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GENETIC STUDIES ON THE INDUCED SIX-ROWED MUTANTS IN BARLEY

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Since De Candolle (1882), students on the origin of cultivated barley have taken a special interest in the two-rowed versus six-rowed character as one of the most important key to this problem. The character pair is conspicuous and easily distinguishable by the basal shape of kernels even in samples excavated from ancient sites. It had been widely accepted until about 1940 that the ancestor of the cultivated barley was a six-rowed type (Tschermak 1914, Nowacki 1920, Schiemann 1932, Åberg 1940). However, since Helbaek (1959, 1966) found two-rowed barley grains with tough rachis at very ancient sites in Jarmo, Iraq, an alternative hypothesis that all cultivated barleys were derived from the two-rowed wild species *Hordeum spontaneum* C. Koch has become predominant. The fact that mutation from two-rowed to recessive six-rowed condition occurred more frequently than in the reverse direction (Trofimovskaja and Zukovskij 1967) favored the latter hypothesis. For this, however, it should be ascertained whether this genic change occurs in the *V* locus on chromosome 2. Nybom (1954) and Hagberg and Persson (1964) confirmed that all their induced six-rowed mutants were attributable to a change in *V* locus. On the other hand, Nötzel (1952) found that one six-rowed and 10 'intermedium' mutants arose from changes in the loci other than *V*. The present authors also found that both of the two six-rowed mutants induced by T. Tsuchiya from two-rowed cultivars, Svanhals and Hakata 2, were resulted from genic changes other than *V* locus (Takahashi and Hayashi 1970, Fukuyama *et al.* 1971, Takahashi *et al.* 1972). Gustafsson and Lundqvist (1980) recently reported that all 36 'six-rowed' mutants arose from a change in *V* locus, but 60 'intermedium' mutants were due to genic changes in nine loci other than *V*.

The present authors have planned to approach the similar problem whether the majority of the induced 'six-rowed' mutants have certainly arisen from changes in the *V* locus, and also how many loci other than *V* have been involved in them. The results will be presented in this paper.

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MATERIALS AND METHODS

The materials for this experiment consisted of 35 mutants which were kindly provided by several authorities, such as listed in Table 1. The mutants may be regarded as six-rowed type because their fertility of lateral florets is recovered almost completely as in a six-rowed plant.

TABLE 1. Six-rowed mutants used for this study

Six-rowed mutant	Abbreviated name	Original two-rowed variety (Mutagen)	Induced and provided by
Xb 388.8	Piro-1	Piroline (X-ray)	Moës, A. (Belgium)
Xc 41.5	Piro-2		
Xd 160.46	Piro-3		
Xf 143.1	Piro-4		
X15 1463	Piro-5		
X15 1508	Piro-6		
X17 2497	Piro-7		
X17 3555	Piro-8		
γ II 3/A	MFB-1	MFB 104 (γ-ray)	Pollhamer, F. (Hungary)
γ III 3/B	MFB-2		
γ 35/3	MFB-3		
γ 49	MFB-4		
γ 225/6	MFB-5		
γ 225/7	MFB-6		
γ 287/1	MFB-7		
γ 486/21	MFB-8		
γ 494/12	MFB-9		
γ 508/8	MFB-10		
γ 550/3	MFB-11		
γ 610/14/13	MFB-12		
γ 644/1	MFB-13		
γ 1109	MFB-14		
γ 1136	MFB-15		
γ 2072	MFB-16		
Mut 2234	AD-1	A. Donaria (X-ray)	Scholz, F. (E. Germany)
Mut 3036	AD-2		
Mut 3844*	Haisa-1	Haisa (X-ray)	
Mut 3885*	Haisa-2		
Mut 4818	Saale-1	Saale (X-ray)	
Mut 4873	Saale-2		
Kmut 27**	Svan	Svanhals (X-ray)	Tsuchiya, T. (U.S.A.)
Kmut 213	Hakata	Hakata 2 (γ-ray)	
38X-197	Gamma	Gamma 4 (X-ray)	Hirai, S. (Tokyo, Japan)
31γ-5	Kirin	Kirin Choku 1 (γ-ray)	
43dES-114	Fuji	Fuji Nijo (DES)	

* These mutants were already genetically investigated by Scholz and Lehmann (1958).

** The mutant was already genetically investigated by Takahashi *et al.* (1972).

Table 1 also shows the abbreviated names of these mutants because the original names were complicated.

