INHERITANCE AND LINKAGE STUDIES IN BARLEY

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Introduction

It is still a desire of the geneticists and plant breeders to pursue studies to elucidate the mode of inheritance and linkage of various plant characters. These characters may or may not be of practical importance, and some have included physiological defects. For such genetical studies, barley with its small number of chromosomes and a large number of clearly distinguishable characters has attracted wide interest among workers, ranking next to maize among important crop plants. Authors attempt to present additional informations on the heredity of some characters of interest on barley.

As pointed out by Vavilov (1925), barley of China and Japan comprise diverse forms varying in both the morphological and physiological characteristics. This facts had attracted considerable attention of Japanese geneticists some two decades ago. The present writers, while making genetical studies on the geographical differentiation of the cultivated barley, have always felt the necessity of accumulating more knowledge on the characters of barley of Far East. During their period of study some valuable materials for linkage analyses were fortunately obtained which has made it possible to advance this work. A series of studies on the inheritance and possible linkage relations of some characters that were of practical or genetical importance were made since. These include works on uzu or semi-brachytic gene which have already been published, and the present report which deals with the location of the genes for ligule-less, bracteate, elevated and "subjacent" hood and fragile stem characters, along with interrelation of three genes in linkage group III.

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Materials and Methods

The experiments were performed during the past several years at the

Ohara Institute. Principal varieties used were so-called "Ligule-less", "Bracteate", Kamairazu, Chengchou No. 5 and Tayeh No. 13. The first three varieties were received from the National Agricultural Experiment Station at Konosu, Japan, and the last two collected in China by the senior author. A number other of Japanese barley were also used to a limited extent, particularly for linkage study. A detailed description of characters of these varieties are given at resprective chapters.

For determining the linkage relations, interaction of the characters in question with the characters listed below were tested principally in F_2 generation, and in some cases in F_3 generation.

Linkage group	Character pairs	Gene symbols
I	Non-six-row vs. six-row	Vv
	Normal vs. long awned glume	Ee
II	Black vs. white palea	Bb
III	Covered vs. naked grain	Nn
	Long vs. short awn	Lklk
	Lax vs. dense ear	Ll
IV	Blue vs. white aleuron layer	Blbl
	Normal hood vs. long awn	Kk
V	Long vs. short haired rachilla	Ss
	Rough vs. smooth awn	Rr
VI	Normal vs. uzu (Semi-brachytic)	Uzuz
	Green vs. white seedling	A_cA_c
	Green vs. white seedling	A_nA_n
VII	Normal vs. brachytic	Brbr
	Normal vs. xantha seedling	X_cX_c

The parental varieties having the marker genes in the respective linkage groups are shown in Table 1.

TABLE 1. *Marker genes involved in different parents.*

Linkage group	Gene symbols	Names of varieties
I	V, e	Iraki Black, Lyallpur, Nigrinudum
II	B	Iraki Black, Nigrinudum
III	n, lk, l	Nigrinudum, Kairyobozu, Suifu
IV	Bl, K	Colsess I, V, Natsudaikon-mugi, Kamairazu, Ligule-less, Cheng-chou No. 2
V	s, r	Iraki Black, Suifu
VI	uz, a_c, a_n	Colsess I, Nigrinudum, Suifu and other Japanese barley
VII	br, x_c	Brachytic, Colsess V

Calculation of recombination percentage was made in general from F_2 data by the use of Immer's tables and formulae. In some cases F_2 and F_3 data or different F_2 data were combined for mean recombination values according to the methods suggested by Robertson et al. (1944) and Kramer and Burnham (1947).

Experimetal Results and Discussion

1. *Location of four genes including al gene for ligule-less character in linkage group* I.

This experiment was planned in order to establish the linkage of the gene for ligule-less character involved in a variant of Japanese origin, called "Ligule-less". This variant, as shown in Fig. 1, is completely deficient not only of the ligule, but also of the auricle on all leaves, and is easily distinguishable from the normal at any stage of the plant growth. The transition part from leaf-sheath to blade is more elongated without any accessory organ or tissue developed thereof, but it is nevertheless distinct because of the differential epidermal tissues of the sheath and the blade. The leaf-blades always stand erect along the stem.

It is well-known to us that there are wild grasses and cereals which involve variants, strains or species that are lacking in ligules or auricles or both. So far as we know, however, no spontaneous mutant of this nature has ever been recorded in barley, although induced ligule-less mutants by X-ray irradiation were obtained by Lutkov (1937) and Nishimura (1952). These induced mutants have well-developed auricles, which differentiate from our material.

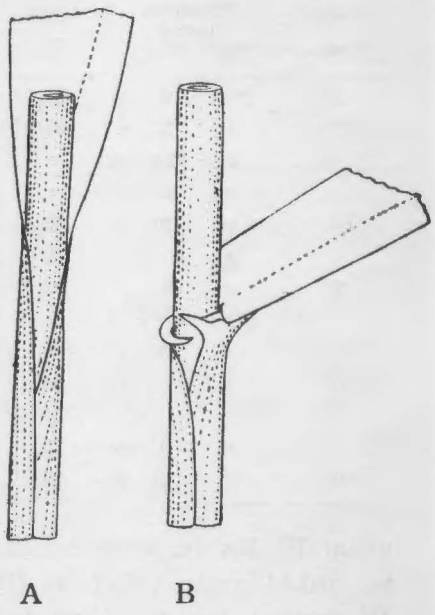

Fig. 1. A leaf without ligule and auricle in "Ligule-less" variety (left), and that of a normal variety (right).

This study was approached in the following way : first, mode of inheritance of ligule-less character and its linkage were determined from F_2 segregations of five crosses. "Ligule-less" was crossed with following parental varieties indicated with their cross numbers in parenthesis : (27) Brachytic, (28) Colsess I, (35) Suifu, (36) Iraki Black, (37) Kairyo-bozu. Next, the order of arrangement of four genes in linkage group I was determined by crossing with H. E. 3649 from Lyallpur, India (briefly called Lyallpur) and noting their segregation in F_2 and F_3 generations.

The F_1 hybrids of these crosses, with one exception, developed normal ligules and auricles, indicating the ligule-less and auricle-less conditions being completely recessive to normal. Situation was, however, somewhat different

in the hybrid with Kairyo-bozu, where this variety, although showed no appreciable difference in form and size of these organs from other normal varieties, ligules and auricles of the F_1 hybrid were apparently intermediate between both parents in size, its leaf-blades being more erect almost alike to those of the ligule-less parent. In the F_2 generation, there appeared normal, intermediate and ligule-less types segregating in a 1 : 2 : 1 ratio. These tests indicated that the presence or absence of ligules and auricles was governed by a single gene. A gene symbol, *al*, was given to the ligulelessness.

In Table 2 are shown the interrelations of *al* with various marker genes in F_2 of the five crosses. The results reveal that *Alal* is inherited independently of the following gene pairs : Black vs. white chaff (*Bb*) in linkage

TABLE 2. *F_2 segregation of character pairs showing independent inheritance in several crosses with Ligule-less variety.*

Linkage group	Genotypes tested Xx	Yy	Cross No.	F_2 phenotypes XY	Xy	xY	xy	Total	χ^2	P
II	Alal	B b	36	265	65	75	34	439	7.181	.07
III	//	N n	37	162	55	49	30	296	8.036	.05
	//	Lk lk	//	163	54	51	28	296	5.343	.15
	//	L l	//	150	67	56	23	296	5.153	.16
IV	//	Bl bl	35	169	51	60	17	297	0.882	v. large
	//	//	37	154	42	53	17	266	1.577	.67
V	//	S s	35	163	57	64	14	299	4.600	.21
	//	//	36	255	75	78	30	438	1.407	.71
	//	R r	//	248	82	81	27	439	0.037	v. large
VI	//	Uz uz	35	163	58	63	15	299	1.855	.55
	//	//	37	173	44	63	16	296	3.988	.26
	//	A_c a_c	28	796	273	278	93	1440	0.012	v. large
VII	//	Br br	27	113	38	31	5	187	5.049	.17

group II; lax vs. dense ear (*Ll*), long vs. short awn (*Lklk*) and covered vs. naked grain (*Nn*) in III group ; blue vs. white aleuron (*Blbl*) in IV group ; long vs. short haired rachilla (*Ss*) and rough vs. smooth awn (*Rr*) in V group ; normal vs. uzu (*Uzuz*) and green vs. white seedling ($A_n a_n$) in VI group ; and also normal vs. brachytic (*Brbr*) in VII group.

