which pertain to the "*Pl*-linkage group". In corroboration of the propriety of this expectation, a linkage test between Pl^{W} and *lg*, a gene which is responsible for liguleless

TABLE 10. F_2 segregation of a cross between colorless with a genotype of $C^{Br}A^+$ and E-44

phenotype	apiculus	purple		pink		white	total	goodness of fit		
	internode	purple, entire	green	light red	white	white				
	leaf blade	purple	green	nearly green	green	green		χ^2	d. f.	p
color type No.		I	II	III	IV	V				
genotype	basic	$C^{Bp}A^E$	$C^{Bp}A^E$	$C^{Br}A^E$	$C^{Br}A^E$	$C^{Bp}+$, $C^{Br}+$				
	modifier	Pl^W	+	Pl^W	+	Pl^W, +				
H-75 ($C^{Br}+$) × E-44	O	159	34	46	77		316			
	C. R.	27	9	9	19					
	C	133.31	44.44	44.44	93.81		316.00	10.469	3	0.02~0.01

TABLE 11. Linkage between Pl^W and lg, in a cross of H-28×E-44

character	apiculus	colored ($C^{Bp}A$, $C^{Bp}A^d$)		colored ($C^{Bp}A$, $C^{Bp}A^d$) colorless ($+A$, $+A^d$)		total	goodness of fit based on R.C.V. of 21.2%		
	internode	colored		colorless					
	ligule	normal	liguleless	normal	liguleless				
genes concerned		Pl^W +	Pl^W lg	+ +	+ lg		χ^2	d. f.	p
(3 : 1)×(9 : 7)	O	81	8	60	27	176			
(R.C.V.=21.2%)	C	86.49	16.68	45.51	27.32	176.00	9.483	3	0.05~0.02

Recombination value=21.2±3.41%.

character in leaf and is known to belong to this group, was demonstrated by the following cross.

A cross was made between two varieties, E-44 and H-28, of which concerning genotypes are C^{Bp} A^{E} Pl^{W} lg^{+} and C^{+} A^{d} Pl^{+} lg respectively. In F_2 of this cross, a linkage takes place between Pl^{W} and lg with a recombination value of 21.2% which is akin to the value previously obtained between Pl and lg (MORINAGA 1938, NAGAO & TAKAHASHI 1952). The numerical record is as shown in Table 11.

Considerations

A view that the basic expression of anthocyanin color in the rice plant is governed by two complementary genes is widely supported by many workers (NAGAO 1951, RAMIAH 1953, JODON 1955, etc.). These two genes are designated as C and A and they correspond to the chromogen base and activator, respectively (JODON 1959). As to the coloration in any part, including leaf, of the rice plant, it has been concluded that in addition to the basic genes there are other genes which are localizing the coloration in particular parts. And further it is also concluded that in addition to these, there are genes for diluting or deppressing the color and for producing various color patterns (cited in KAMATH 1956).

Regarding to leaf color, several segregation ratios of colored vs. colorless, such as 3 : 1, 9 : 7, 3 : 13, 15 : 1, 1 : 3, 7 : 57 and others, are reported by many workers (cited in JODON 1955 and KAMATH 1956). The ratios of 3 : 1, 9 : 7 and 27 : 37 are explained with the help of a localization gene interacting with the two basic genes C and A. The ratios of 1 : 3 and 3 : 13 have been shown to be due to the presence of the suppressor which inhibits the expression of leaf color governed by a localization or distribution gene. The 7 : 57 ratio is explained by the presence of two suppressors which inhibit the expression of color in the leaf.

In the present study the writers estimated the presence of three pairs of suppressors which inhibit the color expression in the leaf blade, and thus pointed out the possibility of the existence of an additional suppressor. At the Central Rice Research Institute of India, three types of colored leaf blade are reported, that is; dark purple, purple wash and faint purple wash. And the interrelationship of the genes controlling coloration in these leaf color types was studied, and the following genic schem was advocated (KAMATH 1956). The gene C and A are the basic for color production, while Lp is the localization gene, B is the basic gene for purple wash color and I-lp is a suppressor which is epistatic over C. Lp' is the gene present in faint purple, and Lp -Lp' -lp are

multiple alleles. *C* is epistatic over *B*. The constitution of the dark purple parent would, therefore, be *A b C Lp i-lp*, and that of purple wash *A B c Lp I-pl*, while that of faint purple wash would be *A B c LP' I-lp*, and that of green-blade parents either *a b c Lp I-lp* or *a b c Lp' I-lp* or *a b c lp I-lp*. In the writers' experiment, however, there is no need of advocating such a gene as *B* mentioned here, and all the segregations obtained are explained fairly well by the multiple alleles *Pl-Pl^{W}-Pl^{+}* and three suppressors, *I-Pl$_1$*, *I-Pl$_2$* and *I-Pl$_3$*, in conjunction with the basic genes, *C* and *A*. The problem of whether *Lp-Lp'-lp* and *Pl-Pl^{W}-Pl^{+}* are identical or not, or whether the previously reported suppressor *I-Pl* of the Japanese varieties corresponds to any one of the suppressors, *I-Pl$_1$*, *I-Pl$_2$* and *I-Pl$_3$*, or not, remains to be solved. The identification of each gene and its inter-relationship with others need to be intensively studied for a proper appreciation of the genetics of anthocyanin coloration.

