ISOLATION OF RECIPROCAL TRANSLOCATION LINES IN RICE

Mutations in rice induced by X-rays III[1]

by

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Studies of X-ray induced chromosome structural changes have been made in many plants (Maize; Anderson 1934, Burnham 1930, Barley; Caldecott 1955). Ramiah (1935) first found a ring chromosome in rice after X-ray treatment. Since then several cases of chromosomal interchanges after X-ray irradiation in rice have been reported. Thus Nishimura (1952), Chang (1955) observed ring chromosomes in semi-sterile plants of X-rayed rice. Oka (1953) proposed a formula for calculating the break point and length of interstitial segment in translocation heterozygote of X-rayed rice.

By way of Yamashita's (1949) suggestion that reciprocal translocation stocks are useful for linkage analysis, the writers initiated X-ray irradiation on rice seeds. The semi-sterile plants with the same cytogenetic behaviour as that reported by previous workers were identified and that homozygotes for interchanges were isolated from the semi-sterile strains by back crossing fertile plants, segregated from semi-sterile plants, to normal ones. Determination of interrelation of homozygotes is still under way, while the procedures and results of obtaining interchanged lines are reported in this paper.

MATERIALS AND METHODS

Germinating seeds of Taichung No. 65 (a representative variety of "Ponlai rice" in Taiwan) were X-rayed on February 14, 1948 and February 17, 1954 at the Plant Breeding Laboratory of Taiwan University and in the University Hospital respectively. X-rays were produced at 80 kv and 4 ma at 30 cm distance and 50–120 minutes for the first treatment. For the second treatment, X-rays were produced at 100 kv and 4 ma through 0.25 mm Aluminium filter for 20–35 minutes. The doses were 5,000 r, 7,000 r, 8,000 r, and 10,000 r.

Panicles of the X_1 generation were planted separately as X_2 lines. The lines segregating into fertile and semi-sterile plants in approximately 1:1 ratio in the X_2 and subsequent generations were selected as BS lines. To test their genetic behaviour, the BS lines were crossed with the original standard variety to see whether the F_1 progeny shows a 1:1 ratio again or not. If so, the lines were further tested by back crossing the fertile plants which segregated from BS lines to the original variety. If the F_1 plants were completely fertile, the male plants were considered as normal

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ones while those being partially sterile were identified as homozygotes for chromosome interchanges and designed them as BS lines.

Cytological observation was made from pollen mother cells of BS lines, to see whether there were ring of four chromosomes in them. Spiklets were taken in the field at 11–12 AM. Farmer's fluid was used as fixative and the ordinary aceto-carmine smear method was applied.

PRESENTATION OF DATA

1) *Isolation of reciprocal translocation lines*

As indicated before, fertile and semi-sterile plants in 1:1 ratio were selected from the semi-sterile plants, the fertile ones bred true, while the semi-sterile ones continued to segregate in the same manner. The segregation ratio of some lines are illustrated in table 1.

Table 1. Genetic behaviour of semi-sterile rice

Strains	% of seed setting of X_2	X_3		X_4		X_5	
		F:S. S.	X^2	F:S. S.	X^2	F:S. S.	X^3
B S 1—3—1	35.3	12 : 17	0.86	12 : 17	0.86	16 : 14	0.13
B S 2—3—3	33.9	12 : 14	0.15	16 : 14	0.13	8 : 8	0.00
B S 3—3—1	28.8	36 : 40	0.21	26 : 28	0.07	12 : 12	0.00
B S 4—4—5	38.9	18 : 17	0.28	12 : 16	0.56	9 : 4	1.92
B S 5—1—1	23.0	10 : 11	0.05	14 : 16	0.13	14 : 13	0.04
B S 6—3—4	33.0	14 : 7	2.30	12 : 8	0.80	12 : 13	0.04
B S 2—1	37.6	12 : 15	0.33	13 : 14	0.04	14 : 14	0.00
B S 9—5—3	—	27 : 24	0.18	27 : 24	0.18	—	—
B S 10—2—7	33.8	—	—	—	—	11 : 12	0.04
B S 11—1—2	33.8	22 : 19	0.22	11 : 10	0.05	14 : 16	0.13
B S 12—1—1	21.8	18 : 22	0.40	20 : 22	0.09	—	—
B S 13—2—1	26.5	33 : 29	0.26	23 : 25	0.08	10 : 10	0.00
B S 14—3—1	29.5	—	—	9 : 10	0.05	12 : 14	0.15
B S 16—1—5	29.4	26 : 12	5.14	15 : 21	1.40	12 : 15	0.33
B S 17—3—1	27.3	8 : 10	0.22	15 : 10	1.00	14 : 13	0.04
B S 18—2—1	24.0	—	—	—	—	12 : 16	0.56
B S 19—2—2	26.0	—	—	—	—	15 : 12	0.33
B S 20—1—2	—	63 : 59	0.13	8 : 9	0.06	—	—

