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INHERITANCE AND LINKAGE STUDIES IN BARLEY

VII. Location of Six New Mutant Genes on Chromosome 3

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According to the latest linkage map for chromosome 3, presented in Barley Genetics Newsletter 13 by Tsuchiya (1983), 18 genes have been definitely located. However, there are many other genes which are known to be on this chromosome, but their locations are not determined as yet. Since we have recently completed linkage analyses of 6 new mutant genes locating on this chromosome, the detailed data will be presented in this paper, although parts of them had already been reported fragmentarily in Barley Genetics Newsletter and others.

MATERIALS AND METHODS

The 6 mutants listed in Table 1 were used for genetic analysis. Their principal characteristics and the gene symbols allotted to the mutants are as shown in the same table. Choshiro Hen was originated

TABLE 1. Characteristics and gene symbols of the materials used in this experiment

Name of mutant	Characteristics	Gene symbol allotted
Choshiro Hen	Awns extremely curly, stem internodes strongly curved, dwarf.	*cu-2*
OUM 5*	Extremely procumbent or lazy growth, dwarf, late maturity.	*lzd*
OUM 148	Short and slender stems, spikes lax with slender kernels.	*sld*
OUM 206	Short awns markedly crooked outwards at their upper portion, rather brittle.	*sca*
OUM 25	Glossy sheath-2, leaf-sheaths and ears lack waxy bloom.	*gs-2*
OUM 231	White striped, most conspicuous under low temperature.	*wst,,j*

* OUM: Okayama University Mutant Accession Number.

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by spontaneous mutation from a Japanese naked, uzu-type cultivar, Choshiro, while five other mutants were all induced by the senior author (T. K.) from a naked, uzu-type cultivar, Akashinriki, by means of EMS (ethyl methanesulfonate) treatment.

Linkages of these mutant genes were studied mostly in the following way: As the first step, a mutant was crossed either to a trisomic set of *Hordeum spontaneum nigrum* provided by Dr. T. Tsuchiya or to some genetic stocks having the chromosome marker genes shown in Table 2.

TABLE 2. Genic constitutions of the six mutants and genetic stocks used in this experiment

Mutant (gene) and genetic stock	Chromosome						
	1	2	3	4	5	6	7
Mutant							
Choshiro Hen (*cu-2*)	*n*	*v*	*uz*, *Als*, X_s	*k*	*b*	*O*	*S*
OUM 5 (*lzd*)	*n*	*v*	*uz*, *Al*	*k*	*b*	*O*	*S*
OUM 148 (*sld*)	*n*	*v*	*uz*, *Al*, *Gs-2* X_c	*k*	*b*	*O*	*S*
OUM 206 (*sca*)	*n*	*v*	*uz*	*k*, *Gl-3*	*b*	*O*	*S*
OUM 25 (*gs-2*)	*n*	*v*	*uz*, *Al*, *Als* *Cu-2* X_c	*k*, *hs*	*b*	*O*	*S*
OUM 231 (*wst,,j*)	*n*	*v*	*uz*, *Al*	*k*	*b*	*O*	*S*
Genetic stock							
Absent Lower Laterals			*Uz*, *als*	*k*	*b*	*O*	
Col-orange	*N*	*v*	*Uz*, x_c	*k*	*b*	*o*	*s*
cu_s·als·Uz		*v*	*Uz*, *als*, *cu-2*	*k*	*b*	*O*	
Ethiopia 321	*N*	*V*	*Uz*			*o*	*s*
Goseshikoku Hen	*N*	*v*	*uz*	*gl-3*	*b*	*O*	*S*
gs-2d	*N*	*v*	*Uz*, *gs-2*	*k*	*b*	*O*	*S*, *r*
L. T. 26	*n*	*V*	*Uz*	*K*, *trd*	*B*	*O*	*s*
Nigrinudum	*n*	*V*	*Uz*	*k*	*B*	*O*	*s*
Russia 82	*N*	*v*	*Uz*, *al*	*Hs*			
Smyrna	*N*	*V*	*Uz*, x_s	*k*			*s*
x_c·a_n (No. 1)	*N*	*v*	*Uz*, x_c, a_n	*K*	*B*	*O*	*s*

And, in order to detect the linkage group to which the mutant gene belongs, all the F_2 segregation data from the latter crosses were tested by calculating the chi-square value for linkage (χ^2_L). Next, the mutant was crossed again to one or more multiple genetic stocks suitable for the multiple linkage test of the mutant gene in question. Recombination percentage was calculated by the formula of maximum likelihood. When two or more values of recombination between the same two genes were obtained from different sources of data, these values were combined and the weighted average value was calculated by the method suggested by Robertson *et al.* (1944) and Kramer and Burnham (1947). Based on these recombination values, the map distances among the genes were estimated using a computer program for the maximum likelihood method developed by Jensen and Jørgensen (1975a).

