INHERITANCE AND LINKAGE STUDIES IN BARLEY

IV. Linkages of Four Variegated Mutants

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White or yellow striped variants of barley occur not rarely as the spontaneous as well as artificial mutations. So far as we know, the majority of them are under genic, but not cytoplasmic, control. Since these mutants are viable and easily distinguishable from normal at the very early growth stage of plants, they are beneficially serviceable for linkage analysis. This paper reports results of linkage studies made of four mutants with white or yellow streaked leaves.

MATERIALS AND METHOD

Three white and one yellow streaked mutants were used in this study. Their names, plant characteristics and the proposed symbols for the mutant genes are listed in Table **1**. As to the character expression in relation to growing temperature, these may be classed into two: low-temperature type and temperature independent type. Manabe, Kanyo 7 and K×M are of the former type. When grown at low temperature, they exhibit wide and numerous streaks on developing leaves, becoming almost albinic or chlorotic, but as the temperature rises, they develop green leaves with only a few white or yellow streaks. An experiment with these materials has indicated that exposure to 3°C for about two weeks immediately after sowing induces distinct streaks on the first and second leaves of the mutant, which enables us to distinguish these from the normal, green plants. "Okina-like" mutant is the exception to this rule. This mutant always develops, irrespectively of height of growing temperature, leaves with fine, narrow white streaks distributing rather uniformly allover. Another feature of this mutant type is that its progeny always includes, besides the characteristic white-streaked plants, about **13~14** per cent of albino plants.

These mutants were each crossed preliminarily with the selected marker stocks which were known to have the gene or genes indicated in Table **1** for providing F_2 linkage tests with at least one marker gene in each of seven established linkage groups. Moreover, reciprocal crosses were made for one or more cross combinations with each mutant in order to know whether the streak character is determined by a nuclear gene and/or transmitted by maternal cytoplasm. The results of these tests were used as a guide for further crosses to determine the position of the mutant genes within the indicated groups.

TABLE 1
Characteristics of the mutants tested and of the marker stocks mated with the mutants

Names	Proposed gene symbol	Chromosome						
		1	2	3	4	5	6	7
Manabe	wst_2	*n*	*v*	*uz*	*k*, *bl*	*b*	*O*	*S*, *R*
Okina-like	wst_3	*n*	*v*	*uz*	*k*	*b*, *Trd*	*O*	*S*
Kanyo 7	wst_4	*N*, *l*	*v*, *E*	*Uz*	*k*, *Hs*	*b*	*O*	*S*
K × M	yst_2	*N*	*v*	*Uz*, *Al*	*k*, *Hs*	*b*, *Trd*	*O*	*S*
Colsess I		*N*, *L*		*Uz*	*K*, *hs*			*s*
Kobai		*n*, *L*		*uz*				
L. T. 12		*n*		*uz*	*K*	*trd*		*s*
L. T. 13		*n*		*uz*		*B*, *trd*		*s*
Nigrinudum		*n*	*V*	*Uz*, a_n	*hs*	*B*		*s*
Orange lemma		*N*		*Uz*	*hs*		*o*	*s*
al–uz				*al*, *uz*				
H. E. 3649			*V*, *e*					
Turkey 179		*N*		*Uz*	*Bl*			*s*, *r*

RESULTS

1. *White Streak 2* (wst_2) *in Manabe*

This mutant was first crossed to two marker stocks, Colsess I and Orange lemma, and later again to Turkey 179 for three point testing. Since all the F_1 plants from these crosses, including those of the reciprocal crosses, were found to be green colored, the streak character was suggested to be governed by a recessive gene, but not transmitted by maternal cytoplasm. The F_2 plants from these crosses were all grown in the field in the fall and their characters were investigated individually. Because of winter killing of the streaked segregants, their head characters could not be known for the crosses with Colsess I and Orange lemma. Table 2 shows the results of F_2 segregation. For all single character pairs F_2 segregation ratio was compared to a 3 : 1 ratio. So far as the data presented in this paper, there was no cases showing significant difference from the theoretical ratio, so χ^2 test was made to determine the fit of the observed numbers to the expected either 9 : 3 : 3 : 1 or 9 : 3 : 4 ratio.