F……Fertile plant
S. S.……Semi-sterile plant
X^2……Chi-square value for 1:1 ratio

As it is shown in table 1, certain cases of segregation did not fit the expected 1:1 ratio, but their previous and later generations satisfied the ratio. This difference might be due to enviromental effects since the heading time of 2nd crop season (July-October) is usually under relatively low temperature. In certain lines, the normal and aborted pollen showed perfect fit for 1:1 segregation ratio as it is shown in table 2.

These lines were test crossed by the above mentioned method and an expected

result was obtained in majority of lines. If there is ring of four chromosomes in pollen mother cells, these lines will be explained as reciprocal translocation heterozygotes without difficulty. This assumption was justified by the result of cytological observation (table 3, 6).

The semi-sterile lines which did not show 1:1 segregation ratio but showed seemingly continuous variation occupied about half of the total lines, and were not studied in detail so far as reciprocal translocations were concerned.

Table 2. Relation between the percentage of normal pollen and seed setting in a semi-sterile strain

Seed setting in per cent	Normal pollen in percent										Total	Segregation ratio (1:1)
	10	20	30	40	50	60	70	80	90	100		
10												
20												
30				3	3	1	1				8	
40				2	2			1			5	15
50							1				1	
60					1						1	
70								1		1	2	
80									1		1	
90					1	1			3	3	8	13
100							1			1	2	
Total				5	7	2	3	2	4	5	28	
Segregation ratio (1:1)			14						14			

Fifty five RT heterozygotes lines were obtained from the two treatments through cytogenetic observation.

2) *Chromosome behaviour of R. T. heterozygotes*

Generally, rice chromosames at the early stages of meiosis i.e. pachytene and zygotene stages, could not be observed clearly owing to unsatisfied staining of Aceto-carmine to chromonema. The chromosome behaviour was mainly observed at diakinesis, 1st metaphase and 1st anaphase. As shown in table 3, quadrivalents and univalents were seen both at diakinesis and at 1st metaphase. Among the chromosome pairing types, 12II and 11V+10II were most frequently seen, while 1IV+9II+2I and 1IV+8II+4I were with rather low frequency, 2Ø4+8II or 1Ø6+9II were observed in some lines. As it is shown in the table 3 and fig. 1, shapes of quadrivalent were ring, chain, spherical, cocoon, Y and cross types. Of these shapes, the ring type was the most comon, and chain type came to next. The percentage of quadrivalents was ranged between 0–100% and being varied in the different lines (fig. 1). Chain and other types of quadrivalent were ranged between 0 to 70%.

Ring of four chromosomes were either "open" or "zigzag" shaped. All "open" type or "open and zigzag" types were found in respective eight and nine lines, while

