イネの第3連鎖群(第3染色体)に座乗する新しい配偶体遺伝子

誌名	育種學雑誌
ISSN	05363683
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巻/号	35巻1号
掲載ページ	p. 25-31
発行年月	1985年3月

Japan. J. Breed. 35 : 25～31 (1985)

New Gametophyte Genes Located in the Third Linkage Group (Chromosome 3) of Rice

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Distorted segregations of *A* (Anthocyanin activator), *Pn* (Purple node) and *d-18*^{h} (hosetsu-waisei) in the third linkage group (Chromosome 3) were detected in F_2 populations of the crosses between H-50 (*A*, *Pn*$^+$, *lax*$^+$, *d-18*$^{h+}$) and linkage testers. Reciprocal backcrossings indicated that the excess segregation of A^d or A^+ is caused by a gametophyte gene (*ga-7(t)*), and it was assumed that the shortage segregation of *Pn*$^+$ is also due to *ga-7(t)* because of the linkage relation between *A* and *Pn*. Further, it was deduced that the shortage segregation of *d-18*^{h} depends on a gametophyte gene through the backcrossing. Since H-50 carried *A* and *d-18*$^{h+}$, it was obvious that *ga-7(t)* and the gametophyte gene linked with *d-18*^{h} are located on different loci. In F_2 population in which the distorted segregation of A^+ was observed, the segregation of *lax* indicated a good fitness to the monogenic segregation ratio. Therefore, it was apparent that *ga-7(t)* is not identical with *ga-8*. Further, it was estimated that *d-18*^{h} is arranged in the sequence of *lax-A-d-18*^{h}, and the gametophyte gene linked with *d-18*^{h} and *ga-8* are located on different loci. Thus, the gametophyte gene linked with *d-18*^{h} was designated as *ga-9*. From these results, it was concluded that *ga-7* and *ga-9* are new gametophyte genes in the third linkage group (Chromosome 3), and the order of the two gametophyte genes was *ga-9-d-18*^{h}*-Pn-A-ga-7-lax*.

KEY WORDS : rice, distorted segregation, gametophyte gene, gene mapping, third linkage group (Chromosome 3).

Introduction

It is known that the gametophyte genes responsible for differential pollen fertilization have been found in F_2 populations of the crosses between distantly related rice varieties (NAKAGAHRA 1972, NAKAGAHRA *et al.* 1972, MORI *et al.* 1973, NAKAGAHRA *et al.* 1974, NAKAGAHRA 1981) and the crosses involving the materials induced by atomic-bomb or gamma irradiation (IWATA *et al.* 1964, MAEKAWA *et al.* 1981).

Since a gametophyte gene causes a segregation distortion of marker gene linked with it, it is important to elucidate the differentiation of gametophyte genes between *Indica* and *Japonica* or within *Indica* or *Japonica* rice varieties.

In the present study, the authors found that H-50, a linkage tester possessed two gametophyte genes which belonged to the third linkage group (Chromosome 3).

Materials and Methods

Materials used in the present experiment were presented in Table 1. A linkage tester, H-50 was derived from the progeny of the cross, Bunwaigata-motsure x A-58 (Kokusho-kuto-2), and carried C^B, *A*, *Pn*$^+$, *d-18*$^{h+}$ and *lax*$^+$.

A (Anthocyanin activator) at which locus six alleles, A^S, A^E, *A*, A^d, A^m and A^+ are known and *C* (Chromogen for anthocyanin) alleles were responsible for the apiculus coloration (TAKAHASHI 1982). C^B and C^{Bp} produced a purple color by a complementary

Received January 9, 1984.

action with A, and all parents used in the experiment possessed C^B or C^{Bp}. As the genotype of H-50 was C^BA, the segregation of A was simply responsible for the apiculus coloration of anthocyanin in the crosses involving H-50.

Recombination values were caculated by the maximum likelihood method.

