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Linkage Studies in Rice (*Oryza sativa* L.) On Some Mutants Derived from Chronic Gamma Irradiation

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Thirteen of the mutant genes induced by gamma irradiation and two of the spontaneous mutant genes of rice were newly described and determined their linkage groups as follows :

Group I; spotted leaf 4 (*spl*₄). Group II; narrow leaf 1 (*nal*₁), yellowish leaf margin (*ylm*) and round kernels 1 (*rk*₁). Group I or III; semi-rolled leaf 2 (*rl*₂). Group IV; spotted leaf 5 (*spl*₅). Group VI; neck leaf 2 (*nl*₂). Group VIII; zebra leaf 2 (*z*₂) and tillering dwarf (*d*, spontaneous). Group X; dwarf (*d*_{*x*-1}), brittle culm 3 (*bc*,) and gold hull 3 (*gh*₃). Group XI; fine culm and tillering (*fc*), spotted leaf 3 (*spl*₃) and virescent 1 (*vi*, spontaneous).

INTRODUCTION

Recently, linkage studies in rice plants have satisfactorily progressed by the use of reciprocal translocations and trisomics (Iwata and Omura, 1971a, b, 1975, 1976; Kinoshita *et al.*, 1975; Sato *et al.*, 1972). However, the number of mutants capable to use for the studies was too limited to complete the more detailed linkage map.

Then, the use of induced mutants for the linkage analysis was planned, and thousands of mutants suitable for the studies have been induced or supplied. Several years ago, more than one hundred of the mutant stocks of Norin 8 were supplied by Dr. S. Tanaka of Institute of Radiation Breeding, National Institute of Agricultural Sciences, Ohmiya, Ibaraki, Japan. Using these stocks, linkage analysis has continued, and as the results, some of linkage relations with marker genes were found.

MATERIALS AND METHODS

The mutants used were induced in the gamma-field of Institute of Radiation Breeding, National Institute of Agricultural Sciences. General conditions of irradiation for inducing the mutants are described by Tanaka (1967). Stock number and their main characteristics are listed in Table 1.

The mutant stocks were crossed with linkage testers having marker genes shown in Table 2 and the linkage relation was tested in F₂. When the linkage was detected, the recombination value was estimated from the segregations in F₂ and in some cases in F₃ progenies by the method of maximum likelihood.

Table 1. The stock number of mutant lines at Kyushu University and their original number at Ohmiya, and their main characteristics.

Stock number at Kyushu	Original number at Ohmiya (1966)	Main characteristics
M 11	265	brittle culm
M 36	46	zebra leaf
M 41	187	spotted leaf
M 45	239	neck leaf
M 50	304	rolled leaf
M 56	512	fine culm, tillering
M 87	781	spotted leaf
M 88	785	yellowish leaf margin, round kernel
M 92	820	dwarf
M 93	846	gold hull
M 100	886	narrow leaf
M 114	971	spotted leaf

Table 2. List of marker genes used and their linkage groups.

Linkage group	Gene symbol	Character	Reference
I	<i>dp₁</i> <i>c</i>	depressed palea 1 chromogen for anthocyanin	Nagamatsu and Omura (1962) Nagao and Takahashi (1963)
II	<i>lg</i>	liguleless	Nagao and Takahashi (1963)
III	<i>A</i>	anthocyanin activator	Nagao and Takahashi (1963)
IV	<i>d₆</i> <i>g</i> <i>Rc</i>	lop-leaved type dwarf long empty glumes brown pericarp	Nagao and Takahashi (1963) Nagao and Takahashi (1963) Nagao and Takahashi (1963)
VI	<i>d₁</i>	Daikoku type dwarf	Nagao and Takahashi (1963)
VIII	<i>sp</i> <i>z</i>	short panicle zebra leaf	Iwata and Omura (1971a) Iwata and Omura (1975)
X	<i>bl₁</i> <i>d_y</i> <i>gh₂</i>	physiological disease showing dark brown discoloration of leaves Waisei-shirasasa type dwarf gold hull 2	Nagao and Takahashi (1963) Iwata and Omura (1971b) Iwata and Omura (1971b)
XI	<i>ch</i> <i>dl</i>	chlorina drooping leaf	Iwata and Omura (1971b) Iwata and Omura (1971b)

RESULTS AND DISCUSSION

F₁ plants of all cross combinations between mutant stocks and linkage testers had normal phenotype. The F₂ segregation modes of all mutant characters tested, except for those of M 88 described later, fitted well the expected ratio of 3:1 as shown in Table 3. The linkage relations between the mutant characters and the marker genes are as follows.