It is evident in the result that the gene wst_2 for the white streaks of this mutant is independently inherited of *n* for naked kernel on chromosome 1, *uz* for semi-brachytic or uzu growth (3), *K* for hooded awn and *Bl* for blue aleurone (both on 4), and *o* for orange lemma (6), but is linked with *r* for smooth awn and *s* for short-haired rachilla both on chromosome 7.

Linkage intensities and relative positions of the three genes, *r*, wst_2 and *s* on chromosome 7 were closely studied by F_3 progenies test of a Manabe × Turkey 179 cross. From the observed frequencies of various F_2 genotypes, together with

TABLE 2
Segregation for green vs. white streak 2 and seven other character pairs in F_2's of the crosses with Manabe (wst_2) mutant

Manabe crossed with	Symbols		Chromosome	F_2 phenotypes				Total	χ^2	p
	Xx	Yy		XY	Xy	xY	xy			
Colsess I	Wst_2wst_2	*Nn*	1	339	103	162		604	1.7391	.5 –.3
	〃	*Uzuz*	3	316	126	162		604	3.8784	.2 –.1
	〃	*Kk*	4	339	103	162		604	1.7391	.5 –.3
	〃	*Ss*	7	294	148	162		604	15.2679	small
Orange lemma	〃	*Oo*	6	181	63	84		328	0.146	.95–.9
Turkey 179	〃	*Nn*	1	411	152	120	43	726	3.912	.3 –.2
	〃	*Uzuz*	3	435	136	128	41	740	2.328	.7 –.5
	〃	*Blbl*	4	421	142	117	46	726	3.299	.5 –.3
	〃	*Rr*	7	389	187	151	13	740	38.748	small
	〃	*Ss*	7	390	186	164	0	740	65.405	small
	Ss	*Rr*	7	463	91	77	109	740	132.673	small

the F_2 data, weighted average values of p between wst_2, r and s were calculated by the method suggested by Robertson et al. (1944) and given in Table 3. The distance between wst_2 and s, calculated from F_3 data only, proved to be 3.65 ± 0.6848 (%), though complete linkage was suggested by F_2 data, while the calculated F_3 data showed a greater distance for wst_2–r than for r–s. It may be safe to conclude that these three genes are arranged in the order of wst_2–s–r. A chromosome map is given in Fig. 1.

TABLE 3
Calculation of weighted average values of p between Wst_2wst_2, Rr and Ss from the F_2 and F_3 data in a Manabe × Turkey 179 cross

Genes	Source of data	p	i	n	I=ni	pI	Weighted p
Wst_2wst_2 –Ss	F_3 AB	0.0303	65.9487	151	9958.2537	301.7351	0.0365± 0.006848
	F_3 Ab	0.0460	42.1762	91	3838.0342	176.5496	
	F_3 aB	0.0400	48.1540	156	7512.0240	300.4810	
Wst_2wst_2 –Rr	F_2	0.2714	1.1942	740	883.7080	239.8384	0.2845± 0.01839
	F_3 Ab	0.3200	5.2750	99	522.2250	167.1120	
	F_3 aB	0.2711	6.2650	143	895.8950	242.8771	
	F_3 AB	0.2920	4.5788	143	654.7684	191.1924	
Rr–Ss	F_2	0.2543	3.7244	740	2756.0560	700.8650	0.2506± 0.016124
	F_3 Ab	0.1053	6.1328	36	220.7808	23.2482	
	F_3 aB	0.2985	3.2991	57	188.0487	56.1325	
	F_3 AB	0.2697	4.0509	168	680.5512	183.5447	

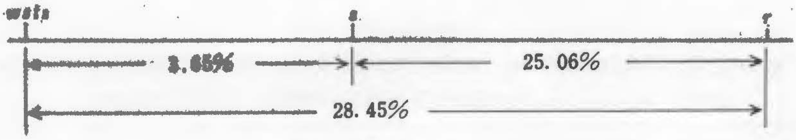

Fig. 1. Map position of *wst₂* on chromosome 7.

