b. ANALYSIS OF GENES FOR COLORATIONS AND OTHER MORPHOLOGICAL CHARACTERS IN RICE

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With the view to re-examining the system of genes established by Drs. Nagao and Takahashi, the writer is being engaged in genetic experiments. The gene marker strains obtained from Dr. Jodon and four from Dr. Nagao, and three local strains belonging to the Ponlai or the 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.

Colorations at apiculus and stigma were observed at the heading time, using the symbol "+" and "−" to represent colored (purple to red) and colorless states, respectively. Colorations in lemma, palea, pericarp and other parts of plants were observed at different stages. The glutinous vs. non-glutinous character of endosperm was determined by the iodine test of grains.

1. Inheritance of coloration at the apiculus

Coloration at the apiculus in parental strains, F_1s and its segregation in F_2 are given in Table 1. In all the crosses given in Table 1. Taichung No. 65 (P–123), is used as the female parent. The apiculus of this strain is colorless or green at the heading time, but show 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.

According to Nagao and Takahashi (1951, 1957), apiculus coloration is determined by the chromogen gene *C* and its activator *Sp*. The gene loci *C* and *Sp* each comprises a multiple allelic series, five genes at the *C*-locus and three at the *Sp*-locus, and their dominance relations are $C^R > C^{Rp} > C^{Rt} > C^{Rr} > c$ and $Sp > Sp^a > sp$ respectively. The phenotype of P–123, apiculus being colorless at the heading time and lightly colored at maturity, is expressed by the combination *Csp*, where *C* may be C^R, C^{Rp}, C^{Rt} or C^{Rr} The genotypes of the two strains, A–58 and H–59, which are the materials used by Drs. Nagao and Takahashi, are already known to be C^R *Sp* and C^R Sp^a 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^R Sp), 3 light red (C^{Rr} Sp_d) and 4 colorles (C^R sp, C^{Rr} sp). When P-123 was crossed with colorless strains such as 7156, 7184 and 7126, the F_1s had a red color, and F_2 segregated into 9 red: 7 colorless at the heading time. Then, the genotype of P-123 may be assumed to be C^{Rr} sp.

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

The genotypes of colorless strains which gave a 3:1 ratio in the F_2 may have csp, since all their F_1s and F_2s were at the heading time colorless, and after maturity, the F_1 and three quarters of the F_2 plants showed a light coloration as seen in P-123.

Further, it was pointed out by Chao (1928), Jodon (1948), Morinaga (1943) and 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 a complementary manner with C and Sp for apiculus coloration. According to Nagao and Takahashi (1951, 1957), both A-58 and H-59 have the 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 plants with colored stigmas always have colored apiculus, but apiculus coloration is not always correlated with colored stigma. In other words, genes for apiculus coloration are epistatic to those for stigma coloration. The data in Table 1 also show that this relation holds good in the data of the present study, though exceptional cases for this rule is reported.

The following four manners of inheritance were found with regard to the coloration of stigmas, as shown in Table 1.

Cases	Stigma color		F_1 stigma color	F_2 stigma color segregation in apiculus colored plants	Male parents
	Female (P-123)	Male			
(1)	−	+	+	1 : 0	A-58, C-12, 7101, 7107
(2)	−	+	−	3 : 13(?)	7111, 7237, C-1
(3)	−	−	−	0 : 1	H-59
(4)	−	−	−	9 : 55(?)	7108

