INHERITANCE AND LINKAGE STUDIES IN BARLEY

V. Locating of Seven New Mutant Genes

Ryuhei TAKAHASHI, Jiro HAYASHI, Takeo KONISHI
and Isamu MORIYA

Barley is among the crop plants of which genetic studies have been made most extensively, but its chromosome map is still far from complete. We have made continued efforts for long years to accumulate linkage data as many as possible, and have recently been in success to locate seven new mutant genes on barley chromosomes 1, 2, 4 and 7. The results are presented in this paper.

MATERIALS AND METHODS

Main characteristics and origin of the seven mutants and the gene symbols allotted to them are listed in Table 1. A further detailed description of each mutant will be given later when necessary.

TABLE 1

Main characteristics and origin of the mutants and the genes allotted to them.

Name of mutant	Characteristics	Gene symbol	Origin
OUM 215	Xantha seedling; heterozygote is chlorina and viable.	X_a	EMS-induced from Akashinriki×L.T. 22 by T. Konishi.
Okaiku 3	Glossy sheath-5, upper leaf-sheaths only lack waxy bloom.	gs_5	Spontaneous mutation in this cultivar.
Goseshikoku-hen	Glossy, waxless leaves.	gl_8	Spontaneous mutaion in a cultivar Goseshikoku.
Kmut 28	Brachytic growth; stems, leaves and awns short, spikes compact.	br_2	X-ray induced from Svanhals by T. Tsuchiya.
Kmut 174	Chlorina plant color (temperature independent), viable.	f_9	X-ray induced from a cultivar Kô A by T. Tsuchiya.
Kmut 27	Semi-six-rowed spike; upper and lower laterals small, sterile and tip-awned or awnless.	v_2	X-ray induced from Svanhals by T. Tsuchiya.
Nagaoka dwarf	Dwarf growth with narrow, erect leaves and curved upper stem-internodes.	*nld*	Spontaneous mutation in F_2 of a Nagaoka×Marumi cross.

The linkage analyses of these mutants were made in the following way: As the first step, a mutant was crossed to a few selected genetic stocks which have been known to involve one or more marker genes on each of the seven chromosomes and determined the linkage group of the mutant gene from the F_2 segregation. Next, the mutant was crossed again to one or two multiple marker stocks appropriate for making the three-point test of the mutant gene in question A list of various genes on different chromosomes involved in each of the new mutants is given in Table 2, and the marker genes and characters of the various genetic stocks crossed to the mutants are shown in Table 3.

TABLE 2

Genic constitutions of the seven mutants used in this investigation.

Mutant (gene)	Chromosome						
	1	2	3	4	5	6	7
OUM 215 (X_a)	*Lk*$_2$, *n*, *L*, *Y*$_c$, *Ac*$_2$	*V*	*Uz*, *Al*	*k*	*Trd*	*O*	*s*
Okaiku 3 (gs_3)	*l*, *n*	*v*, *pr*, *E*, *Li*	*uz*, *An*, *Ac*	*k*, *hs*	*Trd*, *b*	*O*	*S*
Goseshikoku-hen (gl_8)	—	*v*	*uz*, *An*	*k*, *Hs*, *bl*	*b*	—	*S*
Kmut 28 (br_2)	*l*?	*V*	*Uz*	*k*, *Gl*$_8$	—	*O*	*S*
Kmut 174 (f_9)	*N*, *l*?	*V*	*An*	*k*, *Gl*$_8$	*b*	*O*	*S*, *R*
Kmut 27 (v_2)	*N*	*V*, *Li*	*Uz*	*k*	*Trd*, *b*	*O*	*S*
Nagaoka dwarf (*nld*)	*N*	*v*, *pr*	*An*	*k*, *hs*	*b*	*O*	*Fs*, *S*, *R*

In determining independent inheritance or linkage between two pairs of genes, the chi-square test for linkage (χ^2_L) was used throughout. Prior to this test, the fit of the F_2 segregation of each of the single character pairs, say Aa and Bb, to the 3 : 1 or some other expected ratio was tested, and when a poor fit was observed for both of the character pair segregations, the data were discarded. Recombination percentages were calculated by use of maximum likelihood formula. When more than two values of recombination between two genes were obtained from different sources of data, these values were combined and a weighted average value was calculated after the method suggested by Robertson *et al.* (1944) and Kramer and Burnham (1947).

RESULTS AND DISCUSSION

1. *Semidominant Chlorophyll Mutant, OUM 215* (X_a)

This chlorophyll mutant OUM 215 (Okayama University Mutant accession number) was first found by one of the authors, T. Konishi, among

TABLE 3

Marker characters and genetic stocks used in this investigation.

Chromosome	Gene symbol	Character	Genetic stocks
1	ac_2	Albino seedling	Coast II
	yc	Virescent seedling	Coast III
	l	Dense spike	Shiro Ômugi, e-trd, Ligule-less, Kobinkatagi 4
	n	Naked kernel	Nigrinudum, L.T. 16, Kobinkatagi 4, Brachytic
	lk_2	Short awn	Shiro Ômugi, Kobinkatagi 4
	br	Brachytic growth	Brachytic
2	*e*	Elongated glume	e-trd
	Pr	Colored leaf-tip	Nigrinudum, Colsess I, e-trd, Ligule-less, T. 179
	V	Two-rowed spike	Nigrinudum, Svanhals, L.T. 16, Kôyô (ligule-less)
	li	Ligule-less	Ligule-less, Kôyô (ligule-less)
3	*uz*	Uzu or semibrachytic	L.T. 12, L.T. 16, uz-x_3
	a_c	Albino seedling	Colsess I
	al	Albino lemma	Russian 82
	a_n	Albino seedling	Nigrinudum
4	*K*	Hooded appendage	L.T. 12, L.T. 16, Colsess I, IV, and V, K-gl_3
	gl_3	Glossy seedling 3	K-gl_3
	Hs	Hairy leaf-sheath	Ligule-less
	Bl	Blue aleurone	Tawangmiao
5	*trd*	Third outer glume	L.T. 12, L.T. 16, e-trd
	B	Black lemma	Nigrinudum, Minn. 90-5, L.T. 16
6	*o*	Orange lemma	Orange lemma
7	*fs*	Fragile stem	Kamairazu
	s	Short haired rachilla	Orange lemma, Nigrinudum, L.T. 16 Colsess I, IV, and V, T. 179, Syria 439
	r	Smooth awn	T. 179, Syria 439, Minn. 90-5

the M_2 families derived from the EMS-treated seeds of a cross between Akashinriki and Linkage tester (L.T.) 22, and its mode of inheritance and linkage were studied solely by him. The strain was found to segregate three types of seedlings, xantha, chlorina and green, in the M_2 nursery. Because of the deficiency of chlorophyll, the xantha plants were dead at the seedling stage, but the latter two could grow up normally. The chlorina plant contains, like the chlorina plants of Colsess V ($f_c f_c$), total chlorophyll much less than the green plants, but is much higher in chlorophyll a/b ratio. In any way, distinction between chlorina and green plants is quite easy at any stage from the seedling to near maturity whether they are grown in the field or in the green house. Moreover, the chlorina plant is more winter-hardy than Colsess V.

As seen in Table 4, the xantha, chlorina and green seedlings appeared in a 1:2:1 ratio in the progeny of the selfed chlorina plant of OUM 215, while the green plants bred true. On the other hand, in the F_1 generation of the crosses between the chlorina plant of OUM 215 and several testers with green leaves, the chlorina and green plants appeared

TABLE 4

Segregation of three phenotypes in the progenies of the selfed chlorina and green plants, and in F_2 of the crosses of the chlorina plant from OUM 215 with four marker stocks.

