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## GENE MAPPING OF THE FIRST AND SECOND LINKAGE GROUPS IN RICE<sup>1)</sup>

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### Introduction

It is widely accepted that the construction of linkage maps is very important for various kinds of genetic research and breeding projects.

Since NAGAO and TAKAHASHI<sup>2)</sup> first constructed the twelve groups for rice, a great effort has been made to improve and refine the maps by using both genetic and cytological approaches. Among the twelve groups, the first and second groups contain relatively enriched loci, and several genes for economical characters are also mapped on them.<sup>9,10)</sup>

In this report, we have supplemented several loci on both groups.

### Explanation of genes

Marker genes located on the maps are listed in Table 1. In addition, target genes for mapping are explained as follows :

*d-9* A single gene, *d-9* was responsible for the semidwarfness originating from Chinese dwarf. As the gene does not exhibit deleterious effects, there is a possibility that it might be used for the improvement of the short culm variety if an appropriate genetic background were combined.

*I-Pl-2* and *I-Pl-4* It is already known that *Pl<sup>w</sup>* is responsible for the distribution of anthocyanin coloration to the various plant bodies, leaf blade, sheath, pulvinus, internode and pericarp with a high potential of the basic gene combination such as *C<sup>B</sup> A* or *C<sup>Bp</sup> A*.<sup>22)</sup> HSIEH and CHANG<sup>3)</sup> postulated a complementary action of *P<sub>r</sub>p-a* (*P<sub>a</sub>*) and *P<sub>r</sub>p-b* (*P<sub>b</sub>*). Although the genic supposition is different, *Pl<sup>w</sup>* may be equivalent with *P<sub>r</sub>p-b* and *A* corresponds to *P<sub>r</sub>p-a* owing to our identification.

In the combination with a faint coloration genotype due to *C<sup>Bm</sup> A*, *Pl<sup>w</sup>* there

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TABLE 1. Marker genes used for mapping

Linkage group	Symbol	Name	Loci
I	<i>d-4</i>	bunketsu-waito of tillering dwarf	0
	<i>I-Pl-2</i>	Inhibitor for purple leaf-2	
	<i>I-Pl-4</i>	Inhibitor for purple pericarp-4	
	<i>wx</i>	glutinous endosperm	22
	<i>C</i>	Chromogen for anthocyanin	44
	<i>bl-3</i>	brown leaf spot-3	54
	<i>d-9</i>	Chinese dwarf	
II	<i>Pl</i>	Purple leaf	61
	<i>lg</i>	liguleless	92
	<i>Ph</i>	Phenol staining	113
	<i>Pr</i>	Purple hull	137
	<i>rcn-2</i>	reduced culm number-2	
	<i>lk-i</i>	'IRAT 13' long grain	

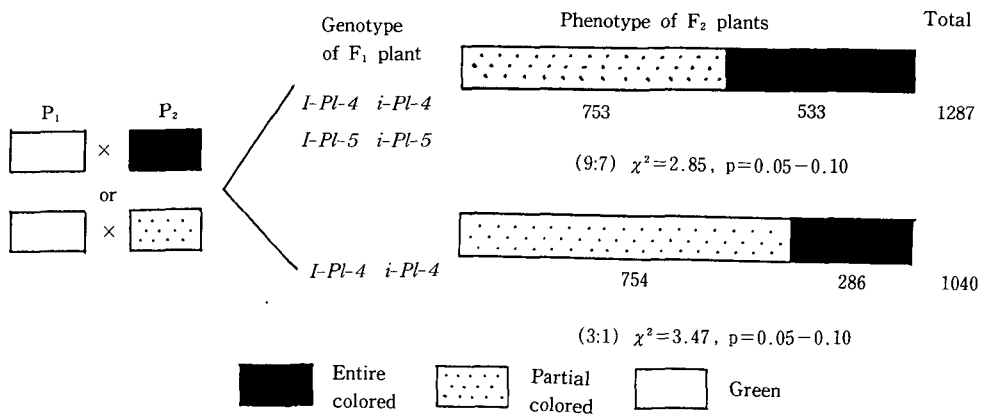


Fig. 1. F<sub>2</sub> segregation of the inhibitors, *I-Pl-4* and *I-Pl-5* which are responsible for purple pericarp.

also develops a purple color in the pericarp without the coloration of other parts.<sup>22)</sup> For the suppression of coloration in leaf blade, *I-Pl-4*, *I-Pl-2* and *I-Pl-3* insert their actions as single, duplicate or triplicate genes.

