INTERRELATIONS OF GENETIC FACTORS IN BARLEY

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INTRODUCTION

The assignment of genetic factors to definite loci in the hereditary mechanism has been a great step in the progress of biology. While this result has been most brilliantly and extensively achieved in Drosophila, confirmation has been found in many other animals and in plants. Genetical investigations in maize, for instance, have resulted in the identification of over ninety genes and the arrangement of twenty-five of these into six linkage groups (HUTCHISON 1922).

Barley is about as favorable as maize for such studies, owing to the existence of a large number of heritable variations; and it has an advantage in that for purposes of experimental breeding it can be raised in the field twice as fast as maize. The smaller number of chromosomes in barley $(n=7)$ as compared with that in maize $(n=10)$ also gives barley an advantage, as the number of chromosomes corresponds with the number of linkage groups, according to the chromosome theory of heredity, and the establishment of linkage groups is relatively easy in species with a small number of such groups. The only serious drawback in genetic work with

barley lies in the excessive amount of labor required in artificial pollination which renders back-crossing impracticable and thus necessitates the study of a large number of individuals to attain a fair degree of accuracy, especially in cases of strong repulsion (HALDANE 1919).

Studies on the inheritance of barley undertaken by previous investigators have elucidated the behavior of numerous simple Mendelian characters, and some linkage relations have been reported by UBISCH (1919), MIYAKE and IMAI (1922) and NILSSON-EHLE (1922). It is the purpose of this study to reveal more interrelations between the genetic factors of barley and prepare the way for further work of the same nature.

<div align="center">MATERIAL AND METHODS</div>

The strains of barley used as parents in the crosses have come from different sources, and nearly all of them were transferred to the writer by Professor R. E. CLAUSEN. Their homozygosity with respect to the characters under investigation is known, as all of them have been grown and studied at the Agricultural Experiment Station at Berkeley for two or more seasons.

The hybrid progenies as well as the parental strains were grown in the field. The work in artificial pollination was carried out in the usual manner, which need not be described here. In nearly all cases the spikes from each individual F_1 and F_2 plant were harvested and stored in an envelope bearing the pedigree number, for laboratory study, while the examination of all the F_3 plants was made in the field.

The first crosses, from which most of the data herein presented were derived, were made in the fall of 1920, and most of these were carried to the F_3 generation. The crosses made in the spring of 1922 have been carried only to the F_2 generation. On account of the limited time several characters had to be dropped out of consideration during the course of the investigation.

In testing the goodness of fit PEARSON'S χ^2 method (PEARSON 1900) is used, and the value of probability, P, is found from ELDERTON'S table. While this mathematical test is undoubtedly a great help in making decisions, weak linkage relations cannot be detected with certainty with a relatively small F_2 population. For instance, with an F_2 population of about a hundred individuals the existence of linkage with a crossover value of forty percent or more will not *per se* make the size of χ^2 significantly too great for the typical Mendelian dihybrid. In such a case the linkage value will be calculated and the size of χ^2 for the assumed linkage relation noted. The probability of linkage is increased if χ^2 for the assumed linkage relation is very small. But too much reliance has not been placed on this

procedure; for it is realized that the data of many of the actual cases of independent assortment can be calculated to show a low linkage intensity with χ^2 smaller than that for independent assortment.

While the data from a single F_2 population may not be conclusive as to linkage relations, further evidence may be secured from other crosses or from F_3 tests. On account of limited facilities it has not been practicable to grow a large number of plants for each F_3 population in these experiments; and the one outstanding difficulty encountered in working with small F_3 populations and weak linkage has been the uncertainty in classifying the populations. Among the progenies of F_2 individuals heterozygous for both factors in the same linkage group, the proportion of populations with the reversed linkage relation to those with the original linkage relation is $c^2 : (1-c)^2$, where c is the amount of crossing over expressed as a decimal fraction. When c is large, populations with the reversed linkage relation are expected to occur frequently. At the same time, it is often difficult to be sure whether a given population represents the original or the reversed linkage relation, for the fluctuations in a small population often make linkage resemble independent assortment and may even make an actual case of linkage in one direction resemble linkage in the opposite direction.

In case the majority of the populations under consideration can be classified with a fair degree of safety, the few doubtful populations are classified in these studies according to whatever slight amount of coupling or repulsion they display. In doing this the writer is fully aware of the possibility of mistakes; but this is the only way of analyzing the F_3 results and comparing them with the assumed relations worked out from the F_2 data, as the F_3 populations taken individually are too small and therefore unreliable for such comparison. The occasional misplacement of one or two populations is not a serious matter when one is aware of such a possibility, as it simply increases the apparent amount of crossing over displayed by the class into which it has been misplaced, and the cross over value displayed by the other class is correspondingly reduced. Such mistakes may be detected from the inequality of crossover values calculated for the class showing original linkage and for that showing the reversed linkage, though there is no definite way of correcting them.

