CHARACTER EXPRESSIONS AND CAUSAL GENES OF SOME MUTANTS IN RICE PLANT[1)]

(Genetical Studies on Rice Plant, XXXIII)

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Received December 11, 1967

Contents

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Introduction

Viable, easily identified mutants are valuable for use in linkage studies and enrich linkage maps. This is one of a series of reports on genic analysis of some mutants in rice plant, spontaneously taken their rise or induced by irradiation, based on a study of crosses with testers of which genic constitutions had been known by the writers and others.

Before going further the writers wish to express their appreciation to Dr. T. KAWAI of the National Institute of Agricultural Science, for giving the writers his own materials which occupy a considerable part of the materials dealt with in the present paper.

Materials and Methods

A majority of mutants of which character expressions are the object of the present examination is obtained from progenies of two rice varieties, Norin-8

TABLE 1. List of mutants of which morphological characteristics are the objects of the present examination

Stock No.	Source	Character expression [1]
M- 5	irradiated Norin-8	brittle culm (MCG-7)
M- 8	ditto	claw-shaped floral glumes (MCG-15)
H-129	E-48×A-31 (Indica×Japonica)	multiform empty glumes
H-131	ditto	ditto, with open tillers and brown spots
H-166	L-34×A-5 (U. S. variety×Japonica)	malformed lemma with high sterility
H- 75	(Indica×Japonica)×Japonica	open tillers of growth habit
H-122	A-13×E-44 (Japonica×Indica)	ditto
M- 19	irradiated Norin-8	spreading growth habit (MCG-181)
N- 62	irradiated Yukara	short stem
M- 15	irradiated Norin-8	dwarf (MCG-106)
M- 17	ditto	ditto (MCG-151)
M- 21	ditto	brown speckles in leaves (MCG-203)
M- 25	ditto	large brown spots in leaves (MCG-207)
M- 26	ditto	ditto (MCG-208)
M- 30	ditto	yellow-spotted leaves (MCG-252)
M- 31	ditto	fine white speckles in leaves (MCG-254)

1) Stock no. or classification no. used by the propositus of the original materials are put in parentheses and have listed them at the end of the descriptive notes of character expression of mutants referred to.

and Yukara. The seeds of these varieties were irradiated with an application of radioisotope ^{32}P and X-ray. The rest of the mutants conducted in the present examination was discovered in progenies from crosses involving Japonica and Indica rice varieties.

Names or stock no.s of these mutants and their ancestral varieties with normal types are as shown in Table 1, together with the concerned characters the mutants have.

These mutants or their derived strains were combined with the writers' testers. Names, character expressions and their causal genes of the testers will be given in the descriptive part where these testers are concerned in.

Experimental Results

A. Brittle culm in M-5

A mutant named M-5 is characterized with its brittle or fragile culm and leaf. When this was crossed with A-5, Akamuro variety of normal culm strength, their F_1 was normal, and the F_2 population segregated into two classes of phenotypes, normal and brittle, in a numerical relation of 243 : 79, which is close to a monogenic segregation of 3 : 1, indicating that the brittleness is resulted by a single recessive gene mutation (Table 2).

A variety known in Japan "Kamairazu (need no sickle)" shows same characteristic as M-5 does. The Kamairazu was found out as a single plant

TABLE 2. F_2 segregation modes in crosses of M-5 (brittle culm mutant) × A-5 (normal) and M-5 × H-9 (brittle culm by *bc* gene)

M-5 (brittle culm)×A-5 (normal)

phenotype	normal	brittle	total	goodness of fit		
genotype	+	*bc*		χ^2	d. f.	p
O.	243	79	322			
C. (3 : 1)	241.5	80.5	322.0	0.04	1	0.8~0.9

M-5 (brittle culm)×H-9 (brittle culm)

phenotype	normal	brittle	total	goodness of fit		
genotype	+ +	bc_1+, $+bc_2$ / $bc_1\ bc_2$		χ^2	d. f.	p
O.	137	96	233			
C. (9 : 7)	131.1	101.9	233.0	0.61	1	0.3~0.5

from the paddy field. This character was confirmed by several workers, to inherit as a simple recessive to the normal type, without exception, and of which responsible gene was designated as *bc*.