Twenty plants each of the mutants, their original two-rowed varieties, and a six-rowed check Natsudaikon Mugi (var *hybernum*) were grown together in fields, and record was taken for the following traits; the presence or absence of hairs on basal leaf-sheaths, anthocyanin pigmentation on lamina joint of flag leaf, rough or smooth awns, heading date, stem length, and diameter of the second internode from the top. At maturity, 10 plants of each mutant were harvested, and measurements were made of the lengths of awns and pedicels of two spikelets from the central portion of the spike on the longest culm within plant. Determination of the rachilla hair type was also made. Then, the central and lateral kernels of the same spike were respectively threshed and weighed.

Allelism tests and genic analyses of mutant genes were made using a total of 259 F_1's from incomplete diallel crosses among 35 mutants (possible 595 crosses) and 70 F_1's crossed with the original two-rowed parents and six-rowed check.

Inheritance and linkage of the six-rowed gene were studied by ordinary method or by trisomic method. The details will be described in the respective sections.

RESULTS

Allelism Test of Six-rowed Mutations

When all mutants were crossed to their respective original two-rowed cultivars (*VV*) and to Natsudaikon Mugi (*vv*), they could be easily classified into two groups according to differences in head types of F_1 plants. As shown in Table 2, one group, consisting of 25 mutants, gave F_1's with heads of two-rowed/six-rowed heterozygote from crosses with the original two-rowed varieties (*VV*), and gave F_1's with six-rowed

TABLE 2. Head types of F_1 plants from crosses between two groups of six-rowed mutants and their original two-rowed variety (*VV*) or six-rowed check Natsudaikon Mugi (*vv*), and F_1 type from inter-group crosses among mutants

Six-rowed mutant group	Number of mutants	F_1 head type when crossed with		
		Original two-rowed vars (*VV*)	Natsudaikon Mugi (*vv*)	Six-rowed mutants of group I
I	25	Heterozygote*(25)**	Six-rowed (25)	Six-rowed (144)
Other	10	Two-rowed (10)	Heterozygote (10)	Heterozygote (86)

* 'Heterozygote' refers to a head type of two-rowed/six-rowed heterozygote.

** Numerals in parentheses represent number of cross combinations.

heads from the cross with six-rowed Natsudaikon Mugi (*vv*). This is just the situation which occurs in F_1 generation when a true six-rowed form with gene *v* is crossed to varieties with allelic gene *V*. Therefore, it is certain that these 25 mutants had an allele *v* in common. It is mentioned also that a total of 144 mutual crosses among them always gave F_1's with six-rowed heads (Table 2). These 25 mutants will be called genetic group I in the following.

The remaining ten mutants constituted the second group; the crosses of the mutants of this group with two-rowed form (*VV*) gave F_1's with two-rowed heads, while the crosses with six-rowed Natsudaikon Mugi (*vv*) gave F_1's with heads of two-rowed/six-rowed heterozygote (Table 2). This indicates that the mutants each have a recessive gene (*x*) for six-rowed heads instead of *v*, where *xx* is epistatic to *VV*, thus crosses with the original two-rowed parents (*VVXX*) give *VVXx* (two-rowed) F_1's and those with six-rowed check (*vvXX*) bring *VvXx* (two-rowed/six-rowed heterozygous) F_1's.

The results of the diallel crosses among these 10 mutants were different from those of genetic group I (Table 3). The mutual crosses of these 10 mutants gave F_1 plants with either two-rowed or six-rowed

TABLE 3. Four different groups of six-rowed mutants classified by incomplete-diallel crosses among them

Six-rowed mutant group	Number of mutants	F_1 head type crossed with group			
		II	III	IV	V
II	1	6-row (selfing)*			
III	5	2-row (5)	6-row (10)		
IV	3	2-row (2)	2-row (3)	6-row (3)	
V	1	2-row (1)	2-row (3)	2-row (2)	6-row (selfing)

* Numerals in parentheses represent number of cross combinations.

TABLE 4. Names of six-rowed mutants belonging to five different genetic groups

Genetic group	No. of mutants	Names of six-rowed mutants
I	25	Piro-4, Piro-6, MFB-1, MFB-3, MFB-4, MFB-5, MFB-6, MFB-7, MFB-8, MFB-9, MFB-10, MFB-11, MFB-12, MFB-13, MFB-14, MFB-15, MFB-16, AD-1, AD-2, Haisa-1, Haisa-2, Saale-1, Saale-2, Kirin, Fuji
II	1	Svan
III	5	Piro-1, Piro-3, Piro-5, Piro-8, Hakata
IV	3	Piro-2, Piro-7, MFB-2
V	1	Gamma

heads. From these results, 10 mutants could be reasonably classified into four genetic groups which were tentatively called genetic group II, III, IV and V. Consequently, it is possible to assume that mutants of each genetic group had a peculiar six-rowed gene different from other genetic groups, all of which were completely recessive to its allele, but were epistatic to *V*. Genes involved in the four genetic groups II, III, IV and V were tentatively allotted symbols v_2, v_3, v_4 and v_5, respectively.