EXPERIMENTAL RESULTS

1. *Curly-2 Mutant* (*cu-2*), *Choshiro Hen*

Lemmas and awns are extremely curly, the rachises are usually bent, and most of the stem internodes are also strongly curved. Some of the leaves are severely rolled and twisted. Takahashi and Hayashi (1966) demonstrated that the mutant character was under the control of a single recessive gene, *cu-2*, but in the F_2 of several simple crosses the mutant-type plants always appeared far less frequently than the expected number on 1 against 3 segregation ratio, which was due to the certation of the pollens involving the mutant gene. Consequently, the linkage group of gene *cu-2* was determined by means of trisomic analysis. The result clearly indicated that the gene was on chromosome 3, but not on chromosomes 1, 4, 5, 6 and 7.

For locating the *cu-2* gene on chromosome 3, the mutant was crossed with a genetic stock, Absent Lower Laterals, which was known to have

TABLE 3. F_2 and F_3 data for linkage of three genes, *cu-2, als* and *uz*, obtained from the cross of Choshiro Hen with Absent Lower Laterals

Linked genes (Aa∼Bb)	Source of data	Phase	Segregation*	Total	Recombination value (%)	Weighted average value (%)
Als als ∼*Cu-2 cu-2*	F_2	R	385 : 166 : 118 : 19	688	36.33	34.75±2.2068
	F_3(AB)	〃	12 : 38 : 45 : 81	176	40.38	
	F_3(Ab)	〃	22 : 27	49	35.53	
	F_3(aB)	〃	44 : 32	76	26.67	
Als als ∼*Uz uz*	F_2	R	366 : 135 : 161 : 23	685	36.81	36.87±2.2472
	F_3(AB)	〃	10 : 36 : 45 : 79	170	38.65	
	F_3(Ab)	〃	26 : 29	55	35.80	
	F_3(aB)	〃	33 : 41	74	35.65	
Cu-2 cu-2 ∼*Uz uz*	F_2	C	428 : 123 : 99 : 35	685	Independ.	Independent
	F_3(AB)	〃	29 : 50 : 46 : 75	200	45.83	
	F_3(Ab)	〃	22 : 30	52	Independ.	
	F_3(aB)	〃	13 : 31	44	45.61	

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

als and *Uz* on chromosome 3. After the F_2 test of the cross, the plants were carried to the F_3 generation for determining the number of genotypes involved. Table 3 gives the summarized results.

The results shown in Table 3 indicate that the location of *cu-2* is 34.75 % apart from *als* on the opposite side of *uz*, the distance between *uz* and *als* being 36.87 %. Furthermore, the distance from *cu-2* to *uz* is known to be 50 % or more. So, it may be safely concluded from these results that three genes, *uz*, *als* and *cu-2*, are arranged in this order on chromosome 3.

2. *Lazy Dwarf Mutant (lzd), OUM 5*

The seedling of this mutant shows an extremely procumbent or so-called "lazy" growth. Short stems, twisted, short and dark-green leaves, late maturity and high responsiveness to GA_3 can be regarded as characteristics of this mutant. And, these characters were found to be controlled altogether by a single recessive gene, named here *lzd*, because all the lazy growth plants, segregated in the F_2 of the cross between the lazy mutant and its original uzu-type variety, Akashinriki, were almost similar to OUM 5. It was further confirmed that among the F_2 population derived from a cross between the mutant (*lzd uz*) and non-uzu isoline (*Lzd Uz*) of Akashinriki, such recombinants as non-uzu dwarf (*lzd Uz*) and normal uzu (*Lzd uz*) were certainly much less than the expected number on independent segregation. This suggested

TABLE 4. F_2 and F_3 data for linkage of three genes, *lzd*, *al* and *uz*, obtained from the cross between OUM 5 and Russia 82