In order to identify the genes for these two brittle culm characters, a test cross was made between M-5 and H-9, the latter being a gene stock of the *bc*. The result is as given in the table, where their F_1 is normal and in F_2 9 normal vs. 7 brittle is recognized, indicating that two different gene loci are involved in this cross. Thus it is most probable that the brittleness in M-5 is said to be a newly obtained mutation, while its character expression is identical with the brittleness caused by the *bc*. Henceforth the *bc*, a common basic symbol for brittlness, should be distinguished by numeral as a subscript; bc_1 (H-9's trait) and bc_2 (M-5's trait).

B. Malformed glumes

1. Claw-shaped floral glumes in M-8

A mutant M-8 has claw-shaped spikelet in which the lemma curves over the abbreviated palea. When this was crossed with a tester A-5 of normal spikelet, the F_1 was also normal and the F_2 gave such a segregation as 208 (normal) : 66 (claw-shaped), which showed close accordance with a ratio of 3 : 1 as shown in Table 3.

2. Multiform empty glumes in H-129 and H-131

In common varieties empty glumes are short, about one-third as long as lemma and palea, while in some varieties they are i) as long as, or ii) longer than, the lemma and palea, and further in some varieties iii) their empty glumes are uneven with respect to either side of lemma and palea. It has been revealed by the writers that the type-i and type-ii are governed by two genes, *g* and *Gm* respectively, and type-iii is a result of coexistence of *g* and its suppressor *Su-g*, which exerts its effect on the long empty glume of lemma side (NAGAO. TAKAHASHI and KINOSHITA 1960). Expressivity and penetrance of these genes are constant and high, giving no spikelet which does not show proper expression of characters governed by the respective gene or genes.

Recently the writers found out a plant with singular type of empty glumes, among progenies from a cross of E-48 (a strain, Rokujunichi-Ki-so) × A-31 (a variety, Fukoku), in which both the parents are normal in their empty glumes. Two derivatives were bred true in respect of this character and were assigned their stock numbers as H-129 and H-131. The character expressions of H-129 and H-131 are the same, giving most striking feature in that four kind of spikelets—spikelets with normal short empty glumes, with long empty glumes, with uneven long empty glumes and without empty glumes—are born

TABLE 3. Inheritance modes of claw-shaped floral glumes in M-8, multiform empty glumes in H-129 and H-131, and malformed lemma in H-166

F_2 from M-8 (claw-shaped floral glumes)×A-5 (normal)

phenotype	normal	claw-shaped	total	goodness of fit		
genotype	+	*cls**		χ^2	d. f.	p
O.	208	66	274			
C. (3 : 1)	205.5	68.5	274.0	0.12	1	0.7~0.8

* basic symbol for this kind of character.

F_2 from H-129 (multiform empty glumes)×A-5 (normal) and H-131 (multiform empty glumes) ×A-43 (normal)

phenotype	normal	multiform	total	goodness of fit		
genotype	+ or ++			χ^2	d. f.	p
A-5×H-129						
O.	375	46	421			
C. (3 : 1)	315.7	105.3	421.0	44.47	1	< 0.01
C. (15 : 1)	394.7	26.3	421.0	15.71	1	< 0.01
A-43×H-131						
O.	253	21	274			
C. (3 : 1)	205.5	68.5	274.0	43.92	1	< 0.01
C. (15 : 1)	256.9	17.1	274.0	0.94	1	0.3~0.5

F_2 from L-34 (normal lemma)×A-5 (normal lemma)

phenotype	normal	malformed	total	goodness of fit		
genotype	+ +			χ^2	d. f.	p
O.	265	13	278			
C. (15 : 1)	260.6	17.4	278.0	1.18	1	0.2~0.3

in the same panicle. This abnormal type, provisionally named as "multiform empty glumes", was examined in its inheritance mode, through crosses of A-5 (normal)×H-129 (multiform) and A-43 (a variety Hokkai-mochi-1, normal)× H-131. Their F_1 s were normal and their progenies, F_2 s, were segregated into two types, the normal and the multiform. As shown in Table 3, numerical relations are 375 (normal): 46 (multiform) in A-5×H-129 and 253

