ANALYSIS ON APICULUS COLOR GENES ESSENTIAL TO ANTHOCYANIN COLORATION IN RICE

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Content

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I. Introduction

Anthocyanin coloration occurs quite commonly in the floral organs, stems, leaves, leaf-sheaths and other parts of rice plant. Those parts of the rice plant which are colored, due to the presence of anthocyanin pigments, show a wide scope of variations in hue and shade of the color. The colors range from pink, red, reddish purple, purple to purplish black.

Several workers have studied the mode of inheritance of the anthocyanin coloration in rice and a considerable amount of data concerning the genic interpretation of this color has been accumulated. These results have been reviewed by such authors as IKENO (1927), YAMAGUCHI (1927 b), MATSUURA (1933), SAKAI (1935), NAGAO (1939, 1951 c), YASUDA (1939), JODON (1948, 1955) et al.

The genic interpretation of this coloration published up to the present, however, is far too complicated and can not be brought together under one general gene scheme. Recently JODON (1955) suggests, from these situation, the possibility of the anthocyanin coloration being controlled by completely different gene systems in different varieties, however, from the author's point of view, the above discordance may be also partly due to the lack of extensive and systematically produced hybridization experiments, and further other causations possibly lie in the difficulty involved in the identification of the hue and shade of colors refered to.

The author produced several crosses from strains or varieties which differ greatly in plant color and has been able to propose an interpretation that encompasses all the results obtained. An outline of decisive information on this interpretation has already been reported (NAGAO and TAKAHASHI 1947, NAGAO 1951), and in these reports the data was presented as if the F_2 generation of the complex crosses were the first to be obtained. Based on this, genic interpretations were formulated and appropriate tests made. However, this was not the actual procedure in all cases. In several instances the results of some of

the simpler crosses were at hand and were used as an aid to the interpretation of the more complex crosses when the latter were obtained.

It is an aim of the present paper, to mention the actual procedure in analysis of genetic relations on this coloration, and to illustrate how the working hypothesis were devised, tested, and discarded, until finally a genic scheme was found that fitted all the data concerned fairly well.

The term "genetic relations" is to include not merely on account of the genic analysis of the material at hand by means of hybridization experiments···though that constitutes the greater part of the paper···but also some considerations on the histological and biochemical aspects on this pigment and its coloration.

The work was conducted at the Hokkaido University in Japan, under the guidance of Prof. S. NAGAO, since 1940. Before going further the author wishes to express his sincere gratitude to Prof. NAGAO, who, throughout the course of the author's research work, has rendered many helpful suggestions and invaluable criticisms, and by his generosity has made the present work possible. The author also wishes to thank a number of persons, too numerous to mention, who are members of or were enrolled at the Plant Breeding Institute of the said University. They assisted the author on many occasions among whom he desires to mention particularly Mr. M. SUZUKI, Mr. T. KINOSHITA and Mr. T. MIYAMOTO. Expense of the present work was partly defrayed with a grant in Aid for Fundamental Scientific Research from the Ministry of Education.

II. Materials

The plant color types discussed in the present paper were obtained mainly from the crossing of varieties or strains in Hokkaido, the north most island in Japan. Almost all of these varieties or strains had been collected in the Plant Breeding Institute of Hokkaido University and have been bred true for many years. The collections also include, in some cases, varieties obtained from other districts in Japan, such as Tohoku and Kanto, and then again collections include some foreign (outside Japan) varieties. Foreign varieties were also used infrequently for the present work.

The names of varieties or strains used in the present work, and their color characters are listed in Table 1.

TABLE 1. List of varieties or strains used in cross experiment.

Name of varieties or strains	color shade of [1] anthocyanin	part colored with [2]	
		anthocyanin at flowering	brown pigment at ripening
Akage	uncolored	none	Ap
Akageshima	"	"	"
Akageshima-ty	"	"	none
Akaine	Blackish red purple	Ap, Lb (mg), Ls (ve), Pu, Nd, In (ve)	not applicable
Akamuro	Rose red	Ap	"
Akanumashiro	uncolored	none	a little at Ap
Anthocyan-furrow	Blackish red purple	Ap, Ls (ve), In (ve)	not applicable
Bozu	uncolored	none	none
Bozu-5-go	"	"	"
Bunketsuwaito	"	"	Ap
Bunwaichogoei	Amaranth purple	Ap, Ls (ve), In (ve)	Ap
Bunwaikamairazu	"	"	"
Bunwaimochi	Blackish red purple	Ap, Gl, Ls (ve), In (ve)	not applicable
Bunwaimomigare	Amaranth purple	Ap, Ls (ve), In (ve)	Ap
Bunwaimotsure-1	uncolored	none	Ap
Bunwaimotsure-2	"	"	none
Bunwaimuyozetsu	"	"	"
Chabo	"	"	Ap, Gl
Chikoto	"	"	"
Chogoei	Amaranth purple	Ap, Ls (ve), In (ve)	Ap
Chogoeimotsure	"	"	"
Chogoei-mochi	Blackish red purple	"	not applicable
Chogoeiyoshinto	Amaranth purple	Ap, Ls, Lb, Pu, Nd, In	Ap
Daikoku	uncolored	none	none
Daikokukamairazu	"	"	"
E-36	"	"	"
Ebisu	"	"	Ap
Ebisumochi	"	"	"
Ebisumochi-kamairazu	"	"	none
Ebisumochishito	Pansy purple	Ap, Ls, Lb, Pu, Nd, In	not applicable
Fukoku	uncolored	none	none
Furenbozu	"	"	"
Fusenshiro	Pansy purple	Pu, Nd	not applicable
Hatsumurasaki	"	Ap, Ls, Lb, Pu, Nd, In	"

TABLE 1. (continued)

Hokamuri	Pansy purple	Ap	not applicable
Hokkai-75-go	uncolored	none	none
Hokkaimochi-1-go	"	"	"
Hokkoshima	"	"	"
Hokkoshima-d6-Ty	"	"	Ap
Hosogara	"	"	a little at Ap
Kaieifunento	"	"	none
Kairyobozu	Pomegranate purple	Ap	Ap
Kamairazu-so	uncolored	none	none
Karasumochi	Blackish red purple	Ap, Gl, Ls (ve)	not applicable
Kitamurawase-2	uncolored	none	none
Kokushokuto	Blackish red purple	Ap, Gl, Ls (ve), Lb (mg), Pu, Nd, In (ve)	not applicable
Kurikaramochi	Pansy purple	Ap, Gl	"
Kuroke	"	"	"
Kuromochi	Blackish red purple	Ap, Gl, Ls (ve), In (ve)	not applicable
Mantaro	uncolored	none	none
Momigare-datsu	"	"	Ap
Momigare-so-1	Pomegranate purple	Ap	not applicable
Momigare-so-2	uncolored	none	Ap
Motsure-datsu	"	"	"
Motsure-so	"	"	"
Murasaki	Pansy purple	Ap, Ls, Lb, Pu, Nd, In	not applicable
Murasakidaikoku	Blackish red purple	"	"
Muyozetsu	uncolored	none	none
Muyozetsu-ty	"	"	"
Muyozetsumotsure	"	"	"
Muyozetsu-motsure-Ty	"	"	Ap
Muyozetsumochi	"	"	none
N-43	"	"	"
N-44	"	"	"
N-48	Seashell pink	Ap	not applicable
Nakasawadaikoku	Blackish red purple	Ap, Ls (ve), In (ve)	"
Norin-20-go	Pomegranate purple	Ap	Ap
Oaoke	uncolored	none	none
Ogimochi	"	"	Ap
Oyobe	"	"	none
Rikuu-132-go	Amaranth purple	Ap, Ls (ve), In (ve)	Ap

TABLE 1. (continued)

Rinshi	uncolored	none	none
Shimadamochi	Blackish red purple	Ap, Ls (ve), In (ve)	not applicable
Shinkodaikoku	uncolored	none	none
Shito	Pansy purple	Ap, Ls, Lb, Pu, Nd, In	not applicable
Tanpaku	uncolored	none	a little at Ap
Tokachikuromomi	Pansy purple	Ap, Gl	not applicable
Tomekichiwase	Tyrian rose	Ap	"
Tsugaruwase	"	"	"
Tsutsuine	uncolored	none	none
ty-1-16-m	"	"	"

1) Blackish red purple . . . . One of the dark purple color group.
Pansy purple . . . . . One of the purple color group.
Amaranth purple . . . . . One of the dark red color group.
Pomegranate purple . . . . One of the red color group.
Tyrian rose . . . . . One of the light red color group.
Rose red . . . . . One of the pink color group.
Seashell pink . . . . . ditto. (refer to Plate I-fig. 2)

2) Abbreviation of the colored part.
Ap . . . apiculus and awn.
Gl . . . glume and empty glume.
Ls . . . leaf sheath.
Lb . . . leaf blade.
Pu . . . pulvinus, ligule and auricle.
Nd . . . stem node.
In . . . inter node.
ve . . . vein.
mg . . . margin (refer to Plate I-fig. 1)

III. Method

In order to examine the mode of segregation, the author conducted the populations and strains in F_2 and F_3 generation, however, in the present paper, because of its brevity, most of mentions will be made up to F_2. The data on F_3 was excluded from the tabulation except in the case of particular necessity.

The plants were cultured in the paddy fields of the Experimental Farm of Hokkaido University. But when close attention was made necessary by the fact that certain coloration exhibited variations in intensity or extent of coloration, they were at the same time cultured under diverse conditions. For this purpose paddy fields in Mizusawa

city, Iwate prefecture, were frequently used.

Since the intensity of color varies to some degree, according to the stage of development, it is indispensable to set the period for observation. The decisive valuation of the coloring in vegetative stage was done in the period immediately after the height of flowering.

The detailed methods on histological and biochemical examination are given in the experimentals, but in general, histological examination was carried out by using both the fresh materials cut by free hand and the fixed sections by paraffin method. Biochemical examination was done by means of ordinal qualitative and quantitative analysis mainly offered by ROBINSON and ROBINSON (1931), HAYASHI and ABE (1952), and BATESMITH (1948).

The "Color Standards and Color Nomenclature" by RIDGWAY (1812), were utilized to identify colors pertaining.

IV. Experimentals

The greatest amount of diversity in terminology is to be found when dealing with descriptions of various colors occurring in different parts of the rice plant, more particularly with those related to the spikelets. For instance, two small glumes at the base of the spikelet are referred to variously as outer glumes, lower glumes, empty glumes, sterile glumes, or glumes I and II. The lemma and palea, which enclose the flower and subsequently the kernel, are referred to variously as the inner glumes, upper glumes, floral glumes, and glumes III and IV. In order to avoid confusion in terminology, and in conformity with usage of NAGAO (1951), brief descriptions of some of the terms used in the present paper are given below.

The first pair, or outer glumes, are designated as empty glumes, and the two inner glumes are designated simply as glumes or as lemma and palea, respectively. The term "apiculus" is applied to part or tip of the lemma and palea and the term "floral glume" is used for part of the spikelet. In awned varieties, the apex of the lemma extends and develops as an awn. The other terms dealt with in the present paper are referred to in figs. 1 and 2 of Plate I.

A. Correlations on Coloration Among Various Parts

Several workers have studied the mode of distribution of anthocyanin colors in rice plant, and it has been shown that often the color-

ation in several parts has developed coincidently, as if the colors of those parts in the group were due to the same gene or genes (HECTOR 1922, JONES 1929, NAKAYAMA 1932, HUTCHINSON and RAMIAH 1938 etc).

For instance, NAKAYAMA reports that a plant, with some coloration in leaf blade or leaf sheath but with colorless apiculus or stigma, has no existence, so far as he is aware, and also that the purple color in ligule and auricle is always associated with some form of coloration in the leaf blade and leaf sheath. According to HUTHINSON and RAMIAH, there exists remarkable association between each pairs of parts; leaf sheath and lemma and palea, leaf blade and internode, ligule and leaf sheath, and auricle and node. They also report that the coloration in leaf blade and empty glume is found only in plants with colored apiculus. HECTOR (1916) also reports that no plants were observed which had colored internodes, leaf sheaths and stigmas, together with colorless apiculus. JONES obtained a singular case of coloration, in which no visible coloration was recognized in apiculus, inspite of showing some colors in internode, node, leaf blade, leaf sheath, auricle and ligule. However, the awn of this plant was colored with red.

With the intention of estimating rough information on mode of color distribution, the author made, prior to cross experiment, an examination on the distribution of anthocyanin color in all strains and varieties collected in the said institute. There were 101 Hokkaido-varieties and -strains, 64 Honshu- or foreign-varieties, and 75 strains bred from varietal crossing.

It required confirmation, first, whether the apiculus coloration may be said to be the basic type of coloration in connection with coloration in all other parts or not, and secondary on the mode of correlations on coloration between the apiculus and other parts. As shown in Table 2, of 240 vraieties or strains under observation, 103 have color in one

TABLE 2. Correlation on anthocyanin coloration between apiculus and all or any other parts.

parts other than apiculus	apiculus		
	colored	colorless	total
colored	103	0	103
colorless	0	137	137
total	103	137	240

or more of the parts, in which there is no variety having colorless apiculus. Of the 103 colored varieties, 60 have awnes and in these the apiculus color pigment always extends to the awnes. Therefore, in so far as the author has examined, there is no variety or strain which has colored apiculus with colorless awn and/or vice versa.

Further the correlations between several parts which bear various mode of coloration were examined, and the results are briefly tabulated in Table 3. It is seen that in every case the positive correlations are calculated and that in two-thirds of the cases they are highly significant. It is particularly noteworthy that among nodes, pulvinus and auricles there exists complete correlations with the r value of 1, showing as if these colorations depend on the pleiotropic effect of single distributing gene pair.

TABLE 3. Correlation on anthocyanin coloration between various parts other than apiculus.

part	number of varieties					r	p
	++	+−	−+	−−	total		
node − auricle	15	0	0	88	103	1.00	0.01
node and pulvinus − 〃	15	0	0	88	〃	〃	〃
〃 − ligule	14	1 1)	0	88	〃	0.96	〃
auricle − 〃	14	1 2)	0	88	〃	〃	〃
leaf blade − leaf sheath	25	0	13	65	〃	0.74	〃
leaf sheath − stigma	21	17	1	64	〃	0.66	〃
leaf blade − 〃	17	8	5	73	〃	0.64	〃
〃 − auricle	13	12	2	76	〃	0.60	〃
〃 − stigma	12	3	10	78	〃	0.59	〃
auricle − leaf sheath	15	0	23	65	〃	0.54	〃
internode − 〃	22	6	16	59	〃	0.53	〃
〃 − node and pulvinus	12	16	4	71	〃	0.46	〃
〃 − leaf blade	15	13	10	65	〃	0.42	〃
stigma − node and pulvinus	9	13	7	74	〃	0.37	〃
〃 − internode	12	10	16	65	〃	0.32	〃

1), 2) Pulvinus or auricle of a variety "Suihakujo" may be colorless.

In general it is revealed that the anthocyanin coloration develops in the vegetative parts only when the color occurs in the apiculus, including the awn and possible the empty glume. It is impossible to

find a plant with colored vegetative parts in which the apiculus is uncolored. It is even more so in vegetative parts that the color occurs coincidently, as if the said coloration depends on the pleiotropic action of simple distributing gene or is due to closed linkage of certain genes, under the co-existence of apiculus coloration.

As a whole, it is emphasized that the color characters of the apiculus are particularly important in analyzing the mode of color inheritance, not only of the apiculus itself but also of other parts of the rice plant.

B. Mode of Inheritance on Apiculus Coloration

From the preceding descriptive notes and accompanying illustrations, it is suggested that apiculus color genes may be the basic ones in connection with anthocyanin coloration in all parts or organs of the rice plant. It follows from this that it is natural to lay emphasis on the genic constitutions of the apiculus color on account of the anthocyanin coloration in rice.

a. Colorless × Colorless.

The anthocyanin color characters of the apiculus may be roughly classified into two groups, colored and colorless (green), the latter becoming in some varieties a brown ripening color called tawny, whereas in other varieties the ripening color is straw white. They are as shown in Table 1.

The tawny coloration may be divided into five grades, including colorless viz. straw white, according to its intensity of color shade. The following is the relation of the color shade of the tawny and the varieties which being representable in each grades, are arranged according to the color intensity in ascending order (fig. 3 of Plate I and fig. 1-B of Plate II).

i	Russet	Ebisumochi, Chabo
ii	Tawny	Akage, Ebisu
iii	Ochraceous buff . . .	Tanpaku, Akanumashiro
iv	Warm buff	Mantaro, Oaoge
v	Straw white	Fukoku, Bozu

Within these grades, iii and iv are sometimes indistinguishable from each other when only a couple of plants are under observation. Further, for the sake of convenience, these two color types will be

TABLE 4. Inheritance of tawny coloration in apiculus in crossing among anthocyanin uncolored varieties that show various grades of tawny color intensity.

P_1		F_1	F_2					
Color shade of tawny	name of variety or strain	color shade	same as P_1 with deep color	same as P_1 with light color	total	χ^2 ($\Sigma\chi_i^2$)	d. f.	p
Russet × Tawny	Ebisumochi × Ebisu	Russet	315	108	423			
	C (3 : 1)		317.25	105.75	423.00	0.064	1	0.9 -0.8
Russet × Warm buff	Mantaro × Momigare-datu	Russet	41	12	53	0.157	"	0.8 -0.7
	Ebisumochi × Momigare-datu	"	367	136	503	0.835	"	0.5 -0.3
	total		408	148	556	(0.992)	2	0.7 -0.5
	C (3 : 1)		417.00	139.00	556.00	0.777	1	0.5 -0.3
Russet × Straw white	Hokkoshima-d6-Ty × Akageshima-ty	Russet	454	154	608	0.018	"	0.95-0.9
	Ebisumochi × Hokkoshima	"	317	86	403	2.879	"	0.1 -0.05
	Momigare-datsu × Rinshi	"	58	21	79	0.106	"	0.8 -0.7
	Bunwaimotsure × Muyozetsu-ty	"	133	56	189	1.694	"	0.2 -0.1
	total		962	317	1279	(4.697)	4	0.5 -0.3
	C (3 : 1)		959.25	319.75	1279.00	0.032	1	0.95-0.9
Tawny × Warm buff	Akage × Mantaro	Tawny	355	104	459			
	C (3 : 1)		344.25	114.75	459.00	1.342	"	0.3 -0.2
Tawny × Straw white	Muyozetsumotsure × Akageshima	Tawny	179	68	247	0.843	"	0.5 -0.3
	Akageshima × Hokkoshima	"	499	155	654	0.590	"	"
	Daikokukamairazu × Akageshima	"	508	187	695	1.347	"	0.3 -0.2
	Ebisu × Muyozetsu-ty	"	230	86	316	0.827	"	0.5 -0.3
	Ebisu × Hokkoshima	"	350	123	473	0.254	"	0.7 -0.5
	Hokkaimochi-1 -gy × Akage	"	412	106	518	5.674	"	0.02-0.01
	total		2178	725	2903	(9.535)	6	0.2 -0.1
	C (3 : 1)		2177.25	725.75	2903.00	0.001	1	0.98-0.95

described en bloc as Ochraceous buff or Warm buff, except when distinction is necessitated.

The author made almost all possible cross combinations among colorless varieties or strains which show all grades of tawny coloration, Russet to Straw white. The F_1s and F_2s data for these combinations are presented in Table 4, 5 and 6. Of these data, the following three results are worthy of notice.

i) As shown in Table 4, between any two color shades of ripening tawny, the differences in color grade are always monogenic, the deep color being dominant over the faint ones, and showing a 3 : 1

TABLE 5. F_2 data showing linkage relation between tawny coloration and endosperm character.

combination		assortment				linkage			
color shade of tawny	name of variety or strain	deep color and non-glutinous	deep color and glutinous	light color and non-glutinous	light color and glutinous	total	phase	recombination value	p*
Russet × Tawny	Ebisumochi × Ebisu	213	102	100	8	423	r	26.6	
Russet × Warm buff	Ebisumochi × Mantaro	241	126	130	6	503	"	20.0	
Russet × Straw white	Ebisumochi × Hokkoshima	227	90	79	7	403	"	29.8	
Tawny × Straw white	Hokkaimochi-1-go × Akage	353	59	57	49	518	c	28.5	
	ditto	1001	154	146	213	1514	"	22.8	
total in coupling combi.		1354	213	203	262	2032		24.2	
C (24%)		1301.75	222.25	222.25	285.75	2032.00			0.2–0.1
total in repulsion combi.		681	318	309	21	1329		25.7	
C (26%)		685.27	311.48	311.48	20.77	1329.00			0.98–0.95

* Goodness of fit under responsible linkage intensities, as in the other tables 8 and 12.

TABLE 6. F_1 and F_2 progenies of crosses between the tawny and the straw white.

P_1		F_1	F_2						
color shade of tawny	name of variety or strain	color shade of antho-cyanin	same as F_1	same as P_1 with tawny color	color-less (straw white)	total	χ^2 ($\Sigma\chi^2$)	d. f.	p
Russet × Straw white	Chikoto × N-44 (crSm)	Blackish red purple	41	12	17	70	0.175	2	0.95~0.9
	Ebisumochi × N-43 (crSM)	"	83	21	32	136	1.465	"	0.5 ~0.3
	total		124	33	49	206	(1.640)	4	0.9 ~0.8
	C (9 : 3 : 4)		115.88	38.63	51.50	206.01	1.509	2	0.5 ~0.3
Tawny × Straw white	test cross in progenies from '50-6	Pansy purple	136	48	73	257			
	C (9 : 3 : 4)		144.56	48.19	64.25	257.00	1.721	2	0.5 ~0.3

ratio in F_2.

ii) F_2 progenies resulting from crosses involving segregations on endosperm character, non-glutinous vs. glutinous, give segregations that undoubtly show the occurrence of a linkage between the gene for tawny and the gene for endosperm (Table 5). The recombinations amount to about 24%, irrespective of the grade of the tawny color shade.

As it has been recognized that the endosperm character is due to a single pair of gene *gl* (details are in CHAO 1928b), these two facts, i) and ii), lead the author to the assumption that there exists a certain series of multiple allelomorphic relation in respect to the tawny coloration in apiculus.

iii) In none of the crosses, straw white × straw white, and tawny colored × tawny colored, do their F_1s and F_2s give types of coloration other than their parental types. While, in some cases of crosses between the tawny and the straw white, progenies show the anthocyanin coloration in their apiculus, together with the fact that there exists a tendency of direct proportion between intensities on tawny colors of parents and that on anthocyanin colors of F_1s. The anthocyanin colored F_1s of such crosses produce in F_2 the three color types, antho-

cyanin colored, green but colored with tawny ripening color, and green with straw white ripenig color, in the relation of 9 : 3 : 4, without exception. This is presented in Table 6.

The results, mentioned in i to iii, suggest that the occurrence of the tawny color character depends on the action of a series of multiple allelomorphs, of which locus is about 24% distant from that of *gl*, the gene for endosperm character. It may be also suggested that the colors in apiculus which are due to anthocyanin pigments are the result of the complementary interaction of at least two genes, one of which being closely related with the gene for tawny coloration.

This intimate connection may be responsible for either a) that they are very closely linked to each other or b) that the tawny gene coincidently is responsible for the formation of chromogen or modifier for the anthocyanin pigment.

b. Colored × Colored

Anthocyanin coloration in apiculus is also classified into four or five types according to the intensity of color shade in ascending order, namely;

i Blackish red purple
ii Pansy purple
iii Tyrian rose
or Rose red
iv White (colorless) (fig. 3 of Plate I and fig. 1-A of Plate II)

In all crosses among every colored varieties or strains, the difference in color shade of parents is always monogenic, the deep color being dominant over faint ones, and giving in F_2 a 3 (deep): 1 (faint) ratio (Table 7). There exists a parallelism between the intensity of color shade and the rank of genetic dominancy among each other, indicating that the differences in the color shade are attributable to the presence of a series of certain genes which are considered to consist of multiple allelomorphic relation. This may be also supported by the fact that every kind of color shade is linked with the endosperm character with recombination value of about 23% all alike, as shown in Table 8.

It is worthy of note that the value of recombination between "tawny" and *gl* is almost equal to that of the recombination between "anthocyanin" and *gl*. This fact may also suggest the intimate con-

TABLE 7. F_1 and F_2 progenies from crosses between anthocyanin colored varieties.