Linked genes (Aa~Bb)	Source of data	Phase	Segregation*	Total	Recombination value (%)	Weighted average value (%)
Lzd lzd	F_2	C	333 : 40 : 28 : 71	472	16.45	21.89±1.4630
~*Uz uz*	F_3(AB)	〃	92 : 32 : 57 : 152	333	21.72	
	F_3(Ab)	〃	7 : 33	40	29.79	
	F_3(aB)	〃	2 : 26	28	13.33	
Lzd lzd	F_2	R	245 : 133 : 94 : 0	472	—	
~*Al al*	F_3(AB)	〃	2 : 19 : 45 : 179	245	15.18	9.97±1.1038
	F_3(Ab)	〃	115 : 18	133	7.26	
	F_3(aB)	〃	80 : 14	94	8.05	
Uz uz	F_2	R	233 : 128 : 106 : 5	472	19.68	16.27±1.3801
~*Al al*	F_3(AB)	〃	1 : 19 : 31 : 182	233	20.58	
	F_3(Ab)	〃	95 : 33	128	14.80	
	F_3(aB)	〃	83 : 23	106	12.17	

* See the foot note of Table 3.

that the gene *lzd* was linked with *uz* on chromosome 3.

For locating the gene *lzd* on chromosome 3, a new cross was made between the mutant (OUM 5) and Russia 82, which involved three marker gene pairs, *Lzd lzd*, *Al al* and *Uz uz*, altogether. The F_2 and F_3 linkage data for three gene pairs are given in Table 4. It is apparent that gene *lzd* is located 9.97 % and 21.89 % apart from *al* and *uz*, respectively, and that three genes are arranged in the order of *lzd*, *al* and *uz*, on chromosome 3.

Since homozygotes of *lzd* are easily identified in segregating population grown in the field or greenhouse even at the seedling stage, the *lzd* gene is thought to be one of the useful viable markers of chromosome 3.

It may be of some interest to note in this connection that four other lazy dwarf mutants (OUM 6∼9) which had also been induced by EMS treatment were found to have the alleles on the same locus as *lzd*. From the viewpoint of mutagenesis, the *lzd* locus may be a so-called " hot spot " or highly sensitive to EMS.

3. *Slender Dwarf Mutant (sld), OUM 148*

The mutant used in this test is characterized by short (about 40 % reduction in stem length compared to the original variety) and slender stems with lax spikes, narrow leaves, and thin kernels. So, it is named a slender-type dwarf mutant.

A preliminary test of linkage has indicated that the mutant character is governed by a recessive gene *sld* and that the slender dwarf gene *sld* was linked with *uz* on chromosome 3, since the recombinants appeared less than the numbers expected from the independent segregation ratio among the F_2 population of the cross between the mutant and a normal or non-uzu isoline of the original variety, Akashinriki (Konishi 1970). Furthermore, the linkage was studied using three crosses between OUM 148 and each of the genetic stocks, Russia 82, $x_c \cdot a_n$ (No. 1) and gs-2d, which included five gene pairs, *Sld sld*, *Uz uz*, *Al al*, X_c x_c and *Gs-2 gs-2* together.

As shown in Table 5, the gene *sld* for slender dwarf is found to be linked with *uz* for uzu type with 4.76∼4.38 %, *al* for albino lemma with 17.48 %, x_c for xantha seedlings with 15.71 % and *gs-2* for glossy sheath-2 with 24.91 % recombination, respectively. From the results, the five genes used in this test are known to be located on chromosome 3 in the order of *al*, x_c, *uz*, *sld*, and *gs-2*.

TABLE 5. Linkage data for five genes, *sld*, *uz*, *al*, x_c and *gs-2*, obtained in the F_2 and F_3 of three crosses of OUM 148 with Russia 82 (A), $x_c \cdot a_n$ (No. 1) (B) and gs-2d (C)

Linked genes (Aa~Bb)	Source of data	Cross	Phase	Segregation*	Total	Recombination value (%)	Weighted average value (%)
Sld sld	F_2	A	C	278 : 11 : 9 : 58	356	6.35	4.76±0.8173
~*Uz uz*	F_3(AB)	〃	〃	99 : 6 : 8 : 165	278	3.82	
	F_3(Ab)	〃	〃	0 : 11	11	—	
	F_3(aB)	〃	〃	0 : 9	9	—	
	F_2	C	〃	282 : 6 : 8 : 61	357	4.38±1.1116	
Sld sld	F_2	A	R	206 : 83 : 65 : 2	356	19.47	17.48±1.6861
~*Al al*	F_3(AB)	〃	〃	3 : 37 : 40 : 126	206	23.27	
	F_3(Ab)	〃	〃	65 : 18	83	12.16	
	F_3(aB)	〃	〃	47 : 18	65	16.07	
Uz uz	F_2	A	R	204 : 83 : 68 : 1	356	13.75	13.84±1.4397
~*Al al*	F_3(AB)	〃	〃	3 : 34 : 34 : 133	204	20.60	
	F_3(Ab)	〃	〃	70 : 13	83	8.50	
	F_3(aB)	〃	〃	53 : 15	68	12.40	
$X_c\ x_c$ ~*Sld sld*	F_3(AB)	B	R	2 : 37 : 37 : 175	251	17.22	15.71±1.5081
	F_3(Ab)	〃	〃	105 : 33	138	13.58	
$X_c\ x_c$ ~*Uz uz*	F_3(AB)	B	R	1 : 29 : 30 : 188	248	13.28	12.17±1.3003
	F_3(Ab)	〃	〃	114 : 27	141	10.59	
Sld sld ~*Gs-2 gs-2*	F_2	C	R	190 : 95 : 67 : 5	357	24.91±4.9089	
Uz uz ~*Gs-2 gs-2*	F_2	C	R	195 : 96 : 60 : 6	357	28.16±4.8106	