(normal) : 21 (multiform) in A-43×H-131. In a monogenic inheritance two types, normal and multiform, should be expected to occur in the relation of 315.7 : 105.3 (A-5×H-129) and 205.5 : 68.5 (A-43×H-131), and to occur in the relation 394.7 : 26.3 (A-5×H-129) and 256.9 : 17.1 (A-43×H-131) when duplicate genes are involved. The actual data, however, did not show any accordance with the expectation from the assumption of monogenic or digenic inheritance either. These are the results obtained from the present examination. But some indications are existent that indicate a possibility of monohybrid segregation, of which causal gene's penetrance is relatively low.

3. Malformed lemma with high sterility in H-166.

In a F_2 population of a cross, L-34 (a U.S. variety)×A-5, certain number of plants which showed a singular type of floral glumes were segregated. Most striking feature of the floral glumes were expressed in their abnormal form of lemma. This deformation usually was accompanied by the relatively low pollen fertility (ranging from 60 to 70%) and very low seed setting percentage (from 0 to 10%). When the F_2 plants were assorted into two types with respect to the normal and the malformed glumes, a numerical relation of 265 vs. 13 was obtained. This shows some agreement of an apriori ratio of 15 : 1, suggesting that each parent possess one of the duplicate genes (Table 3). All of the F_2 segregants with malformed lemma were bred true in the succeeding generation, without producing any other form of the lemma. One of the strains was selected and listed as H-166, for its gene stock number.

C. Growth habit

1. Open tillers in H-75, H-122 and H-131

Normally stem of rice grows upright from the ground, however, one type of growth habit which is called "lazy" has been known. In a lazy plant the stem grows nearly horizontal so that the plant has an extreme spreading or prostrate form. This character is governed by a single recessive gene *la*.

During cross experiment of Japonica×Indica, in progenies from certain cross, the writers found out a couple of plants of which tillers arised at an angle of ca. 60° from the surface of soil, though habit did never took such an extreme spreading form mentioned above. This is temporarily named as "open or medium spreading type" of the growth habit. Strains H-75, H-122 and H-131 are the descendant of the said plants and show the open-type of growth. They were crossed with testers of normal growth habit, A-43 (Hokkaimochi-1, a tester variety), H-127 (a gene stock of color character) and H-163 (ditto). Their F_1 s were open-type and in F_2 generation, throughout all cross combinations, 3 (open) : 1 (erect or nomal) was resulted, of which

numerical data are as given in Tabl 4. The gene for the open type is temporarily designated as *O*.

The *O* was tested for its linkage relationship between some markers. The

TABLE 4. F_2 of crosses between the open type and the normal erect type of growth habit

combination	phenotype	open	erect	total	goodness of fit		
	genotype	*O*	+		χ^2	d.f.	p
H-163×H- 75	O.	243	67	310			
	C.(3 : 1)	232.5	77.5	310.0	1.90	1	0.1~0.2
H-122×H-127	O.	340	116	456			
	C.(3 : 1)	342.0	114.0	456.0	0.05	1	0.8~0.9
A-43×H-131	O.	118	30	148			
	C.(3 : 1)	111.0	37.0	148.0	1.77	1	0.1~0.2
total	O.	701	213	914			
	C.(3 : 1)	685.5	228.5	914.0	1.40	1	0.2~0.3

Homogeneity $\chi^2=2.31$ d.f.=2 p=0.3~0.5

TABLE 5. Combined segregations in F_2, indicating linkages between *O* (open tillers) and *gh* (gold hull), and between *O* and *I-Pl* (one of suppressors for purple leaf)

H-163 (+ +)×H-75 (*O gh*): repulsion

phenotype	straw white type		gold hull		total	recombination value (%)
	open	erect	open	erect		
genotype	*O* +	++	*O gh*	+ *gh*		
O.	184	59	59	8	310	38.0
C.(R.C.V.=38.0%)	166.19	66.31	66.31	11.19	310.00	

