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<https://doi.org/10.5109/23681>

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出版情報 : 九州大学大学院農学研究院紀要. 23 (1/2), pp.85-93, 1978-10. Kyushu University  
バージョン :  
権利関係 :



## **Linkage Studies in Rice (*Oryza sativa* L.) On Some Virescent and Chlorina Mutants**

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(Received August 2, 1978)

Linkage analyses on five virescent and four chlorina mutants were carried out. Six of these mutants,  $v_1, v_2, v_5, ch_1, ch_2$  and  $ch_3$ , were found to belong to the eleventh linkage group. Also, it was found that  $v_3$  and  $ch$ , belonged to the first linkage group, and  $v_4$  to the eighth group. The sequences of the genes in respective linkage groups were made clear, though a few of the loci were undetermined.

### **INTRODUCTION**

Various kinds of chlorophyll mutants are known in rice, however, only a few of the linkage studies on the mutants had been made (Jodon, 1940; Nagao and Takahashi, 1960; Nagamatsu and Omura, 1962) before the authors reported some of them (Iwata and Omura, 1971, 1975, 1978). Most of the chlorophyll mutants are modified their character manifestation by environmental conditions, being clearly distinguishable from the normal in certain conditions but indistinguishable in other conditions. Therefore, the mutants are usable in linkage analysis, when the conditions suitable to character manifestation of the mutants are known.

Recently, many chlorophyll mutants have been obtained, then the authors are carrying on the studies on their character manifestation as shown in some papers (Omura and Tanaka, 1959; Omura *et al.*, 1977; Satoh *et al.*, 1977) on the one hand, and their linkage analyses on the other hand. The present paper described the results of linkage analyses on some of the virescent and chlorina mutants.

### **MATERIALS AND METHODS**

The materials used were five virescent seedlings,  $v_1, v_2, v_3, v_4$  and  $v_5$ , and four chlorina,  $ch_1, ch_2, ch_3$  and  $ch_4$ .

The virescent mutants sprout out white leaves under low temperature condition, but pale green or nearly normal green leaves under high temperature condition, though the mutants have different threshold temperature for chlorophyll accumulation. Contrary, the chlorina mutants sprout out yellowish green leaves, their typical characteristics, under high temperature condition. Their main characteristics and sources are as follows.

$v_1$ : The threshold temperature is 22°C (Omura et al., 1977). When it is sown in late May, ordinary sowing time in Fukuoka, young seedlings are almost whole white but leaves emerging at or after transplanting are pale green with white midrib. Emerging panicles are white in color. It was introduced from Dr. Jodon of U. S. Department of Agriculture.

$v_2$ : The threshold temperature is about 20°C. Differing from  $v_1$ , midrib and panicles are not white but green. Other characteristics are almost the same as  $v_1$ . A spontaneous mutant from a Japanese cultivar "Yaeho".

$v_3$ : The threshold temperature is about 30°C. An induced mutant from a Japanese cultivar "Kinmaze" by *N*-nitroso-*N*-methylurea treatment.

$v_4$ : The threshold temperature is not examined. It is an induced mutant from "Norin 8" by irradiation and introduced from Division of Genetics, National Institute of Agricultural Science (LT 3).

$v_5$ : Except the threshold temperature is probably higher than  $v_3$ , it resembles  $v_3$  in other characteristics. An induced mutant from "Kinmaze" as same as  $v_3$ .

$ch$ : When it is sown in late May, the distinction from the normal seedling is rather difficult, but after transplanting the chlorina character of yellowish green leaves is clearly manifested. A spontaneous mutant stocked in our laboratory (HO 718-721).

$ch_2$ : Leaves of young seedling exhibit orange in color but leaves emerging thereafter are yellowish pale green and finally green (LT 4). The same source as  $v_4$ .

$ch_3$ : It manifested yellowish pale green leaves at just before heading. A spontaneous mutant stocked in our laboratory (HO 717).

$ch_4$ : It is characterized by yellowish green leaves at tillering stage and by fewer culm and somewhat lower viability than the normal. It was induced in gamma field and introduced from Institute of Radiation Breeding, National Institute of Agricultural Science (No. 646).

