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Author(s)	NAGAO, Seijin; TAKAHASHI, Men-emon; KINOSHITA, Toshiro
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GENETICAL STUDIES ON RICE PLANT, XXV

Inheritance of Three Morphological Characters, Pubescence of Leaves and Floral Glumes, and Deformation of Empty Glumes¹⁾

By

Seijin NAGAO, Man-emon TAKAHASHI
and Toshiro KINOSHITA

Plant Breeding Institute, Faculty of Agriculture
Hokkaido University, Sapporo, Japan

Introduction

This is one of a series of reports on genic analysis of characters in foreign rice varieties based on a study of crosses with testers from Japanese varieties of which the genic constitution had been explored. In this paper are presented and discussed three morphological characters and their causal genes. They are pubescence in leaves and floral glumes, and deformed long empty glumes.

Before going further the writers wish to express their thanks to Dr. H. OKA of The National Institute of Genetics, for furnishing to the writers some foreign varieties of which the morphological characters were examined in the present work. Cost of the study was partly defrayed by a Grant in Aid for Fundamental Scientific Research from The Ministry of Education.

Materials and Methods

The names of the varieties and places from where they were introduced are listed in Table 1, together with the concerned characters which they have.

The majority of F₁ hybrids from crosses of these foreign varieties and the Japanese varieties showed high fertility of more than 90% in their seed setting, but in two cases where E-41 and E-45 were combined with Japanese varieties the fertility of their F₁s was relatively low and variable, ranging from 80% to 20%. These low percentages may be due principally to unfavorable photo-thermal conditions under which the plants were grown, but further other

1) Contribution from the Plant Breeding Institute, Faculty of Agriculture, Hokkaido University, Sapporo, Japan.

TABLE 1. List of varieties used.

Varieties		Introduced from	Characters concerned		
Stock no.	Name		pubescence		empty glumes
			leaves	floral glumes	
E-41	Pappaku	Formosa (hills)	medium pubescent	medium pubescent	long & uneven
E-43	Garumbalay	Philippines	glabrous	nearly glabrous	normal short
E-44	Pirurutong	do	thick pubescent with short hairs	do	do
E-45	Betong	Flores (Indonesia)	medium pubescent	shaggy	do
A-12	Bunketsu-waito	Japan	do	medium pubescent	normal short
A-13	Chabo	do	do	do	do
A-43	Hokkaimochi-1	do	do	do	do
A-58	Kokushokuto-2	do	do	do	do
A-77	Shito	do	do	do	do
H-25	"multiple marker"	do	do	do	long & even
H-27	"multiple marker"	do	do	do	do
N-44	"multiple marker"	do	do	do	normal short
N-45	"multiple marker"	do	do	do	do
N-47	"multiple marker"	do	do	do	do

causations may possibly lie in low sexual affinity involved in the difficulties of gametogenesis and/or fertilization. Thus some combinations with low F_1 fertility were disregarded in the present study, except in case of particular necessity.

In order to examine the mode of inheritance, the writers made observations of the populations and strains up to F_3 generation: however, in the present paper, because of its brevity, the greater part of the discussion will be offered on F_1 and F_2 . The plants were cultured in frame beds placed in the green house, but when close attention was made necessary by the fact that certain morphological characters exhibited modifications under diverse conditions, they were at the same time cultured in the ordinary paddy field outdoors.

Starting from the present report the writers intend to use the new system of gene symbolization which has been proposed to The I. R. C. meeting, held in Ceylon in 1959, as "Recommended IRC Standard Symbols for Rice Genes". The gene which will be designated as "*g*" in the present paper is the identical gene which the writers have designated as "*lng*" in the previous papers.