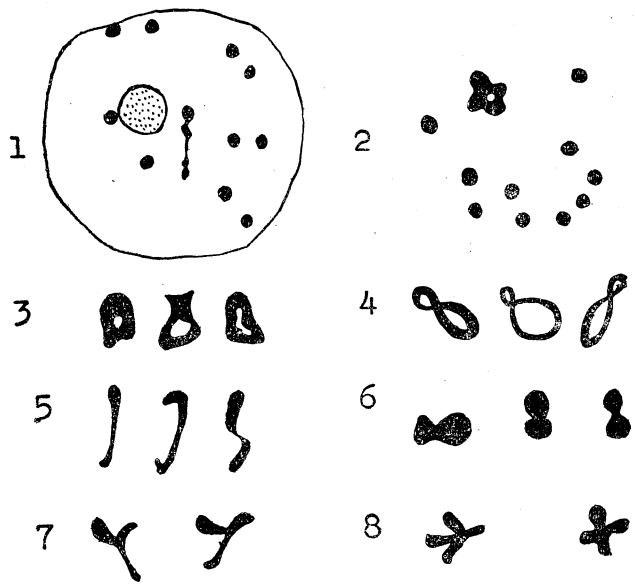


Fig. 1. Various configulations of quadrivalent chromosomes
1. 1 Chain+10II (Diakinesis) 5. Chain shape (Diakinesis)
2. 1 Ring+10II (Metaphase-I) 6. Cocoon shape (Metaphase-I)
3. "open" shaped ring (Metaphase-I) 7. Y shape (Metaphase-I)
4. "Zigzag" shaped ring (Diakinesis) 8. Cross shape (Diakinesis)

lines of those with all "zigzag" rings were never found. As shown in table 4, these rings always connected with 40–70% of pollen abortion. This phenomenon seems to be similar to that observed in Datura (Bergner 1933). Other types of ring and chain also brought about 20–70% of pollen abortion.

Table 3. Frequencies of types of chromosome pairing, quadrivalent and univalent in semi-sterile rice.

Strains	% of seed setting	Frequency of types of chromosome pairing					Frequency of various shaped quadrivalent in %							% of univalent	Total no. of cells observed
		12 II	11 II + 2 I	1 IV + 10 II	1 IV + 9 II + 2 I	1 IV + 8 II + 4 I	ring	chain	spherical	coocoon	Y	cross	Total		
B S 2-3-1	32.2	22		15			21.6	13.5	2.7	2.7			40.5		37
B S 3-3-6	35.3	19		41			41.7	13.4	5.0	8.3			68.4		60
B S 4-4-7	35.5	17	1	13			16.1	9.7	3.2	6.4	3.2	3.2	41.8	6.4	31
B S 5-1-1	42.5	7		12	4		21.7	26.1	4.3	8.6			60.7	34.7	23
B S 6-3-10	72.4	19	2	14			5.7	14.3	8.5	5.7			34.2	11.4	35
B S 7-3-4	29.0	35		5			5.0	2.5	5.0				12.5		40
B S 8-2-9	57.5	32	3	22	1	1		20.3	10.1	8.4			38.8	20.3	59
B S 10-2-8	29.3	29		12	1		11.9	2.4	14.2	2.4			30.9	4.8	42
B S 11-1-6	33.8	6		50			30.3	42.8	5.4	5.4	5.4		89.3		56
B S 12-1-4	27.3	6	1	59			60.5	24.2	3.3	1.5	1.5		91.0	3.0	66
B S 13-2-2	23.4	2		52			70.3	18.5	5.5	1.8			96.1		54