Results

1) Distorted segregation of A

F_2 segregations for A of the crosses between H-50 and the testers carrying C^BA^d, C^BA^+ or $C^{Bp}A^+$ were given in Table 2. Since H-50 possessed C^BA, a monogenic segregation ratio, 3 : 1 was expected for $A : A^d$ or A^+ in the F_2 populations. However, the plants carrying A^d or A^+

Table 1. List of linkage testers used in the experiment

Strain	Marker gene
H-50	C^B, A
A-58	C^B, A, Pn
H-59	C^B, A^d
H-61	C^{Bp}, A, Pn
H-69	C^{Bp}, A^+
H-138	C^B, A
N-46	C^{Bp}, A^+
N-71	d-18^h
No. 12	C^B, A^+, lax
No. 1-344	C^B, A, d-18^h
Taichung 65 (T-65)	C^B, A^+

Table 2. F_2 segregations of the gene, A for Anthocyanin activator in the crosses between linkage testers carrying C^BA^d, C^BA^+ or $C^{Bp}A^+$ and H-50 (C^BA) as a male parent

Famale parent	Genotype for apiculus coloration	F_2 segregation		Total	Goodness of fit (3 : 1)		Percentage of A^d or A^+ (%)
		A	A^d or A^+		χ^2	P	
H-59	C^B A^d	210	128	338	29.9	<0.01	37.9
H-138	C^B A^d	191	84	275	4.5	0.025~0.05	30.5
No. 12	C^B A^+	166	100	266	22.5	<0.01	37.6
H-69	C^{Bp} A^+	214	107	321	11.9	<0.01	33.3
N-46	C^{Bp} A^+	173	78	251	4.9	0.025~0.05	31.1
Total		954	497	1451	66.2	<0.01	34.3
				Homogneity χ^2=6.2, d.f.=4, 0.10<P<0.25			
T-65	C^B A^+	127	92	219	33.8	<0.01	42.0
Total		1081	589	1670	93.9	<0.01	35.3
				Homogeneity χ^2=11.1, d.f.=5, 0.025<P<0.05			

Table 3. B_1F_1 segregations of A^d or A^+ in reciprocal crossings between H-69 and (H-69×H-50) F_1, and between H-59 and (H-59×H-50) F_1

Cross combination	B_1F_1 segregation		Total	Goodness of fit (1 : 1)		Percentage of A^d or A^+ (%)
	A	A^d or A^+		χ^2	P	
H-69×(H-69×H-50)F_1 ($C^{Bp}A^+$) ($C^{Bp}A^+$×C^BA)	43	104[1]	147	25.3	<0.01	70.7
Reciprocal	35	27[1]	62	1.0	0.25~0.50	43.5
H-59×(H-59×H-50)F_1 (C^BA^d) (C^BA^d×C^BA)	38	83[2]	121	16.7	<0.01	68.6
Reciprocal	38	39[2]	77	0.0	>0.95	50.6

[1] Carrying A^+, [2] Carrying A^d

increased significantly in F_2s. A homogeneity chi-square value showed a non-significance among five crosses. On the other hand, the F_2 segregation of T-65 × H-50 gave the highest percentage of A^+ (42%) among six crosses and the chi-square value showed a poor homogeneity for F_2 segregation among six crosses.

Reciprocal crossings between H-69 and (H-69 x H-50) F_1 and between H-59 and (H-59×H-50) F_1 were also conducted (Table 3). When F_1 hybrids were used as female parents, monogenic segregations were obtained, while the B_1F_1 segregations from the reciprocal crosses showed a distortion with the higher percentages of A^d or A^+ than the expected values. Further, F_1 hybrids of the crosses between H-50 and linkage testers showed good seed fertility. From these results, it was suggested that the distorted segregation of A^d or A^+ is due to a gametophyte gene, causing probably differential pollen fertilization. Thus, H-50 carried A and *ga-7(t)*, and H-59, H-138, No. 12, H-69, N-46 and T-65 possessed A^d or A^+ and *ga-7(t)*$^+$.

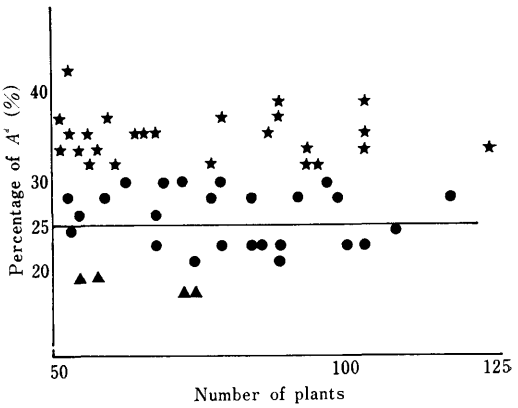

Fig. 1. Frequencies of the percentage of A^d in F_3 progenies derived from heterozygous F_2 plants (AA^d) of the cross, H-138 ×H-50.
Note : ▲ Shortage segregation type (4 lines)
● Normal segregation type (27 lines)
★ Excess segregation type (30 lines)

Recombination value between a gametophyte gene and a marker gene can be estimated from F_3 data when selfing the heterozygous F_2 plants (IWATA *et al.* 1964). If p was designated as a recombination value in the repulsion phase and the observed frequencies of excess, normal and shortage segregation types in F_3 lines were expressed as a, b and c, respectively, then the recombination value was calculated as $p=(2a+b)/2(a+b+c)$ (NAKAGAHRA *et al.* 1972). Among 61 F_3 lines from the heterozygous F_2 plants of the cross, H-138 x H-50, 27 lines showed a normal segregation type within a range of 20 to 30% of the percentage of A^d, as shown in Fig. 1. Four lines belonged to a shortage type and 30 lines to an excess type. Accordingly, the recombination value between A and *ga-7(t)* was calculated to be 28.7±4.1%.