Table 4 shows five genetically different groups and the names of the mutant strains belonging to each of these five groups.

Comparative Morphology of Mutants

As stated before, all mutants have been regarded as a six-rowed type in this study because they recovered fertility of lateral florets. However, there were marked differences among the mutants in the degree of development of lateral florets, such as awn length, kernel weight or pedicel length. Because the six-rowed mutants were induced from different two-rowed parents, awn length or kernel weight can not be directly compared among the mutants. Thus, the ratio of lateral to central row (L/C ratio) was used for comparison of these characters.

There were marked differences in pedicel length of lateral florets among mutants varying from 0.45 to 2.10 mm (Table 5). It is noteworthy that 25 mutants belonging to genetic group I could be easily divided into two subgroups; one group, consisting of 16 mutants, had short pedicels (average, 0.58 mm) close to six-rowed check (0.46 mm), and the remaining 9 mutants had decidedly long pedicels (average, 1.84 mm). These two subgroups will be called respectively subgroup Ia and Ib. The mutants of other genetic groups developed longer pedicels than the six-rowed check. No mutant exceeded its original two-rowed variety in pedicel length.

The L/C ratio for kernel weight varied from 0.155 to 0.796. Sixteen mutants of subgroup Ia had high L/C ratios (average, 0.761) very close to six-rowed check (0.735). While, two mutants (MFB-12 and MFB-15) of subgroup Ib had the lowest L/C ratio.

The L/C ratio for awn length of mutants varied from 0.088 to 0.908; mutants of subgroup Ia had the highest ratio (average, 0.838) very close to six-rowed check (0.879). While, three mutants, Piro-1, Piro-3 and Piro-8, belonging to genetic group III had quite low ratios (0.088～0.125).

Two scatter diagrams were prepared to show the morphological differences among these mutants. Fig. 1 shows that the L/C ratio for kernel weight and awn length was not necessarily correlated. For example, mutants in genetic group IV and subgroup Ia have plump

TABLE 5. Pedicel length of lateral florets and lateral to central (L/C) ratio for kernel weight and awn length in 35 six-rowed mutants and six-rowed check Natsudaikon Mugi

Genetic group	Mutant strain	Pedicel length (mm)	L/C ratio for	
			Kernel weight	Awn length
Ia	MFB-3	0.53	0.766	0.781
	MFB-5	0.45	0.747	0.908
	MFB-6	0.55	0.776	0.816
	MFB-7	0.58	0.788	0.855
	MFB-8	0.58	0.727	0.841
	MFB-9	0.50	0.730	0.856
	MFB-10	0.48	0.754	0.857
	MFB-11	0.50	0.770	0.869
	MFB-13	0.60	0.796	0.857
	MFB-14	0.88	0.756	0.895
	MFB-16	0.53	0.759	0.798
	AD-2	0.53	0.787	0.835
	Haisa-1	0.55	0.735	0.805
	Haisa-2	0.70	0.721	0.852
	Saale-1	0.65	0.781	0.797
	Saale-2	0.68	0.770	0.787
	$\bar{x}$	0.58	0.761	0.838
Ib	Piro-4	1.90	0.374	0.659
	Piro-6	2.10	0.310	0.653
	MFB-1	2.08	0.510	0.723
	MFB-4	1.88	0.433	0.696
	MFB-12	2.05	0.155	0.525
	MFB-15	1.93	0.157	0.708
	AD-1	1.35	0.508	0.702
	Kirin	1.55	0.520	0.700
	Fuji	1.72	0.278	0.450
	$\bar{x}$	1.84	0.361	0.646
II	Svan	1.95	0.499	0.369
III	Piro-1	1.30	0.419	0.110
	Piro-3	1.33	0.472	0.125
	Piro-5	1.18	0.500	0.526
	Piro-8	1.65	0.550	0.088
	Hakata	1.28	0.649	0.601
	$\bar{x}$	1.35	0.518	0.290
IV	Piro-2	0.90	0.654	0.777
	Piro-7	1.03	0.695	0.727
	MFB-2	1.13	0.705	0.771
	$\bar{x}$	1.02	0.685	0.758
V	Gamma	0.71	0.570	0.517
Natsudaikon Mugi		0.46	0.735	0.879