2. *White Streak 3* (*wst₃*) *in Okina-like Mutant*

The original material used in this experiment is an X-ray induced mutant from a commercial naked variety of uzu type, called Akashinriki. This was produced and kindly supplied by Mr. Takashi Ohta, agronomist, Shizuoka Agricultural Experiment Station, Shizuoka, Japan. Because of close similarity in characteristics and genetic behavior with Okina-mugi of which So, Ogura and Imai (1919), So (1921) and Imai (1928, 1935, 1936) studied extensively and reported in detail, this mutant was named as Okina-like mutant.

Inheritance and linkage of the white streak character of this mutant was studied using three crosses. When crossed to normal green tester strains, Nigrinudum, Orange lemma and L. T. (Linkage Tester) 12, all the F_1 plants derived from them were found to be green and normal, and segregation in their F_2 generation occurred in a ratio of 3 green to 1 streak, indicating that the character is governed by a single recessive gene. A gene symbol *wst₃* was allotted to the white-streak character of this mutant.

Interrelationships of the gene pair *Wst₃wst₃* with eight other gene pairs known to be located on different barley chromosomes are shown in Table 4. This clearly indicates that *wst₃* is independently inherited of *n* for naked kernel on chromosome 1, *K* for hooded awn (4), *B* for black hull and *trd* for the third

TABLE 4

Segregation in F_2 generation for green vs. white streak 3 and eight other character pairs in three crosses with Okina-like mutant (*wst₃*)

Mutant crossed with	Symbol		Chromosome	Green		Streak		Total	χ^2	p
	X	x		X	x	X	x			
Nigrinudum	*N*	*n*	1	328	119	132	42	621	3.6978	.3 −.2
	Uz	*uz*	3	461	0	0	175	636	large	small
	B	*b*	5	333	114	117	55	619	7.5842	.1 −.05
	S	*s*	7	324	123	129	45	621	4.5455	.3 −.2
Orange lemma	*N*	*n*	1	275	96	93	35	499	0.6477	.9 −.8
	Uz	*uz*	3	378	0	0	129	507	large	small
	O	*o*	6	273	98	97	31	499	0.5479	.95−.9
	S	*s*	7	283	88	90	38	499	1.9717	.7−.5
L. T. 12	*K*	*k*	4	287	102	99	33	521	0.3390	.98−.95
	Trd	*trd*	5	296	98	106	26	521	2.2832	.7−.5

outer glume (both on 5), *o* for orange lemma (6) and *s* for short-haired rachilla (7). But, this is closely linked with *uz* for semi-brachytic or uzu growth on chromosome 3. Namely, not a single recombinant plant, green-uzu and streak-normal type, was observed among 1143 F_2 plants of the crosses with Nigrinudum and Orange lemma which are both normal type with green leaves.

As stated before, this mutant is characterized by a strange genetic behavior that the progeny of a streaked plant constantly segregates, besides the typical streaked plants, a certain proportion of albino seedlings, though not a single green one is found at all. As seen in Table 5, the frequency of the albino seedlings was 830 or 13.45 % of a total of 6172 viable seedlings. It may be noted also that about 1 % of the streaked seedlings has shown some clear stripes running from the base to top of the first leaves. In order to get some insight into this phenomenon, two experiments were performed.

TABLE 5
Segregation of albino seedlings in the progenies of the streaked Okina-like mutants

Years	Number of seedlings		Total	Percent of albino seedlings
	Streaked	White		
1966	1169	192	1361	14.11
1967 A	2056	331	2387	13.87
1967 B	2117	307	2424	12.67
Total	5342	830	6172	13.45

In the first experiment, it was studied whether the reciprocal crosses between the streaked mutant and normal green varieties behave differently in their F_1 generations. The results presented in Table 6 clearly indicate that albino seedlings have appeared only in the cross in which the streaked mutant had been used as the female parent, whereas all the F_1 plants from their reciprocal crosses have been green. This suggests that the albinism itself is transmitted maternally and irrespectively of the genotype of the pollen plant.