In contrast with this, *I-Pl-3* and *I-Pl-4* inhibits the pericarp coloration only though the various degrees of inhibition were observed (Fig. 1. Plate 1).

*lk-i* A long grain variety, IRAT-13 possessed this gene. Modes of inheritance are explained later.

In the calculation of recombination values, Immer's productive ratio<sup>4)</sup> or a

maximum likelihood method<sup>1)</sup> (plural data) were used.

## Results

### 1. *C-wx* linkage

TAKAHASHI<sup>23)</sup> found the linkage relation between glutinous endosperm and colored awns. Since then, the data shown in Table 2 have been obtained, which support this linkage. By the maximum likelihood method the recombination value was calculated as  $22.9 \pm 0.51\%$ .

### 2. *Pl-lg* linkage

MORINAGA<sup>17)</sup> was the first reported extensive research on the linkage relation between purple leaf and liguleless characters.

Based on the data shown in Table 3, the recombination value was calculated as  $23.7 \pm 0.43\%$ . According to the heterogeneity test, two data significantly differed from the others. It is probable that the recombination values may be affected by various causes such as cross combination, environmental and biological conditions.

TABLE 2. Estimation of the recombination value (R.C.V.) from the  $F_2$  data from different authors for the linkage relation between *C* (Chromogen for anthocyanin) and *wx* (glutinous endosperm)

Linkage phase	Mode of segregation				Total	$\chi^2$	Literature
	<i>C</i> +	<i>C wx</i>	<i>c</i> +	<i>c wx</i>			
c	605	93	80	128	906	0.372	Takahashi 1923
c	778	163	87	128	1156	4.774	"
c	309	30	43	58	440	1.848	Chao 1928
c	67	4	10	17	98	2.366	Yamaguchi 1929
c	214	33	26	51	324	0.986	"
c	1001	154	146	213	1514	0.027	Nagao 1951
c	577	83	84	110	854	0.003	Nagamatsu & Omura 1962
c	1148	175	167	242	1732	0.039	Nagao & Takahashi 1963
r	134	61	60	0	255	2.839	Yamaguchi 1927
r	1732	736	837	31	3336	2.971	"
r	467	228	221	1	917	10.485	"
r	516	209	231	11	967	0.005	Yamaguchi 1929
r	42	21	29	1	93	0.360	"
r	182	80	125	12	399	4.560	"
r	443	176	238	14	871	0.400	Jodon 1957
r	551	273	270	35	1129	20.900	"

R.C.V. =  $22.9 \pm 0.51\%$ , Homogeneity test;  $\chi^2 = 52.850$   $p < 0.001$ .

TABLE 3. Estimation of the recombination value (R.C.V.) from the data from different authors for the linkage relation between *Pl* (Purple leaf) and *lg* (liguleless)

Gene- ration	Linkage phase	Mode of segregation				Total	$\chi^2$	Literature
		<i>Pl</i>	<i>Pl lg</i>	++	+ <i>lg</i>			
F <sub>2</sub>	c	313	40	49	74	476	1.850	Morinaga 1938
F <sub>3</sub>	c	5382	758	818	1263	8221	20.974	"
F <sub>3</sub>	r	1190	510	560	39	2299	1.255	"
F <sub>2</sub>	c	148	21	23	34	226	0.379	Nagao 1951
F <sub>2</sub>	c	303	56	64	56	479	5.900	Nagao & Takahashi 1952
F <sub>2</sub>	c	47	6	5	11	69	6.098	"
F <sub>2</sub>	c	21	5	3	2	31	1.011	"
F <sub>2</sub>	c	101	15	18	23	157	0.003	"
F <sub>2</sub>	c	1325	289	267	272	2153	29.756	Nagao & Takahashi 1963
F <sub>2</sub>	r	394	165	188	14	761	0.947	Iwata & Omura 1971
F <sub>2</sub>	c	490	69	77	109	745	0.862	"
B <sub>1</sub>	c	92	31	33	94	250	1.813	Kinoshita & Takamure 1987

