GENIC ANALYSIS IN RICE

I Coloration genes and inheritance of other characters in rice(1)

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Genic analysis in rice has been reported by Chao (1928), Yamaguchi (1939), Morinaga (1933, 1938, 1940), Kadam and Ramiah (1938), Jodon (1940, 1943, 1948), Nagao and Takahashi (1943, 1946, 1947), and other authors. However, because of differences in the materials, a gene described by an author can not always be compared with similar ones by others. Recently, Nagao and Takahashi (1947, 1951, 1957), have made intensive studies on the inheritance of coloration at apiculus and in other organs and have demonstrated that the expression of colors in various parts of the plants is controlled by the chromogen gene *C* and its activator *Sp* which work in a complementary fashion, and that data by other workers could be explained by this hypothesis.

With the view to re-examine the system of genes established by Drs. Nagao and Takahashi, the writer is being engaged in genetic experiments as reported in this paper. As the materials, strains designated as gene markers by Dr. S. Nagao of the Hokkaido University, Japan and by Dr. N. E. Jodon of the Louisiana Agricultural Experiment Station are used, for which the writer is greatly indebted to the two scholors.

Materials and Method

Ten gene marker strains contributed by Dr. Jodon, four by Dr. Nagao and three local strains belonging to the Ponlai or Japonica type were used as cross parents. The gene symbols given by Dr. Nagao were directly used, while those by Dr. Jodon were rewritten in accordance with the Nagao's system. The putative genotypes of these strains are given in Table 1.

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Table 1. List of strains used as cross parents.

Strain No.	Local name	Putative genic constitution	Description	Note
A-5	Akamuro	C^{Br} *Sp A Rp Rc Rd*	Red apiculus, colored lemma and paplea, Red seed coat.	Nagao's Marker
A-13	Chabo	C^{B} *sp Rp*	Tawny lemma and palea	Nagao's Marker
A-58	Kuromochi	C^{B} *Sp Rp Pn Pla gl*	Purple apiculus, colored lemma and palea, purple node, purple leaf apex and margin, glutinous endosperm.	Nagao's Marker
H-59	Muyozetsto	C^{B} $S_p{}^d$ *lg gl*	Pink apiculus, liguleless, glutinous endosperm.	Nagao's Marker
7101		*Hp Pl*	Purple hull, purple leaf blade.	Jodon's Marker
7107		*Hp*	Purple hull	Jodon's Marker
7108		*Hp*	Ripening red lemma and palea.	Jodon's Marker
7111		*Hw*	Ripening white lemma and palea.	Jodon's Marker
7126		*lh*	Glabrous leaf.	Jodon's Marker
7156		*lh bc*	Glabrous hull, brittle culm.	Jodon's Marker
7165		*nk*	Colorless apiculus, enclosed leaf.	Jodon's Marker
7184			Tizzy	Jodon's Marker
7237		*Ap lgt df hg*	Apiculus purple, long twisted grain, glabrous hull, dwarf.	Jodon's Marker
7245		*df*	Dwarf, clustering spiklet.	Jodon's Marker
P-123	Taichung No. 65		Apiculus ripening brown.	Domestic
C-1	Wu-siang-Keng		Purple apiculus, colored lemma and palea, brown seed coat.	Domestic
C-12			Purple apiculus, colored lemma and palea.	Domestic

The colorations at apiculus and stigma were observed at the heading time, using the symbols "+" and "−" to reoresent colored (purple to red) and colorless states, respectively. Coloration in lemma, palea, pericarp and other parts of plants were also observed at different stages. The glutinous vs. non-glutinous character of endosperm was tested by Iodine tests of grains.

Experimental Results

1. *Inheritance of the coloration at apiculus.*

The coloration at apiculus in parental strains, F_1s, and its segregation in F_2 are given in Table 2.

In all the crosses given in Table 2, Taichung No. 65 or P-123, is used as the female parent. The apiculus of this strain is colorless or green at the heading time, but shows a light brownish color at maturity. Among the male parents, seven have a purple color, two have a red color, and the remaining five are colorless. In all crosses between P-123 and colored (purple or red) strains, the F_1s were colored at the heading time, and the F_2 segregated into 3 colored: 1 colorless without exception.