Experimental

A. Pubescence of leaves

a. Smooth leaves with no hairs:

A Philippine variety E-43 has smooth—glabrous or non-hairy—leaves and floral glumes, except a very few hairs are scatteringly seen in the glume tips (Fig. 1). This was crossed with six Japanese varieties, A-13, A-58, A-77, N-44, N-45 and H-27, all of which are medium pubescent in their leaves and

TABLE 2. F_2 segregations in crosses between the normal (medium pubescent) and the glabrous leaf blade.

leaves floral glumes genotype	med. pub.	glabrous	Total	Goodness of fit (3:1)	
	med. pub.	nearly glab.		χ^2	p
	+	<i>gl</i>			
A-13 × E-43	420	139	559	0.005	0.90-0.95
A-58 × "	247	85	332	0.064	0.70-0.80
A-77 × "	476	162	638	0.052	0.80-0.90
H-27 × "	398	120	518	0.929	0.30-0.50
N-44 × "	414	170	584	5.260	0.02-0.05
N-45 × "	301	128	429	4.647	0.02-0.05

$$\sum \chi_i^2 = 10.957 \quad \text{d.f.} = 6 \quad p = 0.05-0.10$$

floral glumes, though there are a few intervarietal differences in hair length and density. In these crosses the pubescence character of the leaves behaved as single dominant over the glabrous, or the glabrous behaved single recessive to the pubescent, giving pubescent in F_1 s and segregation ratio of 3 pubescent versus 1 glabrous in F_2 s without exception (Table 2).

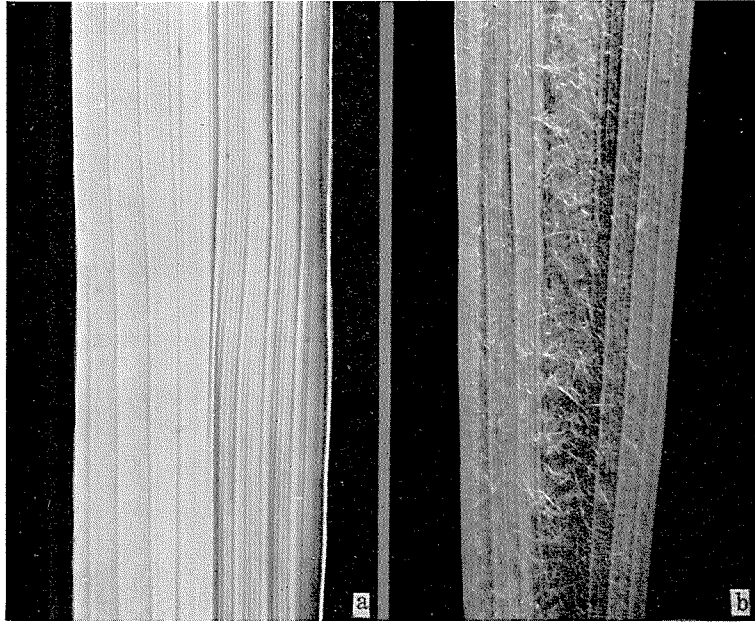


Fig. 1. Pubescence of leaves.

a : glabrous.

b : shaggy with long and thick hairs caused by Hl_aHl_b .

The pubescence of the floral glumes also behaved as incomplete dominant over the glabrous; there existed certain accordance between leaves and glumes in regard to their pubescence, showing that the F_2 and F_3 plants with glabrous leaves scarcely have any hairs in their glumes and that fixed strains of the “double glabrous—types that have smooth leaves and floral glumes together” were easily bred true in F_3 .

Thus it is probable that the gene for glabrous character in leaves—gene symbol “ gl ”—has something to do with the glabrous of the floral glumes, suggesting that it may be caused as a result of the complete linkage between the leaf gene and the floral glume gene or of the pleiotropic effect of the identical gene, gl , most probably the latter.

This gene, gl , was tested for its linkage relationships between 14 marker

TABLE 3. F₂ data of crosses between *gl* and known linkage markers in 11 linkage groups.