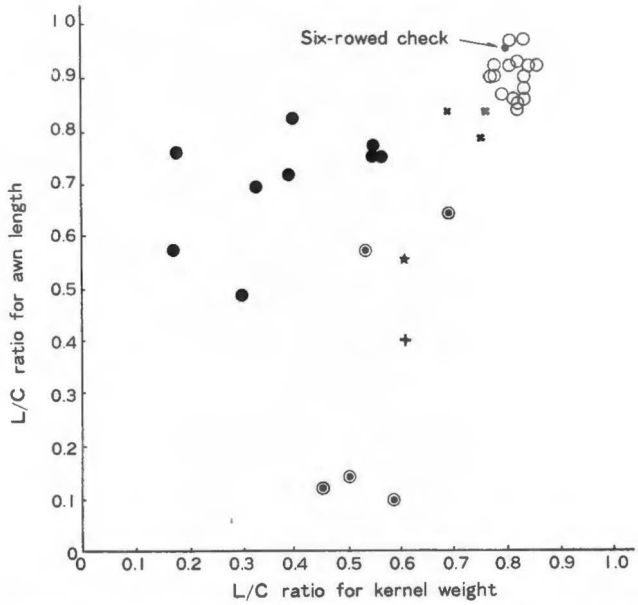

FIG. 1. Interrelationship between L/C ratio for kernel weight and awn length in five different genetic groups of 35 six-rowed mutants. (○) genetic group Ia, (●) group Ib, (+) group II, (◉) group III, (×) group IV, (★) group V.

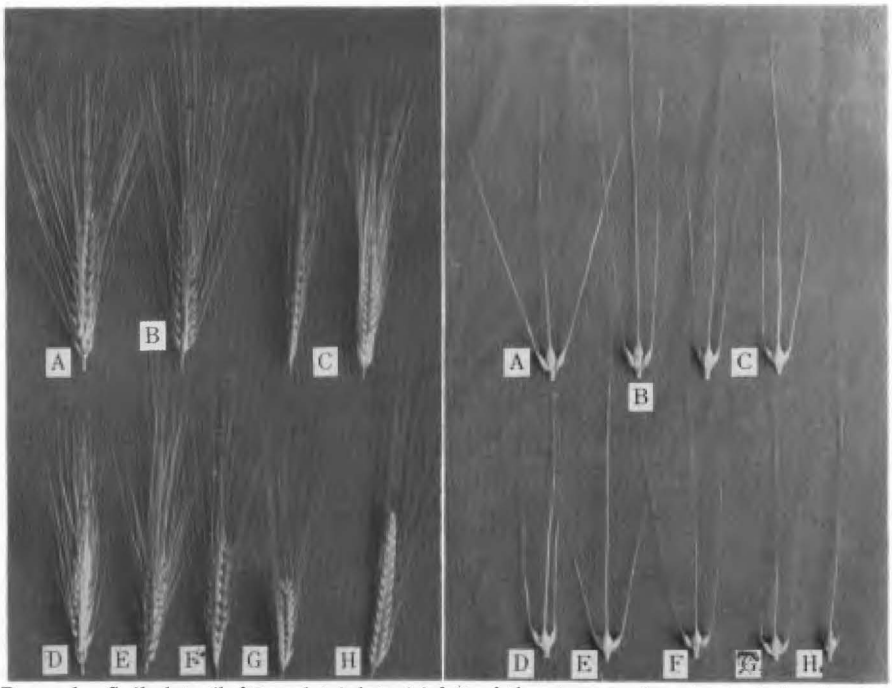

PLATE 1. Spikelets (left) and triplets (right) of the six-rowed mutants belonging to five different genetic groups. (A) six-rowed check Natsudaikon Mugi (*vv*); (B) MFB-5, genetic group Ia (*vv*); (C) Piro-4 (left) and Fuji (right), group Ib (*vv*); (D) Svan, group II (v_2v_2); (E) Hakata, group III (v_3v_3); (F) Piro-2, group IV (v_4v_4); (G) Gamma, group V (v_5v_5); (H) two-rowed var. Piroline (*VV*).

kernels and well-developed lateral awns and alike to those of six-rowed check (Plate I). However, 9 mutants of subgroup Ib are generally lower in L/C ratio for kernel weight but not in the ratio for awn length. The reverse relationship was observed in three mutants of genetic group III (Piro-1, Piro-3, and Piro-8); namely, marked reduction occurred in L/C ratio for awn length, but not in L/C ratio for kernel weight.

The L/C ratio for kernel weight was negatively correlated ($r = -0.870$) with pedicel length (Fig. 2). As shown in the scatter diagram in Fig. 2, mutants belonging to subgroup Ia have well-developed lateral kernels and short pedicels whereas mutants of Ib have lighter laterals and longer pedicels.