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

Then, for explaining "Case 1" in the above table, we must assume that both

Table 1. Segregation for apiculus and stigma colorations in F_2

Crosses	Female parent		Male parent		F_1		Fertility (%)	F_2 Apiculus being				Total	Apiculus			Stigma			Genptype of male parents	
								Colored Stigma		Colorless Stigma										
	ap	*st*	*ap*	*st*	*ap*	*st*		+	−	+	−		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^R *Sp 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^R *Sp 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^R *Sp 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^R *Sp A*	*i*(?) *Ps i*(?)
P-123×7156					R		80		143		125	269	9 : 7	0.912	0.3-0.5	0 : 1			*c Sp A*	
P-123×7184					R				167		110	277	9 : 7	1.837	0.1-0.2	0 : 1			*c Sp 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	*c Sp A*	I_2^{ps} *Ps* i_1*
P-123×7245					R		75		429*		140	569	3 : 1	0.047	0.8-0.9	0 : 1			*c sp A*	
P-123×7156					B		85		288		102	390	3 : 1	0.277	0.5-0.7	0 : 1			*c sp A*	
P-123×7111			P	P	P			115	227		134	476	3 : 1	0.260	0.1-0.2	3 : 13	49.688	0.01>P	C^R *Sp A*	I_2^{ps} *Ps* i_1
P-123×H-59			R		R		80		166		51	217	3 : 1	0.260	0.1-0.2	0 : 1			C^R Sp^d *A*	I_2^{ps} *Ps* I_1^{ps}
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^R *Sp A*	I_2^{ps} *Ps* i_1
P-123×C1			P	P	P		80	73	113		52	238	3 : 1	1.260	0.2-0.5	3 : 13	51.290	0.01>P	C^R *Sp A*	I_2^{ps} *Ps* i_1*
P-123×7108			R		R		78	224	260		116	400	3 : 1	3.413	0.05-0.1	9 : 55	7.400	0.01>P	C^{Rt} *Sp A*	I_2^{ps} *Ps* i_1

Note: 1. P……Purple
P……Red
+……Colored
—……Colorless
2. *……Light brown color after maturation
3. The Taichung No. 65 or P-123 has C^{Rr} *sp* Ai_2 *Ps* I_1^{ps}.

parents have the same dominant *Ps*. For "Case 2" there should be at least two inhibitors, I_1^{ps} and I_2^{ps} which act as complementary genes to inhibit the expression of stigma color, because, P-123 should have *Ps*. For "Case 3", it is necessary that one of the two inhibitors is linked with *Sp*. In this case, the male parent H-59 has Sp^d. It is then possible to assumed that the effect of Sp^d is equal to $Sp+I_2^{ps}$, though it should be confirmed by further tests.

The above considerations lead to the assumption of genotypes that the female parent P-123 has C^{Rr} *sp* i_2^{ps} *A Ps* I_1^{ps}, A-58, C-12, 7101 and 7107 have C^R *Sp i* (?) *A Ps i* (?), 7111, 7237 and C-1 have C^R *Sp* I_2^{ps} *A Ps* i_1^{ps}, H-59 has C^R Sp^d I_2^{ps} *A Ps* I_1^{ps} and 7126 has *cSp* I_2^{ps} *A Ps* i_1^{ps}. However, further experiments are necessary to test whether these assumptions are quite right, or not. In regard to "Case 4", if we assume the genotype of 7108 to be C^{Rt} *Sp* I_2^{ps} *A Ps* i_1^{ps}, the behavior of stigma color can be explained though not conclusive.

3. Coloration of outer and inner glumes or hulls

According to Nagao and Takahashi (1951), the coloration of lemma and palea is due to the distributing gene *Rp* which spreads the pigment produced by *C* and *Sp* over the surface of glumes. The genotype of A-58 which had purple coloration on the surface of the hull, was assumed to be C^R *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^R *Sp Rp*. When these strains were crossed with P-123, the F_1 showed a full coloration of the hull, and the F_2 segreated into 27 purple and 37 green at the time of heading, as shown in Table 2. However, during maturation, the color tone changed according to genotypes, and at least five classes were distinquished at maturity. The genotypes for the color classes were assumed as shown in table 3.

A-13 showed a brownish coloration of glumes at maturity, though was green at the heading time. Its genotype is C^R *sp Rp* according to Nagao (1951). When crossed with P-123 which has C^{Rr} *sp rp*, a 3:1 ratio was found regarding the brown color of glumes at maturity (Table 4). This can be explained in the same manner as for the apiculus color of P-123 which appears at maturity.

Table 2. Segregation ratio for lemma and palea colorations at heading time, in the F_2 of P-123 (C^{Rr} *sp rp*)×7101 (C^R *sp Rp*)

Classes	Apiculus, lemma and palea purple	Apiculus, lemma and palea colorless	Total
	C^R *Sp Rp*	Other gene combinations	
Observed	120	147	267
Expected (27:37)	112.64	154.36	267
$X^2=0.831$		0.3>P>0.5	

Table 3. Segregation ratio for lemma and palea coloration at maturity in the F_2 of P-123 (C^{Br} *sp rp*)×A-58 (C^{B} *Sp Rp*)