Linkage groups	Tester genes (Characters)	F ₂ Segregation					Independence		R. C. V.
		T +	T <i>gl</i>	t +	t <i>gl</i>	Total	χ^2	p	
1. " <i>wx</i> "	<i>wx</i> (waxy endosperm)	185	62	60	25	332	0.969	0.8-0.9	r 53.0
	<i>C</i> (Tawny apiculus)	149	58	59	21	287	2.307	0.5-0.7	c 51.3
	<i>d₂</i> (ebisu dwarf)	152	55	42	18	267	1.917	0.5-0.7	r 52.4
2. " <i>Pl</i> "	<i>Pl</i> (Purple leaf)	240	80	75	34	429	2.304	0.5-0.7	c 45.7
	<i>Pr</i> (Purple hull)	156	63	52	16	287	2.022	0.5-0.7	c 53.9
3. " <i>A</i> "	<i>A</i> (Antho. activator)	329	104	92	35	560	2.241	0.5-0.7	r 52.6
4. " <i>g</i> "	<i>g</i> (long empty glumes)	235	70	73	24	402	0.857	0.8-0.9	r 51.4
5. " <i>I-Bf</i> "	<i>I-Bf</i> (Inhibitor for dark furrows)	193	81	65	22	361	3.238	0.3-0.5	r 47.0
6. " <i>d₁</i> "	<i>gh</i> (gold hull)	139	47	45	16	247	0.068	0.99	c 49.3
7. " <i>fs</i> "	<i>fs</i> (fine stripe)	60	22	18	9	109	1.141	0.7-0.8	r 54.3
8. " <i>la</i> "	<i>la</i> (lazy)	347	114	113	38	612	0.055	0.99	r 50.3
9. " <i>nl</i> "	<i>nl</i> (neck leaf)	51	12	13	8	84	3.111	0.3-0.5	r 60.0
10. " <i>bl</i> "	<i>bl</i> (blackish mottled leaf)	122	46		46*	214	1.934	0.3-0.5	r 54.8
11. " <i>bc</i> "	<i>bc</i> (brittle culm)	138	50		79*	267	3.237	0.1-0.2	r 45.0

Leaf with the genotype of "*bl*" tends to curl at ripening, and the pubescence on brittle plants (*bc*) rubbed off very easily, resulting in their misclassification as glabrous.

To avoid misclassification these plants (* in the Table) are assorted en bloc.

TABLE 4. F_2 segregations of crosses between the thick pubescent and the normal pubescent leaf blade.

Cross		I	II	III	IV	Total	Goodness of fit		
		thick pubescence		medium pub.	glabrous		χ^2	d. f.	p
		long	short						
		leaves	medium pub.	nearly glab.	medium pub.				
floral glumes	$Hl_a Hl_b +$	$Hl_a Hl_b gl$	$Hl_a + +$ $+ Hl_b +$ $+ + +$	$Hl_a + gl$ $+ Hl_b gl$ $+ + gl$					
genotype									
N-45 × E-44	Obs.	177	45	54	21	297	3.01	3	0.3-0.5
	Calc. (9 : 3 : 3 : 1)	167.06	55.69	55.69	18.56	297.00			
A-13 × E-44	Obs.	221	61	147	55	484	2.98	3	0.3-0.5
	Calc. (27 : 9 : 21 : 7)	204.19	68.06	158.81	52.94	484.00			
A-43 × E-44	Obs.	211	59	161	55	486	1.53	3	0.5-0.7
	Calc. (21 : 9 : 21 : 7)	205.03	68.34	159.47	53.16	486.00			
A-58 × E-44	Obs.	204	57	120	42	423	6.77	3	0.05-0.1
	Calc. (27 : 9 : 21 : 7)	178.45	59.48	138.80	46.27	423.00			

genes of 11 linkage groups. The details of the results are abridged here, however, as given in Table 3, in all cross combinations no linkage or association was indicated between genes observed.

b. Leaf hairs of long length :

As listed in Table 1, a Philippine variety E-44 has leaves of which the surfaces are covered with short but thick pubescence, and has floral glumes of which the surface is nearly glabrous. Crosses between this variety and Japanese varieties with medium pubescent leaves gave shaggy—long and thick pubescence—leaves on their offsprings (Fig. 1). Without exception, the F₁s' leaves showed longer hair length but nearly the same thickness of pubescence, when compared with their parents. As to the floral glume hairs, they were nearly the same as those of the Japanese varieties. In F₂, in addition to the parental and the F₁ types, a new type viz., glabrous leaves, appeared. The ratio of the four hair types, shaggy, thick pubescent with short hairs, medium pubescent, and glabrous, were 9:3:3:1 (in a cross of N-45 × E-44) and 27:9:21:3 (A-13 × E-44, A-43 × E-44, and A-58 × E-44), suggesting that these were based on a trigenic scheme of inheritance (Table 4).

