c. GENIC ANALYSIS BY RECIPROCAL TRANSLOCATION METHOD

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1. Isolation for Reciprocal translocation homozygotes

In order to obtain information on artificially induced translocation in rice, dormant seeds, germinating seeds and panicles just before blossoming of two varieties were X-rayed. More than two hundreds strains thus obtained were observed from the second to the fifth generations after the treatment with regard to fertility and other characters.

In a greater part of strains, fertile and semi-sterile plants were found in approximately 1:1 ratio, while in some other strains, either fertile or semi-sterile plants were predominant; in a few strains, the fertility variation seemed to be continuous. In strains segregating into fertile and semi-sterile plants the former produced no sterile plant in their offspring, while the latter continued segregation. In strains showing continuous variation, the progeny of semi-sterile plants generally showed a similar continuous variation.

In a greater part of strains showing segregation of fertile and semi-sterile plants the latter plants were found to form a quadrivalent chromosome in pollen-mother cells, with different frequencies in different strains. The frequency ranged from 2% to 83%. A majority of those quadrivalent chromosomes were ring-shaped, but some of them showed chain or other shapes. Thus, the majority of the strains observed seemed to posses a segmental interchange.

In the majoriy of strains showing segregation of fertile and semi-sterile plants, semi-sterile plants×original stock (non-treated) showed segregation of fertile and semi-sterile plants like the offspring of semi-sterile plants. In contrast to this, fertile plants×original stock produced either semi-sterile or fertile plants, without segregation within the same cross. Such a behavior of sterility was to be expected in a translocation heterozygote.

Fertile plants which produce semi-sterile plants when crossed with the original variety may be homozygous for a translocation. According to the results of these back-cross experiments, 28 translocation homozygotes were selected from different strains. They were quite similar to the original variety in growth habit.

2. Analysis of reciprocal translocations

In order to determine the interrelationship between translocated segments, 28 RT lines isolated by the above mentioned method were intercrossed, and cytological

analysis of the RT lines was made regarding the following respects. In F_1s between two RT lines.

1) If all the chromosome paired normally, the parental lines would have the same translocations.
2) If a quardrivalent chromosome was formed, the chromosomes involved in translocations of both lines would be the same, though it is possible that the translocations are situated in different, for instance 1-3 2-4 and 1-4 2-3.
3) If a ring of six chromosome was formed, the parental lines would have one

Table 1. Segregation of fertile and semi-sterile plants after self-fertilization, behavior of sterility in back-cross experiments, and the presence or absence of a quadrivalent chromosome in different strains

Strain	Self*			Back** cross		Quadri-valent	Strain	Self*			Back** cross		Quadri-valent
	X_2	X_3	X_4	I	II			X_2	X_3	X_4	I	II	
Xg 108 (ear)							Xs 108 (seed)						
1-1-12-11-6	+	+	+	+	+		4-8-5-12-2	+	+	+	+	+	+
2-6-16-1-6	+	+	+	+	+	+	Xg 521 (ear)						
3-1-17	+	+		+	+?	±	1-7-1-5	+	−	+		+	±
3-6-1	+	−	−	−	−	−	1-8-7-3	+	+	+		?	+
3-11-11-1-1	+	+	+?	+?	+	+	1-9-1-3	+	+	+		+	
3-18-15	+	+	−	−	−	−	Xs 521 (seed)						
3-19-1	+	+	−	−	?	±	1-4-2-6-7	+	+	+	+	+	−
3-21-15-11-1	+	+	+	+	?	+	2-5-6-6-7	+	+	+	?	+	+
3-24-13-1-6	+	+	−	−?	+	+	3-4-1-8	+	+	+		?	
3-26-19-2-1	+	+	+?	+	+	+	3-11-3-3	+	+	+		+	−
4-1-2-2	+	+	+		+	+	3-20-15-20	+	+	−		?	+
4-4-2-12	+	+	+		+	+	3-22-1	+	+	+?		+?	
4-5-1-11	+	+	+		+?	−	3-29-2	+	+	+		+	+
4-6-3-1	+	+	+		+	+	3-32-6	+	+?	+		?	+
4-8-3-11	+	−	+		+	+	3-36-11-12	+	+	+		+	+
4-13-2-3	+	−	−		?	+	3-43-1-2	+?	+	+		?	+
4-20-3-2	−	+	−		+?	+	3-45-3	+	+	+		+	
4-21-11-6	+	+	+		?		4-5-4-1	+	+	+		+	+
4-23-2-2	+	+	+		?	+	4-15-2-1	+	+	+		+?	
5-1-3-1	−?	+	+		+?		4-28-6-3	+	+	+		?	+
Xs 108 (seed)							4-37-3-13	+	+	+		+	−
1-4-5-16-5	+	+	+	+	+	+	4-40-1-2	+	+	+		?	
1-10-15-2-6	+?	+	+?	−?	+	+	4-45-7-1	+	+	+		?	
2-1-13-7-6	+	+	+	−?	?	+	4-47-1-3	+	+	+		+?	
4-1-4-13-11	+	+	+	?	?								