Table 2. Segregation for apiculus and stigma colorations in F_2

Crosses	Female parent		male parent		F_1		Fertility	F_2 apiculus being Colored		Colorless	Total	Apiculus			Stigma			Genotype of male parents	
	ap.	*st.*	*ap.*	*st.*	*ap.*	*st.*	%	Stigma +	Stigma −	Stigma + −		Segregation ratio	X^2	P	Segregation ratio	X^2	P	Apiculus	Stigma
P-123×A-58			P	P	P	P	88	354		135	489	3:1	1.632	0.2–0.3	1:0			C^BSp A	$i(?)$ Ps $i(?)$
P-123×C-12			P	P	P	P	80	216		77	293	3:1	0.888	0.3–0.5	1:0			C^BSp A	$i(?)$ Ps $i(?)$
P-123×7101			P	P	P	P	70	406		143	549	3:1	0.321	0.5–0.7	1:0			C^BSp A	$i(?)$ Ps $i(?)$
P-123×7107			P	P	P	P	65	197		76	273	3:1	1.173	0.1–0.2	1:0			C^BSp A	$i(?)$ Ps $i(?)$
P-123×7156					R		80		143	125	268	9:7	0.912	0.3–0.5	0:1			cSp A	
P-123×7184					R				167	110	277	9:7	1.837	0.1–0.2	0:1			cSp A	
P-123×7126					R		82	58	118	135	311	9:7	0.015	0.8–0.9	9:55	51.978	0.01>P	cSp A	I^{ps}_2 Ps i_1
P-123×7245					B		75		429*	140	569	3:1	0.047	0·8–0.9	0:1			csp A	
P-123×7156					B		85		288*	102	390	3:1	0.277	0.5–0.7	0:1			csp A	
P-123×H-59			R		R		80		166	51	217	3:1	0.260	0.1–0.2	0:1			C^BSp^d A	I^{ps}_2 Ps I^{ps}_1
P-123×7111			P	P	P			115	227	134	476	3:1	0.251	0.1–0.2	3:13	49.688	0.01>P	C^BSp A	I^{ps}_2 Ps i_1
P-123×7237			P	P	P		40	117	263	124	504	3:1	0.042	0.8–0.9	3:13	36.155	0.01>P	C^BSp A	I^{ps}_2 Ps i_1
P-123×C-1			P	P	P		80	73	113	52	238	3:1	1.260	0.2–0.3	3:13	51.290	0.01>P	C^BSp A	I^{ps}_2 Ps i_1
P-123×7108			R		R		78	24	260	116	400	3:1	3.413	0.05–0.1	9:55	7.400	0.01>P	$C^{Bt}SpA$	I^{ps}_2 Ps i_1

Note 1. P....Purple. R....Red.
+....Colored. −....Colorless.
2. *....Light brown color after maturation.
3. The Taichung No. 65 or P-123 has C^{Br} sp A i_2 Ps I^{ps}_1.

According to Nagao and Takahashi (1951, 1957), apiculus coloration is determined by the complementary effect of the chromogen gene C and its activator Sp. The gene loci C and Sp each comprises its multiple allelic series, five genes at the C-locus and three genes at the Sp-locus being known, and their dominant relations are $C^B<C^{Bp}>C^{Bt}>C^{Br}>c$ and $Sp>S_p^d>sp$, respectively. The phenotype of P–123, apiculus being colorless at the heading time and lightly colored at maturity, is expressed by the combination $C\ sp$, where C may be C^B, C^{Bp}, C^{Bt}, or C^{Br}. The genotypes of the two strains, A–58 and H–59, which are the materials used by Dr. Nagao, are already known to be $C^B\ Sp$, and $C^B\ S_p^d$ respectively.

When P–123 was crossed with A–58, the F_1 showed the same purple coloration as A–58 and the F_2 at the heading time segregated into 3 colored (purple to red): 1 colorless. When crossed with H–59, the F_1 showed a light red color as seen in H–59, and the F_2 segregated into 9 dark red ($C^B\ S_p$), 3 light red ($C^{Br}\ S_p^d$) and 4 colorless ($C^B\ sp$, $C^{Br}\ sp$). When P–123 was crossed with such colorless as 7156, 7184 and 7126, the F_1s had a red color, and the F_2 segregated into 9 red: 7 colorless at the heading time. Then, genotype of P–123 may be assumed to be $C^{Br}\ sp$.

Regarding the genotypes of strains 7101, 7107, C–12, 7111, 7237 and C–1, their F_1s with P–123, and their colored segregants of F_2, all showed the purple color as that of A–58. Their genotypes may therefore be $C^B\ Sp$. According to Jodon's Correspondence (1955), 7237 has the gene Ap (Apiculus purple). It seems that the Ap corresponds to the C of Nagao.

The genotype of colorless strains which gives a 3:1 ratio in the F_2 may have $c\ sp$, since all their F_1s and F_2s were colorless at the heading time, and after maturity, the F_1 and three quarters of the F_2 plants showed a light brown color as seen in P–123.

Based on these considerations, the genotypes of parental strains were assumed as given in the last column of Table 2.

Further, it was pointed out by Chao (1928), Jodon (1948), Morinaga (1940), Nagao and Takahashi (1956), that there should be the third gene (A by Nagao, or Ap by Morinaga) which is responsible for the spreading of anthocyanin pigment and works in complementary manner with C and Sp for apiculus coloration. According to Nagao and Takahashi (1951), both A–58 and H–59 have dominant gene A; It then seems that all the strains used in the present study have A.

2. *Segregation for stigma coloration in* F_2.

It is generally found that a plant with colored stigma always has colored apiculus, but the colored apiculus is not always correlated with colored stigma. In other words, genes for apiculus coloration are epistatic to those for stima coloration. The data in Table 2 also show that this relation holds good in the data of present study, though exceptional cases for this rule haved been reported (Jones, 1929; Oka unpubl.)

The following four different manners of inheritance were found with regard to the coloration of stigmas as shown in Table 2.