R.C.V. =  $23.7 \pm 0.43\%$ , Homogeneity test;  $\chi^2 = 70.203$   $p < 0.001$

### 3. Mapping of *d-9*, *I-Pl-2* and *I-Pl-4*

In the first linkage group, linkage relations were detected between *d-9* and other markers (Table 4). Putting the data together, the order of five genes was estimated as shown in Fig. 2a. It was also found that *I-Pl-2* is closely linked with *I-Pl-4* and the relations between *wx* and *I-Pl-4* and between *C* and *I-Pl-4* are shown in the Table 5. Four genes were mapped as shown in Fig. 2b.

TABLE 4. Linkage relations involving *d-9* (chinese dwarf)

Gene pair A : B	Linkage phase	R.C.V. (%)	F <sub>2</sub> segregation				Total	Goodness of fit		
			AB	Ab	aB	ab		$\chi^2$	p	
<i>C : d-9</i>	Coup.	31.7 ± 1.28	Obs.	213	43	38	31	325	2.71	0.30-0.50
			Cal.	200.40	43.34	43.34	37.90			
<i>d-4 : d-9</i>	Rep.	47.5 ± 2.88	Obs.	180	51	76	18	325	5.00	0.10-0.20
			Cal.	180.83	62.92	62.92	18.33			
<i>wx : bl-3</i>	Rep.	31.6 ± 4.93	Obs.	92	31	23	2	148	6.76	0.02-0.05
			Cal.	77.69	33.31	33.31	3.69			

### 4. Mapping of *lk-i*

IRAT 13 was crossed with a normal short grained tester, H-165. The F<sub>2</sub> variation of grain lengths is shown in Fig. 3a. The mean of F<sub>1</sub> plants was intermediate between both parents, and F<sub>2</sub> distribution showed a bimodal curve

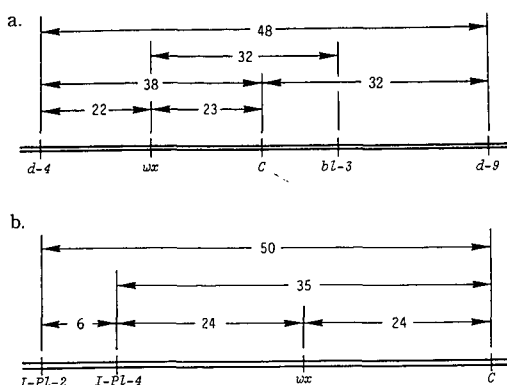


Fig. 2. Mapping of the first linkage group.

a. Gene order of *d-4*, *wx*, *C*, *bl-3* and *d-9*.

b. Gene order of *I-P1-2*, *I-P1-4*, *wx* and *C*.

TABLE 5. Linkage relations involving *I-P1-4* (Inhibitor for purple pericarp-4)

Tester genes		F <sub>2</sub> segregation				Total	Phase of link.	R.C.V. (%)	Fitness $\chi^2$
A	B	AB	Ab	aB	ab				
<i>wx</i>	<i>I-P1-4</i>	224	109	99	9	441	r	23.8	0.896
		100	61	46	1	208	r	$\pm 3.66$	2.180
<i>C</i>	<i>I-P1-4</i>	235	102	88	16	441	r	34.5	0.511
		105	58	41	4	208	r	$\pm 3.39$	1.660
<i>I-P1-2</i>	<i>I-P1-4</i>	143	103	1	11	258	c	6.0	8.66*