Linkage group I

M 114: It is characterized by a kind of physiological disease showing relatively large brown spots in leaves. A gene of the character is designated as

Table 3. F₂ segregation mode in crosses between mutant stocks and normal forms, indicating that each of the mutant characters is governed by single recessive gene.

Mutant lines	Observed number			χ^2 for 3 : 1
	Dominant	Recessive	Total	
M 11	887	270	1,157	1.708
M 36	1,310	413	1,723	0.975
M 41	2,489	812	3,301	0.284
M 45	2,183	734	2,917	0.041
M 50	1,488	448	1,936	3.570
M 56	2,564	804	3,368	2.287
M 87	1,118	341	1,459	2.062
M 92	3,293	1,051	4,344	1.504
M 93	657	214	871	0.086
M 100	1,861	572	2,433	2.881
M 114	772	259	1,031	0.008
HO 568 ¹⁾	1,679	523	2,202	1.832
US 2 ²⁾	954	308	1,262	0.238

¹⁾ A spontaneous dwarf mutant originated from "Bunketsu-to,"

²⁾ A spontaneous virescent mutant introduced from Dr. Jodon.

*spl*₄, because two genes for spotted leaves generated spontaneously, *spl*₁ and *spl*₂, have already been designated by the authors (Iwata and Omura, 1975; Omura and Iwata, unpublished) and another gene for spotted leaves, *spl*₃, will be described later on.

A very close linkage was found between *spl*₄ and *dp*, from the fact that none of the double recessive plant was observed in F₂ in the cross of repulsion phase as shown in Table 4. The weighted mean of recombination value of 1.4 % was calculated from the segregations of F₃ lines from F₂ plants showing such phenotypes as *spl*₄⁺*dp*₁ and *spl*₄*dp*₁⁺.

Table 4. Segregations of *spl*₄ and *dp*₁ in F₂ and F₃.

Items	Segregation mode				Recombination value (%)	χ^2 ¹⁾		
F ₂	Phase	No. of	++	+ <i>dp</i> ₁	<i>spl</i> ₄ + <i>spl</i> ₄ <i>dp</i> ₁	Total	≠0	2.664
	Rep.	4	205 (214.5)	102 (107.3)	122 (107.3)	0 (0)		
F ₃ from F ₂ plants (<i>spl</i> ₄ ⁺ <i>dp</i> ₁)	<i>spl</i> ₄ seg.		<i>spl</i> ₄ non-seg.		Total	0.8±0.8		
	1		59		60			
F ₃ from F ₂ plants (<i>spl</i> ₄ <i>dp</i> ₁ ⁺)	<i>dp</i> ₁ seg.		<i>dp</i> ₁ non-seg.		Total	3.4±1.5		
	5		71		76			
Weighted mean						1.4±0.7		

¹⁾ In Tables 4-17, degree of freedom for χ^2 was 3.

Takahashi *et al.* (1967) reported that a loose linkage relation with the recombination value of about 32 % was detected between one of physiological

disease character, *bl*₃, and waxy, *wx*, belonging to the linkage group I. As *wx* links closely with *dp*₁ with the intensity of 5.5 % (Nagamatsu and Omura, 1962), it is thought that *spl*₄ is not the same as *bl*₃.

Linkage group II

M 100: It is a semi-dwarf with narrow and dark green leaves. The gene for this type is temporarily designated as *nal*₁. A linkage relation between *nal*₁ and *lg* was observed and the recombination value was estimated at 9.5 % in weighted mean from the F₂ and F₃ data (Table 5).

Table 5. Segregations of *nal*₁ and *lg* in F₂ and F₃.

