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New Certation Gene on the First Linkage Group Found by Inter-subspecific Hybridization of Cultivated Rice

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In the hybrid progenies between Japanese testers and exotic varieties of rice plants, the segregation-distortions of four marker genes belonging to the first linkage group, *wx*, *dp₁*, *alk* and *ws*, were found. From the genetic behaviors of the four characters in F_1 , F_2 , F_3 , F_4 and B_1F_1 , it was concluded that the segregation-distortion was not caused by any of the abnormality of germination of F_1 seeds, duplication of genes themselves, complementary fertility genes and cytoplasmic factors, but caused by the linkage between the marker genes and a certation gene, gametophyte gene (*ga₄*). The recombination value between *ga*, and *wx* was calculated on each of the all cross combinations. Based on the linkage intensities, the pollinating ability of *ga*, against *ga₄⁺* pollen grains at the time of pollination of F_1 plants was also calculated. The presence of gametophyte genes shows at least distinct information regarding reproductive isolation, and the fact that the phylogenetic differentiation widely took place in *Oryza sativa* species.

INTRODUCTION

The segregation-distortion in inter-subspecific hybrid population of rice plants has been observed on many marker genes. Among them, the distorted segregation of *wx* (glutinous or waxy endosperm) and *C* (chromogen for anthocyanin coloration) has been well recognized (Oka, 1953a, b, c; Mizushima and Kondo, 1959, etc.). Two hypotheses have been proposed as to the genetic mechanism operating in this phenomenon, one is caused by the complementary fertility genes (Oka, 1953b), the other by genic or chromosomal duplication (Mizushima and Kondo, 1960; Kondo, 1963).

In the previous papers (Nakagahra, 1972; Nakagahra *et al.*, 1972), the distorted segregation of three genes belonging to the eleventh linkage group, *bc* (brittle culm), *dl* (drooping leaf) and *ck* (chlorina leaf), was reported with the causal genetic mechanism different from the above hypotheses.

The present study deals with the newly found segregation-distortion of three genes in addition to *wx*, all of which belong to the first linkage group, chromosome 6.

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MATERIALS AND METHODS

The genetic testers of the Japanese rice plants (*japonica*) were used as one parent possessing four recessive genes, *wx* (waxy or glutinous endosperm), *dp₁* (depressed palea), *alk* (alkali reaction) and *ws* (white striped leaf), all of which show single recessive inheritance and belong to the first linkage group, the chromosome 6 (Iwata and Omura, 1971). The other parental varieties shown in Table 1 are originated in Continental China, Assam, India, Nepal and Sri Lanka. They are so-called *indica* types except for HO 1021. The variety of HO 1021 is one of the collections from Nepal and is considered to be *japonica*.

Table 1. Parental varieties tested.

Variety		Origin	Subspecies or ecotype
No.	Name		
HO 639	Hong She Zu	Continental China	<i>indica</i> or <i>hsieng</i>
HO 1021	Nepal No. 18	Nepal	<i>japonica</i>
HO 1195	Kasa'ath	Assam	<i>indica</i>
HO 1203	Dakanalo	Sri Lanka	<i>indica</i>
HO 1392	Pusur	India	<i>indica</i> or <i>aus</i>
HO 1405	Surjamukhi	India	<i>indica</i> or <i>aus</i>

In the hybrid progenies between a Japanese genetic tester and a foreign variety, examinations were made in the following items; 1) F_1 fertilities of seeds and pollen grains, 2) segregation mode of *wx* in F_1 pollen grains, 3) F_2 segregation modes of *wx*, *dp*, *alk* and *ws*, 4) relationship between the extent of the distorted segregation and semi-sterility and 5) segregations of *wx* in F_3 , F_4 and B_1F_1 .

RESULTS

1) Breeding of F_1 plants and their fertility

If the hybrid semi-sterility is observed in an F_1 plant of the cross of Japanese tester with a foreign variety and there is the linkage between its causal gene so-called complementary fertility genes and a genetic marker gene, the segregation of the marker would be distorted. In the present study, an apparent semisterility was recognized only in the cross combination of the Japanese tester with HO 639. In F_1 hybrids between a Japanese tester and the other foreign varieties, their seed and pollen fertilities were nearly normal (Table 2).