Finally, it must be pointed out a rather strange fact that all mutants belonging to subgroup Ia showed simultaneous changes not only in kernel row number but also in some morphological or physiological traits (Table 6). For example, three six-rowed mutants (AD-2, Saale-1 and Saale-2) induced from A. Donaria and Saale, both of which were hairless on leaf-sheaths, developed hairy leaf-sheaths. MFB-104, two-rowed variety with colored lamina joint of flag leaf and rough awn,

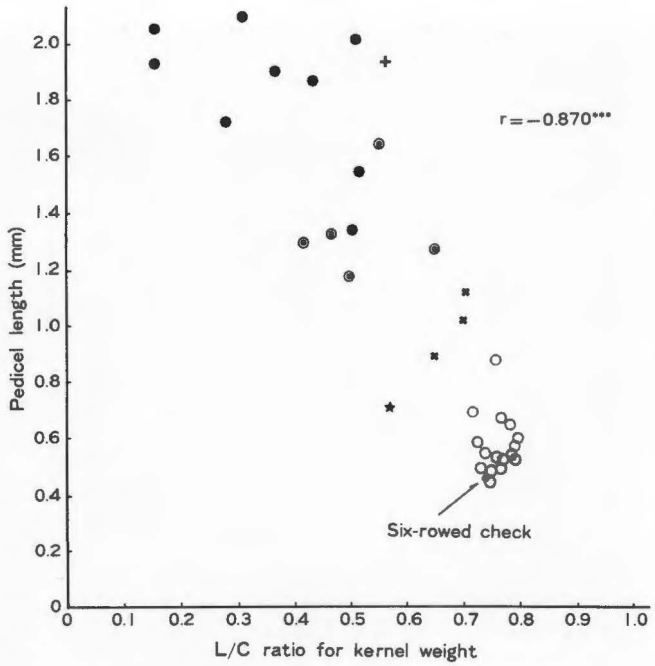

FIG. 2. Interrelationship between L/C ratio for kernel weight and pedicel length in five different genetic groups of 35 six-rowed mutants. (○) genetic group Ia, (●) group Ib, (+) group II, (◉) group III, (×) group IV, (★) group V.
*** Significant at 0.1% level.

TABLE 6. Morphological and physiological characters of six-rowed mutant strains compared with their original two-rowed variety

Genetic group	Mutant strain	Leaf-sheath hair[1]	Plant coloration[1]	Awn barbing[2]	Rachilla hair type[3]	Heading[4] (days)	Stem length[4] (cm)	Central kernel wt[4] (mg)	Stem diameter[4] (mm)
Ia	MFB-3	−	+	S*	S*	+ 4	+18	+ 2.1	+0.2
	MFB-5	−	+	R	S*	+ 6	+17	+ 0.2	0
	MFB-6	−	+	R	S*	+ 4	+20	+ 3.0	+0.1
	MFB-7	−	+	R	L	− 3	+31	+16.9	+0.9
	MFB-8	−	+	R	S*	+12	+31	− 3.5	+0.4
	MFB-9	−	+	R	S*	+13	+27	− 4.6	+0.4
	MFB-10	−	+	R	S*	+12	+25	− 3.5	+0.6
	MFB-11	−	+	R	S*	+10	− 3	−11.1	+0.7
	MFB-13	−	−*	R	L	− 4	+ 5	+16.6	+1.1
	MFB-14	−	+	R	S*	+14	+ 9	−23.3	+0.4
	MFB-16	−	+	S*	L	+ 4	+ 7	+ 1.8	−0.1
	AD-2	+*	+	R	L	− 1	+11	− 1.1	+0.4
	Haisa-1	−	+	R	S*	− 1	+ 9	− 2.1	+0.2
	Haisa-2	−	+	R	S*	− 8	− 6	+ 4.9	0
	Saale-1	+*	+	R	L	− 2	+19	+ 0.8	+1.2
	Saale-2	+*	+	R	L	0	+10	− 8.9	+1.0
Ib	Piro-4	−	+	R	S	− 1	+ 4	− 3.1	0
	Piro-6	−	+	R	S	− 2	− 7	−11.8	+0.1
	MFB-1	−	+	R	S*	+ 2	+18	− 0.9	−0.1
	MFB-4	−	+	R	L	+ 4	+ 3	− 4.9	−0.4
	MFB-12	−	+	R	L	+ 1	− 4	− 3.8	−0.4
	MFB-15	−	+	R	L	0	− 1	− 5.6	−0.4
	AD-1	−	+	R	L	− 2	− 3	− 3.5	+0.1
	Kirin	−	+	R	L	+ 1	+12	+ 2.7	−0.3
	Fuji	−	+	R	L	0	+ 2	+ 2.3	+0.1
II	Svan	−	+	R	L	+ 3	− 3	−11.3	−0.2
III	Piro-1	−	+	R	S	+ 1	+ 8	− 8.6	+0.1
	Piro-3	−	+	R	S	+ 1	+ 3	− 3.3	0
	Piro-5	−	+	R	S	+ 3	+ 1	−13.1	−0.5
	Piro-8	−	+	R	S	+ 3	+ 3	−18.7	+0.1
	Hakata	−	+	R	L	+ 3	− 9	− 9.5	+0.3
IV	Piro-2	−	+	R	S	− 1	+ 6	− 7.4	−0.2
	Piro-7	−	+	R	S	+ 6	+ 8	−23.5	+0.4
	MFB-2	−	+	R	L	+ 2	+10	− 4.3	0
V	Gamma	−	+	R	L	+ 2	−10	−12.3	0

* means discrepancy between the mutant and its original two-rowed variety.