$\chi^2=4.43$ d.f.=3 p=0.2~0.3

H-122 (*O I-Pl*)×H-127 (+ +): coupling

phenotype	suppressing type		self colored		total	recombination value (%)
	open	erect	open	erect		
genotype	*O I-Pl*	+ *I-Pl*	*O* +	+ +		
O.	297	49	43	67	456	22.8
C.(R.C.V.=22.8%)	295.94	46.06	46.06	67.94	456.00	

$\chi^2=0.41$ d.f.=3 p=0.90~0.95

detailed of the results are abridged here, however, as given in Table 5, two cases of linkage, between *O* and *gh* and between *O* and *I-Pl* were indicated. The gene *gh* is responsible for "gold hull" character, and the gene *I-Pl* is one of suppressors for leaf color governed by *Pl* gene. The linkage intensity between *O* and *gh* amounts to 38.0% of cross overs, though this value itself is not so trustworthy in that the value was obtained in the repulsion phase of a single cross combination. The genes *O* and *I-Pl* show more striking linkage in which the recombination value is 22.8%. The gene *gh* is a member of the 6th linkage group of the writers, therefore it is probable that *O* may be inserted into this groups, together with *I-Pl* (TAKAHASHI 1963.).

2. Spreading growth habit in M-19

As noted in Table 1, M-19 shows spreading growth habit, which seemingly is identical with the character expression caused by *la*, the gene for "lazy" in the 8th linkage group. A tester strain, H-50, is one of gene stocks of "lazy", and was crossed with M-19. Their F_1s were spreading or lazy with equal outward appearance, and their F_2s were the very picture of their predecessor, involving no segregant or variant. Thus it is clear that the same mutation, which once spontaneously happend, was over again induced by the artificial irradiation.

D. Short stem and dwarf

1. Short stem in N-62

N-62 is an induced mutant from A-134, Yukara variety in Hokkaido, the northern-most island of Japan, and is featured with shortned stem, being 15 cm shorter than A-134 in ordinary paddy field condition. No other agronomic character, including yielding capacity, differs from A-134, and thus N-62 is considered to be one of the promising breeding materials in promotion of resistance to lodging. The N-62's first propositus was Mr. M. SHIBATA.

N-62 were crossed not only with A-134 from which it arose, but also with A-96, H-21, H-69 and H-143, all of which are normal in their plant height. All of F_1s from these crosses indicate that the long-stemmed viz. normal form is full dominant and in F_2s two phenotypes, which correspond to the long and the short parents respectively, occurred at a ratio of 3 : 1. No segregants which strikingly deviated from the parental forms appeared, indicating that the short-stemmed mutant behaves as monogenic recessive to the normal. The data are as presented in Table 6.

As to linkage relatonship involving a gene for this character (tentatively designated as d_{12}), no positive indication of linkage has been found out, however independent assortment between d_{12} and such genes as *wx* (waxy or glutinous

TABLE 6. F_2 segregation mode when N-62 (short-stemmed form) is crossed with the normal form of plants.

combination	phenotype	normal	short	total	goodness of fit		
	genotype	+	d_{12}		χ^2	d.f.	P
N-62×A-134	O.	123	37	160			
	C.(3:1)	120.0	40.0	160.0	0.30	1	0.5~0.7
N-62×Himehonami	O.	86	30	116			
	C.(3:1)	87.0	29.0	116.0	0.05	1	0.8~0.9
A-96×N-62	O.	426	132	558			
	C.(3:1)	418.5	139.5	558.0	0.54	1	0.3~0.5
H-21×N-62	O.	56	16	72			
	C.(3:1)	54.0	18.0	72.0	0.30	1	0.5~0.7
H-69×N-62	O.	116	30	146			
	C.(3:1)	109.5	36.5	146.0	1.54	1	0.2~0.3
H-143×N-62	O.	111	39	150			
	C.(3:1)	112.5	37.5	150.0	0.08	1	0.7~0.8
total	O.	918	284	1202			
	C.(3:1)	901.5	300.5	1202.0	1.21	1	0.2~0.3

Homogeneity $\chi^2=1.60$ d.f.=5 p=0.9~0.95

endosperm; 1st group), *C* (Chromogen; 1st group), d_7 (cleistogamous dwarf; 4th group), *fs* (fine striped; 7th group), *nl* (neck-leaf; 9th group), bl_1 (10th group) and d_8 (Norin-28 bwarf; 11th group), were presented. The combined segaegation mode on d_{12} and these genes are as shown in Table 7.