B S 14-1-8	32.2	15		19			8.8	14.8	14.7	14.7	2.9		55.9		34
B S 15-8-4	75.3	21	3	7			9.7	3.2	3.2	6.4			22.5		31
B S 16-1-7	29.5	20		28	2		6.0	36.0	10.0	6.0			58.0	8.0	50
B S 17-3-8	28.3	58		28			9.3	11.6	8.1	3.6			32.6		86
B S 18-1-5	38.7	16		34			10.0	26.0	8.0	22.0	2.0		68.0		50
B S 19-2-9	55.4	61		15			3.9	15.8					19.7		76
B S 20-1-14		44		4			8.3						8.3		48
B S 24-3-1	26.5	12		50	3		10.6	60.7		10.7			82.0	9.1	65
B S 25-5	4.8	10		27	17		12.5	46.1	18.5	3.7			80.8	12.8	54
B S 26-9	42.5	9	10	7	15	3	6.8	11.3	27.2	9.1			54.4		44
B S 27-6	45.6	28	6	13	1	1	12.0	20.0	4.0	2.0			38.0	12.0	49
B S 28-9	41.3	30	3	18	3	1	1.8	14.5	18.1	3.6			38.0	29.1	55
B S 29-7	36.3	30	8	11				14.1	14.2	4.1			22.4	32.6	49
B S 30-2	54.1	43	5	2				2.0	2.0				4.0	20.0	50
B S 31-4	34.9	41	2	7			2.0	2.0	4.0	4.0	2.0		14.0	8.0	50
B S 32-6	43.2	39	3	8			2.0	2.0	12.0				16.0	12.0	50
B S 33-8	47.5	33	7	10				8.0	2.0				10.0	28.0	50
B S 34-8	34.3	1		51			42.3	32.7	13.4	7.6	1.9		97.9		52
B S 36-10	44.2	72		1				1.4					1.4		73
B S 37-4	70.0	16	1											11.7	17
B S 38-7	28.4	4		58			75.8	17.7					93.5		62
B S 39-3	60.0	60	1	28			5.6	24.7		1.1			31.4	2.2	89
B S 40-3	42.3	3		45	1		77.6	16.3					93.9	4.1	49
B S 41-3	60.0	34	1	15			14.0	4.0					18.0	4.0	50
B S 42-5	27.8	6	1	43			76.0	4.0		6.0			86.0	4.0	50
B S 43-6	26.0	2		48			90.0	4.0	2.0				96.0		50
B S 44-1	35.3	18	1	31			10.0	6.0	40.0	6.0			62.0	4.0	50
B S 45-1	60.0	16	1	33			30.0	2.0	18.0	16.0			66.0	4.0	50
B S 46-9	32.3	19	4	27			44.0	2.0	6.0	2.0			54.0	6.0	50
B S 48-9	33.6			50			38.0	56.0	6.0				100.0		50
B S 49-8	38.1	1		53			75.0	18.5					93.5		54
B S 52-7	50.0	1		49			34.0	44.0	16.0	4.0			98.0		50
B S 53-8	43.0	1		40			65.8	29.3		2.4			97.5		41
B S 56-4	32.7	1		54			50.9	47.3					98.2		55
B S 58-1	48.6	1		49			72.0	22.0	4.0				98.0		50
B S 59-2	45.8	16	4	32			15.4	53.8	1.9				71.1	15.4	52
B S 61-10	26.2	16	2	32			36.0	16.0	6.0	6.0			64.0	8.0	50
B S 62-8	24.0	2		50			15.1	43.4	18.8	15.0	3.7		96.0	7.5	52
B S 63-1	50.0	16	1	32	3			11.3	43.3	9.4	1.8	1.8	67.6	15.0	52
B S 64-2		33	9	8				2.0	10.0	2.0		2.0	16.0	36.0	50
B S 64-6		1		51			78.8		11.5	5.7	1.9		97.9		52
B S 65-6	60.0	23	3	24			4.0	8.0	24.0	8.0	2.0		46.0	12.0	50
B S 67-5	25.5	1		49			82.0	14.0	2.0				98.0		50
B S 68-4	29.2	10		19			24.1	24.1		17.2			65.4		29

It was found that the correlation coefficient between the frequency of ring chromosome and percentage of seed sterility was as high as r=0.530, while the value between frequency of chain chromosome and seed sterility was r=0.312 which were significant at 5% level. This means the sterility is mainly caused by the segmental interchanges.

Table 4. Pollen abortion observed for translocations with different configulations in Dia-metaphase-I

Chromosome configulations	Pollen abortion in percent						Total lines observed
	20	30	40	50	60	70	
Ring and Chain types	1	2	12	12	8	3	38
All "open" type ring			2	5	1		8
All "Zigzag" type ring							
"Open" & "Zigzag" type ring				6	2	1	9
All chain type							
Total	1	2	14	23	11	4	55

3) *Isolation of R. T. Homozygote*

As mentioned before, when fertile plants produced from R. T. heterozygote were back crossed to the original variety would produce either all sterile or all fertile plants, and the segregation of fertile and sterile plants would never be seen within the same cross; the male parent of former one should be translocation homozygote, while that of later one belongs to normal as original variety. This principle was applied for identification of R. T. homozygote. The result of test cross is shown in table 5.

By using this method, twenty lines of homozygotes for interchanges were selected from fifty five heterozygote lines. A few lines are remained to be checked due to insufficient number of F_1 plants.

Table 5. Segregation of fertile and semi-sterile plants in the hybrids between original variety and fertile plants of the used lines.