All of the F_1 plants were normal in appearance but vigorous in growth as compared with the parental varieties. F_2 seeds obtained from each of F_1 plants germinated as good as normal seeds, and F_2 plants survived normally and produced enough F_3 seeds. The difference in fitness of F_2 plants seemed to be negligible.

2) Distorted segregation in F_2

In all of the four marker characters, the segregation modes in F_2 population were skewed from the expectation of single recessive inheritance. The actual

Table 2. Seed and pollen fertilities and ratio of waxy pollen grains in F_1 anthers of the crosses of the Japanese tester (wx wx) with the foreign varieties (wx^+wx^+).

Foreign variety	F ₁ fertility (%)		Frequency of wx pollen (%)
	Seed	Pollen	
HO 639 ¹⁾	41.4	48.3	49.8
HO 1021	Fertile	Fertile	—
HO 1195	94.9	92.4	49.7
HO 1203	97.4	Fertile	49.8
HO 1392	84.2	Fertile ²⁾	
HO 1405	89.4	Fertile ²⁾	50.5

1): HO 639 having wxwx genotype was crossed with the Japanese tester of wxwx genotype.

2): Fertility of pollen grains was complete, but large and small grains were mixed.

Table 3. Distorted segregation of wx for glutinous endosperm in F_2 of Japanese tester (wxwx) \times foreign variety (wx^+wx^+).

Foreign variety	Segregation in F ₂			Frequency of wx (%)	χ^2 for 3 : 1
	wx ⁺	wx	Total		
HO 639 ¹⁾	1,402	18	1,994	27.7	23.4***
HO 1021	116	210	134	13.4	9.6**
HO 1195	1,145		1,355	19.1	65.2***
HO 1203	518	122	640	16.3	12.0***
HO 3392	1,536	299	1,835	19.2	74.2**
HO 1405	232	55	287	19.2	5.2*

*, ** and *** indicate significance at 5, 1 and 0.1% level, respectively.

3) Since HO 639 has wxwx genotype, the segregation mode was shown by the result of the cross, Japanese tester (wx^+wx^+) \times HO 639 (wxwx). In this case, the frequency of the genotypes from the Japanese tester (wx^+wx^+) is reduced, it means that the increment of wxwx plants is the same phenomenon as that of the other cases.

segregation modes of wx are given in Table 3. The "deficit type" of distorted segregation were observed in all cross combinations except for the cross of the Japanese tester with HO 639. Since the foreign variety HO 639 has wxwx genotype, it was crossed with the Japanese tester of wx^+wx^+ genotype. In this case, the segregation-distortion in F_2 appeared as "excess type." This increase in the frequency of wxwx genotype means that the frequency of wx^+wx^+ , the same genotype as the Japanese tester, was decreased in the F_2 population. Therefore the excess type seems to be the same phenomenon as the deficit type. The frequencies of wx in the populations of deficit type varied between 13.4 and 19.2 percent, so that their decrement from normal frequency (25%) ranged from 11.6 to 5.8 percent (Table 3).

In dp , character, the reduction of proportion of the recessive plants was similar to that of wx. Namely, the frequencies of dp_1 plants varied between 13.4 and 19.2 percent (Table 4), but the extent of distortion was rather stronger than that of wx in respective cross.

Table 5 gives the results of another marker gene, *alk*. The frequency of

Table 4. Distorted segregation of *dp₁* for depressed palea in F₂ of Japanese tester (*dp₁dp₁*) X foreign variety (*dp₁⁺dp₁⁺*).