Cases	Apiculus color		F_1 stigma color	F_2 stigma color segregation ratio in apiculus colored plant			Note
	Female	Male					
				+		—	A-58, C-12
1	—	+	+	1	:	0	7101, 7107
2	—	+	—	3	:	13(?)	7111, 7237, C-1
3	—	—	—	0	:	1	H-59
4	—	—	—	9	:	55	7108

* Complete linkage of *Ps* with apiculus color gene.

In so far as the coloration of stigma is hypostatic to apiculus color, there should be a stigma coloration gene provisionally symboled *Ps*, which is hypostatic to *C*, *Sp*, and *A*. The gene *Ps* may then be considered to be a modifier which spreads the anthocyanin pigment into the stigma.

Then, for explaining "Case 1" in the above Table, we must assume that both parents have the same dominant *Ps*. For "Case 2", we should assume at least two inhibitors, $I^{ps}{}_1$ and $I^{ps}{}_2$ which act in a complementary manner with each other to inhibit the expression of stigma color because P-123 should have *Ps*. For case 3, it is necessary to assume that one of the two inhibitors is linked with *Sp*. In this case, the male parent H-59 has $S_p{}^d$. It is then possible to assume that the effect of $S_p{}^d$ is equal to $Sp+I^{ps}{}_2$, though it should be confirmed by further tests.

The above considerations lead to the assumption of genotypes that the female parent P-123 have C^{Br} $\overline{sp\ i_2}$ *A Ps* $I^{ps}{}_1$, A-58, C-12, 7101, and 7107 have C^B *Sp* (i?) *A Ps* (i?), 7111, 7237, and C-1 have C^B $\overline{Sp\ I^{ps}{}_2}$ *A Ps* i_1, H-59 has C^B $S_p{}^d$ $I^{ps}{}_2$ *A Ps* $I^{ps}{}_1$, and 7126 has *cSp* $I^{ps}{}_2$ *A Ps* i_1. However, further experiments are necessary to test whether these assumptions are right or not.

In regard to "Case 4", if we assume the genotype of 7108 to be C^{Bt} $\overline{Sp\ I^{ps}{}_2}$ *A Ps* i_1, the behavior can be explained though not conclusive.

3. *Inheritance of the colorations in leaf blade, leaf sheath, stem node, and internode.*

The parental strains 7101 and A-58 show a purple coloration at the apex and margin of leaves with fine purple stripes scattered on leaf blade. The gene for this phenotype is *Pla* according to Nagao (1951), which belongs to the *Pl* series, and is linked with *C* and with the glutinous gene *gl*. It is a modifing gene which distributes pigment substance produced by *C* and *Sp* in the leaf blades. The genotype of A-58 was assumed by Nagao to be C^B *Sp Pla*, 7107 might probably have the same genotype regarding this character. When they were crossed with P-123, which had C^{Br} *sp*, the F_2 segregated into 3 colored and 1 colorless among the plants with purple apiculus, as given in Table 6. Then, P-123 should have the recessive allele, *pla*, in addition to C^{Br} *sp*.

The coloration of leaf sheath is always correlated with that of leaf blade. It seems that *Pla* distributes pigment into both the sheath and blade of leaves. The coloration at stem nodes is also a character which behaves in correlation with apiculus coloration. One of our parental strains A-58 showed a purple coloration of nodes. In its cross with P-123, the F_1 had purple nodes, and the F_2 showed a segregation ratio which could be assumed to be 9:7. According to Nagao (1951) and Takahashi (1957), the coloration of the node is expressed by *Pn* which is hypostatic to the *C* series. However, if we take the segregation ratio obtained in the cross P-123×A-58 to be 9:7, there should be two genes with the same effect as *Pn* by Nagao.

A-58 and 7101 have a coloration at internodes. According to Kadam and Ramiah (1943), a gene designated as *Ntp* is responsible for the development of internode color. However, according to Nagao (1951), the occurrence of pigment in the internode is invariably associated with the C^B *Sp* type of apiculus coloration.

4. Coloration of outer and inner glumes or hulls.

According to Nagao and Takahashi (1948), the coloration of lemma and palea is due to a distributing gene *Rp* which spreads pigment produced by *C* and *Sp* over the surface of glumes. The genotype of A-58 which had purple coloration on the hull, was assumed to be C^B *Sp Rp* by Nagao (1951). The strain 7101 might have the same genotype as A-58. For the coloration of glumes in this strain, the gene "*Hp*" was assumed by Jodon (1948), which, however, seems to correspond to C^B *Sp Rp*. When these strains were crossed with P-123, the F_1 showed a full coloration of the hull, and the F_2 segregated into 27 purple and 37 green at the time of heading, as shown in Table 3. However, during the maturation, the color tone changed according to genotypes,

Table 3. Segregation ratio for lemma and palea colorations at heading time in P123 (C^{Br} *sp rp*)×7101 (C^B *sp Rp*).

Classes	Apiculus, lemma and palea purple C^B *Sp Rp*	Apiculus, lemma and palea colorless Other gene combinations	Total
Observed	120	147	267
Expected (27:37)	112.64	154.36	267

$X^2=0.831$ $0.3>P>0.5$

and at least five classes were distinquished at maturity. The genotypes for the color classes were assumed as shown in Table 5.