TABLE 6
Proportion of albino seedlings appeared in the F_1's of two reciprocal crosses between the streak mutant and normal varieties

Mutant crossed with	Streak (♀) × Normal (♂)			Normal (♀) × Streak (♂)		
	Green	Albino	%	Green	Albino	%
Asahi 21	214	32	13.0	121	0	0
Asahi 19	296	36	10.8	81	0	0

For the second experiment a number of caryopses with seemingly white lemma and those with variegated lemma were individually marked after heading and collected separately after ripening, since the variegated plants produced some heads assuming a sectorial mosaic of white and variegated parts. Table 7 shows the number and percentage of albino seedlings arisen from these two kinds of caryopses, which indicates that the rate of albino seedling from the white caryopses is about two times higher than that from the variegated caryopses. It may be noted here that about two thirds of the white kernels became sterile, the cause of which is unknown.

TABLE 7

A comparison of the rates of albino seedlings arisen from the caryopses with white and green (streak) lemma together with fertility of caryopses with white lemma

Plant no.	White caryopses			Green caryopses			Fertility of white kernel	No. of caryopses
	Albino	Streak	%	Albino	Streak	%		
1	11	8	57.9	56	158	26.2	38.2	369
2	5	9	35.7	56	288	16.3	34.9	453
3	19	38	33.3	94	454	17.2	46.8	747
4	10	15	40.0	110	233	32.1	32.2	531
5	16	11	59.3	126	404	23.8	37.6	753
6	8	18	30.8	127	550	18.8	35.4	843
7	5	6	45.5	56	208	21.2	24.0	426
8	2	4	33.3	89	375	19.2	15.9	630
9	1	1	50.0	40	138	22.5	8.3	252
10	9	16	36.0	117	321	26.7	32.1	651
Total	86	126	40.6	871	3129	21.8	34.2	5655

The results obtained from the above-stated experiments may be summed as follows:

1) The variegation (white streak) of this mutant is governed by a single recessive gene wst_3 which is completely linked with *uz* for semi-brachytic growth locating on chromosome 3.

2) The variegated plants always segregate, besides the variegated seedlings, about 13∼14 per cent of albino seedings in their progenies. The albinism is transmitted only by maternal cytoplasm, and it is independent of the genic constitution of the pollen plant.

3) The rate of albino seedlings from the white caryopses obtained from the variegated plants is much higher than that of the variegated caryopses of the same plants.

The genetic behavior of variegation and albinism of this mutant can well be represented by Fig. 2, which is cited from Imai (1928), and it will easily be recognized that this mutant is almost identical with Okina-mugi, of which So, Ogura and Imai (1919) and Imai (1928 and later publications) have studied in detail. Only one difference is that this mutant segregates albino seedlings at somewhat higher rate than the Okina-mugi in which the rate is, according to Imai (1935),