Foreign variety	Segregation in F ₂			Frequency of <i>dp₁</i> (%)	χ^2 for 3:1
	<i>dp₁⁺</i>	<i>dp₁</i>	Total		
HO 639					
HO 1021	672/395	61	834/456	18.4/13.4	18.9***32.9***
HO 1195	1,653	176	1,922	14.0	124.1***
HO 1203	448	128	524	14.5	30.8***
HO 1392	800		928	13.8	62.2***
HO 1405	232	55	287	19.2	5.2*

Table 5. Distorted segregation of *alk* for alkali reaction in F₂ of Japanese tester (*alkalk*) X foreign variety (*alk⁺alk⁺*).

Foreign variety	Segregation in F ₂			Frequency of <i>alk</i> (%)	χ^2 for 3:1
	<i>alk⁺</i>	<i>alk</i>	Total		
HO 639		11		4.7	
HO 1195	748/224	87	835/235	10.4	51.7***
HO 1203					94.7***
HO 1392	295/273	30	345/303	14.9/9.5	20.3***36.8***
HO 1405	978	100	1,078	9.3	142.1***

Table 6. Distorted segregation of *ws* for white striped leaf in F₂ of Japanese tester (*wsws*) X foreign variety (*ws⁺ws⁺*).

Foreign variety	Segregation in F ₂			Frequency of <i>ws</i> (%)	χ^2 for 3:1
	<i>ws⁺</i>	<i>ws</i>	Total		
HO 639	983	129	1,112	11.6	106.5***
HO 1195	1,386	222	1,608	13.8	107.5***
HO 1203	500	110	610	18.0	15.8***
HO 1392	231	61	292	20.9	2.6
HO 1405	206	48	254	18.1	5.0*

the recessive individuals was the lowest in all marker genes used, ranging from 4.7 to 14.5 percent.

In the fourth marker, *ws*, the distorted segregation was also observed, but its reduction was not so notable on the average as compared with that of *alk* (Table 6).

Thus, the apparent segregation-distortion was recognized in all the marker genes of all cross combinations. However, it was simultaneously confirmed that the extent of distortion varied according to difference in the kind of marker genes.

Meanwhile, the gene analysis in the cross between Japanese testers has given the sequence of the four genes being *wx-dp-alk-ws*. The *wx* locus links very closely with *dp*, and *alk* links with *wx* and *ws* with the recombination values of approximately 25 and 14 percent, respectively (Nagamatsu and Omura, 1962; Kudo, 1968).

Then, the relation between gene sequence and the distorted segregation is shown in Fig. 1. The reduction in the frequency of *alk* individuals is larger

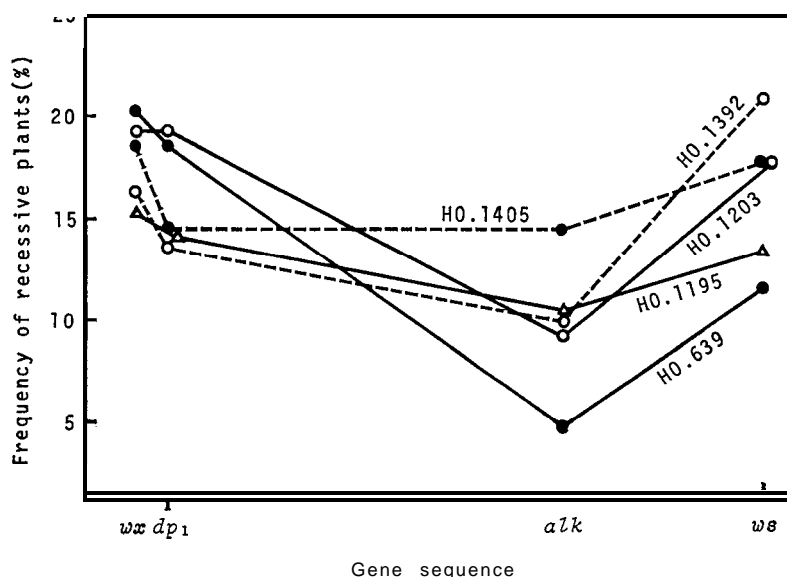


Fig. 1. Relationship between gene sequence and distorted segregation of the four genes on the first linkage group.

than that of any other markers, moreover, the degree of decrease in each character tended to become stronger according as its locus is far distant from *alk* locus. This fact suggests the genic control of the segregation-distortion.