Items		Segregation mode					Recombination value (%)	χ^2	
Phase	No. of cross	++	+ <i>lg</i>	<i>nal</i> ₁ + <i>nal</i> ₁ <i>lg</i>	Total				
F ₂	Rep.	11	1,229 (1,220.6)	632 (604.2)	568 (604.2)	4 (4.1)	2,433	8.2±2.0	3.508
F ₃ from F ₂ plants (<i>nal</i> ₁ ⁺ <i>lg</i>)			<i>nal</i> ₁ seg.	<i>nal</i> ₁ non-seg.	Total				
			35	174	209			9.1±1.5	
F ₃ from F ₂ plants (<i>nal</i> ₁ <i>lg</i> ⁺)			<i>lg</i> seg.	<i>lg</i> non-seg.	Total				
			41	168	209			10.9±1.7	
Weighted mean								9.5±1.0	

On the other hand, two types of the dwarf with narrow leaf linking with *lg* have been described previously. Yen *et al.* (1968) have found that *nal* and *lg* linked each other with the recombination value of 19.1%. Hsieh and Yen (1966) have also found that the *d*₄₂ linked with *lg* and the recombination value was estimated at 10 %. However, the relations among *nal*₁, *nal* and *d*₄₂ remain uncertain.

M 88: It is characterized by a yellowish leaf margin manifesting at the heading stage and round kernels.

These characteristics behaved separately as two of single recessive characters in F₂ as shown in Table 6. So, gene symbols are given as *ylm* for yel-

Table 6. F₂ segregation of M 88 (*rk*₁, *ylm*) and *lg*.

Gene pair	Phase	No. of cross	Segregation mode				Total	Recombination value (%)	χ^2
			AB	Ab	aB	ab			
<i>ylm</i> - <i>lg</i>	Rep.	3	196 (197.0)	98 (97.0)	97 (97.0)	1 (1.0)	392	10.0±5.0	0.015
<i>rk</i> ₁ - <i>lg</i>	Rep.	3	197 (208.1)	85 (84.9)	96 (95.0)	14 (13.1)	392	35.1±4.4	2.086
<i>ylm</i> - <i>rk</i> ₁	coup.	3	230 (237.9)	56 (56.1)	52 (56.1)	14 (14.9)	392	34.7±3.1	2.076

lowish leaf margin and *rk*, for round kernels. Both *ylm* and *rk*, linked with *lg*. The recombination values of *ylm-lg*, *rk₁-lg* and *ylm-rk*, amounted to 10.0 %, 35.1 % and 34.7 %, respectively, suggesting that the order of the genes in the linkage group II would be *lg-ylm-rk*.

The authors reported previously that a round kernel character of "Henpei-to," which was designated as *rk*, had been recognized to belong to the linkage group II by trisomic method (Iwata and Omura, 1975). However, the identification of *rk* and *rk*, has not yet been made.

Linkage group I or III

M 50 : It has semi-rolled leaf, and *rl₂* is used as a gene symbol of the character.

The joint segregation of semi-rolled leaf and colored apiculus was examined in the F₂ of cross between M 50 and a linkage tester having colored apiculus. The apiculus colors by the coexistence of two genes, C and A, belonging to the linkage groups I and III, respectively. In the F₂ given in Table 7, colored and non-colored apiculi segregated in a ratio of 9 : 7. The linkage between apiculus coloration and semi-rolled leaf was observed with the recombination value of 19.5 %, though which of C or A links with *rl₂* was not proved.

Table 7. F₂ segregation of *rl₂* and apiculus color.

Phase	No. of cross	Segregation mode ¹⁾				Total	Recombination value (%)	χ^2
		colored ap.		non-colored ap.				
		+	<i>rl₂</i>	t	<i>rl₂</i>			
coup.	3	198 (192.2)	21 (25.5)	104 (98.0)	64 (71.3)	387	19.5±3.3	2.084

¹⁾ (9 : 7) (3 : 1)

Nagao *et al.* (1964) described that a sort of *rl* gene linked with A with intensity of 41% and belonged consequently to the linkage group III. Against this result, the authors found by trisomic method that this *rl* does not belong to the linkage group III but belong to another linkage group consisting of *nal₂*, *d_B* and *spl₁* (Iwata and Omura, 1975). Therefore, it is clear that *rl* differs from *rl*.