Classes	Apiculus, lemma and palea purple	Apiculus purple, lemma and palea green	Apiculus, lemma and palea tawny	Apiculus tawny, lemma and palea white	Apiculus, lemma and palea are red or green at the heading, became straw white at maturation	Total
	C^{B} *Sp Rp*	C^{B} *Sp rp*	C^{B} *sp Rp*	C^{B} *sp rp*	C^{Br} *sp Rp*, C^{Br} *sp Rp* C^{Br} *sp rp*, C^{Br} *sp rp*	
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 4. Segregation ratio for lemma and palea colorlation at maturity in the F_2 of 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	

4. Linkage between colorlation genes and other characters

The characters dealt with in this study were mostly independent of coloration genes. However, the color gene *Sp* was found to be linked with twisted stem gene ts_1 or (ts_2) in the cross with 7237, Further, the twisted grain gene *ltg* was found to be linked with *df* and ts_1 or ts_2, as shown in Table 5.

As shown in Table 5, *Sp* and *d* (7237) are linked with a recombination value 37.35%. Since the gene *d* carried by 7237 has not been described in the *Sp* linkage group by Nagao, nor by Jodon in his group IV, it may be considered as 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 symboled ts_1 (or ts_2), with a recombination value 22.9%. The ts_1 (or ts_2) gene was further linked with the twisted grain gene *ltg* with a recombination value 29.57% and with *d* with a recombination value 27.72%.

As shown in Table 6, the linkage between purple hull gene *Rp* and liguleless genes *lg* was found in three crosses. Since *Rp* gene is hypostatic to apiculus coloration, purple hulls in apiculus colored plants were counted in combination with liguleless characters in calculating recombination value. The average recombination value between *Rp* and *lg* genes is 31% in coupling phase. This value is comparable with 28.2% calculated by Nagao and Takahashi (1959).

Strain 8001 is a dwarf plant (about 30 cm in plant height) with purple leaf blade. The dwarfness is a monogenic character. In its cross with 521 (the normal plant

Table 5. The F_1 genotypes and recombination values in P-123×7237

Gene pair	F_1 genotype	Phase	AB	Ab	aB	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 (63.62)	11 (11.13)	319	37.35±39	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±24	2.210	0.5-0.7
d—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±16	5.018	0.0-0.2
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±29	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±0.3	2.079	0.5-0.7

height with green leaf blade), linkage was found between *d* and *Pl* genes. Since *Pl* gene is also hypostatic to apiculus coloration the plants having apiculus color were counted in combination of *d* and *Pl* characters in calculating recombination value. The recombination value between *Pl* and *d* was calculated to be 27.4%. According to Nagao and Takahashi (1959), the recombination value between d_3 and *Pl* is 35.2%, between d_2 and *Pl* is 38.1%. The value of 27.4% obtained in the present study may be comparable with that of 35.2%. Then strain 8001 might be situated at the same locus of d_3, otherwise it may be the third dwarf gene belong to group II. However, further study is needed for confirmation.

Linkage between purple leaf blade gene *Pl* and glutinous endosperm gene *gl* was found in the cross between P-138×7102 as shown in Table 6. According to Nagao and Takahashi (1950) *gl* gene is linked with *Pla*, one of allelic genes belongs to *Pl* series, with 44.7% of recombination value. *Pl* gene is independent to *gl* group (or group I). However, 39.6% of recombination value between *Pl* and *gl* was found in the present study. The writer included all purple plants regardless of *Pl*, *Pla* and *Plm* plants in *Pl* class in calculating recombination value, might be the main cause of the difference between two studies. 39.6% recombination value obtained in the present study approches 44.7% that between *Pla* and *gl* genes calculated by Nagao and Takahashi (1959), therefore the *Pl* gene assumed in this study may be the same order as that *Pla*. However, further studies are necessary for this assumption.

One of stigma color genes Ps_1 is linked with the phenol reaction gene *Ph* with 17.8% of recombination value in cross of 108×7108 as seen in Table 6.

In the cross of J-308×A-5, linkage between Ps_1 and *Rp* was found as seen in Table 6. The recombination value between these two genes was calculated to be 26%. Since Ps_1 genes was not included in Nagao's *Pl* group, it may be a new locus to be added to this group.