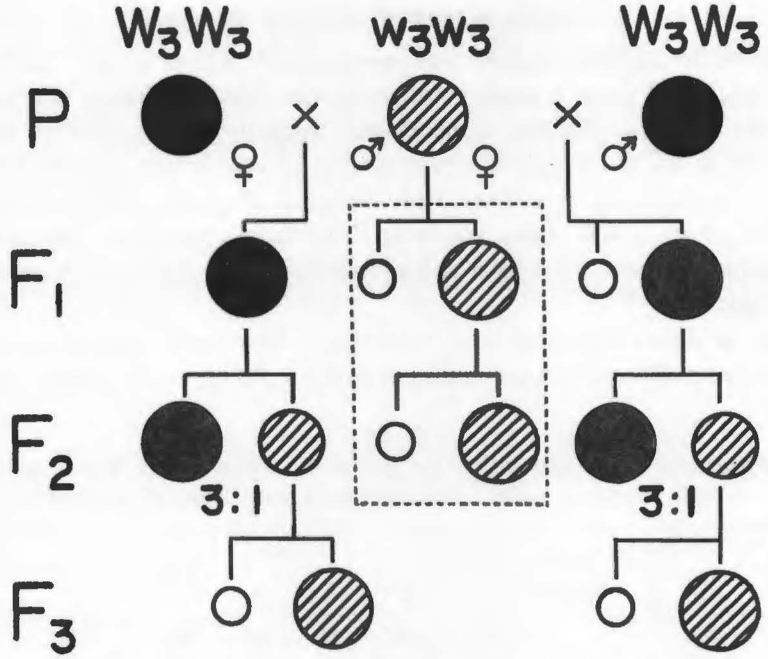

Fig. 2. The inheritance of white streaked and albino plants in Okina-like mutant. Black, white and hatched circles stand for green, albino and streaked plants, respectively. W_3w_3 represents the gene Wst_3wst_3 for green vs. white streak plants.

about 4~7 per cent.

The genetic behavior of this variegated mutant of barley is very peculiar and not comparable with the ordinary variegation studied in various plants. Imai (1928) explained this with the following assumption, which may also be applicable to this mutant: The variegation is transmitted by a recessive gene, but it is not a pattern factor in a strict sense, because the white parts or stripes are due to the distribution of white plastids which have changed their quality permanently. The variegation is, therefore, produced by a factor which alters at times the essential quality of the plastids from normal green to colorless. The original difference between green and variegated barley lies in their allelomorphs for the stability of the plastid, and the variegation is due to the development of white stripes owing to the distribution of the white plastids controlled no longer by genetic factors. Now assume the gene for the plastid mutability as Wst_3wst_3, normal green barley is Wst_3Wst_3, and the variegated barley wst_3wst_3. The plastid of both are originally quite normal in their essential quality. Each of them is designated by g. It is assumed that in the presence of wst_3wst_3 some of the green plastids mutate at times to white plastids w. The plastids of selfgreen barley are all g, while those of the variegated barley consist of g and w. The former g may subsequently be altered in the presence of the factors wst_3wst_3 to become white.

3. *White Streak 4* (wst_4) *in Kanyo 7*

This white streaked mutant was spontaneously arisen at this institute in a cultivar originated from a locality called Kanyo in South Korea. Three crosses were made between this and three testers, including some of their reciprocal crosses. Since all the F_1 plants were normal green, it was suggested that the maternal cytoplasm had no concern with the streak character of this mutant. The segregation of green and streak plants in F_2 of these crosses has shown that the streak character is controlled by a single recessive gene, for which a symbol wst_4 was allotted.

Table 8 shows interrelationships between white streak 4 and nine markers known to be on different chromosomes of barley. As apparent in this table, wst_4 is independently inherited of *n* and *l* for naked kernel and dense head, respectively, both on chromosome 1, *uz* for semi-brachytic growth (3), *K* and *Hs* for hooded awn and hairy leaf-sheaths, respectively, (4), *B* for black hull (5), and *s* for short-haired rachilla (7), but is in linkage with *V* for two-rowed head on chromosome 2.

TABLE 8

Segregation in F_2 generation for green vs. white streak 4 and eight other character pairs in three crosses with Kanyo 7 mutant

Mutant crossed with	Symbol		Chromosome	Green		Streak		Total	χ^2_L	p
	X	x		X	x	X	x			
Kobai	*N*	*n*	1	287	84	77	22	470	0.001	large
	L	*l*	1	255	116	76	31	478	0.410	.7 −.5
	Uz	*uz*	3	280	91	76	38	485	3.354	.1 −.05
Colsess I	*L*	*l*	1	238	98	70	22	428	1.200	.3 −.2
	K	*k*	4	232	107	76	22	437	3.601	.1 −.05
	Hs	*hs*	4	241	101	71	28	441	0.133	.8 −.7
	S	*s*	7	247	89	72	20	428	0.814	.8 −.7
Nigrinudum	*L*	*l*	1	153	60	45	19	277	0.032	.99−.95
	N	*n*	1	173	40	55	9	277	0.385	.7 −.5
	V	*v*	2	178	39	33	31	279	24.297	small
	Hs	*hs*	4	161	52	48	22	283	1.367	.3 −.2
	B	*b*	5	152	61	42	20	275	0.212	.8 −.7
	S	*s*	7	178	35	47	17	277	2.898	.1 −.05

