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

Iwata, Nobuo Laboratory of Plant Breeding, Faculty of Agriculture, Kyushu University

Omura, Takeshi Laboratory of Plant Breeding, Faculty of Agriculture, Kyushu University

https://doi.org/10.5109/23492

出版情報:九州大学大学院農学研究院紀要. 21 (2/3), pp.117-127, 1977-03. Kyushu University バージョン: 権利関係: J. Fac. Agr., Kyushu Univ., 21, 117-127 (1977)

Linkage Studies in Rice (Oryza sativa L.)

On Some Mutants Derived from Chronic Gamma Irradiation

Nobuo Iwata and Takeshi Omura

Laboratory of Plant Breeding, Faculty of Agriculture, Kyushu University 46-01, Fukuoka 812

(Received December 6, 1976)

Thirteen of the mutant genes induced by gamma irradiation and two of the **sponta**neous 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 $(d_s, spontaneous)$. Group X; dwarf (d_{K-1}) , brittle culm 3 (bc_s) 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 handred 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 F_2 . When the linkage was detected, the recombination value was estimated from the segregations in F_2 and in some cases in F_3 progenies by the method of maximum likelihood.

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

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

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

Linkage group	Gene symbol	Character	Reference
I	dp_1	depressed palea 1 chromogen for anthocyanin	Nagamatsu and Omura (1962) Nagao and Takahashi (1963)
II	lg	liguleless	Nagao and Takahashi (1963)
III	A	anthocyanin activator	Nagao and Takahashi (1963)
IV	d ₆ g Rc	lop-leaved type dwarf long empty glumes brown pericarp	Nagao and Takahashi (1963) Nagao and Takahashi (1963) Nagao and Takahashi (1963)
VI	d_1	Daikoku type dwarf	Nagao and Takahashi (1963)
VIII	sp z	short panicle zebra leaf	Iwata and Omura (1971a) Iwata and Omura (1975)
X	$bl_1 \\ d_{\psi} \\ gh_2$	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	ch dl	chlorina drooping leaf	Iwata and Omura (1971b) Iwata and Omura (1971b)

RESULTS AND DISCUSSION

 F_1 plants of all cross combinations between mutant stocks and linkage testers had normal phenotype. The F_2 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

Mutant		χ² for		
lines	Dominant	Recessive	Total	3:1
M 11 M 36 M 41 M 45 M 50 M 56 M 87 M 92 M 93 M 100 M 114 HO 568"	$\begin{array}{c} 887\\ 1,310\\ 2,489\\ 2,183\\ 1,488\\ 2,564\\ 1,118\\ 3,293\\ 657\\ 1,861\\ 772\\ 1,679\\ 0,54\end{array}$	$\begin{array}{c} 270 \\ 413 \\ 812 \\ 734 \\ 448 \\ 804 \\ 341 \\ 1,051 \\ 214 \\ 572 \\ 259 \\ 523 \\ 952$	$\begin{array}{c} 1,157\\ 1,723\\ 3,301\\ 2,917\\ 1,936\\ 3,368\\ 1,459\\ 4,344\\ 871\\ 2,433\\ 1,031\\ 2,202\\ 4,922\\ 2,20$	$\begin{array}{c} 1.708\\ 0.975\\ 0.284\\ 0.041\\ 3.570\\ 2.287\\ 2.062\\ 1.504\\ 0.086\\ 2.881\\ 0.008\\ 1.832\\ \end{array}$

Table 3. F_2 segregation mode in crosses between mutant stocks and normal forms, indicating that each of the mutant characters is governed by single recessive gene.

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 F_2 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 F_3 lines from F_2 plants showing such phenotypes as $spl_4 + dp_1$ and $spl_4 dp_1^*$.

	Items			Segregati	ion mode	•		Recombination value (%)	$\chi^{2^{1)}}$
F	P h a s	e No. (cross	$^{of}++$	$+ dp_1$	<i>spl</i> ₄ + ,	$spl_4 dp_1$	Total		
Гэ	Rep.	4	205 (214.5)	102 (107.3)	122 (107.3)	0 (0)	429	÷0	2.664
F ₃ f	F_3 from F_2 plants		spl ₄ seg.		<i>spl</i> 4 no	n-seg.	Total		
	(<i>spl</i> ₄ +	dp_1)	1		59		60	0.8 ± 0.8	
F ₃ f	F_3 from F_2 plants		dp_1 seg.		dp_1 non-seg.		Total		
	$(spl_4 dp_1^+)$		Ę	ō	7	'1	76	3.4 <u>+</u> 1.5	
Wei	ighted n	nean						1.4 ± 0.7	

Table 4. Segregations of spl_4 and dp_1 in F_2 and F_3 .