1) +, presence; −, absence.

2) R, rough awn; S, smooth awn.

3) L, long rachilla hair type; S, short rachilla hair type.

4) Increase or decrease from two-rowed original variety.

produced six-rowed mutants with colorless (MFB-13) or smooth awn (MFB-3 and MFB-16). Eleven mutants induced from long-haired MFB 104 and Haisa had short-haired rachilla. Most six-rowed mutants in subgroup Ia had very late heading dates and/or were very tall compared with the original variety. Moreover, the central kernel weight of the two six-rowed mutants (MFB-7 and MFB-13) was about 17 mg heavier than the original variety. MFB-14 and Piro-7, on the contrary, had markedly lighter central kernels than those of the two-rowed parents. Table 6 also indicates that the stem diameter of some mutants of Ia was markedly thicker than their original two-rowed parents.

Inheritance of the Six-rowed Character and its Linkage

Crosses were made between two or three representative mutants belonging to genetic groups I~IV, namely, I×III, I×IV, II×III, II×IV and III×IV. Furthermore, MFB-2 of genetic group IV and Gamma of genetic group V were crossed to two-rowed tester stocks.

As shown in Table 7a, the F_2 data of three crosses between six-rowed mutants of genetic group Ib and those of genetic group III and IV gave a close fit to a ratio of 3 two-rowed, 6 two-rowed/six-rowed heterozygous and 7 six-rowed plants. This may be explained on the assumption that these two parental strains differed from each other in

TABLE 7. Segregation of head types in F_2 of (a) mutual crosses of mutants in four different genetic groups and (b) crosses between two six-rowed mutants (MFB-2 and Gamma) and two-rowed tester stocks

Cross combination (genetic group)	Two-rowed	Heterozygote*	Six-rowed	Total	P value of χ^2 for 3:6:7	9:7	3:1
(a) six-rowed mutant × six-rowed mutant							
MFB-12(I) × Piro-3(III)	117	201	223	541	.20–.30		<.001**
Piro-6(I) × Hakata(III)	76	194	189	459	.05–.10		<.001**
MFB-15(I) × Piro-2(IV)	119	200	241	560	.30–.50		<.001**
Piro-1(III) × Svan(II)	317	0	237	554		.50–.70	<.001
Svan(II) × MFB-2(IV)	260	0	186	446		.30–.50	<.001
Hakata(III) × Piro-2(IV)	247	0	193	440		>.90	<.001
(b) six-rowed mutant × two-rowed tester stocks							
MFB-2(IV) × LT 16	334	0	131	465		<.001	.10–.20
MFB-2(IV) × Russian 56	354	0	120	474		<.001	.80–.90
Gamma(V) × LT 16	331	0	120	451		<.001	.30–.50
Gamma(V) × Nigrinudum	367	0	125	492		<.001	.80–.90
Gamma(V) × Russian 56	353	0	126	479		<.001	.50–.70

* Head type of a two-rowed/six-rowed heterozygote.

** Two-rowed and heterozygote plants were combined.

two pairs of gene, *Aa* and *Bb*, and either of the recessive gene pair *aa* or *bb* or both could express the six-rowed character, i. e., *aa* and *bb* were epistatic to *B* and *A* gene, respectively. The gene involved in the mutant of genetic group Ib could express two-rowed/six-rowed heterozygous heads when its genic constitution was heterozygous.

On the other hand, in three crosses among the mutants involved in genetic group II, III or IV, only two-rowed and six-rowed plants were found in F_2 in a ratio of 9 : 7, but not in 3 : 1 ratio (Table 7a). In this case, it is reasonable that these two parental strains differed in two pairs of gene for six-rowed head, and both gene pairs were completely recessive, and again each recessive homozygote was epistatic to another dominant gene.