These modes of segregation can be reasonably explained by the assumption that there exist two complementary genes (proposed gene symbols of *Hl_a* and *Hl_b*) which are responsible for long hair production, and one recessive gene for reducing the effect of *Hl_a* and *Hl_b*, besides a gene or gene-complex for medium pubescence, which is estimated to be in possession of both the Philippines and the Japanese varieties. It is probable that the gene of reducing effect must be the same "g" for glabrous character mentioned in the preceeding section, since in both types of cross combination of the present section there appeared typical glabrous plants in the F₂s. According to this scheme the genic formulae are :

Gene complex for medium pubescence (commonly seen in Japanese varieties)	{	Shaggy (thick & long)	{	Shaggy (thick & long)	<i>Hl_a Hl_b +</i>
		<i>Hl_a Hl_b</i>		Pubescent (thick but short)	<i>Hl_a Hl_b gl</i>
	{	Medium pubescent (medium thick & long)	{	Medium pubescent (medium thick & long)	<i>Hl_a ++, +Hl_b +, +++</i>
		<i>Hl_a +, +Hl_b, ++</i>		Glabrous (non or scarcely)	<i>Hl_a + gl, +Hl_b gl, ++ gl</i>

Thus the genotypes of the parental varieties are given as :

E-44..... $Hl_a Hl_b gl$Thick but short pubescence.

N-45..... $Hl_a + +$ }
 A-13 }Medium pubescence.
 A-43 } $+ + +$
 A-58 }

The reasonableness of this genic scheme was further examined by pedigree culture; in every instance almost all the segregation types in F_3 generation of the above cross combinations, and on others, have appeared (Table 5).

TABLE 5. Segregation types of F_3 strains and their frequencies in the crosses listed in Table 4.

F ₂ Phenotypes	F ₃						Number of plants	
	Types of segregation				Number of pedigrees			
	I	II	III	IV	C ₁ ¹⁾	C ₂		O ²⁾
I thick pubescent with long hairs	1				1	1.2	2	61
	3	1			2	2.4	4	162
	3		1		4	4.8	4	142
	9	3	3	1	8	9.5	8	332
	9		7		4	4.8	8	318
	27	9	21	7	8	9.5	7	213
II thick pubescent with short hairs		1			1	1.2	1	8
		3		1	4	4.8	4	129
		9		7	4	4.8	2	61
III medium pubescent			1		7	8.3	14	436
			3	1	14	16.6	20	745
IV glabrous				1	7	8.3	2	56
Total					64	76.2	76	2663

1) C₁ indicates the theoretical ratio and C₂ indicates the theoretical numbers.

2) O indicates the total of observed numbers in three crosses, (A-13×E-44, A-43×E-44 and A-58×E-44).

On the whole, therefore, these results lead the writers to the conclusion that in addition to a gene complex for medium pubescence and the recessive gene for glabrous character (*gl*), there exist complementary genes, Hl_a and Hl_b , the causal genes for thick and long hairs when they co-exist together. On close observation, Hl_a and Hl_b were found to exert their pleiotropic effects on hair length of panicle branches but no remarkable effect was seen in pubescence of floral glumes.

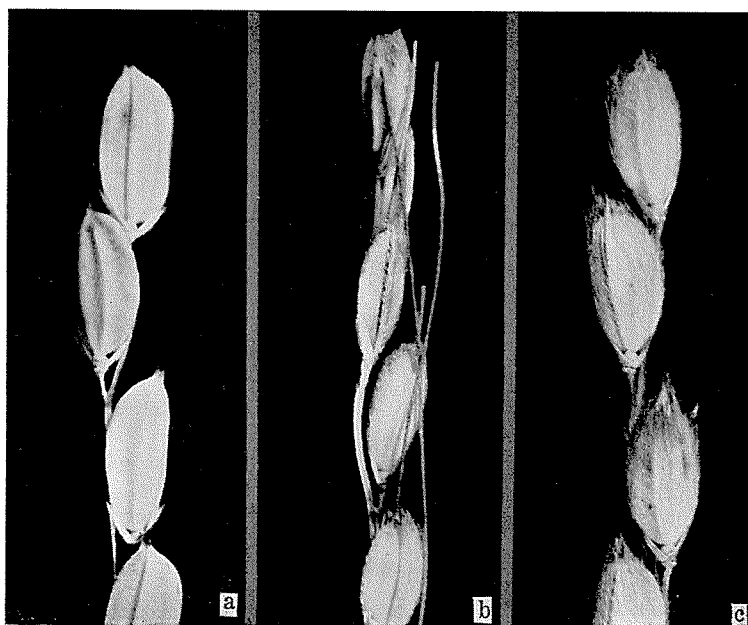


Fig. 2. Pubescence of floral glumes.