3) Effect of fertility on the distorted segregation

The hybrid-sterility observed in the inter-subspecific cross breeding causes the distorted segregation of marker genes (Oka, 1953a, b). In the present study, semi-sterility was observed in the progenies in and after F_1 generations of the cross of HO 639 with a Japanese marker line, and after F_2 of the cross between a Japanese tester and each of HO 1392 and HO 1405. Assuming that there are some correlation between the semi-sterility and the segregation-distortion in the above cases, it was examined whether or not the segregation for *wx* genotype in F_3 lines is skewed by the degree of the sterility of their parental F_2 plants.

Table 7 shows that the segregation-distortion of *wx* gene was not directly related to the semi-sterility of F_2 individuals. The complementary fertility genes can thus be considered to be independent of the distortion, so that there must be a different factor controlling the phenomenon.

4) Genetic mechanism of the distorted segregation

It now appears, as mentioned above, that none of the following three factors, viz. 1) sterile factors named complementary fertility genes, 2) differential fitness between phenotypes of a marker and its wild alleles, and 3) diversity in the expressiveness of respective marker characters, are causal in the mechanism inducing the distorted segregation. Additionally, the segregation-distortion was not affected in pattern and extent by the reciprocal crosses. Therefore, cyto-

Table 7. The relationship between fertility and frequency of glutinous plants in F_2 segregations of the cross, Japanese tester (wxwx) \times foreign variety (wx^+wx^+).

Variety	No. of crosses	Fertility of $F_2^{(1)}$	No. of genotypes			Frequency of wx+wx (%)	χ^2 for independence
			wx+wx+	wx+wx	Total		
HO 639 ²⁾	3	N			55		
		SS	12	43	69	78.2	
			14	55		79.7	0.000
		S+HS	25	89	114	78.1	(N - S+HS)
		Total	51	187	238	78.6	
HO 1392	2	N	14	19			
		SS	29	42	33	57.6	
		S+HS		84	71	59.2	0.003
			36	99	140	60.0	(N - S+HS)
		Total	50	144	194	60.3	
HO 1405	1	N	35	65			
		SS+S+HS	40	65	105	65.0	0.099
			75	130	105	67.9	(N - SS+S+HS)
		Total	75	130	205	63.4	

1) The symbol of N, SS, S and HS indicates normal fertility (fertile more than 80%), partial sterility (60-80%), semi-sterility (30-60%) and high sterility (less than 30% in fertility), respectively.

2) HO 639 having wxwx genotype was crossed with the Japanese tester of wx^+wx^+ genotype.

plasmic factors also can be considered to have no particular influence on the distortion.

From these facts it would be very reasonable to assume that a certation gene is the main causal factor to induce the segregation-distortion as reported in the previous papers (Nakagahra, 1972; Nakagahra *et al.*, 1972); in which the segregation-distortion of the three markers belonging to the eleventh linkage group (chromosome 5) were dealt with. Further evidence to justify this assumption will be described under. When a marker gene links with such a certation gene as a gametophyte gene, the F_1 male gametes possessing a marker gene will pollinate less to female gametes on account of the strongness of their linkage relationship. Consequently, the frequency of marker plants in an F_2 population will be expected to become lower than normal frequency of 25 percent. In F_3 lines derived from the heterozygous F_2 plants, three different types of segregation modes should appear. The first is the "deficit type," the same segregation as F_2 , the second is the normal one showing the Mendelian expectation, and the third is the "excess type" produced as a result of recombination between a marker gene and a gametophyte gene.

Fig. 2 gives an actual result of the F_3 observation in the cross of the Japanese tester (wx) with HO 1405. Many lines of deficit and normal types appeared, and a few lines of excess type were newly observed.