OUM 215 chlorina ×	Phenotypes			Total	χ^2 for 1:2:1	P
	Xantha	Chlorina	Green			
Selfed chlorina (OUM 215)	80	167	82	329	0.100	.99—.95
Selfed green (OUM 215)	0	0	87	87	—	—
Shiro Ômugi	161	297	140	598	1.502	.5—.3
Orange lemma	368	740	397	1,502	1.533	.5—.3
Russian 82	162	324	157	643	0.117	.95—.9
L. T. 12	295	604	307	1,206	0.242	.9—.8

in a 1:1 ratio, and in the progenies of the chlorina F_1 plants from these four crosses, three types occurred in a 1:2:1 ratio. These results have led to the conclusion that only a single gene pair conditions these character expressions, and the chlorophyll deficient condition is semidominant over the green. Now denotes the gene pair $X_a x_a$, $X_a X_a$ and $x_a x_a$ are xantha and green, respectively, while the heterozygote $X_a x_a$ is chlorina.

Interrelationships between the gene $X_a x_a$ and a number of marker genes were studied using the crosses of the chlorina plants from OUM 215 with four genetic stocks. The F_2 results, shown in Table 5, indicate that the chlorophyll deficiency gene X_a is inherited independently of *l* (1),

TABLE 5

Independent inheritance of the chlorina seedling ($X_a x_a$) and several markers in F_2 generation of the four crosses with OUM 215.

OUM 215 ($X_a x_a$) chlorina type ×	Symbol		Chromosome	Chlorina ($X_a x_a$)		Green ($x_a x_a$)		Total	χ^2_L(*)	P
	Y	y		Y	y	Y	y			
Shiro Ômugi	*Lk*₂	*lk*₂	1	217	60	76	56	409	19.910	small
	N	*n*	1	218	59	107	25	409	0.216	.5—.3
	L	*l*	1	196	81	88	44	409	0.685	.5—.3
	V	*v*	2	204	72	102	31	409	0.294	.7—.5
Orange lemma	*N*	*n*	1	261	63	155	21	500	4.183	< .05
	V	*v*	2	171	53	103	23	350	1.495	.3—.2
	O	*o*	6	253	71	135	41	500	0.085	.8—.7
Russian 82	*N*	*n*	1	254	69	127	19	469	3.073	.1—.05
	V	*v*	2	245	78	112	34	469	0.028	.9—.8
	Al	*al*	3	243	80	109	37	469	0.018	.9—.8
	S	*s*	7	257	66	111	35	469	0.786	.5—.3
L.T. 12	*Uz*	*uz*	3	200	85	116	59	460	1.629	.3—.2
	K	*k*	4	216	69	135	40	460	0.159	.7—.5
	Trd	*trd*	5	212	73	135	40	460	0.495	.5—.3

* Calculated on the basis of a 6:2:3:1 segregation ratio.

v (2), *uz* (3), *K* (4), *trd* (5), *o* (6) and *s* (7), but is linked with lk_2 for short awn on chromosome 1. As to *n* for naked kernel on the same choromosome, on the other hand, a loose linkage was suggested by somewhat langer χ^2_L only in a cross with Orange lemma, but not in two other crosses, and no linkage was indicated any more between X_a and *l* from the F_2 results.

In order to obtain more reliable linkage data for these four genes, an F_3 progeny test was made for the cross between OUM 215 and Shiro Ômugi which included four gene pairs, Lk_2lk_2, *Nn*, *Ll* and X_ax_a altogether. In addition, relations of X_a with a_{c2} and y_c, both of which were known to be on the same chromosome, were studied by seedling test of the F_2 plants from the crosses with Coast II and Coast III. The summarized results of these linkage analyses are presented in Tables 6 and 7.

TABLE 6

The F_2 and F_3 data for linkages between X_ax_a and three gene pairs, Lk_2lk_2, *Nn*, and *Ll* obtained in a cross between the chlorina plant (X_ax_a) of OUM 215 and Shiro Ômugi.

Linked gene pairs X x Y y	Source of data	Phase	F_2 phenotypes or genotypes* xx YY	xx Yy	Xx YY	Xx Yy	xx yy	Xx yy	Total	Reocmbination value (%)	Weighted average value of recombination (%)
X_ax_a Lk_2lk_2	F_2	R	76		217		56	60	409	34.38	35.25±2.2470
	F_3	R	20	56	65	152	56	60	409	35.88	
X_ax_a *N n*	F_2	C	107		218		25	59	409	42.43	40.70±2.5627
	F_3	C	55	52	81	137	25	59	409	39.73	
X_ax_a *L l*	F_2	R	88		196		44	81	409	43.43	44.40±2.6012
	F_3	R	28	60	72	124	44	81	409	45.10	

* xx=green; Xx=chlorina. XX=lethal xantha and not included in this table.

TABLE 7

Interrelationships between X_ax_a and two gene pairs, $A_{c2}a_{c2}$ and Y_cy_c, in F_2 of the two crosses with Coast II and Coast III.

OUM 215 chlorina ×	Symbol X x	Y y	Green (xxY-)	Chlorina (XxY-)	Xantha (XXY-)	Albino or virescent (—yy)	Total	χ^2*	P	Recombination value (%)
Coast II	X_ax_a	$A_{c2}a_{c2}$	98	228	136	137	599	7.957	<.02	38.90± 5.1807
Coast III	X_ax_a	Y_cy_c	80	135	85	100	450	3.185	.5—.3	independent

*Compared with the calculated numbers on the ratio of 3:6:3:4.

According to Table 6, the X_a locus is considerably apart from all of the three other gene loci, but judging from the recombination values, X_a is on the leftmost, and lk_2, *n* and *l* are arranged to the right. Since the

gene order of the latter three suggested from this result is in accord with that confirmed by Takahashi *et al.* (1953), it may be possible to conclude that the gene order is X_a-lk_2-n-l. If so, it follows that both a_{c2} and y_c would be more distant than l from X_a. The F_2 data shown in Table 7 verify this: X_a and y_c were independent, and X_a and a_{c2} are quite loosely linked each other.

By the way, Takahashi and Hayashi (Barley Newsletter 2, 1959) had previously made a study on the relationships among the six genes, lk_2, n, l, a_{c2}, y_c and br in chromosome 1 in order to demonstrate by the conventional genetic method that linkage groups III and VII of barley are on one chromosome (cf. Kramer *et al.* 1954). Since the information may be

TABLE 8

F_2 and F_3 data for linkages between the gene pairs, Lk_2lk_2, Nn, Ll, $A_{c2}a_{c2}$, $Y_c y_c$ and $Brbr$, on chromosome 1 in three crosses indicated (repulsion phase).

Cross	Linked genes	Source of data	Segregation*	Total	Recombination value (%)	Weighted average value of recombination (%)
Coast II × Kobinkatagi 4	$A_{c2}a_{c2}$ ~Lk_2lk_2	F_2	409:167:205	781	36.08	19.38±1.6372
		$F_3(A_{c2}\ Lk_2)$	3 : 40 : 33 :173	249	17.67	
		$F_3(A_{c2}\ lk_2)$	86 : 45	131	20.74	
	$A_{c2}a_{c2}$ ~Nn	F_2	397:179:205	781	26.02	11.87±1.2673
		$F_3(A_{c2}\ N)$	2 : 22 : 26 :206	256	10.82	
		$F_3(A_{c2}\ n)$	94 : 30	124	13.76	
	$A_{c2}a_{c2}$ ~Ll	F_2	390:186:205	781	17.68	5.79±0.8790
		$F_3(A_{c2}\ L)$	0 : 11 : 15 :231	257	5.23	
		$F_3(A_{c2}\ l)$	106: 17	123	7.42	
Coast III × Kobinkatagi 4	Y_cy_c ~Lk_2lk_2	F_2	278:111:150	539	37.94	39.21±3.2086
		$F_3(Y_c\ Lk_2)$	16 :4 6 : 45 : 94	201	40.76	
		$F_3(Y_c\ lk_2)$	41 : 50	91	37.88	
	Y_cy_c ~Nn	F_2	266:123:150	539	22.67	37.99±3.2962
		$F_3(Y_c\ N)$	15 : 44 : 40 : 92	191	41.31	
		$F_3(Y_c\ n)$	47 : 54	101	36.49	
	Y_cy_c ~Ll	F_2	248:141:150	539	complete	36.26±3.1917
		$F_3(Y_c\ L)$	13 : 45 : 41 : 95	194	38.21	
		$F_3(Y_c\ l)$	48 : 50	98	34.25	
Coast II × Brachytic	$A_{c2}a_{c2}$ ~Nn	F_2	327:162:140	629	7.83	10.26±1.4418
		$F_3(A_{c2}\ N)$	1 : 23 : 13 :131	168	12.13	
		$F_3(A_{c2}\ n)$	80 : 14	94	8.05	
	$A_{c2}a_{c2}$ ~$Brbr$	F_2	364:125:140	629	independ.	
		$F_3(A_{c2}\ Br)$	25 : 55 : 49 : 79	208	independ.	
		$F_3(A_{c2}\ br)$	20 : 34	54	45.95	