Linkage group IV

M 87: It is also characterized by a kind of physiological leaf spots. This mutant shows relatively small reddish brown spots scattering extensively in leaves in comparison with M 114 (*spl₄*). A gene for this leaf spots is designated as *spl₅*.

The linkage relations were found in F₂ of crosses between the *spl*, and such three genes as *d₆*, *g* and *Rc*. From the F₂ data shown in Table 8, the recombination values of *spl₅-d₆*, *spl₅-g* and *spl₅-Rc* were estimated at 19.8%, 20.1% and 13.5 %, respectively. The arrangement of *d₆-g-Rc* on the group have previously been confirmed from numerous F₂ data (Iwata and Omura, 1971b; Nagao and Takahashi, 1963). Thus, the sequence of the four genes at the map of linkage group IV may be *d₆-g-spl₅-Rc*.

Table 8. Linkage relation between *spl₅* and genes belonging to the linkage group IV.

Gene pair	Phase	No. of cross	Segregation mode in F ₂				Total	Recombination value (%)	χ ²
			AB	Ab	aB	ab			
<i>spl₅-d₆</i>	Rep.	1	100 (100.9)	52 (47.6)	44 (47.6)	2 (2.0)	198	19.8±6.8	0.692
<i>spl₅-g</i>	Rep.	1	101 (101.0)	17 (16.1)	8 (8.5)	38 (37.1)	198	20.1±6.8	0.684
<i>spl₅-Rc</i>	coup.	1	135 (136.1)	17 (12.4)	8 (12.4)	38 (37.1)	198	13.5±2.6	3.298

Linkage group VI

M 45: It is characterized by a imperfect degeneration of a bract arising at the panicle base. However, its bract is not so large as that of neck leaf mutant governed by *nl* gene, of which bract is large enough to cover the panicles, but much the same as that of the heterozygous plants for *nl*. F₁ plants from the cross between M 45 and normal testers were completely normal. Then, a gene symbol for the character of M 45 is designated as *nl₂*, and thus *nl* should be altered hereafter as *nl₁*.

As shown in Table 9, the *nl₂* showed a linkage relation with *d₁* and its recombination value came to 20.9 %.

Table 9. F₂ segregation of *nl₂* and *d₁*.

Phase	No. of cross	Segregation mode				Total	Recombination value (%)	χ ²
		++	+ <i>d₁</i> 75	<i>nl₂</i> +	<i>nl₂</i> <i>d₁</i> 4			
Rep.	2	194 (192.1)	75 (89.9)	103 (89.9)	4 (4.1)	376	20.9±4.9	4.000

Linkage group VIII

M 36: It is a kind of chlorophyll mutants having zebra leaves, of which color is yellowish pale green. It appears more clearly in the stage from seedling to tillering. It has fine culm and inferior growth. A gene for the character is designated as *z₂*, because the F₁ hybrids between M 36 and another zebra leaf, *z*, manifest normal phenotype. Now, the *z* is altered as *z₁*.

A striking linkage relationship was observed in F₂ populations of a cross between M 36 and a tillering type dwarf, which originated from "Bunketsu-to" and was governed by a single recessive gene, *d₁* (see Table 3). A linkage intensity was given as 5.9 % from a segregation mode of *z₂* in the F₃ lines from F₂ plants having the phenotype of *z₂⁺ d₁*, though double recessive plants were not observed in the F₂ segregants (Table 10).

On the other hand, a linkage relation with recombination value of about 35 % was observed between *d₁* and *sp* (Table 11). Therefore, it is concluded that the *z₂* belongs to the linkage group VIII. Then the linkage intensities of *z₂-sp* were estimated from F₂, F₃ and their weighted mean at 41.5 %, 23.6 % and 35.7 %, respectively, showing indistinct linkage relation between them (Table 12).

Table 10. Segregations of z_2 and d_t in F_2 and F_3 .

Items		Segregation mode					Recombination value (%)	χ^2
Phase	No. of cross	++	+ d_t	z_2	+ z_2	d_t	Total	
F_2	Rep. 2	205 (201.5)	97 (100.8)	101 (100.8)	0 (0)	403	$\doteq 0$	0.201
F_3 from F_2 plants ($z_2^+ d_t$)		z_2 seg.		z_2 non-seg.		Total		
		9		72		81	5.9 ± 2.0	

Table 11. F_2 segregation of d_t and sp .