P_1		F_1	F_2					
color shade of antho-cyanin	name of variety or strain	color shade	same as F_1 or deeply colored P_1	same as lightly colored P_1	total	χ^2 ($\Sigma\chi_i^2$)	d. f.	p
Blackish red purple × Pansy purple	Tokachikuromomi ×Kokushokuto	Blackish red purple	229	92	321	2.302	1	0.2 -0.1
	Hatsumurasaki ×Shimadamochi	"	172	53	225	0.250	"	0.7 -0.5
	total		563	197	760	(2.609)	3	0.5 -0.3
	C (3 : 1)		570.00	190.00	760.00	0.344	1	0.7 -0.5
Blackish red purple × Rose red	Akamuro ×Kokushokuto	Blackish red purple	570	196	766	0.141	"	0.8 -0.7
	Akamuro ×Akaine	"	835	298	1133	1.090	"	0.3 -0.2
	total		1405	494	1899	(1.231)	2	0.7 -0.5
	C (3 : 1)		1424.25	474.75	1899.00	1.026	1	0.5 -0.3
Blackish red purple × white	N-44 (crSm) ×Anthocyan-furrow	Blackish red purple	412	136	548			
	C (3 : 1)		411.00	137.00	548.00	0.098	"	0.8 -0.7
Pansy purple × Tyrian rose or Rose red	Hatsumurasaki ×Akamuro	Pansy purple	451	150	601	0.001	"	0.99-0.98
	Tomekichiwase ×Shito	"	217	86	303	1.853	"	0.2 -0.1
	Tsugaruwase ×Shito	"	180	57	237	0.114	"	0.8 -0.7
	total		848	293	1141	(1.968)	3	0.7 -0.5
	C (3 : 1)		855.75	285.25	1141.00	0.028	1	0.9 -0.8
Pansy purple × white	Muyozetsumochi ×Shito	Pansy purple	395	113	508	2.058	1	0.2 -0.1
	ditto	"	975	303	1278	1.136	"	0.3 -0.2
	ditto	"	140	42	182	0.350	"	0.7 -0.5
	total		1510	458	1968	(3.544)	3	0.5 -0.3
	C (3 : 1)		1476.00	492.00	1968.00	3.133	1	0.1 -0.05
Rose red × white	Akamuro ×N-44 (crSm)	Rose red	81	26	107			
	C (3 : 1)		80.25	26.75	107.00	0.028	1	0.9 -0.8

TABLE 8. F_2 data showing linkage relation between anthocyanin coloration and endosperm character.

combination		assortment					linkage		
color shade of anthocyanin	name of variety or strain	deep color and non-glutinous	deep color and glutinous	light color and non-glutinous	light color and glutinous	total	phase	recombination value	p
Blackish red purple × pansy purple	Hatsumurasaki × Shimadamochi	125	47	46	7	225	r	37.4	
	Hatsumurasakl × Kokushokuto	106	56	45	7	214	"	33.4	
Blackish red purp. × Rose red	Akamuro × Kokushokuto	408	162	189	7	766	"	20.4	
Blackish red purp. × white	N-44 (crSm) × Anthocyan-furrow	367	45	53	83	548	c	20.2	
Pansy purple × white	Muyozetsumochi × Shito	354	41	54	59	508	"	22.8	
	ditto	847	128	138	165	1278	"	24.5	
	ditto	121	19	18	24	182	"	23.8	
total in coupling combi.		1689	233	263	331	2516		23.1	
C (23%)		1611.81	275.19	275.19	353.81	2516.00			÷ 0.01
total in repulsion combi.		639	265	280	21	1205		27.3	
C (27%)		621.33	282.44	282.44	18.83	1205.00			0.5–0.3

nection of the tawny with the anthocyanin. How this connection is to be interpreted genetically will be illustrated in the following descriptive note on crosses between the colored and the colorless.

c. Colored × Colorless

On the basis of the rank of color intensity, the following corresponding series of cross combinations between the anthocyanin colored and the tawny colored were, made, and their F_1s and F_2s were produced. They are presented in Table 9.

TABLE 9. F_1 and F_2 progenies of crosses between anthocyanin colored and tawny colored varieties, in corresponding series of grade of color intensity.

P_1		F_1	F_2					
color shade of tawny × anthocyanin	name of variety or strain	color shade	same as F_1 or anthocyanin colored P_1	same as tawny colored P_1	total	χ^2 ($\Sigma\chi_i^2$)	d. f.	p
Russet × Blackish red purple	Bunketsuwaito ×Kuromochi	Blackish red purple	333	131	464	2.586	1	0.2 -0.1
	Bunketsuwaito ×Murasakidaikoku	"	315	109	424	0.113	"	0.8 -0.7
	Bunwaimotsure ×Kokushokuto	"	216	45	261	8.380	"	0.01
	Ogimochi ×Bunwaimochi	"	316	99	415	0.354	"	0.7 -0.5
	total		1180	384	1564	(11.43)	4	0.05-0.02
	C (3 : 1)		1173.00	391.00	1564.00	0.167	1	0.7 -0.5
Tawny × Pansy purple	Tokachikuromomi ×Motsure-so	Pansy purple	67	22	89	0.003	"	0.98-0.95
	Hokamuri ×Akageshima	"	233	67	300	1.138	"	0.3 -0.2
	Kurikaramochi ×Akage	"	275	105	380	1.404	"	"
	Akage ×Hatsumurasaki	"	1037	344	1381	0.006	"	0.95-0.9
	Akage ×Tokachikuromomi	"	719	262	981	1.561	"	0.3 -0.2
	Tokachikuromomi ×Akage	"	176	56	232	0.092	"	0.8 -0.7
	total		2507	856	3363	(4.204)	6	0.7 -0.5
	C (3 : 1)		2522.25	840.75	3363.00	0.369	1	"
Warm buff × Rose red	Progeny from Mantaro ×Shito	Rose red	106	39	145			
	C (3 : 1)		108.75	36.25	145.00	0.279	1	0.7 -0.5

Anthocyanin	*Tawny*
Blackish red purple	Russet
Pansy purple	Tawny
Rose red	Warm buff

The F_1 plants showed anthocyanin colored apiculus and in F_2 two phenotypes, which are identical with the color types of both parents

respectively, occurred at a ratio of 3 colored : 1 colorless, which changes into tawny at ripening). No segregants appeared which bear anthocyanin and tawny color at the same time, indicating that anthocyanin color behaves as monogenic dominant over tawny color.

It may be worthy of note, in the case of these cross combinations, that there are no linkage relationships between the anthocyanin coloration and the endosperm character. It is shown in Table 10.

TABLE 10. F_2 of some crosses showing independent assortment on anthocyanin coloration and endosperm character.

combination		assortment					linkage		
color shade of anthocyanin	name of variety or strain	colored with anthocyanin, and non-glutinous	colored with anthocyanin, and glutinous	colored with tawny, and non-glutinous	colored with tawny, and glutinous	total	phase	recombination value	p
Russet × Blackish red purple	Bunketsuwaito × Kuromochi	270	63	110	21	464	r	46.5	
	Bunwaimotsure × Kokushokuto	159	57	29	16	261	"	55.4	
Tawny × Pansy purple	Kurikaramochi × Akage	210	65	81	24	380	"	49.4	
total		639	185	220	61	1105		49.4	
C (50%; 9 : 3 : 3 : 1)		621.56	207.19	207.19	69.06	1105.00			0.3-0.2

Further, the colored varieties or strains were crossed with the colorless, in which ripening color is straw white. Their F_1s were colored with anthocyanin pigment, and in F_2 two types of segregation ratio on colored vs. colorless were recognized, one being a ratio of 3:1 and the other 9:7 (Table 11).

The colorless segregants from the former segregation, 3:1, showed straw white color at ripening without exception. While in the latter, 9:7, the colorless segregants were classified into two types of ripening color, tawny and straw white, with the phenotypic ratio of 3:4 respectively. This also indicates that the expression of anthocyanin coloration needs the complementary effect of two genes, one of which being

TABLE 11. F_1 and F_2 progenies from crosses between anthocyanin colored and colorless; the ripening color of the later is straw white.

a: (3 : 1)

P_1		F_1	F_2						
color shade of anthocyanin colored parent	name of variety or strain	color shade	same as anthocyanin colored P_1 or F_1	colorless but changes into tawny at ripening	colorless, same as colorless P_1	total	χ^2 ($\Sigma\chi_i^2$)	d. f.	p
Blackish red purple	N-44 ×Anthocyan-furrow	Blackish red purple	412	0	136	548			
	C (3 : 1)		411.00	0.00	137.00	548.00	0.098	1	0.8 -0.7
Pansy purple	Muyozetsumochi ×Shito	Pansy purple	1510	0	458	1968	3.133	"	0.3 -0.05
	Progeny from Fusenshiro ×N-44	"	446	0	163	609	1.012	"	0.5 -0.3
	ditto	"	433	0	141	574	0.058	"	0.9 -0.8
	total		2389	0	762	3151	(4.203)	3	0.3 -0.2
	C (3 : 1)		2363.25	0.00	787.75	3151.00	1.122	1	"
Rose red	Akamuro ×N-44	Rose red	81	0	26	107			
	C (3 : 1)		80.25	0.00	26.75	107.00	0.028	1	0.9 -0.8

b: (9 : 3 : 4)

Blackish red purple	Daikoku ×Kuromochi	Blackish red purple	273	89	103	465	2.551	2	0.3 -0.2
	Fukoku ×Kuromochi	"	492	176	215	883	0.852	"	0.7 -0.5
	Hokkaimochi-1-go ×Kuromochi	"	201	63	79	343	0.905	"	"
	Hokkaimochi-1-go ×Akaine	"	384	100	174	658	5.507	"	0.1 -0.05
	Oyobe ×Akaine	"	100	31	34	165	1.831	"	0.5 -0.3
	Fukoku ×Akaine	"	273	73	99	445	4.694	"	0.1 -0.05
	Kokushokuto ×Muyozetsu-ty	"	89	28	42	159	0.239	"	0.9 -0.8
	Muyozetsu-ty ×Kokushokuto	"	120	54	52	226	3.943	"	0.2 -0.1
	total		1932	614	798	3344	(20.52)	16	0.3 -0.2
	C (9 : 3 : 4)		1881.00	627.00	836.00	3344.00	3.384	2	0.2 -0.1

TABLE 11. (b: continued)

Pansy purple	Muyozetsumotsure ×Shito	Pansy purple	342	95	155	592	2.881	〃	2.3 -0.2
	Hokkai-75-go ×Shito	〃	127	37	46	210	1.616	〃	〃
	Bozu-5-go ×Shito	〃	70	29	44	143	3.438	〃	0.2 -0.1
	Bozu ×Shito	〃	121	35	44	200	1 529	〃	0.5 -0.3
	Shito ×Tsutsuine	〃	236	74	84	394	3.090	〃	0.3 -0.2
	Muyozetsu-ty ×Hatsumurasaki	〃	157	57	70	284	0.325	〃	0.9 -0.8
	Hokkaimochi-1-go ×Kuroke	〃	670	193	267	1130	4.391	〃	0.2 -0.1
	Daikoku ×Tokachikuro-momi	〃	142	44	50	236	2.019	〃	0.5 -0.3
	total		1865	564	760	3189	(19.30)	16	0.3 -0.2
	C (9 : 3 : 4)		1793.81	597.94	797.25	3189.00	6.492	2	0.05-0.02
Rose red	Daikoku ×Akamuro	Rose red	546	447		993	0.646	1	0.5 -0.3
	Hokkoshima ×Akamuro	〃	318	240		558	0.124	〃	0.8 -0.7
	Akamuro ×Furenbozu	〃	186	166		352	1.662	〃	0.2 -0.1
	total		1050	853		1903	(2.432)	6	0.9 -0.8
	C (9 : 7)		1070.44	832.56		1903.00	0.892	1	0.5 -0.3

to the gene for the tawny coloration. Here, it is pointed out that there appeared a new type of coloration viz. tawny in addition to the parental types, and that the difference of genic constitution between the anthocyanin colored segregants and the tawny colored ones may be considered to be monogenic, just as seen in Table 10.

Though the same type of segregation, 3 colored : 1 colorless, are obtained from crosses presented in Table 10 and in Table 11 a, linkage relations with endosperm characters are quite different from each other. In Table 10 there was no linkage relationship between the apiculus color and the endosperm character, while in Table 11 a approximately 23% recombination value, which is similar to the value as presented in Table 8, was recognized. This is shown in Table 12a in detail. This indicates that the gene or genes for apiculus coloration dealt with in Table 10 may not be the same, as is dealt with in Table 11.

The same relation of the linkage was recognized from crosses shown

TABLE 12. Linkage relations between apiculus color and endosperm character, that are shown in F_2 from crosses, colored ×colorless (ripening straw white).

a: (3 : 1) (3 : 1)

combination		assortment					linkage		
color shade of anthocyanin colored P_1	name of variety or strain	colored with anthocyanin, and non glutinous	colored with anthocyanin, and glutinous	uncolored with anthocyanin, and non glutinous	uncolored with anthocyanin, and glutinous	total	phase	recombination value	p
Blackish red purple	N-44 × Anthocyan-furr.	367	45	53	83	548	c	20.2	
Pansy purple	Muyozetsumochi ×Shito	1322	188	210	248	1968	"	24.3	
	Progeny from ×Fusenshiro N-44	385	61	89	74	609	"	21.2	
Rose red	Akamuro ×N-44	70	11	12	14	107	"	25.1	
total in coupling combi.		2144	305	364	419	3232		24.3	
C (24%)		2070.50	353.50	353.50	454.50	3232.00			=0.01

b: (9 : 7) (3 : 1)

Blackish red purple	Hokkaimochi-1-go ×Akaine	322	62	167	107	658	c	26.4	
	Muyozetsu-ty ×Kuromochi	62	27	60	10	159	r	16.9	
	Fukoku ×Kuromochi	349	143	315	76	883	"	35.1	
	Daikoku ×Kuromochi	178	95	162	30	465	"	9.0	
	Fukoku ×Kokushokuto	152	61	109	25	347	"	34.1	
Pansy purple	Hokkaimochi-1-go ×Kuroke	612	58	297	163	1130	c	18.8	
	Hokkaimochi-1-go ×Hatsumurasaki	178	20	94	57	349	"	19.7	
total in coupling combi.		1112	140	558	327	2137		21.6	
C (29%)		1057.82	144.25	544.94	390.00	2137.01			=0.01
total in repulsion com.		741	326	646	141	1854		29.1	
C (29%)		726.85	316.02	663.65	147.48	1854.00			0.8–0.7

in Table 11b, that is to say; when their F_2 plants are sorted into colored vs. uncolored in respect of anthocyanin coloration, the segregation between this character and endosperm character is seen, with an approximate 22% recombination value (Table 12b). But in the case of yet another classification, in which the straw white is excluded from consideration and therefore the ratio is 9 (3) colored and 3 (1) tawny, there is no sign of linkage between apiculus color and endosperm character.

In addition to this, in several crosses between colored and colorless (straw white), it is also noticeable that the degree of color intensity in the tawny appeared in F_2 segregants always corresponds to the color intensity in the anthocyanin of colored parents. For instance, if a colored parent is Blackish red purple, the color shade of the tawny segregants in F_2 is Russet, and if the F_2 segregants bears a tawny color of warm buff its colored parent is always of a Rose red anthocyanin color shade. As colorless parents have no tawny color, it follows that the occurrence of the tawny in F_2 must be attributed to a certain genic force of other parents in which the apiculus is colored with anthocyanin.

To summarize the above;

i) Genetically the expression of the anthocyanin color in apiculus depends on the complementary effect of two genes.

ii) One of them seems to consist of multiple allelomorphic series of gene, in which at least four alleles are noticeable, located in same linkage groups as in endosperm gene *gl*, with recombination values of about 23% between them.

iii) Some of the colorless plants with anthocyanin, either in parental varieties or F_1s and F_2s, show a brown ripening color called tawny in four grades of color intensity. This color may also be caused by the presence of a kind of multiple allelomorphs which consists of at least four alleles. This gene links with *gl*, with a recombination value of about 24%.

iv) As to the degree of color intensity, there exists a remarkable accordance between the anthocyanin and the tawny, suggesting that it may be caused as a result of the pleiotropic effect of an identical multiple allelomorphic series of genes.

C. Proposition of Multiple Allelomorphic Series of Genes *C* and *Sp*

Considering the results of the examinations mentioned above, the following working hypothesis on a genic scheme of apiculus coloration may be most probable.

The production of anthocyanin coloration in apiculus requires the complementary effect of two genes, one of which is comprised of four alleles of a multiple allelomorphic series. In the case of absence of both of these two genes, the anthocyanin color does not appear and the apiculus is colorless. But on ripening and if the multiple allelomorphs are present, alone, viz. without another complementary gene, they make the apiculus brown viz. tawny in several intensities of color shade depending on which allele of this locus is concerned. This will be designated as the *C*-series of multiple allelomorphus, the alleles comprised of this locus being as follows:

C^B (Russet)$>C^{Bp}$ (Tawny)$>C^{Br}$ (Warm buff)$>C^+$ (Straw white).

C links with *gl* with the intensity of 23% recombination values.

The other complementary gene may exert its modifying effect on the *C* and turn the tawny or its precursor to anthocyanin. This gene, in itself, causes no coloration with anthocyanin or tawny, and it is free-assorted with *gl*. This is designated as *Sp*.

Thus, the color types and their genic schemes may be represented as:

Genotype	Hue or Shade of color		
	at flowering	at ripening	
$C^B\,Sp$	Blackish red purple		
$C^{Bp}\,Sp$	Pansy purple		
$C^{Br}\,Sp$	Rose red		
$C^B\,Sp^+$	Colorless	Russet	tawny
$C^{Bp}\,Sp^+$	"	Tawny	tawny
$C^{Br}\,Sp^+$	"	Warm buff	tawny
Combination with C^+	"	Colorless (Straw white)	

a. Colored × Colorless, continued.

For further verification of this scheme of genes, several crosses of colored × colorless were made, in which each parent differed from each other in the degree or rank of intensity of color shade in regards to anthocyanin and tawny coloration.

The details of the results, being tedious, are abridged here, however

TABLE 13. F_1 and F_2 segregation from representative crosses between colored-with-anthocyanin and uncolored, in which apiculus color differs from each other in grade of color intensity of anthocyanin and tawny respectively.

P_1			F_1
color shade	name of variety or strain, crossed	genic constitution	color shade
1. Pansy purple ×Blackish red purple	Hatsumurasaki ×Shimadamochi	$C^{Bp}Sp \times C^{B}Sp$	Blackish red purple
2. Rose red ×Blackish red purple	Akamuro ×Kokushokuto	$C^{Br}Sp \times$ 〃	〃
3. White (Straw white) ×Blackish red purple	N-44 ×Anthocyan-furrow	$C^{+}Sp \times$ 〃	〃
4. White (Tawny) ×Blackish red purple	Ebisu ×Chogoei-mochi	$C^{Bp}Sp^{+} \times$ 〃	〃
5. White (Warm buff) ×Blackish red purple	Mantaro ×Shimadamochi	$C^{Br}Sp^{+} \times$ 〃	〃
6. White (Straw white) ×Blackish red purple	Fukoku ×Kuromochi	$C^{+}Sp^{+} \times$ 〃	〃
7. Rose red ×Pansy purple	Akamuro ×Hatsumurasaki	$C^{Br}Sp^{+} \times C^{Bp}Sp$	Pansy purple
8. White (Straw white) ×Pansy purple	Muyozetsumochi ×Shito	$C^{+}Sp \times$ 〃	〃
9. White (Russet) ×Pansy purple	Chabo ×Kurikaramochi	$C^{B}Sp^{+} \times$ 〃	Blackish red purple
10. White (Warm buff) ×Pansy purple	Oaoke ×Shito	$C^{Br}Sp^{+} \times$ 〃	Pansy purple
11. White (Straw white) ×Pansy purple	Muyozetsumotsure ×Shito	$C^{+}Sp^{+} \times$ 〃	〃
12. White (Straw white) ×Rose red	N-44 ×Akamuro	$C^{+}Sp \times C^{Br}Sp$	Rose red
13. White (Russet) ×Rose red	Chikoto ×Akamuro	$C^{B}Sp^{+} \times$ 〃	Blackish red purple
14. White (Tawny) ×Rose red	Ebisu ×Akamuro	$C^{Bp}Sp^{+} \times$ 〃	Pansy purple
15. White (Straw white) ×Rose red	Daikoku ×Akamuro	$C^{+}Sp^{+} \times$ 〃	Rose red
16. White (Straw white) ×White (Russet)	N-44 ×Chikoto	$C^{+}Sp \times C^{B}Sp^{+}$	Blackish red purple
17. White (Straw white) ×White (Tawny)	test cross in progeny from '50-6	〃 $\times C^{Bp}Sp^{+}$	Pansy purple
18. White (Tawny) ×White (Russet)	Ebisu ×Ebisumochi	$C^{Bp}Sp^{+} \times C^{B}Sp^{+}$	White (Russet)
19. White (Straw white) ×White (Russet)	Muyozetsu-ty ×Bunwaimotsure-1	$C^{+}Sp^{+} \times$ 〃	〃
20. White (Warm buff) ×White (Tawny)	Mantaro ×Akage	$C^{Br}Sp^{+} \times C^{Bp}Sp^{+}$	White (Tawny)
21. White (Straw white) ×White (Tawny)	Daikokukamairazu ×Akageshima	$C^{+}Sp^{+} \times$ 〃	〃

All the combinations except $C^{+}Sp \times C^{Br}Sp^{+}$, $C^{Br}Sp^{+} \times C^{B}Sp^{+}$ and $C^{+}Sp^{+} \times C^{Br}Sp^{+}$ are listed in the above.

TABLE 13. (continued)

continued on the right side of the preceding table

	F_2												
	mode of segregation								segregation ratio	χ^2 ($\Sigma\chi_i^2$)	d. f.	p
	Blackish red purple	Pansy purple	Rose red	Russet	Tawny	Warm buff	Straw white	total				
	C^BSp	$C^{Bp}Sp$	$C^{Br}Sp$	C^BSp^+	$C^{Bp}Sp^+$	$C^{Br}Sp^+$	$\frac{C^+Sp}{C^+Sp^+}$					
1.	172	53						225	3:1	0.250	1	0.7 –0.5
2.	570		196					766	"	0.141	"	0.8 –0.7
3.	412		136					548	"	0.098	"	"
4.	180	63		70	22			335	9:3:3:1	1.240	3	"
5.	166		64	63		27		320	"	3.955	"	0.3 –0.2
6.	492		156				215	863	9:3:4	0.852	2	0.7 –0.5
7.		451	150					601	3:1	0.001	1	0.99–0.98
8.		1510					458	1968	"	3.133	"	0.1 –0.05
9.	213	65		70	25			373	9:3:3:1	0.520	3	0.95–0.9
10.		65	25		17	8		115	"	1.606	"	0.7 –0.5
11.		342			95		155	592	9:3:4	2.881	2	0.3 –0.2
12.			81			26		107	3:1	0.028	1	0.9 –0.8
13.	488		132	122		68		810	9:3:3:1	16.739	3	0.01
14.		613	198		189	64		1064	"	1.009	"	0.8 –0.7
15.			546			447		993	9:7	0.646	1	0.5 –0.3
16.	41			12			17	70	9:3:4	0.175	2	0.95–0.9
17.		136			48		73	257	"	1.721	"	0.5 –0.3
18.				315	108			423	3:1	0.064	1	0.9 –0.8
19.				133			56	189	"	1.695	"	0.2 –0.1
20.					355	104		459	"	1.342	"	0.3 –0.2
21.					508		187	695	"	1.347	"	"

as given in Table 13, in all cross combinations, numerical relations were found between the several color types and also between the several classes of behavior which is reasonably close to the expectation.

The propriety of above genic scheme was further confirmed by pedigree culture in F_3. In every instance all the segregation types expected in F_3s of these crosses have appeared. Table 14 represents one of these crosses, in which parental varieties and their assumed genotypes are expressed as Kuromochi ($C^B Sp gl$) and Akage ($C^{Bp} Sp^+ gl^+$) respectively.

Here, it is also pointed out that all F_3 plants derived from the anthocyanin colored F_2 parents bear neither anthocyanin nor tawny coloration of which color intensity grades are heigher than that of their

TABLE 14. Segregation types of F_3 strains and their frequencies in a cross, $C^{Bp}Sp^+ \times C^B Sp$.

F_2		F_3								
phenotype	genotype	type of segregation				number of [1] strains			χ^2	p
		Blackish red purple	Pansy purple	Russet	Tawny	O	C_1	C_2		
Blackish red purple	$C^B\ C^B\ Sp\ Sp$	1				12	1	11.4		
〃	$C^B\ C^{Bp} Sp\ Sp$	3	1			25	2	22.9	2.687	0.5–0.3
〃	$C^B\ C^B\ Sp\ Sp^+$	3		1		16	2	22.9	(d.f.=3)	
〃	$C^B C^{Bp} Sp\ Sp^+$	9	3	3	1	50	4	45.8		
total						103	9	103.0		
Pansy purple	$C^{Bp} C^{Bp} Sp\ Sp$		1			17	1	19.7	0.565	〃
〃	$C^{Bp} C^{Bp} Sp\ Sp^+$		3		1	42	2	39.3	(d.f.=1)	
total						59	3	59.0		
Russet	$C^B\ C^B\ Sp^+ Sp^+$			1		7	1	7.5		
〃	$C^B\ C^{Bp} Sp^+ Sp^+$			3	1	17	2	15.0	0.600	0.8–0.7
Tawny	$C^{Bp} C^{Bp} Sp^+ Sp^+$				1	6	1	7.5	(d.f.=2)	
total						30	4	30.0		

1) C_1 indicates the theoretical ratio and C_2 indicates the theoretical numbers.

parental F_2, and that there are no plants which would be expected to appear on a supposition that the gene for anthocyanin color may closely be linked with that for tawny.

Therefore, it is natural to consider that these two colors are produced as a result of the dual effect of an identical gene, *C*, which is responsible for the production of chromogenic substance of the anthocyanin.

b. Some considerations on C-chromogen.

Though, more detailed experiments including geneticohistological or physicochemical examinations are necessary to determine the above proposition conclusively, its propriety or possibility may be supported, to some extent, under the following reviews which have been made by many workers from a biochemical point of view.

Considering the nature of anthocyanin pigment, it has been revealed that, throughout various plants, when anthocyanins coexist with flavonols, their basic constitutions viz. glucosides and aglucons show an intimate connection; that is, e.g., cyanidin-quercetin or myricetin-delphinidin. By what course or courses, these two kinds of substances coexist with each other, is not yet ascertained, however, the opinions advocated by KLEIN and WERNER (1925) or SAND, MILNER and SHERMAN (1935), that the flavonol is a precursor of the anthocyan, is worthy of note. Notably, the latter reveales a possibility that anthocyanin might be produced as a reduction product of flavonol. It is also revealed that the flavone or flavonoin compounds widely exist in cell sap of several parts or organs of higher plants, including gramineae (ANDERSON and PERKIN 1931, ENDO 1956). Flavonol is one of the flavone group and shows a yellowish brown color. This color shade becomes intense in proportion, as the hydroxyl group in it increases. In fact certain flavonol pigments are used as dyes.

In accordance with the above information and with consideration to the intimate connection between the anthocyanin and the tawny color in the rice, it is possible to assume that the expression of the tawny color may be due to the presence of a kind of substance such as flavone, and that the occurrence of the anthocyanin color may be expected as a result of a chemical change; flavone→anthocyanin.

Thus, one of the suppositions that every two pair of genes, which belong to different loci of two multiple allelomorphs, may be closely linked with each other, in corresponding series of their rank of domi-

nancy, is considered invalid.