* F_2 phenotypes: AB : Ab : (aB+ab)
F_2 genotypes, doubly dominant: AABB : AaBB : AABb : AaBb
singly dominant: AAbb : Aabb

of use in constructing a map of genes on this chromosome, the summarized results of the F_2 and F_3 tests are given in Table 8. This clearly indicates that these genes are arranged in the order of *lk*$_2$-*n*-*l*-*a*$_{c2}$-*y*$_c$-*br*, and at the same time the former linkage groups III and VII should be grouped into one.

Fig. 1 showing a map of genes on chromosome 1 was prepared from the present results and some other linkage data previously reported pertaining to these genes. It may be of interest to note that the new gene X_a occupies the distal end of the long arm of chromosome 1, and hence will be used as the marker in place of *lk*$_2$ for the cytogenetic study of this chromosome arm.

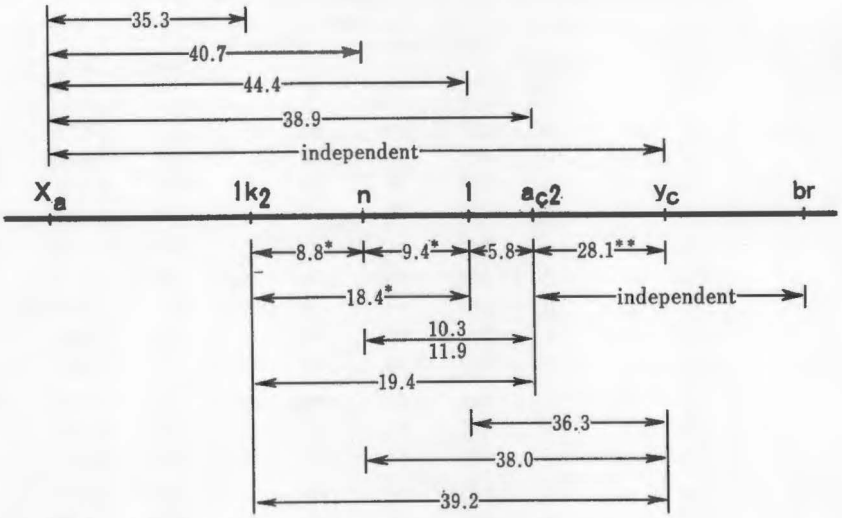

Fig. 1. A map of seven genes on chromosome 1.
* and ** are cited from Takahashi *et al.* (1953) and Haus (1958), respectively.

2. *Glossy Sheath* (*gs*$_5$) *in Okaiku 3*

Okaiku 3 is a naked variety of uzu type which was bred at Okayama Prefectural Agricultural Experiment Station in 1930's. This is characterized by absence of wax coating on the upper leaf-sheaths only. Like other *eceriferum* mutants, this glossy sheath character proved to be conditioned by a single recessive gene. In our preliminary report (Barley Newsletter 9, 1966), the gene was designated *gs*$_7$, but later changed to *gs*$_8$, since *gs*$_7$ was used for the gene in Kogane Mugi at the publication of its linkage data (Takahashi and Hayashi, 1966). Recently, however, McProud (1971) have shown that *gs*$_8$ in Okaiku 3 is allelic to *gs*$_5$ in Jotun which was studied by Rasmusson and Lambert (1965), so that gene symbol *gs*$_5$ will be used for this mutant in this paper.

A genetic study was commenced using the crosses of this mutant with Nigrinudum, Colsess I and Orange lemma for testing its relations with various chromosome markers, but two additional crosses were employed for determining its location on chromosome 2.

Table 9 gives the F_2 data for those genes which have proved to be independently inherited of gs_5. The followings are the marker genes and number of chromosomes on which each of them are known to be located: *n* and *l* (1), *uz*, a_c and a_n (3), *K* and *Hs* (4), *B* and *trd* (5), *o* (6) and *s* (7).

TABLE 9

Independent inheritance of the glossy sheath (gs_5) and several markers in F_2 generation of the five crosses with Okaiku 3.

Okaiku 3(gs_5) crossed with	Symbol		Chromosome	Non-glossy		Glossy		Total	χ^2_L	P
	X	x		X	x	X	x			
Nigrinudum	*Uz*	*uz*	3	233	148	83	61	525	1.6764	.2—.1
	A_n	a_n	3	381	—	144	(151)*	676	4.2663**	.2—.1
	B	*b*	5	295	86	120	24	525	2.4231	.2—.1
	S	*s*	7	295	86	112	32	525	0.0256	.9—.8
Colsess I	*N*	*n*	1	226	71	66	22	385	0.0487	.9—.8
	Uz	*uz*	3	214	83	59	29	385	0.6929	.5—.3
	A_c	a_c	3	297	—	88	(132)*	517	1.0125**	.7—.5
	K	*k*	4	241	56	69	19	385	0.3951	.7—.5
	S	*s*	7	227	70	64	24	385	0.4851	.5—.3
e-trd	*N*	*n*	1	202	61	56	25	344	1.8656	.2—.1
	Uz	*uz*	3	212	51	67	14	344	0.0827	.8—.5
	Trd	*trd*	5	200	63	66	15	344	0.8734	.5—.3
Ligule-less	*N*	*n*	1	193	56	83	20	352	0.6111	.5—.3
	L	*l*	1	175	74	79	24	352	1.4596	.3—.2
	Uz	*uz*	3	193	56	82	21	352	0.3232	.7—.5
	Hs	*hs*	4	173	76	70	33	352	0.3232	.7—.5
Orange lemma	*Uz*	*uz*	3	167	49	48	23	287	2.6671	.2—.1
	O	*o*	6	165	51	51	21	282	0.8920	.5—.3

* Total number of the albino plants.

** Compared with the calculated number on a 9:3:4 ratio.

Since it was found from the F_2 tests that the gene gs_5 was on chromosome 2, the F_2 plants from the cross between Okaiku 3 and Nigrinudum, which involved three gene pairs, Gs_5gs_5, *Prpr* and *Vv* altogether, were further subjected to F_3 progenies test. Table 10 shows the summarized results obtained from the F_2 and F_3 tests for the linkages of five gene pairs, gs_5, *Pr*, *v*, *e* and *li*, and the recombination values calculated from each of these data. The weighted average values of recombination among the three genes, gs_5, *Pr* and *v*, are also given in the same table, in which two values were calculated and listed; one from the

TABLE 10

F_2 and F_3 data for linkages of five genes, gs_5, *Pr*, *v*, *e* and *li*, obtained in the crosses of Okaiku 3 with (A) Nigrinudum, (B) Colsess I, (C) e-trd and (D) Ligule-less.