A three point test was then made with a new cross between Kanyo 7 and H. E. 3649 from Lyallpur, Pakistan. F_2 data for the interrelationships among three genes, wst_4, *v* and *e* for white streak 4, six-row and long-awned glume, respectively, are given in Table 9. Based on these and the F_3 data obtained by their F_3 progeny test, weighted average values of p were calculated and given in Table 10. The results clearly indicate wst_4 being very close to *e*, and this makes it difficult to determine on which side of *e* the gene wst_4 is truly located. According

TABLE 9

Interrelationships between wst_4 for white streak 4 in Kanyo 7 and v and e in F_2 of a cross with H. E. 3649

Gene		Symbol		Phase	F_2 phenotypes				Total	χ^2 for 9:3:3:1	Recombination %	χ^2 for linkage
X	x	Y	y		XY	Xy	xY	xy				
Wst_4	wst_4	V	v	Coupl.	257	62	54	46	419	28.08	33.29	0.526
〃	〃	E	e	Repl.	216	103	100	0	419	40.95	0	0.446
V	v	E	e	Repl.	219	92	97	11	419	16.62	32.16	0.151

TABLE 10

Calculation of weighted average values of p between Wst_4wst_4, Vv and Ee from the F_2 and F_3 data in a Kanyo 7 × H. E. 3649 cross

Genes	Source of data	p	i	n	I=ni	pI	Weighted p
Wst_4wst_4 $-Vv$	F_2	0.3329	2.7859	419	1167.2921	388.5915	0.3431± 0.02248
	F_3 Ab	0.2858	3.3350	66	220.1100	62.9074	
	F_3 AB	0.3928	2.0491	240	491.7840	193.1728	
Wst_4wst_4 $-Ee$	F_3 Ab	0.0899	20.5814	97	1996.3953	179.4760	0.0651± 0.009955
	F_3 aB	0.0303	64.2841	34	2185.6594	66.2255	
	F_3 AB	0.0696	28.2436	209	5902.9124	410.8427	
$Vv-Ee$	F_2	0.3216	1.2800	419	536.3200	172.4805	0.3482± 0.027779
	F_3 Ab	0.3134	5.3898	88	474.3024	148.6464	
	F_3 aB	0.4563	3.8014	75	285.1050	130.0934	

to the F_2 results, the distance of wst_4-v was slightly larger than that of v-e, while quite a reverse relation was suggested by the F_3 progeny test. Judging from their average weighted values, calculated by combining all the data altogether, it may be tentatively concluded that wst_4 is located in a close proximity to e and on the same side of v relative to e. The position of wst_4 on chromosome 2 is shown in Fig. 3.

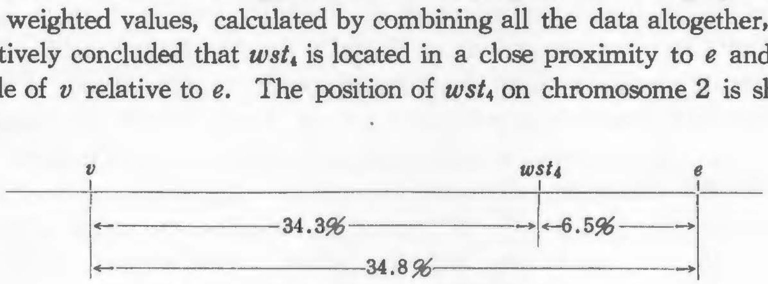

Fig. 3. Map position of wst_4 on chromosome 2.

