Chromosomal Location of an Earliness Gene *Ef₁* of Rice, *Oryza sativa* L.

Shigetoshi SATO, Ichiroh SAKAMOTO¹⁾, Kohji SHIRAKAWA and
Satoshi NAKASONE²⁾

College of Agriculture, University of the Ryukyus, Nishihara,
Okinawa, 〒 903-01

To map earliness gene(s) on the 7th chromosome of rice, *Oryza sativa* L., three early-heading isogenic lines T 65·ER-1, T 65·ER-5 and T 65·ER-6, were bred after 9 or 10 backcrosses with Taichung 65 (a cultivar from Taiwan) to two interchange homozygotes T 3-7 and RT 7-11, and a linkage tester HO 775, respectively. Each early-heading isogenic line carried a dominant earliness gene. The earliness gene was one of the allele of *Ef₁* locus (early flowering), which is identical with or isoallelic to *Ef₁^b*. *Ef₁* was linked with seven breakpoints involving the 7th chromosome, 7-11, 6-7, 3-7, 7-8 b, 7-9, 7-8 a, and 2-7 a, and two genes on the chromosome, *fgl* (faded green leaves) and *pgl* (pale green leaves), recombination values being 2.2, 3.0, 7.8, 11.9, 23.3, 25.9, 28.5, 15.3 and 29.0%, respectively. *Ef₁* was estimated not to be located on the 9th chromosome, but on the 7th, and the early observation of a linkage between *Ef₁^b* and the lazy growth-habit gene *la* on the 9th chromosome was not correct. The arrangement of four linked genes and seven breakpoints on the 7th chromosome were estimated as *pgl*-7-8 b-*Rf₁*-*fgl*-7-11-*Ef₁*-6-7-3-7-7-9-7-8 a-2-7 a.

KEY WORDS : *Oryza sativa* L., *japonica*, heading time, earliness gene, linkage analysis.

Introduction

Heading time or time of floral initiation is an important agronomic character which is responsible for the regional and seasonal adaptation of varieties.

Early genetical studies on this trait of rice, *Oryza sativa* L., mainly dealt with the genes for photoperiodic sensitivity, while CHANG *et al.* (1969) suggested that there exist two or three earliness genes controlling the basic vegetative growth. TSAI and OKA (1965, 1966 and 1968) bred early-heading lines having the same genetic background as that of Taichung 65 (a *japonica* cultivar from Taiwan), and detected an earliness gene *Ef₁* which is inferred responsible for the basic vegetative growth. TSAI (1973) observed a linkage relationship between *Ef₁* and the lazy gene *la* which belongs to the VIII linkage group corresponding to NISHIMURA's 9th chromosome (IWATA and OMURA 1971, SATO 1976). Later, SATO and SHINJO (1983) suggested that an earliness gene is linked with the fertility restoring gene *Rf₁* on the 7th chromosome.

To map the earliness gene on the 7th chromosome suggested by SATO and SHINJO (1983), three early-heading isogenic lines of Taichung 65 were bred, and linkage studies were carried out, using other isogenic lines with interchanges involving the 7th chromosome and marker genes on it.

Received June 2, 1987.

Present address : ¹⁾Tohbi Agricultural Extension Center, Wake, Wake-gun, Okayama, 〒709-04

²⁾Chubu Agricultural Extension Center, Takaesu, Gushikawa, 〒904-22

Materials and Methods

Two interchange homozygotes T 3-7 and RT 7-11, and a linkage tester HO 775 were used as donor parents of earliness genes. T 3-7 was obtained from Kokushokuto-2 (or A-58; a native variety in Hokkaido) after the gamma-ray treatment (SATO *et al.* 1975). RT 7-11 was derived from an unknown rice variety exposed to the atomic bomb in Nagasaki (IWATA 1970). HO 775 carries a marker gene *pgl* (pale green leaves) on NISHIMURA's 7th chromosome (SATO and SHINJO 1985). Taichung 65 (abbreviated as T 65) was used as the recurrent parent for backcrossing.

An early-heading line T 65·ER-1 carrying an earliness gene derived from T 3-7 was obtained after 10 successive backcrosses with T 65, in which plants showing early-heading and semisterility were selected for further backcrossings till B_5F_1 . An early-heading fertile plant was obtained in B_6F_1 . Such early-heading fertile plants were selected also in subsequent backcrosses. T 65·ER-1 was selected from the $B_{10}F_3$ progeny. On the other hand, early-semisterile plants were also backcrossed with T 65 till B_9F_1 .

An early-heading line T 65·ER-5, which has an earliness gene originated from RT 7-11, was obtained after 9 successive backcrosses with T 65. This line carried the interchange chromosome 7-11.