In the F_2 generation of the two crosses between a six-rowed mutant MFB-2 and two two-rowed tester stocks, only two-rowed and six-rowed plants appeared in a ratio of 3 : 1, and no two-rowed/six-rowed heterozygous plant was found. (Table 7b). The same segregation ratio was observed in crosses between a six-rowed mutant Gamma and three two-rowed tester stocks. The results indicated that six-rowed heads of MFB-2 of genetic group IV and Gamma of genetic group V were controlled by a single recessive gene. Thus, all results stated above lead to the conclusion that six-rowed heads of mutants in genetic group I were controlled by an incompletely recessive gene *v*, while those of genetic group II, III, IV or V were controlled by a single recessive gene v_2, v_3, v_4 or v_5, respectively.

For linkage study of gene v_3 in Hakata, trisomic method was applied. Table 8 shows that in F_2 of crosses with 'Pale' and 'Purple' including

TABLE 8. Linkage data for gene v_3 in Hakata by trisomic method

Trisomic type (extra chromosome)	Disomic		Trisomic		Total	P value of χ^2 for 3:1
	Two-rowed	'Six-rowed'	Two-rowed	'Six-rowed'		
Pseudo-normal (5)	92	4	48	0	144	<.001*
Pale (3)	76	20	38	15	148	.70–.80
Purple (6)	79	20	25	14	138	>.90

* P value of χ^2 for 8:1 in disomic class was >.05.

extra chromosome 3 and 6, respectively, the segregation of two-rowed and six-rowed plants occurred in a 3 : 1 ratio, but in F_2 of the cross with 'Psuedo-normal (5)', the observed number of two-rowed and six-rowed plants much differed from the expected numbers on a 3 : 1 segregation ratio, but fitted a trisomic ratio of 8 : 1 in disomic class. Though F_2 segregation in other possible crosses including trisomic stocks

'Bush (1)', 'Slender (2)', 'Robust (3)', and 'Semi-erect (7)' have not been investigated, the above-mentioned results might be sufficient to indicate that gene v_3 was located on chromosome 5.

Table 9 shows the interrelationships between gene v_4 in MFB-2 and the seven marker genes involved in two-rowed linkage tester stocks, LT 16 and Russian 56. Gene v_4 was independently inherited of *n* on chromosome 1, *K* on 4, *B* and *trd* on 5, *o* on 6 and *s* on 7, but linked with gene *uz* for 'uzu' or semi-brachytic growth on chromosome 3 with recombination of 27.55 ± 4.24 %.

Finally, the linkage of gene v_5 in Gamma was studied using crosses with three two-rowed tester stocks, Nigrinudum, LT 16 and Russian 56.

TABLE 9. Interrelationships between gene v_4 in MFB-2 and the seven marker genes involved in two-rowed tester stocks, LT 16 and Russian 56

MFB-2 ×	Symbol		Chromosome	V_4(two-rowed)		v_4(six-rowed)		Total	P value of χ^2 for linkage
	X	*x*		*X*	*x*	*X*	*x*		
LT 16	*N*	*n*	1	263	71	91	40	465	.20–.30
LT 16	*Uz*	*uz*	3	239	94	122	9	464	<.001*
LT 16	*K*	*k*	4	254	80	99	32	465	>.90
LT 16	*B*	*b*	5	241	93	101	30	465	.70–.80
LT 16	*Trd*	*trd*	5	245	89	97	34	465	>.90
Rus. 56	*O*	*o*	6	266	88	91	29	474	>.90
LT 16	*S*	*s*	7	251	83	94	37	465	.80–.90

* Recombination value (repulsion): 27.55 ± 4.24%.

TABLE 10. Interrelationships between gene v_5 in Gamma and the seven marker genes involved in two-rowed tester stocks, Nigrinudum, LT 16 and Russian 56

Gamma ×	Symbol		Chromosome	V_5(two-rowed)		v_5(six-rowed)		Total	P value of χ^2 for linkage
	X	*x*		*X*	*x*	*X*	*x*		
Nigri.	*N*	*n*	1	282	85	98	27	492	>.90
LT 16	*N*	*n*	1	253	78	98	22	451	.50–.70
LT 16	*Uz*	*uz*	3	275	56	93	25	449	.80–.90
LT 16	*K*	*k*	4	301	30	38	82	451	<.001*
LT 16	*B*	*b*	5	245	86	86	34	451	>.90
Nigri.	*B*	*b*	5	279	89	89	36	493	.70–.80
LT 16	*Trd*	*trd*	5	258	73	89	31	451	.80–.90
Rus. 56	*O*	*o*	6	254	99	91	35	479	>.90
Nigri.	*S*	*s*	7	271	96	95	31	493	>.90

* Recombination value (coupling): 16.21 ± 1.93%.

According to Table 10, gene v_5 was inherited independently of *n* (1), *uz* (3), *B* and *trd* (5), *o* (6) and *s* (7), but apparently linked with gene *K* for hooded lemma appendage on chromosome 4. The recombination value between v_5 and *K* was calculated to be 16.21 ± 1.93 %.