2. Dwarf in M-15

Short grained dwarf with stout panicle axis is the characteristic of the mutant, M-15. In outward appearance this dwarf is, in some way, different from all of the dwarf formes governed by those genes which previously reported by the writers; from d_1 to d_{11} (NAGAO and TAKAHASHI 1963). F_1 plant from a cross, M-15 (dwarf)×A-5 (normal) is normal, and in F_2 a ratio of 3 normal: 1 dwarf is given, indicating that this character is resulted from a single gene mutation. The actual data are presented in Table 8, in which the causal gene is provisionally designated as d_{13}.

TABLE 7. Combined segregations in F_2 from crosses, between d_{12} and seven linkage testers, *wx*, *C*, d_7, *fs*, *nl*, bl_1 and d_8

C (1st group): A-96×N-62

gene pair	AB	Ab	aB	ab	total	χ^2	d.f.	p
O. (C and d_{12})	319	97	107	35	558			
C. (9 : 3 : 3 : 1)	313.9	104.6	104.6	34.9	558.0	0.69	3	0.8~0.9
C (ditto): H-69×N-62								
O. (C and d_{12})	91	21	25	9	146			
C. (9 : 3 : 3 : 1)	82.1	27.4	27.4	9.1	146.0	2.65	3	0.3~0.5
wx (1st group): A-96×N-62								
O. (*wx* and d_{12})	337	107	89	25	558			
C. (9 : 3 : 3 : 1)	313.9	104.6	104.6	34.9	558.0	6.89	3	0.05~0.1
d_7 (4th group): N-7×N-62								
O. (d_7 and d_{12})	53	24	12	1	90			
C. (9 : 3 : 3 : 1)	50.6	16.9	16.9	5.6	90.0	7.13	2	0.02~0.05
fs (7th group): H-69×N-62								
O. (*fs* and d_{12})	85	22	31	8	146			
C. (9 : 3 : 3 : 1)	82.1	27.4	27.4	9.1	146.0	1.77	3	0.5~0.7
nl (9th group): H-69×N-62								
O. (*nl* and d_{12})	88	24	28	6	146			
C. (9 : 3 : 3 : 1)	82.1	27.4	27.4	9.1	146.0	1.92	3	0.5~0.7
bl_1 (10th group): H-21×N-62								
O. (bl_1 and d_{12})	41	12	15	4	72			
C. (9 : 3 : 3 : 1)	40.5	13.5	13.5	4.5	72.0	0.23	2	0.8~0.9
d_8 (11th group): N-58×N-62								
O. (d_8 and d_{12})	82	28	41	8	159			
C. (9 : 3 : 3 : 1)	89.4	29.8	29.8	9.9	158.9	5.30	3	0.1~0.2

TABLE 8. F_2 in crosses between normal and two dwarf forms caused by d_{13} and d_{14} genes

M-15 (dwarf)×A-5 (normal)

phenotype	normal	dwarf	total	goodness of fit		
genotype	+	d_{13}		χ^2	d.f.	p
O.	79	27	106			
C. (3 : 1)	79.5	26.5	106.0	0.01	1	0.9~0.95

M-17 (dwarf)×A-5 (normal)

phenotype	normal	dwarf	total	goodness of fit		
genotype	+	d_{14}		χ^2	d.f.	p
O.	108	14	122			
C. (3 : 1)	91.5	30.5	122.0	11.90	1	< 0.001