4. *Yellow Streak 2 (yst_2) in K×M*

The original material used in this experiment was found at this institute as a spontaneous mutant among an F_5 population of a Kuromugi 148 × Mensury C cross, and hence named K×M for the brevity's sake. As in the cases with aforementioned three mutants, F_1, F_2 and F_3 behaviors of the several crosses with

TABLE 11
Segregation in F_2 generation for green vs. yellow streak 2 and nine markers in four crosses with K×M mutant

Mutant crossed with	Symbol		Chromosome	Green		Streak		Total	χ^2	p
	X	x		X	x	X	x			
Nigrinudum	*N*	*n*	1	235	88	100	24	447	4.9675	.2−.1
	V	*v*	2	244	80	103	33	460	5.1749	.2−.1
	Hs	*hs*	4	230	94	119	42	485	0.2495*	.7−.5
	B	*b*	5	253	70	95	29	447	3.8192	.3−.2
	S	*s*	7	248	75	98	27	448	3.3968	.5−.3
L.T. 13	*N*	*n*	1	294	80	84	30	488	3.4536	.5−.3
	Uz	*uz*	3	353	157	187	5	702	67.0869	small
	Trd	*trd*	5	392	147	105	52	696	1.7267*	.2−.1
	B	*b*	5	279	94	88	26	488	1.0055	.8−.7
	S	*s*	7	282	93	97	20	492	4.0098	.3−.2
Orange lemma	*Hs*	*hs*	4	264	99	77	41	481	2.5468*	.2−.1
	O	*o*	6	289	74	76	33	472	6.6365	.1−.05
	S	*s*	7	284	79	83	27	473	2.8735	.5−.3
Colsess I	*K*	*k*	4	230	83	44	13	370	0.3471	.7−.5

* Values for χ^2_L

this mutant have indicated that its yellow streak character is governed by a single recessive gene, named here ***yst*$_2$**, and not affected by maternal cytoplasm. In Table 11 are given the observed frequencies of F_2 phenotypes in the crosses between this mutant and four kinds of testers. It is evident in the results that the gene ***yst*$_2$** is independently inherited of ***n*** for naked kernel on chromosome 1, ***v*** for six-row (2). *K* for hooded awn and *Hs* for hairy leaf-sheath (both on 4), *B* for black hull (5), *o* for orange lemma (6) and *s* for short-haired rachilla (7), but is in linkage with ***uz*** for semi-brachytic growth on chromosome 3.

In order to determine the position of ***yst*$_2$** on chromosome 3, one more cross was made with a tester plant having ***al*** (albino lemma) and ***uz*** combined. Table 12 shows the recombination values and also average weighted values of p between two each of the four genes, ***yst*$_2$**, ***al***, ***uz*** and ***a*$_n$**, which were calculated from the F_2 and F_3 data in three crosses with the yellow streak mutant, K × M. As apparent in the table, ***yst*$_2$** is 8.2% apart from ***a*$_n$** which is involved in Nigrinudum, and very close to ***al***, because no doubly recessive plant (***yst*$_2$ *al***) was found at all among the F_2 population of the cross between K × M and ***al–uz***, and only 0.9% recombination value was obtained by the F_3 test of the same cross. Probably on this account, some difficulties were encountered in determining the relative position of ***yst*$_2$** with ***al*** and ***uz***. Whereas the F_2 data obtained from the cross with ***al–uz*** tester suggested that the order of genes was ***uz–yst*$_2$*–al***, inasmuch as the distance of ***uz*** to ***yst*$_2$** (12.2%) was about 3% larger than that of ***uz*** to ***al***

TABLE 12

Calculation of average weighted values of p between four genes, *yst_2*, *al*, *uz* and *a_n* in the three crosses of yellow streak mutant with (1) Nigrinudum, (2) al-uz tester and (3) L. T. 13