Table 4. Segregation ratio for lemma and palea coloration at maturity in P–123 (C^{Br} *sp rp*)×A–58 (C^{B} *Sp Rp*).

Classes	Apiculus, lemma and palea purple C^{B} *Sp Rp*	Apiculus purple, lemma and palea green C^{B} *pS rp*	Apiculus lemma and palea tawny C^{B} *sp Rp*	Apiculus tawny, lemma and palea white C^{B} *sp rp*	Apiculus, lemma and palea are red or green at the heading time, became straw white at maturation C^{Br} *sp Rp*, C^{B} *sp Rp* C^{Br} *sp rp*, C^{B} *sp rp*	Total
Observed	200	69	70	19	80	438
Expected (27:9:9:3:16)	184.78	61.59	61.59	20.54	109.5	438

$X^2=11.241$ $0.02<P<0.05$

Table 5. Segregation ratio for lemma and palea coloration at maturity in P–123 (C^{Br} *sp rp*)×A–13 (C^{B} *sp Rp*).

Classes	lemma and palea ripening tawny	lemma and palea ripening white	Total
	C^{B} *sp Rp*, C^{Br} *sp Rp*	C^{B} *sp rp*, C^{Br} *sp rp*	
Observed	431	139	570
Expected (3:1)	427.5	142.5	570

$X^2=0.115$ $0.7<P<0.8$

A–13, shows a brownish coloration of glumes at maturity, though green at the heading time. Its genotype is C^{B} *sp Rp* according to Nagao. When crossed with P–123 which has C^{Br} *sp rp*, a 3:1 ratio is seen regarding the brown color of glumes at maturity. This can be explained in the same manner as for the apiculus color of P–123 which appears at maturity.

5. Inheritance of seed coat color.

According to Nagao and Takahashi (1951), the red coloration of seed coat is due to the complementary effect of the genes *Rc* and *Rd*; but *Rc* alone gives a light brown color. Strains 7156 and 7101 showed a light brown color of pericarp. Then, their genotype may be assumed to be *Rc rd*. In their crosses with P–123 which is colorless, segregation of plants with brown and white seeds in a 3:1 ratio was found. The genotype of P–123 in regard to pericarp coloration may then be assumed to be *rc rd*.

6. Inheritance of other characters.

Brittle culm: The stem, leaf, and other vegetative parts of strain 7156 are easily broken by applying a small pressure. This brittleness is, according to Jodon (1933, 1948), Morinaga and Fukushima (1943), controlled by a reccesive gene *bc*. A 3:1 segregation was also found by the writer in its cross with P–123, as shown in Table 6. Within the data of the pressent study, no linkage relation with other genes was found for the gene *bc*.

Table 6. Segregation ratios for various characters in F_2

Characters	Crosses	Observed number			Segregation ratio	X^2	P
		Dominant	Recessive	Total			
Brown pericarp (*Rc*)	P123×C-1 P123×7101 P123×7156	180 395 171	63 147 68	243 542 239	3:1 3:1 3:1	0.111 1.301 1.518	0.7-0.8 0.2-0.3 0.2-0.3
Purple leaf blade (*Pla*)	P123×A-58 P123×7101	276 293	209 252	485 545	9:7 9:7	0.147 1.371	0.7-0.8 0.2-0.3
Purple node (*Pn*)	P123×A-58	517	415	932	9:7	0.229	0.5-0.7
Purple internode (*Ntp*)	P123×7101 P123×7111	402 371	147 145	549 516	3:1 3:1	0.932 2.646	0.3-0.5 0.1-0.2
Purple pulvinus *Ppv*	P123×A-58	268	170	438	9:7	4.336	0.02-0.05
Purple ligule (*Plg*)	P123×A-58	279	203	482	9:7	0.524	0.3-0.5
Purple auricle (*Pau*)	P123×A-58	280	99	379	3:1	0.254	0.5-0.7
Glutinous endosperm (*gl*)	P123×A-58 P123×H-59	725 173	207 41	932 214	3:1 3:1	3.869 3.894	0.05-0.10 0.05-0.10
Brittle culm (*bc*)	P123×7156	192	47	239	3:1	3.628	0.05-0.10
Glabrous hull (*lh*)	P123×7126 P123×7156 P123×7237	241 181 228	80 62 71	321 243 299	3:1 3:1 3:1	0.001 0.034 0.251	0.90-0.95 0.80-0.90 0.5-0.7
Liguleless-ness (*lg*)	P123×H-59	178	36	214	3:1	7.632	0.01
Short ligule (*lg₁ lg₂*)	P123×A-5	351	257	608	9:7	0.541	0.3-0.5
Shattering (*Sh*)	P123×7237	228	90	318	3:1	1.849	0.1-0.2
Long twisted grain (*ltg*)	P123×7237	235	84	319	3:1	0.302	0.5-0.7
Awn (*An*)	P123×A-5 P123×A-13	338 416	271 151	609 567	9:7 3:1	0.139 0.805	0.7-0.8 0.3-0.5
Long empty glume (*lng*)	P123×H-25	625	196	821	3:1	0.558	0.3-0.5
Lazy (*la*)	P123×H-25	627	194	821	3:1	0.975	0.3-0.5

Glabrous hull: The hulls of 7126 are lacking hairs. A recessive gene *lh* was assigned for this character by Jodon (1948). The crosses of P–123 with 7126 and 7156, showed a 3:1 ratio regarding this character.