- a : glabrous.
- b : medium pubescence in a Japanese variety.
- c : shaggy with extremely long hairs due to *Hg*.

B Pubescence of floral glumes

It has been reported by many workers that the glabrous floral glumes behave as single recessive to the medium pubescence which is commonly seen in Japanese varieties, and it is generally accepted that the glabrous character is governed by a single recessive gene "*gl*", probably with the gene mentioned above.

An Indonesian variety E-45 has extremely long hairs ranging from 2 to 3 mm on its floral glumes and auricles (Fig. 2 and 3). This was crossed with the Japanese varieties, A-12, N-45 and H-27, which are medium pubescence type in their glume hairs. F_1 s were about intermediate as to hair length, but in F_2 , by grouping the hair length into two classes; "N-45 and F_1 types" and "Japanese type", a ratio of 3:1 was obtained, indicating that the extremely long hairs of the floral glume are governed by a single incomplete dominant gene (Table 6). This assumption as to genes was verified by F_3 observation too. This gene is designated as "*Hg*". As to the pleiotropic effect of the *Hg*, it has an effect on auricles, leaf margins and panicle branches similar to its effect on the glumes (Fig. 3).



Fig. 3. Pubescence of auricles.

a : medium pubescence in a Japanese variety.

b : long hairs due to a pleiotropic effect of *Hg*.

TABLE 6. F_2 segregations in crosses between the medium pubescence and the long pubescence glume types.

floral glumes genotype	shaggy	med. pub.	Total	Goodness of fit (3:1)	
	<i>Hg</i>	+		χ^2	p
A-12 × E-45	93	33	126	0.095	0.7-0.8
H-27 × "	35	12	47	0.007	0.9-0.95
N-45 × "	141	43	184	0.261	0.5-0.7

$$\sum \chi^2_i = 0.363 \quad \text{d.f.} = 3 \quad p = 0.90-0.95.$$

C. One sided long empty glumes

In common varieties, the empty glumes are short, about one-third as long as the lemma and palea, while in some varieties they are i) as long as, or ii) longer than, the lemma and palea. It is generally accepted that the type-i glume behaves as recessive to the normal short type (PARNEL et al. 1917, JONES 1934, MORINAGA and FUKUSHIMA 1943, etc.) and type-ii behaves as incomplete

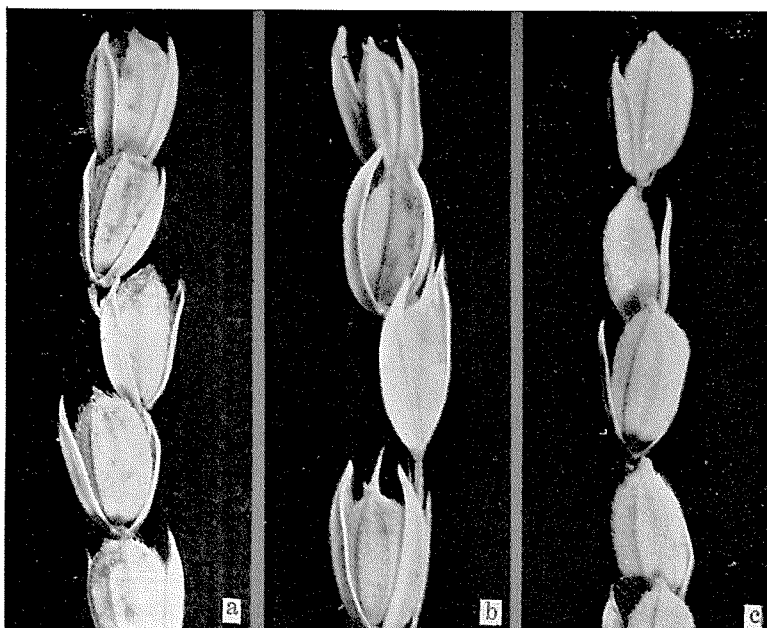


Fig. 4. Long empty glumes.