* See the footnote of Table 3.

4. *Short and Crooked Awn Mutant* (*sca*), *OUM 206*

This mutant is characterized by short awns which are 2 cm long and crooked outwards at their upper portion. Its stem length is slightly shorter than that of the original variety.

Mode of inheritance and linkage was studied using three crosses with the tester stocks, Nigrinudum, Goseshikoku Hen and Ethiopia 321. The F_2 data from these crosses have revealed that these characteristics are controlled simultaneously by a single recessive mutant gene. So, a gene symbol *sca* (short, crooked awn) is allotted to the mutant. The *sca* gene is inherited independently of *n* (chromosome 1), *v* (2), *gl-3* (4), *B* (5), *o* (6) and *s* (7), but is in linkage with *uz* which is known to be on chromosome 3 (Table 6).

For determining the locus of the mutant gene *sca* on chromosome 3, a cross was newly made between the mutant OUM 206 and Russia 82,

TABLE 6. Independent inheritance of the short, crooked (*sca*) and several markers in the F_2 generation of the three crosses with OUM 206

Cross*	Symbol		Chromosome	Normal		Short, crooked		Total	χ^2_L	P
	X	x		X	x	X	x			
A	*N*	*n*	1	269	74	76	23	442	0.170	0.7 – 0.5
B	*N*	*n*	1	215	56	79	28	378	1.130	0.3 – 0.2
C	*V*	*v*	2	125	49	50	20	244	0.029	0.9 – 0.8
A	*Uz*	*uz*	3	324	19	16	86	445	246.205	v. small
B	*Gl-3*	*gl-3*	4	195	77	76	33	381	0.318	0.7 – 0.5
C	*B*	*b*	5	134	40	51	19	244	0.466	0.5 – 0.3
A	*O*	*o*	6	250	93	80	22	445	1.259	0.3 – 0.2
A	*S*	*s*	7	257	86	64	38	445	5.543	0.02–0.01
C	*S*	*s*	7	130	44	53	17	244	0.029	0.9 – 0.8

* Cross A: OUM 206 × Ethiopia 321. Cross B: OUM 206 × Goseshikoku Hen. Cross C: OUM 206 × Nigrinudum.

TABLE 7. F_2 and F_3 data for linkage of three genes, *sca*, *al* and *uz*, obtained from the cross between OUM 206 and Russia 82

Linked genes (Aa∼Bb)	Source of data	Phase	Segregation*	Total	Recombination value (%)	Weighted average value (%)
Sca sca	F_2	R	336 : 172 : 141 : 0	649	—	
∼*Al al*	F_3(AB)	〃	0 : 8 : 1 : 323	332	1.36	1.38 ± 0.3239
	F_3(Ab)	〃	164 : 7	171	2.09	
	F_3(aB)	〃	135 : 3	138	1.10	
Sca sca	F_2	C	462 : 46 : 50 : 91	649	17.23	16.94 ± 1.1465
∼*Uz uz*	F_3(AB)	〃	116 : 51 : 41 : 249	457	16.28	
	F_3(Ab)	〃	5 : 41	46	19.61	
	F_3(aB)	〃	6 : 43	49	21.82	
Al al	F_2	R	344 : 133 : 168 : 4	649	16.88	16.17 ± 1.1331
∼*Uz uz*	F_3(AB)	〃	6 : 38 : 42 : 253	339	14.84	
	F_3(Ab)	〃	88 : 43	131	19.63	
	F_3(aB)	〃	119 : 48	167	16.78	

* See the footnote of Table 3.

and the interrelationships among three genes, *sca*, *uz* and *al*, involved in the cross, were studied further.

