J. Fac. Agr. Hokkaido Univ., Vol. 64, Pt. 3 : 208~217 (1990)

GENE MAPPING OF THE FIRST AND SECOND LINKAGE GROUPS IN RICE[1)]

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Received February 1, 1990

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[21)] 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.[9,10)]

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^w 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 $C^B A$ or $C^{Bp} A$.[22)] HSIEH and CHANG[3)] postulated a complementary action of *Prp-a* (P_a) and *Prp-b* (P_b). Although the genic supposition is different, Pl^w may be equivalent with *Prp-b* and *A* corresponds to *Prp-a* owing to our identification.

In the combination with a faint coloration genotype due to $C^{Bm} A$, Pl^w there

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1) Contribution from the Plant Breeding Institute, Faculty of Agriculture, Hokkaido University, Sapporo 060, Japan.

2) This work was supported in part by Grant-In-Aid for Co-operative Research, No. 62304013 from the Ministry of Education, Science and Culture, Japan.

TABLE 1. Marker genes used for mapping

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

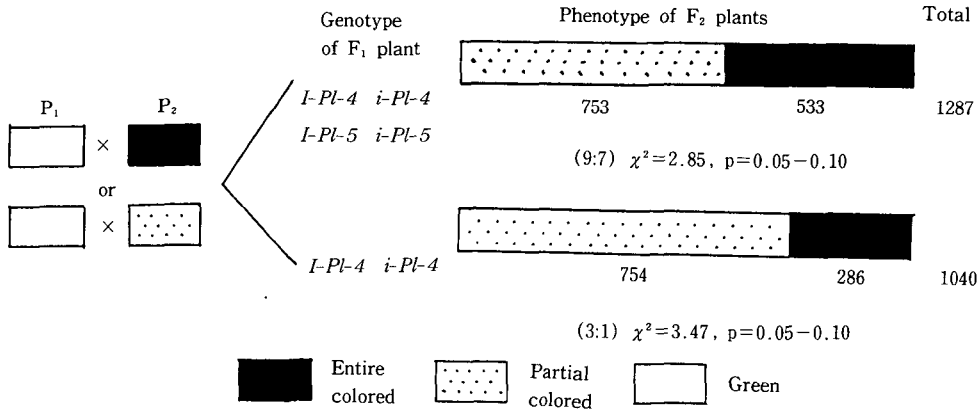

Fig. 1. F_2 segregation of the inhibitors, *I-Pl-4* and *I-Pl-5* which are responsible for purple pericarp.

also develops a purple color in the pericarp without the coloration of other parts.[22] 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[4] or a

maximum likelihood method[1] (plural data) were used.

Results

1. *C-wx* linkage

TAKAHASHI[23] 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[17] 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	χ^2	Literature
	C +	*C wx*	*c* +	*c wx*			
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	χ^2	Literature
		Pl	*Pl lg*	+ +	+ *lg*			
F_2	c	313	40	49	74	476	1.850	Morinaga 1938
F_3	c	5382	758	818	1263	8221	20.974	〃
F_3	r	1190	510	560	39	2299	1.255	〃
F_2	c	148	21	23	34	226	0.379	Nagao 1951
F_2	c	303	56	64	56	479	5.900	Nagao & Takahashi 1952
F_2	c	47	6	5	11	69	6.098	〃
F_2	c	21	5	3	2	31	1.011	〃
F_2	c	101	15	18	23	157	0.003	〃
F_2	c	1325	289	267	272	2153	29.756	Nagao & Takahashi 1963
F_2	r	394	165	188	14	761	0.947	Iwata & Omura 1971
F_2	c	490	69	77	109	745	0.862	〃
B_1	c	92	31	33	94	250	1.813	Kinoshita & Takamure 1987

R.C.V. = 23.7±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_2 segregation AB	Ab	aB	ab	Total	Goodness of fit χ^2	p
C : d-9	Coup.	31.7±1.28	Obs.	213	43	38	31	325		
			Cal.	200.40	43.34	43.34	37.90	325.00	2.71	0.30−0.50
d-4 : d-9	Rep.	47.5±2.88	Obs.	180	51	76	18	325		
			Cal.	180.83	62.92	62.92	18.33	325.00	5.00	0.10−0.20
wx : bl-3	Rep.	31.6±4.93	Obs.	92	31	23	2	148		
			Cal.	77.69	33.31	33.31	3.69	148.00	6.76	0.02−0.05