- a : even-long ; type-i.
 b : even-long ; type-ii.
 c : uneven-long ; due to a suppressive effect of *Su-g*.
 normal short type of empty glumes are seen in
 Fig. 2.-a, b and c.

dominant over the normal short (RAMIAH et al 1931, JODON 1957). These two types are considered to be governed by two genes, *g* and *Gm*. In these long empty glumes, both empty glumes, attached on the lemma side and the palea side, are ordinarily like in their shape and size.

These are the prevailing types of long empty glumes. However, there is still another type of such glumes in which the length of the empty glumes is uneven with respect to either side of lemma and palea, giving a long empty glume in the palea side in spite of existence of a short empty glume in the lemma side, as shown in Fig. 4.

A Formosan variety E-41 is one that has this type of peculiar empty glumes; in the present paper, this is temporarily termed as "one-sided long empty glumes or uneven long empty glumes". For analysing this empty glume type two kinds of cross combinations were made by the writers. They are "long empty glumes due to *g* gene (temporarily termed as even long empty glumes)" × "uneven long" and "normal short" × "uneven long".

In the first combination Japanese variety H-25 which was revealed to have gene *g* was crossed with E-41. This cross gave "uneven long type" in F_1 ; it segregated in F_2 into two classes of phenotypes, "uneven long" and "even long" in a ratio of 3:1, suggesting that monogenic difference exists between the parental varieties, under the genic situation that both the parents possess the *g* gene for even long glumes in common (Table 7).

TABLE 7. F_2 segregation of a cross between the uneven long type and the even long type of empty glume length.

Cross	empty glume	uneven long	even long	Total
	genotype	<i>g, Su-g</i>	<i>g, +</i>	
H-25 × E-41	Obs.	247	85	332
	Calc. (3:1)	249.0	83.0	332.0

$$\chi^2 = 0.0643 \quad \text{d.f.} = 1 \quad p = 0.70-0.80$$

Here it is pointed out that in their empty glume length when compared with the parental uneven type, E-41, there remain some possibilities of existing minor or modifying genes which have something to do with the phenotypic expression of the uneven long empty glumes; detailed analysis on the presence of these genes is in progress at present.

The monogenic inheritance of the major gene for the uneven type was confirmed through the following observation on F_3 plants, too. All the plants of 7 F_3 strains derived from F_2 plants of the even-long type were also even-long, and no others appeared. Further, 25 F_3 strains of which parental F_2 plants were uneven-long were assorted into two groups with regard to their segregation types, that is: 8 strains of which the empty glumes were uneven-long throughout individual plants, and 17 strains which showed the same segregation mode as in the F_2 . These are results that can be reasonably explained by the scheme of a dominant modifier—gene symbol "*Su-g*"—which exerts its effect on the long empty glume of lemma side, when *Su-g* co-exists with *g* for even long empty glumes. Thus the genotypes of the parental varieties may be given as *g Su-g* in E-41 and *g+* in H-25.

For verification of the above, three crosses were made between E-41 (uneven long) and Japanese varieties with normal short empty glumes (genotype of g^+), A-43, N-45 and N-47. Here, F_1 s should show "normal short" and their F_2 progenies should segregate into three types, normal short ($+ Su-g, ++$), uneven long (*g Su-g*) and even long ($g+$) in a ratio of 12:3:1. The result from the cross of N-47 × E-41 closely fitted with the expectation (Table 8). How-

ever in other crosses, A-43 × E-41 and N-45 × E-41, F₂ segregations were not so close to the expectation.

TABLE 8. F₂ segregation of crosses between the normal short type and the uneven long type of empty glumes.

empty glumes	normal short	uneven long	even long	Total	Goodness of fit (12:3:1)	
genotype	+ <i>Su-g</i> ++	<i>g Su-g</i>	<i>g +</i>		χ ²	p
A-43 × E-41	205	87	17	309	17.943	0.01
N-45 × "	216	78	18	312	8.000	0.01-0.02
N-47 × "	286	60	26	372	1.864	0.30-0.50

As presented in Table 9, however, the propriety of the above genic scheme was recognized by the pedigree culture of F₃ from A-43 × E-41, in which almost all the segregation types expected in F₃ generation of this cross combination, and no others, were obtained.

TABLE 9. Segregation types of F₃ strains and their frequencies in the cross, A-43 × E-41, listed in Table 8.