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 F_2 and F_3 data (Table 5).

	Items			Segregation mode						Recombination value (%)	χ^2
	Phase	No. cross	of	++	+	⊦ lg	$nal_1 +$	nal ₁ lg	Total		
F ₂	Rep.	11	1 (1	, 229 , 220.	6) (6	32 04.2)	568 (604.2)	4 (4.1)	2,433	8.2 <u>+</u> 2.0	3.508
\mathbf{F}_{3}	from F2 p	lants		nal	seg.		nal ₁ n	on-seg.	Total		
	(nal_{1}^{+})	lg)			35		1	74	209	9.1 <u>+</u> 1.5	
F_3	from F2 p	lants		lg	g seg	£	lg non	-seg.	Total		
	$(nal_1 l_2)$	g+)			41		16	8	209	10.9±1.7	
W	/eighted m	lean								9. 5 <u>+</u> 1.0	

Table 5. Segregations of nal_1 and lg in F_2 and F_3 .

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 F_2 as shown in Table 6. So, gene symbols are given as **ylm** for yel-

Cono pair	Phase	No. of		Segrega	Recombination	o./2			
Gene pair		cross	AB	Ab	аB	ab	Total	value (%)	x-
ylm-lg	Rep.	3	$(196 \\ (197.0)$	98 (97. 0)	97 (97. (1 0) (1. 0)	392	10.0 ± 5.0	0.015
rk ₁ -lg	Rep.	3	$197 \\ (208.1)$	85 64 . 9)	96 252 0	14 (12 1) (46	392	35.1 <u>+</u> 4.4	2.086
ylm-rk ₁	coup.	3	230 (237.9)	(56. 1)	(56.1) (41.9)	392	34.7t3.1	2.076

Table 6. F_2 segregation of M 88 (*rk*,, *ylm*) and *lg*.

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lowish leaf margin and **rk**, for round kernels. Both *ylm* and **rk**, linked with lg. The recombination values of *ylm-lg*, rk_1 -*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 rl_2 is used as a gene symbol of the character.

The joint segregation of semi-rolled leaf and colored apiculus was examined in the F_2 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 F_2 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 rl_2 was not proved.

NT C -	Segregation mode ¹⁾							
Phase No. of cross		colored ap). r	on-color	ed ap.	Tatal	Recombination	χ^{2}
,	-	+ /	$\cdot l_2$	t	rl_2	Total		
coup.	3	198 (192.2) (25.	104 5) (98.0	64)) (71.3)	387	19.5 <u>±</u> 3.3	2.084

Table 7. F_2 segregation of rl_2 and apiculus color.

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 nal_2, d_B and spl_1 (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 (spl_4). A gene for this leaf spots is designated as spl_5 .

The linkage relations were found in F_2 of crosses between the **spl**, and such three genes as d_6 , **g** and **Rc**. From the F_2 data shown in Table 8, the recombination values of spl_5-d_6 , spl_5-g and spl_5-Rc were estimated at 19.8%, 20.1% and 13.5%, respectively. The arrangement of d_6 -g-Rc on the group have previously been confirmed from numerous F_2 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 d_6 -g-spl_5-Rc.

Cono pair	Dhasa	No. of	S	egregatio	on mode	Recombination			
	1 mase	cross	AB	Ab	aB	ab	Total	value	(%) ^x
spl_5-d_6	Rep.	1	$100 \\ (100.9)$	52) 51⁴7. (6) $\frac{44}{44}$ 7.6	$)_{1}^{2}$ a	198	19.8 <u>+</u> 6.8	0.692
spl ₅ -g	Rep.	1	101 (101.0)	(47. 17 ⁵⁾	(47. 8 ⁵⁾	(2.0) 38	198	20.1 ± 6.8	0.684
spl ₅ -Rc	coup.	1	$ \begin{array}{r} 135 \\ (136.1) \end{array} $	(12.4)	(12.4)	(37.1)	198	13.5 <u>+</u> 2.6	3.298

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

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 nl_2 , and thus nl should be altered hereafter as nl_1 .