The above result suggests *al* being located in linkage group I. In fact, this was verified in a cross with Iraki Black barley, since *al* was not inherited independently of, but was linked with *v* for six-row that had been known to be in group I. The recombination percentage was 38.54 ± 2.09.

Interrelations of *Alal* with *Vv*, *Ee*, *Prpr* were studied in a cross between "Ligule-less" and Lyallpur, where *Ee* is a gene for normal vs. long outer glume and *Prpr*, an assumed symbol for purple vs. green basal leaf sheath. The F_2 data shown in Table 3 indicate these four genes being in a linkage group, although recombination value of *Alal* and *Ee* was over 50 per

TABLE 3. *Linkage of the four genes in linkage group I. calculated from F2 data of a Lyallpur × Ligule-less cross*

Symbol		F_2 phenotypes				Total	Recombination values (%)	Fit to the theoretical. P
Xx	Yy	XY	Xy	xY	xy			
Alal	Prpr	504	239	240	28	1011	30.98	.41
//	Vv	735	220	171	112	1238	39.29	.07
//	Ee	682	236	237	83	1238	50.02	v. large
Prpr	Vv	514	229	266	2	1011	9.09	.24
Vv	Ee	647	271	295	25	1238	28.06	.76
Prpr	Ee	602	141	151	117	1011	34.08	.51

cent owing to a great distance between them. The observed number in each of the two character combination afforded a good fit to the calculated on the basis the respective recombination percentages.

In order to make the result more accurate, F_3 progenies derived from F_2 plants of the same cross were raised to determine their F_2 genotypic constitutions. The observed number of different genotypes involved in this F_2 population is shown in Table 4. From the data in Table 4, it was possible to calculate the recombination values and combined informations between any two combination of the four character pairs. The recombination percentages of each character combination thus obtained from the F_2 and F_3 data were combined to secure a value which best satisfies both F_2 and F_3 data. In Table 5 are given the combined weighted values of recombination and their standard error between each two of the four character pairs studied. A chromosome map showing the order of the four genes is also given in Fig. 2.

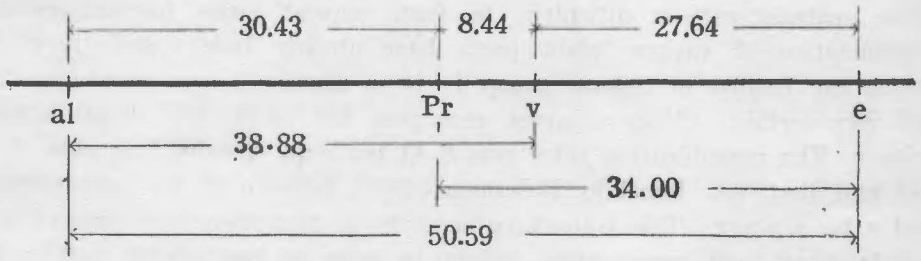

Fig. 2. Arrangemeent of the four geenes on the first chromosome in barley.

Bose et al. (1937) first demonstrated that *Ee* for normal vs. long awned outer glume and *Vv* for non-six-row vs. six-row were linked with a recombination value of 24. 7 per cent. This was verified further by Robertson et al. (1944), Swenson et al. and also Immer et al. (1943). The recombination values reported by them were 26.6 ± 0.6, 26.7 ± 1.7, and 28.0 ± 1.2 per cent respectively. It is obvious that the value obtained here, 27.64 ± 1.96, agrees well with those shown above, and that we have dealt with

TABLE 4. *Number of various F_2 genotypes as determined by F_3 progeny test.*

	VV	Vv	vv	EE	Ee	ee	PrPr	Prpr	prpr
AlAl	19	23	20	21	29	12	12	27	23
Alal	19	53	19	23	41	27	22	57	12
alal	8	16	18	13	17	12	23	16	3
PrPr	2	12	43	26	21	10			
Prpr	13	74	13	27	52	21			
prpr	31	6	1	4	19	15			
EE	3	22	32						
Ee	15	50	22						
ee	28	20	3						

TABLE 5. *The average weighted percentages of recombination and their standard error found from a combination of F_2 and F_3 data in a Lyallpur × Ligule-less Cross.*

Character combination	Percentage recombination	Character combination	Percentage recombination
Ligule and purple sheath (Alal-Prpr)	30.43±2.02	Ligule and kernel rows (Alal-Vv)	38.88±1.78
Purple sheath and kernel rows (Prpr-Vv)	8.44±1.35	Purple sheath and empty glumes (Prpr-Ee)	34.00±1.80
Kernel rows and empty glumes (Vv-Ee)	27.64±1.96	Ligule and empty glumes (Alal-Ee)	50.59±1.92

the same gene in question.

While the presence or absence and the shade of anthocyanin pigmentation in a certain plant part is considerably modified by external conditions, such a character is none the less heritable, and appropriate materials enable us genic analysis without dificulty. In fact, several genes for anthocyanin pigmentation of various plant parts have already been found, most of which are located in linkage group I. It is mentioned here although still not very certain, of an apparent new gene for purple leaf sheath linked with *v*. The recombination value was 8.44 per cent, a value very close to 9 per cent that was found by Robertson (1933) between *Pr* for purple stem and *v* for six-row. This coincidence suggests us that these two characters, purple sheath and purple stem, might be more or less related with each other, although speculative. Here, rather than giving another name for purple sheath gene, the same *Pr* for purple stem is used. We may mention here that Morinaga and Fukushima dealing with rice crosses, had found a gene for anthocyanin pigmentation of a certain plant parts being linked with a gene for deficiency of ligule and auricle.

2. *A gene for bracteate ear in linkage group* II.

The material of this study was a strain called "Bracteate" that may have been the same one used by Miyake and Imai (1922) in their experiment.

The distinguishing characteristic of this strain is the presence of a bract or a so-called third outer glume outside the two empty glumes of each central spikelet. Size of the lowest bract is always the largest, embracing in some cases about one half of the very compact and short head, and it becomes smaller and smaller toward the top of the head. Wada (1936) in his rather extensive study on the differentiation of wheat ear, recognized that a leaf primordia or a bract in a young head corresponds to a normal leaf, a spikelet to a tiller or an axillary bud, and empty glumes to a prophyll; and that this leaf primordia or bract of a young head generally degenerates at its earliest stage in ordinary variety. It can be reasonably supposed that this strain in question is possessed with a peculiar nature of continuing the growth of the leaf primordia, which otherwise is destined to be degenerated. Two typical bracts of this strain are shown in Fig. 3. Miyake and Imai (1922) have already demonstrated that the bracteate character of this or similar variant was inherited as a simple recessive to normal, but they did not establish its linkage relation.