In this connection, it may be worthy of note that one of the writers TAKAHASHI had an opportunity of observing Mr. JODON's F_2 materials from crosses among genetic stocks and varieties in the United States on which he continued his genetic works. Among these, the following three combinations gave the similar type of segregation mode to the writers' crosses described in the present paper. The cross combinations are;

Pl (a genetic stock with purple apiculus, leaf and pericarp)
× Hb (a genetic stock with colorless? apiculus, leaf and pericarp)
Scl (a genetic stock with purple apiculus, leaf and pericarp)
× Nato (U. S. variety with colorless? apiculus, leaf and pericarp)
Scl (do)
× Zenith (the same as Nato)

Their F_2 segregation modes, examined by Mr. JODON, are as shown in Table 12. On these results, he might possible make public his most appropriate genic scheme that encompasses all the data he obtained, however, results can also be explained to some extent by applying the writers' scheme under the supposition that the parental genetic stocks and varieties may gave such genic constitutions as; *C^{Bp} A^{E} Pl^{W} Pn* (Pl), *C^{B} A^{E} Pl^{W} Pn^{+}* (Scl), and *C^{Bm} A^{E} Pl^{+} Pn^{+}* (Hb, Nato and Zenith). Detailed accounts are omitted here, but for brief information the table may be of sufficient value.[1]

It is well known that in many crosses of rice plants there are segregations for the presence of anthocyanin color to its absence in a large number of organs,

1) In a plant with completely awnless apiculus no noticeable "faint-red" dots are recognized in its apiculus even though it has a potentiality of presenting "faint-red" color in its very tip of the apiculus and awns. In Table 12 segregants with the mark of ✻ are assumed to be this type of plant.

TABLE 12. Application of the writers' present scheme to the JODON's data obtained in F_2 from crosses between purple leaved and colorless varieties

a. Purple leaf ($C^{Bp}\,A^{E}\,Pl^{W}\,Pn$)×colorless ($C^{Bm}\,A^{E}$++)

phenotype	apiculus	purple				white or almost white		total	goodness of fit		
	internode	purple		green		green					
	leaf blade	purple		green[1)]	green	green					
	node	purple	purple streak on both sides	purple	purple	green					
	pericarp	purple	purple	white	white	purple	white				
possible genotype based on the writers' scheme	basic	$C^{Bp}\,A^{E}$	$C^{Bp}\,A^{E}$	$C^{Br}\,A^{E}$	$C^{Bp}\,A^{E}$	$C^{Bm}\,A^{E}$	$C^{Bm}A^{E}$				
	modifier	$Pl^{W}\,Pn$	Pl^{W} +	+ Pn	++	$Pl^{W}Pn$,Pl^{W}+	++				
Pl ($C^{Bp}A^{E}Pl^{W}Pn$) × Hb ($C^{Bm}A^{E}$++)	O	291	107	108	33	114 *	32 *	685			
	C. R.	27	9	9	3	12	4				
	C	288.98	96.33	96.33	32.11	128.44	42.81	685.00	6.989	5	0.30~0.20

1) Some of them are purple margined.

b. Cololess ($C^{Bm}A^E$+)×purple ($C^BA^EPl^W$)

phnotype	apiculus	purple		white		total	goodness of fit		
	internode	purple, entire	purple lining	green			χ^2	d. f.	p
	leaf blade	purple	green	green					
	pericarp	purple	white	purple	white				
possible genotype based on the writers' scheme	basic	$C^B A^E$	$C^B A^E$	$C^{Bm} A^E$	$C^{Bm} A^E$				
	modifier	Pl^W	+	Pl^W	+				
Nato ($C^{Bm}A^E$+) × Scl ($C^BA^EPl^W$)	O	199	79	71 *	34 *	383			
	C. R.	9	3	3	1				
	C	215.44	71.81	71.81	23.94	383.00	6.213	3	0.20～0.10
Zenith ($C^{Bm}A^E$+) × Scl ($C^BA^EPl^W$)	C	122 [1]	44	48	15	229			
	C. R.	9	3	3	1				
	O	128.81	42.94	42.94	14.31	229.00	1.017	3	0.80～0.70