Table 7 shows the results obtained from the F_2 and F_3 tests of the cross, which clearly indicates that gene *sca* is located rather close to *al* (about 1 % recombination), on the opposite side of *uz*. Thus, three genes, *sca*, *al* and *uz*, are arranged in this order on chromosome 3.

5. *Glossy Sheathed Mutant* (*gs-2*), *OUM 25*

Among the 15 EMS-induced glossy sheathed mutants from a cultivar, Akashinriki, two mutants, OUM 19 and 25, were shown to have the alleles on the same locus (*gs-2*) as gs-2d from Vantage (Konishi 1973). Interrelationships between *gs-2* and a number of marker genes were studied using four crosses of OUM 25 with genetic stocks, Smyrna, Col-orange, Russia 82 and Nigrinudum. The F_2 data indicated that the glossy sheath gene *gs-2* is inherited independently of *n* (chromosome 1), *v* (2), *al* (3), *K* and *Hs* (4), *B* (5), *o* (6) and *s* (7), but is linked with *uz* on chromosome 3 (Table 8).

TABLE 8. Independent inheritance of the glossy sheath–2 (*gs-2*) and several markers in the F_2 generation of the four crosses with OUM 25

Cross*	Symbol		Chromo-some	Normal		Glossy		Total	χ^2_L	P
	X	x		X	x	X	x			
A	*N*	*n*	1	240	97	83	28	448	0.571	0.5 – 0.3
B	*N*	*n*	1	145	59	48	12	264	1.946	0.02–0.1
C	*N*	*n*	1	301	95	85	31	512	0.347	0.7 – 0.5
A	*V*	*v*	2	253	84	79	32	448	0.671	0.5 – 0.3
D	*V*	*v*	2	147	63	51	16	277	1.043	0.5 – 0.3
C	*Al*	*al*	3	274	122	89	27	512	2.920	0.1 – 0.05
C	*Uz*	*uz*	3	323	73	74	42	512	14.670	v. small
D	*Uz*	*uz*	3	171	39	44	23	277	6.675	v. small
B	*K*	*k*	4	150	58	43	13	264	0.546	0.5 – 0.3
C	*Hs*	*hs*	4	289	88	107	28	512	0.420	0.7 – 0.5
D	*B*	*b*	5	148	62	52	15	277	1.396	0.3 – 0.2
B	*O*	*o*	6	145	59	48	12	264	1.946	0.2 – 0.1
A	*S*	*s*	7	250	87	82	29	448	0.004	0.95
B	*S*	*s*	7	153	55	40	16	264	0.061	0.9 – 0.8

* Cross A: OUM 25 × Smyrna. Cross B: OUM 25 × Col-orange.
Cross C: OUM 25 × Russia 82. Cross D: OUM 25 × Nigrinudum.

In order to raise more detailed linkage data about *gs-2*, one more cross was made between OUM 25 and a tester stock, cu-2·als·Uz, and the F_2 and F_3 tests were made for two crosses of OUM 25 with cu-2·als·Uz and Col-orange. Linkage data in Table 9 indicate that *gs-2* is linked closely with *als* (5.04 %), but loosely with x_c (40.58 %), *uz* (30.57 %) and *cu-2* (37.28 %). Thus, these genes are shown to be arranged in the order of x_c, *uz*, *gs-2*, *als* and *cu-2* on chromosome 3.

TABLE 9. F_2 and F_3 data for linkage of five genes, *gs-2*, *uz*, x_c, *als* and *cu-2*, obtained from two crosses of OUM 25 with Col-orange (X_c x_c) (A) and cu-2·als·Uz (B)