Linked genes	Source of data	Cross	Phase	Segregation**	Total	Recombination value (%)	Weighted average value (%)
	F_2	A	C	309:72:85:59	525	35.64	
	F_2	A	C	248:59:50:44	401	32.76	
	$F_3(Gs_5\ Pr)$	A	C	50:53:55:142	300	42.28	36.18±1.6754
Gs_5gs_5 ~*Prpr*	$F_3(Gs_5\ pr)$	A	C	14:55	69	33.74	
	$F_3(gs_5\ Pr)$	A	C	25:68	93	42.37	
	F_2	B	C	222:75:51:37	385	39.54	(35.94±1.2542)*
	F_2	C	C	215:48:43:38	344	31.94	
	F_2	D	C	189:60:54:49	352	35.88	
	F_2	A	C	328:53:66:78	525	25.28	
	F_2	A	C	267:47:31:56	401	22.07	
Gs_5gs_5 ~*Vv*	$F_3(Gs_5\ V)$	A	C	70:44:39:163	316	23.14	24.20±1.3210
	$F_3(Gs_5\ v)$	A	C	10:43	53	31.75	
	$F_3(gs_5\ V)$	A	C	14:58	72	32.56	
Gs_5gs_5 ~*Ee*	F_2	C	R	177:86:81:0	344	complete linkage	
Gs_5gs_5 ~*Lili*	F_2	D	R	186:63:78:25	352	independ	
	F_2	A	C	360:34:34:97	525	13.93	
	F_2	A	C	284:30:23:64	401	14.80	
Prpr ~*Vv*	$F_3(Pr\ V)$	A	C	88:36:34:202	360	15.75	15.09±1.0283
	$F_3(Pr\ v)$	A	C	6:27	33	30.77	
	$F_3(pr\ V)$	A	C	4:24	28	29.42	

* Calculated by combining all the linkage data obtained from the crosses, A, B, C and D.

** F_2 phenotypes=AB:Ab:aB:ab. F_3(AB)=AABB:AaBB:AABb:AaBb. F_3(Ab)=AAbb:Aabb. F_3(aB)=aaBB:aaBb.

data obtained from a cross with Nigrinudum (A) only, and the other by combining all the data from the four crosses. It is apparent in the table that the gene gs_5 is located very close to *e*, but far apart from *li*, and that four genes are arranged in chromosome 2 in the order of *li*-*Pr*-*v*-gs_5. However, relative position of gs_5 and *e* could not be determined in this test.

Rasmusson and Lambert (1965) have estimated the recombination value of gs_5 with *e* to be 2.5% and with *v* 32.0%, while the distance between *e* and *v* to be 31.0%, which have suggested the gene order of *v*-*e*-gs_5. McProud (1971) has indicated that the distance between *v* and gs_5 is 24.4% or 27.3%. In Fig. 2 is given a map of five genes on chromosome 2 constructed from the linkage data obtained by various authors.

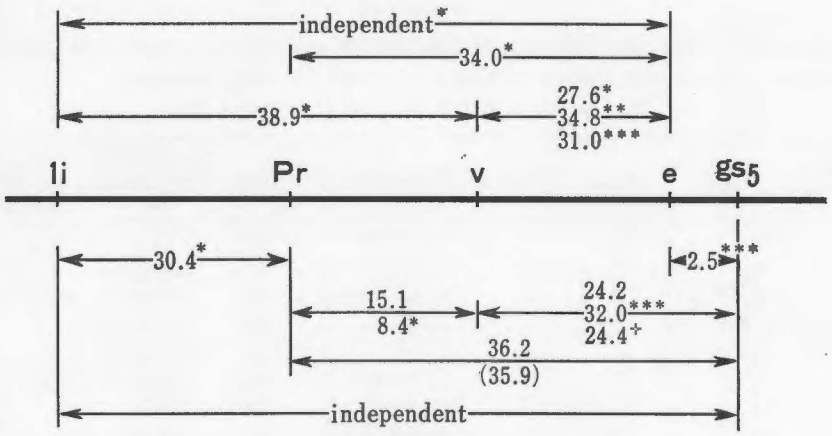

Fig. 2. A map of five genes on chromosome 2.
*, **, *** and † are cited from Takahashi *et al.* (1953), Takahashi and Moriya (1969), Rasmusson and Lambert (1965) and McProud (1971), respectively.

3. *Glossy Leaf Character in Goseshikoku-hen* (gl_3)

The original material was kindly provided by Dr. K. Hirata, Professor of Niigata University. Because of lack of waxy bloom on all leaf-blades, this mutant has shiny or glossy appearance and is easily distinguished from the normal type at almost all life stages. The mutation is supposed to occur spontaneously in the Japanese covered barley of uzu type, called Goseshikoku. Just as in the *gl* and gl_2 mutants, the glossy leaf character proved to be governed by a single recessive gene. An allelism test made among these three mutants has indicated that the gene in Goseshikoku-hen is different from both *gl* and gl_2. So, a gene symbol gl_3 was assigned to this mutation. In this test, it was eventually found that the *gl* and gl_2 mutants, both received from Dr. D. W. Robertson of Colorado State University, were allelic, as was confirmed also by Dr. T. Tsuchiya (Personal communication). It is noted that Goseshikoku-hen is much more winter-hardy and better suited to linkage study than the *gl* and gl_2 mutants.

In order to detect linkage of gl_3, Goseshikoku-hen was crossed to Nigrinudum and Colsess IV. The F_2 segregations of various character pairs are shown in Table 11, which indicates that gl_3 is independently inherited of *v* (2), *uz* and a_n (3), *B* (5) and *s* (7), but linked with *K* for hooded character on chromosome 4. The linkage intensity between gl_3 and *K* was estimated to be 32.85%. Furthermore, a loose linkage between gl_3 and *Hs* was suggested by a bit larger χ^2_L value due to an excessive parental types in the cross with Colsess IV. The recombination value was 42.18%. Nevertheless, this was not confirmed in the cross with Nigrinudum.

TABLE 11

Interrelationships between gl_3 for glossy leaf character in Goseshikoku-hen and several markers in F_2 of two crosses with Nigrinudum and Colsess IV.

Goseshikoku-hen (gl_3) ×	Symbol X	Symbol x	Chromosome	Non-glossy X	Non-glossy x	Glossy X	Glossy x	Total	χ^2_L	P
Nigrinudum	*V*	*v*	2	496	165	168	56	885	0.0001	>.99
	Uz	*uz*	3	483	154	181	68	886	1.0158	.5—.3
	A_n	a_n	3	357	—	116	(164)*	637	1.7574**	.5—.3
	Hs	*hs*	4	466	159	195	63	883	0.1058	.8—.7
	B	*b*	5	480	149	184	71	884	1.8100	.2—.1
	S	*s*	7	513	171	151	49	884	0.0181	.9—.8
Colsess IV	*Uz*	*uz*	3	242	88	79	30	439	0.0306	.9—.8
	Hs	*hs*	4	232	92	88	20	432	4.2140	<.05
	K	*k*	4	262	63	59	52	436	33.7656	small
	S	*s*	7	232	83	88	29	432	0.1029	.8—.7

* Total number of the albino seedlings.
** Compared with a 9:3:4 segregation ratio.

Along with this experiment, other linkage studies had been in progress at that time using two different mutants, brachytic 2 (br_2) and chlorina plant (f_9), and from the results these two mutant genes were found to be on the same chromosome. Consequently, a revised plan to investigate the interrelationships among the genes, gl_3, br_2, f_9, *K* and *Bl*, was put into execution by utilizing a genotype $KKgl_3gl_3$ (represented hereafter as K-gl_3) which was newly arisen in F_3 of the cross between Goseshikoku-hen and Colsess IV. In these circumstances, it seems adequate to state the results of the studies on linkages of br_2 and f_9 first, leaving the discussion of linkage intensity between *K* and gl_3 till later on.

4. *Brachytic Growth (br_2) in Kmut 28*

The brachytic mutant Kmut 28 was induced from a two-rowed cultivar Svanhals by X-ray irradiation and provided us for use by Dr. Tsuchiya. Short plant height and the dense spike with very short awn are its chief characteristics. Its stem length is about 2/3 and its awn length about 1/3 of the original variety Svanhals. Its kernels, too, are somewhat short and small as compared with those of Svanhals. Thus, this mutant has appearance very similar to the uzu or semi-brachytic type plant. Nevertheless, the brachytic type can be distinguished from the uzu type by the differences in size and shape of their coleoptiles. Comparison of the mean lengths of the coleoptiles of the F_2 segregants in several crosses has revealed that, while the uzu type is about one half of the normal type, the brachytic type is about 2/3 as long as the normal type in cole-

optile length. Moreover, a tiny projection and a notch are often found at the apex of the coleoptile of the uzu type, whereas neither of these characters persent in the coleoptile of the brachytic type. Since the simultaneous reduction in length of various plant parts in Kmut 28 proved to be due to a single recessive gene which was different from *br* in another brachytic mutant occurred in Himalaya, a gene symbol br_2 was assigned to this new mutant.