An early-heading line T 65·ER-6 possessing an earliness gene derived from HO 775 was obtained after 10 backcrosses with T 65, in which plants carrying an earliness gene and *pgl* in the heterozygous state were selected till B_5F_1 . A single early-heading plant homozygous for *pgl*⁺ was obtained in B_6F_1 . Such plants were selected also in subsequent backcrosses, and the early-heading line T 65·ER-6 was obtained from the progeny. Heterozygotes on both traits were also successively backcrossed till B_6F_1 .

T 65·*Efl*^b, which is an isogenic line of T 65 with an earliness allele *Efl*^b derived from Bozu 5 (a native variety in Hokkaido) on the *Efl* locus (early flowering), was also used in this study. It was bred after 20 backcrosses with T 65 (TSAI 1976).

The F_1 plants of T 65·ER-5/T 65//T 65 were observed with regard to the genetic behaviour of heading time and its linkage relation with the breakpoint 7-11. The F_1 plants of T 65·ER-1/T 65//T 65 and T 65·ER-1/T 65//T 65·ER-1, and the F_2 plants of T 65·ER-1/T 65 were tested to estimate the number of earliness genes carried by T 65·ER-1. The B_7F_1 to B_9F_1 plants bred parallel with T 65·ER-1, and selfed progenies of B_5F_1 to B_7F_1 plants showing early-heading and semisterility were also tested to estimate the number of genes carried by T 65·ER-1 and the linkage relation between heading time and breakpoint 3-7. For the same purpose, two sorts of segregating plants were tested; one was the B_6F_1 to B_9F_1 plants obtained parallel with T 65·ER-6, and the other was the selfed progenies of early-heading plants homozygous for *pgl*⁺ which were selected from the B_6F_1 and B_7F_1 plants. The genotype of B_nF_1 plants for *pgl* was determined by testing 30 B_nF_2 seedlings per B_nF_1 plant. The reason why such the plants not to segregate for the chlorophyll-mutant trait were used, is that the trait pleiotropically delayed heading time. Allelic relationships between earliness genes of T 65·ER-1, T 65·ER-5, T 65·ER-6 and T 65·*Efl*^b, were studied by three-way crosses of three of them.

Since the four early-heading lines were found to have an earliness gene at the same

Table 1. Interchange homozygotes used and their breakpoints

Interchange homozygote	Interchange chromosome	Breakpoint	Origin	Number ¹⁾ of backcrossings
RT 2-7 a·T 65	2, 7	2-7 a	Taichung 65 : T-14	10
RT 6-7·T 65	6, 7	6-7	Atomic bombed rice : AP 39	8
RT 7-8 a·T 65	7, 8	7-8 a	Okute-Asahi : AC 13	8
RT 7-8 b·T 65	7, 8	7-8 b	Okute-Asahi : X-205	9
RT 7-9·T 65	7, 9	7-9	Okute-Asahi : A ₁ -7	9

¹⁾ Backcrossed with Taichung 65.

locus, as mentioned later, linkage relations of the earliness gene to *fgl* (faded green leaves), and five breakpoints involving the 7th chromosome, were examined. The 5 interchange homozygotes, RT-lines were obtained after 8 or more backcrosses with T 65 (Table 1). The linkage tester T 65·*fgl* was obtained after 8 backcrosses with T 65. The heading time of backcrossed interchange homozygotes and the F₁ hybrid between T 65·*fgl* and T 65 was similar to that of T 65, although T 65·*fgl* headed significantly later than T 65. The delation of heading time of T 65·*fgl* was considered to be resulted from the pleiotropical effect of the chlorophyll-mutant character expressed by *fgl*, as well as by *pgl*. Consequently, these lines were regarded as isogenic lines of T 65 having interchanges or the marker gene.

Three-way crosses RT-lines/T 65·ER-1//T 65 were observed to examine the linkage relations between heading time and breakpoints. The linkage relation between heading time and *fgl* was also tested by the three-way cross T 65·*fgl*/T 65·ER-6//T 65. The genotype for *fgl* of each plant was estimated by testing 30 selfed seedlings per three-way-cross F₁ plant.

Linkage intensities between two genes, *pgl* and *fgl*, and breakpoint 2-7 a, were examined in the F₂ plants of T 65·*pgl*/RT 2-7 a·T 65 and T 65·*fgl*/RT 2-7 a·T 65.

The experimental plants were grown in the first and the second cropping seasons in 1980 to 1986 in the experimental field of College of Agriculture, University of the Ryukyus (26°16' N). Seeding date was February 1st to 14th for the first cropping, and was August 1st for the second. Seedlings at about 4.5 leaf age were transplanted with a 15×20 cm spacing. Fertilizers (1.2 kg/a each of N, P₂O₅ and K₂O) were applied at a ratio of 5 : 3 : 2 for basal, and first and second top dressings.