On the whole, therefore, the interpretation on genes for apiculus coloration should be developed as follows.

Anthocyanin coloration in apiculus depends on the complementary effect of gene *C* and *Sp*. *C* is reponsible for the formation of chromogenic substance and *Sp* exerts its modifying—possibly reducting—effect on *C* and turns the chromogen to anthocyanin. Pigmentation occurs in the apiculus as well as awns, as a result of the interaction of said two genes. *C* alone causes the site to brown viz. tawny at ripening. Four alleles are listed at the *C* locus, namely in ascending order, $C^{B}>C^{Bp}>C^{Br}>C^{+}$, and two at the *Sp* locus, $Sp>Sp^{+}$.

c. Cross combination involving Sp^{a}, another allele at Sp locus.

The apiculus color in genotype of $C^{Br}Sp$ is Rose red at flowering, but on ripening becomes discolored and turns into Straw white. There is another apiculus color type in which tawny color begins to develop at ripening, in spite of showing similar color shades to $C^{Br}Sp$ at flowering. This type of coloration, tentatively designated as "Y-type", is classified into the following two types in their intensity of color shade.

	Anthocyanin color at flowering	Tawny color at ripening	Varieties belong to
i	Amaranth purple	Russet, but somewhat light	Chogoei, Rikuu-132-go,
ii	Pomegranate purple	Tawny, „	Norin-20-go, Kairyobozu

(fig. 3 of Plate I and fig. 1-B of Plate II)

The crosses between Y-type and $C^{B}Sp^{+}$ or $C^{Bp}Sp^{+}$, which is colorless but turns into tawny, gave Y-type in F_1 and segregated in F_2 as two classes of phenotypes, colored (Y-type) and colorless (tawny at ripening) in a ratio of 3:1, as shown in Table 15.

If the Y-type colored plants in these crosses possess *Sp*—the modifier for *C*-chromogen—some progenies or segregants with Blackish red purple or Pansy purple apiculus, having genotypes of $C^{B}Sp$ or $C^{Bp}Sp$, should appear in F_1 and F_2. However, as mentioned above, the result was quite different, and it was brought forward to indicate that the Y-type should have another modifier, somewhat different from *Sp*, instead of *Sp*.

This is supposed to be another allele at *Sp*-locus which is designated

TABLE 15. F_1 and F_2 from crosses between the Y-type and $C^{B}Sp^{+}$ or $C^{Bp}Sp^{+}$.

a. $C^{B}Sp^{+} \times$ Y-type

P_1 combination	F_1 color shade	F_2 Amaranth purple	Pomegranate purple	White (tawny)	total	χ^2 ($\Sigma\chi_i^2$)	d. f.	p
Chikoto ×Y-type (Chogoei)	Blackish red purple	302		120	422	2.657	1	0.2–0.1
Chabo ×Y-type (Chogoei)	"	272		80	352	0.970	"	0.5–0.3
Ebisumochi ×Y-type (Bunwaimomigare)	"	183		62	245	0.012	"	0.95–0.9
Ebisumochi ×Y-type (Bunwaikamairazu)	"	217		66	283	0.425	"	0.7–0.5
Muyozetsumotsure ×Y-type (Chogoeiyoshinto(	"	190		74	264	1.293	"	0.3–0.2
total		1164		402	1566	(5.357)	5	0.5–0.3
C (3 : 1)		1174.50		391.50	1566.00	0.375	1	0.7–0.5

b. $C^{Bp}Sp^{+} \times$ Y-type

Ebisu-hen ×Y-type (Chogoei)	Blackish red purple	209	78	94	381	0.751	2	0.7–0.5
Ebisu ×Y-type (Bunwaikamairazu)	"	138	43	77	258	3.371	"	0.2–0.1
total		347	121	171	639	(4.122)	4	0.5–0.3
C (9 : 3 : 4)		359.44	119.81	159.75	639.00	1.225	2	0.7–0.5
Akage ×Y-type (Chogoei)	Blackish red purple	489		180	669	1.296	1	0.3–0.2
Ebisu ×Y-type (Chogoei)	"	243		92	335	1.084	"	"
Ebisu ×Y-type (Bunwaimomigare)	"	217		60	277	1.647	"	0.2–0.1
total		949		332	1281	(4.027)	3	0.3–0.2
C (3 : 1)		960.75		320.25	1281.00	0.567	1	0.5–0.3
Ebisu ×Y-type (Norin-20-go)	Pansy purple		294	99	393			
C (3 : 1)			294.75	98.25	393.00	0.008	"	0.95–0.9

as Sp^d (d means dilute). As to the action of Sp^d, it will be assumed that this allele is less potent than Sp, and the color shade of anthocyanin in the C^BSp^d or $C^{Bp}Sp^d$ is only able to reach a mere Amaranth purple or Pomegranate purple respectively, in spite of having higher rank allele of C-locus, C^B or C^{Bp}, which is sufficient in presenting Blackish red purple or Pansy purple in coexistence with Sp.

According to this assumption, and examining another cross combination, Y-type $\times C^+Sp^+$, in which a parent has no chromogenic gene or its modifier, F_1 showed the same type of coloration as that of Y-type parent, while in F_2 in addition to the parental types of coloration, a new type viz. colorless at flowering and tawny colored at ripening, appeared (Table 16). The ratio of three types of coloration, red (Amaranth purple or Pomegranate purple en block) flowering color with tawny ripening color, flowering colorless with ripening tawny, and flowering colorless with Straw white ripening color, is approximately 9:3:4, which suggests that it is based on a digenic scheme of segregation, the parental Y-type being double dominant over the parental colorless, C^+Sp^+. It is natural to consider that these two genes may be C (C^B or C^{Bp}) and Sp^d respectively.

TABLE 16. F_1 and F_2 from crosses between the Y-type and C^+Sp^+.

P_1 combination	F_1 color shade	F_2							
		Amaranth purple	Pomegranate purple	White		total	χ^2 ($\Sigma\chi_i^2$)	d. f.	p
				tawny	white				
Shinkodaikoku ×Y-type (Chogoei)	Amaranth purple	153		50	75	278	0.595	2	0.8–0.7
Daikoku ×Y-type (Chogoei)	"	85		27	46	158	1.471	"	0.5–0.3
ty-1-16-m ×Y-type (Chogoei)	"	343		104	120	567	5.194	"	0.1–0.05
total		581		181	241	1003	(7.260)	6	0.3–0.2
C (9 : 3 : 4)		564.19		188.06	250.75	1003.00	1.145	2	0.7–0.5
Daikoku ×Y-type (Momigareso-1)	Pomegranate purple		92	22	47	161	3.376	"	0.2–0.1
Muyozetsu-ty ×Y-type (Momigareso-1)	"		52	21	25	98	0.561	"	0.8–0.7
total			144	43	72	259	(3.937)	4	0.5–0.3
C (9 : 3 : 4)			145.69	48.56	64.75	259.00	1.468	2	"

If it be so, which of the alleles of *C*-locus, C^B or C^{Bp}, does Chogoei, Rikuu-132-go, Norin-20-go, Kairyobozu and Norin-20-go have? In this respect, some test crosses were made (Table 17). The F_1 phenotype and F_2 segregation in these crosses were very close to expectation, on the basis of genic constitutions that Chogoei and Rikuu-132-go are C^BSp^d, and Norin-20-go and Kairyobozu are $C^{Bp}Sp^d$.

TABLE 17. F_1 and F_2 from crosses between Y-type varieties and some genotypic plants of C^BSp or $C^{Bp}Sp$.

P_1	F_1	F_2							
combination (Y-type tester)	color shade	Blackish red purple C^BSp	Pansy purple $C^{Bp}Sp$	Amaranth purple C^BSp^d	Pomegranate purple $C^{Bp}Sp^d$	total	χ^2 ($\Sigma\chi_i^2$)	d. f.	p
Chogoei ×C^BSp	Blackish red purple	684		216		900	0.480	1	0.5 –0.3
Bunwaimomigare ×C^BSp	"	150		51		201	0.015	"	0.95–0.9
Rikuu-132-go ×C^BSp	"	295		106		401	0.440	"	0.7 –0.5
total		1129		373		1502	(0.935)	3	0.9 –0.8
C (3 : 1)		1126.50		375.50		1502.00	0.022	1	"
Chogoeiyoshinto ×$C^{Bp}Sp$	Blackish red purple	449	164	219		832	1.763	2	0.5 –0.3
Chogoeiyoshinto ×$C^{Bp}Sp$	"	426	151	172		749	2.088	"	"
total		875	315	391		1581	3.851	4	"
C (9 : 3 : 4)		889.31	296.44	395.27		1581.00	1.438	2	"
Kairyobozu ×C^BSp	Blackish red purple	177	63	58	24	322	1.050	3	0.8 –0.7
Norin-20-go ×C^BSp	"	453	156	141	42	792	2.020	"	0.7 –0.5
total		630	219	199	66	1114	(3.070)	6	0.8 –0.7
C (9 : 3 : 3 : 1)		626.63	208.88	208.88	69.63	1114.02	1.160	3	"
Kairyobozu ×$C^{Bp}Sp$	Pansy purple		283		89	372	0.229	1	0.7 –0.5
Kairyobozu ×$C^{Bp}Sp$	"		243		64	307	2.824	"	0.1 –0.05
total			526		153	679	(3.053)	2	0.3 –0.2
C (3 : 1)			509.25		169.75	679.00	2.204	1	0.2 –0.1

What type of coloration will result when Sp^d coexists with C^{Br}, the less potent chromogenic allele at *C*-locus, and does a variety in which the genotype is assumed to be $C^{Br}Sp^d$, exist or not?

For verification of the above, two crosses were examined. In these, F_2 progenies from $C^BSp^d \times C^{Br}Sp$ should segregate into four types of coloration, Blackish purple (C^BSp), Y-type (C^BSp^d), Rose red ($C^{Br}Sp$) and $C^{Br}Sp^d$ in a ratio of 9:3:3:1. As presented in Table 18 a F_2 segregants which should have genotype of $C^{Br}Sp^d$ were colorless; to be exact whitish orange or pale orange (Seashell pink; fig. 3 of Plate I and fig. 1-B of Plate II). This was also ascertained from a cross between C^BSp (Kuromochi) and the whitish orange which had been bred from a progeny of the above cross. If a whitish orange parent was $C^{Br}Sp^d$, the mode of F_2 segregation should result in the same as the above cross, $C^BSp^d \times C^{Br}Sp$. The result closely fitted with the expectation (Table 18 b). Because of a small quantity of chromogenic substance and a lesser potency of action of the modifier, it seems probable that anthocyanin

TABLE 18. F_1 and F_2 from crosses, $C^BSp^d \times C^{Br}Sp$ and $C^{Br}Sp^d \times C^BSp$.

a. $C^BSp^d \times C^{Br}Sp$

P_1 combination	F_1 color shade	F_2 Blackish red purple C^BSp	Amaranth purple C^BSp^d	Rose red $C^{Br}Sp$	Seashell pink or White $C^{Br}Sp^d$	total	χ^2 ($\Sigma\chi_i^2$)	d. f.	p
Bunwaichogoei ×Akamuro	Blackish red purple	215	65	74	21	375	0.920	3	0.9 -0.8
Chogoei ×Akamuro	"	245	77	84	29	435	0.449	"	0.95-0.9
total		460	142	158	50	810	(1.369)	6	0.98-0.95
C (9 : 3 : 3 : 1)		455.63	151.88	151.88	50.63	810.02	0.950	3	0.9 -0.8

b. $C^{Br}Sp^d \times C^BSp$

N-48 ×Karasumochi	Blackish red purple	100	33	37	12	182	0.368	3	0.95-0.9
N-48 ×Kokushokuto	"	245	65	75	27	412	2.797	"	0.5 -0.3
total		345	98	112	39	594	(3.165)	6	0.8 -0.7
C (9 : 3 : 3 : 1)		334.13	111.38	111.38	37.17	594.02	2.068	3	0.7 -0.5

pigment is unable to appear in $C^{Br}Sp^{d}$ plant.

As to the demonstration of existence of the genotypic variety, $C^{Br}Sp^{d}$, a result of the examination presented in Table 19 may answer the purpose, showing that the genic constitution of Kitamurawase-2, one of the known varieties, is none other than $C^{Br}Sp^{d}$.

TABLE 19. F_1 and F_2 from crosses, involving Kitamurawase-2 and Kaieifunento.

P_1 combination	F_1 color shade	F_2 Pansy purple $C^{Bp}Sp$	Pome-granate purple $C^{Bp}Sp^{d}$	Rose red $C^{Br}Sp$	Sea-shell pink or white $C^{Br}Sp^{d}$	total	χ^2 ($\Sigma\chi_i^2$)	d. f.	p
Kitamurawase-2 × $C^{Bp}Sp$	Pansy purple	180	52	54	26	312	3.351	3	0.5–0.3
ditto	"	191	68	67	17	343	1.250	"	0.8–0.7
Kaieifunento × $C^{Bp}Sp$	"	208	56	49	28	341	7.927	"	0.05–0.02
total		579	176	170	71	996	(12.528)	9	0.2–0.1
C (9 : 3 : 3 : 1)		560.25	186.75	186.75	62.25	996.00	3.946	3	0.3–0.2

From the result of these cross experiments as presented in Table 15–19, it is possible to conclude that in addition to Sp and Sp^{+}, there exists another allelic gene Sp^{d} which is recessive to Sp and dominant over Sp^{+}.

Hence the Sp locus comprises the following three alleles, namely:

$$Sp > Sp^{d} > Sp^{+}.$$

Considering the nature of action of Sp^{d} from a physicochemical point of view, one could assume that this gene can utilize, in the formation of anthocyanin pigment, only a fraction of the chromogenic substance produced. This would account for the light red, rather than purple, color of the $C^{B}Sp^{d}$ or $C^{Bp}Sp^{d}$ phenotype and also for the tawny color of the apiculus at ripening, when the remaining quantity of unchanged chromogenic substance will turn into brownish pigment.

An opinion which have been advanced by SAND, MILNER and SHERMAN (1935) from a biochemical standpoint of view will support the above assumption, namely: when only a fraction of flavonol in plants is turned into anthocyanin by certain causes, the remainder should remain

unchanged, and consequently the flavonols and the corresponding anthocyanins should coexist with each other. It is, therefore, natural to assume that this remaining flavon or some other relative substances may be responsible, directly or indirectly, for the formation of brown pigment viz. tawny.

D. Color Distribution, Caused by *C*, in Itself or Coexistent with *Sp*

With regard to the action of *C* or *CSp*, for the sake of brevity the description has been kept within the coloration on apiculus, however, in actuality the color distribution or sphere of coloration caused by *C* and *CSp* is not restricted to the apiculus but includes some other sites, according to whatever allele at *C*-locus is concerned.

Throughout a considerable amount of cross examinations, several genotypic plants segregated from a combination of alleles of *C* and *Sp* loci show various types of color distribution as well as color shade. In this respect, the detailed accounts are mentioned as follows.

C^B: In combination with *Sp*, this allele gives deep purple (Blackish red purple) color in apiculus, awn, empty glumes and stigma, and purple lines on internode and leaf sheath. With Sp^a it gives pale red (Amaranth purple) at the time of flowering and tawny (somewhat paler than Russet) at the time of ripening in the above sites or parts, and with Sp^+ it makes these parts colorless (green or white) at flowering and tawny (Russet) at ripening.

C^{Bp}: In combination with *Sp*, this allele gives light purple (Pansy purple) in apiculus, awn, empty glumes and stigma. No colors are seen in internode or leaf sheath. This is an outstanding phenotypic difference between C^BSp and $C^{Bp}Sp$, though faint stripes are seldom seen in the intermode of $C^{Bp}Sp$ when it is exposed to direct sun light for a long time. With Sp^a it makes the same parts as the above light red (Pomegranate purple) except that the stigma is uncolered, and with Sp^+ gives green (or white) at flowering and tawny at ripening; the shade of the tawny being somewhat paler than tawny.

C^{Br}: With *Sp*, C^{Br} produces pale red or pink (Rose red) in apiculus, awn and empty glumes, but white stigmas and green internode and leaf sheath. When combined with Sp^a detectable anthocyanin or tawny coloration is not seen, with the apiculus and other parts remaining whitish orange or straw color both at flowering and at ripening. With

TABLE 20. Color distribution of genotypes from every combination between *C* and *Sp* loci genes.

	C-locus	*Sp*-locus	Anthocyanin color shade	mode of coloration			
				awn	apiculus	empty glume	stigma
1.	C^B	*Sp*	Blackish red purple	full	full	full	full
		Sp^d	Amaranth purple	ditto	ditto	ditto	not detectable
2.	C^{Bp}	*Sp*	Pansy purple	ditto	ditto	ditto	full
		Sp^d	Pomegranate purple	ditto	ditto	colored at apex	— [2]
3.	C^{Bt} [1]	*Sp*	Tyrian rose	ditto	ditto	ditto	—
		Sp^d	may be Salmon buff	undetermined			
4.	C^{Br}	*Sp*	Rose red	ditto but faint at apex	ditto	ditto	—
		Sp^d	Seashell pink or white	only at basal site	only at apex	not detectable	—
5.	C^+	*Sp*	White	—	—	—	—
		Sp^d	White	—	—	—	—

(continued)

	mode of coloration			tawny color shade in apiculus in the absence of *Sp* and Sp^d
	inner surface of leaf sheath	internode	outer surface of internode	
1.	colored at lower part	striped	striped	Russet
	ditto	ditto	ditto	
2.	faintly colored at lower part	—	—	Tawny
	not detectable	—	—	
3.	—	—	—	Ochraceous buff
4.	—	—	—	Warm buff
	—	—	—	
5.	—	—	—	Straw white
	—	—	—	

1) C^{Bt}: refer to following section.

2) — : indicates "uncolored".

Sp^+ these parts are colorless at flowering but the apiculus becomes pale brown (Warm buff) at ripening.

C^+: No chromogenic substance is formed and no colors appear during any part of vegetative or maturing periods.

These results are tabulated as in Table 20, in which it is pointed out that every allele at *C*-locus gives rise to respective color shades, in cooperation with any one of the allele at *Sp*-locus, in awn and empty glumes as well as in apiculus. In addition to this, it is worthy of note that besides these coloring parts some other parts are coincidently colored as a result of the presence of the allele at *C*-locus, indicating that the action of the *C*-gene is pleiotropic in regards to the location or distribution of color. It is further noticeable that the expanse of coloring parts is proportional to the rank of dominancy of allele in *C*-locus. (fig. 1-A, B of Plate II).

E. Genic Scheme on Glume Coloration

One of the most striking color types in glumes is the coloration over the entire surface of the floral glumes viz. lemma and palea. Glumes of rice plant are self colored in the following shades of color; Blackish red purple, Pansy purple, Amaranth purple or Pomegranate purple in coexistance with apiculus genes, C^BSp, $C^{Bp}Sp$, C^BSp^d or $C^{Bp}Sp^d$ respectively (NAGAO and TAKAHASHI 1947 · 1948 b · 1952 b, NAGAO 1951). Japanese names of some varieties such as Karasu-mochi, Kuro-mochi, Kuro-uruchi or Kuro-momi are well associated with the mode of said coloration.

Table 21 represents the genetic behavior on these colorations, indicating that in addition to the apiculus genes *C* and *Sp*, there is a single dominant gene which is responsible for the distribution of pigment substance produced in the apiculus over the entire surface of lemma and palea. This gene is designated as *Rp*. (fig. 2 of Plate II).

On which gene, *C* or *Sp*, does this gene *Rp* exert its effect? It is most probable that *Rp* acts on *C*, since segregants which are colored with tawny over their entire surface of lemma and palea came out in F_2 from crosses presented in Table 21. This is also ascertained with crosses of which parental varieties have self colored glumes with tawny (Table 22).

TABLE 21. Genic relation between apiculus color and glume color with anthocyanin.

a. $C^{B}SpRp^{+}$ (apiculus colored)×$C^{B}SpRp$ (full colored)

P_1 combination	apiculus	F_2 Blackish red purple $C^{B}\ Sp$		Pansy purple $C^{Bp}\ Sp$		Amaranth purple $C^{B}\ Sp^{d}$		Pomegranate purple $C^{Bp}\ Sp^{d}$	
	glume	ditto	green	ditto	green	ditto	green	ditto	green
		Rp	Rp^{+}	Rp	Rp^{+}	Rp	Rp^{+}	Rp	Rp^{+}
Shimadamochi ×Kuromochi		519	152						
Akaine ×Kuromochi		549	161						
total		1068	313						
C (3 : 1)		1035.75	345.25						

b. $C^{Bp}Sp^{d}\ Rp^{+}$ (apiculus colored)×$C^{B}SpRp$ (full colored)

Kairyobozu ×Kokushokuto		134	43	45	18	43	15	17	7
Norin-20 -go ×Karasumochi		348	105	119	37	97	44	30	12
total		482	148	164	55	140	59	47	19
C (27:9:9:3:9:3:3:1)		469.97	156.66	156.66	52.22	156.66	52.22	52.22	17.41

c. $C^{Br}Sp^{+}Rp^{+}$ (white)×$C^{B}SpRp$ (full colored)

Mantaro ×Kuromochi		354	126						
C (27 : 9 : 12 : 16)		358.59	119.53						

d. $C^{+}Sp^{d}\ Rp^{+}$ (white)×$C^{B}SpRp$ (full colored)

Muyozetsu ×Kokushokuto		154	44			26	19		
Kamairazu-so ×Bunwaimochi		93	44			42	13		
total		247	88			68	32		
C (27 : 9 : 9 : 3 : 16)		245.11	81.70			81.70	27.23		

e. $C^{+}Sp^{+}Rp^{+}$ (white)×$C^{B}SpRp$ (full colored)

Fukoku ×Kuromochi		354	138						
Daikoku ×Kuromochi		200	73						
Hokkaimochi-1-go ×Kuromochi		144	57						
Muyozetsu-ty ×Kokushokuto		64	25						
total		762	293						
C (27 : 9 : 9 : 3 : 16)		780.47	260.16						

f. $C^{+}Sp^{+}Rp^{+}$ (white)×$C^{Bp}SpRp$ (full colored)

Hokkaimochi-1-go ×Kuroke				497	173				
Daikoku ×Tokachikuromomi				108	34				
total				605	207				
C (27 : 9 : 12 : 16)				576.28	192.09				

TABLE 21. (continued)

continued on the right side of the preceding table.

a.

F_2									
Rose red	Russet		Tawny		Warm buff or White	total	χ^2	d.	p
$C^{Br}Sp$	$C^{B}Sp^{a}$		$C^{Bp}Sp^{+}$		other genotypes				
green	ditto	Straw white	ditto	Straw white	green or Straw white		($\Sigma\chi_i^2$)	f.	
Rp, Rp^{+}	Rp	Rp^{+}	Rp	Rp^{+}	Rp, Rp^{+}				
						671	1.972	1	0.2 –0.1
						710	2.045	„	„
						1381	(4.017)	2	„
						1381.00	4.017	1	0.05–0.02
b.									
						322	1.856	7	0.98–0.95
						792	5.981	„	0.7 –0.5
						1114	(7.837)	14	0.9 –0.8
						1114.02	4.610	7	0.8 –0.7
c.									
154	216					850			
159.38	212.50					850.00	0.648	3	0.9 –0.8
d.									
					78	321	11.793	4	0.02–0.01
					68	260	5.026	„	0.3 –0.2
					146	581	(16.819)	8	0.05–0.02
					145.25	581.00	3.648	4	0.5 –0.3
e.									
	127	49			215	883	4.060	4	0.5 –0.3
	66	23			103	465	3.510	„	„
	46	17			79	343	2.284	„	0.7 –0.5
	18	10			42	159	2.291	„	„
	257	99			439	1850	(12.145)	16	0.8 –0.7
	260.16	86.72			462.50	1850.01	5.981	4	0.3 –0.2
f.									
			193		267	1130	4.650	3	0.3 –0.2
			44		50	236	2.100	„	0.7 –0.5
			237		317	1366	(6.750)	6	0.5 –0.3
			256.13		341.50	1366.00	5.767	3	0.2 –0.1

TABLE 22. F_1 and F_2 of crosses on tawny coloration in glumes involving *Rp*.

a. F_2 segregation.

$C^BSp^+Rp \times C^{Bp}SpRp$ (full colored with tawny and anthocyanin)

P_1 combination	F_1 color shade	F_2 anthocyanin full $C^B(C^{Bp})Sp(Sp^d)Rp$	anthocyanin apiculus $C^B(C^{Bp})Sp(Sp^d)Rp^+$	tawny full $C^B(C^{Bp})Sp^+Rp$	tawny apiculus $C^B(C^{Bp})Sp^+Rp^+$	total	χ^2 $(\sum\chi_i^2)$	d. f.	p
Chabo × Kurikara-mochi	full; Blackish red purple	213 65		70 25		373			
C (9 : 3 : 3 1)		209.81 69.94		69.94 23.31		373.00	0.520	3	0.95-0.9
$C^BSp^+Rp \times C^BSp^dRp^+$ (full colored with tawny; apiculus colored with anthocyanin)									
Chikoto × Chogoei	full; Amaranth purple	240	71	90	31	432	2.864	3	0.5-0.3
Chabo × Chogoei	"	195	65	67	24	351	0.262	"	0.98-0.95
total		435	136	157	55	783	(3.126)	6	0.8-0.7
C (9 : 3 : 3 : 1)		440.44	146.81	146.81	48.94	783.00	2.450	3	0.5-0.3

b. F_1 coloration.