Phase	No. of cross	Segregation mode				Total	Recombination value (%)	χ^2
		++	+ sp	d_t +	d_t sp			
Rep.	2	199 (196.9)	79 (81.4)	82 (81.4)	11 (11.4)	371	35.0 ± 4.5	0.112

Table 12. Segregations of z_2 and sp in F_2 and F_3 .

Items		Segregation mode					Recombination value (%)	χ^2	
Phase	No. of cross	++	+ sp	z_2 +	z_2 sp	Total			
F_2	Rep. 4	427 (414.9)	161 (158.1)	146 (158.1)	30 (32.9)	764	41.5 ± 3.0	1.588	
F_3 from F_2 plants ($z_2^+ sp$)		z_2 seg.		z_2 non-seg.		Total			
		29		47		76	23.6 ± 4.3		
Weighted mean								35.7 ± 2.4	

The linkage relation between z_2 and z_1 was obscure.

Linkage group X

M 92: It is a dwarf form characterized by a extremely shortened top internode, and consequently the panicle emergence is more or less imperfect. The shape and length of panicle is rather normal.

A gene for this character is designated as d_{K-1} . As shown in Table 13, the linkage relationship with recombination value of 13.8 % was observed in the F_2 segregation of cross between d_{K-1} and bl_1 . However, significant linkages were not observed between d_{K-1} and two genes, d_w and gh .

M 11: It is featured with rather short height, imperfect emergence of panicles and especially its brittle or soft culm. The brittleness of culm and panicle axis of the mutant is, however, not so distinct as that of bc_1 and bc_2 genes described by Takahashi et al. (1967). Then, a gene for this character is

Table 13. Linkage relations between some genes newly described and marker genes belonging to the linkage group X.

Gene pair	Phase	No. of cross	Segregation mode in F ₂				Total	Recombination value (%)	χ^2
			AB	Ab	aB	ab			
$d_{K-1}-bl_1$	Rep.	2	326 (297.8)	128 (144.7)	134 (144.7)	2 (51.8)	590	13.8±4.0	5.618
$d_{K-1}-d_w$	Rep.	4	397 (398.1)	128 (123.2)	119 (123.2)	54 (56.6)	695	54.0±2.7	0.336
$d_{K-1}-gh_2$	Rep.	4	499 (490.8)	151 (160.9)	164 (160.9)	8 (56.8)	868	51.2±2.5	0.894
$d_{K-1}-bc_3$	Rep.	2	213 (198.5)	(99.3)	(99.3)	0 (0)	397	≐0	2.844
gh_3-bl_1	Rep.	1	92 (92.5)	45 (43.3)	42 (43.3)	2 (2.0)	181	20.9±7.1	0.108

designated as bc_3 .

In a total of 397 F₂ segregants from the cross between bc_3 and d_{K-1} , none of the double recessive plant was observed as shown in Table 13, suggesting a close linkage relation between them.

M 93: It has golden yellow colored hulls and internodes at maturity, and it is alike to the phenotypes of gh_1 belonging to the linkage group VI and gh_2 . A gene symbol of the character is designated as gh_3 .

The linkage relation was observed between gh_3 and bl_1 with a intensity of 20.9 % (Table 13), while it did not between gh_3 and bl_1 (Iwata and Omura, 1971b).

Therefore, it was proved that three genes, d_{K-1} , bc_3 and gh_3 , belong together to the linkage group X, though the sequence of these genes and others at the group is so far not established.

Linkage group XI

M 56: As it is characterized by many tillers with fine culm and normal

Table 14. Segregations of fc and ch in F₂ and F₃.

Items	Phase	No. of cross	Segregation mode				Total	Recombination value (%)	χ^2
			+ +	+ ch	fc +	$fc ch$			
F ₂	Rep.	4	400 (375.2)	160 (170.8)	159 (170.8)	9 (11.2)	728	24.8±3.4	3.570
F ₃ from F ₂ plants ($fc^+ ch$)			fc seg. 36		fc non-seg. 47		83	27.7±4.4	
F ₃ from F ₂ plants ($fc ch^+$)			ch seg. 37		ch non-seg. 47		84	28.2±4.5	
Weighted mean								26.5±2.3	

height, a gene for the character is designated as *fc*.