The heading time of a main culm was recorded except for B₆F₁, B₅F₂ and B₆F₂ plants segregating for interchange breakpoint 3-7, in which the date of emergence of the first panicle was recorded as heading date. The segregation patterns for heading time in the first cropping season were bimodal and continuous, but those in the second were discontinuous. For the plants remaining undecided whether they were early or late-heading types, progeny test was made with 5 selfed progenies per individual.

Three chromosomal types of interchanges in segregating populations are distinguishable by seed fertility; interchange heterozygotes are semisterile, while interchange homozygotes and the normal are fertile.

Linkage intensities were calculated from the F₂ and B_nF₂ data by the product method (JOACHIM 1947), and those from three-way cross, backcross and B_nF₁ data were obtained

by the maximum likelihood method (FISHER 1928).

Results

Gene analysis of heading time is shown in Table 2. Segregation of heading time in the F_1 's of T 65·ER-1/T 65//T 65 and successive backcrosses (B_nF_1) which were bred parallel with T 65·ER-1, fitted a 1 early : 1 late ratio which is expected by postulating one gene segregation, except for B_8F_1 . The biased data in B_8F_1 seemed to be accidental error, since the segregation in grand total of the above data fitted the 1 early : 1 late ratio, also. The F_2 plants of T 65·ER-1/T 65 and successive backcrosses were segregated

Table 2. Gene analysis of heading time

A : T 65·ER-1					
Generation and cross-combination	Number of plants			Expected ratio	χ^2 value (d. f. =1)
	Early	Late	Total		
B_7F_1	39	39	78	1 : 1	0.000
B_8F_1	166	215	381	1 : 1	6.302*
B_9F_1	148	160	308	1 : 1	0.468
F_1 (T 65·ER-1/T 65//T 65)	526	522	1,048	1 : 1	0.015
Grand total	879	936	1,815	1 : 1	1.790
B_5F_2	222	79	301	3 : 1	0.249
B_6F_2	162	51	213	3 : 1	0.127
B_7F_2	285	81	366	3 : 1	1.607
B_7F_2	263	113	376	3 : 1	5.121*
F_2 (T 65·ER-1/T 65)	361	126	487	3 : 1	0.198
Grand total	1,293	450	1,743	3 : 1	0.621
F_1 (T 65·ER-1/T 65//T 65·ER-1)	368	0	368	1 : 0	
B : T 65·ER-5					
Cross-combination	Number of plants			Expected ratio	χ^2 value (d. f. =1)
	Early	Late	Total		
F_1 (T 65·ER-5/T 65//T 65)	215	245	460	1 : 1	1.957
C : T 65·ER-6					
Generation	Number of plants			Expected ratio	χ^2 value (d. f. =1)
	Early	Late	Total		
B_6F_1	38	40	78	1 : 1	0.051
B_7F_1	287	256	548	1 : 1	1.770
B_8F_1	222	226	448	1 : 1	0.036
Grand total	547	520	1,067	1 : 1	0.666
B_6F_2	269	85	354	3 : 1	0.185
B_7F_2	318	113	431	3 : 1	0.341
Grand total	587	198	785	3 : 1	0.021

* : Significant at the 5% level.

Table 3. Distribution of heading time in F₁ generation of three early-heading lines/T 65·ER-1//T 65

Cross-combination	Cropping season	Seed fertility	Number of plants heading on																										Total plants	χ^2 value (1:1)		
			Sep. 29		Oct. 1		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23			24	25
T 65	2nd '84												6	8	9	6	6	2	2												39	
T 65· <i>Ef_I^b</i>							19	15	5																						39	
T 65·ER-1							2	14	17	6	1																				40	
F ₁ (T 65· <i>Ef_I^b</i> /T 65·ER-1)							7	6	6	1																					20	
F ₁ (T 65· <i>Ef_I^b</i> /T 65·ER-1//T 65)							4	23	94	119	42	8																			290	
T 65	2nd '84 ¹⁾																1	4	9	16	17	23	6	6	1	3	2				88	
T 65·ER-1							3	14	28	23	13	7	2																		90	
F ₁ (T 65·ER-5/T 65·ER-1//T 65)		Fertile					3	37	39	17	3	3																			102	0.043 ²⁾
		Semisterile					10	36	37	15	4	2	1																		105	
T 65	2nd '85												1	1	3	7	8	7	9	6	4	3	1								50	
T 65·ER-6							1	3	2	3	1																				10	
T 65·ER-1							1	2	5	14	5	1	2																		30	
F ₁ (T 65·ER-6/T 65·ER-1)							2	5	1	1	1																				10	
F ₁ (T 65·ER-6/T 65·ER-1//T 65)							2	9	28	64	69	39	23	1																	235	

¹⁾ Plants were grown in netted field (shading rate was about 20%).²⁾ Degree of freedom was 1.

into a 3 early : 1 late ratio. The second trial of B_7F_2 was an exception. The biased data seemed to occur occasionally from the same reason mentioned above. All the F_1 plants from T 65·ER-1/T 65//T 65·ER-1 showed early heading and no trace of segregation. It was, then, asserted that T 65·ER-1 had a dominant earliness gene. The F_1 plants of T 65·ER-5/T 65//T 65 segregated into 1 early : 1 late. Successively backcrossed F_1 plants which were obtained parallel with T 65·ER-6 showed a 1 early : 1 late ratio and the F_2 plants showed a 3 early : 1 late ratio. Therefore, T 65·ER-5 and T 65·ER-6 were asserted to possess a dominant earliness gene.