TABLE 12

Interrelationships between br_2 for brachytic growth 2 and several markers in F_2 of the four crosses with Kmut 28.

Kmut 28 (br_2) crossed with	Symbol		Chromosome	Normal		Brachytic		Total	χ^2_L	P
	X	x		X	x	X	x			
Orange lemma	L_x	l_x	(?)	197	87	74	41	399	1.9184	.2—.1
	V	v	2	313	105	108	39	565	0.1229	.8—.7
	O	o	6	323	95	96	51	565	8.5902	<0.01
	S	s	7	309	109	111	36	565	0.1434	.3—.2
Colsess IV	V	v	2	420	139	131	38	728	0.3516	.7—.5
	K	k	4	503	60	65	100	728	161.2918	small
	S	s	7	418	141	126	43	728	0.0024	>.95
uz-x_3	Uz	uz	3	379	111	120	27	637	0.8793	.5—.3
Nigrinudum	S	s	7	124	36	39	11	210	0.0021	>.95

TABLE 13

F_2 and F_3 data for the linkages of two gene pairs, br_2~K and br_2~gl_3, obtained in the crosses of Kmut 28 (br_2) with (A) Colsess IV and (B) K-gl_3.

Linked genes	Source of data		Phase	Segregation**	Total	Recombination value (%)	Weighted average of recombination (%)
Br_2br_2 ~Kk	Cross A	F_2	C	503:60:65:100	728	20.09	19.38±1.1357
		$F_2(Br_2\ K)$	C	51:26:18:113	208	17.27	
		$F_3(Br_2\ k)$	C	2:21	23	16.00	
		$F_3(br_2\ K)$	C	5:19	24	34.49	
	Cross B	F_2	C	241:35:46:70	392	21.61	22.75±1.9827
		$F_3(Br_2\ K)$	C	30:21:21:74	146	24.85	
		$F_3(Br_2\ k)$	C	3:17	20	26.09	
		$F_3(br_2\ K)$	C	4:22	26	26.67	(20.49±1.1357)*
Br_2br_2 ~Gl_3gl_3	Cross B	F_2	R	199:116:77:0	392	—	1.29±0.5121
		$F_3(Br_2\ Gl_3)$	R	0:2:1:109	112	1.35	
		$F_3(Br_2\ gl_3)$	R	53:1	54	0.93	
		$F_3(br_2\ Gl_3)$	R	58:2	60	1.69	

* Calculated from the combined data of the two crosses A and B.

** See the footnote of Table 10.

For the linkage study of br_2, Kmut 28 was crossed first to the four tester stocks, Orange lemma, Colsess IV, Nigrinudum and uz-x_s, and later to K-gl_3. As shown in Table 12, it became evident that br_2 was independently inherited of *v* (2), *uz* (3), *s* (7) and also a gene for dense spike on unknown chromosome. In spite of larger χ^2_L for br_2 and *o*, these two are still conceived to be independent, because excessive double recessive type plants, which chiefly contributed to the larger χ^2 value, can hardly be attributable to the linkage of these genes in repulsion phase. On the other hand, linkage of br_2 with *K* for hooded lemma appendage is doubtless.

Linkage intensities between br_2 and *K* and also between br_2 and gl_3 were estimated from the F_2 and F_3 data obtained in the crosses of Kmut 28 with Colsess IV and K-gl_3 testers. The results are shown in Table 13. The weighted average values of recombination calculated by combining the separate data indicate that br_2 is only 1.3 map units apart from gl_3, and about 20.5 units apart from *K* on chromosome 4.

5. *Chlorina Mutant* (f_9), *Kmut 174*

The chlorina mutant Kmut 174, which was used in this investigation, was induced by Dr. Tsuchiya by X-ray irradiation of the seed of two-rowed cultivar Kô A. This mutant always develops conspicuous chlorina leaves indifferently of height of temperature at all growth stage. Since Colsess V is a chlorina mutant of lowtemperature type, this can be easily distinguished from Kmut 174 type plant by growing these two types together in a condition of rather high temperature. Slightly compact spike and lateness in heading, as compared with the original variety Kô A, are the other characteristics of Kmut 174. The mutant character is simple recessive to the normal. A gene symbol f_k was previously assigned to this by the present authors, but later amended to f_9 by Dr. D.W. Robertson (1970).

Table 14 shows the segregation of green vs. chlorina and a number of marker character pairs in the F_2 generation of the crosses of Kmut 174 with five genetic marker stocks. It is apparent in this table that the gene f_9 is independently inherited of *n* (1), *v* (2), a_n (3), *B* (5), *o* (6), and *r* and *s* (7), but linked with *K* for hooded lemma appendage on chromosome 4.

In order to raise more reliable data for estimation of the distances from f_9 to *K* and gl_3, almost all but the doubly recessive F_2 plants of the cross between Kmut 174 and K-gl_3 were carried through the F_3 generation to determine their genotypes. In Table 15 are given the F_3 data, together with the F_2 results regarding the linkages, and the recombination values calculated from each of them. The weighted average value of recombination between f_9 and gl_3 and that between f_9 and *K* were further calculated, which were 40.07 ± 2.12 (%) and 23.29 ± 1.6546 (%), respectively.

TABLE 14

Interrelationships between green vs. chlorina plants (F_9f_9) and the marker character pairs on chromosomes 1~7 in F_2 of the crosses with the chlorina mutant, Kmut 174.

Kmut174 (f_9) crossed with	Symbol		Chromosome	Green		Chlorina		Total	χ^2_L	P
	X	x		X	x	X	x			
Nigrinudum	*N*	*n*	1	281	91	90	23	485	0.6930	.5—.3
	A_n	a_n	3	382	—	113	(154)*	649	1.8261**	.5—.3
	B	*b*	5	286	86	76	37	485	3.7535	.1—.05
	S	*s*	7	286	86	84	29	485	0.3136	.7—.5
Minn. 90-5	*B*	*b*	5	268	105	83	37	493	0.3085	.7—.5
	R	*r*	7	268	105	82	39	494	1.3947	.3—.2
Orange lemma	*L*	*l*	(1?)	258	119	48	16	441	2.4694	.2—.1
	V	*v*	2	298	83	58	9	448	0.6967	.5—.3
	O	*o*	6	287	93	59	20	459	0.0293	.9—.8
	S	*s*	7	262	117	42	23	444	0.0160	.95-.9
K-gl_3	*V*	*v*	2	267	83	99	29	478	0.0753	.8—.7
	K	*k*	4	307	43	57	71	478	97.0051	small
	Gl_3	gl_3	4	254	97	102	26	479	2.7560	.1—.05
Colsses V	*V*	*v*	2	267	110	76	28	481	0.3514	.7—.5
	K	*k*	4	317	60	57	47	781	34.9552	small
	S	*s*	7	288	89	74	30	481	1.0998	.3—.2

* Total number of albino plants.

** Compared with the calculated numbers on the segregation ratio of 9 : 3 : 4.

TABLE 15

F_2 and F_3 data for the linkages of the gene pairs, F_9f_9~Gl_3gl_3 and F_9f_9~Kk, obtained from a K-gl_3 × Kmut 174 (f_9) cross, and the recombination values calculated therefrom by the method of maximum likelyhood.