3. Dwarf in M-17

A mutant M-17 also is one of the dwarf forms. But the stem is relatively long, and therefore the M-17 bears a resemblance, in some respects, to "Norin-28 dwarf" of which causal gene, d_8, is a marker of the 11th linkage group. A cross, M-17 (dwarf)×A-5 (normal) was made and in their F_1s the normal form exhibited almost complete dominant. About 30% of F_2 plants were too late to emerge panicles. Hence these plants are excluded from the data presented in Table 8. A serious deficiency in the number of dwarf segregants would be pointed out in this table, provided that the dwarf form is single recessive to the normal form. An appropriate explanation of this is not yet forthcoming, however, it is possible to consider that this is essentially monohybrid inheritance and the allele for the dwarf form links or correlates with an inherent trait of late maturity which is brought by M-17. In the fact, a considerable part of the immatured F_2 plants were suggestive of the dwarf form, even though without an actual observation of panicles final decision is apt to fail. In Table 8, d_{14} denotes the causal gene of this dwarf.

E. Brown spots or speckles, and yellow spots

1. Brown-spotted leaves in H-131

There is a group of singular color types in which discoloration of chlorophyll appears first in leaves as brown spots or speckles resembling fungus lesions. Sometimes the spots spread and extend into stems and panicles.

In this plant, H-131, brown spots begin to develop after panicle emergence. The brown spots first take place on the leaves and by maturity extend into

the surface of glumes. H-131 was discovered as a single plant in the F_2 population from a cross between E-48 (a Chinese variety) and A-31 (Fukoku, a Hokkaido variety). E-48 and A-31 are normal green in their leaves and panicles. All of the selfed progenies from the discovered plant have been brown-spotted and thus bred true.

When H-131 was crossed with A-43 (normal green) the brown-spotted form behaved as simple recessive to the normal green. The actual segregation pattern is as shown in Table 9. It is natural to assume that this character

TABLE 9. F_2 segregation modes of several types of brown spots or brown speckles in leaves, caused by genes, bl_3, bl_4, bl_5 and bl_6

Brown spotted leaves in H-131

combination	phenotype	normal	spotted	total	goodness of fit		
	genotype	+	bl_3		χ^2	d.f.	p
H-131 (spotted) × A-43 (noamal)	O.	115	33	148			
	C. (3 : 1)	111.0	37.0	148.0	0.58	1	0.5~0.7

Brown speckles in leaves of M-21

combination	phenotype	normal	spotted	total	goodness of fit		
	genotype	+	bl_5		χ^2	d.f.	p
M-21 (speckled) × A-58 (normal)	O.	107	24	131			
	C. (3 : 1)	98.3	32.7	131.0	3.12	1	0.05~0.1

Large brown spots in leaves of M-25

combination	phenotype	normal	spotted	total	goodness of fit		
	genotype	+	bl_4		χ^2	d.f.	p
M-25 (spotted) × A-5 (normal)	O.	132	43	175			
	C. (3 : 1)	131.3	43.7	175.0	0.02	1	0.95~0.98
M-25 (spotted) × H-9 (normal)	O.	163	31	194			
	C. (3 : 1)	145.5	48.5	194.0	8.42	1	< 0.01

Large brown spots in leaves of M-26

combination	phenotype	normal	spotted	total	goodness of fit		
	genotype	+	bl_6		χ^2	d.f.	p
M-26 (spotted) × A-5 (normal)	O.	209	78	287			
	C. (3 : 1)	215.3	71.7	287.0	0.73	1	0.3~0.5

spontaneously arose as a single gene mutation, of which gene symbol is designated as bl_3.

Here it must be noted that the causal gene of this trait showed an indication of linkage with *wx*, a marker gene of first rank in the 1st linkage group. A recombination value of 32% was calculated in a cross of H-131 × A-43, though phase of linkage was repulsion (Table 10).