Linked genes (Aa∼Bb)	Source of data	Cross	Phase	Segregation*	Total	Recombination value (%)	Weighted average value (%)
Gs-2 gs-2	F_2	A	R	193 : — : 71 : —	264	43.95	40.58±1.5506
∼X_c x_c	F_3(AB)	″	″	19 : 43 : 32 : 99	193	43.37	
	F_3(aB)	″	″	33 : 38	71	36.54	
Gs-2 gs_2*-2*	F_2	B	C	406 : 83 : 88 : 91	668	29.13	30.57±1.5506
∼*Uz uz*	F_3(AB)	″	″	97 : 74 : 67 : 168	406	29.27	
	F_3(Ab)	″	″	25 : 58	83	46.30	
	F_3(aB)	″	″	17 : 71	88	32.38	
Gs-2 gs-2	F_2	B	R	302 : 187 : 178 : 1	668	6.80	5.04±0.6142
∼*Als als*	F_3(AB)	″	″	2 : 37 : 10 : 253	302	8.87	
	F_3(Ab)	″	″	176 : 11	187	3.03	
	F_3(aB)	″	″	162 : 16	178	4.71	
Gs-2 gs-2	F_2	B	R	383 : 106 : 163 : 16	668	35.44	37.28±1.8757
∼*Cu-2 cu-2*	F_3(AB)	″	″	52 : 106 : 77 : 148	383	45.98	
	F_3(Ab)	″	″	59 : 47	106	28.48	
	F_3(aB)	″	″	70 : 93	163	39.91	
Uz uz	F_3(AB)	A	R	1 : 21 : 10 : 131	163	10.76	10.09±1.4491
∼X_c x_c	F_3(aB)	″	″	17 : 84	101	9.19	
Uz uz	F_2	B	R	335 : 145 : 159 : 29	668	38.13	32.50±1.6832
∼*Als als*	F_3(AB)	″	″	31 : 67 : 82 : 155	335	44.95	
	F_3(Ab)	″	″	88 : 57	145	24.46	
	F_3(aB)	″	″	90 : 69	159	27.71	
Uz uz	F_2	B	R	394 : 152 : 100 : 22	668	41.98	42.09±1.9116
∼*Cu-2 cu-2*	F_3(AB)	″	″	59 : 78 : 116 : 141	394	44.67	
	F_3(Ab)	″	″	53 : 99	152	32.45	
	F_3(aB)	″	″	51 : 49	100	48.29	
Als als	F_2	B	C	416 : 130 : 64 : 58	668	37.16	39.74±1.7570
∼*Cu-2 cu-2*	F_3(AB)	″	″	83 : 96 : 96 : 141	416	39.07	
	F_3(Ab)	″	″	49 : 81	130	45.25	
	F_3(aB)	″	″	22 : 42	64	48.84	

* See the footnote of Table 3.

6. *White-striped Mutant (wst,,j), OUM 231*

The white-stripe character of OUM 231, induced from EMS-treated Akashinriki, is sensitive to low temperature. When grown in the field through winter, its leaf sheath and most of the leaf blades became whitish or white-striped, and only the leaf tip and central portion along the midrib of the blade remained green in general. However, the stripe character was not expressed at a temperature above 20°C.

Inheritance and linkage of the mutant character was investigated in the F_2 generation of two crosses of OUM 231 with L. T. 26 and Col-orange. The white-stripe was inherited as recessive to normal, and the gene was independent of *n* (chromosome 1), *v* (2), *K* (4), *B* and *trd* (5), *o* (6) and *s* (7), but was linked with *uz* on chromosome 3 (Table 10).

TABLE 10. Independent inheritance of the white-stripe (*wst„j*) and several markers in the F_2 generation of the two crosses with OUM 231

Cross*	Symbol		Chromosome	Normal		White stripe		Total	χ^2_L	P
	X	x		X	x	X	x			
A	*N*	*n*	1	301	109	84	44	538	2.876	0.1 - 0.05
B	*V*	*v*	2	297	104	116	35	552	0.464	0.5 - 0.3
A	*Uz*	*uz*	3	394	16	18	120	548	381.668	v. small
B	*Uz*	*uz*	3	380	21	24	127	552	387.791	v. small
A	*K*	*k*	4	315	95	103	33	546	0.066	0.8 - 0.7
B	*K*	*k*	4	314	87	112	39	552	0.931	0.5 - 0.3
B	*B*	*b*	5	293	108	107	44	552	0.390	0.7 - 0.5
B	*Trd*	*trd*	5	229	102	121	30	552	2.013	0.2 - 0.1
A	*O*	*o*	6	319	91	108	29	547	0.059	0.9 - 0.8
A	*S*	*s*	7	307	103	99	33	542	0.001	0.99-0.95
B	*S*	*s*	7	292	109	121	30	552	3.298	0.1 - 0.05

* Cross A: OUM 231 × Col-orange. Cross B: OUM 231 × L. T. 26.