P_1 name	P_1 color shade [1]	P_1 genotype	F_1 mode of coloration
N-44 ×Chikoto	White full; Russet	$C^+SpRp^+ \times C^BSp^+Rp$	full; B-r-p
N-43 × "	" " ; "	" × "	" ; "
Akamuro × Nakazawadaikoku	apiculus; Ro-r × apiculus; B-r-p	$C^{Br}SpRp \times C^BSpRp^+$	" ; "
" ×Shimadamochi	" ; " × " ; "	" × "	" ; "
" ×Akaine	" ; " × " ; "	" × "	" ; "
" ×Chogoei	" ; " × " ; Am-p	" $\times C^BSp^dRp^+$	" ; "
" ×Ebisumochi	" ; " × " ; Russ	" $\times C^BSp^+Rp^+$	" ; "
" ×Murasaki	" ; " × " ; Pa-p	" $\times C^{Bp}SpRp^+$	" ; Pa-p
" ×Shito	" ; " × " ; "	" × "	" ; "
" ×Hatsumurasaki	" ; " × " ; "	" × "	" ; "
" ×Norin-20-go	" ; " × " ; Po-p	" $\times C^{Bp}Sp^dRp^+$	" ; "
" ×Ebisu	" ; " × " ; Ty	" $\times C^{Bp}Sp^+Rp^+$	" ; "
" ×Akageshima	" ; " × " ; "	" × "	" ; "
" ×Momigare	" ; " × " ; "	" × "	" ; "
" ×Motsure-so	" ; " × " ; "	" × "	" ; "
" ×Motsure-datsu	" ; " × " ; "	" × "	" ; "

1) B-r-p: Blackish red purple. Pa-p: Pansy purple. Am-p: Amaranth purple. Po-p: Pomegranate purple. Ro-r: Rose red. Russe Russet. Ty: Tawny.

The genic constitution of self colored glumes may be then represented as: Blackish red purple ($C^{B}SpRp$), Pansy purple ($C^{Bp}SpRp$), Amaranth purple ($C^{B}Sp^{d}Rp$), Pomegranate purple ($C^{Bp}Sp^{d}Rp$), Russet ($C^{B}Sp^{+}Rp$) and Tawny ($C^{Bp}Sp^{+}Rp$). In genotypes of $C^{B}Sp^{d}Rp$ and $C^{Bp}Sp^{d}Rp$ which show a reddish color at flowering, tawny color overlaps at ripening. This is also shown in Table 21 and fig. 2 of Plate II.

In connection with this, it is worthy of note that in genotypes of $C^{Br}SpRp$ and $C^{Br}Sp^{+}Rp$, there is no sign of coloration in floral glumes except in apiculus and empty glumes. There are no differences of color types in each two genotypes between $C^{Br}SpRp$ and $C^{Br}SpRp^{+}$, or between $C^{Br}Sp^{+}Rp$ and $C^{Br}Sp^{+}Rp^{+}$. This phenomena probably is due to the fact that C^{Br} produces too small an amount of chromogenic substance to distribute pigment all over the lemma and palea. The propriety of this assumption was demonstrated by cross examination in which Akamuro variety was used as a parent. This is presented in Table 22-b and 23.

In this variety a Rose red color is restricted only to the apiculus and empty glumes, showing phenotypically the same type of coloration as that in $C^{Br}SpRp^{+}$. The F_1 from the cross between Akamuro and other varieties with uncolored glume, however, shows a new type of coloration viz. full-colored glumes, and in F_2, the full-colored behaves as single dominant over colorless with respect to the extension of glume color. This mode of segregation cannot be understood unless Akamuro possesses the distributing gene *Rp*.

As to the distribution of color by *Rp*, it is considered that it extends from floral glumes to rachis, when *Rp* coexists with $C^{B}Sp$ or $C^{Bp}Sp$.

Thus the genotypes and their phenotypes on floral glumes may be classified as mentioned below. In this description, symbols of glume color types and examples of actual varieties are given in parenthesis.

i) Colored types: Anthocyanin color came out in the flowering stage, and the color remains up to the ripening stage.

$C^{B}SpRp$—Floral glume and rachis are Blackish red purple, internode and leaf sheath have purple lines. (I; Kuromochi, Kurouruchi, Kokushokuto).

$C^{Bp}SpRp$—Floral glumes and rachis are Pansy purple; the internode is green. (II; Takachikuromomi, Kuroke, Kurikaramochi).

$C^{B}SpRp^{+}$—Apiculus, including empty glumes, are Blackish red purple; internode and leaf sheath have purple lines. (III; Shimadamochi, Akaine, Nakazawadaikoku).

TABLE 23. Anthocyanin and tawny coloration in floral glumes of F_1 and F_2 plants in crosses involving $C^{Br}SpRp$, a genotype of variety Akamuro.

a. $C^B(C^{Bp})Sp^+Rp \times C^{Br}SpRp$

P_1 combination	F_1 color shade	F_2 anthocyanin: Blackish red purple or Pansy purple, full: $C^B(C^{Bp})Sp\,Rp$	anthocyanin: Blackish red purple or Pansy purple, apiculus: $C^B(C^{Bp})Sp\,Rp^+$	anthocyanin: Rose red, apiculus: $C^{Br}SpRp^+$ / $C^{Br}Sp\,Rp^+$	tawny: Russet or Tawny, full: $C^B(C^{Bp})Sp^+Rp$	tawny: Russet or Tawny, apiculus: $C^B(C^{Bp})Sp^+Rp^+$	tawny: Warm buff or Straw white, full & apic.: $C^{Br}Sp^+$ or without $C^B \sim C^{Br}$	total	χ^2 ($\Sigma\chi_i^2$)	d. f.	p
Chikoto × Akamuro	full; Blackish red purple	488		132	122		68	810			
C (9 : 3 : 3 : 1)		455.63		151.88	151.88		50.63	810.02	16.739	3	0.01

b. $C^B(C^{Bp})Sp^+Rp^+ \times C^{Br}SpRp$

Ebisu × Akamuro	full; Blackish red purple	412	134	173	135	52	64	970	1 631	5	0.9–0.8
Ebisumochi × Akamuro	,,	298	96	115	92	77		678	1.881	4	0.8–0.7
total		710	230	288	227	193		1648	(3.512)	9	0.95–0.9
C (27:9:12:9:7)		695.25	231.75	309.00	231.75	180.25		1648.00	2.765	4	0.7–0.5

c. $C^+Sp^+Rp^+ \times C^{Br}SpRp$

Daikoku × Akamuro	apiculus; Rose red			465			368	833			
C (36 : 28)				468.56			364.44	833.00	0.108	1	0.8–0.7

$C^{Bv}SpRp^+$—Apiculus and empty glumes are Pansy purple; internode and leaf sheath are green. (IV; Shito, Murasaki, Hatsumurasaki).

ii) Colored-tawny types: Anthocyanin color occurs in flowering stage, the color changing to tawny in the ripe stage.

C^BSp^dRp—In the flowering stage the color of glumes is red (Amaranth purple), while the internode and leaf sheath have pale red lines.

The color changes to tawny in the ripe stage. (V; H–60).

$C^{Bp}Sp^{d}Rp$—Similar to V, except for green internode and leaf sheath, and somewhat lighter color shade than V, both in anthocyanin (Pomegranate purple) and tawny (light Tawny). (VI).

$C^{B}Sp^{d}Rp^{+}$—Apiculus and empty glumes are Amaranth purple, changing to tawny (Russet) at ripening, while pink lines are evident on internode and leaf sheath. (VII; Chogoei, Rikuu-132-go, Tomoenishiki, Otamochi, Isawomochi).

$C^{Bp}Sp^{d}Rp^{+}$—Similar to VII, except for green internode and leaf sheath, and somewhat light color shade in anthocyanin and tawny. (VIII; Minamochi, Norin-20-go, Kairyobohzu, Hokkai-87-go).

iii) Colored-green types: Anthocyanin color occurs in the flowering stage and disappears with ripening.

$C^{Br}SpRp$, $C^{Br}SpRp$—Colors of apiculus, awn and empty glumes are Rose red in flowering and Straw white at ripening. There is no phenotypic difference between these two genotypes. (IX; Akamuro).

iv) Green-tawny types: Green in the flowering stage, with brownish or tawny color appearing at certain sites of floral glumes at ripening.

$C^{B}Sp^{+}Rp$—Tawny color (Russet) spreads over the entire surface of glumes as well as apiculus and empty glumes, on Cripening. (X; Chabo Chikoto).

$C^{Bp}SpRp$—Same as above, except color is light (tawny). (XI; B–12).

$C^{B}SpRp^{+}$—Russet color is restricted to apiculus and empty glumes. (XII; Bunketsuwaito, Ebisumochi).

$C^{Bp}Sp^{+}Rp^{+}$—Same color shade as XI is restricted to apiculus and empty glumes. (XIII; Akage, Ebisu).

v) Green types: Green in the flowering and Straw white at ripening.

$C^{Br}Sp^{d}Rp$, $C^{Br}Sp^{d}Rp^{+}$—Apiculus are faintly colored with whitish color, but change to straw white at ripening. (XIV; Kitamurawase-2, Kaieifunento. N–48).

$C^{Br}Sp^{+}Rp$, $C^{Br}Sp^{+}Rp^{+}$—Colorless in the flowering and scarecely colored (Warm buff) at ripening. (XV: Mantaro).

Other combinations without C—Colorless in both flowering or ripening stage. (XVI; Bozu, Fukoku, Hokkaimochi-1-go).

F. Brief of Genic Scheme on Coloration in Other Vegetative Parts

With respect to coloration of certain parts other than apiculus and glumes, NAGAO and the author (1951a·b, 1952a) have reported on the presence of genes, *Pl*, *Pn* and *Ipl*, which are responsible for the coloration occurring in such parts as leaf blade, leaf sheath, stem node, ligule, pulvinus and auricle. Detailed accounts on examinations of analysing these genes, being not the principal subject on the present paper, are abridged here, and in this section, mention will be made of conclusive and a brief description on the nature of these genes so that the illustration in the following section will be easier to be comprehended.

The following three types of coloration in leaf blade are distinguished as follows;

i) Full colored: This is a self colored leaf character designated as "Murasakiine or Shito" type.

ii) Colored leaf spex and margins: The pigment appears mainly at the apex and margins, with scattered, irregular, fine colored stripes here and there on the leaf surface. This is designated as "Akaine" type.

iii) Colored midrib: The pigment is found primarily in the midrib and is especially distinct on the lower surface of the leaf. This is designated as "Shimadamochi" type.

Of these three types of coloration, the genetic mechanism which is responsible for "Shinadamochi" type is still obscure, although, as mentioned before, it is known that the pleiotropic action of apiculus gene, C^B and C^{Bp}, is generally responsible in combination with *Sp* or Sp^d. Two other types, "Murasakiine" and "Akaine", are concluded to be developed in the presence of genes *Pl* and *Pn* respectively, in coexistence with apiculus genes, *C* and *Sp*.

The phenotypic expression of *Pl* and *Pn* are largely dependent on the constitution of genes responsible for apiculus coloration. They are presented as in Table 24 and Plate III. As shown in this table, *Pl* and *Pn* may be said to be the modifiers which are related with the distribution of the pigment substance produced in apiculus. And it is also shown that the distributing effect of these genes varies according to which allele of *C* and *Sp* loci coexist with; that is to say it varies according to the color intersity in the apiculus. For example,

TABLE 24. Mode of color distribution due to *Pl*, *Pn* and *Ipl*, in cooperation with *C* and *Sp*.

genes concerned		*Pl*		*Pn*		*Pl Ipl*	
		$C^B(C^{Bp})Sp$	$C^B(C^{Bp})Sp^d$	$C^B(C^{Bp})Sp$	$C^B(C^{Bp})Sp^d$	$C^B(C^{Bp})Sp$	$C^B(C^{Bp})Sp^d$
color shade		purple	red	purple	red	purple	red
part colored	rachis	entirety	entirety	—	—	entirety	entirety
	leaf blade	〃	〃	apex and margin	apex and margin	part attached to pulvinus	part attached to pulvinus
	leaf sheath	〃	〃	intervening part of vascular bundle [1]	intervening part of vascular bundle [1]	entirety	entirety
	auricle and ligule	〃	〃	entirety	entirety	〃	〃
	pulvinus	〃	〃	〃	〃	〃	〃
	node	〃	〃	〃	〃	〃	〃
	internode	part exposed to the sun	part exposed to the sun	intervening part of vascular bundle [1]	intervening part of vascular bundle [1]	part exposed to the sun	part exposed to the sun
	pericarp	entirety [2]	entirety [2]	—	—	entirety [2]	entirety [2]

1) Limited to C^BSpPn or C^BSp^dPn.
2) Found only in the case of clipping operated caryopsis.

purple pigment can occur in leaf blades when *Pl* and *Pn* are present in combination with either C^B *Sp* or C^{Bp} *Sp*; but when the apiculus color constitution is $C^{Br}Sp$, no color develops in leaf blade or leaf sheath. They remain green no matter what leaf-color gene are present. Furthermore, the purple leaf colors beceme paler when *Pl* and *Pn* are combined with C^BSp^d or $C^{Bp}Sp^d$, appearing as greenish red instead of dark purple.

Therefore, the apiculus color genes have an effect here similar to their effect on the development of glume color, and also, with respect to the modes of color distributions caused by *Pl* and *Pn*, typical distributions are given in the presence of apiculus genes C^BSp or $C^{Bp}Sp$.

TABLE 25. Summary of F_2 segregations of color in leaf blade, involving *Pl*.
(full colored $C^B(C^{Bp})SpPl \times$ colorless).

apiculus color	phenotype	purple		red (tawny)		pink	green	total	number of cross combinations	χ^2	d. f.	p
	genotype	$C^B(C^{Bp})Sp$		$C^B(C^{Bp})Sp^d$		$C^{Br}Sp$	$C^B(C^{Bp})Sp^+, C^{Br}Sp^d$ $C^{Br}Sp^+, C^+Sp$ C^+Sp^d, C^+Sp^+					
leaf color	phenotype	purple	green	red	green	green	green			($\Sigma\chi_i^2$)		
	genotype	*Pl*	*Pl*+	*Pl*	*Pl*+	*Pl*, *Pl*+	*Pl*, *Pl*+					
$C^B(C^{Bp})Sp$ [1]	0	1372	450					1822	4	0.069	1	0.8 –0.7
	(3 : 1)	3	1					4		(2.342)	4	0.7 –0.5
	C	1366.50	455.50					1822.00				
$C^B(C^{Bp})Sp^d$	0	249	80	86	25			440	2	0.461	3	0.95–0.9
	(3 : 1) (3 : 1)	9	3	3	1			16		(2.250)	6	0.9 –0.8
	C	247.50	82.50	82.50	27.50			440.00				
$C^B(C^{Bp})Sp^+$	0	1583	504				681	2768	8	1.043	2	0.7 –0.5
	(3 : 1) (3 : 1)	9	3				4	16		(7.377)	16	0.98–0.95
	C	1557.06	519.00				692.00	2768.00				
$C^{Br}Sp$	0	321	130			150		601	2	3.519	2	0.2 –0.1
	(3 : 1) (3 ; 1)	9	3			4		16		—	—	—
	C	338.06	112.69			150.25		601.00				
$C^{Br}Sp^d$	0	134	46	38	14	54	26	312	1	6.116	5	0.3 –0.2
	(9:3:3:1) (3:1)	27	9	9	9	12	16	64				
	C	131.63	43.88	43.88	14.63	58.50	19.50	312.02				
$C^{Br}Sp^+$	0	133	52			58	73	316	2	1.769	3	0.7 –0.5
	(9 : 3 : 4) (3 : 1)	27	9			12	16	64		(3.205)	6	0.8 –0.7
	C	133.31	44.44			59.25	79.00	316.00				
C^+Sp^d	0	322	91	87	45		171	716	3	8.368	4	0.1 –0.05
	(9 : 3 : 4) (3 : 1)	27	9	9	3		16	64		(10.500)	8	0.7 –0.5
	C	302.06	100.69	100.69	33.56		179.00	716.00				
C^+Sp^+	0	805	286				792	1883	7	3.067	2	0.3 –0.2
	(9 : 7) (3 : 1)	27	9				28	64		(18.105)	14	0.5 –0.3
	C	794.39	264.80				823.81	1883.00				

1) Genes in colum 1 indicate genotype for apiculus color in parental varieties in which leaf blade colors are green.

TABLE 26. Summary of F_2 segregations of color in stem node, involving *Pn*.
(colored node $C^B(C^{Bp})$ $\overline{SpPn}$ × colorless).

apiculus color	phenotype / genotype	purple $C^B(C^{Bp})\,Sp$		red (tawny) $C^B(C^{Bp})\,Sp^d$		pink $C^{Br}\,Sp$	green $C^B(C^{Bp})Sp^+, C^{Br}Sp^d$ $C^{Br}\,Sp^+, C^+\,Sp$ $C^+\,Sp^d, C^+\,Sp^+$	total	number of cross combinations	χ^2 ($\Sigma\chi_i^2$)	d. f.	p
node color	phenotype genotype	purple *Pn*	green *Pn*+	red *Pn*	green *Pn*+	green *Pn*, *Pn*+	green *Pn*, *Pn*+					
$C^B(C^{Bp})\,Sp$ [1]	0	1659	582					2241		1.13	1	0.3–0.2
	(3 : 1)	3	1					4	4			
	C	1680.75	560.25					2241.00		(4.27)	4	0.5–0.3
$C^B(C^{Bp})\,Sp^d$	0	721	89	82	163			1055		5.19	3	0.2–0.1
	(; 18%)	323 (8)	40 (1)	40 (1)	81 (2)			484	3			
	C	704.06	87.19	87.19	176.56			1055.00		(12.41)	9	"
$C^B(C^{Bp})\,Sp^+$	0	2981	378				1154	4513		1.12	2	0.7–0.5
	(3 : 1) (57 : 7)	171	21				64	256	7			
	C	3014.54	370.21				1128.25	4513.00		(11.60)	14	"
$C^{Br}\,Sp$	0	1042	358			496		1896		1.61	2	0.5–0.3
	(3 : 1) (3 : 1)	9	3			4		16	2			
	C	1066.50	355.50			474.00		1896.00		(1.67)	4	0.8–0.7
$C^+\,Sp^+$	0	824	118				702	1644		3.23	2	0.3–0.2
	(9 : 7) (8 : 1)	72	9				63	144	6			
	C	823.62	101.12				719.26	1644.00		(10.57)	12	0.7–0.5

1) Genes in column 1 indicate genotypes for apiculus color in parental varieties in which node colors are geen.

Thus the genes *Pl* may be said to be concerned with the color distribution of the entire surface of leaf blade, leaf sheath, pulvinus, auricle, ligule, rachis, and node and internode exposed direct to the sun; and also the gene *Pn* may be said to be related with the distribution of color in leaf apex, leaf marins, and entire surface of node, pulvinus, auricle and ligule. The most striking colored parts caused by *Pl* and *Pn* are the entire leaf blade and the stem node respectively, so *Pl* is said to be a gene for leaf blade coloration while *Pn* is a gene for node coloration. The gene symbol "*Pl*" denotes "purple leaf" and "*Pn*" denotes "Purple node".

The experimental data concerning the relation between apiculus color genes, *CSp*, and leaf color gene *Pl*, and between *CSp* and node color gene *Pn* are given in Table 25 and 26 respectively.

In these tables and in regards to the theorecical segregation ratio on node coloration, an 8:1 ratio for colored vs. colorless is shown. As reported before (NAGAO and TAKAHASHI 1951a), this is the ratio due to the existence of a linkage between *Pn* and *Sp* with a recombination value of approximately 18% in coupling phase. The data presented in these tables are in close accordance with the expectation based on the information mentioned sbove.

In addition to the genes *Pl* and *Pn*, there exists another gene for leaf coloration. The effect of *Pl* is diminished by the presence of an inhibitor for *Pl* that inhibits the coloration at the center of leaf blade as shown in fig. 1 of Plate IV. This gene is designated as *Ipl*, and the mode of coloration and their inheritance, involving *Pl* and *Ipl* are presented in Table 27.

G. Supplements on Apiculus Color Genes

In this section, illustration will be made on the genic interrelation between vegetative-part-color gene, *Pn* and *Pl*, and apiculus gene, laying emphasis on the estimation of the presence of the third apiculus gene *A*, and of an additionan chromogenic gene C^{Rt}; a member of the alleles at *C*-locus.

a. Proposition of third gene for apiculus coloration.

According to the principal hypothesis mentioned in the previous articles, the expression of anthocyanin color character of apiculus is determined by the combination of multiple alleles at *C* and *Sp* loci. And from this scheme of genes, monohybrid or dihybryd segregation

TABLE 27. F_2 from crosses, $C^{Bp}Sp^{d}Pl^{+}Ipl$ (Kairyobozu) × $C^{Bp}SpPlIpl^{+}$ (Shito and Ebisumochishito), involving *Pl* and *Ipl*.

phenotype	apiculus	purple		
	leaf sheath	purple		green
	leaf blade	green	purple	green
genotype		$C^{Bp}Sp\,Pl\,Ipl$	$C^{Bp}Sp\,Pl\,Ipl^{+}$	$C^{Bp}Sp\,Pl^{+}\,Ipl$ $C^{Bp}Sp\,Pl^{+}\,Ipl^{+}$
Kairyobozu × Shito		143	63	77
" × Ebisumochishito		138	55	50
total		281	118	127
(9 : 3 : 3 : 1) (3 : 1)		27	9	12
C		286.45	95.48	127.31

(continued)

red			total	χ^2 ($\Sigma\chi_i^2$)	d. f.	p
red		green				
green	red	green				
$C^{Bp}Sp^{d}Pl\,Ipl$	$C^{Bp}Sp^{d}\,Pl\,Ipl^{+}$	$C^{Bp}Sp^{d}Pl^{+}\,Ipl$ $C^{Bp}Sp^{d}Pl^{+}Ipl^{+}$				
50	14	25	372	5.089	5	0.5–0.3
30	12	22	307	9.625	"	0.1–0.05
80	26	47	679	(14.714)	10	0.2–0.1
9	3	4	64			
95.48	31.83	42.44	678.99	9.486	5	0.1–0.05

ratios of the apiculus color, as in case of 3:1, 9:7, 9:6:1, 9:3:4, 9:3:3:1 or 15:1 can be reasonably explained—a detailed explanation will be gived in General Considerations—by the *C-Sp* combination scheme.

However, some workers such as LEE (1927) and CHIAO (1928 a), notably the latter, have reported another ratio of colored to coloress, as in 27:37, indicating that at least three genes are involved in apiculus coloration. To all outward appearance this result cannot be explained

by the *C-Sp* scheme, but as a matter of fact, it is not inconsistent with the author's scheme of genes. The means by which to explain the trihybrid segregation under the author's scheme is already reported and a new gene *A* was additionally proposed (NAGAO and TAKAHASHI 1956 a). It may be an aid to the present section, to mention the actual procedure in proposition of this gene.

Among several kinds of cross combinations involving foreign varieties, the combinations in which the colorless variety E–36 was combined with testers Akaine (apiculus and node are a blackish red purple, under a genic constitution of $C^{B}SpPn$) and Ebisu (originally colorless, but apiculus color turns into tawny at ripening; $C^{Bp}SpPn^{+}$) showed the following segregations.

The F_1 of E–36 × Akaine showed the same type of coloration as that of Akaine, having a colored apiculus and node, while in F_2, in addition to the parental types, a new type viz. colorless apiculus with colored node appeared. This type, tentatively called "Xp type", is decidingly unique, in that, the color of the node may develop even in the absence of the apiculus color, which phenomena have never been observed in cross combinations among Japanese varieties (fig. 2 of Plate IV). Though the apiculus are colorless visually, slightly colored cells are revealled scattered, in microscopical examination, and when the glumes are awned a faint hint of purple colors appears in their apicis alone, therefore to a cursory view the awn seems also to be cololess. And at ripening the tawny color does not appear in the apiculus or awn and remains Straw white without exception. The ratio of three color types, purple apiculus with puple node, Xp-type, and colorless, is approximately 9 : 3 : 4, suggesting that it is based on a digenic scheme of inhertance. But in colorless segregants, there are some plants which have the same coloration as the Xp-type in their apiculus and awns. This type, tentatively called "X-type", also shows a straw color at ripeining.

This mode of segregation cannot be illustrated with the *C* and *Sp* combination alone; be that as it may, the fact that the F_2 segregants with colored apiculus are invariably accompanied by colored node sugests the presence of *Pn* gene in E–36 variety likewise, and the fact that the colors of awns and apiculus of colorless segregants do not change to tawny in the ripening indicates that a certain cause or causes of modifying the effect of *C* may exist in genotype of CSp^{+}.

In the progenies from E–36 × Ebisu, which is the combination

between colorless varieties, F_1 showed a colored apiculus and colored node in the same manner as in F_1 from E-36 × Akaine, and F_2 populations were classified under the following five types of coloration with regard to the apiculus and node colors, namely; i) colored apiculus with colored node, ii) colored apiculus with colorless node, iii) Xp-type, iv) X-type or colorless apiculus (straw white at ripening), and v) colorless apiculus with tawny ripening color. As mentioned above, the apiculus coloration of Xp-type and X-type may be regarded as colorless, in accordance with the assumption that these two types are colorless, and separating the F_2 populations into colored vs. colorless groups, the actual numbers come to 106:141, which is a close fit to the calculated relation of 27:37. This result gives support to the view that in this cross combination there exists a trigenic inheritance in regard to the apiculus coloration.

When apiculus coloration including the node color is classified, these frequencies are very singular, that; colored apiculus with colored or colorless node, Xp-type, X-type or colorless apiculus and node, and colorless apiculus which turns into tawny, are in numerical relation of 106:30:89:22.

Ebisu consists of the genic constitution C^{Bp}, Sp^+ and Pn^+, and the F_1 from E-36 × Ebisu shows purple apiculus and node. Therefore E-36 must contain the dominant gene *Sp* and *Pn*. If so, the determination as to whether E-36 posses the gene *C* or not, the determination as to what genotype of the Xp-type remains.

In order to solve these problems, Xp-type plants were bred true and the pure breds were crossed with two testers, C^+Sp^+ and CSp^+, with the results of colored apiculus in the F_1s, indicating that the Xp-type posses not only *Sp* but also *C*. Therefore, in spite of having identical genotype for *C* and *Sp* loci, there exists a monogenic difference between the following two types of apiculus color, colored apiculus with colored node and Xp-type in the F_2 from E-36 × Akaine. This fact indicates that it is necessary to assume that another gene for the expression of apiculus color in addition to *C* and *Sp* exists.