4. Mapping of *lk-i*

IRAT 13 was crossed with a normal short grained tester, H-165. The F_2 variation of grain lengths is shown in Fig. 3a. The mean of F_1 plants was intermediate between both parents, and F_2 distribution showed a bimodal curve

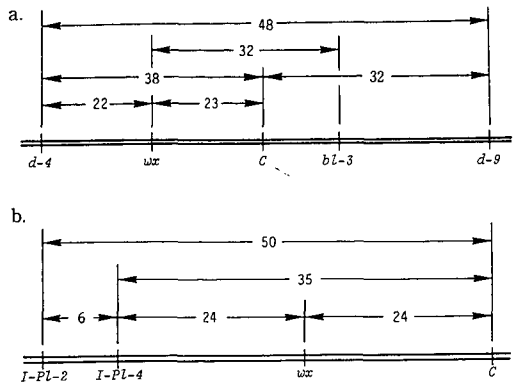

Fig. 2. Mapping of the first linkage group.
a. Gene order of *d-4*, *wx*, *C*, *bl-3* and *d-9*.
b. Gene order of *I-Pl-2*, *I-Pl-4*, *wx* and *C*.

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

Tester genes		F_2 segregation					Phase of	R.C.V.	Fitness
A	B	AB	Ab	aB	ab	Total	link.	(%)	χ^2
wx	*I-Pl-4*	224	109	99	9	441	r	23.8	0.896
		100	61	46	1	208	r	±3.66	2.180
C	*I-Pl-4*	235	102	88	16	441	r	34.5	0.511
		105	58	41	4	208	r	±3.39	1.660
I-Pl-2	*I-Pl-4*	143	103	1	11	258	c	6.0	8.66*

* Calculation by Immer's method.

devided 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*.[24] From the F_2 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[6,8], the first linkage group corresponds to KURATA's K6[14] 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-

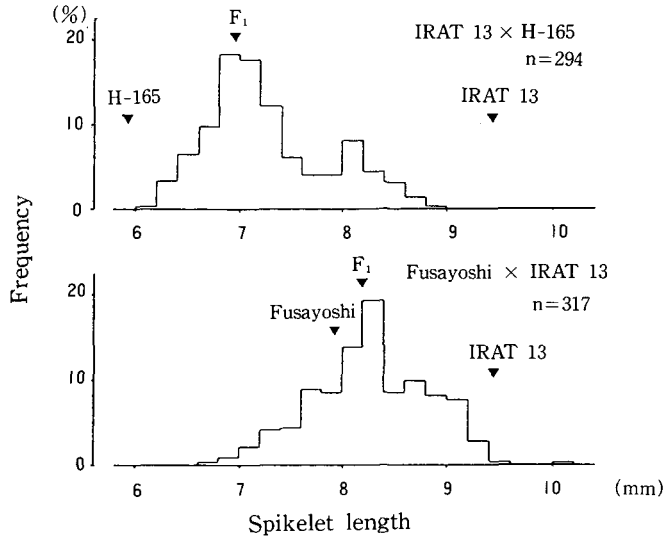

Fig. 3. Frequency distribution of spikelet length in F_2 population of the crosses between IRAT 13 and testers, H-165 (short grain) and Fusayoshi (long grain).

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

Grain type	Normal +	Long *lk-i*	Total	Ratio	Goodness of fit	
					χ^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_2 population of the cross between IRAT 13 and A-58

Gene pair A : B	Linkage phase	R.C.V. (%)		F_2 segregation AB	Ab	aB	ab	Total	Goodness of fit χ^2	p
Pr : lk-i			Obs.	78	17	18	14	127		
	Coup.	33.2±3.6	Cal.	77.67	17.58	17.58	14.17	127.00	0.03	>0.99
Ph : lk-i			Obs.	101	32	29	15	177		
	Coup.	43.2±3.5	Cal.	102.78	29.97	29.97	14.28	177.00	0.24	0.95−0.98
Pr : Ph			Obs.	85	10	12	20	127		
	Coup.	19.3±2.7	Cal.	84.18	11.07	11.07	20.68	127.00	0.21	0.95−0.98

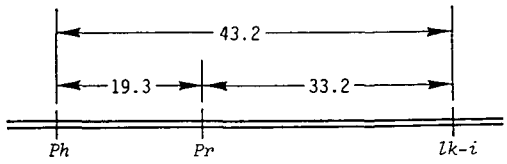

Fig. 4. Mapping of the three loci, *Ph*, *Pr* and *lk-i* in the second linkage group.