Cross combinations	Percentage of seed setting										Total	Remarks
	10	20	30	40	50	60	70	80	90	100		
Taichung No. 65 × B F 1—8								2	2		4	*
× B F 2—3					1	1	1	2	2	1	8	**
× B F 2—7				1		1			3	8	13	*
× B F 3—7									1	6	7	*
× B F 3—3				2							2	***
× B F 4—4					1?		1	1	2	3	8	*
× B F 4—6		1	2	2		2					7	***
× B F 5—5	1	1	1	4	5			1?		1?	14	***
× B F 5—8					2	2	4	1	1		10	**
× B F 6—4		1	2	1	3						7	***
× B F 6—8										6	6	*
× B F 7—3							1	1	2	1	5	*
× B F 7—7			2		1						3	***
× B F 8—2									1	5	6	*
× B F 9—1			2	2	2						6	***

× B F 9—6	5				1						6	***
× B F10—8							1	1	2	2	6	*
× B F11—5	12	4	1	1	4					1?	23	***
× B F11—8			1	5	6	1	2			1?	16	***
× B F12—8				7	4		1				12	***
× B F13—3									2	4	6	*
× B F14—1	1			4	3						8	***
× B F14—5		1		2	1	1					5	***
× B F15—2					4						4	***
× B F16—4	2	1		7	2						12	***
× B F16—8									5	5	10	*
× B F17—5				2	3						5	***
× B F17—6										9	9	*
× B F20—3				3	3	1	1				8	***
× B F21—1									3	3	6	*
× B F24—3							2	1	2	3	8	*
× B F25—3		3	2	1							6	***
× B F29—2			2	2	3						7	***
× B F36—1			1		1						2	**
× B F41—7				1							1	**
× B F44—6	1										1	**
× B F45—8	1	1									2	**
× B F57—6	1										1	**
× B F59—4	1										1	**

Remarks: * Normal plant same as original variety
** Might be the R. T. Homozygote
*** R. T. Homozygote

Table 6. Relation between segregation ratio of fertility and quadrivalent chromosomes

Strains	Selfing	Meiosis	Back cross	Strains	Selfing	Meiosis	Back cross	Strains	Selfing	Meiosis	Back cross
B S 1	+	±	*	B S24	+	+	*	B S44	—	+	*
B S 2	+	±	**	B S25	+	+	***	B S45	—	+	**
B S 3	+	+	***	B S26	+	+		B S46	+	+	
B S 4	+	±	***	B S27	—	±		B S47	+		
B S 5	+	+	***	B S28	+	±	**	B S48	+	+	
B S 6	+	±	***	B S29	+	±	***	B S49	+	+	
B S 7		±	***	B S30	+	±		B S50	+		
B S 8	+	±	*	B S31	—	±		B S51	—		
B S 9	+	±	***	B S32	—	±		B S52	—	+	
B S10	+	±	*	B S33	—	±	**	B S53	+	+	
B S11	+	+	***	B S34	—	+		B S54	+		
B S12	+	+	***	B S35	+			B S55	+		
B S13	+	+	**	B S36	—	±	**	B S56	+	+	
B S14	+	+	***	B S37	—	—		B S57	+		**
B S15	+	±	***	B S38	+	+		B S58	+	+	
B S16	—	+	***	B S39	+	±		B S59	+		**
B S17	+	±	***	B S40	+	+	**	B S60	+		
B S18	+	+		B S41	+	±		B S61	+	+	
B S19	+	±		B S42	—	+					
B S20	+	±	***	B S43	+	+					

Note: Selfing + Fertility showed 1:1 segregation ratio in each generation
— Fertility did not fit 1:1 segregation ratio in certain generation
Meiosis + Parcentage of quadrivalent is above 50%
± Percentage of quadrivalent is below 50%
— No quadrivalent is found
Back cross *** Confirmed R. T. homozygote was obtained
** R. T. homozygote is doubtful
* No R. T. homozygote was obtained

DISCUSSION

Sterility occurring in plant may be caused either by genetic or by chromosomal changes. The genetic behaviour of semi-sterile plant in the present study is that the semi-sterile plant give the typical 1 normal: 1 semi-sterile segregation, the later continuing to segregate while the fertile ones bred true. This is similar to that reported by Nishimura (1953), Oka (1953) and Chang (1955).

As the result of cytological observation, ring and other shaped quadrivalents were found and were found to be correlated with percentage of seed sterility ($r=0.530$). From these results, it was concluded that the sterility was attributable to chromosome interchanges. Ring chromosome found in microsporocytes included "open" and "zigzag" types. Theoretically, "zigzag" type gives alternate segregation, while "open" type gives Adjacent I or Adjacent II segregation" as described by McClintock. If the above mentioned three types of segregation were equally frequent and no crossing over occured, 66.7% sterility would be expected. In the present study, strains which form mostly ring chromosomes have approximately 40–60% sterility, this suggests that the "open" and "zigzag" type ring chromosomes may be equally frequent as it is known in Maize.