2) Distorted segregation of *d-18*^{h}

Hosetsu-waisei is an extremely short stature controlled by a single recessive gene, *d-18*^{h} (SHINBASHI *et al.* 1976, SHINBASHI 1982), and the locus of *d-18*^{h} is on the third linkage group (Chromosome 3) (IWATA *et al.* 1979). In F_2 population of the cross between N-71 carrying *d-18*^{h} and H-50, a distorted segregation of *d-18*^{h} was obtained as shown in Table 4. The homogeneity chi-square value for reciprocal crossings between N-71 and H-50 showed no significance and the reciprocal difference was not observed. In B_1F_1 population of the cross, N-71 x (H-50 x N-71)F_1, a shortage segregation type of *d-18*^{h} was shown. Therefore, it was deduced that the distorted segregation of *d-18*^{h} is caused by a gametophyte gene linked with *d-18*^{h}. Since linkage relation between a gametophyte gene and a recessive marker gene in the coupling phase was responsible for the shortage

Table 4. Distorted segregations of hosetsu-waisei, *d-18*^{h} in F_2s of the crosses between N-71 and H-50, and in B_1F_1 of N-71×(H-50×N-71)F_1

Cross combination	Phenotype: Normal (*d-18*$^{h+}$)	Phenotype: hosetsu-waisei (*d-18*^{h})	Total	Goodness of fit (3 : 1): χ^2	Goodness of fit (3 : 1): P	Percentage of *d-18*^{h} (%)
F_2 population						
N-71×H-50	266	43	309	20.3	<0.01	13.9
H-50×N-71	540	64	604	66.8	<0.01	10.6
Total	806	107	913	85.9	<0.01	11.7
			Homogeneity χ^2=2.2, d.f.=1, 0.10<P<0.25			
B_1F_1 population						
N-71×(H-50×N-71)F_1	174	104	278	17.6[1)]	<0.01	37.4

[1)] Chi-square value for 1 : 1

segregation of the recessive gene in F_2, and H-50 possessed *d-18*$^{h+}$, it was considered that H-50 carried the dominant gene for the gametophyte gene linked with *d-18*^{h}. Consequently, it was obvious that the gametophyte gene which caused the distorted segregation of *d-18*^{h} is located on different locus from *ga-7(t)*. Thus, the genotype of H-50 and N-71 were *d-18*$^{h+}$, ga$^+$ and *d-18*^{h}, *ga*, respectively.

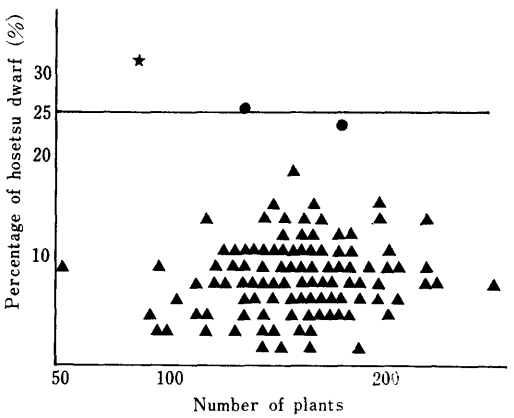

Fig. 2. Frequencies of the percentage of hosetsu dwarf (*d-18*^{h}) in F_3 progenies derived from heterozygous F_2 plants of the cross, N-71×H-50.
Note : ▲ Shortage segregation type (156 lines)
● Normal segregation type (2 lines)
★ Excess segregation type (1 lines)

The recombination value between *d-18*^{h} and *ga* was calculated from the ratio of shortage : normal : excess type in F_3 lines. The frequencies of *d-18*^{h} in 159 F_3 lines were presented in Fig. 2. In this case, the normal segregation type of *d-18*^{h} was entered into the range of 22 to 28%, and the ratio of 1 excess : 2 normal : 156 shortage segregation type was obtained. Thus, the recombination value between the two was estimated to be 1.3±0.6%.