*……Self-fertilization, + shows a distinct segregation of fertile and semi-sterile plants.

**……Back-cross experiments, colums I and II show the results of (semi-sterile plant × original variety) and (fertile plants × original variety) respectively; + shows that the results of back-crosses agree with the expectation.

Table 2. Percentage of quardrivalents in PMCs in F_1s of intercrosses of 13 reciprocal translocation homozygotes (108)

		1	2	3	4	5	6	7	8	9	10	11	12	13
1	12II	30.53												
	1(4)	69.47												
2	12II	55.56	70.16											
	1(6)	37.37	29.84											
	2(4)	7.07												
3	12II	84.00	11.38	45.65										
	1(4)	16.00	38.83	54.35										
	2(4)		49.80											
4	12II	60.36	26.32	29.33	77.07									
	1(4)	22.50	26.97	25.96	22.74									
	1(6)	17.14	46.71	44.71										
5	12II	23.25	18.85	22.50	16.67	71.85								
	1(4)	44.30	39.34	61.88	64.59	28.15								
	2(4)	32.45	41.81	15.62	15.76									
6	12II	4.14	8.07	20.69	6.51	57.07	66.67							
	1(4)	21.89	38.04	41.38	26.05	8.70	33.33							
	2(4)		53.89	37.93	67.44									
	1(6)	73.97				34.23								
7	12II	30.20	3.85	19.11	3.33	38.48	12.76	66.00						
	1(4)	52.97	33.08	40.13	21.67	43.03	41.27	34.00						
	2(4)	16.83				8.49	15.95							
	1(6)		63.08	10.76	75.00									
8	12II		44.90	26.17	2.97	39.38	12.96	12.99	62.83					
	1(4)		37.24	50.47	50.54	45.00	53.70	48.05	37.17					
	2(4)		17.86	23.36	46.53	15.63	33.33	39.96						
9	12II	82.00	20.32	11.31		1.01	80.53	1.20		4.41				
	1(4)	17.00	52.94	49.40		38.38	19.47	9.64		95.59				
	2(4)		20.74	39.29				89.16						
	1(6)	1.00				60.61								
10	12II	9.71		32.84	16.93	35.48	13.43		75.00	4.93	22.12			
	1(4)	47.57		43.53	50.79	35.48	43.28		26.62	52.11	61.00			
	2(4)	42.72		18.63		29.03	43.28		2.38	42.96	16.81			
	1(6)				32.28									
11	12II	1.88	7.65	1.97	13.74	5.56	81.16				5.82	11.97		
	1(4)	28.64	46.94	42.36	86.26	83.33	52.04				54.50	60.68		
	2(4)	69.48	45.41			11.11					39.68	27.35		
	1(6)						39.80							
12	12Ik	41.14	7.73	6.67		14.65	5.50	5.67	18.79	1.88	9.57	0.96	52.45	
	1(4)	22.08	63.40	56.66		56.69	15.00	42.55	52.35	48.87	49.87	1.90	47.55	
	2(4)			36.67		28.66			28.86		42.55			
	1(6)	36.80	28.87				79.50	51.77		49.25		97.14		
13	12II	4.40	28.57	1.89		39.81	1.76			12.00	9.23	12.26	7.18	22.32
	1(4)	19.78	41.35	50.94		44.49	27.06			48.00	34.62	31.60	42.54	77.68
	2(4)					15.74	71.18			40.00	56.15	56.13	50.28	
	1(6)	75.82	30.08	47.17										

Note: 1(4)…one ring of four 2(4)…two rings of four 1(6)…one ring of six

chromosome in common in their translocations.

4) If two rings of four were found, the parental lines would have quite different translocation.