F ₂	F ₃						Number of plants
	Types of segregation			Number of pedigrees			
	I	II	III	C ₁	C ₂	O	
I normal short	1			4	8	6	88
	3	1		2	4	6	101
	3		1	2	4	3	37
	12	3	1	4	8	7	209
II uneven long		1		1	2	4	129
		3	1	2	4	4	63
III even long			1	1	2	2	33
Total				16	32	32	660

In this connection it may be worthy of note that the presence of this particular gene, *Su-g*, was also ascertained in a cross, E-43 (normal short) × H-27 (even long). F₂s from this cross gave such a segregation mode as, normal short (++, +*Su-g*): uneven long (*g Su-g*): even long (*g+*) in a ratio of 12:3:1, indicating that the E-43 possesses the genotype of "+*Su-g*", in spite of having normal short type of empty glumes in outward appearance (Table 10).

TABLE 10. F_2 segregation of a cross, H-27 \times E-43, involving *Su-g* gene.

empty glumes	normal short	uneven long	even long	Total
genotype	+ <i>Su-g</i> , ++	<i>g Su-g</i>	<i>g</i> +	
Obs.	322	81	32	435
Calc. (12 : 3 : 1)	326.25	81.56	27.19	435.00

$$\chi^2 = 0.911 \quad \text{d.f.} = 1 \quad p = 0.50-0.70$$

Consideration

Pubescence is one of the characters by which some phylogenetical and genecological analysis of the rice plant have been made (MATSUO 1952, NAGAMATSU and ISHIKAWA 1956, OKA 1953 etc). Furthermore the glabrous leaves and glumes are very desirable characteristics from the grower's standpoint because of freedom from dust in harvesting and hull removing. In several instances the glabrous leaves behave as single recessive to the normal pubescence (RAMIAH 1937, JODON 1955), but besides this, RAMIAH (1937) found a case where a 15:1 ratio was given in F_2 , of which double recessive is glabrous. As to the pubescence of floral glumes, OKA (1953) demonstrated digenic scheme of inheritance for glabrous type, and again he assumed the presence of minor genes for the development of the hair length.

In the writers' experiment, as described above, it has been shown that there exist three kind of major genes, Hl_a , Hl_b and gl , all of which are responsible for an expression and development of the pubescence of the leaves. The identification of the genes of the writers and other workers' will be left for further studies; however, in connection with leaf pubescence, it should be mentioned that the gene gl exerts an effect not only on glumes but also on leaves. As a result of the present work the following hair types on glumes and leaves have been accounted for, as combining three genes mentioned here plus a dominant gene Hg for floral glume hairs.

floral glumes	leaves	genic constitution
haired	haired	$Hl_a Hl_b Hg$
haired	hairless	$Hg gl$
hairless	haired	$Hl_a Hl_b gl$
hairless	hairless	gl

Besides the gene for recessive long empty glumes (g) and the dominant

long empty glumes (*Gm*; recommended symbol of JODON), by which two types of monogenic segregation mode are caused. CHAO (1928) reported a case where duplicate genes for short type are existent, giving a F_2 of 15 normal : 1 long. The gene *Su-g* suggested by the writers is apparently another type of gene, since it gives rise to uneven long empty glumes when it co-exists with *g*.

In the present work it has been indicated that gene *gl* does not pertain to any other 11 linkage groups. BREAU (1940) found out a linkage between awnedness (*An*) and glabrous characters with the intensity of 41% of recombination value. Thus it is probable that *gl* and *An* make the 12th linkage group of rice plant.

Summary

The genic constitution of three characters, which are carried on some foreign varieties, were studied by crossing with testers from Japanese varieties. These characters are pubescence of leaves and floral glumes, and deformed—uneven—long empty glumes. Through the present work their causal genes were estimated to be as follows.

gl... A gene for glabrous leaves and floral glumes. The plants with *gl* have smooth glumes and leaves. There is an indication that the *gl* and *An* (for awnedness) make the 12th linkage group of rice plant.

Hl_a and *Hl_b*... Complementary genes for long pubescence of leaves. When these genes co-exist with *gl*, however, the hairs are remarkably shortened.

Hg... A gene for long pubescence on floral glumes. This gene exerts its pleiotropic effect on pubescence of leaf margins, auricles and panicle branches.

Su-g... A gene for empty glume length; it has a suppressive effect on the empty glume of the lemma side, when it co-exists with *g* for long empty glumes.

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