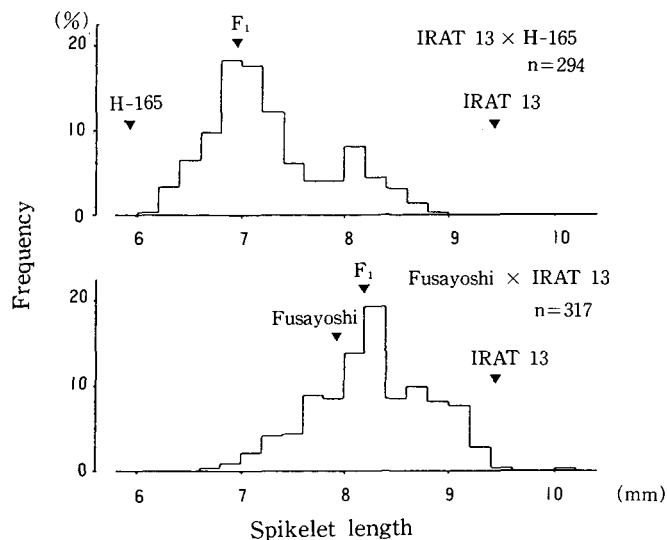
\* Calculation by Immer's method.

divided into normal (short) and long grain groups. As to the feature of grain shape, it was detected that a single recessive gene is responsible for the long grain of IRAT 13 (Table 6). IRAT 13 was crossed with Fusayoshi which possesses the other long grain gene, *Lk-f*.<sup>24)</sup> From the F<sub>2</sub> distributions of the cross between them (Fig. 3b), it was inferred that an independent relation exists between the two genes showing a continuous variation in a wide range. New linkages involving *lk-i* were found in the second linkage group (Table 7). The order of the three genes was estimated as shown in Fig. 4.

### Discussion

Detailed maps of the first and second linkage groups are presented in Fig. 5, depending on the linkages reported hitherto.

According to the trisomic analysis in both Japonica and Indica rice<sup>6,8)</sup>, the first linkage group corresponds to KURATA's K6<sup>14)</sup> or Triplo 3 and the second group to K4 or Triplo 12. Because the chromosome numbering system is not standardized, a different number is allotted to the same chromosome. If the location of centromere, arm ratio and other features of chromosome is character-



**Fig. 3.** Frequency distribution of spikelet length in F<sub>2</sub> population of the crosses between IRAT 13 and testers, H-165 (short grain) and Fusayoshi (long grain).

**TABLE 6.** Inheritance mode of the long grain character originating from IRAT 13

Grain type	Normal +	Long <i>lk-i</i>	Total	Ratio	Goodness of fit	
					$\chi^2$	p
Obs.	219	75	294	3:1	0.04	0.8-0.9

**TABLE 7.** Combined segregations between *lk-i* and marker genes in F<sub>2</sub> population of the cross between IRAT 13 and A-58

Gene pair A : B	Linkage phase	R.C.V. (%)	F <sub>2</sub> segregation				Goodness of fit			
			AB	Ab	aB	ab	Total	$\chi^2$	p	
<i>Pr : lk-i</i>	Coup.	33.2±3.6	Obs.	78	17	18	14	127	0.03	>0.99
			Cal.	77.67	17.58	17.58	14.17	127.00		
<i>Ph : lk-i</i>	Coup.	43.2±3.5	Obs.	101	32	29	15	177	0.24	0.95-0.98
			Cal.	102.78	29.97	29.97	14.28	177.00		
<i>Pr : Ph</i>	Coup.	19.3±2.7	Obs.	85	10	12	20	127	0.21	0.95-0.98
			Cal.	84.18	11.07	11.07	20.68	127.00		

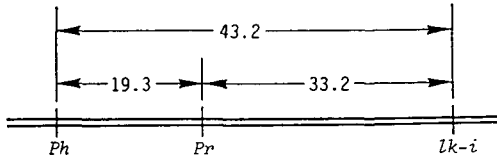


Fig. 4. Mapping of the three loci, *Ph*, *Pr* and *lk-i* in the second linkage group.