Linkage was detected in  $F_2$  by the trisomic and conventional methods. Trisomics used were some types described by Iwata and Omura (1975). Marker genes used in conventional method are listed in Table 1. Recombination

**Table 1.** List of marker genes used and their linkage groups.

Linkage group	Gene symbol	Character	Reference
I	<i>wx</i>	waxy endosperm	Nagamatsu and Omura (1962)
	<i>dp_1</i>	depressed palea 1	"
	<i>C</i>	chromogen for anthocyanin	"
	<i>ws</i>	white striped leaf	"
	<i>Cl</i>	clustered spikelets	Nagao and Takahashi (1963)
VIII	<i>la</i>	lazy	Iwata and Omura (1971)
	<i>sp</i>	short panicle	"
XI	<i>ch_1</i>	chlorina 1	"
	<i>fc</i>	fine culm, tillering	Iwata and Omura (1977)
	<i>bc_1</i>	brittle culm 1	Iwata and Omura (1971)
	<i>dl</i>	drooping leaf	"

$$u = (a + b) / 3(c + d) .$$

Gene pair	Items			Segregation mode				Recombination value (%)	$\chi^2_{(3)}$
	Phase	No. of	++	+fc	ch, +	ch <sub>2</sub> fc	Total		
<i>ch<sub>1</sub>-fc</i>	F <sub>2</sub> Coup.	4	461 (469.9)	90 (98.6)	111 (98.6)	96 (90.14)	758	30.8±2.1	2.763
	Rep.	6	587 (556.3)	246 (253.0)	232 (253.0)	16 (8)	1,079	24.9±2.8	4.087
	F <sub>3</sub> from F <sub>2</sub> plants			Seg.	Non-seg.		Total		
	<i>(ch<sub>1</sub><sup>+</sup> fc)</i>			37	47		84	28.2±4.5	
	<i>(ch<sub>1</sub> fc<sup>+</sup>)</i>			36	47		83	27.7±4.4	
	Weighted mean							28.5±1.5	
<i>ch<sub>2</sub>-bc</i>	Phase	No. of	AB	Ab	aB	ab	Total		
	F <sub>2</sub> Coup.	2	413 (404.1)	135 (144.2)	147 (144.2)	36 (38.6)	731	54.1±2.9	1.008
	Rep.	3	419 (425.5)	131 (146.8)	167 (146.8)	46 (0)	763	48.0±2.8	4.675
	Weighted mean							50.9±2.0	
	<i>ch<sub>1</sub>-dl</i>	F <sub>2</sub> Rep.	4	628 (629.5)	204 (215.0)	227 (215.0)	67 (66.5)	1,126	48.6±2.3
<i>fc-bc</i>	F <sub>2</sub> Coup.	1	119 (109.7)	22 (26.8)	27 (26.8)	14 (18.7)	182	35.8±4.6	2.829
	Rep.	7	751 (702.0)	258 (282.7)	268 (282.7)	36 (45.5)	1,313	37.2±2.3	8.339
	Weighted mean							37.0±2.1	
	<i>fc-dl</i>	F <sub>2</sub> Rep.	9	1,014 (970.4)	324 (346.6)	338 (346.6)	80 (92.4)	1,756	45.9±1.9
<i>bc<sub>1</sub>-dl</i>	F <sub>2</sub> Coup.	18	2,335 (2,283.0)	641 (648.8)	627 (648.8)	306 (328.5)	3,909	42.0±1.1	3.547
	Rep.	4	647 (616.1)	204 (207.4)	190 (207.4)	67 (1)	1,098	49.4±2.3	4.586
	Weighted mean							43.4±1.0	

## RESULTS AND DISCUSSION

As it was found that *ch*, belonged to the eleventh linkage group by the translocation method (Iwata and Omura, 1971), it was used as one of the marker genes of this group. The interrelation of the marker genes are shown in Table 2. The sequence of *ch*<sub>1</sub>—*fc*—*bc*<sub>1</sub>—*dl* is suggested from respective recombination values, though that of *bc*<sub>1</sub>—*dl*—*ch*<sub>1</sub> was previously reported (Iwata and Omura, 1971). The recombination values of *v*<sub>1</sub>—*fc* and *v*<sub>1</sub>—*bc*<sub>1</sub> were both 17.9 % (Table 3), and that of *fc*—*bc*, was 37.0 % (Table 2). Consequent-

Table 3. Linkage relations between *v*<sub>1</sub> and genes belonging to the eleventh linkage group.