The allelic relationships among the earliness genes carried by four lines, T 65·ER-1, T 65·ER-5, T 65·ER-6 and T 65· Ef_1^b , were examined. The results are shown in Table 3. Heading time in each of F_1 's of three-way crosses distributed in a narrow range as that of their early-heading parents, showing no segregation. This shows that these early-heading lines have alleles of similar action located at the same locus. Since T 65· Ef_1^b has the allele Ef_1^b on the locus Ef_1 , the earliness genes carried by these early-heading lines were determined to be alleles on the locus. Segregation for fertility in the F_1 plants of T 65·ER-5/T 65·ER-1//T 65 also fitted a 1 fertile : 1 semisterile ratio, as expected.

Heading time of every line grown in netted field (shading rate was about 20%) was significantly later than that in a open field (Table 3).

The relationships of Ef_1 with seven interchange breakpoints involving the 7th chromosome and with two genes locating on this chromosome were tested by the data of three-way-cross F_1 , backcross, B_nF_1 and B_nF_2 populations. As shown in Table 4, the chi-square values for independence were significant at the 0.1% level. This indicates that the Ef_1 gene was located on the 7th chromosome, because these interchanges are involved in this chromosome. Table 5 shows the linkage relation between Ef_1 and an interchange breakpoint 3-7. Recombination values of 8.1 and 7.5% between them were obtained from B_nF_1 and B_nF_2 data, respectively. A weighted mean of 7.8% was obtained from the two sorts of data. As shown in Table 6, recombination values between Ef_1 and other six breakpoints, 7-11, 6-7, 7-8 b, 7-9, 7-8 a and 2-7 a, were estimated to be 2.2, 3.0, 11.9,

Table 4. Test of independence between Ef_1 , and seven interchange breakpoints and two marker genes

Breakpoint and marker gene	χ^2 value (d. f. = 1)	Cross observed
2-7 a	78.123***	F_1 of three-way cross
3-7	539.047***	B_nF_1
	240.527***	B_nF_2
6-7	378.576***	F_1 of three-way cross
7-8 a	115.396***	F_1 of three-way cross
7-8 b	274.576***	F_1 of three-way cross
7-9	107.947***	F_1 of three-way cross
7-11	420.870***	B_1F_1
<i>pgl</i>	93.341***	B_nF_1
<i>fgl</i>	212.752***	F_1 of three-way cross

*** : Significant at the 0.1% level.

Table 5. Linkage relation between *Ef₁* and interchange breakpoint 3-7

Generation	Number of plants ¹⁾					Recombination value (%)	χ^2 value (d. f. =3)
	EF	ES	LF	LS	Total		
B ₇ F ₁	3 (3.5) ²⁾	36 (35.5)	35 (35.5)	4 (3.5)	78	9.0±3.2	0.157
B ₈ F ₁	13 (14.0)	153 (176.5)	200 (176.5)	15 (14.0)	381	7.3±1.3	6.401
B ₉ F ₁	15 (13.5)	133 (140.5)	148 (140.5)	12 (13.5)	308	8.8±1.6	1.134
Grand total	31 (31.0)	322 (352.5)	383 (352.5)	31 (31.0)	767	8.1±1.0	5.278
B ₅ F ₂	78 (90.6)	144 (135.2)	60 (59.9)	19 (15.3)	301	11.5±2.7	3.220
B ₆ F ₂	62 (60.6)	100 (99.1)	44 (45.9)	7 (7.4)	213	7.5±2.6	0.141
B ₇ F ₂	95 (102.1)	190 (172.4)	70 (80.9)	11 (10.6)	366	6.2±1.8	3.774
B ₇ F ₂	91 (103.9)	172 (178.1)	100 (84.1)	13 (9.9)	376	5.6±1.7	5.788
Grand total	326 (357.6)	606 (584.4)	274 (270.4)	50 (43.6)	1,256	7.5±1.1	4.578

Weighted mean of recombination value=7.8%

¹⁾ EF, ES, LF and LS indicate early-fertile, early-semisterile, late-fertile and late-semisterile plants, respectively.