As shown in Table 9, the nl_2 showed a linkage relation with d_1 and its recombination value came to 20.9 %.

Table 9.	F_2	segregation	of nl	and and	d_1 .
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No. of	No. of	Segregation mode					Recombination	ou ²
Fnase	cross	++	$+ d_1$	$nl_2 +$	$nl_2 d_1$	Total	value (%)	X
Rep.	2	$\underset{(192.1)}{\overset{194}{}}$	(89. 9)	103 (89.9)	(4. 1)	376	20.9 <u>+</u> 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 z_2 , because the F_1 hybrids between M 36 and another zebra leaf, z, manifest normal phenotype. Now, the z is altered as z_1 .

A striking linkage relationship was observed in F_2 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, d_t (see Table 3). A linkage intensity was given as 5.9 % from a segregation mode of z_2 in the F_3 lines from F_2 plants having the phenotype of $z_2^+ d_t$, though double recessive plants were not observed in the F_2 segregants (Table 10).

On the other hand, a linkage relation with recombination value of about 35 % was observed between d_t and sp (Table 11). Therefore, it is concluded that the z_2 belongs to the linkage group VIII. Then the linkage intensities of z_2 -sp were estimated from F_2 , F_3 and their weighted mean at 41.5 %, 23.6 % and 35.7 %, respectively, showing indistinct linkage relation between them (Table 12).

	Items		Seg	regation mod	e	I	Recombination value (%)	χ^2
F	Phase	No. of cross	++ +	$d_t z_2 +$	$z_2 d_t$	Total		
Г2	Rep.	2	205 (201.5)	97 101 (100.8) (100.8	0 3) (0)	403	. €0	0.201
$\mathbf{F_3}$ t	from F ₂	plants	z_2 seg.	Z ₂ non-seg	<u>g</u> .	Total		
	$(z_2^+ a)$	d_t)	9	72		81	5.9±2.0	
			Table 11.	F2 segregati	on of c	d_t and sp .		
DI	No. 0	f	Seg	gregation mod	e		Recombination	
Phas	e cross	* +-	+ + <i>sp</i>	d_t +	$d_t sp$	Total	value (%)	χ²
Rep.	2	199 (196.	79 (81. 4)	82 (81. 4)	11 (11 . 4)	371	35.0 <u>±</u> 4.5	0.112
		Ta	ble 12. Seg	regations of	z_2 and z_2	sp in F ₂ a	und F ₃ .	
	Items	Ta	ble 12. Seg S	regations of	z₂ and and a solution	sp in F ₂ a	nd F3. Recombination value (%)	χ^2
	Items Phase	Ta No. of cross	ble 12. Seg S ++ -	Tregations of Gegregation model $+ sp = z_2 + z_2$	z_2 and z_2 and z_2 sp	sp in F ₂ a	nd F ₃ . Recombination value (%)	χ²
F ₂	Items Phase Rep.	Ta No. of cross 4	ble 12. Seg S ++ - 427 (414.9) (regations of Gegregation mo + <i>sp z</i> ₂ + 161 146 158.1) (158.1	z_2 and z_2 and z_2 sp $z_2 sp$ (32)	sp in F ₂ a 7 Total 9)	nnd F ₃ . Recombination value (%) 41.5±3.0	X ² 1.588
F ₂	Items Phase Rep. from F ₂	Ta No. of cross 4 plants	ble 12. Seg S ++ - (414.9) (<i>z</i> ₂ seg.	aregations of degregation model + sp z_2 161 146 158.1) (158.1) z_2 non-state	z_2 and z_2 ode $z_2 sp$ 30 - (32.) 30 - (32.)	sp in F ₂ a 7 Total 764 70tal	nd F ₃ . Recombination value (%) 41.5 <u>+</u> 3.0	χ² 1.588
F ₂ F ₃	Items Phase Rep. from F_2 $(z_2^+ s_2)$	No. of cross 4 plants	ble 12. Seg S ++ - (414.9) (22 seg. 29	aregations of degregation model + sp z_2 161 146 158.1) (158.1) z_2 non-s 42	z_2 and z_2 sp z_2 sp (32. sp) (32. sp)	sp in F ₂ a Total 764 764 764	nd F ₃ . Recombination value (%) 41.5±3.0 23.6±4.3	x ² 1.588