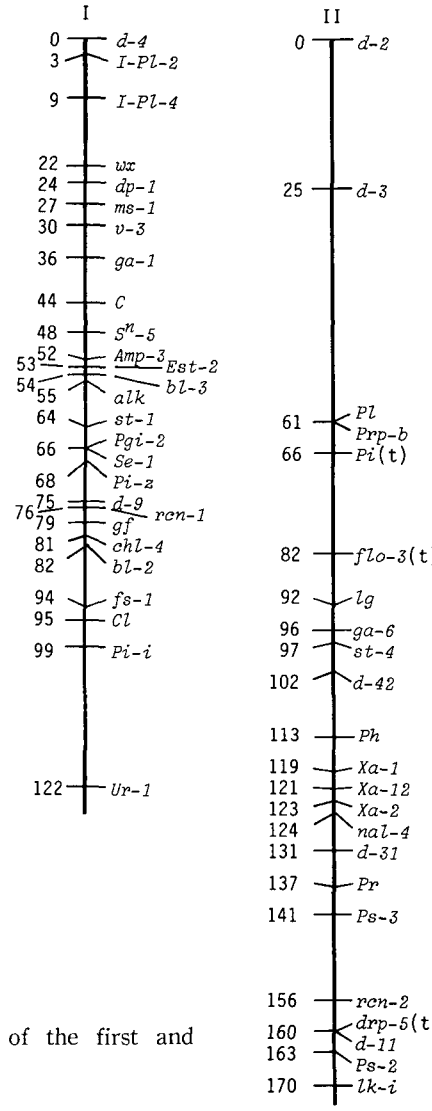

Fig. 5. Linkage maps of the first and second groups.

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.[13,15] 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.[16] 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±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±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 grtoup.

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 formely found for long grain of Fusayoshi.

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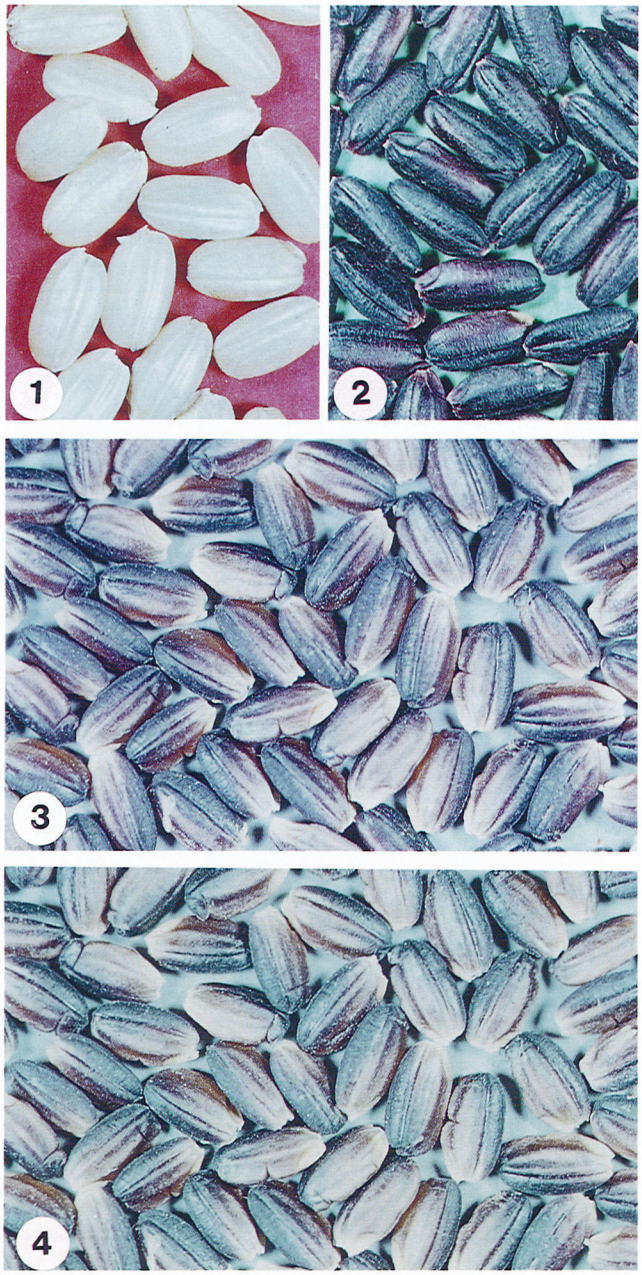

Explanation of Plate

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