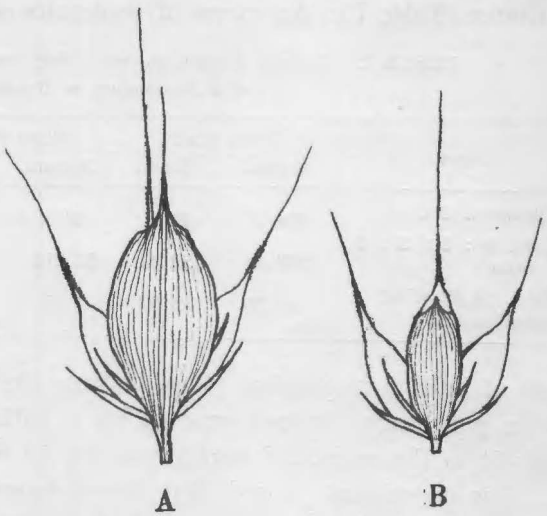

Fig. 3. A bract on the lowest spikelet triplets (A), and that of middle portion (B) in a head of the "Bracteate" variety.

Although the existence of such a mutant is very rare, Vavilov (1929) found a similar variant in Afghanistan, and designated it as var. *afghanicum* Vav. This material was later genetically studied by Ivanova (1937), who found that the bracteate character was inherited as a simple recessive to normal, and that the gene for the character was linked with black chaff color. The linkage value was determined to be 15.35～16.94 per cent.

Owing to a close resemblance of characteristics between the variants from Afghanistan and Japan, it may be possible to infer these two to have occurred by reccurent mutations. Hence, based upon this inference, a cross between Nigrinudum and "Bracteate" was made to see if there is a linkage between bracteate character and black chaff of linkage group II.

The heads of F_1 hybrid appeared quite normal, and in F_2 generation a monohybrid segregation was observed. Therefore, the gene responsible for the bracteate character was designated as *trd*, according to Robertson et al. (1941) who suggested it for this type of character.

Interrelation of *trd* with various marker genes are indicated in Table 6.

TABLE 6. *Independent inheritance of trd for bracteate character with several marker genes observed in a Nigrinudum × Bracteate cross.*

Linkage group	Symbol Xx	Symbol Yy	F_2 phenotypes observed XX	Xy	xY	xy	Total	x^2	P
I	Trdtrd	Vv	385	103	113	48	655	4.298	.24
III	//	Nn	383	109	129	34	655	3.617	.31
V	//	Ss	353	141	124	37	655	3.732	.30
VI	//	A_nA_n	493	—	161	—	655	0.062	v. large

It is obvious that *Trd trd* was inherited independently of *Vv* in linkage group I, *Nn* in group III, *Ss* in group V and A_nA_n in group VI. However, segregation of *Trd trd* and *Bb* for black chaff color in the F_2 generation of the same cross did not fit well to a 9 : 3 : 3 : 1 ratio for independent inheritance (Table 7). An excess of segregates of parental types indicates exis-

TABLE 7. *Linkage of black vs. white chaff and normal vs. bracteate in the F_2 of a Nigrinudum × Bracteate cross.*

Items	Black chaff Normal	Black chaff Bract.	White chaff Normal	White chaff Bract.	Total	x^2	P
Observed. No.	454	49	40	112	655		
Calc. 9 : 3 : 3 : 1 ratio	368.44	122.81	22.814	40.95	655	v. large	v. small
Calc. 14.83 % of recombination	446.28	44.97	4.97	118.78	655	1.4381	.70

tence of linkage in coupling phase between the two gene pairs. The recombination percentage obtained was 14.83 ± 1.03. The observed data afforded good fit to the calculated segregation for 14.83 per cent.

This experiment proved that the distance between the bracteate gene, *trd*, involved in this material and *B* in the second chromosome was in agreement with that obtained by Ivanova in a cross with a variant from Afghanistan. This fact suggests that these mutants may had occurred reccurrently by the same mutation at two remote places.

3. *Three genes for ear and awn characters in linkage group* III.

Covered vs. nakedness of grain, ear density and awn length are the characters of barley ears so striking and of such practical importance, that they have attracted for a long time special attention of barley taxonomists and breeders ; and there have accumulated numerous reports of works done on the inheritance of these characters and their linkage relations. Authors have gathered additional informations on these subjects for this report. But, for all these efforts, there still remains some unsolved problems.

As seen in the reviews of the subject presented by Smith and the present authors, there are a number of major or minor genes that are respon-

sible for the ear density and the awn length. In this study we confined ourselves to deal with the major gene or genes commonly involved in Japanese dense ear varieties. On the awn length, a major gene, *lk*, that reduces the awn length to about one half of the normal (*LkLk*) ones, and makes pleiotropically the awn texture more fine and flexible.

Ando (1918) dealing with a natural hybrid of Japanese barley, first demonstrated linkage between covered vs. naked grains (*Nn*) and lax vs. dense ear (*Ll*) with about 14 per cent of recombination. Soon later, So, Ogura and Imai (1919) suggested that three different gene pairs were responsible for the ear density, each being linked with *Nn* with 12.5, 25 and 33 per cent of recombination respectively. Two of the above were later confirmed by Miyake and Imai (1922). So et al. also reported the recombination between a gene for awn length and *Nn* being about 5 per cent. The interaction of the genes for awn length and ear length studied in Japanese barley crosses by Takezaki (1927) and Ubisch (1917, 1919) gave the recombination percentages of respectively about 25 and 20.

From the results of these authors, it is certain that the three character pairs under consideration are located in linkage group III, but their order of arrangement is not known, since there are considerable discrepancies seen among the authors as to the number of major genes involved for ear density and the linkage intensity with *Nn* or *Lklk*.

For our study fifteen varieties of barley were selected. The varieties characterizing naked kernel, short awn or dense ear were of Japanese origin, with the exception of Mammut. Their names arranged according to their ear characters are shown below. The number in parenthesis before each variety is used in this chapter for indicating the corresponding variety.

Covered	Lax, Long-awn	(1)	Natsudaikon-mugi, (2) Rokkaku Chevalier
		(3)	Indian barley
	Lax, Short-awn	(4)	Mammut
	Dense, Long-awn	(5)	Sekitori, (6) Zairai-Tambo
Naked	Lax, Long-awn	(7)	Oitahadaka, (8) Mitsukiko-1
		(9)	Kobinkatagi
	Lax, Short-awn	(10)	Kairyobozu
	Dense, Long-awn	(11)	Kochi-wase, (12) Yakko-52
	Dense, Short-awn	(13)	Aizu-hadaka-3, (14) Kobinkatagi-4
		(15)	Honen-6

Several simple and back crosses, each involving two or three character pairs in question were made between these varieties, and five of them were tested for their segregations in F_2 and F_3 in 1943 and 1944, and the other six including four backcrosses in 1948.

All of these crosses gave F_1 hybrids with covered, lax and long-awned characters as generally recognized by other workers, indicating these characters to be dominant over the respective allelic character. It was also confirmed

that covered vs. naked as well as long vs. short awn segregated in ratios of 3 : 1 in F_2 and 1 : 1 in backcrosses with doubly recessive types. No difficulty was encountered in distinguishing between the paired characters. The segregation of lax and dense forms in some crosses were determined by measuring the lengths of rachis internodes and ear lengths of all F_2 individuals. This accompanied F_3 progeny tests. These experiments proved that lax and dense ear forms segregate clearly in a 3 : 1 ratio, and that the distinction of both classes was nearly always possible by mere visual observation (Takahashi 1951). The actual numbers of phenotypes determined from these crosses by either of the methods proved a good fit to the calculated on the basis of monofactorial segregation.

Next, the results on the interaction of covered vs. naked and lax vs. dense ear character pairs from the above crosses are shown in Table 8. It is obvious that the two character pairs are not inherited independently, but in linkage with each other, and that the observed numbers in each of the crosses fitted well to the numbers expected for the respective recombination value obtained by following Immer's product method, in spite of considerable discrepancies in the recombination values not only among different crosses, but also between F_2 and the backcross, both of which were dealt with the same parental forms. A weighted mean value of recombination was estimated from these data based on the assumption that we have dealt with the same major gene for ear density involved in these crosses.