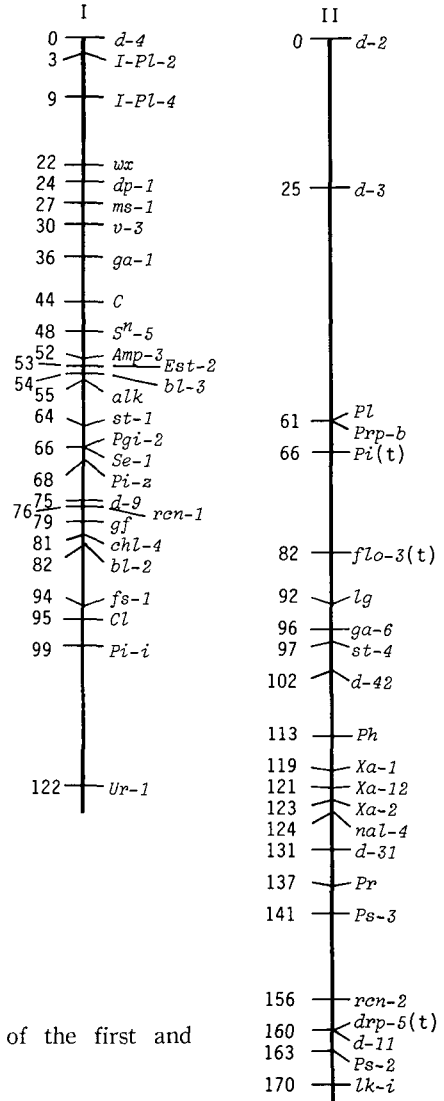


Fig. 5. Linkage maps of the first and second groups.

ized, the detailed chromosome maps will be established in the near future.

Recently the use of RFLP (restriction fragment length polymorphism) and other biochemical markers for rice has developed rapidly.<sup>13,15)</sup> Two RFLP maps are now available for the first and second linkage groups. We are planning to make an integrated map by using near-isogenic lines.<sup>16)</sup> If these studies progress, more refined linkage maps will be available for efficient use in various kinds of genetic and breeding research. Further, studies on expression and regulation of the rice genes must be developed using modern tools complemented with both molecular and conventional genetics.

### Summary

In order to improve and refine the linkage maps in rice, the determination of the new gene loci and the recalculation of recombination values were carried out in the first and second linkage groups.

Recombination values between *C* (Chromogen for anthocyanin) and *wx* (glutinous endosperm) were calculated as  $22.9 \pm 0.51\%$  depending on the data from various authors.

As well as this, the recombination value between *Pl* (Purple leaf) and *lg* (liguleless) was  $23.7 \pm 0.43\%$  though the two data significantly differed from the others. There is a possibility that various causes due to environmental and biological conditions may affect the recombination values.

Marker genes, *d-9*, *I-Pl-2* and *I-Pl-4* were newly mapped in the first linkage group, while the locus of *lk-i* was determined in the second linkage group.

The suppression of purple pericarp was explained by the complementary effect of *I-Pl-4* and *I-Pl-5*. In addition, it is noted that the  $F_2$  variation of spikelet length indicated an independent relation between *lk-i* and *Lk-f* which was formerly found for long grain of Fusayoshi.