In the F_4 lines derived from the heterozygous F_3 line of the deficit type, the same results as in the F_3 generation should be expected. On the contrary, in the case of the excess type, most of the lines should be excess and normal types. This expectation was sufficiently justified by the experimental results. The former case is shown in Fig. 3. Many lines of deficit type and several lines of normal type were observed, but excess type expected as a recombinant was not recognized, presumably because the number of F_4 lines used was not enough

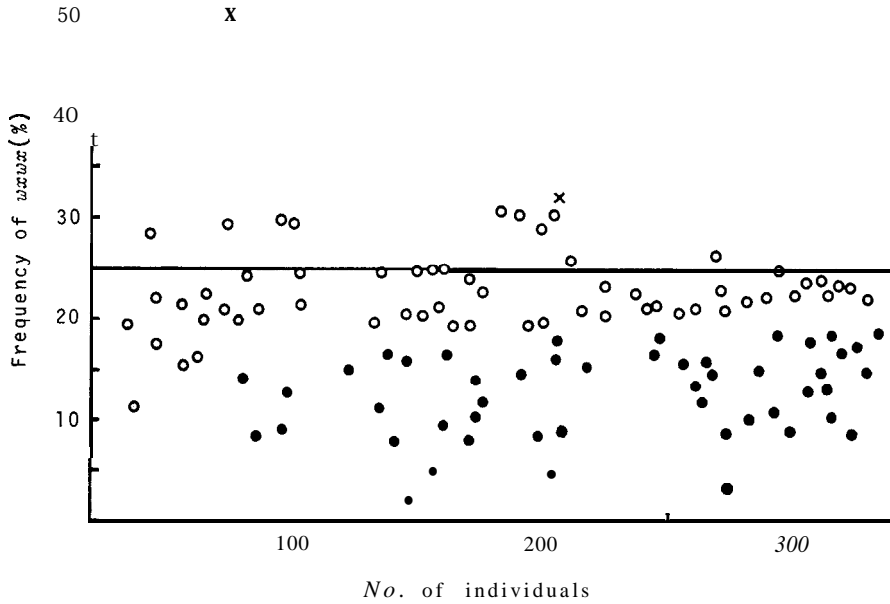


Fig. 2. Segregation pattern of wx in F_3 lines derived from F_2 plants (wx^+wx) of the cross of Japanese tester ($wxwx$) \times HO 1405 (wx^+wx^+), foreign variety.
 ○: Normal type, ●: Deficit type and ×: Excess type of segregations.

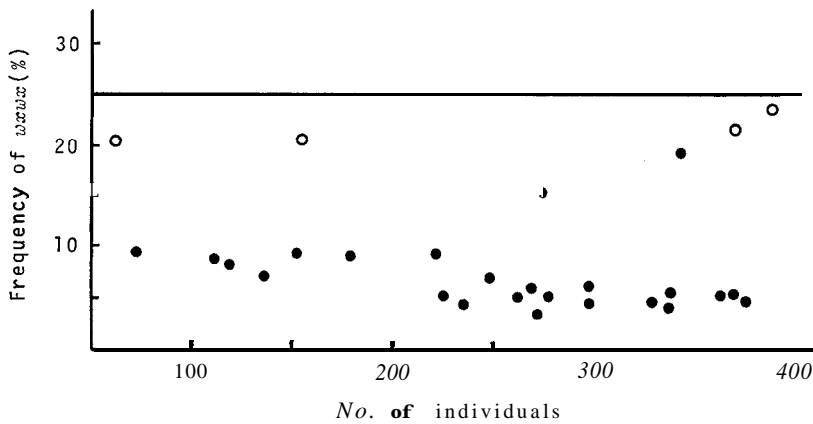


Fig. 3. Segregation pattern of wx in F_4 lines derived from the F_3 line showing the deficit type of segregation. ○: Normal type and ●: Deficit type of segregations.

to contain the lines of the excess type. The latter case is shown in Fig. 4. Both the excess and the normal type were recognized in many F_4 lines, but the deficit type was observed in only two lines.