²⁾ Number in parenthesis shows the expected value calculated on the basis of recombination value.

Table 6. Linkage relations between *Ef₁* and six interchange breakpoints

Breakpoint	Number of plants ¹⁾					Recombination value (%)	χ^2 value (d. f. =3)
	EF	ES	LF	LS	Total		
2-7 a	164 (151.5) ²⁾	57 (60.5)	64 (60.5)	139 (151.5)	424	28.5±2.2	2.468
6-7	210 (208.0)	10 (6.5)	3 (6.5)	206 (208.0)	429	3.0±0.8	3.808
7-8 a	212 (183.5)	67 (64.0)	61 (64.0)	155 (183.5)	495	25.9±2.0	9.134*
7-8 b	209 (208.0)	27 (28.0)	29 (28.0)	207 (208.0)	472	11.9±1.5	0.081
7-9	141 (145.0)	48 (44.0)	40 (44.0)	149 (145.0)	378	23.3±2.2	0.948
7-11	8 (5.0)	207 (225.0)	243 (225.0)	2 (5.0)	460	2.2±0.7	6.480

* : Significant at the 5% level.

¹⁾ EF, ES, LF and LS indicate early-fertile, early-semisterile, late-fertile and late-semisterile plants, respectively.

²⁾ Number in parenthesis shows the expected value calculated on the basis of recombination value.

Table 7. Linkage relations between *Ef₁* and two genes, *pgl* and *fgl*

Gene pair	Phase	Number of plants ¹⁾					Recombination value (%)	χ^2 value (d. f. = 3)
		AaBB	AaBb	aaBB	aaBb	Total		
<i>Ef₁-pgl</i>	Repulsion	81	196	179	72	528	29.0 $\pm$ 2.0	1.300
		(76.5) ²⁾	(187.5)	(187.5)	(76.5)			
<i>Ef₁-fgl</i>	Coupling	175	36	32	200	443	15.3 $\pm$ 1.7	1.902
		(187.5)	(34.0)	(34.0)	(187.5)			

¹⁾ A, B : Dominant genes. a, b : Recessive genes.

²⁾ Number in parenthesis shows the expected value calculated on the basis of recombination value.

Table 8. Linkage relations between a breakpoint 2-7a and two genes, *pgl* and *fgl*

Marker gene	Number of plants ¹⁾					Recombination value (%)	χ^2 value (d. f. = 3)
	AF	AS	aF	aS	Total		
<i>pgl</i>	187	207	67	67	528	$\geq$ 50.0	1.051
	(198.0) ²⁾	(198.0)	(66.0)	(66.0)			
<i>fgl</i>	114	122	40	30	306	31.8 $\pm$ 6.8	0.769
	(109.7)	(119.8)	(43.3)	(33.2)			

¹⁾ AF, AS, aF and aS indicate dominant-fertile, dominant-semisterile, recessive-fertile and recessive-semisterile, respectively.

²⁾ Number in parenthesis shows the expected value calculated on the basis of recombination value.

23.3, 25.9 and 28.5, respectively.

When these recombination values were used for calculating the expected values, the observed numbers showed a good fitness to the expected numbers (Tables 5 and 6). The three-way cross involving interchange homozygote RT 7-8 a · T 65 was an exception, possibly because some bias in segregation occurred occasionally for *Ef₁*.

Linkage relations between *Ef₁* and two chlorophyll-mutant genes, *pgl* and *fgl* were shown in Table 7. *Ef₁* was linked with two genes, *pgl* and *fgl*, recombination values being 29.0 and 15.3%, respectively. Taking their recombination values in account, observed segregation patterns fitted the expected ones well.

As shown in Table 8, linkage intensities for 2-7 a—*pgl* and 2-7 a—*fgl* were estimated to be 50.0 and 31.8%, respectively.

Discussion

The variation of heading time in a hybrid population is often continuous, even if it was controlled by a small number of major genes. Isogenic lines with particular heading-time genes are useful for gene analysis, as proposed by TSAI (1976).

This study aimed at not only mapping the earliness gene on NISHIMURA's 7th chromosome found by SATO and SHINJO (1983), but also comparing it with the *Ef₁* gene detected by TSAI and OKA (1965, 1966, 1968), and TSAI (1973). Therefore, it was necessary in this study to breed isogenic lines with the same genetic background as that of the early-heading isogenic line bred by TSAI and OKA. Then, we developed three isogenic lines of T 65 with the earliness gene on the 7th chromosome which was derived from three

donors, i. e., two interchange homozygotes including the chromosome, T 3-7 and RT 7-11 and a linkage tester HO 775 having a marker gene *pgl* on it, by nine or ten backcrosses with T 65. We selected early-heading plants in early backcross generations with the aid of close linkages of earliness with the cytological and genetical markers, i. e., the interchange breakpoints 3-7 and 7-11 and the gene *pgl* by the same method proposed by YOKOO *et al.* (1979, 1980). The selection was repeated until the progeny showed a bimodal distribution for heading time. Then, respective recombinants were selected and backcrossed successively with T 65.