As shown in Table 14, the linkage relation was observed between *fc* and *ch*, and the recombination value was estimated from F_2 and F_3 . Namely, the value of 24.8 %, 27.7 % and 28.2 % were calculated from F_2 and F_3 from F_2 plants showing such phenotypes as *fc⁺ch* and *fc ch⁺* respectively, and thus weighted mean of 26.5 % was obtained.

On the other hand, a linkage relation was also found between *fc* and a virescent seedling mutant which had been introduced from Dr. N. E. Jodon. Although this virescent mutant is governed by a single recessive gene, v_1 , its linkage group had been unknown. The linkage intensities between *fc* and v_1 were, as shown in Table 15, calculated from F_2, F_3 and their weighted mean at 15.9 %, 19.5 % and 17.8 %, respectively. This fact shows that v_1 also belongs to the linkage group XI.

Table 15. Segregations of *fc* and v_1 in F_2 and F_3 .

Items		Segregation mode					Recombination value (%)	χ^2	
Phase	No. of cross	++	+ v_1	<i>fc</i> +	<i>fc v_1</i>	Total			
F_2	Rep.	4	340 (315.4)	140 (151.8)	140 (151.8)	3 (3.9)	623	15.9±3.9	3.961
	F_3 from F_2 plants (<i>fc v_1⁺</i>)		v_1 seg.		v_1 non-seg.		Total		
			29		60	89		19.5±3.6	
Weighted mean								17.8±2.6	

M 41: It is also characterized as well as M 114 (*spl₄*) and M 87 (*spl₅*) by a kind of physiological leaf spots, and named as *spl₃*. Although it is slightly different from *spl₅*, distributing smaller reddish brown spots over the whole surface of leaves, it is difficult to distinguish them. Also, it differs distinctly from *spl₁* and *spl₂*.

The linkage relationship was observed between *spl₃* and *dl*. The recombi-

Table 16. Segregations of *spl₃* and *dl* in F_2 and F_3 .

Items		Segregation mode					Recombination value (%)	χ^2	
Phase	No. of cross	++	+ <i>dl</i>	<i>spl₃</i> +	<i>spl₃ dl</i>	Total			
F_2	Rep.	6	680 (658.3)	301 (309.2)	297 (309.2)	12 (13.3)	1,290	20.3±2.7	1.541
	F_3 from F_2 plants (<i>spl₃ dl⁺</i>)		<i>dl</i> seg.		<i>dl</i> non-seg.		Total		
			35		52	87		25.2±4.1	
Weighted mean								21.7±2.2	

nation values of *spl₃-dl* were estimated at 20.3 % from F₂, 25.2 % from F₃, and thus their weighted mean of 21.7 % (Table 16).

In order to know the sequence of four genes, *fc*, *spl₃*, *dl* and *ch*, in the linkage group XI, the linkage intensities among each genes were calculated from F₂ data. As shown in Table 17, the linkage intensities of *fc-dl*, *spl₃-fc* and *spl₃-ch* were 44.3 %, 43.4% and 47.4 %, respectively. In addition, a non-linkage relationship was known already between *dl* and *ch* (Iwata and Omura, 1971a). Consequently, the sequence of genes at the linkage group is probably *dl-spl₃-fc-ch* or *spl₃-dl-fc-ch*.

Table 17. Another linkage relation of genes belonging to the linkage group XI.

Gene pair	Phase	No. of cross	Segregation mode				Total	Recombination value (%)	χ^2
			AB	Ab	aB	ab			
<i>fc-dl</i>	Rep.	5	514 (494.7)	174 (181.1) 76	174 (181.1) 88	39 (44.2) 20	901	44.3±2.7	1.921
<i>spl₃-fc</i>	Rep.	2	210 (215.6)	95 (79.9)	99 (79.9)	27 (18.6)	394	43.4±4.0	1.262
<i>spl₃-ch</i>	Rep.	2	289 (283.6)	98 (98.9)	99 (98.9)	27 (28.6)	510	47.4±3.4	0.346

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