By the above method the RT lines were grouped on the basis of their behavior in respective crosses. The results are shown in Table 2.

3. Agronomic characters in RT Homozygotes

The X-ray induced RT homozygotes did not show any marked difference in morphological characters from normal plants. Therefore, it seems that no major genic changes are involved in the translocation lines. However, in agronomic characters which are controlled by polygenes, some changes may or may not occur together with translocations. In view of this respect a number of translocation homozygotes were compared regarding agronomic characters. The RT homozygotes, 10 lines of 108 and 7 lines of 521, 10 lines of 504 were used for field experiment. The results of analysis with regard to various agronomic characters are shown in Table 3.

Table 3. Analysis of variance for various agronomic characters of RT Homozygotes

Strains	Source of variation	D. F.	Heading time		Plant height		Number of tiller		Number of panicles		Grain yield	
			Mean square	F value	Mean square	F value	Mean square	F value	Mean square	F value	Mean square	F value
108TH	Between lines	10	140.260	0.026	36.166	13.405**	1.445	1.02	0.764	1.07	0.02140	2.780*
	Replication	2	8.450		0.555		8.351		2.970		0.01950	
	Error	20	5,452.260		2.698		1.415		0.739		0.00770	
521TH	Between lines	7	1.749	2.580	10.930	2.726	1.435	1.14	1.760	1.45	0.00307	1.480
	Replication	2	0.263		6.210		1.540		1.440		0.05560	
	Error	14	0.679		4.010		1.240		1.210		0.02070	
504TH	Between lines	10	0.625	0.197	23.150	2.514	1.124	1.75	0.907	1.87	0.00640	1.391
	Replication	2	0.930		39.870		1.315		0.820		0.04400	
	Error	20	0.318		9.210		0.644		0.484		0.00460	

*……Significant at 5% level.
**……Significant at 1% level.

As the table shows, no marked differences among lines were seen with regard to various agronomic characters except for a few lines of variety 108. It may be said that translocation lines are generally homogenious in agronomic characters and may be regarded as having the same genotype except for translocations. Accordingly, the translocation method may be used to some extent for locating quantitative characters on chromosomes.

4. Genic analysis by reciprocal translocation method

(a) Linkage between the point of breakage and the glutinous gene or the apiculus color gene.

Some of the above mentioned RT homozygores were crossed with glutinous varieties with different combinations of the genes for apiculus coloration (*C* and *Sp*), to investigate the linkage relation of translocations with those genes. The relation between fertility and segregation for the glutinous gene is shown in Table 4.

When a genic difference is involved in a chromosome with translocated segment, the heterozygous plant for that gene should be heterozygous for the translocation, and semi-sterility will result. As Table 4 shows, in the crosses 160×108 TH-6, 563×521 TH-3b and 563×521 TH-6, semi-sterile plants were found mostly among those

Table 4. Relation between fertility and apiculus coloration, and between fertility and glutinous vs. non-glutinous endosperm, in F_2s of crosses between a glutinous strain and strains homozygotes for translocations

Crosses	Seed fertility in F_1	Class	Apiculus		X^2	Endosperm			X^2
			Colored	Colorless		++	+*gl*	*gl gl*	
160×108									
TH-1	29%	F	26	5	0·130	5	17	8	2.23
		S	53	15		5	46	16	
TH-4	26	F	26	12	0.135	7	18	13	2.16
		S	41	16		11	33	13	
TH-6	31	F	22	10	0.528	8	9	15	5.29**
		S	35	11		7	25	14	
TH-8	24	F	34	9	0.038	6	21	13	3.82
		S	54	13		21	31	15	
TH-9	23	F	37	6	1.720	9	17	16	0.01
		S	43	14		12	23	21	
TH-11	30	F	18	6	0.435	3	13	7	1.45
		S	31	15		7	19	29	
TH-12	33	F	40	13	0.413	8	20	25	1.12
		S	40	17		10	24	20	
TH-13b	16	F	30	4	3.014	5	20	9	1.32
		S	46	17		5	37	21	
TH-15	29	F	24	11	1.090	8	18	8	0.69
		S	50	14		11	40	13	
108	87	F	66	14	—	8	51	21	—
563×521									
TH-1	30	F	26	16	0.114	10	24	8	0.64
		S	31	22		9	33	10	
TH-3b	20	F	22	17	0.142	12	20	7	8.58**
		S	29	19		4	29	17	
TH-4b	16	F	30	20	3.416	8	25	17	2.89
		S	18	26		2	24	15	
TH-4c	23	F	22	18	0.191	13	23	4	3.83
		S	22	22		9	24	11	
TH-6	24	F	14	7	0.539	6	10	5	2.60
		S	20	15		5	24	6	
TH-8	24	F	23	28	1.450	14	23	14	0.66
		S	28	21		12	26	11	

F: Fertile plants.
S: Semi-sterile plants.