In addition, an other experiment has also been performed to prove our hypothesis. If the segregation-distortion in F_2 is induced by the linkage between a marker gene and a gametophyte gene, the distortion will also be observed in

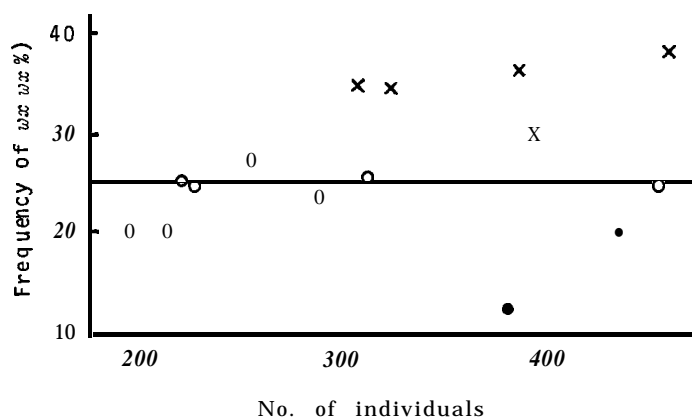


Fig. 4. Segregation pattern of wx in F_4 lines derived from the F_3 line showing the **excess** type of segregation. ○: Normal type, ●: Deficit type and ×: Excess type of segregations.

Table 8. Distorted segregation of wx in B_1F_1 compared with its estimation from F_2 .

Foreign variety	Item	Segregation in B_1F_1			Frequency of wx (%)	χ^2 for 1: 1	χ^2 for Heterogeneity	Distortion type in F_2
		wx^+	wx	Total				
HO 639	Observation	42	60.6	102	58.8	3.176	0.006	Excess
	Estimation	41.4		102.0	59.4	3.614		
HO 1195	Observation	122	54.3	175.0	30.3	27.206***	0.020	Deficit
	Estimation	120.7		175	31.0	25.194***		
HO 1405	Observation	49	41	90.0	45.6	0.711	0.005	Deficit
	Estimation	48.5	41.5		46.1	0.544		

B_1F_1 segregation when the F_1 plant is used as a paternal parent. The actual segregation modes of wx in B_1F_1 and their expectation, which is estimated from F_2 data by the equation given in the previous paper (Nakagahra, 1972), are shown in Table 8. The results show a good fit between the observed and the calculated segregation mode.

These evidences described above certainly reconfirm that the segregation-distortion in the present case is caused by the existence of a gametophyte gene linked with the marker genes examined. Then, the present gametophyte gene is temporarily symbolized as ga . The genotypes concerned with wx and ga , therefore, can be estimated as follows: HO 1021, HO 1195, HO 1203, HO 1392 and HO 1405 are expressed as $wx^+ga_i^+/wx^+ga_i^+$, and their cross pairs, the Japanese testers have the genotype of $wxga_i/wxga_i$. On the contrary, in the cross combination of the Japanese tester x HO 639, the genotype of the tester parent can be put on wx^+ga_i/wx^+ga_i and that of HO 639 $wxga_i^+/wxga_i^+$.

5) Calculation of the recombination value between ga and wx , and of the pollinating ability of ga ,

As the recombination value between wx and ga , cannot be calculated in F_2 , it is done from the frequency of segregation types in F_3 lines. When the

recombination value between ga_4 and wx is put on p , and the number of lines exhibiting deficit, normal and excess types of segregation in F_3 lines is expressed as a , b and c respectively, the recombination value is given by the following equations (Nakagahra *et al.*, 1972). In the case of the cross of $wxga_4/wxga_4 \times wx^+ga_4^+/wx^+ga_4^+$,

$$p = (b+2c) / 2(a+b+c)$$

and in the case of the cross of $wx^+ga_4/wx^+ga_4 \times wxga_4^+/wxga_4^+$,

$$p = (2a+b) / 2(a+b+c)$$

The standard deviation (s_p) is

$$s_p = \sqrt{p(1-p) / 2(a+b+c)}$$

When the recombination value is given by the above formulae, the pollinating ability (k) can be estimated by the following equations (Nakagahra *et al.*, 1972). In the case of the deficit type of distortion,

$$k = (p-2f) / \{2f - (1-p)\}$$

and in the case of the excess type of distortion,

$$k = \{(1-p) - 2f\} / (2f - p)$$

where f is the frequency of recessive individuals in F_2 population.