Ligulelessness: According to Chao (1928) and Jodon (1948), this character is also cotrolled by a recessive gene *lg*. The ligule is deficient in the strain H–59. The F_2 ratio found between P–123 and H–59 was assumed to be 3:1, though the chi-square value from the expected numbers was large enough to be significant. The reason for the number of *lg* plants being smaller than expected is left for further study.

Both the strains P–123 and A–5 have short ligules (about 1 cm). The F_1 between them, however, had long ligules (about 2 cm). In the F_2, plants with long and short ligules were found in a 9:7 ratio (Table 9). This indicates that there is a set of two complementary genes. Two genes lg_1 and lg_2 were designated by the writer. The genotype of P–123 and A–5 may then be assumed to be $Lg_1\ lg_2$ and $lg_1\ Lg_2$, respectively. No linkage relation was found between these and other genes.

Twisted grains: The grains of 7237 are slightly twisted. A recessive gene *lgt* was assigned for this character by Jodon. The writer's experiment also showed that it was a monogenic recessive character.

Glutinous endosperm: It was confirmed that all the progeny of glutinous ×glutinous was glutinous, and that of non-glutinous×non-glutinous was non-glutinous. The gene symbol *gl* was used by Nagao (1951), though it is *wx* by Jodon (1948). The expected 3:1 ratio was found in both P–123×A–58 and P–123 ×H–59.

Dwarfness: The plant heights of 7237 and 7245 were about 75 cm and 30 cm, respectively. Both of them were found to be a single recessive character and the F_2 ratios fitted to a 3:1 ratio. This character appeared to be linked with *Sp* as shown in Table 8.

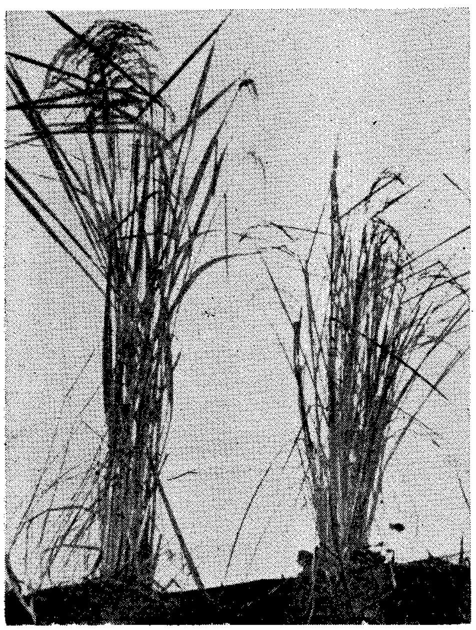
Long empty glumes: The empty glumes of H–25 are as long as its lemma and palea. This character was found to be simple recessive to the common short empty glume, as reported by Jones (1933), Morinaga and Fukushima (1943). The gene *lng* was used by Nagao (1951) for this character.

Lazy: The stem of H–25 grows obliquently. The gene symbol *la*, which might be corresponded with Nagao's *sg*, was assumed by Jodon (1948). No linkage relation was found between this and other characters.

Twisted stem: The stem of 7237 is somewhat twisted. This character seemed to be controlled by two complementary genes designated as ts_1 and ts_2 by the writer.

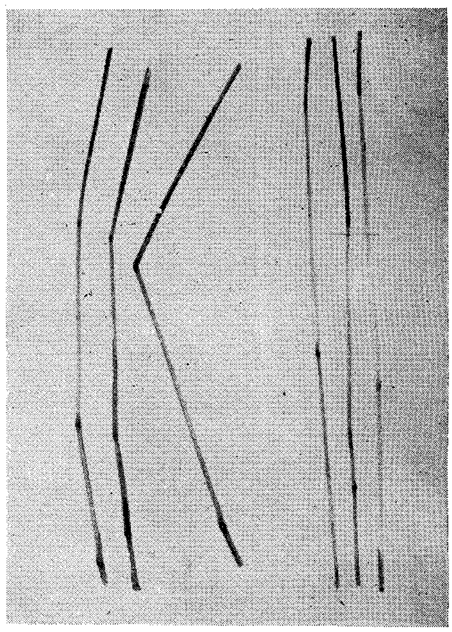
However, the twisted growing habit of stems, always brings about spreading of tillers and may be easily affected by enviromental conditions.

Fig 1. Long twisted (A) and normal (C) grairs.



Normal Dwarf

Fig 2. Dwarf plant (7237) compared with normal.



Twisted Normal

Fig 3. Twisted stems compared with normal.

7. *Linkage between color genes and other characters*

The characters dealt with in this study were mostly independent of coloration gene as shown in Table 7. However, the color gene *Sp* was found to be linked

Table 7. Tests of independence between color genes and other characters.