Table 9 shows interrelation between *Nn* and the gene *Lklk* for long vs. short awn from several crosses. The results reveal a fact that both genes are apparently linked in the coupling phase, and the linkage intensities of various crosses were nearly alike. A weighted average recombination value was as shown at the bottom of the column in the Table.

Undoubtedly from the above data *Ll* and *Lklk* must be in the same lin-

TABLE 8. *Segregation of covered vs. naked and lax vs. dense ear character pairs in F_2 of the various simple crosses and some backcrosses.*

Crosses	Covered		Naked		Total	Recomb. value (%)	Fit to Calc. Recomb. (P)
	Lax	Dense	Lax	Dense			
(13) × (1)	386	28	38	132	585	11.33	.14
F_1 (13×1) × (13)	67	9	2	73	151	7.28	.19
F_1 (1×8) × (8)	24	3	2	28	57	8.77	v. large
(14) × (2)	386	46	40	119	591	15.15	.42
F_1 (14×2) × (14)	78	5	6	95	184	5.97	.63
F_1 (1×15) × (15)	97	2	6	115	220	3.63	.51
(11) × (3)	131	12	9	37	189	11.67	v. large
(7) × (6)	143	73	89	1	306	10.30	.36
(8) × (5)	162	96	91	3	352	16.10	.36
(12) × (4)	315	30	38	87	470	12.88	.30
Weighted mean Recombination %						9.038±0.6088	

TABLE 9. *Interrelation of covered vs. naked and long vs. short-awn character pairs.*

Crosses	Long-awn		Short-awn		Total	Recomb. value (%)	Fit to Calc. Recomb. (P)
	Covered	Naked	Covered	Naked			
(13) × (1)	393	28	21	142	584	8.27	.15
F1 (13×1) × (13)	66	7	10	68	151	11.27	v. large
(14) × (2)	406	29	26	130	591	9.53	.77
F1 (14×2) × (14)	76	9	7	92	184	8.70	.62
F1 (15×1) × (15)	93	12	6	109	220	8.18	.36
(1) ×(10)	223	8	16	61	308	7.86	.37
Weighted mean Recombination %						8.75±0.6499	

kage group. As further shown in Table 10, the recombination values between *Ll* and *Lklk* were about 20 per cent with two exceptions where the distance between *Nn* and *Ll* may have been too short.

TABLE 10. *Interrelation of long vs. short awn and lax vs. dense ear character pairs.*

Crosses	Long-awn		Short-awn		Total	Recomb. value (%)	Fit to Calc. Recomb. (P)
	Lax	Dense	Lax	Dense			
(13) × (1)	369	52	55	108	584	19.45	.04
F1 (13×1) × (13)	57	16	12	66	151	18.55	.76
(14) × (2)	370	65	55	100	590	22.00	.43
F1 (14×2) × (14)	71	14	13	86	184	14.67	.69
F1 (15×1) × (15)	91	14	12	103	220	11.81	v. large
(12) × (4)	244	111	109	4	468	19.13	v. large
(9) × (14)	249	43	32	54	378	22.50	.62
Weighted mean recombination %						18.40±0·9066	

From these various results obtained, it may be plausible to assume that the same gene pair for covered vs. naked character was involved in those different crosses, and perhaps similarly for the awn length. However, in the case of ear density we are bewildered as to how to explain the result showing large discrepancies in the recombination values. It is certain that two different genes located in more or less remote loci on a chromosome should generally result in different linkage value with respect to another gene, but the reverse is not necessarily true. Takezaki (1925) confirmed in his extensive work that a large number of crosses among Japanese varieties belonging to the same ear type (varieties similar in ear length, density and awn length) did not segregate out any individual that had different ear type, indicating that in these different crosses were involved respective only one gene for ear density which also accounted for awn length, but he obtained considerably different recombination values between the gene for ear length and that for awn length : the recombination values recalculated by Immer's method from the data shown in his paper proved to vary from 14.7% to 36.33 %, with a weighted mean value of 22.65 %. It was almost similar

in the case of Ubisch (1919), who dealt with a single cross repeatedly in different years and yielded 11.5 % to 27 % with a weighted mean value of 17.67 %.

So, Ogura and Imai (1919), on the other hand, have concluded that the ear density is determined by three different genes that are linked with *Nn* with 12.5, 25, and 33.3 per cent of recombination respectively. In their series of experiments, it is ably pointed out that a lax ear parent (Shiromugi) in a group of crosses in which L_2 gene pair was identified, was again used as a dense ear parent in other group of crosses wherein l_3 gene was further identified, which apparently indicates L_2 being different from L_3 and L_7. These two genes, L_3 and L_7, are still obscure whether or not they were originally of different loci, and we have no means of pursuing further on this relationship.

It must be admitted that the mode of inheritance of the ear density is so complicated that it is far from being thorough in understanding of it, but the data hitherto accumulated may indicate that Japanese native varieties with very dense ear involve a major recessive gene in common. And, if so, we may conclude from this experiment that three gene pairs, that is, *Lklk* for long vs. short awn, *Nn* for covered vs. naked kernel and *Ll* for lax and dense ear are located on the third chromosome of barley in the order of *lk - n - l*. A chromosome map showing this relation is given in Fig. 4.

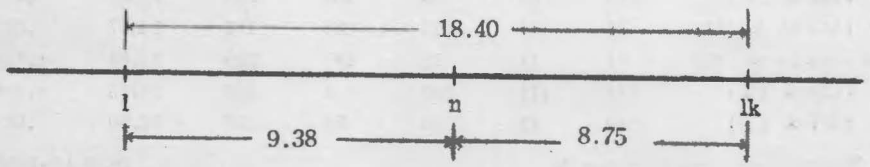

Fig. 4. Arrangement of the three genes for ear and awn characters on the third chromosome in barley.

4. *The trifurcate awns.*

Barley whose tip of the outer paleas grow into three pronged appendages or their like are as a whole called a hooded barley. But it may be further subdivided into three types, i. e. normal, elevated and subjacent hooded ; although alternative classifications may be given according to some such heritable characters, as shape, size, and presence or absence of a fine awn on the hood. The most common and more or less familiarized type is the normal or sessile hood (Fig. 5 C and D). Its appendages of paleas are apparently of trifurcate structure, consisting of a deformed floret at its center with two triangular leaf-like projections called lemma wings. It is noted that the supernumerary floret in the hood is always attached upside down to the top of the outer palea of the first normal floret, as if two florets are connected mutually top to top. The supernumerary florets often contain stamens filled with fertile pollen grains and occasionally bear kernels within them.

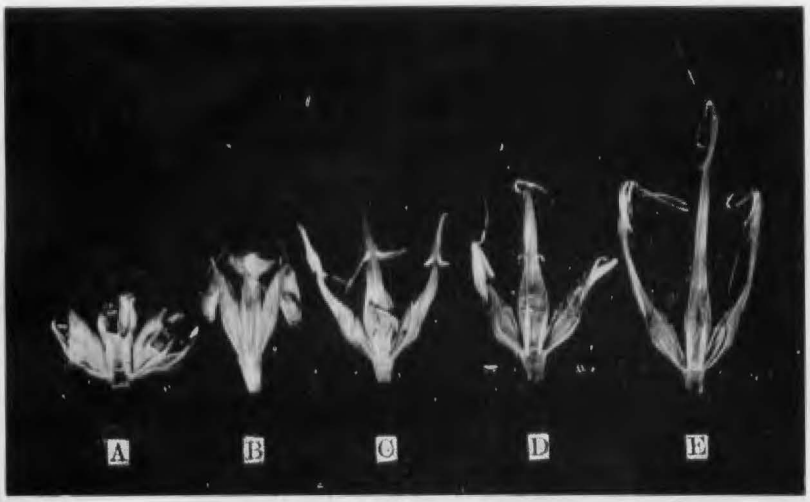

Fig. 5. Spikelet triplets of various hooded barley: (A) subjacent hood of "Sekitori-hen", (B) subjacent hood of Tayeh-13, (C) and (D) normal hood and (E) elevated hood of Chengchou-5.