What then, is the nature of the action of this new gene, and on which gene, *C* or *Sp*, does this new gene—gene symbol "A"—exerts its effect? It is most probable that *A* has a distributing effect on *C*, since there is no appearance of tawny coloration in colorless F_2 segregants from E-36 × Akaine. Thus the genic constitution of the Xp-type is estimated to be $CSpPnA^+$. From the fact that in the colorless F_2

TABLE 28. Inheritance of color in apiculus in crosses involving C^+ and A^+ alleles of the C and A loci.

P_1		F_1	F_2		
combination	apiculus color	color type	phenotype	colored (purple)	
			genotype	$CSp\,A$ [1]	
	node color		phenotype	colored	colorless
			genotype	Pn	Pn^+
E-36 × Akaine $C^+\overline{SpPn}A^+$ $C\overline{SpPn}A$		same as Akaine	0 (3 : 1) (3 : 1) C	200 9 203.62	
" × Ebisu $C\overline{Sp^+Pn^+}A$		"	0 (27:9:9:19) (8:1) C	106 27 104.20	

(continued)

F_2							
colorless in visual, but faintly colored		colorless (white)		total	χ^2	d. f.	p
		Straw white at ripening	tawny at ripening				
$CSp\,A^+$		CSp^+A^+, C^+SpA C^+SpA^+, C^+Sp^+A $C^+Sp^+A^+$	CSp^+A				
colored	colorless	colorless	colorless				
Pn	Pn^+	Pn, Pn^+	Pn, Pn^+				
62	100			362			
3	4			16			
67.88	90.50			362.00	1.571	2	0.5-0.3
30	89		22	247			
$8(=9\times\frac{8}{9})$	$20\,(=9\times\frac{1}{9}, 9, 3, 3, 3, 1)$		9	64			
30.88	77.19		34.72	247.00	6.830	3	0.1-0.05

1) C denotes C^B or C^{Bp}, as in the other tables, 29, 30 and 31.

segregants of E–36 × Ebisu the tawnys outnumber the non-tawnys, it is natural to assume that E–36 locks the dominant gene *A* and has the genic constitution of $C^+ Sp Pn A^+$.

In accordance with this genic scheme and with consideration to the mode of inheritance of F_1 and F_2 in E–36 × Akaine and E–36 × Ebisu, the theoretical ratios of F_2 segregations and their deviations from observed numbers of segregants are as shown in Table 28. In this table, in regard to the theoretical segregation ratio on node coloration, an 8:1 ratio for colored vs. colorless is shown. As mentioned before this is the ratio apriorily calculated from the linkage relationship between the gene *Sp* and *Pn* with a recombination value of about 18% in coupling phase. The observed results are in close accordance with the expectation based on these assumptions.

For further varification of the genic scheme as proposed by the author, a strain called H–61 has been bred from E–36 × Ebisu and shows a Xp-type coloration and is assumed to have the genic constitution of $C Sp Pn A^+$, were crossed with some tester varieties as described below;

Kokushokuto ($C Sp Pn A$) . . .	The same as in Akaine.
Akage ($C Sp^+ Pn^+ A$)	The same as in Ebisu.
N–44 ($C^+ Sp Pn^+ A$)	Colorless apiculus, straw white at ripening.
Akamuro ($C^{Br} Sp Pn^+ A$)	Pink apiculus with colorless node.

The details of the results, being tedious, are abridged here, however as given in Table 29, in all combinations, numerical relations were found between the several coloration types and also between the several classes of behavior which is reasonably close to the expectation.

Furthermore the propriety of these genic interpretations were confirmed by pedigree culture, and in every instance almost all the segregation types expected in F_3 generation of the above mentioned cross combinations, and no others, have appeared (Table 30).

On the whole therefore, these results lead the author to the conclusion that besides the gene *C* and *Sp* there exists another gene *A* for apiculus coloration, and according to this view the expression of the anthocyanin color in apiculus depends on the complementary effect of *C*, which is concerned with the formation of chromogen, *Sp* which is responsible for the formation of the modifier for *C* (chromogen→ anthocyanin), and *A* which is responsible for spreading the chromogen

TABLE 29. F_2 segregations and their ratios expected from the genic assumption "Basic genes *C–Sp* and presence of their modifier *A*".

combination	apiculus color	phenotype	purple		pink
		genotype	*C Sp A*		*C^{Br} Sp A*
	node color	phenotype	colored	colorless	colorless
		genotype	*Pn*	*Pn*+	*Pn, Pn*+
Fusenshiro×Kokushokuto *C Sp Pn A*+ *C Sp Pn A*		0 (3 : 1) C	618 3 612.75		
" × Akage *CSp*+*Pn*+*A*		0 (9 : 3 : 3 : 1) (8 : 1) C	137 24 (=27×8/9) 126.50	11 3 (=27×1/9) 15.81	
" × N-44 *C*+*SpPn*+*A*		0 (9 : 3 : 4) (3 : 1) C	244 27 248.48	93 9 82.83	
" × Akamuro *C^{Br}SpPn*+*A*		0 (9 : 3 : 3 : 1) (3 : 1) C	356 36 347.63		

(continued)

white in visual but faintly colored		white		total	χ^2	d. f.	p
		Straw white at ripening	tawny at ripening				
C Sp A+		*CSp*+*A*+, *C^{Br}SpA*+ *C^{Br}Sp*+*A*+, *C*+*SpA* *C*+*SpA*+, *C*+*Sp*+*A* *C*+*Sp*+*A*+	*C Sp*+ *A*				
colored	colorless	colorless	colorless				
Pn	*Pn*+	*Pn, Pn*+	*Pn, Pn*+				
199 1 204.35				817 4			
43 8 (=9×8/9) 42.17	21 4 (=9×1/9, 3) 21.08		41 9 47.44	253 48 253.00	3.226	4	0.7–0.5
94 9 82.83	160 19 174.86			589 64 589.00	3.656	3	0.5–0.3
95 9 86.91	71 7 67.59			618 64 618.01	4.537	3	0.3–0.2

TABLE 30. Segregation types of pedigrees and their frequencies in F_3 progenies from the crosses mentioned in Table 29.

Fusenshiro×Kokushokuto

F_2 phenotype	F_3 type of segregation [1]						number of strains [2]			number of plants
	Pp	P	R	Xp	G(T)	X, G(t)	C_1	C_2	0	
Pp	1						1	4.5	7	396
"	3			1			2	9.0	7	411
Xp				1			1	4.5	4	357
total							4	18.0	18	1164
Fusenshiro×Akage										
Pp	1						20	0.8		
"	3	1					9	0.4		
"	3			1			40	1.6	2	202
"	3				1		9	0.4		
"	9	3		3		1	18	0.7		
"	9			3	3	1	18	0.7		
"	8	1			3		40	1.6	2	228
"	2	1			1		2	0.1	1	144
"	24	3		8	9	4	80	3.2	3	348
"	6	3		2	3	2	4	0.2	1	115
P		1					1	0.0		
"		3			1		9	0.4	1	120
"		3				1	2	0.1		
"		9			3	4	18	0.7	1	77
Xp				1			20	0.8	4	300
"				3		1	18	0.7	1	84
"				2		1	40	1.6	1	99
"				1		1	2	0.1		
G(T)					1		30	1.2	1	67
"					3	1	60	2.4		
X, G(t)						1	40	1.6	1	100
total							480	19.3	19	1884
miscellaneous [3]									1	102
Fusenshiro×N-44										
Pp	1						1	0.3	1	72
"	3	1					2	0.7		
"	3			1			2	0.7		
"	3					1	2	0.7	1	119
"	9	3				4	4	1.4	2	204

TABLE 30 (continued)

Fusenshiro×N-44 (continued)

Pp	9			3		4	4	1.4	1	102
"	9	3		3		1	4	1.4	1	123
"	27	9		9		19	8	2.8	3	339
P		1					1	0.3		
"		3				1	4	1.4	2	128
"		9				7	4	1.4	2	144
Xp				1			1	0.3	1	152
"				3		1	4	1.4	2	169
"				9		7	4	1.4	2	232
X, G (t)						1	19	6.5	4	240
total							64	22.1	22	2024
miscellaneous									1	22

Fusenshiro×Akamuro

Pp	1						1	0.3		
"	3	1					2	0.6	2	140
"	3		1				2	0.6		
"	3			1			2	0.6	1	112
"	9	3	4				4	1.3		
"	9	3		3		1	4	1.3		
"	9		3	3		1	4	1.3	3	213
"	27	9	12	9		7	8	2.5	3	303
P		1					1	0.3	2	145
"		3	1				2	0.6	1	73
"		3				1	2	0.6		
"		9	3			4	4	1.3	2	188
R			1				4	1.3		
"			3			1	8	2.5	1	63
Xp				1			1	0.3		
"				3		1	4	1.3	1	84
"				9		7	4	1.3	2	112
X, G (t)						1	7	2.2	2	140
total							64	20.2	20	1573
miscellaneous									2	195

1) Pp denotes the coloration type as purple apiculus with colored node, P as purple apiculus with colorless node, R as pink apiculus with colorless node, G (T) as colorless but ripening tawny, and G (t) as colorless and straw white at ripening.

2) C_1 indicates the theoretical ratio, C_2 indicates the theoretical numbers, and 0 indicates the observed numbers.

3) These pedigrees contain unexpected segregatic or show singular ratios of segregation which may be due to natural crossing or inadequately small plant numbers in determining the mode of segregation.

of *C* to the entirety of the apiculus, awns and the apices of empty glumes. *A* in itself, however, or in combination with *Sp* does not produce any pigment.

On the basis of the above interpretation on the trigenic of apiculus coloration, it is concluded that the reformed *C–Sp–A* scheme proposed as a basic interpretation of the apiculus coloration is substantiated, in so far as it is possible to determine.

As mentioned before since the color development in node (and also in pulvinus, ligule, auricle and leaf margin) does not necessitate the presence of *A*, it is natural to assume that *A* is one of the distributing genes for anthocyanin pigment, as it is in the same category as *Pl* and *Pn*. However, it is pointed out in this connection that in actual cross examinations, in which A^+ and *Pl* are involved, such plants as colorless apiculus with colored leaf blade, having a genotype of $A^+ C Sp Pl$, were scarcely observed. The cause of this phenomenon is not determined at the author's satisfaction as yet, a single F_2 progeny resulting from a cross of a H–61 (Xp-type, $C^{Bp} Sp Pn A^+ Pl^+$) × N–45 (purple

TABLE 31. F_2 of cross between gene for apiculus color (*A*) and leaf blade color (*Pl*), showing linkage relation in coupling. Fusenshiro (*CSpPnPl*$^+$*A*$^+$) × Ebisumochishito (*CSpPn*$^+$*PlA*).

apiculus color	purple			faintly colored			total	χ^2	d. f.	*p*
	A			*A*$^+$						
leaf blade color	colored	colorless		colored	colorless					
	Pl	*Pl*$^+$		*Pl*	*Pl*$^+$					
node color	colored	colored	colorless	colored	colored	colorless				
	Pn, *Pn*$^+$	*Pn*	*Pn*$^+$	*Pn*, *Pn*$^+$	*Pn*	*Pn*$^+$				
0	415	10		4	78	29	536			
(56:1:1:18) (3:1)	224	4		4	54	18	304			
O	394.95	7.05		7.05	95.21	31.74	536.00	6.877	4	0.2–0.1

A–Pl linkage (coupling)

A Pl	*A Pl*$^+$	*A*$^+$ *Pl*	*A*$^+$ *Pl*$^+$	total
415	10	4	107	536

Recombination value: 2.70%

apiculus and leaf blade, $C^{Bp}SpPn^{+}APl$) gave a segregation that showed an occurrence of the colored leaf blade with colorless apiculus which depends on the action of *Pl* in cooperation with *C*, *Sp* and A^{+}, and furthermore the occurrence of a linkage between *A* and *Pl*. As presented in Table 31, the progeny from a selfed F_1 heterozygous for *A* and *Pl*, may be classified into four types of coloration as regards apiculus and leaf blade colors, namely purple apiculus with purple leaf blade, purple apiculus with colorless leaf blade, faint colored apiculus (Xp or X) with purple leaf blade, and faintly colored apiculus with colorless leaf blade, totaling 536 plants, in the numerical relation of 415:10:4:107. These four types should be expected to occur in the relation 301.5:100.5:100.5:33.5 in independent assortment between *A* and *Pl*. The observed deviations from the expectations may be caused by *A*–*Pl* linkage in the coupling phase, and the ovserved result is in close accordance with the expectation based on an approximate 3% recombination value between *A* and *Pl*. This is also presented in the same table.

b. Suggestion on presence of an apiculus gene C^{Bt}, fifth member of the C series of multiple allelemorphs.

The gene C^{Bt}, which will be explained here, is said to be one of the alleles at *C*-locus. As to the conclusive information of the nature of C^{Bt}, it is less potent than C^{Bp} and more potent than C^{Br}, showing an apiculus color shade as Tyrian Rose when co-existing with *Sp*. The C^{Bt} itself, viz. $C^{Bt}Sp^{+}$, makes the apiculus or awns Ochraceous buff at ripening; a somewhat deeper color shade than Warm buff caused by C^{Br}. Phenotypic discrimination between $C^{Bt}Sp$ and $C^{Br}Sp$ or between $C^{Bt}Sp^{+}$ and $C^{Br}Sp^{+}$ is sometimes difficult when these genotypic plants are compared individually, but in the case of group or mass comparison there is no trouble in distinguishing one from the other (fig. 3 of Plate I and fig. 1–A of Plate II).

As a result of possessing more potency in C^{Bt} than in C^{Br}, the gene *Pl*, in coexistence with $C^{Bt}Sp$, is able to exert its distributing effect over leaf and stem node, though the location of color is limited to the pulvinus or node, showing but a faint color shade. Cross examinations involving C^{Bt} have been carried out. Among these, for example, the cross combinations in which the $C^{Bt}SpPl^{+}$ (pink apiculus with colorless leaf) was combined with Shito (Apiculus and entire leaf blade are purple, under genotype of $C^{Bp}SpPl$) showed a segregation that is pre-

TABLE 32. F_2 segregation in apiculus and leaf color, involving *Pl* and new allele, C^{Bt}, at *C*-locus.

a. $C^{Bt}SpPl^+ \times C^{Bp}SpPl$

apiculus color	phenotype	purple		pink		green		total	χ^2	d. f.	p
						tawny	straw white				
	genotype	C^{Bp} *Sp*		C^{Bt} *Sp*		$C^{Bp}Sp^+$	$C^{Bt}Sp^+$				
leaf color	phenotype	purple, entirety	green	pink, at the center	green	green	green		$(\Sigma\chi_i^2)$		
	genotype	*Pl*	Pl^+	*Pl*	Pl^+	*Pl*, Pl^+	*Pl*, Pl^+				
Tomekichiwase ×Shito		164	53	59	27			303	4.017	3	0.3–0.2
Tsugaruwase × 〃		139	41	38	19			237	2.694	〃	0.5–0.3
total		303	94	97	46			540	(6.711)	6	〃
(3 : 1) (3 : 1)		9	3	3	1			16			
C		303.75	101.25	101.25	33.75			540.00	5.046	3	0.2–0.1

b. $C^{Bt}Sp^+Pl^+ \times C^{Bp}SpPl$

Tanpaku ×Shito	65	17	25	4	34	11	156	2.109	4	0.8–0.7
Akanumashiro × 〃	117	34	31	14	52	16	264	1.913	5	0.9–0.8
Hosogara × 〃	53	24	23	6	32	12	150	3.648	〃	0.7–0.5
total	235	75	79	24	118	39	570	(7.670)	14	0.95–0.90
(9 : 3 : 4) (3 : 1)	27	9	9	3	12	4	64			
C	240.47	80.16	80.16	26.72	106.88	35.63	570.02	2.226	5	0.9–0.8

sented in Table 32a.

The F_1 of this cross gave the same type of coloration as that of Shito, having a purple apiculus and leaf, and in F_2 a ratio of 3 purple : 1 pink, with respect to apiculus color, was observed. The pink did not change into tawny at ripening, and showed a similar mode of coloration to genotypic individuals as $C^{Br}SpPl$ or $C^{Br}SpPl^+$. However, leaves and nodes of three-quarters of the pink segregants were colored with a faint color shade. On the whole, this cross gave the following four phenotypes, in F_2, namely; purple apiculus with purple leaf, purple apiculus with colorless (green) leaf, pink apiculus with pink leaf, and pink apiculus with colorless leaf. These plants appeared in a ratio of

9:3:3:1 respectively, clearly indicating that *Pl* is involved in the plants with pink apiculus as well as in the plants with purple apiculus color.

In a case of a cross between $C^{Bt}Sp^{+}Pl^{+}$ (colorless apiculus and leaf) and $C^{Bp}SpPl$, their F_1 showed purple apiculus and node, similar to that of the colored parent, and segregations which are presented in Table 32 b occurred in F_2. In this table, it is also pointed out that *Pl* exert its effect over leaf or node of the plants with pink apiculus.

These patterns of leaf coloration in the pink apiculus plants are apparently similar to that in such a genotypic plant as $C^{B}Sp^{a}$ *Pl* or $C^{Bp}Sp^{a}Pl$. However, the evidence in support of the assumption that these colorations are not due to the presence of Sp^{a} is substantiated by the following facts.

i) If the pink color of these plants depend on a genic constitution such as $C^{B}Sp^{a}$ or $C^{Bp}Sp^{a}$, their apiculus color should convert into tawny at ripening. But, such plants did not appear in actual observation, showing that the chromogenic substance in apiculus color had completely changed into anthocyanin.

ii) And if these pink colors depend on the presence of Sp^{a}, colorless parents and all colorless F_2 segregants, presented in Table 32 b, should give tawny colored apiculus in the ripening stage. But actual results were quite different. The ripening color of the colorless parents were straw white, and one-quarter of colorless F_2 segregants remain straw white at ripening.

These results are naturally interpreted on the basis of the assumption that these peculiar natures of the pink apiculus coloration depends on the presence of another chromogenic allele at *C*-locus. The above mentioned evidence suggests the presence of a fifth member, C^{Bt}, of the *C* series, which may be stated as;

$$C^{B} > C^{Bp} > C^{Bt} > C^{Br} > C^{+} .$$

H. Genetico-histological and Biochemical Informations on Anthocyanin and Tawny Coloration

The preceding parts of the present paper deals with a presentation of color types of anthocyanin pigmentation and with the results of the genic analysis thereof. As pointed out, the plant color in rice is of a variable character both in its hue or shade and pattern of distribution.

This article is devoted to the histological observation on the location

of pigments which were undertaken with the genetical studies on coloration, and an attempt is made at a biochemical analysis of said pigments. The term "genetico-histological information" refers to that the histological observations on characteristics which are already analysed or estimated genetically.

a. Histological aspects.

All observations were made using fresh materials cut freehand, as well as using fixed sections cut by paraffin method. In the case of observation on general topography rather than in detail, it was found desirable to make thick sections using fresh materials cut freehand. However, in case in which pigment was apt to flow out or when the amount of the pigment was insufficient for close detection, the materials were fixed by the following agents, and mounted and cut by paraffin method. The ingredients of the fixative worked out by the author are 25% lead acetate (40 vols.), 90% alcohol (5 vols.) and 10% caustic potash (1 vol.). This fixative is favorable in detaining anthocyan and like substances, converting them into a insoluble precipitation with black or deep violet color. The procedureas devised by the author is as follows.

In detecting tiny anthocyanin pigment without its being obscured by other cell contents, preservation of this pigment is the primary objective, if the preparations are for histological study by paraffin method. As a rule, it is considered practical to use lead acetate which causes the precipitation of anthocyanin in a form of lead acetate. However, free acid contained in the lead acetate solution is likely to cause the precipitated anthocyanin to dissolve again. And also the lead acetate causes the coagulation of some liquid albinoids, and consequently prevents rapid penetration of the fixing liquid into tissue. To avoid these obstacles, K ion of KOH is added as swelling-ingredient in the fixative.

Alcohol is also used for dissolving lipoid which is considered to prevent the rapid penetration of the fixing liquid. As a foundation of this fixative, it is advisable to use lead subacetate, rather than lead acetate, to prevent the lead from becoming insoluble as a result of neutralization by KOH. Thus, as for the most satisfactory fixing agent, the above mentioned formula is proposed.

In the descriptive note given below, the genic assignment on the third gene, *A*, will be excluded. In every genic constiution, the gene

A is held in common except in the case when particular remarks will be made.

Coexistence of *C* and *Sp*:

Apiculus color—As mentioned before, under the complementary effect of two series of multiple allelomorphic genes, *C* and *Sp*, more than six differences in hue or shade of anthocyanin color resulted, according to which allele at *C* and *Sp* loci are concerned. Histologically, the intratissual location of the pigment has no essential difference on the above six; it is dissolved in cell sap in the epidermis of apiculus and empty glumes (fig. 1-B, B', E of Plate V).

It is worthy of note, however, that when genotypic plants have *Sp* in common and differ from each other in allele at *C*-locus, the differences in color shade to the eye are mainly attributed to the differences in density of colored cell distribution rather than the differences in the intensity of cell sap color; and when plants have *C* in common and differ from each other in allele at *Sp*-locus, the visual color differences seem to be mainly due to the differences in color intensity of the cell sap rather than the differences in the density of colored cell distribution.

As mentioned before, it could assumed that Sp^a is less potent than *Sp* and can utilize in the formation of anthocyanin pigment only a fraction of the chromogenic substance produced. If so, the mode of colored cell distribution between C^BSp and C^BSp^a and between $C^{Bp}Sp$ and $C^{Bp}Sp^a$ should be similar to each other respectively, and on the other hand the color shade of the cell sap in the C^BSp or the $C^{Bp}Sp$ should be deeper than in the C^BSp^a or the $C^{Bp}Sp^a$ respectively. Here, the propriety of these assumptions are also histologically ascertained.

In every case the color is most intense in the apiculus and spreads down thin along the vein to the middle of the glume. This is because the colored cells are sparsely distributed downward.

Colors in other parts—In C^BSp and $C^{Bp}Sp$ stigmas are colored; this is the pigmentation of papilla cell sap (fig. 1-D of Plate V). $C^{Bp}Sp$, $C^{Bp}Sp^a$, $C^{Bt}Sp$ or $C^{Br}Sp$ produce usually no color in leaf sheath, but in some cases the light red color is observed on the inside of the lower part of the sheath of the $C^{Bp}Sp$. This is due to the presence of colored cell distributed in epidermal layer (fig. 1-Q of Plate V). In C^BSp the color intensity of that part is darker than in $C^{Bp}Sp$, because of dense distribution of the pigmented cells.

As for the noticeable characteristics of the C^BSp and C^BSp^a, they

produce respectively purple and red lines in internode and mid-rib of leaf blade. The pigment in the internode is present in a single layer of the parenchyma cells adjacent to the bundle sheath of larger vascular bundle; and sometimes pigment is found in the parenchyma cells arranged in horseshoe form arround the small vascular bundly adjacent to the hypodermis. The mid-rib usually consists of assimilation tissue, assuming triangle form with hollows, in some parts of which the large vascular bundles lie. The colored lines of the mid-rib are due to pigment dissolved in cell sap of parenchyma adjacent to the large vascular bundle. The colored lines also extend to the leaf sheath, which is divided into an outer and an inner part by a lacuna; this colored line is due to the pigment of a single cell layer of the outer parenchyma tissue. (fig. 2-M, M′ and fig. 4-K, K′, Q of Plate V).

Coexistence of *CSp* with *Rp*:

When $C^{B}Sp$, $C^{Bp}Sp$, $C^{B}Sp^{d}$ or $C^{Bp}Sp^{d}$ coexists with *Rp*, apiculus colors are distributed over the entire surface of glumes and on the rachilla. These colorations are caused by the dense distribution of the colored epidermal cells (fig. 3-B of Plate V). In this connection it must be remembered that under visual observation, genotypic plants such as $C^{Br}SpRp$ do not show any phenotypical difference from $C^{Br}SpRp^{+}$ with regard to the mode of color expression in glume, while having colored apiculus but uncolored glumes. This is also ascertained histologically, on the supposition that the gene C^{Br} may not have a sufficient amount of the chromogenic substance to distribute the pigment all over the entirety of the glumes even when it coexists with *Rp*.

Coexistence of *CSp* with *Pl* and *Pn*:

The gene *Pl* is responsible for coloration in leaf sheath, leaf blade, ligule, pulvinus, internode and stem node. The color of the leaf blade is due to the presence of pigment in epidermal cells, motor cells and sclerenchyma cells located outside the phloem. The purple ($C^{B}SpPl$ or $C^{Bp}SpPl$) or red ($C^{B}Sp^{d}Pl$ or $C^{Bp}Sp^{d}Pl$) appearance of the entire surface of the leaf blade is a result of the dense distribution of colored cells, though a considerable number of uncolored cells are interspersed among them (fig. 6-K, K′, K″ of Plate VI). The color of the leaf sheath is due to the pigment in the single layer of parenchyma cells surrounding the bundle sheath and in the intervening epidermis of each bundle. The internode color is caused by the distribution of cells with

colored cell sap in parenchymatous tissue; and the coloration in the ligule, auricle, pulvinus and the stem node is caused by pigment in the cells sap of the epidermis (fig. 6-Q, M, J of Plate VI).

If lemma and palea are partly cut off soon after anthesis, the coloration begins to develop in a pericarp layer of this caryopsis as a result of pleiotropic action of *Pl.* This coloration corresponds to the pigmentation in cell saps of epicarp, mesocarp or seed coat or both. But the seed coat color is considerably lighter compared with the color in the pericarp.