Genes	Source of data	p	i	n	I	pl	Weighted p value	
yst_2-a_n	F_3 AB (1)	0.0759	25.7525	200	5150.5000	390.9230	0.0815 ±0.0134	
	F_3 Ab 〃	0.1538	6.1047	65	396.8055	61.0287		
yst_2-al	F_2 (2)	0.0000	—	546	—	—	0.0094 ±0.0037	
	F_3 AB 〃	0.0106	193.9247	190	36845.6930	390.5643		
	F_3 Ab 〃	0.0120	179.9146	84	15112.8264	181.3539		
	F_3 aB 〃	0.0085	233.3349	59	13766.7591	117.0175		
yst_2-uz	F_2 (2)	0.1223	1.0376	546	566.5296	69.2866	0.0776	0.0997 ±0.0091
	F_3 AB 〃	0.0749	26.2610	195	5120.8950	383.5550		
	F_3 Ab 〃	0.0748	26.2975	79	2077.5025	155.3972		
	F_3 aB 〃	0.0741	26.5531	58	1540.0798	114.1199		
	F_2 (3)	0.1824	1.0852	702	761.8104	138.9542	0.1731	
	F_3 AB 〃	0.1696	10.4653	103	1077.9259	182.8162		
	F_3 Ab 〃	0.2128	8.1169	57	462.6633	98.4548		
	F_3 aB 〃	0.1290	13.9645	35	488.7575	63.0497		
uz-al	F_2 (2)	0.0919	10.0263	546	5474.3598	503.0937	0.0869 ±0.0102	
	F_3 AB 〃	0.0793	16.9554	237	4018.4298	318.6615		
	F_3 aB 〃	0.1539	4.5097	12	54.1164	8.3285		

(9 %), F_3 data from the same cross indicated the latter being larger, though slightly, than the former. By the F_2 and F_3 tests of the cross with L. T. 13, on the other hand, the distance between ***uz*** and ***yst_2*** was estimated as **17.3 %**. So, all the linkage data of ***uz*** and ***yst_2***, obtained from these two crosses, were combined and a weighted average value was calculated. It was **10.0 %**. It may therefore be concluded, though not confidently, that the order of four genes on chromosome 3 is ***uz-al-yst_2-a_n***. A map of chromosome 3 is given in Fig. 4.

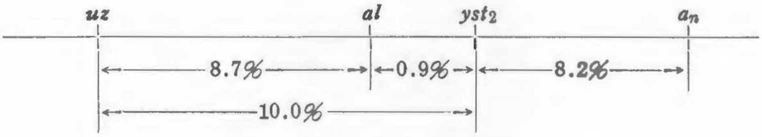

Fig. 4. Map position of *yst_2* on chromosome 3.

SUMMARY

This paper deals with the results of linkage studies of three white and one yellow streak mutant characters of barley. In three mutants, Manabe, Kanyo 7 and K × M, their characteristic streaks are conspicuously expressed under rather

low growing temperature, while in Okina-like mutant white streak appears almost irrespectively of height of growing temperature. The results obtained may be summed as follows:

1) The gene wst_2 for white streak of Manabe is located very closely to *s* for short-haired rachilla and on the opposite side of *r* for smooth awn on chromosome 7.

2) The gene wst_3 for white streak in Okina-like mutant is completely linked with *uz* for semi-brachytic growth on chromosome 3. Like Okinamugi of which So et al. (1918) and Imai (1928) have reported, all the variegated plants having this gene always segregate about 13~14 per cent of albino seedlings in their progenies. The albinism is transmitted by maternal cytoplasm and has no connection with the genic constitution of pollen plant.

3) The gene wst_4 for white streak in Kanyo 7 is on chromosome 2. Its location is very close to *e* for elongated glume and on the same side of *v* relative to *e*.

4) The gene yst_2 for yellow streak in K × M mutant is very close to *al* for albino lemma on chromosome 3. Four genes, *uz*, *al*, yst_2 and a_n are arranged in this order.

5) Figs. 1, 3 and 4 show map position of wst_2, wst_4 and yst_2, respectively.

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