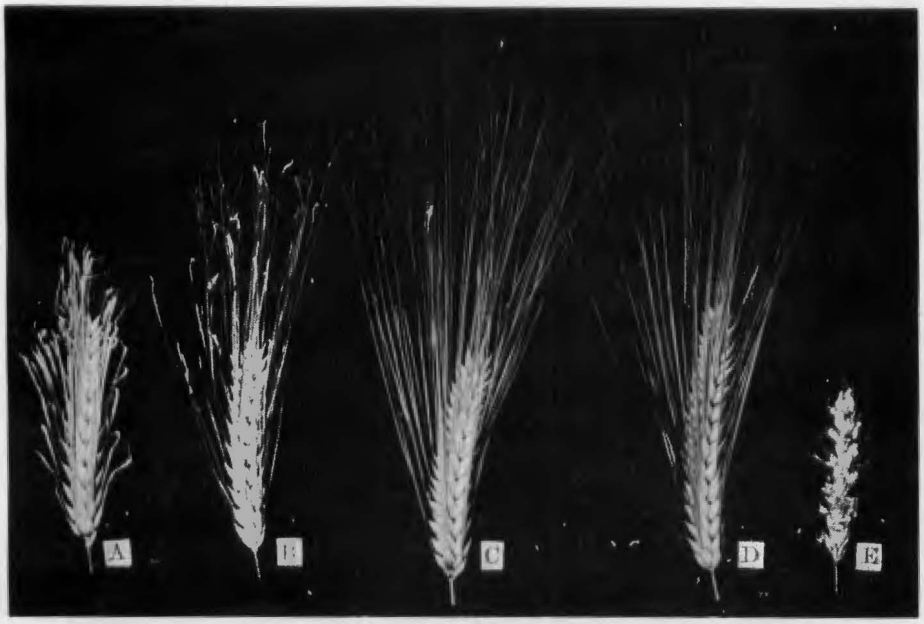

Fig. 6. Various types of hooding appeared in a cross between the elevated and the subjacent hooded barley (Chengchou-5 × Tayeh-13), showing (A) and (E) parental types, (B) F_1 (elevated × subjacent hooded) type, (C) F_1 (elevated × long-awned) type, and (D) long-awned type.

Fig. 7. Different degree of hooding apepared in F_1 of the crosses of Chenchou - 5 (an elevated hooded variety) with long-awned varieties, (A) Coast II, (B) Nigrinudum and (C) Koyo covered barley.

Fig. 8. Two kinds of subjacent hooded plants segregated from a cross between the normal hooded and the subjacent hooded varieties.

In some cases, an additional floret, consisting of tiny outer and inner paleas, is found on the top of the second floret, in which case, the direction of the third floret again reverses with respect to the secondary one, attaching base to base with each other.

Another type of hood is called the elevated or awned hood, or curly simply from its appearance. The appendages of this type are elevated on awns of 1 - 2 cm. or longer, and less differntiated than those of the normal type. Lemma wings are much reduced in size, and the supernumerary floret, too, involves a mere spur of floral organs within it (Fig. 5 E).

A third one was designated temporarily by the present authors as the "subjacent" hood. As shown in Fig. 5 A and B, the central cup-like cavity or its modification is generally situated below the top of the outer palea of the first floret, with no lemma wing existing. Owing to the shortening of the outer palea, the kernel is more or less exposed. It should be pointed out that no spur of flower organ can be detected within the cavity of the subjacent hood.

Mode of inheritance of the normal hood and its linkage are almost clear at present. It may be concluded from the facts established by a number of workers that normal hood is singly dominant, though in many cases more or less intermediate, over long awn, and the gene pair, *Kk* for normal hood vs. long-awn is linked with *Blbl* and I^h *l i* for intermedium, both located in linkage group IV. Moreover, *K* seems to be partly or completely hypostatic to some genes of abreviating awn length, such as *lk* and *lr* (Smith 1951, Takahashi and Yamamoto 1949).

The heredity of hood other than normal type, on the other hand, has scarcely been understood. Michels (1936) reported a segregation of approximately 3 hooded : 1 awned in a cross between normal hood and elevated hooded varieties, but this was not confirmed by G. A. Wiebe who repeated the same experiment. According to L. Smith (1951), Fung from her own work and that of Biffen, Lewis, and Ubisch, concluded that these elevated hoods were not readily analyzable genetically. It seems that possibly they are dependent on at least two duplicate factors that are recessive to the factor for normal hoods and also recessive to the factor for awn. Finally, it is only possible to point out that there is no knowledge about the "subjacent" hooded character, except that Ubisch had ever found "Sekitori-hen" like plants among the F_2 segregates of a cross between Nepal barley and Sekitori, a Japanese uzu or semi-brachytic barley variety.

A study was planned to elucidate the mode of inheritance and linkage relation of elevated hood and also of "subjacent" hood in relation to the normal hooded and the long-awned characters. As the materials, the following varieties or strains were used :

Normal hooded : Konosu hooded, Chengchou – 2, Colsess I.

Elevated hooded : Chengchou – 5.

Subjacent hooded : Tayeh－13 (Normal type), Sekitori-hen (Uzu type).
Long-awned : Natsudaikon-mugi, Brachytic, Nudideficiens, Nigrinudum, Coast II, Koyo covered barley.

The elevated hooded barley, such as Chengchou－5 and other similar specimens were collected along with the normal hooded barley by the senior author, Takahashi, in the subverbs of Chengchou city and Chiao-chuang, which is about 170 km. south of Chengchou, Honan, Central China. It was observed at that time that this form did not occur alone in any field, but in a mixture of very small proportion with long or short awned barley. According to Lewis (1933), a plant with elevated hood was first discovered by Love at Keiteh, Honan, and a later observation showed that this type of barley was distributed rather widely throughout the plains region of Honan Province, occurring as an impurity of about 5 per cent in fields of normally awned barley. As a consequence, our elevated hooded barley can be suspected to be quite similar to that of Lewis as to their origin.

One of the "subjacent" hooded forms happened to be found by Takahashi growing singly in a barley field consisting of long-awned form near Tayeh, Hupei Province, Central China, where any other kind of hooded barley was not found. The other subjacent hooded, called Sekitori-hen, obtained from Konosu, is thought as a spontaneous mutant perhaps isolated from Sekitori, a semi-brachytic covered barley grown widely in Kwanto District in Japan.

All possible combinations of crosses were made between representative varieties of different hooded or awned forms listed above, and their F_2 segregations were studied.

a) Interrelation between the normal hood, the elevated hood and the long-awned characters.

The F_1 hybrids of the normal hooded with the elevated hooded and the long-awned were all normal hooded, indicating almost complete dominancy of normal hood over the other two. In their F_2 generations of these crosses, as shown in Table 11, monohybrid segregations was always observed. Separation of normal hooded from elevated hooded or long-awned segregates was rather easy, inasmuch as there appeared no intermediate form in both cases.

Situation was more or less different in an elevated hood × long-awned variety cross : F_1 hybrid of the cross was almost like to the long-awned one at its first sight, but differed only in a characteristic detectable by careful observation. The distinguishing characteristic was that there existed within one ear several awns with a tiny projection near the top mixed among many normal awns. This condition was observable without exception in every ears and plants. In other words, dominancy of the hooded condition was very slight in this case. It should, however, be noted that the degree of domi-

nancy of hooded condition varied with crosses. As seen in Fig. 7, the appearance of awns on the hybrid plants was markedly different, even though the same elevated hooded variety (Chengchou - 5) was mated with long awned varieties that are seemingly equal as to their awn character.