Table 6. F_1 genotypes and recombination values between characters

Genes in Inkage	Crosses	F_1 Genotype	Phase	AB	Ab	aB	ab	Total	Recombination value %	X^2	P	Linkage group
Rp—lg (3:1) (3:1)	J-308×7041	$\frac{C^{Br}\ Sp\ Rp\text{-}lg}{C^{B}\ Sp\ Rp\text{-}Lg}$	C	180 (187.44)	40 (36.06)	30 (36,06)	39 (38.44)	298	28.1±2.90	1.7532	0.9–0.95	I I
Rp—lg (3:1) (3:1)	P-167×7101	$\frac{C^{Br}\ sp\ rp\text{-}lg}{C^{B}\ Sp\ Rp\text{-}Lg}$	C	133 (134.27)	29 (27.72)	27 (27.72)	27 (26.27)	216	30.3±3.37	0.0990	0.99	II
Rp—lg (3:1) (3:1)	J-398×A-5	$\frac{C^{Br}\ Sp\ rp\text{-}lg}{C^{B}\ Sp\ Rp\text{-}Lg}$	C	138 (140.79)	33 (31.70)	32 (31.70)	27 (25.78)	230	33.0±3.51	0.1460	0.7–0.3	II
Pl—d (3:1) (3:1)	521×8001	$\frac{C\ sp\ pl\text{-}D}{C^{Bp}\ Sp\ Pl\text{-}d}$	N	39 (43.57)	17 (19.42)	26 (19.42)	2 (1.57)	84	27.4±0.47	3.0100	0.3–0.5	II
(?) *Pla—gl* (3:1) (3:1)	P-138×7102	$\frac{C^{Br}\ sp\ Pl\text{-}gl}{C^{Br}\ Sp\ Pl\text{-}Gl}$	C	86 (94.99)	24 (25.76)	32 (25.76)	19 (14.49)	161	39.6+4.51	3.8860	0.2–0.3	I
Ph—Ps_1 (3:1) (9:7)	108×7108	$\frac{Ph\text{-}Ps_1\ Ps_2}{ph\text{-}Ps_1\ Ps_2}$	C	95 (82.69)	40 (32.91)	5 (4.42)	14 (19.25)	154	17.8±7.04	4.9120	0.1–0.2	II
Rp—Ps_1 (3:1) (9:7)	J-308×A-5	$\frac{C^{Br}\ Sp\ rp\text{-}Ps_1\ ps_2}{C^{Br}\ Sp\ Rp\text{-}ps_1\ Ps_2}$	C	107 (109.44)	68 (61.56)	16 (18.81)	37 (38.19)	228	26.0±0.49	1.1850	0.7–0.8	I I
Lro—C(Sp) (3:1) (9:7)	P-163×9783	$\frac{Lro\text{-}C^{Br}\ sp}{lro\text{-}c\ sp}$	C	160 (138.37)	81 (86.37)	27 (30.37)	32 (44.62)	300	32.2±4.85	7.6890	0.05-0.1	I or IV

Strain 9783 is a roll-leaved dwarf. A gene *lro* was assigned by Kadam (1943) to this character, *lro* is linked with one of apiculus color genes either *C* or *Sp* with 32.2% of recombination value. It may belong to Nagao's group I or group IV though needed further studies.

DISCUSSION

Hsieh: Experiments done by other sections can be related with the low yield problem in tropical and subtropical regions. But it seems difficult to link this work to the title of the joint project. Any comment on this point will be much appreciated.

Oka: Genic analysis is a basic research not easily correlated with yield of rice. However, the joint work is based on varietal differences, when different varieties are used there exists genetic problems.

Hsu: Various characters dealt with in your experiment, such as colorations at various organs of the plant, or spreading habit etc, can be related with the yield problem, can't they?

Hsieh: Usually quantitative characters are more closedy related with yield than characters controlled by major genes. It seems however, that genetics on major gene should be done first.

Oka: Segregation ratios, such as 3:1 or 9:7, will be meaningless without studying linkage relations with other characters.

Hsieh: Linkage studies have been our main purpose, before calculating linkages, it is necessary to find the genetic behavior of each characters.

Wu: Genetic study occupies one of the important parts in this joint work. You should deal more with quantitative characters which can be related with yield than major genes such as coloration at various plant organs. Another thing I want to suggest is that the name, Pai-kan-tao, a liguleless variety, must be standarized.

Hsieh: Yes, we will improve this situation.