Ef₁ was considered to locate on the 9th chromosome, since TSAI (1973) reported that it was linked with the marker gene *la* (lazy growth habit) of the 7th linkage group of NAGAO and TAKAHASHI's, and IWATA and OMURA (1971) and SATO (1976) reported that *la* was carried by the 9th chromosome. However, it was concluded in this study that *Ef₁* was located on the 7th chromosome, since it was clearly linked with each of seven interchange breakpoints involving the chromosome, and two genes on it. It is not doubtful that the gene *la* is located on the 9th chromosome. The linkage observed between *Ef₁* and *la* was spurious, as the recombination value of 38% obtained by TSAI (1973) was considerably large.

It was estimated that three genes, *pgl*, *Rf₁* (fertility-restoring gene) and *fgl* were linked in the order (SHINJO 1975). The linkage intensity 29.0% for *pgl*—*Ef₁* was larger than that 11.9% for *fgl*—*Ef₁* and 20.4% for *pgl*—*fgl* (SHINJO 1975). Then, the arrangement of these four genes was estimated as *pgl*—*Rf₁*—*fgl*—*Ef₁*. The breakpoint 7-8 b was located between two genes, *pgl* and *Rf₁* (SATO and SHINJO 1985). It was postulated in this study that breakpoint 7-8 b existed on the chromosomal segment between *pgl* and *Ef₁*, as the recombination value between these two genes was considerably larger than each of values between the genes and the breakpoint, namely, values for *pgl*—7-8 b and for *Ef₁*—7-8 b was obtained as 3.6 and 11.9%, respectively (SATO and SHINJO 1985). If the arrangement of genes and breakpoints was determined on the basis of a simple comparison of recombination values, it may be considered as *fgl*—7-8 b—*Ef₁*, since values for *fgl*—7-8 b (2.1%, SATO and SHINJO 1985) and for *Ef₁*—7-8 b were smaller than that for *fgl*—*Ef₁* (15.3%). However, the recombination considerably reduces near the breakpoint, when the interchange exists in the heterozygous state (SATO 1976). Thus, the order of *pgl*—7-8 b—*fgl*—*Ef₁* was estimated. Two breakpoints, 6-7 and 7-11, were closely linked with *Ef₁*, recombination values being 3.0 and 2.2%, respectively. Then, these breakages were near the gene. Since the linkage intensity for *fgl*—7-11 was reported to be 4.3% (SATO and SHINJO 1985), and this value as well as that for 7-11—*Ef₁* was much smaller than that for *fgl*—*Ef₁*, the breakpoint 7-11 was considered to be located between these two genes. The recombination value between *fgl* and *Ef₁* in the heterozygous condition for breakpoint 7-11 was calculated as about 6.3%, based on values between the genes and breakpoint 7-11. The value was smaller than that for *fgl*—6-7 (10.4%, SATO and SHINJO 1985). Then, breakpoint 6-7 was estimated to locate on the distal segment of the *Ef₁* locus. Two breakpoints, 2-7 a and 3-7 were also considered to be located on the distal side of the *Ef₁*, from the comparison of linkages between four genes, *pgl*, *Rf₁*, *fgl* and *Ef₁*, and each of two breakpoints, 2-7 a and 3-7. It is evident that two breakpoints,

7-8 a and 7-9, are not located on the segment between two genes, *pgl* and *Ef₁*. However, it was not determined on which of distal segments they were located, from recombination values between two genes, *pgl* and *Ef₁*, and these two breakpoints. This suggests that recombination values between genes and breakpoints from the *F₂* data tend to lack preciseness when they are larger than about 25%. Linkages between *Rf₁* and six breakpoints were obtained from three-way crosses (SATO and SHINJO 1985) and the two sorts of data were used for determining chromosomal location of two breakpoints 7-8 a and 7-9. Recombination values between *Rf₁* and two breakpoints 7-8 a and 7-9 were larger than those between *Ef₁* and these two breakpoints, respectively. These two breakpoints were, then, located on the distal segment of the *Ef₁* locus. The order of *Ef₁* and five breakpoints locating on the distal side was considered as *Ef₁*-6-7-3-7-7-9-7-8 a-2-7 a, from the comparison of values between *Ef₁* and these breakpoints.

Based on the discussion mentioned above, a linkage map of the 7th chromosome including four genes and seven interchange breakpoints was constructed as shown in Fig. 1.