The chain type might be the result of unequal length of exchanged pieces, i.e. one short and one long. If pachytene chromosomes of rice could be detected clearly under microscope as it has been done in Maize, the length of translocated segment and break point could be cytologically observed. Further technical improvement is necessary for this purpose of study in rice.

According to Terao (1921), there were occassionally semi-sterile plants segregated in fertile strains of rice. The genetic behaviour of such semi-sterile plant was same as that reported here, Terao believed that semisterile would not be caused by chromosomal structural changes, but by a lethal factor which affected the female gametes only. Oka (1953), Sampath and Mohanty (1954), and Hsieh (1957) reported that hybrid sterility between distantly related rice variety is not due to translocation nor due to the failure of the parental chromosomes to pair; there is no detectible cytological abnormality at mataphase I.

In contrast, Venkataswamy (1957) found "true breeding semi-sterile plants" in the progeny of distant crosses in rice, in which quadrivalant chromosomes were detected and assumed that those semi-sterile plants might be homologous for duplications and deficiency of small chromosome segments. Cua (1952) refered to several reports which attributes the observed sterilityto segmental interchanges even in the absence of rings. From these results, it may be assumed that translocation occurs in rice in natural conditions as it has been assumed in other plants. The translocated segments might be so short that it is difficult to detect cytologically. However such a big translocations as dealt with in the present study or in other similar ones which are induced by irradiations can not be found in cultivated varieties of rice under natural conditions. Only small translocations may play a role in the evolution of rice as assumed

by Hwang (1958), though the reason for this can not be explained clearly.

SUMMARY

The semi-sterile plants induced by X-ray irradiation were studied cytogenetically. It was found that, semi-sterile plants gave 1 fertile and 1 semi-sterile segregation ratio; fertile ones bred true, while the semi-sterile ones continue to segregate as above mentioned manner. When the former was back crossed to original variety, it produced either all sterile or all fertile plants, and segregation of fertile and sterile plants was never seen whthin the same cross. Such a behaviour of inheritance of fertility was concluded as attributable to chromosomal interchanges caused by X-ray irradiation. Frequency of ring, chain and other types of quardrivalents which were varied 0-100% were found to be significantly correlated with percentage of seed sterility. It was assumed that "ring" and "zigzag" configulated chromosomes were equally frequent in the observed strains. Fifty five lines of heterozygote for interchange and twenty lines of homozygote for interchange were isolated from the two treatments, and the analysis of interrelation of chromosomes is being carried out.

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水稻染色體相互轉座系統之分離

水稻經X線處理後所發生的突然變異之第三報

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本研究係探討在第一報所報告，X線處理後所發生的半不稔稻之細胞遺傳行爲。半不稔稻在次代分離爲結實稻及半不稔稻兩種，其比例爲1：1，結實稻即固定並遺傳至後代，但半不稔稻則再以1：1之比例分離結實稻及半不稔稻。若將前者與原來未處理品種回交則產生全結實稻或全半不稔稻而無如上述之分離現象。若將後者與未處理原來品種回交則與上述同樣方式分離出，1 結實稻及 1 半不稔稻。此種結實率之遺傳行爲與相互轉座體者相似。爲檢定相互轉座系統之眞實性乃觀察其花粉母細胞之染色體行爲，結果在肥厚期及第一中期發現環形 (Ring type)，鏈形 (Chain type)，蛹形 (Ocoon type) 十字形 (Cross type) 及Y形等各種形狀之四價染色體。其出現頻度介於 0—100%之間。此等四價染色體與不稔率之間有顯著的相關 ($r=0.530$)。此結果表示上述半不稔稻係由於染色體之相互轉座所致。

水稻之相互轉座可能在自然界中亦有發生，但所交換的染色體斷片 (Interchanged segment) 可能甚短不易察見，且可能不易產生如本研究中所發現之大轉座。

經過上述試驗已分離出53系統的轉座異型體 (Reciprocal translocation heterogyzote) 及20系統的轉座同型體，轉座同型體 (R. T. Homozygote) 間之分析正在進行中。