Linked genes	Source of data	Phase	Segregation*	Total	Recombination value (%)	Weighted average value of recombination (%)
F_9f_9 ~Gl_3gl_3	F_2	R	254: 97 10:2: 26	479	44.36	40.07±2.1200
	$F_3(F_9\ Gl_3)$	R	13 : 49 : 52 :113	227	36.13	
	$F_3(F_9\ gl_3)$	R	39 : 54	93	40.91	
	$F_3(f_9\ Gl_3)$	R	42 : 51	93	37.78	
F_9f_9 ~Kk	F_2	C	307: 43 : 57 : 71	478	23.39	23.29±1.6546
	$F_3(F_9\ K)$	C	63 : 42 : 37 :140	282	23.75	
	$F_3(F_9\ k)$	C	4 : 34	38	19.05	
	$F_3(f_9\ K)$	C	6 : 42	48	22.22	

* See the footnote of Table 10.

6. *Determination of the locations of gl_3, br_2, f_9, K and Bl on chromosome 4.*

Since *Bl* for blue aleurone color has been frequently used as a marker gene of chromosome 4, information about the linkage of *Bl* with gl_3 and

K was thought to be of use. An additional cross was made between K-gl_3 and a Chinese variety Tawangmiao with dark blue aleurone to fulfil the requirement. In the F_2 generation of this cross the plants with blue aleurone appeared too many to given a good fit to a 3 blue to 1 white ratio. But, as the segregations of both *Kk* and Gl_3gl_3 occurred in the expected ratio, linkage of *Bl* with *K* and gl_3 could be confirmed from the results. A part of these F_2 plants of this cross were then subjected to F_3 test in order to determine the F_2 genotypes. The F_2 and F_3 data obtained in these tests and the recombination value calculated each of them are shown together in Table 16. In the same table you can find the weighted average value of recombination between *Bl* and gl_3 and that between *Bl* and *K*, which are 13.60% and 34.74%, respectively.

TABLE 16

F_2 and F_3 data for the linkages of the gene pairs, Gl_3gl_3~*Blbl* and *Blbl*~*Kk*, obtained from a cross, Tawangmiao (*Bl*)×K-gl_3 tester stock, and the recombination values calculated therefrom by the method of maximum likelyhood.

Linked genes	Source of data	Phase	Segregation*	Total	Recombination value (%)	Weighted average value of recombination (%)
Gl_3 gl_3 ~*Bl bl*	F_2	C	364:63:15:74	516	14.22	13.60±1.3677
	F_3(*Gl*$_3$ *Bl*)	C	43: 9 :14:88	154	11.94	
	F_3(gl_3 *Bl*)	C	3 :24	27	20.00	
Bl bl ~*K k*	F_2	R	308:119:80: 9	516	33.08	34.74±2.8195
	F_3(*Bl K*)	R	7 : 38:26:64	135	37.12	
	F_3(*Bl k*)	R	22:24	46	35.29	

* See the footnote of Table 10.

Now, let us give an account of the linkage intensity between *K* and gl_3. As stated in this and the preceeding three sections, we have used four crosses each involving these two pairs of genes, and can estimate the recombination value from their F_2 and F_3 data. Table 17 shows a grand average value of recombination between *K* and gl_3 being 24.37±1.0356 (%), although the average values, calculated cross by cross, differ considerably, ranging from 19.07% to 31.86%.

Finally, collecting all the results of a series of experiments separately dealt with before, we could easily build up a map of the five genes on chromosome 4 as is shown in Fig. 3. In this map, the values obtained by three-point tests are mainly referred to, but those values estimated by combining all the available data, too, are shown besides in parenthesis. It is worthy to note that, as far as we know, the f_9 is the gene which is located at the most distal end of the short arm of chromosome 4, as the distance between f_9 and *K* is farther than that between *I* or I^h and *K*

TABLE 17

F_2 and F_3 data for linkage between *Kk* and Gl_3gl_3 and their recombination values obtained from the four crosses indicated.

Crosses	Source of data	Phase	Segregation*	Total	Recombination value (%)	Weighted average value of recombination (%)
Goseshikoku × Colsess IV	F_2	C	262:63:59:52	436	32.85	31.86±2.5042
	$F_3(K\ gl_3)$	C	8:44	52	26.67	
	$F_3(k\ Gl_3)$	C	10:46	56	30.30	
K-gl_3 × Kmut 28 (br_2)	F_2	R	214:101:73:4	392	19.63	23.90±2.3424
	$F_3(K\ Gl_3)$	R	5:23:20:73	121	26.19	
	$F_3(K\ gl_3)$	R	30:21	51	25.93	
	$F_3(k\ Gl_3)$	R	32:19	51	22.89	
K-gl_3 × Kmut 174 (f_9)	F_2	R	247:108:117:6	478	22.64	19.07±1.5293
	$F_3(K\ Gl_3)$	R	1:36:40:146	223	19.68	
	$F_3(K\ gl_3)$	R	70:37	107	20.90	
	$F_3(k\ Gl_3)$	R	67:30	97	18.29	
K-gl_3 × Tawang-miao	F_2	R	268:120:111:17	516	35.34	31.43±2.4753
	$F_3(K\ Gl_3)$	R	6:24:26:60	116	33.90	
	$F_3(K\ gl_3)$	R	19:21	40	35.59	
	$F_3(k\ Gl_3)$	R	27:13	40	19.40	
Grand average value of recombination (%)						24.37±1.0356

* See the footnote of Table 10.

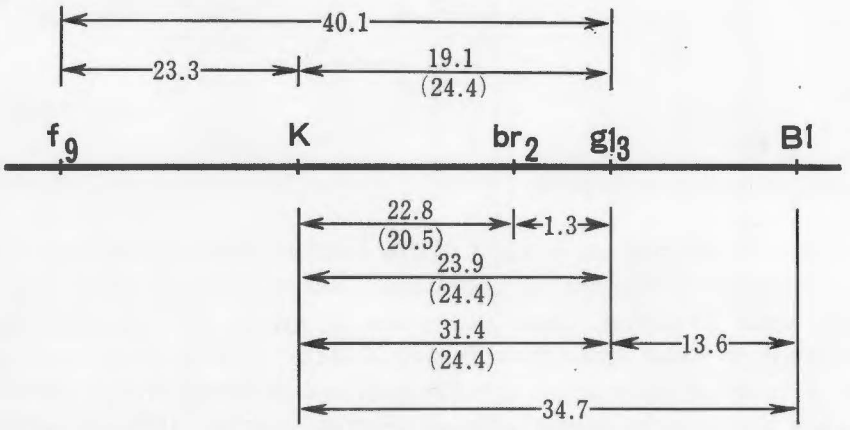

Fig. 3. A map of five genes on chromosome 4, in which are shown the weighted average values obtained by the three-point tests for each of the three genes concerned. The values in parenthesis are those calculated by combining all the data obtained from different crosses.

which has been estimated to be 14.3% by Leonard (1942) and 15.1% by Robertson (1937).

7. *A Semi-six-rowed Mutant, Kmut 27*

The semi-six-rowed mutant Kmut 27 was induced by X-ray irradiation from a two-rowed barley Svanhals and given us for use by Dr.

Tsuchiya. This appears almost similar to the ordinary six-rowed barley, but the upper and lowermost two or three lateral spikelets are somewhat underdeveloped in general and often become tip-awned or awnless and sterile. The genetic behavior of this mutant character was found to be different from that of the ordinary six-rowed character. As shown in Table 18, when crossed to a two-rowed form, the resultant F_1 plant had

TABLE 18

Segregation of non-six-row and six-row phenotypes in F_2 of the crosses of Kmut 27 (v_2) with the ordinary two-rowed and six-rowed varieties.