TABLE 11. F_2 and F_3 data for linkage of three genes, *wst„j*, *uz* and *al*, obtaind from the cross between OUM 231 and Russia 82

Linked genes (Aa~Bb)	Source of data	Phase	Segregation*	Total	Recombination value (%)	Weighted average value (%)
Wst wst	F_2	C	292 : 15 : 16 : 68	391	8.77	10.02 ± 1.1307
~*Uz uz*	F_3(AB)	〃	80 : 21 : 22 : 169	292	11.60	
	F_3(Ab)	〃	1 : 14	15	12.50	
	F_3(aB)	〃	0 : 12	12	—	
Wst wst	F_2	R	217 : 90 : 80 : 4	391	23.24	22.54 ± 1.7560
~*Al al*	F_3(AB)	〃	4 : 45 : 30 : 138	217	21.95	
	F_3(Ab)	〃	53 : 37	90	25.87	
	F_3(aB)	〃	47 : 24	71	20.34	
Al al	F_2	R	216 : 81 : 92 : 2	391	16.73	14.99 ± 1.4097
~*Uz uz*	F_3(AB)	〃	0 : 25 : 34 : 154	213	15.11	
	F_3(Ab)	〃	56 : 19	75	14.50	
	F_3(aB)	〃	68 : 23	91	14.47	

* See the footnote of Table 3.

After a few years, the F_2 and F_3 tests were performed using a new cross between OUM 231 and Russia 82 in order to obtain more accurate linkage data about the gene, *wst,,j*, for white-stripe. A summarized result is given in Table 11. The weighted average P value in per cent, estimated from the recombination values obtained from the F_2 and F_3 segregations, is presented also in this table. The results show that the arrangement of three genes is in the order of *al*, *uz* and *wst,,j*.

CONSTRUCTION OF A LINKAGE MAP OF CHROMOSOME 3 AND DISCUSSION

A series of linkage studies described above have disclosed that the six mutant genes tested are on chromosome 3, and enabled us to construct a tentative linkage map of chromosome 3 using the obtained recombination values of these six genes in relation to four markers, *al*, x_c, *uz* and *als*, as shown in Fig. 1. However, the linkage data may include some inconsistent values, because they were obtained from several different genetic experiments. It is, therefore, desirable to estimate the most probable map distances among these ten genes based on all the estimated recombination values and their standard deviations, and finally to reconstruct a more reliable linkage map of chromosome 3. Fortunately, Jensen and Jørgensen (1975a) have already developed a computer program of the maximum likelihood method just applicable to such a case, and kindly allowed us to use it.

In the first place, map distances were calculated using all the values of recombination and their standard deviations obtained in this series of experiments, on the assumption that the ten genes are arranged in the order of *lzd*, *sca*, *al*, x_c, *uz*, *sld*, *wst,,j*, *gs-2*, *als* and *cu-2*. The result gave a highly significant chi-square value for inconsistency ($\chi^2=30.673$, d. f. = 19). Therefore, the recalculations were tried by dropping some of the seemingly inconsistent values one by one. As the result, a non-significant chi-square value ($\chi^2=13.472$, d. f. = 16) was finally obtained when two values, 40.58 ± 1.5506 (%) for x_c~*gs-2* and 42.09 ± 1.9116 (%) for *uz*~*cu-2*, were excluded.

Another question involved is whether three genes are truly arranged in the order of *gs-2*, *als* and *cu-2*, as shown in Fig. 1, or *als*, *gs-2* and *cu-2*, because *gs-2* was found to be very closely linked with *als*. So, the map distances among the ten genes were estimated again, based on the latter gene order, namely *als*, *gs-2* and *cu-2*. This claculation has resulted in a much larger chi-square value ($\chi^2=35.502$, d. f. = 19), suggesting the gene order being improbable. Therefore, it may be safe to conclude that, so far as the available data are concerned, the ten genes are arranged on chromosome 3 in the former order, namely, *lzd*, *sca*, *al*, x_c,

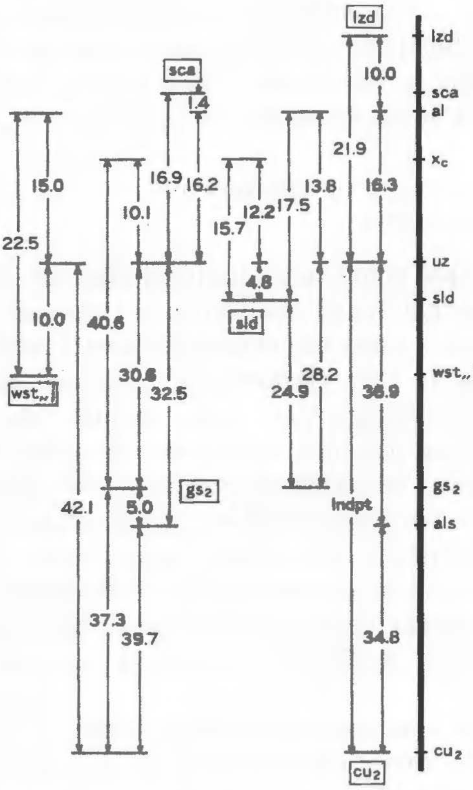

Fig. 1. Linkage relationships among 10 genes on chromosome 3.