YOSHIMURA *et al.* (1982) observed linkages of the *rk₂* (round kernel) gene with four breakpoints used in this study, 2-7 a, 7-8 a, 7-9 and 7-11, recombination values being 0.8, 4.2, 2.5 and 16.4%, respectively. This shows that *rk₂* is located near breakpoint 2-7 a, and suggests that the order of two breakpoints, 7-8 a and 7-9 are reversible, for the recombination value between *rk₂* and 7-8 a was slightly larger than that between the gene and 7-9.

Summarizing the results mentioned above, it was concluded that the earliness gene(s) detected by SATO and SHINJO (1983) which was considered to occupy the different locus from that of *Ef₁* (SATO and SHINJO 1983), is identical or isoallele to *Ef₁^b* on the *Ef₁* locus, and that the locus locates on the 7th chromosome. The linkage order of four genes on the chromosome and seven interchange breakpoints including *Ef₁* was estimated as *pgl*-7-8 b-*Rf₁*-*fgl*-7-11-*Ef₁*-6-7-3-7-7-9-7-8 a-2-7 a.

Fig. 1. Linkage map of the seventh chromosome.

1) and 2) : Quoted from SHINJO (1975) and SATO and SHINJO (1985), respectively.

The basic vegetative growth is one of important agronomic characters. However, informations of genes responsible for the trait were not sufficient, namely, three genes, *Ef₁*, *If₂* (late flowering, TSAI 1985 b) and *m-Ef* (a modifier gene to *Ef₁*, on the 10 th chromosome, TSAI 1985 a) were detected only. Segregations on the trait can not be always explained fully with above three genes. It is, then, necessary hereafter to identify new other earliness genes.

Acknowledgments

We express our hearty thanks to Prof. C. SHINJO, University of the Ryukyus, Dr. H. I. OKA, National Institute of Genetics, Misima and Associate Prof. K. H. TSAI, National Chung-Hsing University, Taiwan for their invaluable suggestions and advice during the course of the experiment. This work was partly supported by a grant from the Ministry of Education, Science, and Culture of Japan.

Literature Cited

- CHANG, T. T., C. C. LI and B. S. VERGARA. 1969. Component analysis of duration from seeding to heading in rice by the basic vegetative phase and the photoperiod-sensitive phase. *Euphytica* **18** : 79~91.
- IWATA, N. 1970. Cytological studies on the progenies of rice plants exposed to atomic radiation in Nagasaki. *Sci. Bull. Fac. Agr., Kyushu Univ.* **25** : 1~53.
- and T. OMURA. 1971. Linkage analysis by translocation method in rice plants (*Oryza sativa* L.). II. Linkage groups corresponding to the chromosome, 5, 6, 8, 9, 10 and 11 *Sci. Bull. Fac. Agr., Kyushu Univ.* **25** : 137~153.
- FISHER, R. A. 1928. Statistical methods for research workers. Second edition. Edinburgh : Oliver Boyd.
- JOACHIM, G. S. 1947. The product method of calculating linkage from *F₂* data involving semisterility ; and its application to a barley translocation. *Genetics* **32** : 580~591.
- NAGAO, S. and M. E. TAKAHASHI. 1963. Genetical studies on rice plant, XXVII. Trial construction of twelve linkage groups in Japanese rice. *J. Fac. Agr., Hokkaido Univ.* **53** : 72~130.
- NISHIMURA, Y. 1961. Studies on the reciprocal translocation in rice and barley *Bull. Natl. Inst. Agric. Sci., Japan Ser. D* **9** : 171~235.
- SATO, S. 1976. Linkage analysis of rice plant, by the use of reciprocal translocation lines. *Bull. Coll. Agr., Univ. Ryukyus* **23** : 73~104.
- , T. KINOSHITA and M. E. TAKAHASHI. 1975. Genetical studies on rice plant, LXII. Linkage analysis of rice plant by the use of reciprocal translocation lines induced from linkage testers. *Memo. Fac. Agr., Hokkaido Univ.* **9** : 193~199.
- and C. SHINJO. 1983. An experiment of genetic study on heading time in rice, *Oryza sativa* L. *Bull. Coll. Agr., Univ. Ryukyus* **30** : 145~153.
- and ———. 1985. Construction of a new linkage group corresponding to the Nishimura's seventh chromosome in rice, *Oryza sativa* L. *Bull. Coll. Agr., Univ. Ryukyus* **32** : 11~19.
- SHINJO, C. 1975. Genetical studies of cytoplasmic male sterility and fertility restoration in rice, *Oryza sativa* L. *Bull. Coll. Agr., Univ. Ryukyus* **22** : 1~57.
- TSAI, K. H. 1973. Comparison of intra-allelic structure related to the major earliness genes involving in isogenic and radiation-induced early-maturing lines of a rice variety, Taichung 65. *J. Agric. Assoc. China, N. S.* **84** : 23~47.
- . 1976. Studies on earliness genes in rice, with special reference to analysis of isoalleles at the *E* locus. *Jpn. J. Genet.* **51** : 115~128.
- . 1985 a. Genic analysis of the emphatic gene, *m-Ef*, of early-flowering in rice. *J. Agric. Assoc. China, N. S.* **130** : 1~15.
- . 1985 b. Analysis of genes for late heading in rice. *In* New Frontiers of Breeding Research. *Proc. Intern. Congr. SABRAO*, p. 221~236. Kasetsart Univ. Bangkok.