In the presence of *Pn*, when associated with basic genes *CSp*, anthocyanin color extends into leaf apex, leaf margin, midrib, ligule, auricule, pulvinus and stem node, and further, in the genotypes $C^{B}SpPn$ and $C^{B}Sp^{a}Pn$ the broad colored lines are present in leaf sheath. The purple lines in the midrib are due to the pigmentation of the cell sap of stereom surrounding phloems of vascular bundles present on the lower side of the leaf (fig. 5–K, K′ of Plate VI). This is histologically, quite different from the situation caused by $C^{B}SpPn^{+}$, where the coloration occurs in parenchyma cells, although the appearance of the colored midrib to the eye is similar in both two cases. The colored lines of the leaf margin and the colored wash of the leaf apex are caused by pigment in cell saps of the motor cells and epidermis (fig. 5–K″ of Plate VI). The color of the leaf sheath is due to pigment in epidermal cells. The outward appearance of this coloration shows wide colored stripes, because the epidermis is intersected regularly by the stereom, which remains colorless (fig. 5–Q, Q′ of Plate VI). Thus it is pointed out that this mode of localization of colored cells by *Pn* is quite different from that by $C^{B}SpPn^{+}$, inspite of showing similar patterns in visual observation. The coloration in the auricle, ligule, pulvinus and the stem node is the same as in the case of *Pl.*

Throughout these observation, it may be emphasized that as a general rule the color shade of several parts, when compared with the color shade of cell sap therein, is darker, since the coloration of the anthocyanin overlaps with the color of chlorophyll located in the assimilation tissue when seen to the eys. In addition to this, it is also noticeable that the intra-genotypic variation on color intensity of cell sap is considerably larger than the author has expected.

Ç in itself:

The chromogenic substance in the cell sap is converted into brown

pigment, the tawny, at the time of ripening. With the lapse of time the cell sap loses water. Therefore the brown pigment should eventually settle on the cell wall at full ripening. Histologically this was also ascertained. Figure 3 of Plate IV shows the tissual location of this pigment in glumes of genotypic plant of C^BRpSp^+.

As regards the amount of the brown pigment in the cell wall, it is somewhat less in the genic combination of Sp^a with *C*-alleles than in that of *Sp* with *C*-alleles.

Location of the tawny color in other vegetative parts is rather difficult to determine, however, in a genotype of C^BPl for instance, a tint of brown pigment can be detected in leaf blade, to some extent.

In connection with this, a short examination was made. Some strains or individuals which show various modes of tawny color distribution, were cellected before they were beginning to turn tawny. They were separated into two parts respectively; (a) parts in which the tawny would begin to develop at the time of ripening and (b) parts which remain colorless at ripening. Every 2 gr. of these samples were extracted with hot water of 50 cc for 30 minutes. With the lapse of time, a considerable amount of red precipitate appeared in the extract from (a), whereas scarcely any appeared in that from (b) without exception. This indicates that the chromogenic substance for the tawny may be water soluble at an early stage of flowering but changes to insoluble as a result of conversion into the tawny substance.

As a whole, it is concluded that coloration with anthocyanin is histologically the pigmentation in cell sap without exception, and that the coloration with the tawny is the pigmentation on the inner surface of cell wall as a result of the desiccation of the cell.

To sum up the above descriptions, they are tabulated as in Tables 33 and 34.

TABLE 33. Histological location of anthocyanin pigment due to complementary effect of *C* and *Sp*, in coexistence with *A*.

colored part	awn	apiculus	empty glume	stigma	inner surface of leaf sheath	stripes of internode	outer surface of leaf sheath
histological location of the pigment	epidermal cell	epidermal cell	epidermal cell	papilla cell	epidermal cell	parenchyma cell adjacent to vascular bundle	a single layer of outer parenchyma tissue

TABLE 34. Histological location of anthocyanin pigment caused by distributing genes *Rp*, *Pl* and *Pn*, in cooperation with *CSpA*.

colored part		lemma and palea	rachilla	rachis	midrib of leaf sheath	stripe of leaf sheath	leaf margin
Histological location of the pigment	*Rp*	+	+	−	−	−	−
		epidermal cell	epidermal cell				
	Pl	−	−	+	+	+	+
				epidermal cell ?	stereom adjacent to phloem of vascular bundle	epidermal cell and parenchyma adjacent to bundle sheath of vascular bundle	epidermal and motor cell
	Pn	−	−	−	+	+	+
					ditto	epidermal cell	epidermal cell

continued on the right side of the above

	auricle and ligule	pulvinus	node	intervening part of stripes in internode	entire leaf blade	entire leaf sheath	pericarp
Rp	−	−	−	−	−	−	−
Pl	+	+	+	+	+	+	+
	epidermal cell	epidermal cell	epidermal and parenchyma cells	parenchyma cell	epidermal and motor cell	epidermal cell and parenchyma adjacent to bundle sheath	epicarp [1] and mesocarp layers
Pn	+	+	+	−	−	−	−
	ditto	ditto	epidermal cell				

1) Only in a case of clipping operated caryopsis.

b. Biochemical aspect

In the preceding descriptive note and accompanying illustrations on genic interpretation, the color produced by the action of apiculus genes *CSpA* and their distributing modifiers *Rp*, *Pl* and *Pn* were deductively, viz. in apriori, dealt with as the color with anthocyanin pigment.

To take an objective view of the genic scheme of the author, an examination of the following problems is expected; (a) whether various color intensities, i.e. Blackish red purple to Rose red, are caused by an identical anthocyanin or not, and (b) what kind of aglucones do these anthocyanins consist of, and further (c) what is the chemical nature of the chromogenic substance provided it is presumable, and consequently what kind of substance is the tawny color ?

In these connections the author made some chemical experiments. These were accomplished using strains which have been bred true for coloration with regard to said genes, and in a few cases some genotypic sib-plants derived from F_2 were used.

Anthocyanin pigment:

The detailed results of the examination on anthocyanin is already reported by NAGAO, TAKAHASHI and MIYAMOTO (1956b) but in outline they are as follows.

The apiculus, awn, leaf blade and other various coloring parts were taken and collected at the time of two or three days after anthesis, and anthocyanins contained in the above parts were extracted with 1% solution of hydrochloric acid. A paper-chromatographical separation of the anthocyanins in the extracts was conducted by the use of a mixture of N-butanol, glacial acetic acid and distillated water in a ratio of 4:1:2, as advocated by BATE-SMITH (1948). The result of one dimentional separation is as in Table 35.

In this table it is pointed out that almost all genotypes of the apiculus, as well as awn, show similar values of Rf, ranging from 0.41 to 0.43, and also the same Rf value is obtained in the extracts from another colored part, in which the expression of color is dependent upon the distributing effect of *Rp*, *Pl* and *Pn* in the presence of *C*, *Sp* and *A*. This result lead the author to the conclution that there are no differences among the several genotypes in regards to the quality of anthocyanin concerned.

Further, to clarify the aglucone of this anthocyanin, the colored

TABLE 35. Rf values of anthocyanins extracted from various parts of different genotypic plants. ("*A*" presents, in-common).

distributing modifier	mode of color distribution by modifier	basic genotype	stock no. of materials examined	part selected for examination	Rf value
Rp+ *Pl*+*Pn*+	apiculus and awn	*C*^{B} *Sp*	A- 2	apiculus and awn	0.42
			A- 58	" and "	"
		C^{Bp} *Sp*	A-107	" and "	0.41
			A- 77	apiculus	0.43
		C^{B} *Sp*^{d}	A- 18	"	0.42
		C^{Bp} *Sp*^{d}	A- 83	"	"
		C^{Br} *Sp*	A- 5	apiculus and awn	"
Rp Pl+ *Pn*+	entire glume and rachilla	*C*^{B} *Sp*	A- 58	glume	"
		C^{Bp} *Sp*	A-107	"	0.43
Rp+ *Pl Pn*+	entire leaf blade, and sheath, ligule, pulvinus, auricle, node and internode	*C*^{B} *Sp*	D- 25	leaf blade	0.42
		C^{Bp} *Sp*	A- 77	"	"
				leaf sheath	"
				node	0.43
			A- 38	leaf blade	0.42
			N- 45	"	"
		C^{B} *Sp*^{d}	N- 4	"	"
Rp+ *Pl*+ *Pn*	leaf margin, leaf sheath, ligule, pulvinus, auricle and node	*C*^{B} *Sp*	A- 65	leaf margin	0.41
			A- 2	"	0.42
				ligule	"
				node	0.41
			A- 58	leaf margin	"
				node	0.42

leaf blade with the genic constitution of $C^{B}SpAPl$ was treated according to the quatitative analysis of aglucone effered by ROBINSON and ROBINSON (1931). The water solution of aglucone showed the following results of examination.

(a) The sample shows a violet color when sodium acetate is added to its amyl alcohol extract and ferric chloride changes the said violet to dark blue. (b) The sample is fairly stable in a solution of 10% sodium hydroxide. (c) A small portion of aglucone is extracted when the solution is shaken in an equal volume of a mixture of cyclohexanol (1 vol.) and toluene (5 vols.). (d) And it is also extracted, to a certain extent, in a 5% solution with an equal volume of amyl ethyl ether (1 vol.) and anisol (4 vols.).

Identical results are obtained from materials from genotype $C^{Bp}SpAPl$, using the same method. These results seem to indicate that the anthocyanin, which is present in rice plant, and which depends on the multiple allelic series of gene, *C* and *Sp*, has cyanidin as its aglucone.

To verify this assumption, this aglucone was paperchromatographically identified, and compared with a cyanidin specimen, by means of HAYASHI and ABE's method (1952). According to this one dimentional paperchromatography the Rf value of all samples invariably show the same values and are equal to that of the cyanidin.

On the whole therefore, the anthocyanin pigments presented by every combination of genes, *C*, *Sp*, *Rp*, *Pl* and *Pn*, are the same, with no qualitative differences in spite of numerous variations in color hue and shade as well as in location of colors.

Tawny pigment:

As to the chemical aspect on the tawny the author has not yet arrived at a satisfactory conclusion. NAGAO and TAKAHASHI (1947) have introduced a tentative interpretation that the chromogenic substance of the anthocyanin may be such a kind of substance as flavon, on which production gene *C* is concerned directly or indirectly. However, this assumption has not always been positively ascertained in the course of the author's later biochemical examination, though some indications of the presence of the flavon is noticeable.

On the other hand MIYAMOTO (1956, unpublished) made some chemical examinations on the same tawny by using qualitative and quantitative analysis worked out by KLEIN (1932) and ISHII and OSHIMA (1940) re-

spectively. MIYAMOTO asserts that the extract from parts in which the tawny would begin to develop, at the stage of ripening, mainly contain such a kind of substance as catechine, including catechol tannin. He also asserts that the content of the estimated catechine and catechol tannin show a tendency of direct proportion to the rank of dominancy in alleles of *C*-locus.

From a biochemical point of view, it is well known that the catechine and the catechol tannin is converted into phlobaphane, in which case the color hue is brown. Since the tawny in color shade comes under brown, it is also probable, to some extent, that the tawny coloration in rice may be caused by phlobaphane pigment.

As for a common precursor of the anythocyanin and the tawny, however, it may be difficult to assume that the catechine or the catechol tannin is responsible. The reason will be dealt with in the following General Considerations.

V. General Considerations, with Special Reference to Critical Identification of Genic Schemes Proposed by Other Workers

NAGAO and TAKAHASHI have briefly accounted for the degree of anthocyanin coloration by assuming multiple alleles at two loci, *C* and *Sp* (1947, 1951). In the present paper, abundant results have been brought forward by the author to prove that the above genic interpretation is able to encompass all data concerned, and in addition, some chemical and histological examinations have been produced to supplement the above.

In the present paper the author will be in a position to give critical identification of genic schemes proposed by other workers based on the author's scheme.

A. (Apiculus and Glume Coloration)

With regard to apiculus and glume coloration, more than ten color types were recognized as due to genes at three loci, exclusive of gene *A*. This is described as follows. The expression of anthocyanin or tawny color characters of apiculus is determined by the combination of alleles at *C* and *Sp* loci, in cooperation with *A*. And in addition to this, *Rp* is proposed for glume color. *Rp* is responsible for distributing the pigment substance produced in the apiculus over the entire

surface of palea and lemma. Thus the genotypes and their phenotypes, and the segregation ratios expected from the combination of above genes may be summarized as in Table 36.

In the past it has been considered that there exists a single pair of genes which in itself produces an anthocyanin coloration on apiculus, and that there also exists a linkage between this gene and a gene which refers to non-glutinous vs. glutinous endosperm, with an intensity of about 20% cross overs (TAKAHASHI 1923·1935, YAMAGUCHI 1926·1927·1929, CHAO 1928a, BREAUX 1940, JODON 1948, JODON and CHILTON 1946, and COMEAUX 1946 etc.). This is one of the well known relationships of linkage in rice plant, and is inserted in the *gl*-linkage group of NAGAO and TAKAHASHI (1947·1948) or in the Group-1 of JODON (1948).

Further, it has been assumed that various color shades of the anthocyanin necessitate the existence of a modifier which controls the color intensity in addition to a chromogenic gene. YAMAGUCHI (since 1921), NAGAI (1921), LEA (1927) and JONES (1930·1933) are the advocators of these schemes. And CHAO (1928) proposed two pair of duplicate genes for the expression of color in apiculus, on the basis of dihybrid segregation ratio of 15 colored to 1 colorless.

However the author have not yet come upon such occasions as to need the above mentioned complicated assumption, in so far as in crosses with which he is concerned, and it is emphasized that the production of the apiculus color or the expression of color hue or shade has been satisfactorily explained by the "*C–Sp*" scheme.

YAMAGUCHI (1926·1927·1929·1931) has made a cross experiments between two varieties, Karasumochi, which is blackish red purple in apiculus and glume color, and Shinriki, with colorless or green apiculus and glumes. Their F_1 plants had blackish red purple apiculus and glumes, and gave in F_2 the following five phenotypes in the apiculus and glume color, namely; blackish red purple in apiculus and glumes, blackish red purple at apiculus, reddish brown in apiculus and glumes, reddish brown at apiculus, and colorless or green in the ratio of 27:9:9:3:16 respectively. Based on these results he assumed three genes, *B*, *R* and *S* which concern the apiculus and glumes colors. According to him, *S* is a gene responsible for the development of reddish brown color at apiculus; *B* is a gene responsible for converting the reddish brown color to blackish red purple; and *R* is a gene responsible for spreading the pigment produced by *S* or *SB* over the entire surface of the glumes. *S* is linked with *gl*, giving 21.4% recombination values.

TABLE 36. Summary of the types of anthocyanin color characters in floral glumes and their ratios expected from combination of alleles of *C*, *Sp* and *Rp*, in the presence of *A*.

antho-cyanin	apiculus	purple		red purple		dark red		red		pink	
	glume	ditto	green	ditto	green	ditto	green	ditto	green	pinkish green	green
tawny	apiculus										
	glume										
genotype		$C^B\,Sp\,Rp$	$C^B\,Sp+$	$C^{Bp}\,Sp\,Rp$	$C^{Bp}\,Sp+$	$C^B\,Sp^d\,Rp$	$C^B\,Sp^d+$	$C^{Bp}Sp^dRp$	$C^{Bp}Sp^d+$	$C^{Bt}\,Sp\,Rp$	$C^{Bt}\,Sp+$
color type		I	III	II	IV	V	VII	VI	VIII	IX-a	IX-b
C^BSpRp	× ++++	27	9								
$C^{Bp}SpRp$	× 〃			27	9						
$C_{Bt}SpRp$	× 〃									27	9
$C^{Br}SpRp$	× 〃										
C^BSp^dRp	× 〃					27	9				
$C^{Bp}Sp^dRp$	× 〃							27	9		
C^BSpRp	$\times C^B++$	9	3								
〃	$\times C^{Bp}++$	27	9	9	3						
〃	$\times C^{Bt}++$	27	9							9	3
〃	$\times C^{Br}++$	27	9								
〃	$\times +Sp+$	9	3								
〃	$\times +Sp^d+$	27	9			9	3				
〃	$\times C^{Bt}Sp^d+$	27	9			9	3			9	3
〃	$\times C^{Br}Sp^d+$	27	9			9	3				
$C^{Br}SpRp$	$\times C^BSp^d+$	27	9			9	3				
C^B+Rp	$\times C^{Br}Sp^d+$					27	9				
〃	$\times +Sp+$	27	9								
$C^{Bp}+Rp$	$\times C^{Br}Sp^d+$							27	9		
〃	$\times +Sp+$			27	9						
C^B+Rp	$\times C^B++$										
〃	$\times C^{Bp}++$										
〃	$\times C^{Bt}++$										
〃	$\times C^{Br}++$										
〃	× ++++										

TABLE 36. (continued)

continued on the right side of the preceding table

pink	pale orange or wht.	pale orange or wht.	white							
green	green	green	green							
			dark brown		brown		light brown		straw white	
			ditto	straw white	ditto	straw white	ditto	straw white	ditto	total
$C^{Br}SpRp$ $C^{Br}Sp+$	$C^{Bt}Sp^{d}Rp$ $C^{Bt}Sp^{d}+$	$C^{Br}Sp^{d}Rp$ $C^{Br}Sp^{d}+$	$C^{B}+Rp$	$C^{B}++$	$C^{Bp}+Rp$	$C^{Bp}++$	$C^{Bt}+Rp$ $C^{Bt}++$	$C^{Br}+Rp$ $C^{Br}++$	$+SpRp$, $+Sp+$ $+Sp^{d}Rp$, $+Sp^{d}+$ $++Rp$, $+++$	
IX-c	XIV-a	XIV-b	X	XII	XI	XIII	XV-a	XV-b	XVI	
			9	3					16	64
					9	3			16	"
							12		16	"
36 (9)								12 (3)	16 (4)	" (16)
			9	3					16	"
					9	3			16	"
			3	1						16
			9	3	3	1				64
			9	3			4			"
12			9	3				4		"
									4	16
									16	64
	4									"
12		4								"
12		4								"
		12	9	3				4		"
			9	3					16	"
		12			9	3		4		"
		12			9	3			16	"
			3	1						4
			9	3	3	1				16
			9	3			4			"
			9	3				4		"
			9	3					4	"

Thus YAMAGUCHI concluded that the genic constitution for apiculus and glumes color in Karasumochi is *B R S* and in Shinriki B^+ R^+ S^+.

In the author's opinion, however, this type of segregation should be explained under one general scheme, "*C–Sp–Rp*"; the genotypes of Karasumochi and Shinriki may be $C^B SpRp$ (exactly $AC^B Sp\ Rpgl$) and $C^+ Sp^d Rp^+$ (exactly $AC^+ Sp^d gl^+$) respectively. The F_2 segregation ratio expected from this assumption should correspond to the results obtained by YAMAGUCHI;

27 $C^B Sp\ Rp$	blackish red purple in apiculus and glumes
9 $C^B Sp\ Rp^+$	blackish red purple at apiculus
9 $C^B Sp^d Rp$	reddish brown in apiculus and glumes
3 $C^B Sp^d Rp^+$	reddish brown at apiculus
9 $C^+ Sp\ Rp$	colorless or green
3 $C^+ Sp\ Rp^+$	
3 $C^+ Sp^d Rp$	
1 $C^+ Sp^d Rp^+$	

In this scheme, a linkage between *C* and *gl* should be phenotypically represented as a linkage between a gene for apiculus color and a endosperm gene *gl*, and the differential affection between *Sp* and Sp^d should appear as a differential situation on a intensifier for color intensity, viz. presence or absence of the emphassor.

The corroboration of the propriety of this opinion was already demonstrated by NAGAO and TAKAHASHI (1952 b), using the same materials as YAMAGUCHI, which is briefly as follows.

Cross 1: Karasumochi × Kuromochi ($C^B SpRpgl$)—Kuromochi shows the same color type as Karasumochi, and its genotype is known as $C^B SpRpgl$. The F_1 from the cross 1 was phenotypically the same as their P_1s, and in F_2 there appeared no segregation type with respect to the color type and the endosperm character.

Cross 2: Karasumochi × Ebisu ($C^{Bp} Sp^+ Rp^+ gl^+$)—A cross combination in which the author discovered the first case of linkage relation between *C* and *gl* was Kuromochi × Akage (colorless, $C^{Bp} Sp^+ Rp^+ gl^+$). Ebisu, a parental variety in the cross 2, was also ascertained to have an identical genotype with the Akage. As presented in Table 37, F_1 from the cross 2 showed the same coloration as Karasumochi, and gave in F_2 the same segregation type and consequently the same recombination value—between apiculus and endosperm gene—as in F_2 from Kuromochi × Akage.

TABLE 37. F_2 of cross between Karasumochi ($C^B SpRp gl$) and Ebisu $C^{Bp} Sp^+ Rp^+ gl^+$.

apiculus color	Blackish red purple		Pansy purple		Blackish red purple		Pansy purple		green, and tawny color at ripening				total	χ^2	d. f.	p
glume color	ditto		ditto		green		green		ditto		Straw white					
genotype	$C^B Sp\ Rp$		$C^{Bp} SpRp$		$C^B SpRp^+$		$C^{Bp} SpRp^+$		$C^B Sp^+ Rp$ $C^{Bp} Sp^+ Rp$		$C^B Sp^+ Rp^+$ $C^{Bp} Sp^+ Rp^+$					
	gl^+	gl	gl^+	gl	gl^+	gl	gl^+	gl	gl^+	gl	gl^+	gl				
0	84	32	39	2	26	7	18	1	42	15	14	3				
	116		41		33		19		57		17		283			
C. R.	27		9		9		3		12		4		64			
C	119.39		39.80		39.80		13.27		53.06		17.68		283.00	4.087	5	0.7–0.5

C-gl linkage (repulsion)

$C^B gl^+$	$C^B gl$	$C^{Bp} gl^+$	$C^{Bp} gl$	total
110	39	57	3	209

Recombination value: 25.1%

TABLE 38. F_2 from Karasumochi × Norin-20-go and Karasumochi × N-48, showing appearance of reddish brown segregants.

a. Karasumochi ($C^B Sp\, Rp\, gl$) × Norin-20-go ($C^{Bp} Sp^d\, Rp^+\, gl^+$)

apiculus color	Blackish red purple		Pansy purple		Blackish red purple		Pansy purple		Amaranth purple		Pome-granate purple		Amaranth purple		Pome-granate purple		total	χ^2
glume color	ditto		ditto		green		green		ditto		ditto		green		green			
genotype	$C^B Sp\, Rp$		$C^{Bp} Sp Rp$		$C^B Sp Rp^+$		$C^{Bp} Sp Rp^+$		$C^B Sp^d Rp$		$C^{Bp} Sp^d Rp$		$C^B Sp^d Rp^+$		$C^{Bp} Sp^d Rp^+$			
	gl^+	gl	gl^+	gl	gl^+	gl	gl^+	gl	gl^+	gl	gl^+	gl	gl^+	gl	gl^+	gl		
0	247	101	112	7	68	37	31	6	67	30	38	6	17	13	12	0		
	348		119		105		37		97		44		30		12		792	
C. R.	27		9		9		3		9		3		3		1		64	
C.	334.10		111.40		111.40		37.10		111.40		37.10		37.10		12.40		792.00	5.981

d. f.: 7 & p: 0.7–0.5

C-*gl* linkage (repulsion)

$C^B gl^+$	$C^B gl$	$C^{Bp} gl^+$	$C^{Bp} gl$	total
399	181	193	19	792

Recombination value: 29.4%

TABLE 38. (continued)

b. Karasumochi ($C^B Sp Rp gl$) × N-48 ($C^{Br} Sp^d Rp gl^+$)

apiculus color	Blackish red purple		Amaranth purple		Rose red		Seashell pink or white		total	χ^2	d. f.	p
glume color	ditto		ditto		green		green					
genotype	$C^B Sp Rp$		$C^B Sp^d Rp$		$C^{Br} Sp Rp$		$C^{Br} Sp Rp^d$					
0	197	94	71	26	100	3	30	4	525			
	291		97		103		34					
C. R.	9		3		3		1		16			
C.	295.31		98.44		98.44		32.81		525.00	0.388	3	0.98–0.95

1) In each column of color types, the left is gl^+ and the right is gl.

C-gl linkage (repulsion)

$C^B gl^+$	$C^B gl$	$C^{Br} gl^+$	$C^{Br} gl$	total
268	120	130	7	525

Recombination value: 22.9%

Hence, from the results of these crosses, the genotype of Karasumochi is undoubtedly $C^B Sp Rp gl$ of the author's scheme. Furthermore, to clarify the genotype of reddish brown apiculus color in F_2 from Karasumochi × Shinriki and to determine whether it is due to $C^B Sp^d$ or not, namely whether the Shinriki variety possesses Sp^d or not, the following two crosses were made.

Cross 3: Karasumochi × Norin 20 ($C^{Bp} Sp^d Rp^+ gl^+$), Karasumochi × N-48 ($C^{Br} Sp^d Rp gl^+$)—As to a tester which should cross with Karasumochi, genotypic plants such as $C^+ Sp^d Rp gl^+$ (colorless with non glutinous endosperm) would be most desirable. But the author was compelled to use plants of $C^{Bp} Sp^d Rp^+ gl^+$ and $C^{Br} Sp^d Rp gl^+$ as the next best testers. F_1s and F_2s from those crosses, however, came up to the author's expectation, segregating in F_2 as a reddish brown color type due to $C^B Sp^d$, as shown in Table 38. Substituting the C^+ for the C^{Bp}, in the cross 3, the mode of the F_2 segregation presented in Table 39 should result as being identical to that of F_2 segregation from the cross of Karasu-

TABLE 39. Mode of F_2 segregation, when C^{Bp} in Table 38 is substituted by C^+.

apiculus color	purple				reddish brown				white		total	χ^2	d. f.	p
glume color	ditto		green		ditto		green		green					
genotype	$C^B Sp\ Rp$ ($B\ S\ R$)		$C^B Sp\ Rp^+$ ($B\ S\ r$)		$C^B Sp^d\ Rp$ ($b\ S\ R$)		$C^B Sp^d\ Rp^+$ ($b\ S\ r$)		C^+SpRp , C^+SpRp^+ C^+Sp^dRp, $C^+Sp^dRp^+$ ($B\ s\ R$, $B\ s\ r$ $b\ s\ R$, $b\ s\ r$)					
	gl^+	gl	gl^+	gl	gl^+	gl	gl^+	gl	gl^+	gl				
0	247	101	68	37	67	30	17	13	193	19				
	348		105		97		30		212		792			
C.	334.10		111.40		111.40		37.10		198.00		792.00	5.477	4	0.3–0.2
(C. R.)	(27)		(9)		(9)		(3)		(16)		(64)			

mochi × Shinriki by YAMAGUCHI. Here, it is natural that the linkage between *C* and *gl* should be represented as the linkage between *S* and *gl*, and it follows that it is most probable that the genotype of Shinriki may be $C^{+}Sp^{a}Rp^{+}$.