*……Significant at 5% level.
**……Significant at 1% level.

heterozygous for glutinous vs. non-glutinous endosperm. It seems that the glutinous endosperm gene +:*gl* is involved in the translocated chromosomes. The apiculus coloration gene *C* is linked with *gl*. However, no correlation between semi-sterility and apiculus coloration was found. It may be due to the distance between *C* gene and the point of interchange.

The recombination value between *gl* and interchange point was calculated according to the following formula.

	AA	Aa	aa
Fertile group	$\frac{1}{4}(1-2p+2p^2)$	$p\ (1-p)$	$\frac{1}{4}(1-2p+2p^2)$
Semi-sterile group	$\frac{1}{2}p\ (1-p)$	$\frac{1}{2}(1-2p+2p^2)$	$\frac{1}{2}p\ (1-p)$

Solving the equations obtained by maximum linkelihood method, the recombination value between *gl* and interchange point in 108×H-6, 521 TH-3b and 521 TH-6 were estimated to be 26%, 39% and 25% respectively.

(b) Relation between translocations and quantitative characters.

Variations in heading date and plant height were compared between fertile and semi-sterile classes of F_2 plants to see if genes for these quantitative characters are involved in the translocations under observation. The results obtained is shown in Table 5.

Table 5. Variations in heading date and plant height among fertile and semi-sterile F_2 plants

(a) Heading date

Cross	Class	Sep.						Oct.			No. of plants	X^2
		20	22	24	26	28	30	2	4	6		
160×108-TH-1	F		1		17	16	15	4			53	15.58**
	S	1			5	10	26	13	1	1	57	

(b) Plant height

Cross	Class	cm 70	75	80	85	90	95	100	105	110	115	120	125	130	No. of plants	X^2
180×108-TH-1	F					7	2	5	11	2	2	8		1	31	10.78*
	S	2		2		7	15	22	8	5	5		1	1	68	
563×521-TH-4c	F		1	6	2	13	14	4							40	22.88**
	S		3	11	15	12	2	1							44	

*.....Significant at 5% level.
**.....Significant at 1% level.

As the data in the table shows, in 160×108 TH-2, heading dates in the semi-sterile group were later than those of the fertile group, and the difference was statistically significant. Heading date showed a continuous variation. It then seems that there may be a number of genes are concerned in heading date, and some of them are located in the chromosomes involved in the translocation.

Similar phenomona were also recognized with regard to plant height. As Table 5 (b) shows, in the crosses 180×108 TH-1 and 563×521 TH-4c, the semi-sterile group was lower in plant height than the fertile group being statistically significant. This may indicate that some genes controlling plant height were involved in the chromosome with a translocated segment.

DISCUSSION

Chang: I would like to suggest Mr. Chiu to add one glutinous variety of Taichung No. 65 which was selected in the genetic loboratory of Provincial Taichung College of Agriculutre in order to test the effect of high temperature to nutrient absobtion in relation to the glutinous gene. How about the idea?

Hsu: I think it is a good idea, you had better cousult this matter with Mr. Chiu, so that you can make chemical analysis.

Tan: I think major genes should be studied in relation with polygenes.

Oka: Yes, we can study them at the same time but it seems necessary to make clear the genetic behavior of major genes first.

Hsieh: I think you had better make reciprecal translocation analysis in more details to get 12 different RT homozygotes which involves all the chromosomes.

Chang: Yes, I am just doing this work and expect to complete this RT analysis in near future. Since it takes quite a lot of cytological labor, I think this work still need some time.

Hsu: What is the difference of your work from Mr. Hsieh's.

Chang: Essentially the same, but the method is different. The linkage relation between genes is usually determined by the common method as practiced by Mr. Hsieh. By the RT method, the genes can be related directly to the chromosomes. Therefore, the linkage groups can be acurately corresponded to the chromosomes. But this method is more laborous than the former.