Kmut 27 (v_2) crossed with	F_2 phenotypes		Total	χ^2 for 3:1	P	χ^2 for 9:7	P
	non-6-row	6-row					
Svanhals (2-row)	315	112	427	0.3443	.7-.5	53.2623	small
Nigrinudum (2-row)	388	87	475	11.3168	small	124.8618	small
L.T. 16 (2-row)	301	113	414	1.4483	.3-.2	45.5525	small
Ligule-less (Kôyô) (2-row)	315	91	406	1.1627	.3-.2	75.1034	small
Orange lemma (6-row)	274	204	478	79.6680	small	0.2211	.7—.5
Colsess V (6-row)	312	200	512	54.0000	small	4.5714	.05-.02

two-rowed heads, but not the intermediate ones, and in the F_2 generation the semi-six-rowed plant appeared in a ratio of one against 3 normal two-rowed ones. On the other hand, a cross with the ordinary six-rowed

TABLE 19

Interrelationships between non-six-row vs. 'six-row' (V_2v_2) and the marker character pairs on chromosomes 1~7 in F_2 of the crosses with the 'six-row' mutant, Kmut 27.

Kmut 27 (v_2) crossed with	Symbol		Chromo-some	Non-6-row		6-row		Total	χ^2_L	P
	X	x		X	x	X	x			
Nigrinudum	*N*	*n*	1	289	99	65	22	475	0.0049	.95—.9
(2-row)	*B*	*b*	5	294	94	61	26	475	0.9292	.5—.3
	S	*s*	7	258	130	85	2	475	31.8467	small
L. T. 16	*N*	*n*	1	236	65	90	23	414	0.1299	.8—.7
(2-row)	*Uz*	*uz*	3	241	60	85	28	414	0.9028	.5—.3
	K	*k*	4	222	79	86	27	414	0.2416	.7—.5
	B	*b*	5	240	61	87	26	414	0.2415	.7—.5
	Trd	*trd*	5	229	72	88	25	414	0.1814	.7—.5
	S	*s*	7	213	88	106	7	414	25.1304	small
Ligule-less (Kôyô) (2-row)	*Li*	*li*	2	239	76	72	19	406	0.3164	.7—.5
Orange lemma	*O*	*o*	6	214	60	159	45	478	0.0043*	.95—.9
(6-row)	*S*	*s*	7	195	79	159	45	478	2.8972*	.1—.05
Colsess V	*K*	*k*	4	233	79	143	57	512	0.5181*	.5—.3
(6-row)	*S*	*s*	7	226	86	164	36	512	5.4768*	.02—.01

* Calculated on the basis of a 27:9:21:7 segregation ratio.

variety gave the F_1 plants with spikes of so-called intermediate appearance, and in the F_2 generation non-six-row and six-row plants appeared in a 9 : 7 segregation ratio. The results clearly indicate that the semi-six-rowed character of this mutant is conditioned by a gene which is different from *v* for ordinary six-rowed spike and completely epistatic to *V*. A gene symbol v_2 was assigned to this mutant gene.

Linkage of v_2 with several markers was studied using five crosses between Kmut 27 and testers with two-rowed or six-rowed head. Table 19 shows the summarized results of the F_2 segregations. It is apparent in this table that v_2 for the semi-six-rowed character is inherited independently of *n* (1), *li* (2), *uz* (3), *K* (4), *B* and *trd* (5) and *o* (6), but is linked with *s* on chromosome 7, although in the cross with Orange lemma with six-rowed spikes the observed F_2 frequencies fitted well to the expected ratio for independent assortment. An F_3 progeny test was made for the cross with Nigrinudum only. In Table 20 are shown the data for linkage between v_2 and *s* obtained in the crosses with L. T. 16 and Nigrinudum. The weighted average value of recombination was 18.98±1.4572 (%).

TABLE 20

The linkage data for v_2 and *s*, and the weighted average value of recombination.

Kmut 27 (v_2) ×	Source of data	Phase	Segregation*	Total	Recombination value (%)	Weighted average value of recombination (%)
L. T. 16	F_2	R	213: 88 :106: 7	414	25.93	
Nigrinudum	F_2	R	258:130: 85 : 2	475	14.78	
〃	$F_3(V_2\ S)$	R	7 : 18 : 27 :131	183	17.71	18.98±1.4572
〃	$F_3(V_2\ s)$	R	81 : 49	130	23.22	
〃	$F_3(v_2\ S)$	R	61 : 23	84	15.86	

* See the footnote of Table 10.

8. *Narrow-Leaved Dwarf Mutant, Nagaoka Dwarf (nld)*

This mutant was first found among the F_2 population of a cross between two Japanese cultivars, Nagaoka and Marumi 16, in our experimental farm. For the simplicity's sake, it was named Nagaoka dwarf. Its leaves are narrow, thick, dark-green colored and erect with prominent midribs. Auricles are degenerated to tiny projections, though ligules are normal. Most of the stem-internodes are short and the uppermost one is markedly curved as seen in Fig. 4. The spikes are dense, and its spikelets are relatively small and sometimes infertile.

The linkage of the gene *nld* for this mutant character as stated above was studied by trisomic analysis and found to be located on chromosome 7, but neither on chromosome 2 nor 6 (Takahashi and Hayashi 1966).

Fig. 4. A photograph of the upper part of the narrow-leaved dwarf mutant (*nld*) with markedly curved, short stem-internodes (uzu type).

Along with the trisomic analysis, a conventional genetic analysis was started simultaneously using the crosses of Nagaoka dwarf with Nigrinudum, Orange lemma and Colsess IV, and after finding the chromosome on which *nld* was located, two additional crosses were made to locate *nld* on chromosome 7.

Table 21 shows the segregation of normal vs. dwarf and several chromosome marker character pairs in F_2 of the five crosses with Nagaoka dwarf. The results clearly indicate that *nld* is independently inherited of *n* (1), *v* and *Pr* (2), a_n (3), *K* and *Hs* (4), *B* (5) and *o* (6), but linked with *s* for short-haired rachilla and also *fs* for fragile stem on chromosome 7.

In order to determine the location of *nld* by three point test, analyses were made with the cross between Nagaoka dwarf and T. 179, which involves *Rr*, *Ss* and *Nldnld* altogether. The data obtained from this and a few other sources are given in Table 22.

It became evident from the results that *nld* was located 37% apart from *s* on the opposite side of *r*. This led to an assumption that *fs* might lie between *nld* and *s*, as the distance between *fs* and *s* had been known to be 26~20% (Takahashi *et al.* 1953). F_2 tests made with two crosses, Nagaoka dwarf × Kamairazu (*fs*) and Syria 439 × Kamairazu, have shown that the map distance between *fs* and *nld* is 18.61%, while that between *nld* and *s* is 36.86%. Thus, the assumption stated above was verified by this experiment (Table 23). It may be safe to conclude from these results that four genes, *nld*, *fs*, *s* and *r* are arranged in this order on chromo-

TABLE 21

Interrelationships between normal vs. narrow leaved dwarf (*Nldnld*) and several marker character pairs on chromosomes 1～7 in F_2 of the crosses with Nagaoka dwarf mutant.

Nagaoka dwarf (*nld*) ×	Symbol		Chromosome	Normal		Dwarf		Total	χ^2_L	P
	X	x		X	x	X	x			
Nigrinudum	*N*	*n*	1	345	114	128	47	634	0.3091	.7—.5
	V	*v*	2	348	112	142	35	637	1.7096	.2—.1
	Pr	*pr*	2	356	104	135	41	636	0.0112	.95—.9
	A_n	a_n	3	460	—	177	(193)*	830	4.0585**	.2—.1
	Hs	*hs*	4	331	130	117	59	637	2.5538	.2—.1
	B	*b*	5	348	112	126	50	636	1.2327	.3—.2
	S	*s*	7	318	142	144	33	637	10.2998	small
Orange lemma	*O*	*o*	6	245	68	95	21	429	0.7835	.5—.3
	S	*s*	7	236	77	108	8	429	15.8013	small
Colsess IV	*K*	*k*	4	200	56	62	25	343	1.6330	.3—.2
	Hs	*hs*	4	179	74	67	20	340	1.3386	.3—.2
	S	*s*	7	178	78	70	17	343	4.1364	< .05
T. 179	*Pr*	*pr*	2	235	123	86	68	512	0.1050	.8—.7
	S	*s*	7	260	98	138	16	512	20.0556	small
	R	*r*	7	263	95	121	33	512	1.6806	.2—.1
Kamairazu	*Fs*	*fs*	7	242	116	138	5	501	50.0388	small

TABLE 22

F_2 and F_3 data for the linkages of three genes, *nld*, *s* and *r*, obtained in the crosses of Nagaoka dwarf with T. 179, Nigrinudum and Orange lemma.