Gene pair	Items		Segregation mode					Recombination value (%)	$\chi^2_{(3)}$
	Phase	No. of cross	++	+ <i>fc</i>	<i>v</i> <sub>1</sub> +	<i>v</i> <sub>1</sub> <i>fc</i>	Total		
<i>v</i> <sub>1</sub> - <i>fc</i>	F <sub>2</sub> Rep.	4	340 (315.4)	140 (151.8)	140 (151.8)	3 (3.9)	623	15.9±3.9	3.916
	F <sub>3</sub> from F <sub>2</sub> plants		Seg.		Non-seg.		Total		
	( <i>v</i> <sub>1</sub> + <i>fc</i> )		29		60		89	19.5±3.5	
	Weighted mean							17.9±2.7	
<i>v</i> <sub>1</sub> - <i>bc</i> <sub>1</sub>	Phase	No. of cross	++	+ <i>bc</i> <sub>1</sub>	<i>v</i> <sub>1</sub> +	<i>v</i> <sub>1</sub> <i>bc</i> <sub>1</sub>	Total		6.886
	F <sub>2</sub> Rep.	3	353 (320.8)	142 (154.0)	135 (154.0)	3 (4.3)	633	16.5±3.8	
	F <sub>3</sub> from F <sub>2</sub> plants		Seg.		Non-seg.		Total		
	( <i>v</i> <sub>1</sub> + <i>bc</i> <sub>1</sub> )		27		57		84	19.1±3.6	
	Weighted mean							17.9±2.6	

Table 4. Linkage relations between *v*<sub>2</sub> and genes belonging to the eleventh linkage group.

Gene pair	Phase	No. of cross	Segregation mode in F <sub>2</sub>					Recombination value (%)	$\chi^2_{(3)}$
			AB	Ab	aB	ab	Total		
<i>v</i> <sub>2</sub> — <i>bc</i> <sub>1</sub>	coup.	15	1,952 (1,910.0)	396 (397.7)	382 (397.7)	347 (371.5)	3,077	30.5±1.0	3.171
	Rep.	3	388 (359.6)	151 (169.9)	162 (169.9)	6 (6.6)	706	19.3±3.6	5.103
	Weighted mean								29.7±1.0
<i>v</i> <sub>2</sub> — <i>dl</i>	coup.	11	1,411 (1,388.5)	244 (245.0)	238 (245.0)	285 (299.5)	2,178	25.8±1.1	1.271
	Rep.	9	1,142 (1,118.9)	474 (501.9)	509 (501.9)	38 (4)	2,161	26.7±2.1	2.274
	Weighted mean								26.0±1.0

Table 5. Linkage relation between  $v_5$  and  $ch_1$  belonging to the eleventh linkage group.

Items		Segregation mode					Recombination value (%)
Phase	No. of cross	+ +	+ $ch_1$	$v_5$ +	$v_5 ch_1$	Total	
F <sub>2</sub> Rep.	2	193	93	59	0	345	$\div 0$
F <sub>3</sub> from F <sub>2</sub> plants		Seg.	Non-seg.			Total	
$(v_5^+ ch_1^-)$		3	83			86	1.8±1.0
$(v_5^- ch_1^+)$		2	35			37	2.8±2.0
Weighted mean							2.0±0.9

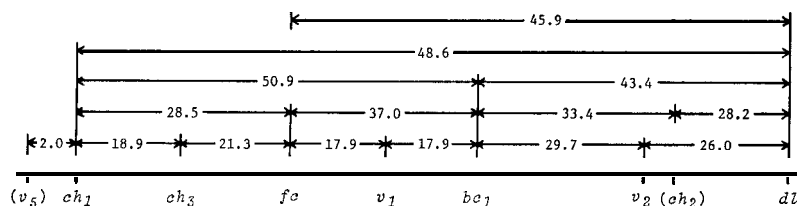
Table 6. Linkage relations between two genes,  $ch$ , and  $ch_1$ , newly described and marker genes belonging to the eleventh linkage group.