TABLE 10. Data of F_2 segregations, including linkages between bl_3 and *wx*, and between bl_4 and bc_1

A-43 (+ *wx*) × H-131 (bl_3 +): repulsion

phenotype	normal green		brown spots		total	recombination value (%)
	non waxy	waxy	non waxy	waxy		
genotype	+ +	+ *wx*	bl_3 +	bl_3 *wx*		
O.	92	23	31	2	148	
C. (R.C.V. = 32.2%)	77.84	33.16	33.16	3.84	148.00	32.2

$\chi^2 = 6.12$ d.f. = 2 p = 0.02 ~ 0.05

M-25 (bl_4 +) × H-9 (+ bc_1): repulsion

phenotype	normal		brown spots		total	recombination value (%)
	narmal	brittle	normal	brittle		
genotype	+ +	+ *bc*	bl_4 +	bl_4 bc_1		
O.	124	39	29	2	194	
O. (corrected)	124.0	48.5	50.8	4.0	227.3	
C. (R.C.V. = 28.5%)	118.3	52.2	52.2	4.6	227.3	28.5

$\chi^2 = 0.61$ d.f. = 2 p = 0.7 ~ 0.8

2. Small brown speckles in leaves of M-21

A mutant M-21 is characterized with a kind of physiological disease showing small brown speckles with the size of sesame seed on leaf blades. In a cross of M-21 (brown speckles) × A-58 (normal green; a variety named Kokushokuto-2), brown speckles behave as monogenic recessive to the normal green, though the goodness of fit was not so high (Table 9). The causal gene is provisionally designated as bl_5.

3. Brown spots in leaves of M-25

A mutant M-25 is featured with relatively large brown spots in leaves. This trait proved itself as simple mendelian recessive when M-25 was crossed with two testers of normal green leaves, A-5 and H-9 (a gene stock of bc_1). The actual data on segregation modes in F_2 are as given in Table 9. The

gene symbol bl_4 was employed in this character.

The bl_4 and the bc_1, a gene for "brittle culm" in the 11th linkage group, gave combined segregation mode which indicated an existence of linkage between them. This is as shown in Table 10. In calculating linkage intensity a correction was made with respect to the frequency in the recessive classes of bl_4. This is because of the fact that a deficiency in the number of brown spotted segregants in F_2 from M-25×H-9 was noted. The recombination value was estimated as 29% in a repulsion phase.

4. Brown spots in leaves of M-26

M-26 is a mutant with brown-spotted leaves, of which discoloration pattern of chlorophylls is similar to that of M-25. M-26's brown spot behaved as recessive to the normal green in F_1 of a cross, M-26×A-5. And in F_2 a segregation ratio of 3 normal: 1 brown-spotted was observed, indicating that this trait is governed by a single recesive gene which provisionally designated as bl_6 (Table 9).

5. Yellow spots in leaves of M-30

A mutant M-30 shows yellow spots in its leaves. When M-30 was crossed with a normal green type (H-69), the normal green was full dominance in F_1, and in F_2 a segregation of 393 (normal green): 95 (yellow spot) was obtained (Table 11). This suggests an existence of a single recessive gene, temporarily designated as *ysl*, for yellow spots, though the numerical relation was not so close to an approximation of a 3 : 1 ratio, giving a deficiency in

TABLE 11. F_2 segregation modes in crosses of M-30 (yellow spots in leaves)×H-69 (normal green), and of M-31 (fine white speckles in leaves)×A-5 (normal green)

M-30 (yellow spotted)×H-69 (normal green)

phenotype	normal	spotted	total	goodness of fit		
genotype	+	*ysl*		χ^2	d.f.	p
O.	383	95	478			
C. (3 : 1)	358.5	119.5	478.0	6.70	1	< 0.01

M-31 (fine white speckles)×A-5 (normal green)

phenotype	normal	speckled	total	goodness of fit		
genotype	+	fs_2		χ^2	d.f.	p
O.	185	51	236			
C. (3 : 1)	177.0	59.0	236.0	1.45	1	0.2~0.3

the number of yellow-spotted segregants. In this connection, the writers have noted the phenomenon that plants with yellow-spotted leaves frequently died during their cultivation, not only in a nursery bed but also in a paddy field.

F. Chlorophyll deficiency in M-31, featured with fine white speckles of leaves

This is one of the variegated types in chlorophyll deficiencies. White and fine speckles in leaves are the feature of this mutant. Unlike such variegated types "fine stripes in leaves, by *fs* gene" and "green and white stripes, by *gw* gene", the character expression of this mutant is constant, giving stable expressivity and high penetrance.