DISCUSSION

It has been reported so far that almost all of the induced 'six-rowed' mutants were due to genic changes in the *V* locus on chromosome 2 (Nybom 1954, Hagberg and Persson 1964, Gustafsson and Lundqvist 1980). One exception was the 'six-rowed' mutant induced by Nötzel (1952), which was confirmed to result from a genic change in other than *V* locus, though its locus was not decided. A number of mutants classified into 'intermedium' type, on the other hand, were attributed to genic changes in loci other than *V* (Nötzel 1952, Gustafsson and Lundqvist 1980).

A series of our genetic investigations have disclosed that 35 'six-rowed' mutants are classified into five genetic groups and mutants of these five groups are controlled by five different genes, *v*, v_2, v_3, v_4 and v_5 locating on chromosome 2, 7, 5, 3 and 4, respectively, and four genes other than *v* are completely recessive.

As stated before, 16 mutants belonging to genetic group Ia with well-developed lateral florets alike to six-rowed check showed simultaneous changes from the original two-rowed variety not only in kernel row number but also in some morphological or physiological traits, such as hairiness on leaf-sheaths, anthocyanin pigmentation, awn barbing, rachilla hair type, heading date, stem length, central kernel weight or stem diameter (Table 6). As is well-known, some of these traits are controlled by a major gene, such as *Hs*, *r* or *s*. So, it must be assumed that mutations in two different loci simultaneously occurred in these mutants, though such events are very rare. Moreover, differences between mutants and their original two-rowed parents in some physiological traits can hardly be explained by pleiotropy of their mutated gene '*v*' from *V*. Because, according to Takahashi *et al.* (1976), gene pair *VV* or *vv* does not affect so strong on heading date, stem length or stem diameter.

The remaining 9 mutants (group Ib) from a change in *V* locus had somewhat underdeveloped lateral florets with long pedicels (Plate I). They did not show the morphological or physiological changes mentioned above with the exception of MFB-1 which had short haired rachilla though its original two-rowed variety MFB 104 was of the long-haired type. In these 9 mutants, two possibilities may be considered in regard to poorer development of lateral florets. One is that the gene involved in these mutants may be allelic gene to *v*. It is well-known that there are

many alleles located on the *V* locus, such as V^a, V^t, V^p, *lr* or *Lk*. Another possibility is that the poor development of laterals may be due to an interaction between gene *v* and some modifier(s), such as I^h or *I* controlling lateral grain development (Leonard 1942, Woodward 1949).

Ten of 35 mutants arose from genic changes in four different loci other than *V*. Almost all of these 10 mutants had underdeveloped awns and kernels in the lateral row, and long pedicels (Plate I). No morphological or physiological change was found in these 10 six-rowed mutants.

Our results lead to the conclusion that, excepting mutants belonging to genetic group Ia, all 'six-rowed' mutants developed somewhat undersized lateral florets. But, they had almost completely fertile lateral florets. In this sense, we regard them as a six-rowed type though Gustafsson and Lundqvist (1980) have suggested that our materials should be classified into 'intermedium' type.

Trofimovskaja and Zukovskij (1967) treated three winter barleys by ethyl methanesulfonate and reported that mutations from two-rowed to six-rowed condition were more frequent than in the reverse direction. As stated before, this problem is very important on the origin of cultivated barley. Therefore, more detailed experiments may be needed for the problem.

SUMMARY

A total of 35 six-rowed mutants were studied to know how many mutants have resulted from genic changes in *V* locus, and also how many other loci have been involved in six-rowed mutations.

The mutants were crossed to a six-rowed check Natsudaikon Mugi with gene *v* and to the respective two-rowed original variety with gene *V*. Further, 294 cross combinations among mutants were used for allelism test of gene for six-rowed heads.

Of 35 six-rowed mutants, 25 resulted from a change in *V* locus. However, nine of the 25 were classified into a different subgroup because of their underdeveloped lateral florets with somewhat elongated pedicels compared with the remaining 16 six-rowed mutants.

According to differences in genetic behavior, the other 10 six-rowed mutants could be classified into four genetic groups having a peculiar gene, tentatively named v_2, v_3, v_4 and v_5, respectively. They were all completely recessive to their allelic genes but epistatic to *V* for two-rowed heads.

Linkage analysis using trisomic method indicated that gene v_3 was on chromosome 5. It was confirmed by conventional F_2 method that gene v_4 was located 27.55 ± 4.24 units apart from *uz* on chromosome 3 and that gene v_5 was 16.21 ± 1.93 units apart from *K* on chromosome 4.

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