In the F_2 generation of this cross, there appeared various types of hood, ranging from parental type to F_1 type, besides the true long-awned form. No sessile hooded plant was found. Since discrimination of true elevated hooded plants from intermediate class was difficult, the F_2 population was classified into hooded and awned, the result of which is shown in Table 11. It is evident from the result in this table, that the elevated hood vs. long-awn is governed by a single pair of gene, with imperfect dominancy of the hooded condition.

TABLE 11. *Segregation in the F_2 generations in three possible hybrid combinations among the normal hooded (1. Konosu hooded and 2. Chengchou-2), the elevated hooded (3. Chengchou-5) and the long-awned (4. Natsudaikonmugi) varieties.*

Cross No.	Character combination (X type) × (Y type)			F_2 phenotypes X type	F_2 phenotypes Y type	Total	χ^2	P
25	Norm. hood (1)	×	Long awn (4)	248	89	337	.357	.58
29	// (2)	×	// (4)	294	110	404	1.069	.32
22	Elev. hood (3)	×	// (4)	211	75	286	.228	.68
23	Norm. hood (4)	×	Elev. hood (3)	301	92	393	.530	.48

From the results stated above, it may be safe to conclude that the normal hood, the elevated hood and the long-awn are determined by an allelic series of genes. Therefore, the gene for elevated hooded character of this material was designated as K^e.

As stated before, linkage relation between K for normal hood and Bl for blue aleuron character was established by Buckley (1933), Immer et al. (1934), Robertson et al. (1932) and Myler and Stanford (1942) ; their recombination values obtained were 40. 6, 44, 22 and 24. 72 per cent respectively. Therefore, K^e as well as K involved in these crosses are expected to be linked with Bl with the same intensities of linkage. Fortunately, studies on interrelation of K and Bl, K^e and Bl as well, were made possible by mating two hooded parents, Konosu-hooded and Chengchou - 5 with white aleuron and Natsudaikon-mugi, a long-awned parent with blue aleuron. The results are presented in Table 12. It is obvious from this that both K and K^e are linked with Bl, and moreover, their recombination values of K-Bl and K^e - Bl were almost equal and conformed to those revealed by Robertson and Myler. The fact thus obtained may be an evidence, though indirect and mere supplementary, to support the multiple allelic hypothesis of the normal and elevated hooded characters.

Since it is admitted as an established fact that the elevated hooded plants arise sometimes from the crosses between the normal hooded and long-

TABLE 12. *Linkage of for normal hood and K^c for elevate hood with Bl for blue aleuron character.*

Long awn crossed with (Cross No.)	Items	Hooded		Awned		Total	x^2	P
		Blue	white	Blue	white			
Normal hooded (No. 25)	Observed. No.	171	75	85	4	335		
	Calc. 9 : 3 : 3 : 1	188.45	62.81	62.81	20.94	335	25.514	v. small
	Calc. 21.8 % of recombination	171.48	79.77	79.77	3.97	335	.632	v. large
Elevated hooded (No. 22)	Observed. No.	134	76	71	5	286		
	Calc. 9 : 3 : 3 : 1	160.92	53.64	53.64	17.88	286	28.721	v. small
	Calc. 23.5 % of recombination	146.87	67.63	67.63	3.87	286	2.662	.56

awned varieties (Biffen, Ubisch, Buckley and others), it seemed rather natural that Lewis (1933) supposed that the elevated hooded barley obtained from Honan, China, too, have originated by such a natural cross. Judging from the genetical behaviours, however, there may exist two forms of elevated hooded barley, though phenotypically similar, differing in their genetical causes. And, so far as those from Honan Province, China, are concerned, it seems to be more reasonable to suspect that they might have arisen by a spontaneous mutation perhaps directly from the varieties, such as *pallidum* Sér. or *horsfordianum* Wittm. distributed widely in these district.

b) Inheritance of the subjacent hooded character, and its relation to two other hooded charactecs.

A subjacent hooded barley from Tayeh, Hupei Province, China was used chiefly for this experiment. This variety is characterized by slender and short stems provided with rather narrow and short leaves, small number of spikelets of low fertility, and a high liability to outcrossing with others due to its floral structure.

Genetical behaviour of this subjacent hood was proved to be different from those stated above. F_1 hybrids of Tayeh - 13 and also Sekitori-hen with several long-awned varieties were always long-awned, and did not show any sign of hooded character. To the normal hood it also behaved as completely recessive. However, a cross with the elevated hoods gave F_1 plants that rather resembled those between the elevated and the long-awned varieties, where projections appeared on almost all of the awns (Fig. 6 B).

The F_2 segregation of the crosses between subjacent hooded and long-awned varieties revealed, as seen in Table 13, that the subjacent hooded condition was inherited as a simple Mendelian recessive to the long-awn, although observed number of the recessive type was to an extent smaller than would be expected in general. A gene symbol, *sk*, was given to the gene for the subjacent hooded character.

TABLE 13. *F_2 segregation of long-awn and subjacent hood characters in the crosses between Tayeh-13, a subjacent hooded and three long-awned varieties.*

Tayeh-13 crossed with	Long awn	Subjac. hood	Total	x^2	P
Natsudaikon-mugi	283	96	379	0.022	v. large
Brachytic	327	84	411	4.562	.03
Nudideficiens	391	91	482	9.628	.002

Interrelation of subjacent hood with normal hood and elevated hood was studied repeatedly in 1949 and 1951. The results are given in Table 14. In the F_2 generation of these crosses, there appeared long-awned type as well as two parental types, their segregation ratio being 9 normal hood : 3 awned : 4 subjacent hood, wherein, however, somewhat fewer number of the subjacent hooded plants than expected were observed, which would perhaps be due to certation or competition between pollen tubes of different genotypes. Segregation in the F_2 of the elevated hood × subjacent hood cross was also quite similar, when the plants having different degree of hooding are classified together as the hooded (Fig. 6). These results indicate clearly that *sk* is inherited independenly of *K* - series.

It was noticed at the second test, however, that two different types were involved in the segregates that had formerly been classified as the subjacent hooded on the whole. As shown in Fig. 8, one of them resembled Tayeh - 13 with large cup-like cavities and strong awns on it (here, this is called simply "awned"), and the other a type provided with small appendages in the outer paleas and resembling Sekitori-hen (awnless). The observed number of the four phenotypes thus classified in the two crosses are shown in Table 14, which reveals that they have a good fit to the calculated for independent inheritance.

TABLE. 14. *Interaction of the subjacent hood with the normal hood and elevated hood characters.*

Tayeh-13 crossed with	Norm. or elev. hood	Long-awn	Subjacent hood		Total	x^2	P
			awnless	awned			
Chengchou-5 (elev. hooded)	484	169	186		839	3.866	.15
Konosu hooded ('49)	186	49	62		297	4.972	.08
〃 ('50)	227	87	61	25	400	4.551	.21
Colsess I	311	119	94	44	568	5.196	.16

Compared with a calculated 9 : 3 : 4 or 9 : 3 : 3 : 1 ratios.