On the whole therefore, these results are enough to substantiate the author's estimation that the necessity of introducing apiculus gene *S* and color emphassor *B*, as advocated by YAMAGUCHI, is invalid. The same estimation of the author may hold true in the cases reported by other workers who have proposed similar schemes of genes as YAMAGUCHI.

C–Sp scheme may also be applicable in such cases as digenic segregation due to duplicate genes. For instance, the result of cross as by CHAO (1928 a) can be explained on the assumption that the genotypes of parental varieties may be $C^{Bp}Sp \times C^{Bt}Sp^{a}$ (colored × colorless) or $C^{Bp}Sp^{a} \times C^{Bt}Sp$ (colored × colored). And in these crosses the F_2 ratio of 15 colored : 1 coloress is well within reason.

TABLE 40. Application of the present scheme to the JONES' result obtained in F_2 from a cross, Nilo Vialone × Caloro.

phenotype		all organs purple	leaf and leaf sheath purple striped (colorless node)	awn and apiculus red (colorless node)	all organs green	total	χ^2	d. f.	p
0		100	15	30	62	207			
JONES' interpretation	genotype	*A C P*	*a C P*	*A C p* *a C p*	*A c P* *A c p* *a c P* *a c p*				
	C. R.	27	9	12	16	64			
	C	87.33	29.11	38.81	51.75	207.00	12.708	3	0.01
interpretation by linkage	genotype	$C^{B}\overline{SpPn}$	$C^{B}\overline{SpPn}^{+}$	$C^{Br}\overline{SpPn}$ $C^{Br}\overline{SpPn}^{+}$	$C^{B}\overline{Sp^{+}Pn}$ $C^{B}\overline{Sp^{+}Pn}^{+}$ $C^{Br}\overline{Sp^{+}Pn}$ $C^{Br}\overline{Sp^{+}Pn}^{+}$				
	C. R. (9:3:4) (8:1)	72	9	27	36	144			
	C	103.50	12.94	38.81	51.75	207.00	4.475	3	0.3–0.2

Further, from this point of view, the remainder of the data as presented by several workers can be explained by the author's scheme, revealing that monohybrid or dihybrid segregation ratios of apiculus coloration as in the case of 3:1, 9:7, 9:6:1, 9:3:4, and 9:3:3:1 (HOSHINO 1915, HECTOR 1916, KATO 1916, MITRA et al 1928, NAGAI 1921, 1926, PARNELL et al 1917, 1922, Van der STOCK 1908 etc) can be interpreted by the "*C–Sp*" combination itself. Full accounts are omitted here, however for brief informotion Table 36 may be of sufficient value.

It has been already illustrated that trihybrid segregation on the apiculus coloration is settled by a modified *C–Sp–A* scheme. In connection with this, the result obtained by LEE (1927) is worthy of note. He demonstrated that a purple coloration in stem node may develop even in the absence of color in the apiculus. According to him a purple stemmed variety with pale yellow apiculus when crossed with other varieties which are green stemmed and have also pale yellow apiculus gave F_1 plants which were purple in both parts. The F_2 population divided into five types of coloration, namely; purple apiculus and node, pale yellow apiculus and purple node, purple apiculus with green node, red apiculus with green node, and pale yellow apiculus and green node. Based on this, he assumed that the purple coloration in the apiculus is due to the cooperation of three genes, *C*, *R* and *B*, and that in the stem node to the co-operation of *A*, *R* and *B*. The genic scheme is represented as:

Genotype	*stem node color*	*apiculus color*
A C R B	purple	purple
A c R B	"	pale yellow
a C R B	green	purple
A C R b	"	red
other combinations	"	pale yellow

Applying the author's scheme to the above, LEE's genes, *B–b*, *R–r*, *C–c* and *A–a*, may correspond to the author's genes, C^B (C^{Bp})–C^{Br}, *Sp–Sp*$^+$, *A–A*$^+$ and *Pn–Pn*$^+$, respectively.

MORINAGA et al (1943) briefly reported the presence of a linkage relationship among the gene for apiculus color, *Ap*, the gene for phenol reaction, *Ph*, and the gene for liguleless, *lg*. As *Ph* and *lg* are inserted into the *Pl*-linkage group (NAGAO and TAKAHASHI 1952a), it is most probable to consider that *Ap* is also linked with *Pl*. The author's *A*

gene also links with *Pl*. Whether *Ap* is identical with *A* or not, the question, however, is left for the present.

Hitherto, some workers have assumed that tawny color may be genetically due to a single pair of genes, *Ty*, of which they, except NAGAI (1922) and JODON (1948), had little consideration with respect to genetical or biochemical relationship to the anthocyanin coloration. In so far as the author is aware, NAGAI is the first worker who suggests the intimate genetical connection between the tawny and the anthocyanin color, though he was unsuccessful in the generalization of his gene scheme. He assummed the following four genes in color of the apiculus; a chromogen gene *C*, a chromophlein gene *O* that converts the chromogenic substance to the brown-this may be the tawny-pigment, a red anthocyanin gene *R* in the presence of *C*, and a purple anthocyanin gene *R'* in the presence of *C* and *R*. The genes *C* and *O* were supposed to be completely linked, or to constitute a single gene complex. Thus the scheme of genes of NAGAI may be given as:

Genotype	*apiculus and awn color*
$\overline{C\ O}\ R\ R'$	purple
$\overline{C\ O}\ R\ r'$	red
$\overline{C\ O}\ r\ R'$, $\overline{C\ O}\ r\ r'$	brown (tawny)
combination without $\overline{C\ O}$	white

As to the linkage between the tawny and the endosperm character, CHAO (1928a) reported a recombination value of about 17% between *Ty* and *gl*. This value is similar to the value obtained between *C* and *gl* (21% on the average), indicating that the tawny of CHAO is probably identical with the *C* of the author.

On the whole therefore, the *C-Sp-A* scheme proposed as the apiculus coloration has been, if not completely substantiated, or at least rendered highly probable.

It is worthy to emphasize that in connection with the apiculus coloration and in accordance with the *C-Sp-A* scheme, the following two problems which have been debated for a considerable length of time seems to be settled to some extent. One of these is the explanation for such types of coloration as light colored apiculus with deep colored leaf and blade, and the other is the question as to whether plants with colorless apiculus but with some coloration in other parts exist or not.

If in a plant which has a genic constitution of $C^{B}SpA$ and shows a deep coloration in several parts, A is substituted with A^{+}, and the distribution of colored cells in the apiculus becomes scarce, resulting in the shade of the apiculus color showing a phenomenal decrease in comparison with that of the other parts. And if a plant, which has a genic constitution of $C^{Bp}Sp^{a}APl$ or C^{Bp} $Sp^{a}APn$ and shows a light coloration in apiculus and other parts such as leaf or node, loses the dominant gene A, its apiculus may scarcely show any coloration in which case the apiculus is considered to be colorless to the eye in spite of having colored leaf or node.

B. (Coloration in Other Vegetative Parts)

Up to the present, many workers have concentrated on the full colored leaf character designated as Murasakiine (purple rice plant), reporting several types of segregation such as 3:1 (NAKAYAMA 1931, PARNELL 1917 etc), 9:7 (PARNELL et al 1917, YAMAGUCHI 1932, NAKAYAMA 1932 etc), or 27:37 TAKEZAKI 1921·1923, JONES 1930, NAKAYAMA 1932, YAMAGUCHI 1932 etc) in respect of full colored vs. non full colored.

According to the author's scheme this color character develops in the presence of a gene *Pl* in combination with apiculus color genes, *C* and *Sp*, and *Pl* may be said to be a modifier that is responsible for distributing the pigment substance produced by the apiculus genes over the entire surface of the leaf blade and leaf sheath. If F_2 populations from crosses involving *Pl* are classified in two groups, full colored leaf vs. non full colored, they should show various segregation ratios, such as 3:1, 9:7 and 27:37, depending on which allele of apiculus color genes coexist with *Pl*.

It follows from this that among several genes, which have been worked out by other workers with respect to full colorationin the leaf, there exists some genes that may be considered to be the apiculus genes rather than being complementary genes.

The *Pl* is a representative gene in *Pl*-linkage group, and is linked with a gene for liguleless, *lg*, with the recombination value of 27% (NAGAO and TAKAHASHI 1952 a). MORINAGA et al (1938, 1942, 1943) obtained a linkage relation between *lg* and a plant color gene, with a 22% recombination value. It is probable that MORINAGA's color gene is identical with the author's gene *Pl*.

The effect of *Pl* is depleted by the presence of *Ipl* that inhibits the coloration in the leaf blade. Same color types and same modes

of segregation have been also reported by many workers, e. g., KADAM (1936) in India, YAMAGUCHI (1937) in Japan, and JODON (1945) in the United States, all of whom proposed similar inhibitor.

As regards the coloration in stem node—including pulvinus, auricle and ligule—considerable work has been done, and various segregation ratios of colored vs. colorless were reported; 3:1 (JONES 1930), 9:7 (HECTOR 1922, JONES 1930, BOREAUX 1940), 27:37 (HECOR 1922, CHAO 1928 a, JONES 1930) etc. The genic schemes were also conflicting and up to the present at least three which are concerned with production of node color have been proposed (KADAM and RAMIAH 1943, JODON 1948).

According to NAGAO and the authors' scheme (1951 a) however, under the coexistence of apiculus genes, only a single pair of gene *Pn* is required for node coloration, neverthless several types of segregation ratio are presented, when they are conducted either in leaving the apiculus color out of consideration or in taking them into consideration. The multiplicity of type of segregation ratio result not only from differences of genotype of the apiculus but also from the existence of linkage relationship between *Pn* and *Sp*, one of the apiculus gene.

Therefore, it may be open to discussion as to whether so many genes as estimated by other workers are necessary, viz. exist, or not, with respect to the node, pulvinus, auricle or ligule coloration.

CHAO (1928 a) explained his results by assuming three complementary genes, Lg_1, Lg_2 and Lg_3, in which Lg_3 is closely linked with a pericarp gene Pr_2. Only triple dominat plants show coloration in ligule, and a similar situation is reported by HECTOR (1922). According to NAGAO and TAKAHASHI (1946, 1947, 1948), *Sp* is found to be closely linked with a pericarp color gene, *Rd*, the recombination value being less than 0.3%. As *Sp* is indispensable for the production of anthocyanin pigment, *Sp* and *Pn* are said to be complementary to each other. Thus, CHAO's gene Lg_3 may be the equivalent rather to the author's *Sp* than to ligule color gene in itself.

BREAUX (1940) also demonstrated that pulvinus color is due to the co-operation of two genes, *Jpa* and *Jpb*, in which *Jpa* links with a endosperm gene *gu* (identical with the author's gene *gl*) with a 23% of recombination value. *Jpa* is recognized to be identical with an apiculus gene *Ap* by JODON (1948), and is linked with an endosperm gene *wx* (identical with *gl* or *gu*), with about a 20% (though varying from 7% to 30%) recombination value. Based on this linkage relationship and considering from the mode of inheritance in tawny color, it

is probable that *Jpr* is identical with the chromogene gene *C*. If so, it may be a natural result than *Jpa* behaves as a complementary gene for pulvinus coloration. Thus, the genic constitution of the cross combination, *C*1400×*C*1422, that BREAUX worked upon, may be represented by the author's scheme as $\overline{C\,gl^{+}\;Sp\,Pn}\times\overline{C^{+}gl\;Sp^{+}Pn^{+}}$, $\overline{C\,gl^{+}\;Sp\,Pn^{+}}\times\overline{C^{+}gl\;Sp^{+}Pn}$ or similarly. Here, a recombination value of about 23% in *C–gl* should be expected, which value is same as that of *Jpa–gu* by BREAUX.

An inheritance of color in leaf and leaf sheath was studied by JONES (1930), in a cross between Niro vialone, an Italian colored variety, and Caloro, a colorless variety. In this cross F_2 gave the following mode of segregation in actual numbers of segregants as 100 all organs purple, 15 leaves and leaf sheaths purple striped, 30 apiculus red, and 62 all organs green. As an explanation of this result, he proposed a 3-gene hypothesis, though the numbers do not agree well with the expected ratio, 27:9:12:16. And as to the shortcoming of 27:9:12:16 ratio, be assumed that some disturbing forces may be affecting the result in this case. By the application of the author's *Pn–Sp* schème, however, the deviation from the observation in the above may be lessened. Assuming that the genotypes of the parental varieties, Niro Vialone and Caloro, are $C^{B}\overline{Sp\,Pn}$ and $C^{Br}\overline{Sp^{+}Pn^{+}}$ respectively, their F_2 should give a segregation type as presented in Table 40. The F_3 from this F_2 is also satisfactorily explained by this scheme rather than by JONES', and this scheme is consistent with other datas and their genic interpretation by JONES.

Further, as regards node color, JONES described a singular ratio of segregation, 1 colored : 1 colorless, in F_2 from a cross Colusa × Italian Red, without success in their genic interpretation. To this result, the author's scheme is also applicable, under the supposition that Colusa is $C^{B}\overline{Sp\,Pn}$ or $C^{Bv}\overline{Sp\,Pn}$ and Italian Red is $C^{+}\overline{Sp^{+}Pn^{+}}$. From these genic constitutions, the segregation ratio of the node coloration, apart from the consideration on apiculus coloration, should be given as 1 colored vs. 1 colorless (exactly 513:5111 respectively) as a result of the linkage relation between *Sp* and *Pn*, with a recombination value of 18% in the repulsion phase.

As a whole, it may be concluded that the results of these critical examinations further support the propriety of the author's genic scheme in indicating that there is no necessary for estimiting so many color

genes for the vegetative part itself as the other workers seem to find necessary.

C. (Histologicals)

So far as the author is aware, little work on histological illustration on the anthocyanin coloration, in connection with their genic constitutions, has been reported previous to this time. Even when it was presented, its description is rather obscure. For example HATCHINSON and RAMIAH (1938) have reported on the coloration on the following histological color location in leaf blade, without detailed observation. According to them: "Among the purples, apart from the grades of intensity, three types may be distinguished, (i) one with self color only, where the color is confined to the parenchcymatous tissue between vascular bundles, (ii) one with purple line only, i.e. the color confined to the vascular bundles, the intervening tissue being green, and (iii) where the color is present in both the bundles and the intervening tissue".

According to the results presented in the present paper, which tissues of what organ are colored varies; depending on the differences of the organs and on the genes. For instance, in genotypes of *CSpPn*$^+$ and *CSpPn* which externally refer to producing the similar purple lines in midrib of leaf blade, the former has the pigmentation of parenchyma attached to bundle sheath, while in the latter the pigmentation is found at sclerenchyma outside the bundle. Further in examining the location of colored cells by an identical gene, for instance as regards the purple color in leaf blade and leaf sheath by *Pl*, the pigmentation in parenchyma attached to bundle sheath which appears in the sheath, is no longer found in the bundle, in which case the pigment begins to develop in sclerenchyma.

Therefore, it is not only incorrect to decide the coloring part on a mere visual observation, but a thorough microscopic examination of various parts which are colored by identical gene is necessary.

Histologically, the coloration with anthocyanin is the pigmentation in cell sap without exception, and the coloration with tawny substance is the pigmentation inside the cell wall as a result of the desiccation of the cell. As to the tissual location of the pigmented cells, it is briefly refered to in Table 33 and 34.

D. (Biochemicals)

It has been reported that at least one of aglucons involed in the rice anthocyanin is identified as cyanidin by HAYASHI (1944 · 1946). However this study was carried out only from a chemical point of view, by using purple leaf blades of a single type of colored variety; Murasaki-ine. It is unfortunate that the genic constitution of HAYASHI's sample is not ascertained.

Identical result were obtained by the author, and further it is substantiated that the anthocyanin pigment presented by every combination of genes are the same, with on qualitative differences in spite of showing remarkable variations in color shade as well as in tissual location of colors.

As to the biochemical cause of occurence of the variation in color shade, two possible causes have been recognized; (a) depends on quantitative differences of anthocyanins, or (b) is based on qualitative differences in co-pigments of the anthocyanin or in complex salts of the anthocyanin. The later was advocated by ROBINSON et al. (1931), SHIBATA et al. (1918), MIYAMICHI (1943) or other workers as a result of examinations between remarkably different color hues in some kinds of flowers. Which is the more probable explanation, the former or the later, in the case of rice plant, is not yet ascertained at present, however, the fact that the color hue in rice does not vary so greatly, with similar color hues of cell sap, seems to indicate that it may be enough to be explained by the former alone. This is also supported to some extent by the biochemical aspect mentioned above.

It may be said in this connection that the differences of the affection of multiple alleles at *C*-locus are to be regarded as quantitative, and same should be considered to hold in the case of *Sp*-locus.

As regards the common precursor of the anthocyanin and the tawny, the author made auggestions, in the preceding part, that catechin might be hard to be considered as the substance produced by the direct affect of *C*. This is because of the difficulty in changing from the catechin to the anthocyanin; and rather than this, as already mentioned before, another estimated case that the common precursor of the tawny and the anthocyanin may be a kind of flavon and that the expression of the tawny color may be due to the presence of such a kind of substance as flavonol is more probable, since the chemical change, flavon→anthocyanin, is recognized and admitted by some biochemists.

Therefore, at present, the author will only give a following amending interpretation on biochemical aspect of the action of *C*, that is; *C* may be responsible for the formation of a common precursor of the flavon and the anthocyanin and possible the catechin.

Biochemically, the anthocyanin, the flavon and the catechin are all ingredients of the flavonoid, and from the work of ROBINSON (1935) it has been advanced that they should be derived from a common precursor.

VI. Conclusion

Whether the genic scheme of the author described in the present paper is adepuate must be left to the judgement of others, however, it, at any rate, is certain, that not only from the author's own data but also from a review of literature of other workers as conducted by the author revealed that several modes of segregation on rice coloration, notably apiculus color, can be reasonably explained by the author's scheme.

By way of conclusion, the genes proposed by the author are arranged and classified into the following three groups of causal genes, according to how many other genes are necessary when the proper gene exerts its effect to the eye.

Basic group

C : fundamental gene for apiculus coloration.
Sp : ditto
A : sub-basic; gives some modifying effect on *C*.

Distributing gene group

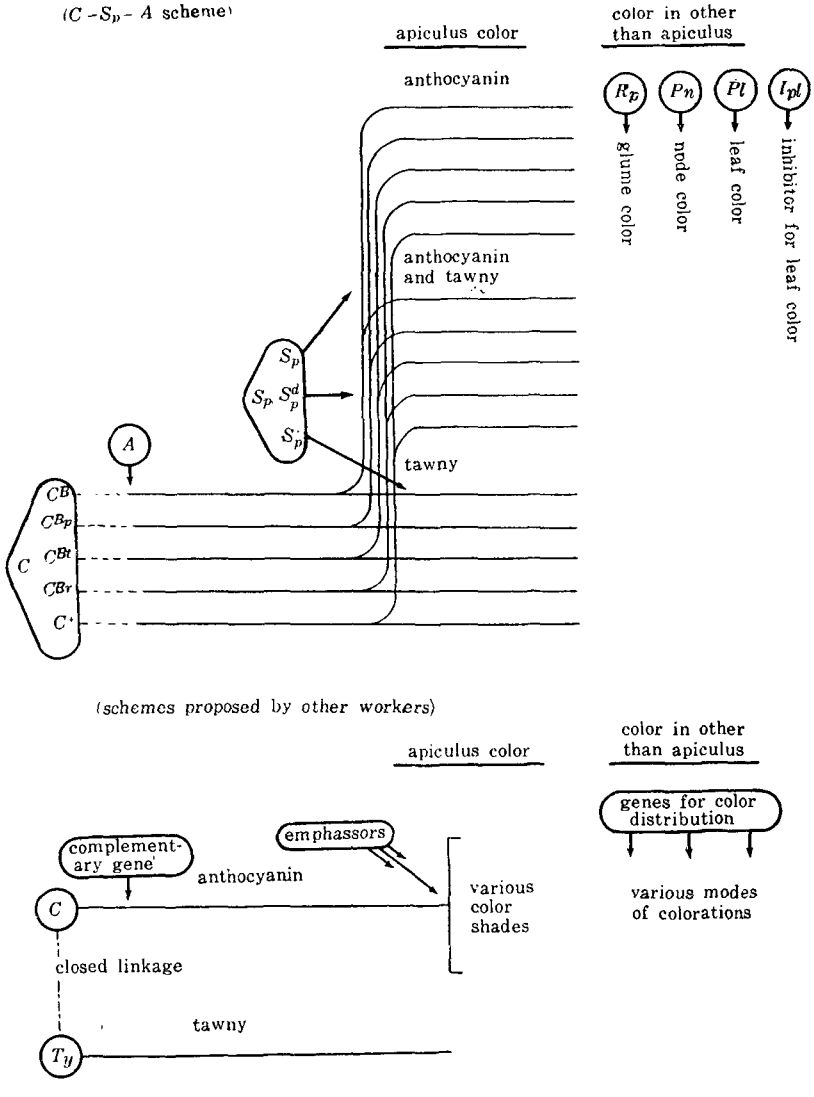
Rp : exerts its effect, under the existence of basic gene.
Pl : ditto
Pn : ditto

Inhibitor group

Ipl: exerts its influence, only when it coexists with a gene *Pl*

The genic interrelation and the mode of color expression caused by these genes are diagramatically represented as in Table 41, in comparison with other genic schemes that have been previously supported by many workers.

TABLE 41. Diagramatic illustration of the "*C-Sp-A*" scheme of gene, in comparison with other previous schemes.



VII. Summary

1. In the present paper, anthocyanin color characters in several parts of plant, notably in apiculus, are genetically described and illustrated, and some of their histological and biochemical natures are discussed with an emphasis on the production of further evidence of the propriety of the genic scheme that has been briefly proposed by NAGAO and the author.

2. The occurence of anthocyanin color in rice depends on the complementary effect of gene *C* and *Sp*; *C* is the fundamental gene for the production of chromogen, and *Sp* exerts its modifying effect on *C* and turns the chromogen into anthocyanin. *C* and *Sp* each comprises multiple allelic series of genes; five alleles are found at *C*-locus, and three at *Sp*-locus. They are arranged according to the rank of dominancy as follows;

$$C^{B} > C^{Bp} > C^{Bt} > C^{Br} > C^{+} \text{ and } Sp > Sp^{a} > Sp^{+}$$

3. Biochemically, *C* is considered to be responsible for the production of such substances as flavon or catechine, or is considered to be the common precursor. *Sp* is connected with the conversion into anthocyanin pigment, or is related with the prevention of changing of substances into other substances.

4. Aglucon of the anthocyanin was identified to be cyanidin without exception, there being no qualitative differences among the various hues and shades of color and consequently throughout every combination of color genes.

5. The expression of anthocyanin color character of apiculus is essentially attributed to the complementary effect of *C* and *Sp*, 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 *Sp*, for another gene *A* to exist, which is concerned with spreading chromogenic substance over the entirety of the apiculus.

6. The majority of varieties, as a matter of fact however, possess *A* in common, it follows that principal color types on the apiculus color can be genetically explained as a result of combinations of any alleles of the *C* and *Sp* loci.

7. The rank of dominancy of every allele at *C* and *Sp* loci is in direct proportion to the potency of chromogen production and also to the utilizing ability of chromogenic substance in the formation of

anthocyanin pigment, respectively.

8. In the case of absence of *C* or *Sp* and/or either one of them, the anthocyanin color does not appear and the plant is uncolored at the time of flowering, but on ripening and if *C* is present alone or with Sp^d, that is when it is without *Sp*, *C* makes the apiculus brown viz. tawny in several intensities of color shade, depending on which alleles of *C*-locus is concerned.

9. To this phenomena, it is assumed that, when *Sp* is absent, the chromogenic snbstance produced by *C* changes to brown pigment which may be a kind of substance such as flavonol or phlobaphane. Sp^d is less potent than *Sp*, that is, only a fraction of the chromogenic substance produced can be utilized in the formation of anthocyanin pigment, and therefore when *C* coexists with Sp^d the remaining quantity of unchanged chromogenic substance is turned into tawny pigment. This is the reason why certain genotypic plants, e. g. C^BSp^d and $Cp^{Bp}Sp^d$, show a particular mode of coloration in which the anthocyanin and the tawny colors overlap each other.

10. Thus it is apparent that the coloration with anthocyanin and tawny pigment have an intimate connection with each other. The following is the relation of hue and shade of apiculus color according to dominancy of any allele in the ascending order.

		C^B	C^{Bp}	C^{Bt}	C^{Br}	C^+
Sp	a. f.	purple	red purple	red	pink	white
	t. r.	not detectable				
Sp^d	a. f.	deep red	red	whitish orange	whitish orange	white
	t. r.	brown	light brown	yellowish white	white	white
Sp^+	a. f.	white	white	white	white	white
	t. r.	dark brown	brown	light brown	yellowish white	white

a. f. . . . . anthocyanin color at flowering.
t. r. . . . . tawny color at ripening.

11. Every allele at *C*-locus, in cooperation with any allele at *Sp*-locus, gives rise to respective color shades in awnes and empty glumes

as well as in apiculus. And further, when a high ranking allele at *C*-locus is involved, some other parts are also colored as a result of a pleiotropic action of the said allele. The expanse of coloring parts by any allele of *C*-locus is proportional to the rank of dominancy of *C*-allele, as tabulated in Table 33.