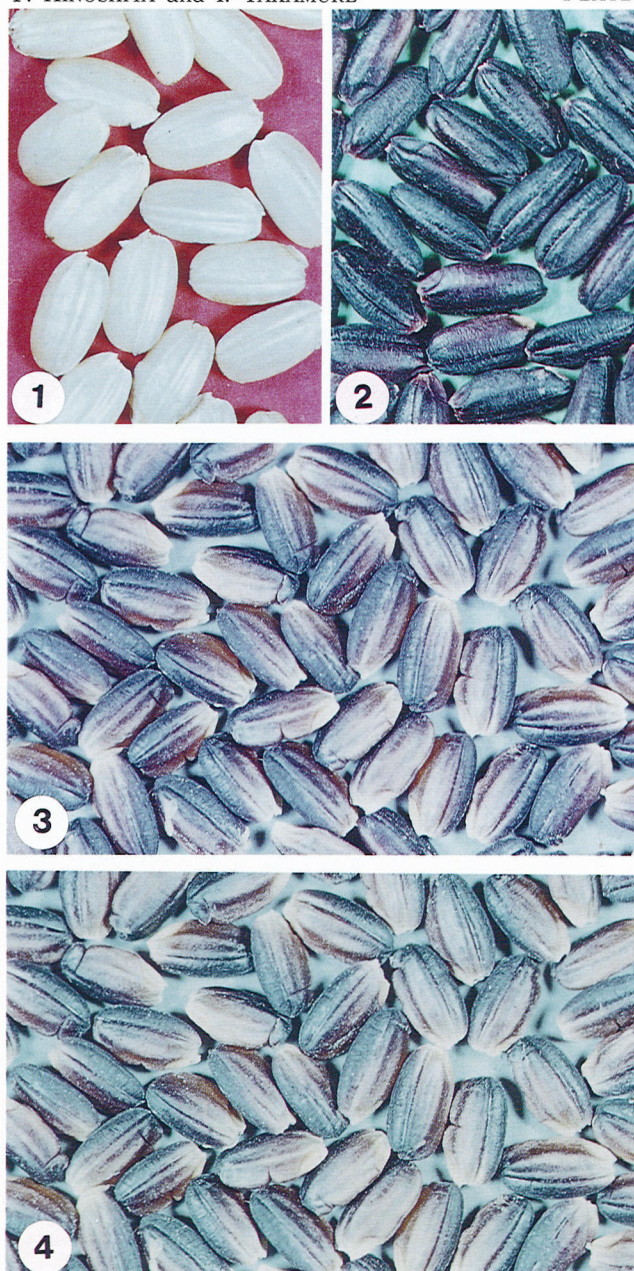
### Literature Cited

1. ALLARD, R. W. : Formulas and tables to facilitate the calculation of recombination values in heredity. *Hilgardia*. **24** : 235-278. 1956
2. CHAO, L. F. : Linkage studies in rice. *Genetics* **13** : 133-169. 1928
3. HSIEH, S. C. and T. M. CHANG : Genic analysis in rice. IV. Genes for purple pericarp and other characters. *Jpn. J. Breed.* **14** : 141-149. 1964
4. IMMER, F. R. : Formulae and tables for calculating linkage intensities. *Genetics* **15** : 81-98. 1930
5. IWATA, N. and T. OMURA : Linkage analysis by reciprocal translocation method in rice plant (*Oryza sativa* L.) II. Linkage group corresponding to the chromosome 5, 6, 8, 9, 10 and 11. *Sci. Bull. Fac. Agr. Kyushu Univ.* **25** : 137-153. 1971 (Japanese with English summary)
6. IWATA, N. and T. OMURA : Studies on the trisomics in rice plant (*Oryza sativa* L.) VI. An accomplishment of a trisomic series in *japonoca* rice plants. *Jpn. J. Genet.* **59** : 199-204. 1984
7. JODON, N. E. : Inheritance of some of the more striking characters in rice. *J. Hered.* **48** : 181-192. 1957
8. KHUSH, G. S., R. J. SINGH, S. C. SUR and A. L. LIBROJO : Primary trisomics of rice. Origin, morphology, cytology, and use in linkage mapping. *Genetics* **107** : 141-163. 1984
9. KINOSHITA, T. : Gene analysis and linkage map. In *Biology of Rice* (Tsunoda, S. and N. Takahashi eds.) 187-274. Tokyo, 1984
10. KINOSHITA, T. : Report of the committee on gene symbolization, nomenclature and linkage groups. IV. Current linkage map. *Rice Genet. Newsletter* **4** : 11-37. 1987
11. KINOSHITA, T. and I. TAKAMURE : Inheritance and linkage relationship on zebra chlorosis