- and H. I. OKA. 1965. Genetic studies on yielding capacity and adaptability in crop plants. 1. Characters of isogenic lines in rice. Bot. Bull. Acad. Sinica **6**: 19~31.
- and ———. 1966. Ditto. 2. Analysis of genes controlling heading time in Taichung 65 and other rice varieties. Bot. Bull. Acad. Sinica **7**: 54~70.
- and ———. 1968. Ditto. 3. Further observation on the effect of an earliness gene, *E*, in the genetic background of a rice variety, Taichung 65. Bot. Bull. Acad. Sinica **9**: 75~78.
- YOKOO, M., F. KIKUCHI and A. NAKANE. 1979. Genic analysis of heading time by aid of close linkage with blast resistance in rice. JARQ. **13**: 215~221.
- , ———, ——— and H. FUJIMAKI. 1980. Genetical analysis of heading time by aid of close linkage with blast resistance in rice. Bull. Natl. Agric. Sci., Japan Ser. **D 31**: 95~126.
- YOSHIMURA, A., N. IWATA and T. OMURA. 1982. Linkage analysis by reciprocal translocation method in rice plants (*Oryza sativa* L.). III. Marker genes located on chromosomes, 2, 3, 4 and 7. Japan. J. Breed. **32**: 323~332.

イネ早生遺伝子 *Ef₁* 座の同定

佐藤茂俊・坂本一朗・白川浩二・仲宗根智

(琉球大学農学部, 沖縄県西原町, 〒 903-01)

イネ第7染色体に座乗する早生遺伝子がこれまでに見出されている(佐藤・新城 1983). この早生遺伝子と蔡・岡(1968)が報告した早生遺伝子 *Ef₁^b* との関係を調べるとともに, この早生遺伝子の染色体上の位置を決めることを目的として, 相互転座系統 T 3-7 と RT 7-11 ならびに標識遺伝子系統 HO 775 を早生遺伝子の供与親とし, 台中 65 号を反復親とする 9 ないし 10 回の連続戻し交雑により, 早生の同質遺伝子系統 T 65-ER-1, T 65-ER-5 および T 65-ER-6 を育成した. T 3-7 は北海道の在来イネ品種である黒色稲-2 をガンマー線処理して作出された系統であり(佐藤ら 1975), RT 7-11 は長崎の原爆被曝イネから見いだされた系統である(岩田 1970). また, HO 775 は第7染色体に座乗する淡緑色葉遺伝子 *pgl* を持つ標識遺伝子系統である. なお, B₅F₁ までの初期世代では出穂期と転座点あるいは *pgl* との連鎖を利用することにより, 第7染色体の早生遺伝子を確実に選抜した.

出穂期の遺伝分析の結果, 上記の3早生系統はいずれも第7染色体に属する1対の完全優性の早生遺伝子をもつことを明らかにした. これら3系統ならびに TSAI (1976) の育成した北海道在来のイネ品種である坊主5号に由来する早生遺伝子 *Ef₁^b* を持つ同質遺伝子系統の間で早生遺伝子に関する対立性検定を行なった結果, いずれの早生遺伝子も第7染色体の *Ef₁* 座に存在し, また類似した作用力を持つ遺伝子であることを明らかにした.

第7染色体の相互転座点および標識遺伝子と *Ef₁* の連鎖関係を調べた. *Ef₁* は転座点 7-11, 6-7, 3-7, 7-8b, 7-9, 7-8a および 2-7a とそれぞれ 2.2, 3.0, 7.8, 11.9, 23.3, 25.9 および 28.5% の組換え価で連鎖しており, また *fgl* (退緑色葉) および *pgl* とともに 15.3 および 29.0% の組換え価でそれぞれ連鎖していることを明らかにした. したがって, 蔡(1973)は *Ef₁^b* と第9染色体のもつれ性遺伝子 *la* との連鎖を報告したが, それは見掛けの連鎖であったと本研究の結果から推察した.

先に報告された SHINJO (1975) および佐藤・新城(1985)の成績と本実験の成績を併せ考え, *Ef₁*, *pgl* および *fgl* の3遺伝子, ならびに稔性回復遺伝子 *Rf₁* と転座点の配列は *pgl*-7-8b-*Rf₁*-*fgl*-7-11-*Ef₁*-6-7-3-7-7-9-7-8a-2-7a であると推定した.