It is supposed from the above results that the genetic constitutions of both parents are *KKLkLkSkSk* for normal hooded and *kkLkLksksk* for subjacent hooded, and consequently, the four phenotypes to appear in the F_2 generation will be as follows (where *Lk* is responsible for long awn) :

Normal hood : *KK LkLk SkSk*, *Kk LkLk Sksk*, etc.
Long awn : *kk LkLk SkSk*, *kk LkLk Sksk*, etc.
Awned subjacent hood : *KK LkLk sksk* and *Kk LkLk sksk*
Awnless subjaecnt hood : *kk LkLk sksk*

Prior to conclude as above, however, it is desirable to corroborate that *sksk* is truly epistatic to *KK*, in a sense that *sk* in homozygous condition exerts its effect in forming a subjacent hood or lowering the position of hood even in the presence of *KK* and *LkLk* genes. There are two ways for the test : one is to investigate F_3 progenies of two different subjacent hooded segregates in F_2, and the other, which seems more effective, to test the behaviours of the hybrids between the subjacent hooded plants in F_2 and pure long awned variety (*kk LkLk SkSk*).

Among the F2 segregates in a Colsess I × Tayeh - 13 cross, seventeen plants of awned subjacent hood and twelve or eleven plants of awnless subjacent hood were selected and tested in their F_3 families or hybrids with Indian barley, a long awned form. The result was as follows :

Subjacent hood (putative genotypes)	Phenotypes observed in F_3	Phenotypes observed in Crosses with long awn (kk LkLk SkSk)	No. of Strains F_3	No. of Strains Crosses
Awnless				
(a) KK LkLk sksk	awnless only	normal hood only	5	4
(b) Kk LkLk sksk	awned + awn-less	normal hood + long awn	6	8
Awned				
kk LkLk sksk	awned only	long awn only	17	17

The result shown above proved to be nearly satisfactory. For, phenotypes that appeared in their next generation were just as expected, and also the ratio of genotypes (a) and (b) in awnless class was about 1 : 2, although a plant that was in reality of genotype (b) did not segregate awned subjacent hood in F_3, perhaps owing to too small a number of plants being tested.

c) Relation between two subjacent hoooded varieties originated from China and Japan.

Both varieties of subjacent hood, Tayeh - 13 from China and Sekitori-hen from Japan, agree in the features that the hood-like appendages are generally situated below the top of the outer paleas, and that no spur of floral organ exists within the hood-like appendages. But, both varieties differ from each other in some such points as presence or absence of awn, size and form of the appendages, etc. In order to know the genetical bases of these differences, a cross was made between them. The F_1 hybrid thus obtained was found to be an exact replica of Tayeh-13 parent, and in the F_2 appeared only the parental types with some exceptional long-awned plants (Table 15). As pointed out before, the subjacent hooded barley is liable to outcross

TABLE 15. *Segregation of different types of subjacent hood in F_2 generation of a Tayeh—13 × Sekitori-hen cross.*

	Tayeh-13 type (Normal)	Sekitori-hen type (uzu type)	long* awn	Total	χ^2	P
F_2 selfed	54	26	1	81	2.40	.12
F_2 open	238	72	8	318	0.52	.47

* These individuals were excluded for the χ^2 test.

owing to the structure of paleas, so that the exceptional plants are thought to have been brought about by outcrossing with other pollens, even in the artificially selfed plot due to missing the time of bagging. If so, the F_2 segregation is deemed as a simple Mendelian with dominance of the Tayeh type. It is further noted here that while the Tayeh type segregates were all recognized normal type, Sekitori-hen type segregates were semi-brachytic or uzu type only. Therefore, it may be plausible to conceive that both parental varieties involve one and the same gene, *sk*, for subjacent hood, but the hood shape etc. were modified further by the action of the uzu gene, as it is generally recognized that this uzu gene exerts its effect in shortening almost all parts of a plant, and in fact this often lower the site of normal hood just as it was found by Ubisch in a cross between normal hooded barley and awned uzu barley. So, we may conclude that Tayeh-13 and Sekitori-hen were both arisen by reccurent recessive mutations of *Sk* locus independently in different localities.

In this connection, we are also interested in a hooded mutant discovered by Harlan (1931). The characters of this mutant was described by him as follows : "This plant was nearly leaf-less, the leaf blades on the upper nodes being reduced to mere spurs. Despite the special care, the plant did not thrive well, and one culm only could eventually head out. The ear on that culm was found to be provided with hoods, contrary to the expectation from the parental forms with long awns. It was sterile, so it could not be tested further," etc.

A careful comparison of the head of this mutant shown in his paper with those of the subjacent hooded barley from Tayeh reveals that these two resemble one another in details. It was further recognized that Tayeh - 13, which originally possesses short and narrow leaves, have segregated several leaf-less plants in F_2 of a cross with Colsess I, although the leaves of the "leaf-less" plants were somewhat longer than those of Harlan's mutant. There are some reasons to suppose, therefore, that these two variations might have occurred from a very similar, if not identical, mutation. So, Harlan's belief that occurrence of the mutant is so significant as to throw light on the origin of hooded barley seems to be overestimated.

d) Interrelation of *sk* gene with several marker genes.

For the determination of the linkage group of the *sk* gene, a few cros-

ses were made and their F_2 segregations were studied, but it was not successful. As shown in Table 16, the gene *sk* was inherited independently of *Vv* (I), *Nn* (III), *Ss* (V), A_cA_c (VI), and *Brbr* (VII). Independence with *K*-series in group IV was shown before. The gene *sk* might therefore be located in linkage group II, although no conclusive evidence can be presented.

TABLE 16. *Segregation of character pairs showing independent inheritance in a few crosses with Tayeh—13, a subjacent hooded barley.*

Tayeh-13 crossed with	Linkage group	Genotypes tested		F_2 phenotypes				Total	χ^2	P
		Xx	Yy	XY	Xy	xY	xy			
Nndideficiens	I	Sksk	Vv	295	96	61	30	482	12.016	.007
//	III	//	Nn	299	92	71	19	481	11.137	.018
Brachytic	//	//	Nn	254	73	62	22	411	5.977	.113
//	VII	//	Brbr	255	72	63	21	411	6.247	.102
Colsess I	V	//	Ss	334	96	105	33	568	1.891	.598
//	VI	//	A_cA_c	430	—	138	—	568	0.150	.703

5. *Fragile stem character in linkage group V.*

Mode of inheritance and linkage of fragile stem character in barley have never been reported in Japan nor in foreign countries. In this study, a six-rowed covered barley with compact ear, called Kamairazu was used. This strain is characterized by the extraordinary fragility of the stems and leaves, being easily broken between fingers. In spite of the fragility, the stems of this variant become more flexible than those of the normal at a stage previous to its maturity. Such mutants as this have been found rather frequently in rice and barley in Japan, whereas it has never been recorded in foreign countries. For example, Uchida (1947) reported the occurence of spontaneous mutation in a rice variety "Sotoku" and in the offsprings of a barley hybrid between Miho - 65 and Shirochinko. A similar barley mutant was also discovered by the present authors, although this was proved to have arisen by a mutation at a different locus (unpublished).

Kamairazu was crossed with four varieties, each possessing some of the marker genes of the seven different chromosomes.

Since F_1 hybrids from these crosses always produced almost normal tough stem, and in F_2 segregated tough stem and fragile stem plants ina 3 : 1 ratio. The gene for fragile stem was designated as *fs*. Table 17 gives various character pairs inherited independently of *Fsfs*. The segregation in F_2 indicated a good agreement between the observed and the calculated ratios for independent inheritance. It seems probable, therefore, that *Fsfs* for tough vs. fragile stem is independent of the gene pairs as follows : *Vv* in group I, *Bb* in group II, *Nn*, and *Lklk* in group III, *Blbl* in group IV, *Uzuz* in group VI and also *Brbr* in group VII.