3) Genic identification among the gametophyte genes in the third linkage group (Chromosome 3)

From these results, it was revealed that H-50 possessed the two gametophyte genes, belonged to the third linkage group (Chromosome 3). On the other hand, NAKAGAHRA (1981) reported the existence of *ga-8* from the crosses between *Indica* and *Japonica* varieties, causing the distorted segregations of *eg*, *lax* and *d-10* in the third linkage group (Chromosome 3). In F_2 population of the cross between No. 12 which possessed A^+ and *lax* and H-50, the distorted segregation of A^+ was observed (Table 2). However, the segregation of *lax* showed a good fitness to the monogenic segregation as shown in Table 5. Further, F_2 segregation of *Pn* for Purple node linked with *A*(NAGAO and TAKA-

Table 5. F_2 segregations of *lax* and *Pn* belonging to the third linkage group (Chromosome 3) in the crosses between linkage testers and H-50

Cross combination	Marker gene	F_2 segregation		Total	Goodness of fit (3 : 1)		Precentage of recessive type (%)
		Dominant	Recessive		χ^2	P	
No. 12×H-50	*lax*	194	72	266	0. 6	0. 25～0. 50	27. 0
A-58×H-50	*Pn*	280	54	334	13. 9	<0. 01	16. 2
H-61×H-50	*Pn*	260	53	313	10. 9	<0. 01	16. 9
Total		540	107	647	24. 7	<0. 01	16. 5

Homogeneity $\chi^2=0.1$, d. f. $=1$, $0.75<P<0.90$

Table 6. Combined segregations among *A*, *lax* and *d-18^h* belonging to the third linkage group (Chromosome 3) in F_2 of the cross between No. 1-344 (*A*, *d-18^h*) and No. 12 (*A*$^+$, *lax*)

gene pair		Phase of linkage	F_2 segregation				Total	Goodness of fit (9 : 3 : 3 : 1)		R. C. V. (%)
A	*B*		*AB*	*Ab*	*aB*	*ab*		χ^2	P	
A	*lax*	Coup.	63	20	12	9	104	4. 2	0. 25～0. 50	39. 1±6. 4
A	*d-18^h*	Rep.	65	18	15	6	104	1. 9	0. 50～0. 75	>50
lax	*d-18^h*	Rep.	62	13	18	11	104	5. 6	0. 10～0. 25	>50

[1] Recombination value

HASHI 1963) was examined in the crosses, A-58×H-50 and H-61×H-50. Since A-58, H-50 and H-61 possessed C^BA or $C^{Bp}A$(H-61), the monogenic segregation ratio of 3 *Pn*: 1 *Pn*$^+$ was expected. However, as shown in Table 5, the shortage segregation of *Pn*$^+$ were observed in the two crosses. Because of the linkage relation between *A* and *Pn*, the distorted segregation of *Pn*$^+$ was attributed to *ga-7(t)*. These results demonstrated that *ga-7* and *ga-8* are identified as independent loci.

Linkage relations among *lax*, *A* and *d-18^h* were investigated in F_2 of the cross, No. 1-344(*A d-18^h*)×No. 12 (*A*$^+$ *lax*) (Table 6). Although *lax* was apart from *A* with the recombination value of 39. 1±6. 4%, *d-18^h* was nearly independent from *A* and *lax*. Thus, the sequence of the three genes was considered to be *lax-A-d-18^h*, and it was assumed that *ga-8* which caused the distorted segregation of *lax* did not influence the segregation of *d-18^h*. Accordingly, it was concluded that the *ga* gene which caused the distorted segregation of *d-18^h* is located on different locus from *ga-8* and *ga-7*. Then, we have proposed the new gametophyte gene to symbolize *ga-9*.

Discussion

In rice, seven gametophyte genes were reported hitherto, namely *ga-2* and *ga-3* (NAKAGAHRA *et al.* 1972) in the eleventh linkage group (Chromosome 5), *ga-4* (NAKAGAHRA *et al.* 1974) and *ga-5*(MORI *et al.* 1973) in the first linkage group (Chromosome 6) and *ga-8*(NAKAGAHRA 1981) in the third linkage group (Chromosome 3) which were detected from F_2s of the crosses between *Indica* and *Japonica* rice varieties. On the other hand, *ga-1*(IWATA *et al.* 1964) in the first linkage group (Chromosome 6) and *ga-6*(MAEKAWA *et al.* 1981) in the second linkage group (Chromosome 11) were induced by an atomic-bomb exposure and gamma irradiation of *Japonica* varieties, respectively. The present experiment revealed that two gametophyte genes are located on the third