(a) When two gene loci are concerned.

Genes concerned (Aa Bb)	Crosses	Combined characters				Total	Segregation ratio	X²	P
		AB	A*b*	*a*B	*ab*				
Sp/sp —+/*lh*	P123×7237	169	66	59	25	319	9:3:3:1	2.351	0.5–0.7
Sp/sp —+/*lgt*	P123×7237	166	66	73	18	323	9:3:3:1	4.635	0.1–0.2
Sp/sp —*Sh*/+	P123×7237	168	60	60	30	318	9:3:3:1	5.824	0.1–0.2
Sp/sp —+/*gl*	P123×H-59	129	35	44	6	214	9:3:3:1	5.815	0.1–0.2
Sp/sp —+/*lg*	P123×H-59	133	29	45	7	214	9:3:3:1	7.896	0.02–0.05
Rc/rc —+/*lh*	P123×7156	124	56	47	13	240	9:3:3:1	3.851	0.2–0.3
Rc/rc —+/*bc*	P123×7156	143	27	52	18	240	9:3:3:1	9.362	0.02–0.05
Rc/rc —*Ntp/ntp*	P123×7101	293	102	105	43	543	9:3:3:1	3.937	0.2–0.3
Rc/rc —*Sp/sp*	P123×C-1	140	42	49	12	243	9:3:3:1	1.053	0.7–0.8
Rc/rc —*Sp/sp*	P123×7101	297	110	98	43	548	9:3:3:1	3.377	0.2–0.3
Rp/rp —*An/an*	P123×A-13	322	94	109	45	570	9:3:3:1	4.075	0.2–0.3
+/*lh* —+/*lgt*	P123×7237	175	63	58	22	318	9:3:3:1	0.637	0.8–0.9
+/*lh* —+/*d*	P123×7237	183	52	67	17	319	9:3:3:1	2.386	0.3–0.5
+/*lh* —*Sh/sh*	P123×7237	165	70	63	20	318	9:3:3:1	3.073	0.3–0.5
Lgn/lgn—*Sh/sh*	P123×7237	174	70	54	20	318	9:3:3:1	2.469	0.3–0.5
+/*d* —*Sh/sh*	P123×7237	186	63	44	25	318	9:3:3:1	6.058	0.1–0.2
+/*lng* —+/*la*	P123×H-25	475	150	152	44	821	9:3:3:1	2.451	0.3–0.5

(b) When three gene loci are concerned.

Genes concerned (Aa Bb Cc)	Crosses	Combined characters				Total	Segregation ratio	X²	P
		ABC	AB*c*	A*b*C *a*BC *ab*C	A*bc* *a*B*c* *abc*				
C/c, *Sp/sp* — +/*lh*	P123×7126	135	39	96	41	311	27:9:21:7	2.325	0.5–0.7
C/c, *Sp/sp* — +/*bc*	P123×7156	106	20	89	28	243	27:9:21:7	7.056	0.02–0.05
C/c, *Sp/sp* — *Rc/rc*	P123×7156	95	47	79	23	244	27:9:21:7	6.300	0.10–0.20
Ntp_1/ntp_1, Ntp_2/ntp_2—+/*lh*	P123×7126	121	48	108	32	309	27:9:21:7	1.673	0.5–0.7
Pla_1/pla_1, Pla_2/pla_2—*Rc/rc*	P123×7101	210	76	185	72	543	27:9:21:7	4.529	0.2–0.3
Pla_1/pla_1, Pla_2/pla_2—+/*gl*	P123×A-58	220	56	167	42	485	27:9:21:7	6.029	0.1–0.2
Pn_1/pn_1, Pn_2/pn_2 —+/*gl*	P123×A-58	207	59	178	40	484	27:9:21:7	6.725	0.05–0.10
+*lh* — Ts_1/ts_1, Ts_2/ts_2	P123×7237	134	45	101	39	319	27:9:21:7	0.506	0.3–0.5
Sh/sh — Ts_1/ts_1, Ts_2/ts_2	P123×7237	132	46	97	43	318	27:9:21:7	2.528	0.3–0.5

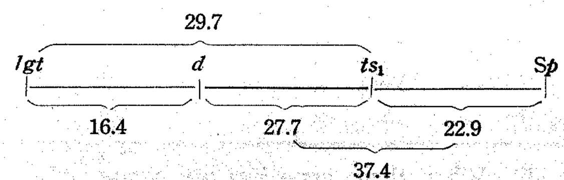
with dwarf gene *d* and twisted stem gene ts_1 (ts_2) in the cross with 7237. Further, the twisted grain gene *ltg* was found to be linked with *d* gene and ts_1 (or ts_2), as shown in Table 8.

Table 8. Chi-square values showing linkages found from the test of independence in P123×7237.

Genes concerned (A) (B)	Combined character				Total	X^2
	AB	A*b*	*a*B	*ab*		
Sp—*d*	170	80	58	11	319	11.321*
Sp—$ts_1(ts_2)$	115	113	64	27	319	13.463*
ltg—$ts_1(ts_2)$	147	88	32	52	319	15.878*
d —$ts_1(ts_2)$	155	95	24	45	319	16.621*
ltg—*d*	218	17	32	52	319	103.430*

* Significant from the expected number.