- and zebra necrosis in rice. -Genetical studies on rice plant, LIIIVIII.- *J. Fac. Agr. Hokkaido Univ.* **61** : 445-445. 1984
12. KINOSHITA, T. and I. TAKAMURE : Linkage studies by the use of backcross data in rice. -Genetical studies on rice plant, XCV.- *J. Fac. Agr. Hokkaido Univ.* **63** : 136-143. 1986
  13. KISHIMOTO, N., M. YANO, T. TANAKA, K. SAITO, A. SAITO, T. NAGAMINE, S. KUHARA, M. KAWASE, M. KATSUTA, S. YOSHIMURA, A. YOSHIMURA, M. NAKAGAHARA and N. IWATA : Linkage mapping of RFLP markers of rice nuclear DNA, morphological markers and isozyme loci in rice (*Oryza sativa* L.) *Proc. of the 6th internatl. Congr. of SABRAO* : 489-492. 1989
  14. KURATA, N., N. IWATA and T. OMURA : Karyotype analysis in rice. 2. Identification of extra chromosomes in trisomic plants and banding structure on some chromosomes. *Jpn. J. Genet.* **56** : 41-50. 1981
  15. MCCOUCH, S. R., G. KOCHERT, Z. H. YU, Z. Y. WANG, G. S. KHUSH, W. R. COFFMAN and S. D. TANKSLEY : Molecular mapping of rice chromosomes. *Theor. Appl. Genet.* **76** : 815-829. 1988
  16. MUEHLBANER, G. J., J. E. SPECHT, M. A. THOMAS-COMPTON, P. E. STASWICK and R. I. BERNARD : Near-isogenic lines - A potential resources in the integration of conventional and molecular marker linkage maps. *Crop Sci.* **28** : 729-735. 1988
  17. MORINAGA, T. : Inheritance in rice. *Oryza sativa* L. II. Linkage between the gene for purple plant color and the gene for liguleless. *Jpn. J. Bot.* **9** : 121-129. 1938
  18. NAGAMATSU, T. and T. OMURA : Linkage study of the genes belonging to the first chromosome in rice. *Jpn. J. Breed.* **12** : 231-236. 1962
  19. NAGAO, S. : Genic analysis and linkage relationship of characters in rice. *Advances in Genetics* **4** : 181-212. 1951
  20. NAGAO, S. and M. TAKAHASHI : Genetical studies on rice plant. XIV. The order and distance of some genes belonging to *Pl*-linkage group. *Jpn. J. Breed.* **1** : 237-240. 1952 (in Japanese with English summary)
  21. NAGAO, S. and M. TAKAHASHI : Trial construction of twelve linkage groups in Japanese rice. Genetical studies on rice plant, XXVIII. *J. Fac. of Agr. Hokkaido Univ.* **53** : 72-130. 1963
  22. NAGAO, S., M. TAKAHASHI and T. KINOSHITA : Genetical studies on rice plant, XXVI. Mode of inheritance and causal genes for one type of anthocyanin color character in foreign rice varieties. *J. Fac. of Agr. Hokkaido Univ.* **52** : 20-50. 1962
  23. TAKAHASHI, N. : An example of linkage in rice (Preliminary report). *Jpn. J. Genet.* **2** : 23-30. 1923 (in Japanese)
  24. TAKEDA, K. and K. SAITO : Major genes responsible for grain shape in rice. *Jpn. J. Breed.* **30** : 280-282. 1980 (in Japanese)
  25. YAMAGUCHI, Y. : Kreuzungsuntersuchungen an Reispflanzen. II. Über die zweite (S-M-) Koppelungsgruppe mit besonderer Berücksichtigung ihrer korrelativen Beziehung zur Blütezeit, Vorläufige Mitteilung. *Ber. Ohara Institut. f. landw. Forsch.* **3** : 1-126. 1927 (in German)
  26. YAMAGUCHI, Y. : Supplementary information on S-M linkage relation in rice. *Nogaku -Kenkyu* **13** : 135-172. 1929 (in Japanese)

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PLATE



#### Explanation of Plate

1. White pericarp
2. Purple pericarp (entire)
3. Moderate inhibition of purple pericarp (partial)
4. Strong inhibition of purple pericarp (partial)