TABLE 17. *F_2 segregations of several character pairs showing independent inheritance in several crosses with Kamairazu, a fragile stem variety.*

Linkage group	Kamairazu crossed with	Cross No.	Characters tested Xx	Yy	F_2 phenotypes XY	Xy	xY	xy	Total	x^2	P
I	Iraki Black	31	Vv	Fsfs	250	104	99	22	475	6.713	.08
II	〃	〃	Bb	〃	259	100	90	26	475	2.063	.56
III	〃	〃	Ll	〃	243	103	105	23	475	9.098	.03
〃	Kairyo-	32	〃	〃	188	80	60	31	359	7.429	.06
〃	Bozu	〃	Nn	〃	209	60	58	25	352	2.535	.48
〃	〃	〃	Lklk	〃	207	67	61	24	359	0.609	v. large
IV	〃	〃	Blbl	〃	203	54	63	28	351	3.131	.37
VI	〃	〃	Uzuz	〃	207	68	61	23	359	0.737	v. large
〃	Suifu	33	〃	〃	172	45	51	12	280	4.178	.25
VII	Brachytic	26	Brbr	〃	216	85	61	25	387	4.015	.26

The gene for fragile stem may be inferred to be in linkage group V. Interrelation between *Fsfs* and *Rr* for rough vs smooth awn and *Ss* for long vs. short haired rachilla was studied by using three crosses. The results shown in Table 18, reveals that the gene pair *Fsfs* is apparently linked

TABLE 18. *Linkage relation of Fsfs with Ss and Rr*

Cross No.	Symbol Xx	Yy	Items	F_2 phenotypes XY	Xy	xY	xy	Total	x^2	P
33	Ss	Fsfs	Obsvd. No.	159	54	64	2	279		
			9 : 3 : 3 : 1 ratio	157.0	52.3	52.3	17.4	279	16.328	small
			20.35% recomb.	142.3	66.9	66.9	2.9	279	4.852	0.19
31	Ss	Fsfs	Obsvd. No.	237	112	117	9	475		
			9 : 3 : 3 : 1 ratio	267.2	89.1	89.1	29.7	475.1	32.50	small
			26.12% recomb.	245.7	110.6	110.6	8.1	475	0.796	large
31	Rr	Ss	Obsvd. No.	309	45	58	63	475		
			9 : 3 : 3 : 1 ratio	267.2	89.1	89.1	29.7	475.1	95.524	small
			25.1% recomb.	304.2	52.1	52.1	66.6	475	1.906	0.59
31	Rr	Fsfs	Obsvd. No.	258	91	109	17	475		
			9 : 3 : 3 : 1 ratio	267.2	89.1	89.1	29.7	475.1	10.239	0.02
			38.61% recomb.	255.2	101.1	101.1	17.7	475.1	1.683	0.65
36*	Rr	Ss	Obsvd. No.	282	51	47	58	438		
			9 : 3 : 3 : 1 ratio	246.2	82.2	82.2	27.4	438	66.295	small
			25.99% recomb.	279.0	49.5	49.5	60.0	438	0.271	large

* Iraki Black × Ligule-less

with *Ss* and *Rr*. As a matter of course, *Rr* and *Ss* were also linked with each other. The recombination values between these three gene pairs were as follows :

	Cross No.	Recombination values (%)
fs — s	33 (repulsion)	20.35 ± 3.84
	31 (〃)	26.12 ± 2.85
fs — r	31 (repulsion)	38.61 ± 2.60
r — s	31 (coupling)	25.10 ± 1.59
	36 (〃)	25.99 ± 1.69

The fit of the observed data to the calculated segregation based on the respective recombination percentages proved to be very good. Linkage of *Rr* and *Ss* has been confirmed by several workers, whose recombination percentages being 28.1, 30, 30.8, 34.6, ca. 35 and 42.7 respectively. These values are all somewhat larger than that obtained in this experiment, but the discrepancies are not so large in some cases. Therefore, it is possible to conclude safely that *Fsfs* for tough vs. fragile stem character is located in linkage group V, and the three genes occur on the fifth chromosome in the order of *Fsfs*, *Ss*, and *Rr* as is shown in Fig. 9.

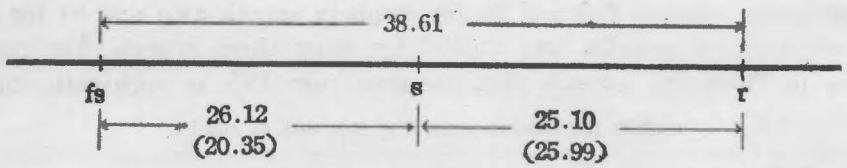

Fig. 9. Arrangement of the three genes on the fifth chromosome.

Summary

This paper presents results of studies on the inheritance and linkage of several characters of practical or genetical interest. They are summarized as follows :

1. Ligule- and auricle-less and purple leaf-sheath, both involved in a mutant variety, "Ligule-less" behaved as simple Mendelian characters. The gene pair *Alal* for normal vs. ligule-less and *Prpr* for purple vs. green sheath were found to be linked with *Ee* for normal vs. long-awned outer glume and also with *Vv* for non-six-row vs. six-row. These four genes are arranged in the order of $al - pr - v - e$ on the first chromosome (Fig. 2). Independent inheritance of *Alal* with genes known to be in six other linkage groups was also confirmed.
2. A mutant variety of Japanese origin, called "Bracteate" is characterized by the presence of bracts or third outer glumes on each of the central spikelets of its head. The gene, *Trd trd*, for this character pair was found to be linked with *Bb* for black vs. normal chaff colour with about 15 per cent of recombination, but was inherited independently of *Vv* (I), *Nn* (III), *Ss* (V), and also $A_n a_n$ (VI). It was inferred that this character was result of another mutation in the same locus that produced var. *afghanicum* Vav.

3. It seemed probable from our experiments and many other instances that, so far as the Japanese barleys are concerned, the lax vs. dense ear as well as the long vs. short awn character pairs are both chiefly governed by a single respective major gene, *Ll* and *Lklk*, located in linkage group III. Studies on interrelation of the two genes with *Nn* for covered vs. naked kernel indicated that *Lklk*, *Nn* and *Ll* were arranged in that order on the third chromosome in barley (Fig. 4).
4. According to the site of hoods on the outer paleas, the hooded barley were classified into normal or sessile hood, elevated hood and subjacent hood (Fig. 5). All possible combinations of crosses were made between representative varieties of these different hooded or awned forms, and their interrelation were studied.

   It was shown that the normal hood, the elevated hood and the long-awn were governed by a multiple allelic series *K*, K^e and *k*. The gene *K* for normal hood was almost completely dominant over K^e for elevated hood and *k* for long-awn, while K^e was only slightly dominant over *k*. The multiple allelic hypothesis seemed to be supported by the fact that *K* and K^e are both linked with *Bl* for blue aleuron in linkage group IV with almost equal intensity.
5. The subjacent hood was shown to be due to a gene, *sk*, recessive to the long-awned condition, which was independent of *K*-series. The gene, *sk*, in homozygous condition behaved epistatic to *K* and K^e, lowering the site of hood even in the presence of *K* or K^e gene. Linkage of the *Sksk* gene was not yet established, although this was proved to be independent of *Vv* (I), *Nn* (III), *Ss* (V), $A_c a_c$ (VI), and *Brbr* (VII).
6. It was shown that two different subjacent hooded barley from China and Japan, respectively, Tayeh - 13 and Sekitori-hen originated from the same mutation at the *sk* locus, although the latter is somewhat different in the apearance of hood from the former due to the uz gene. It was also pointed out that a hooded mutant discovered by Harlan resembled the subjacent hooded strain from China in the major characteristics.
7. A fragile stem character of a Japanese mutant barley, Kamairazu, was inherited as simple recessive to normal. The gene pair, *Fsfs* was proved to be linked with *Ss* for long vs. short-haired rachilla aud *Rr* for rough vs. smooth awn. The order of the arrangement of these three genes on the fifth chromosome is $fs - s - r$. *Fsfs* was confirmed to be independent of several genes located in the other six linkage groups.

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