As shown in Table 9, *Sp* and *d* is linked with each other with a 37.35% recombination value. Since the *d* gene (possessed by 7237) has not been described in the *Sp* linkage group by Nagao, nor by Jodon in his group II, this may be a new locus to be added to this group. The apiculus color gene *Sp* was also found to be linked with the twisted stem gene provisionally symbled ts_1 (or ts_2) with a 22.92% recombination value. The ts_1 (or ts_2) was further linked with the twisted grain gene *ltg* with a 29.67% recombination value, and with *d* with a 27.72% recombination. Based on these findings, we may assume the order of genes in the *Sp* group as shown below.



Discussion

It has been shown by Nagao and Takahashi (1956, 1958) that the anthocyanic pigmentation of apiculus in rice is due to three complementary genes, *C*, *Sp* and *A*. Though the crosses observed in this study did not include one segregating for *A*: *a*, all the data obtained for apiculus coloration could be explained by the genic system established by Nagao and Takahashi. The genotype of Taichung No. 65, a representative Japonica variety in Taiwan, was found to be C^{Br} *sp A* for apiculus coloration.

In contrast, the genic system for stigma coloration appeared to be a more complicated one. As worked out by former workers (Ramiah, 1953; Takahashi, 1958), stigma coloration was hypostatic to apiculus coloration in the crosses observed, and a dominant gene which spreads into stigmas the pigment produced by the genes for apiculus coloration was assumed. In some crosses between strains with colored and colorless stigmas, however, the F_1 was colorless, and

Table 9. The F_1 genotypes and recombination values in P-123×7237.

Gene pair	F_1 genotype	Phase	A B	A*b*	*a*B	*ab*	Total	Recombination value %	X^2	P
Sp——*d* (3:1) (3:1)	$\frac{C^{Br}\ sp\ +}{C^B\ Sp\ d}$	R	170 (170.63)	80 (68.62)	58 (68.62)	11 (11.13)	319	37.35±0.039	3.535	0.3-0.5
Sp——ts_1 (ts_2) (3:1) (9:7)	$\frac{C^{Br}\ sp\ Ts_1\ Ts_2}{C^B\ Sp\ ts_1\ ts_2}$	R	115 (122.75)	113 (116.50)	64 (56.69)	27 (23.06)	319	22.92±0.024	2.210	0.5-0.7
ltg——ts_1 (ts_2) (3:1) (9:7)	$\frac{Lgt\ +}{lgt\ d}$	C	218 (215.27)	17 (23.93)	32 (23.93)	52 (55.77)	319	16.37±0.016	5.018	0.1-0.2
ltg——ts_1 (ts_2) (3:1) (9:7)	$\frac{Lgt\ Ts_1\ Ts_2}{lgt\ ts_1\ ts_2}$	C	147 (149.20)	88 (90.05)	32 (30.24)	52 (49.51)	319	29.67±0.029	0.306	0.95-0.98
d—— ts_1 (ts_2) (3:1) (9:7)	$\frac{+\ Ts_1\ Ts_2}{d\ ts_1\ ts_2}$	C	155 (150.89)	95 (88.38)	24 (28.55)	45 (51.18)	319	27.72±0.003	2.079	0.5-0.7

in F_2, colorless plants were more than colored ones. Thus, for fully explaining the data, at least two inhibitors for the dominant stigma coloration gene, which are complementary with each other to suppress stigma coloration, should be assumed. It should be assumed further that one of them is linked with the apiculus coloration gene *Sp*. In addition to these, it is known that in some particular crosses, the general rule that stigma coloration is hypostatic to apiculus coloration does not hold good, and plants with colorless apiculus and colored stigma occur (Jones, 1929, Oka unpubl.).

It seems that colorations in other parts such as leaf and stem are due to similar genic systems as for stigma coloration, and the whole system for coloration comprises a number of genes which interact with one another in complicated manners. This study is a preliminary survey and does not furnish enough data to look into the whole genic system for coloration. It may, however, be pointed out that investigation of the inheritance of coloration may form an important part in genic analysis of rice.

Recently, Nagao and Takahashi (1959) have found out ten linkage groups. However, only three genes, *Sp*, *Rd* (red pericarp), and *Pn* (purple node), have been known to belong to the *Sp* group. The present study added three new genes, ts_1 (twisted stem), *d* (dwarf) and *lgt* (long twisted grain), to the group. Using these genes, whether the *Sp* locus is involved or not in a given segregation pattern for coloration may easily be detected.

Another thing to be discussed is that in some crosses, segregation ratios showed significantly large deviations from expectations, though in other respects the assumption of genes seemed to be correct. This might be due to certation or gametic selection which occurs as results of hybrid sterility. It should be noticed that when distantly related strains are crossed, fertility variation should be investigated together with the segregation of characters for which the investigation is made.