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

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

Gene pair Phase		No. of		Segrega	Recombination	· · 2			
		cross	AB	Ab	aB	ab	Total	value (%	5) ^x
$d_{K-1}-bl_1$	Rep.	2	326 (297.8)	128 (144.7)	134 (144.7)	(2.51^{2})	590	13.8 <u>+</u> 4.0	5.618
$d_{K-1} - d_W$	Rep.	4	397 (398.1)	128 (123.2)	119 (123.2)	(50. 54 6)	695	54.0 <u>+</u> 2.7	0.336
d_{K-1} - gh_2	Rep.	4	499 (490.8)	151 (186 2)	164 (<u>168</u> 2)	(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

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

designated as bc,.

In a total of 397 F_2 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_1 .

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, 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

Items				Segregat	tion mode	Recombination χ^2 value (%)		
	F	Phase No. of cross		+ + + ch	fc + fc ch	Total		
r	Γ ₂	Rep.	4	400 160 (375.2) (170.8)	159 (11. (170.8) 2)	728	24.8 <u>+</u> 3.4	3.570
F ₃ fr		rom F₂ p	lants	fc seg.	fc non-seg.	Total		
_	$(fc^+ ch)$			36	47	83	27.7 <u>+</u> 4.4	
	F_3 from F_2 plants			ch seg.	ch non-seg.	Total		
		$(fc \ ch^+)$		37	47	84	28.2±4.5	
Weighted mean			ean				26.5 <u>+</u> 2.3	

Table 14. Segregations of fc and ch in F_2 and F_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.

	Items		Segregat	ion mode	Recombinatio value (%)	$n \chi^2$				
F	Phase	No. of cross	$++$ + ν_1	$fc + fc v_1$	Total					
F ₂	Rep.	4	340 140 (315.4) (151.8)	$\begin{array}{ccc} 140 & 3\\ (151.8) & (3.9) \end{array}$	623	15.9 <u>+</u> 3.9	3.961			
F_3 from F_2 plants			v_1 seg.	v_1 non-seg.	Total					
_	$(fc v_1^+)$		29	60	89	19.5 <u>+</u> 3.6				
Weighted mean						17.8 <u>+</u> 2.6				

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

M 41: It is also characterized as well as M 114 (spl_4) and M 87 (spl_5) by a kind of physiological leaf spots, and named as spl_3 . Although it is slightly different from spl_5 , distributing smaller reddish brown spots over the whole surface of leaves, it is difficult to distinguish them. Also, it differs distinctly from spl_1 and spl_2 .

The linkage relationship was observed between spl_3 and dl. The recombi-

Items			Segregation mode				Recombination χ^2 value (%)		
n	Phase	No. of cross	++	+ dl	$spl_3 +$	spl ₃ dl	Total		
Γ 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 (spl ₃ dl ⁺)			dl seg.		dl non-seg.		Total		
			35		52		87	25.2 <u>+</u> 4.1	
Weighted mean								21.7±2.2	

Table 16. Segregations of spl_3 and al in F_2 and F_3 .

nation values of spl_3 -dl were estimated at 20.3 % from F_2 , 25.2 % from F_3 , and thus their weighted mean of 21.7 % (Table 16).

In order to know the sequence of four genes, fc, spl_3, dl and ch, in the linkage group XI, the linkage intensities among each genes were calculated from F_2 data. As shown in Table 17, the linkage intensities of fc-dl, spl_3-fc and spl_3-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 $dl-spl_3-fc-ch$ or $spl_3-dl-fc-ch$.

Conon	air Dhaca	No. of cross	Segregation mode					Recombination	n
Gene p	all Fllase		AB	Ab	аB	ab	Total	value (%)	(%) ^{X*}
fc-dl	Rep.	5	514 (494.7)	$174 \\ (181 1) \\ 76 $	174 (181 1)	$(44. 20)^{2}$	901	44.3 <u>+</u> 2.7	1.921
spl ₃ -fc	Rep.	2	210 (215.6)	(7 9. 9) 95	(79.9) 99	(18.6) 27	394	43. 4±4.0	1.262
spl ₃ -ch	Rep.	2	289 (283.6)	(98.9)	(98,9)	(28.6)	510	47.4±3.4	0.346

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

ACKNOWLEDGEMENT

The authors are grateful to Dr. S. Tanaka for his kind supply of the mutant stocks.

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