1) A single plant with white pericarps made its appearance here.

as if a single gene is responsible for the expression of color in these various parts. In accordance to the association between the presence of color in the different parts, the question often arises whether this association is due to close linkage or pleiotropy. In the case where the gene Pl^W (and Pl) involved, the writers could not rule out the possibility of linkage playing its part, however, in so far as the present results indicate, it at any rate, is certain, that Pl^W (and Pl) has an pleiotropic effect for localizing color not only in the leaf but also in such parts as internode, node, collar, ligule, auricle and pericarp, since, throughout F_2s from all cross combinations, no decisive recombination class was present in the joint segregation with regard to coloration between leaf and any other parts mentioned above.

JODON (1955) considered it to be possible that the different gene systems are responsible for the expression of anthocyanin coloration in different varieties. And in this connection, it is worthy of note that in one of crosses between Japanese and Indian varieties, MIZUSHIMA and KONDO (1959, 1960) obtained an anomalous segregation mode which is followed by the suggestion that, as far as the *C*-locus is concerned, there may be a structural difference of chromosome, between the two varieties used. In the present examination of the writers, however, no valuable information is obtained in this matter.

Summary

1. Mode of inheritance and causal genes for one type of anthocyanin color character in the Philippine varieties were studied by crossing with Japanese testers.

2. This color type is characterized by the following color expression as; i) scatteringly colored leaf blade, ii) colored ligule, auricle and pericarp, iii) deeply and all over colored internode, iv) node and collar with colored streak on the sides.

3. Through the present study, the existence of single color distribution or localization gene, Pl^W, and its three suppressors, I-Pl_1, I-Pl_2 and I-Pl_3, are estimated. And further, the new alleles at the C and A loci are proposed.

4. Pl^W is responsible for the distribution of anthocyanin and/or its related tawny colors, which are the product of $C\,A$ and $C\,A^+$ respectively, into leaf (in its entirety), internode (in its entirety), node (on the sides), collar (on the sides) and pericarp (in its entirety, but a higher accumulation is seen on the dosal side).

5. The shade or intensity of the colored parts by Pl^W is connected with the basic genes C and A, and therefore, when Pl^W coexists with high potent gene combinations such as $C^B\,A$ and $C^{Bp}\,A$ the color in respective parts is

purple, and if Pl^W coexists with less potent genes such as C^{Br} A, Pl^W distributes pink color in the respective parts except in the pericarp where relatively intense color is accumulated, and further, in a case where Pl^W combined with C alone viz. without any alleles at A-locus, brown, so-called tawny, color is seen in the respective parts.

6. The mode of coloration by Pl^W is nearly the same as that by Pl, which has been known as a gene for puple leaf, however, they are different from each other principally in the following points. i) Color by Pl^W almost fades out in the later part of the growing period, whereas color by Pl does not show any noticeable change up to maturity. ii) Pl^W causes pericarp purple (or red) regardless of its exposure to direct sun light or not during its development, while pericarp color by Pl is expressed only when it is exposed to the direct sun light. iii) As to internode coloration striking expression is given as the preiotropy of Pl^W but to node or collar coloration Pl is more effective than Pl^W.

7. Pl^W and Pl, together with Pl^+, consist of multiple allelomorphic genes in which the order of dominancy is arranged in two ways as given below.

i) Based on color expression in leaf, node or collar; $Pl > Pl^W > Pl^+$

ii) Based on color expression in pericarp; $Pl^W > Pl > Pl^+$

8. The effect of Pl^W is diminished by the interaction of three suppressors, $I\text{-}Pl_1$, $I\text{-}Pl_2$ and $I\text{-}Pl_3$, which are multiple in their suppression effect for Pl^W and which diminishes the coloration at the leaf blade as shown in the figure. Among these $I\text{-}Pl_1$ exerts its effect on the color by Pl likewise. The other two genes, $I\text{-}Pl_2$ and $I\text{-}Pl_3$, are effective principally to the color by Pl^W. A problem whether $I\text{-}Pl_1$ of the writers' is identical with $I\text{-}Pl$, or not is unsolved yet.

9. In connection with the proposition of Pl^W, new alleles at the loci of basic genes C and A, are considered. They are temporalily designated as C^{Bm} and A^E, and are inserted into the respective loci, in the order of;

$$C^B > C^{Bp} > C^{Bl} > C^{Br} > C^{Bm} > C^+$$

$$A^E > A > A^a > A^+$$

To arrive at an adequate conclusion that these two alleles must exist, however, further studies, which are partly in progress at pressent, should be made.

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