Gene pair	Phase	No. of cross	Segregation mode in F <sub>2</sub>					Recombination value (%)	$\chi^2_{33}$
			AB	Ab	aB	ab	Total		
$ch_2-bc_1$	Rep.	2	212 (201.6)	92 (84.9)	69 (84.9)	9 (10.6)	382	$33.4 \pm 4.5$	4.350
$ch_2-v_2$	Rep.	2	175	106	101	0	382	$\div 0$	
$ch_2-dl$	Rep.	3	303 (305.7)	139 (135.3)	134 (135.3)	0 (0)	588	$28.2 \pm 3.7$	0.145
$ch_3-ch_1$	Rep.	2	181 (178.6)	84 (84.6)	84 (84.6)	3 (3.1)	351	$18.9 \pm 5.1$	2.199
$ch_3-fc$	coup.	2	220 (227.4)	35 (35.8)	39 (35.8)	57 (51.9)	351	$23.1 \pm 2.6$	1.039
	Rep.	2	193 (188.2)	93 (90.8)	84 (90.8)	2 (2.2)	372	$15.2 \pm 4.9$	0.703
Weighted mean								$21.3 \pm 2.3$	

ly, it is concluded that  $v_1$  is located between  $fc$  and  $bc_1$ . Jodon (1940) found that a virescent gene ( $v$ ) linked with  $gu$  ( $wx$  in our symbol),  $as$  ( $C$ ) and  $Cl$ . This fact indicates that  $v$  belongs to the first linkage group, however, Takahashi and Morimura (1968) could not find the linkage relations, using a virescent gene introduced from Dr. Jodon. It is uncertain whether  $v_1$  is identical with  $v$  or not, though  $v_1$  is also introduced from Dr. Jodon.

Two virescent genes,  $v_2$  and  $v_5$ , were found to belong to this group. The recombination values of  $v_2-bc_1$  and  $v_2-dl$  were 29.7 and 26.0 %, respectively (Table 4). Then, the sequence of  $bc_1-v_2-dl$  is reliable. The recombination value of  $v_5-ch_1$  was calculated in F<sub>3</sub> from two kinds of singly dominant F<sub>2</sub> at 2.0% (Table 5). This value shows that  $v_5$  is located near by  $ch_1$ .

Two chlorina genes,  $ch$ , and  $ch_1$ , belonged also to this group. The recombination values of  $ch_2-bc_1$  and  $ch_2-dl$  were estimated at 33.4 and 28.2 %, respectively (Table 6). The recombination value of 43.4 % have already been obtained between  $bc_1$  and  $dl$  (Table 2). From these results, the sequence of  $bc_1-ch_2-dl$  was confirmed.



**Fig. 1.** Sequence of the nine genes at the eleventh linkage group.

Table 7. Linkage relations between  $v_3$  and genes belonging to the first linkage group.