Summary

In order to investigate the systems of genes for colorations at various parts and other characters of the rice plant, established by Nagao and Takahashi (1951–1959) and by Jodon (1948–1955), strains designated as gene markers by these authors were crossed with a strain of Taichung No. 65, a representative Japonica variety of Taiwan. The anthocyanic coloration of apiculus is controlled by three complementary genes symboled by Nagao (1951) *C*, *Sp*, and *A*. Their combinations in the used strains were determined first based on F_2 segregation ratios. Next, the coloration of stigmas is usually hypostatic to that of apiculus. A gene *Ps*, which spreads the pigment produced by *C*, *Sp*, and *A* into stigmas, was assumed for this character. It should be assumed further, however, that there are two complementary inhibitors which suppress the action of *Ps*, symboled $I^{ps}{}_1$ and $I^{ps}{}_2$, and that the latter is linked with *Sp*. Further, genes for colorations in other parts of the plant, *i.e.* glumes, leaf sheath, node, and internode, which were generally hypostatic to apiculus coloration, were surveyed.

Genes for various morphological traits were also investigated in addition. The twistedness of stems was found to be controlled by duplicated recessive genes ts_1 and ts_2. One of them was linked with *Sp*. Around the *Sp* locus, further, linkage relations were found between ts_1 (or ts_2) and *ltg* (long twisted grain), ts_1 (or ts_2) and *d* (dwarfness in Strain 7237), and between *Sp* and *d*, and recombination fractions were estimated for each. Brittleness of culms, glabrousness of hulls, ligulessness, long empty-glumes, and lazyness were each found to be controlled by a recessive gene. No linkage relation could be detected for them in the materials used.

稻之遺傳因子分析

第一報　水稻顏色遺傳因子及其他性狀之遺傳

謝　順　景

為探討水稻各部位之顏色及其他性狀之遺傳因子系統，曾利用 Jodon，長尾及高橋各氏之遺傳因子標識稻 (gene markers) 與臺灣蓬萊種臺中65號等雜交，並觀察顏色及各性狀之分離情形。根據長尾氏 (1951)，支配稻稃尖顏色之因子有 *C*, *Sp* 及 *A* 之三對。本試驗根據此等因子系統對供試稻品種加以分析並曾定供試系統之遺傳因子型。

柱頭之着色一般在稃尖着色之下位 (Hypostatic) 而受由 *C*, *Sp* 及 *A* 三因子之相互作用所產生之色素分佈至柱頭之 *Ps* 因子支配。除此之外柱頭色又受有互助作用 (Complementary) 關係之 $I^{ps}{}_1$ 及 $I^{ps}{}_2$ 之兩對抑制因子 (Inhibitors) 所支配，其中之 I^{ps} 與 *Sp* 有完全連鎖之關係。對於稃尖以外之植物體，即穎色，葉鞘，葉節及節間等之顏色的遺傳亦認為係在稃尖着色之下位。

此外對各形態遺位因子亦曾作研究。曲莖受 ts_1 及 ts_2 之兩對穩性因子所支配，而其中之一與 *Sp* 有連鎖關係。在 *Sp* 因子座之附近，曾發現 ts_1 (或 ts_2) 與 *ltg* (長曲粒)，ts_1 (或 ts_2) 與 *d* (7237之矮性)，*Sp* 與 *d* 之間有連鎖關係，其因子之交換值 (Recombination Value) 均有計算。植物體脆弱性 (Brittle culm) 谷粒無毛 (glabrous hull)，無葉舌 (Ligulelessness)，長護穎 (Long empty glumes) 及散開性 (Lazy) 等均受單穩性因子控制此等性狀在本研究之範圍內未能找到連鎖關係。(摘要)

Literature Cited

CHAO L. F.: Linkage studies in rice. Genetics 13: 133-169, 1928.

JONES J. W.: Inheritance of anthocyanin pigmentation in rice. Jour. Agr. Res. 40: 1105-1123, 1930.

KADAM B. S. and K. RAMIAH: Symbolization of genes in rice. Ind. Jour. Genet. and Plant Breed. 3: 7-27, 1943.

JODON N. E.: Summary of linkage data. Report of Plant Industry Station U. S. D. A., No. 112 cc: 1-32, 1948.

_______: Present status of rice genetics. Jour. Agr. Assoc. of China. New ser. 10: 5-21, 1955.

MORINAGA T.: Linkage between phenol reaction gene and some other genes. Jap. Jour. Genet. 19: 206-218, 1940.

NAGAO S.: Genic analysis and linkage relationship of characters in rice. Advances in Genetics. 4: 181-212, 1951.

_______ and M. TAKAHASHI: The third gene in apiculus coloration in rice. Jap. Jour. Bot. 15: 141-151, 1956.

TAKAHASHI M.: Analysis on apiculus color genes essential to anthocyanin coloration in rice. Jour. Faculty of Agr., Hokkaido Univ. 50 Pt 3: 266-362, 1957.

_______: Genetical studies on rice plant XXI. Genes for localization of anthocyanin pigment in stigma. Jap. Jour. Breed. 8: 142-148, 1952.

YAMAGUCHI Y.: Inheritance of rice. Jap. Jour. Genet. 15: 1-9, 1939.