The recombination values and pollinating ability of ga_4 , calculated by the above formulae are shown in Table 9. The recombination values between ga_4 and wx ranged from 11.8 to 42.9 percent. The pollinating ability of pollen grains with ga_4 , against those with ga_4^+ differed considerably among the parental foreign varieties, but all of them, except for HO 1405, took lower value than 0.5.

Table 9. Recombination value (p) between ga_4 and wx , and pollinating ability (k) of ga_4 .

Foreign variety	No. of lines of segregation types in F_3				Frequency of wx in F_2 (f)	Recombination value (%) (p)	Pollinating ability (k)
	Deficit (a)	Normal (b)	Excess (c)	Total			
HO 639	16	58	31	105	0.297	42.9±3.4	-0.139
HO 1021	34	18	1	53	0.134	18.9±3.8	0.145
HO 1195	60	14	2	76	0.155	11.8±2.6	0.335
HO 1203	51	16	6	73	0.191	19.2±3.3	0.446
HO 1392	26	31	6	63	0.168	34.1±4.2	0.015
HO 1405	63	43	7	113	0.231	25.2±2.9	0.734

DISCUSSION

Two marker genes belonging to the first linkage group, wx and C , have been known to show the segregation-distortion in the progenies of inter-subspecific hybrid of rice plants (Chao, 1928; Oka, 1953a, b, c; Mizushima and Kondo, 1959, 1960, 1961; Kondo, 1963; Kudo, 1968). In the present study, other genes such as dp_1 , alk and ws , all belong to the same linkage group, were supplemented as the new distortion markers.

Concerning the genetic mechanism of the segregation-distortion, Oka (195313) proposed a hypothesis that the distorted segregations of wx and C were

caused by the linkage between these genes and one of the complementary fertility genes, gametic development genes. In the present paper, however, segregation-distortion has appeared differently, indicating that the gene frequency is not concerned with the hybrid sterility. Consequently, it was concluded that the gene frequency of the marker genes belonging to the first linkage group was influenced by a certation gene, named gametophyte gene which linked with the marker genes. The existence of a gametophyte gene in rice plants was first reported by Iwata *et al.* (1964), and the distorted segregations of genes located on the eleventh linkage group were clearly illustrated by the existence of gametophyte genes (Nakagahra, 1972; Nakagahra *et al.*, 1972). Therefore, the gametophyte gene may be generally accepted as a causal factor of the segregation-distortion. The gametophyte gene is distinguishable from the duplicate sterility genes by having the pollinating ability of pollen grains, but more detailed relationship between them should be clarified.

Because the degree of segregation-distortion was stronger in *alk* than in any other genes (Fig. 1), it may be said that *ga₄* is located near the *alk* locus. Moreover, as shown in Table 9, the recombination value between *wx* and *ga₄*, and the pollinating ability of *ga₄* against *ga₄⁺* differed considerably among cross combinations. This fact seems to suggest that "ga," contains some genes, though it was tentatively regarded as single gene. However, it has been well known that the recombination value between certain two genes, and the pollinating ability of a certain gametophyte gene varied on account of the cross combination and environmental factors. Therefore, it remains obscure whether "ga₄" is a gene or genes.

The species of cultivated rice plant, *Oryza sativa* L., has a great number of varieties different in morphological, physiological and biochemical characteristics. The presence of various ecotypes shows that rice plants have a long history of the origin of the species. Therefore, the existence of the gametophyte and the complementary fertility genes must be recognized as one of the results of occurrence of wide differentiation. Further, these genes would give the strong influence on the formation of new ecotypes or subspecies as one of the factors operating on the reproductive isolation.

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