Linked genes	Nagaoka dwarf ×	Source of data	Phase	Segregation*	Total	Recombination value (%)	Weighted average value of recombination (%)
Nldnld ～*Ss*	T. 179	F_2	R	260: 98 :138: 16	512	34.29	36.86±2.4799
	〃	F_3(*Nld S*)	R	11 : 29 : 35 : 73	148	39.80	
	〃	F_3(*Nld s*)	R	27 : 31	58	36.47	
	〃	F_3(*nld S*)	R	34 : 44	78	39.29	
	Orange lemma	F_2	R	236: 77 :108: 8	429	30.00	
	Nigrinudum	F_2	R	318:142:144: 33	637	40.64	
Nldnld ～*Rr*	T. 179	F_2	R	263: 95 :121: 33	512	46.04	47.97±2.5757
	〃	F_3(*Nld R*)	R	15 : 35 : 39 : 60	149	48.29	
	〃	F_3(*Nld r*)	R	19 : 38	57	50.00	
	〃	F_3(*nld R*)	R	20 : 45	65	52.94	
Ss～ *Rr*	T. 179	F_2	C	341: 57 : 43 : 71	512	22.42	21.54±1.6733
	〃	F_3(*S R*)	C	45 : 21 : 26 : 97	189	20.37	
	〃	F_3(*S r*)	C	3 : 34	37	15.00	
	〃	F_3(*s R*)	C	4 : 21	25	27.59	

* See the footnote of Table 10.

some 7. A map of the genes in this part of chromosome 7 is shown in Fig. 5.

TABLE 23

Linkage data for four genes, *fs*, *nld*, *r* and *s*, obtained in F_2 of two crosses, Kamairazu×Nagaoka dwarf and Kamairazu×Syria 439.

Kamairazu crossd with	Symbol Xx	Symbol Yy	Phase	F_2 phenotypes XY	Xy	xY	xy	Total	χ^2_L	Recombination value (%)
Nagaoka dwarf	*Fsfs*	*Nldnld*	R	242	138	116	5	501	50.0388	18.61±4.281
Syria 439	*Fsfs*	*Ss*	R	279	124	105	11	519	20.4112	30.42±3.9290
〃	*Fsfs*	*Rr*	R	321	82	102	14	519	2.3603	independent
〃	*Rr*	*Ss*	C	351	72	33	63	519	77.8439	22.78±2.1457

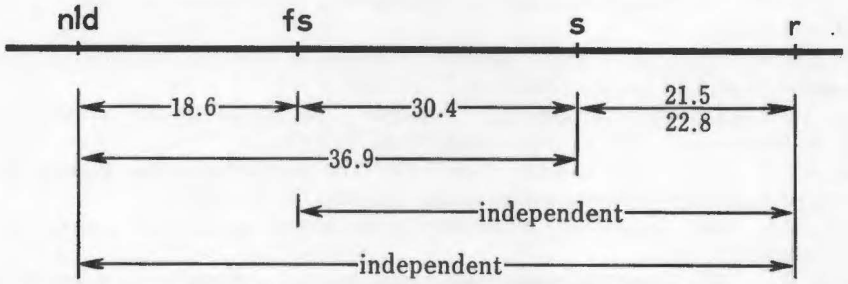

Fig. 5. A map of genes on chromosome 7.

Acccording to the map of chromosome 7, prepared by Robertson (1971), *fs* locus is placed on the proximal end of the long arm, while Hayes and Rana (1966) has suggested *ddt* to be on the short arm. It is possible to suppose, therefore, that *nld* is located on the short arm of this chromosome and might be close to *ddt*.

SUMMARY

This paper presents the gene linkages and character descriptions of seven new mutants of barley. The results may be summarized as follows.

The semidominant chlorophyll mutant OUM 215, induced by EMS treatment, segregates xantha (lethal), chlorina and green plants in a 1:2:1 ratio. The gene X_a is located 35.3% apart from *lk*, and occupies the distal end of the long arm of chromosome 1 (Fig. 1).

The glossy sheath character in Okaiku 3 is shown by this genetic analysis to be the same as that of Jotun. The gene gs_5 is on chromosome 2 and closely linked with *e* (Fig. 2).

Three genes, gl_3 for glossy leaves in Goseshikoku-hen, br_2 for brachytic growth 2 in Kmut 28, and f_9 for chlorina plant of Kmut 174, are all on chromosome 4. Arrangement of the five genes are f_9-*K*-br_2-gl_3-*Bl* (Fig. 3).

A semi-six-rowed mutant character induced from a two-rowed cultivar Svanhals is conditioned by v_2 which is linked with *s* on chromosome 7 with 19% recombination.

The narrow-leaved dwarf mutant called Nagaoka dwarf has a gene *nld* on chromosome 7. Since it is 18.6% apart from *fs*, it is inferred that *nld* is located close to *ddt* on the short arm of chromosome 7 (Fig. 5).

ACKNOWLEGMENT: The writers wish to express their sincere thanks to Dr. T. Tsuchiya, Associate Professor of Colorado State University, and also to Dr. K. Hirata, Professor of Niigata University, for the materials.

LITERATURE

Haus, T. E. 1958. A linkage between two sections of a chromosome in barley. J. Hered. 49 : 179–180.

Hayes, J. D. and Rana, M. S. 1966. Genetic resistance to DDT in *Hordeum*. I. Linkage studies in diploid barley. Heredity 21 : 581–593.

Kramer, H. H. and Burnham, C. R. 1947. Methods of combining linkage intensity values from backcross, F_2 and F_3 data. Genetics 32 : 379–390.

Kramer, H. H., Veyl, R. and Hanson, W. D. 1954. The association of two genetic linkage groups in barley with one chromosome. Genetics 39 : 159–168.

Leonard, W. H. 1942. Inheritance of fertility in the lateral spikelets of barley. Genetics 27 : 299–316.

McProud, W. L. 1971. Genetics, phenotypes, agronomic and malting performance of glossy sheath mutants in barley, *Hordeum vulgare* L. Ph. D. thesis, Montana State University.

Rasmusson, D. C. and Lambert, J. W. 1965. Inheritance of the glossy-sheath character in barley, *Hordeum vulgare* L. Crop Sci. 5 : 251–253.

Robertson, D. W. 1937. Inheritance in barley. II. Genetics 22 : 443–451.

Robertson, D. W. 1970. Recent information of linkage and chromosome mapping. Barley Genetics II : 220–242.

Robertson, D. W., Immer, F. R., Wiebe, G. A. and Stevens, H. 1944. The location of two genes for mature plant characters in barley linkage group I. Jour. Amer. Soc. Agron. 36 : 66–72.

Takahashi, R. and Hayashi, J. 1959. Association of linkage groups III and VII. Barley Newsletter 2 : 22–23.

Takahashi, R. and Hayashi, J. 1966 Inheritance and linkage studies in barley. II. Assignment of several new mutant genes to their respective linkage groups by the trisomic method of analysis. Ber. Ohara Inst. landw. Biol. Okayama Univ. 13 : 185–198.

Takahashi, R., Hayashi, J., Moriya, I. and Hirao, Ch. 1966. Linkage studies. Barley Newsletter 9 : 68–69.

Takahashi, R. and Moriya, I. 1969. Inheritance and linkage studies in barley. IV. Linkages of four variegated mutants. Ber. Ohara Inst. landw. Biol. Okayama Univ. 15 : 35–46.

Takahashi, R., Yamamoto, J., Yasuda, S. and Itano, Y. 1953. Inheritance and linkage studies in barley. Ber. Ohara Inst. landw. Forsch. 10 : 29–52.