12. With regard to the anthocyanin coloration in some parts other than apiculus, three remarkable genes, *Rp*, *Pl* and *Pn* are proposed. The occurrence 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 *Rp*, *Pl* and *Pn* coexist with any gene combination at *C* and *Sp* loci. And in a case that the apiculus are colorless, no color develops in other part no matter whether three these genes are present.

13. Thus *Rp*, *Pl* and *Pn* are recognized to give rise to distributing the apiculus color into respective parts. *Rp* is responsible for distributing the apiculus color over the entire surface of lemma and palea, and in some cases rachilla. This is also holds good in the tawny coloration of these parts. *Pl* is concerned with the color distribution over the entire surface of leaf blade, leaf sheath, pulvinus, auricle, ligule, stem, stem node and rachis. *Pn* is connected with the distribution of color in leaf apex, leaf margin and entire surface of stem node, pulvinus, auricle and ligule. The most striking colored parts by *Pl* and *Pn* are the leaf blade and stem node.

14. The effect of *Pl* is diminished by the presence of an inhibitor for *Pl*, that inhibits the coloration at the center of leaf blade. This gene is designated as *Ipl*.

15. On the whole, therefore, the apiculus color genes are indespensable in analysing the mode of color inheritance, not only in the apiculus but also in all other parts, and it is concluded that *C* and *Sp* are the basic, while *A* is the sub-basic, gene in connection with anthocyanin coloration in rice.

16. Histologically the coloration with anthocyanin is the pigmentation in cell sap without exception, and the coloration with tawny color is the pigmentation on innersurface of cell walls as a result of the desiccation of the cell. The tissual location of the colored cells, however, varies somewhat, according to which of the color genes are concerned. This diagramatically presented in Table 34 and 35.

17. It is worthy of note that when plants have *Sp* in common and differ from each other in allele at *C*-locus, the differences in visual

color intensity can mainly be attributed to the differences in density of distribution of the colored cell, rather than the differences in the intensity of cell sap color; and when plants have *C* in common and differ from each other in allele of *Sp*-locus, the visual color differences are mainly due to the differences in color intensity of the cell sap.

18. From the author's own data and from a review of literature by other workers, various modes of inheritance on anthocyanin coloration in several parts of rice, especially in apiculus, can be reasonably explained by the author's gene scheme described above.

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EXPLANATION OF PLATES

Plate I.

Fig. 1. Natural figure of rice plant.
a, panicle; b, leaf, node and internode; c, glume.

Fig. 2. Principal parts of rice plant represented diagramatically.
A, apiculus; B, lemma; C, palea; D, stigma; E, empty glume; F, rachilla; G and H, rachis; I, leaf sheath; J, node; K and L, leaf blade; M, internode; N, ligule; O, auricle; P, pulvinus; Q, outer-surface of leaf sheath; R, innersurface of leaf sheath.

Fig. 3. Color-squares and their nomenclature.
a, Blackish red-purple; b, Pansy purple; c, Amaranth purple; d, Pomegranate purple; e, Tyrian rose; f, Rose red; g, Seashell pink; h, Russet; i, Tawny; j, Ochraceous-buff; k, Warm buff; l, Straw white.

Plate II.

Fig. 1. Coloration of apiculus both in flowering and in ripening stages.

A. Colors produced by the combination of *Sp* with all *C*-alleles.

	genotype	*color type*	*color shade at flowering*
a.	$C^{B}\,Sp$	III	Blackish red-purple
b.	$C^{Bp}Sp$	IV	Pansy purple
c.	$C^{Bt}Sp$	IX–b	Tyrian rose
d.	$C^{Br}Sp$	IX–c	Rose red
e.	$C^{+}\,Sp$	XVI	White

B. Colors produced by the combination of Sp^{d} with all *C*-alleles.

	genotype	*color type*	*color shade at flowering*
f.	$C^{B}\,Sp^{d}$	VII	Amaranth purple
g.	$C^{Bp}Sp^{d}$	VIII	Pomegranate purple
h.	$C^{Bt}Sp^{d}$	XIV–a	Seashell pink ?
i.	$C^{Br}Sp^{d}$	XIV–b	Seashell pink
j.	$C^{+}\,Sp^{d}$	XVI	White

C. Colors produced by the combination of Sp^{+} with all *C*-alleles at flowering and at ripening.

	genotype	*color type*	*color shade* *at flowering*	*at ripening*
k.	$C^{B}\,Sp^{+}$	XII	White	Russet
l.	$C^{Bp}Sp^{+}$	XIII	"	Tawny

m. $C^{Bt}Sp^{+}$ . . . XV-a . . . " . . . Ochraceous-buff
n. $C^{Br}Sp^{+}$ . . . XV-b . . . " . . . Warm buff
o. C^{+} Sp^{+} . . . XVI . . . " . . . Straw white

(Colored squares shown on the right side of each glumes indicate the expression of internode colors occurred as a pleiotropic effect of *C* and *Sp* alleles.

Fig. 2. Expression of glume color due to *Rp* affected by the presence of *CSp* or CSp^{+}.

	genotype	*color type*	*color shade at flowering*	*at ripening*
a.	C^{B} *Sp Rp*	I	Blackish red-purple	
b.	C^{Bp}*Sp Rp*	II	Pansy purple	
c.	C^{B} $Sp^{d}Rp$	V	Amaranth purple	Tawny
d.	$C^{Bp}Sp^{d}Rp$	VI	Pomegranate purple	(light) Tawny
e.	C^{B} $Sp^{+}Rp$	X	Green	Russet
f.	$C^{Bp}Sp^{+}Rp$	XI	"	Tawny

Plate III.

Fig. 1. Expression of plant color character due to *Pl*, affected by the presence of *C* and *Sp* series of genes.

a. C^{B} *Sp Pl*
b. C^{Bp}*Sp Pl* . . . . full purple leaf, (a) being darker than (b).
c. C^{B} $Sp^{d}Pl$
d. $C^{Bp}Sp^{d}Pl$ . . . . reddish green leaf, (c) being darker than (d).
e. $C^{Bt}Sp$ *Pl* . . . . green leaf with pink tint around pulvinus and node.

Fig. 2. Colors of leaf margin, node and pulvinus, caused by *Pn*, in cooperation with *C* and *Sp* series of genes.

a. C^{B} *Sp Pn*
b. C^{Bp}*Sp Pn* . . . . purple node and pulvinus with colored leaf margin, (a) being darker than (b).
c. C^{B} $Sp^{d}Pn$
d. $C^{Bp}Sp^{d}Pn$ . . . . red node and pulvinus, the red disappearing in the leaf margin.
e. Neither *Pl* nor *Pn* present.

Plate IV.

Fig. 1. Color expression due to an inhibitor *Ipl* for *Pl*, in cooperation with *C* and *Sp* genes.

a, $C^{B}SpPl\,Ipl$; b, $C^{B}Sp^{d}Pl\,Ipl$. It is shown that *Ipl* makes the purple or the red leaf blade colorless or green.

Fig. 2. Apiculus, awn and node color of "Xp-type", based on genotype of $C^{Bp}SpA^{+}Pn$.

a and b, awnes and glumes dotted with purple stippling; c, location of color by *Pn*.

Fig. 3. Comparative illustration of histological location of three kinds of colors, anthocyanin, tawny and gold, in glumes.

a. anthocyanin . . pigmentation in cell sap.
b. tawny . . . . . pigmentation on innersurface of cell wall.
c. gold . . . . . coloration in cell wall occurring as an effect of a pigment other than (a) and (b).

Plate V and VI.

Histological location of anthocyanin color developed in some genotypic plants.

Fig. 1. Location of colored cells with $C^{Bp}Sp$.

Fig. 2. Location of colored cells with $C^{B}Sp$.

Fig. 3. Glume color due to *Rp*, in cooperation with $C^{B}(C^{Bp})Sp$.

Fig. 4. Vegetative part coloration occurring as a pleiotropic expression of $C^{B}Sp$.

Fig. 5. Leaf and node color due to *Pn*, in cooperation with $C^{B}(C^{Bp})Sp$.

Fig. 6. Leaf, node and internode colors due to *Pl*, in cooperation with $C^{B}(C^{Bp})Sp$.

B. cross section of glume.
B′. enlarged figure of (B).
D. stigma.
E. cross section of empty glume.
J. cross or longitudinal section of node.
K. cross section of midrib of blade.
K′. enlarged figure of (K).
K″. cross section of leaf margin.
M. cross section of internode.
M′. enlarged figure of (M).
Q. cross section of midrib of sheath.
Q′. enlarged figure of (Q).

bs, bundle sheath; c, assimilation tissue; cav, cavity of inter-node; e, epidermis; h, hypodermis; ie, epidermal cell on innersurface; l, lemma; lac, lacuna; lsh, leaf sheath; m, motor cell; mav and miv, vascular bundle; mx, metaxylem; oe, epidermal cell on outer surface; p, palea; par, parenchyma; ph, phloem; px, protoxylem; pi, pith; s, stereom, sg, papilla cells of stigma; spv, spiral vessel; st, stem (internode); sy, style; t, trichome; v, vascular bundle.

(Black arrows indicate the location of colored cells).

Fig. 1

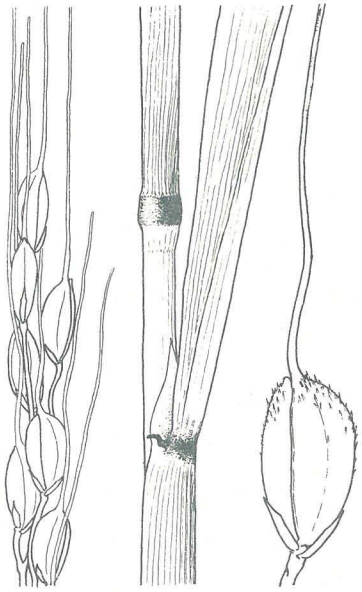

Fig. 2

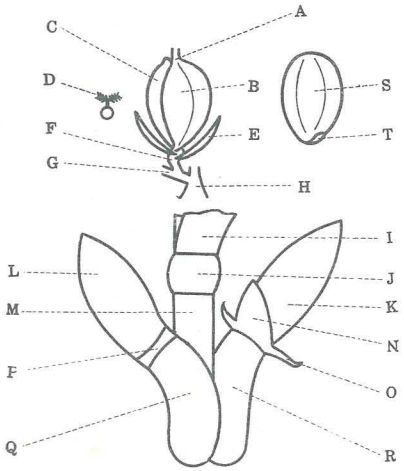

Fig. 3

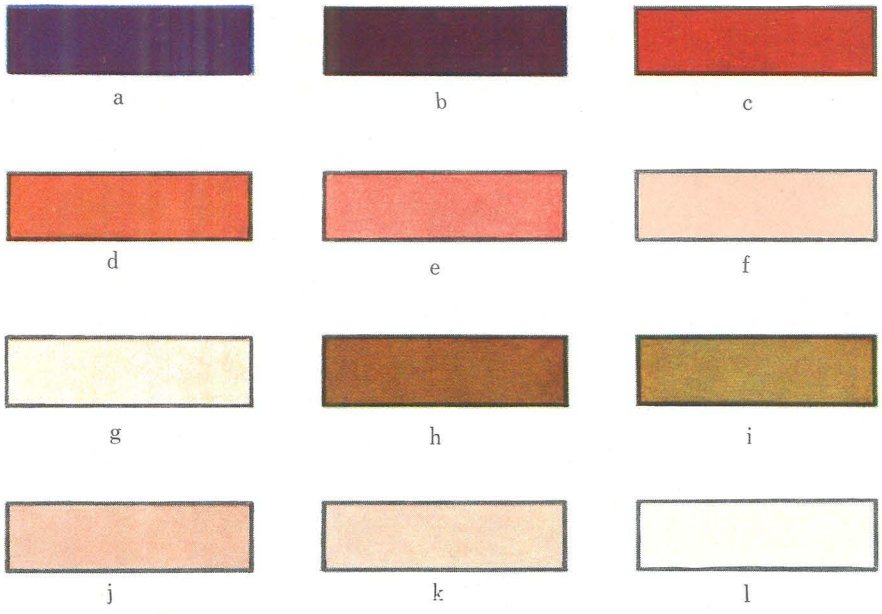

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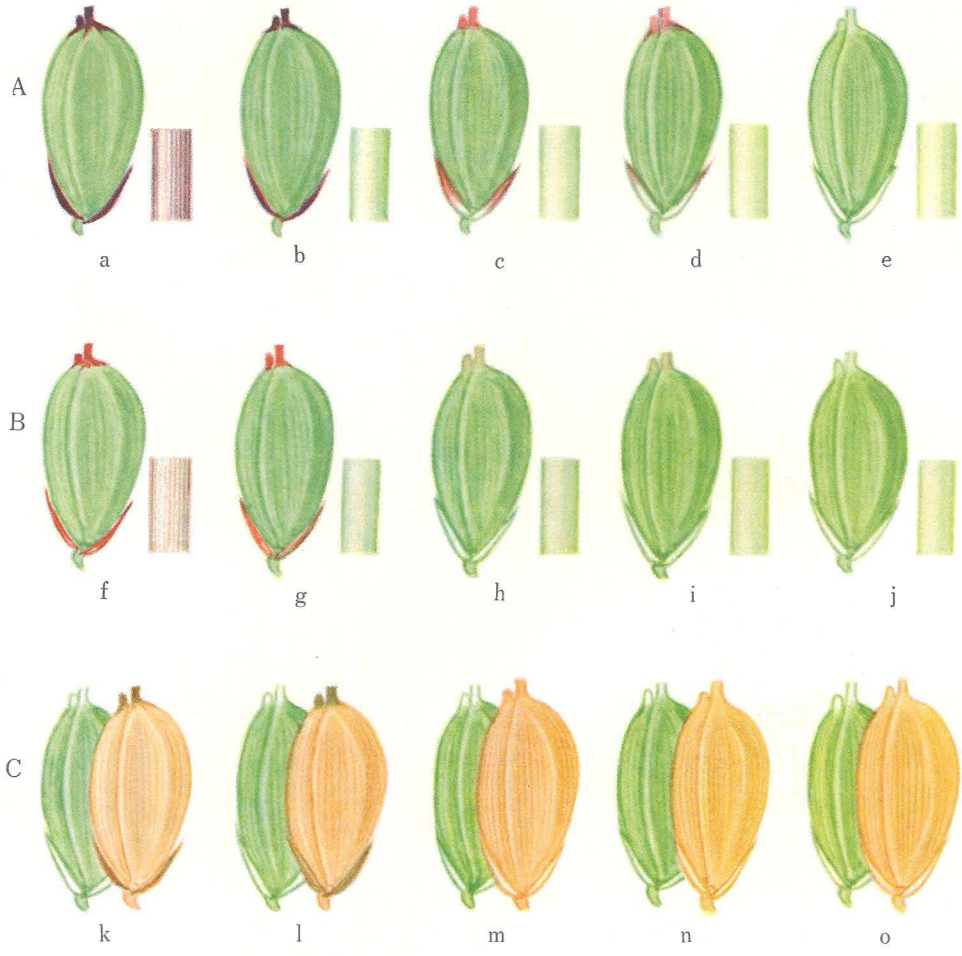
Fig. 1



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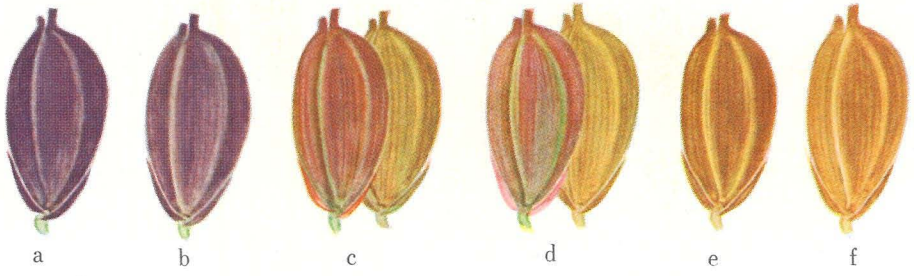

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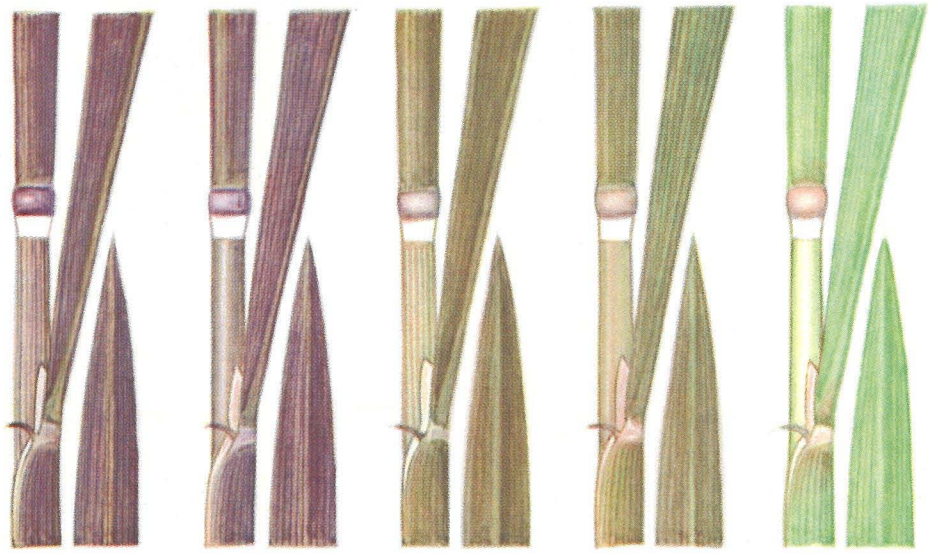
Fig. 1



a b c d e

Fig. 2

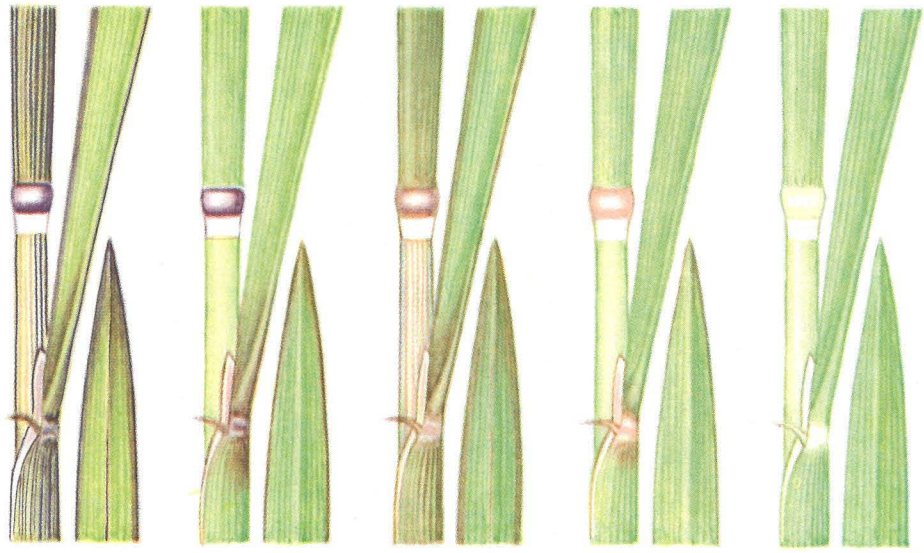


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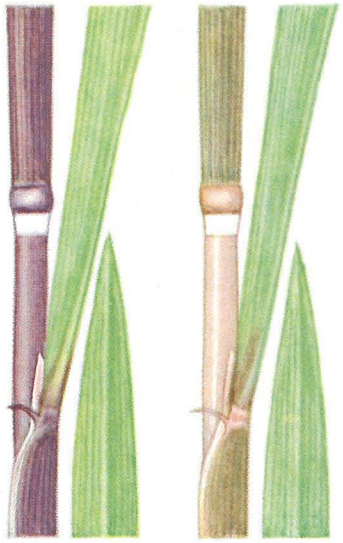
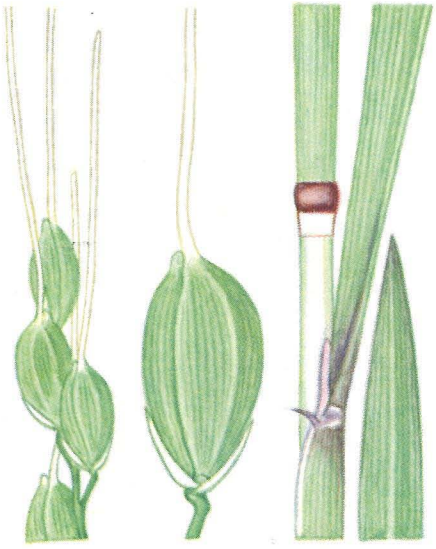
Fig. 1



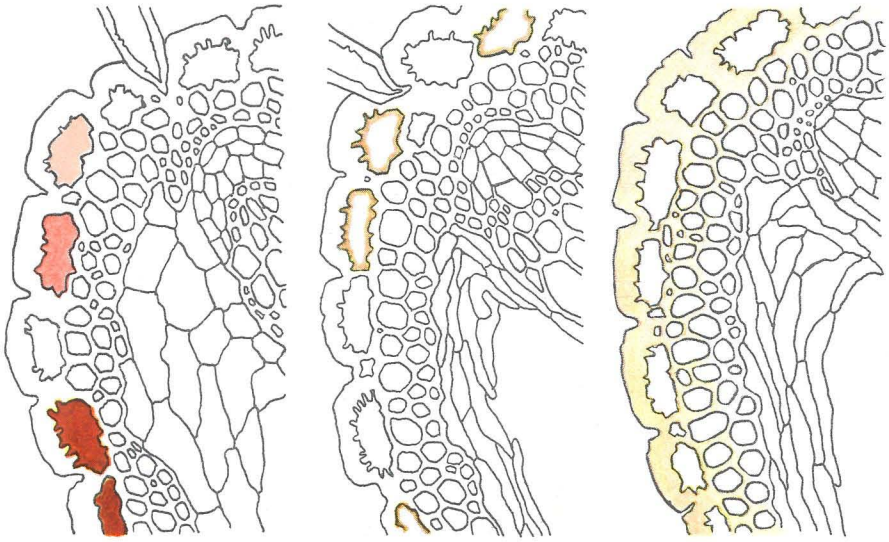
a b

Fig. 2



a b c

Fig. 3



a b c

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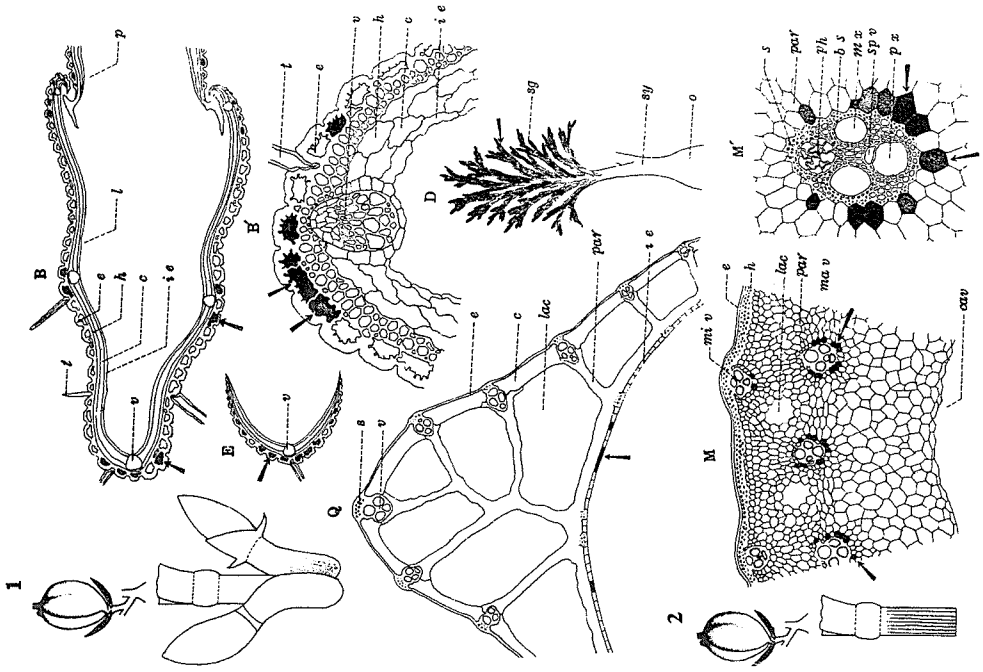

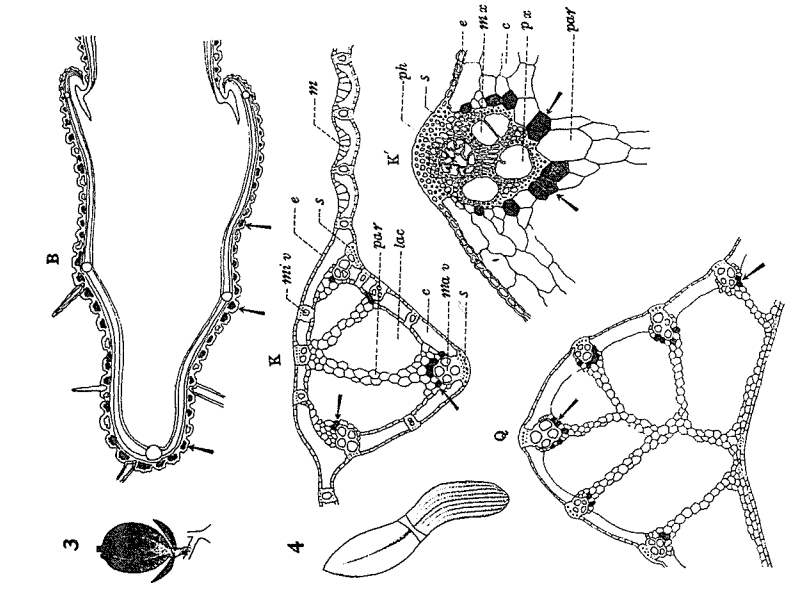

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