Gene pair	Items		Segregation mode						Recombination value (%)	$\chi^2_{(3)}$
	Phase	No. of cross	++	$+dp_1$	$v_3+$	$v_3dp_1$	Total			
$v_3-dp_1$	F <sub>2</sub> Rep.	1	192 (183.3)	85 (88.2)	83 (88.2)	2 (2.3)	362	16.0±5.1	0.874	
	F <sub>3</sub> from F <sub>2</sub> plants		Seg.	Non-seg.		Total				
	$(v_3^+ dp_1)$		19	61		80	13.5±3.1			
	$(v_3 dp_1^+)$		1	25		26	2.0±2.0			
	Weighted mean		6.3±1.6							
$v_3-wx$	Phase	No. of cross	+		$v_3$		Total			
			++	wx	wxwx	++	wx	wxwx		
	F <sub>2</sub> Rep.	1	12	92	40	39	4	0	187	8.6±2.1
	F <sub>3</sub> from F <sub>2</sub> plants		Seg.	Non-seg.		Total				
	$(wx v_3^+)$		9	29		38	13.4±4.4			
Weighted mean		9.5±1.9								
$v_3-C$	Phase	No. of cross	AB	Ab	aB	ab	Total			
	F <sub>2</sub> Coup.	2	246 (254.3)	31 (23.7)	20 (30.7)	75 (68.1)	372	14.3±2.0	3.430	
$v_3-Cl$	F <sub>2</sub> Coup.	1	113 (102.5)	(29.5)	(29.5)	(14.5)	176	42.7±5.2		3.915

The close linkage relation was observed between  $ch_2$  and  $v_2$ , however, the recombination value was not calculated, because none of the doubly recessive plant was segregated in F<sub>2</sub> in repulsion phase (Table 6). As mentioned above,  $v_2$  was also located between  $bc$ , and  $dl$ , therefore, the loci of  $ch$ , and  $v_2$  should be adjacent each other, although accurate distance of them is so far uncertain. The recombination values of 18.9 and 21.3 % were calculated in  $ch_3-ch_1$  and  $ch_3-fc$ , respectively (Table 6). As the value of  $ch_1-fc$  was 28.5 % (Table 2),  $ch$ , is located between  $ch_1$  and  $fc$ . Based on these results, the sequence of the nine genes at the eleventh linkage group is tentatively drawn

as shown in Fig. 1.

The other virescent gene ( $v_3$ ) linked with marker genes of the first linkage group (Table 7). The recombination values between  $v_3$  and  $wx$ ,  $dp_1$ ,  $C$  and

Table 8. Trisomic segregation of  $ch_4$  in  $F_2$  of a cross with B type of trisomics.

Portion of population	Observed number			$\chi^2$	
	Dominant	Recessive	Total	Disomic 3 : 1	Trisomic
					$\frac{8:1}{\text{for } 2x}$ $\frac{44:1}{\text{for } 2x+1}$
2x	139	1	84		<b>0.596</b>
2x+1	83	15	237		<b>0.412</b>
Total	222			44.063***	

\*\*\* Significant at 0.1% level.

Table 9. Linkage relations between  $ch_4$  and genes belonging to the first linkage group.

Gene pair	Items		Segregation mode				Recombination value (%)	$\chi^2_{(3)}$	
	Phase	No. of cross	AB	Ab	aB	ab			Total
<i>ch<sub>4</sub>-dp<sub>1</sub></i>	F <sub>2</sub> Rep.	4	506 (497.1)	203 (189.9)	170 (189.9)	37 (39.1)	916	41.3±2.7	3.261
<i>ch<sub>4</sub>-C</i>	F <sub>2</sub> Coup.	1	106 (111.3)	36 (26.7)	20 (26.7)	22 (19.3)	184	35.3±4.6	5.549
<i>ch<sub>4</sub>-ws</i>	Phase	No. of cross	++	+ws	<i>ch<sub>4</sub>+</i>	<i>ch<sub>4</sub>ws</i>	Total		
	F <sub>2</sub> Rep.	4	418 (416.9)	189 (190.1)	142 (141.9)	9 (9.1)	758	24.5±3.4	0.010
	F <sub>3</sub> from F <sub>2</sub> plants		Seg.	Non-seg.		Total			
	<i>(ch<sub>4</sub>+ws)</i>		37	115		152		13.9±2.3	
	Weighted mean								17.2±1.9
<i>ch<sub>4</sub>-Cl</i>	Phase	No. of cross	+Cl	++	<i>ch<sub>4</sub>Cl</i>	<i>ch<sub>4</sub>+</i>	Total		
	F <sub>2</sub> Coup.	2	244 (246.6)	49 (46.4)	15 (16.6)	20 (18.4)	328	27.5±3.0	0.466