When M-31 was crossed with A-5, a normal green type, their F_1 was normal and in F_2 the normal and the speckled segregants were given in a numerical relation of 185 : 51 (Table 11). This is fairly good agreement of an expectation of 3 : 1, where the speckled type is a single recessive to the normal type. The fs_2 is a temporary gene symbol of this trait. In this connection it must be noted that the gene symbol "*fs*" which has been employed in the "fine striped seedling" should be changed into fs_1.

Conclusion and Summary

The genic constitution of some morphological characters, which are features of some natural or artificially induced mutants, were studied by crossing with testers or gene stocks of the writers. These characters are i) brittleness of culm (1 mutant), ii) malformed glumes (3 mutants), iii) growth habit characterized with spreading or open tillers (2 mutants), iv) short stem or dwarf (3 mutants), v) brown or yellow spots in leaves and glumes (5 mutants), and vi) chlorophyll deficiency featured with white speckles in leaves (1 mutant).

Character expressions, segregation modes in F_2 generation, estimated causal genes, and their provisionally proposed gene symbols, are briefly as follows.

1. Brittle culm in M-5 : The culms and the leaves are so brittle that they can be picked easily by hand. Single gene recessive to the normal. Different from a gene *bc* (brittle culm) in the writers' 11th linkage group. Thus designated as bc_2 in its gene symbol.

2. Claw-shaped floral glumes in M-8 : The lemma curves over the abbreviated palea, giving an claw-shaped appearance of spikelet. Single recessive to the normal. Basic gene symbol of *cls* has been preserved for this form of character.

3. Multiform empty glumes in H-129 and H-131 : Spikelets with empty glumes of various form or length are borne in the same panicle. Possively monohybrid character.

4. Malformed lemma with high sterility in H-166: An abnormal form of lemma, with low fertility of seed setting. Presumably double recessive to the noramal. No gene symbol is designated, because of the inadequate experimental data.

5. Open tillers, the growth habit in H-75, H-122 and H-131: Tillers arise at an angle of ca. 60° from the ground. Single dominant over the normal, erect form. Tentatively designated as *O*. Links with *gh*, gold hull, in an intensity of 38% R.C.V. and with *I-Pl*, one of suppressors for purple-leaf gene *Pl*, in a magnitude of 22.8% R.C.V., thus possibly belongs to the 6th linkage group.

6. Spreading growth habit in M-19: Governed by an identical gene with *la* for lazy growth habit. The same mutation, which once spontaneously happened, was over again induced artificially.

7. Short stem in N-62: An induced mutant from Yukara variety. Agronomically important characters, other than plant height, show no difference from Yukara. Monogenic recessive to the normal. A causal gene, d_{12}, is independent from markers in the 1st, 4th, 7th, 9th, 10th, and the 11th linkage groups.

8. Dwarf in M-15: Short grained dwarf with stout panicle axis. Single recessive (d_{13}) to the normal.

9. Dwarf in M-17: Bears an resemblance, in some respects, to the dwarf caused by d_8 gene. Presumably monohybrid inheritance, attributable to d_{14} gene.

10. Brown-spotted leaves in H-131: Brown spots begin to appear after panicle emergence and spread in leaves. Simple recessive to the normal. The causal gene bl_3 gives an indication of linkage to *wx* (waxy) in the 1st group, with 32% cross-over values.

11. Small brown speckles in leaves of M-21: Deep brown speckles with the size of a sesame seed distribute over the leaf blade. Single recessive to the normal. A causal gene is provisionally desingated as bl_5.

12. Brown spots in leaves of M-25: Featured with relatively large reddish brown spots in leaves. Monogenic recessive character caused by bl_4. The bl_4 links with bc_1 (brittle culm) of the 11th group, in 29% R.C.V.

13. Brown spots in leaves of M-26: Similar pattern to M-25, and caused by a single recessive gene bl_6 (tentative symbol).

14. Yellow-spots in leaves of M-30: Yellow spots in leaf blades. A simple mendelian recessive, and governed by *ysl* (temporary designation).

15. Fine white speckles of leaves in M-31: A kind of chlorophyll deficiency, caused by fs_2 gene.

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