linkage group (Chromosome 3). One is linked with *A* and *Pn*, and the other linked with *d-18*^{h}. NAKAGAHRA (1981) already reported that *ga-8* is linked with *eg*, *lax* and *d-10* in the third linkage group (Chromosome 3) and the order of the genes is *ga-8-eg-lax-d-10*. In F_2 of the cross between No. 12 and H-50, the distorted segregation of A^+ and the normal segregation of *lax* were observed, and it was estimated that *d-18*^{h} is located in the order of *lax-A-d-18*^{h}. From these results, it was obvious that the loci of *ga-7* and *ga-9* linked with *A* and *d-18*^{h}, respectively are different from that of *ga-8*. Accordingly, the order of the genes concerned in the third linkage group (Chromosome 3) was estimated to be *ga-9-d-18*^{h}*-Pn-A-ga-7-lax*.

MATSUURA *et al.* (1983) found hybrid chlorosis in F_2 populations of the crosses between Japanese rice varieties, and postulated the differentiation of the genes for the hybrid chlorosis within native rice varieties in Japan. Both the gametophyte gene and the hybrid chlorosis are considered to be the barriers for reproductive isolation (NAKAGAHRA *et al.* 1972). H-50, a linkage tester derived from the cross, Bunwaigata-motsure x A-58, carried *ga-7* and *ga-9*$^+$, whereas other linkage testers possessed *ga-7*$^+$ and *ga-9*.

Since in F_2s involving A-58, distorted segregation of *A* and *d-18*^{h} was not observed, it was considered that *ga-7* and *ga-9*$^+$ existed in Bunwaigata-motsure. These results suggested that the gemetophyte genes might be differentiated within Japanese rice varieties.

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イネの第3連鎖群（第3染色体）に座乗する新しい配偶体遺伝子

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標識遺伝子型系統である H-50 (C^B, A, Pn^+, lax^+, $d\text{-}18^{h+}$) と他の数種の標識遺伝子型系統とを交雑した F_2 集団で，第3連鎖群（第3染色体）に所属する A（アントシアニン活性化），Pn（茎葉節紫色）と $d\text{-}18^h$（豊雪矮性）遺伝子の異常分離を見出した．A 遺伝子座については，A^d，A^+ の劣性遺伝子が過剰となり，Pn と $d\text{-}18^h$ 遺伝子座では劣性遺伝子が過少分離を示した．戻し交雑の結果と，F_1 が良好な種子稔性を示したことから，A と $d\text{-}18^h$ の異常分離は花粉の受精競争に起因するもので，配偶体遺伝子の関与していることが判明した．H-50 は A と $d\text{-}18^h$ 遺伝子座に関して優性遺伝子を有しており，F_2 集団で A 遺伝子座の劣性遺伝子が過剰となり，また，$d\text{-}18^h$ 遺伝子が過少となったことから，A と $d\text{-}18^h$ の異常分離にはそれぞれ別の配偶体遺伝子が関与していることは明らかであった．したがって，A と $d\text{-}18^h$ に連鎖する配偶体遺伝子を *ga-7(t)*, *ga* とした．中川原（1981）は既に，第3連鎖群（第3染色体）に *ga-8* が座乗し，*eg*, *lax*, *d-10* と連鎖していることを報告した．そこで，*ga-8* と *ga-7(t)*, *ga* との位置関係を標識遺伝子との連鎖関係から明らかにした．すなわち，A^+ が過剰分離となった F_2 で，*lax* は正常の 3：1 の単遺伝子分離を示した．また，*Pn* 遺伝子の過少分離も A と *Pn* の連鎖関係から *ga-7(t)* によると考えられ，これらのことは，*ga-7(t)* の遺伝子座は *ga-8* 座と異なることを示していた．さらに，$d\text{-}18^h$ 座は *lax-A-d-18*^{h} と推定され，$d\text{-}18^h$ に連鎖する *ga* も *ga-8* とは座を異にしていた．そこで，$d\text{-}18^h$ と連鎖する配偶体遺伝子を *ga-9* とした．以上のことから，第3連鎖群（第3染色体）に新しい配偶体遺伝子 *ga-7* と *ga-9* が座乗し，それぞれの座位は *ga-9-d-18*^{h}*-Pn-A-ga-7-lax* であった．各系統の遺伝子型については H-50 が *ga-7*, *ga-9*$^+$，他の標識遺伝子型系統が *ga-7*$^+$, *ga-9* を有していた．