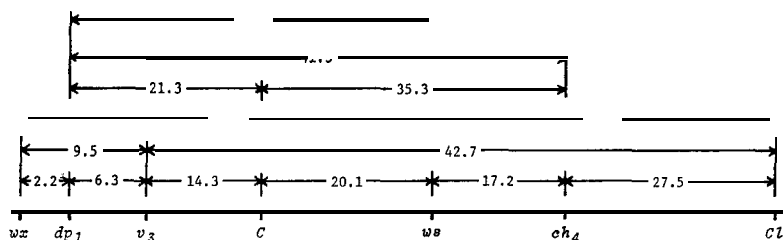


Fig. 2. Sequence of the seven genes at the first linkage group.



**Table 10.** Trisomic and disomic segregations of  $v_4$  in  $F_2$  of a cross with G type of trisomics.

$F_1$ plants	Observed number			$\chi^2$ for 3 : 1	Ratio of domi.: rece.	
	Dominant	Recessive	Total		Theoretical	Observed
Trisomic	183	6	189	48.016*** 0.269	8 : 1-44 : 1	30.5 : 1
Disomic	367	129	496		3 : 1	

\*\*\* Significant at 0.1% level.

**Table 11.** Linkage relations between  $v_4$  and genes belonging to the eighth linkage group, and between  $la$  and  $sp$ .

Gene pair	Items		Segregation mode					Recombination value (%)	$\chi^2_{(3)}$
	Phase	No. of cross	++	+ $la$	$v_4$ +	$v_4la$	Total		
$v_4-la$	$F_2$ Coup.	3	343 (342.7)	33 (27.0)	21 (27.0)	96 (96.3 2)	493	11.6±1.6	0.024
		2	215 (224.2)	118 (108.1)	107 (108.1)	(2.7)	443	15.5±4.6	
	$F_3$ from $F_2$ plant		Seg.	Non-seg.		Total			
				14	75	89		8.5±2.3	
				14	64	78		9.9±2.6	
	Weighted mean							10.8±1.1	
$la-sp$	$F_2$ Rep.	1	54 (63.4)	37 (29.6)	31 (29.6)	2 (1.4)	124	21.1±8.5	3.569
		24	2,831 (2,884.5)	455 (443.3)	448 (443.3)	703 (691.0)	4,437	22.5±0.7	
	Rep.	7	669 (642.5)	266 (285.3)	281 (285.3)	(24.0)	1,237	27.8±2.6	2.831
	Weighted mean							22.9±0.7	

$Cl$  were 9.5, 6.3, 14.3 and 42.7 %, respectively, so the gene sequence was thought to be  $wx-dp_1-v_3-C-Cl$ . It was confirmed that  $ch_4$  belonged to the first linkage group by means of the trisomic segregation in  $F_2$  of a cross with B type of trisomics (Table 8). The recombination values between  $ch_4$  and  $dp_1$ , C and ws were calculated at 41.3, 35.3, 17.2 and 27.5 %, respectively (Table 9). Combining these values and the value of 30.6 % between ws and Cl reported by Iwata and Omura (1971), it is concluded that  $ch_4$  is located between ws and Cl. Therefore, the sequence of these genes at the first linkage group is as shown in Fig. 2.

Takahashi and Morimura (1968) reported the linkage between a chlorina gene ( $chl$ ) and C, Cl and wx with the recombination values of 33.0, 39.5 and 34.5 %, respectively. This chlorina gene ( $chl$ ) sent by us is identical with  $ch_4$ . As above mentioned,  $ch_4$  belongs to the eleventh linkage group and

never links with marker genes of the first linkage group.

Lastly,  $v_4$  was found to belong to the eighth linkage group, showing the trisomic segregation in  $F_2$  of a cross with G type of trisomics (Table 10). The recombination values of  $v_4-la$ ,  $v_4-sp$  and  $la-sp$  were 10.8, 21.1 and 22.9 %, respectively (Table 11). Therefore, their sequence is either  $la-v_4-sp$  or  $v_4-la-sp$ . Linkage relations between  $v_4$  and the other marker genes of this group are under examination.

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