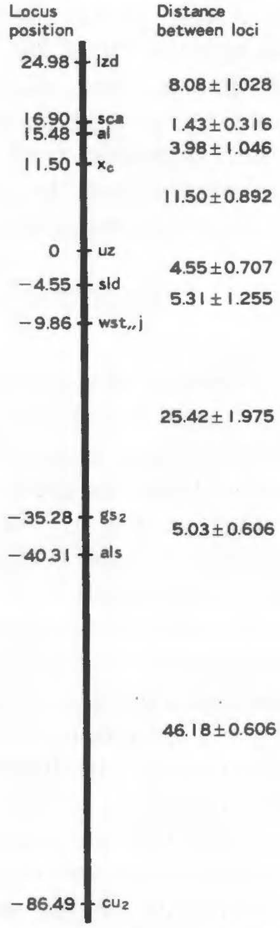

Fig. 2. A linkage map of 10 genes on chromosome 3, showing their map positions in centimorgan (cM).

uz, sld, wst,,j, gs-2, als and *cu-2,* with map distances shown in the right side of Fig. 2.

It seems quite reasonable to indicate a number of gene loci on the same chromosome by the distances in centimorgan (cM) from the centromere. Using telotrisomics, Tsuchiya (1983) has been in success to locate the centromere of chromosome 3 between *yst* and *zb.* But, no trials to estimate the map distances between the centromere and these two or many other gene loci have ever been made. Therefore, a chromosome map is usually constructed by using the distances (recombination values) from a gene locating on a putative distal end of the chromosome to the various loci.

From the practical point of view, however, the proposal of Jensen and Jørgensen (1975b) appears to be most pertinent. According to them, (1) the gene location is indicated by the map distance from a certain locus (origin) which is frequently used as a marker for linkage test, and which is close to the centromere, and (2) each locus on short and long arms of the chromosome is shown in the map distance from the origin with the positive and negative signs, respectively. If we adopt this system of chromosome map representation for barley chromosome 3, the gene *uz* is considered to be well qualified as the origin by the following three reasons: (1) the *uz* locus is close to the centromere of the chromosome, (2) the uzu type plants are easily distinguishable from the seedling stage to maturity, and (3) the *uz* gene has often been used as a good marker for linkage test. Since Tsuchiya (1983) has located *al* and x_c on the short arm of chromosome 3 and *uz*, *als* and *cu*–2 on the long arm, the former two loci should be indicated with the positive sign and the latter three loci with the negative sign. Furthermore, we reconstructed a linkage map including the newly located 6 genes and 4 markers according to the method proposed by Jensen and Jørgensen (1975b), and presented in Fig. 2.

SUMMARY

The character descriptions of six new mutants and linkage relationships between their mutant genes and several markers on chromosome 3 of barley are presented in this paper. The results are summarized as follows.

1) Choshiro Hen is mainly characterized by curly lemmas and awns, and strongly curved stem internodes. These characters are controlled by a single recessive gene, *cu-2*, which is located 34.75% apart from *als* on the opposite side of *uz*.

2) A lazy dwarf mutant, OUM 5, induced by EMS treatment, shows lazy or extremely procumbent growth with twist, dark-green leaves. Late maturity and high GA_3 sensitivity are also characteristics of this mutant. These characteristics are pleiotropically conditioned by a recessive gene, *lzd*, located 9.97% apart from *al* on the opposite side of *uz*.

3) The slender dwarf character of EMS-induced mutant, OUM 148, is governed by *sld* gene, locating close to *uz*, apart from *al*.

4) An EMS-induced mutant, OUM 206, is characterized by short and crooked awns, and slightly short stems, controlled simultaneously by a single recessive gene, *sca*. The gene is located rather close to *al* on the opposite side of *uz*.

5) One of the glossy sheath gene, *gs-2*, of OUM 25 induced by EMS treatment, is closely linked with *als* with 5.04% recombination.

6) The white-stripe character of EMS-induced mutant, OUM 231, is of a low-temperature sensitive type, and its mutant gene, *wst,,j*, is linked with *uz*, apart from *al*.

7) Arrangement of the six mutant genes and four markers on chromosome 3 is *lzd*, *sca*, *al*, x_c, *uz*, *sld*, *wst,,j*, *gs-2*, *als* and *cu-2*, as shown in Fig. 1. The relationships among genes are also indicated as the map distance in the centimorgan (cM) in Fig. 2.

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