Besides using YULE's coefficient of association with a table of calculated corresponding linkage values as suggested by COLLINS (1912), formulae for the calculation of linkage values directly from the F_2 data have been worked out by EMERSON (1916) and HALDANE (1919). Professor CLAUSEN has suggested a method (unpublished) for the calculation

of linkage values which is more convenient than the others in use in conjunction with the χ^2 test for the goodness of fit. The method consists essentially of obtaining a balanced linkage ratio from the given data so that the square root of the double recessive class reveals the gametic ratio. The balancing of the ratio depends on the principle that theoretically the amount by which the different zygotic classes in a linkage distribution differ from the corresponding classes in independent assortment remains constant. For, assuming the gametic series to be

$$(m+a)AB : (m-a)Ab : (m-a)aB : (m+a)ab,$$

the zygotic series is:

$$AB = 9m^2 + (2ma + a^2)$$
$$Ab = 3m^2 - (2ma + a^2)$$
$$aB = 3m^2 - (2ma + a^2)$$
$$ab = \ m^2 + (2ma + a^2)$$

Assuming the gametic series to be

$$(m-a)AB : (m+a)Ab : (m+a)aB : (m-a)ab,$$

the zygotic series is:

$$AB = 9m^2 - (2ma - a^2)$$
$$Ab = 3m^2 + (2ma - a^2)$$
$$aB = 3m^2 + (2ma - a^2)$$
$$ab = \ m^2 - (2ma - a^2)$$

The method suggested by Professor CLAUSEN is employed in this paper and will be indicated at the first instance of calculation of linkage value. Since the value calculated by this method does not differ from that calculated by HALDANE's method, HALDANE's formula for the probable error of linkage value is here used. The formula is

$$\pm .477 \sqrt{\frac{(2+p^2)\ (1-p^2)}{(1+2p^2)\ n}}$$

where n is the total number of individuals under consideration, p is the crossover value in case of repulsion, and $1-p$ is the cross over value in case of coupling.

A consideration of the size of the probable error is a guide to the significance of the difference in linkage values and another means of ascertaining the existence of weak linkage. With respect to the latter function the use of the probable error is subject to the same limitations as encountered in the use of χ^2, as the difference between the calculated linkage value and the value for independent assortment may not exceed the probable error of the former (or the latter[1]) so much as to be significant.

[1] The probable error for independent assortment (i.e., with P equal to 0.5) and χ^2 for independent assortment are both useful in ascertaining what calculated amount of linkage intensity may be considered as significant.

THE MULTIPLE ALLELOMORPH SERIES A, a^s, a^f

The lateral floret of barley exhibits four main grades of fertility upon which HARLAN (1918) has classified the four species of barley (which are probably better ranked as sub-species of *Hordeum sativum* Jess.); namely,

(1) *Hordeum vulgare*   lateral floret fully fertile;
(2) *Hordeum intermedium*[2]   lateral floret partially fertile;
(3) *Hordeum distichon*   lateral floret staminate;
(4) *Hordeum deficiens*   lateral floret rudimentary.

That 1, 3 and 4 form a multiple-allelomorph series was first pointed out by ENGLEDOW (1920), based on the investigations of BIFFEN (1906, 1907) and his own.   Data obtained from the present investigation confirming this case of multiple allelomorphism are assembled in tables 1, 2 and 3.

TABLE 1

Hordeum vulgare $\times$ *H. distichon or reciprocal.*

NUMBER OF F₂ CULTURE	NON-*vulgare*	*Vulgare*
22215	15	10
23215	194	56
22216	41	6
22219	28	13
23219	154	47
22221	10	4
23221	63	21
22224	22	4
23224	87	25
22228	135	53
23228	73	26
22235	66	19
23235	107	27
*21201	34	11
*21202	38	16
*21208	27	13
Total..................	1094	351
Calculated.............	*1083.75*	*361.25*

Deviation, 10.25 ± 11.10

The prefixes 21, 22, 23 indicate the years 1921, 1922 and 1923, respectively, when the plants were grown.

224 and 219 are from reciprocal crosses of the same parents.

*Cross made by Professor R. E. CLAUSEN.

[2] HARLAN and HAYES (1920) have shown that *H. intermedium* may be secured as a recombination product by crossing *H. distichon* with a certain type of *H. vulgare*.

TABLE 2

Hordeum vulgare × *H. deficiens or reciprocal.*

NUMBER OF F_2 CULTURE	NON-*vulgare*	*Vulgare*
22226	39	12
23226	54	22
23236	172	83
156×205	162	58
Total.................	427	175
Calculated	*451.5*	*150.5*

Deviation 24.5 ± 7.17

TABLE 3

H. distichon × *H. deficiens.*

NUMBER OF F_2 CULTURE	NON-*distichon*	*Distichon*
22217	71	33
23217	234	69
Total.................	30 ؛	102
Calculated.............	*305.25*	*101.75*

Deviation, 0.25 ± 5.89

If the assumption of multiple allelomorphism is correct, crossing any two of these forms should not give rise to the third form. The fulfillment of this requirement is at once clearly seen in the *vulgare*×*distichon* and *distichon*×*deficiens* crosses. In the *vulgare*×*deficiens* crosses the lateral floret of the F_1 is similar to that of *H. distichon*. But all such forms in F_2 were found to be heterozygous, and hence are genetically distinct from the true-breeding *H. distichon*. Data supporting this statement are recorded by BIFFEN (1907) and are furnished by this study. Thirty-six F_2 plants of culture 22226 were carried to the F_3 generation. Of these the seven *vulgare* plants bred true; so did all the fourteen plants of the *deficiens* type. The fifteen intermediate plants similar to *H. distichon* all bred like the F_1.

The symbols A, a^s, and a^f are here used to indicate the factors for *deficiens, distichon* and *vulgare*, respectively.

CROSSES INVOLVING A a^s a^f AND L l

The rachilla of the barley spike is covered either with long and unbranched hairs or with short branched hairs. This difference in the type

of hair on the rachilla has long been made use of in distinguishing otherwise closely similar strains of barley, and the mode of inheritance resulting from crossing the two types has been reported by UBISCH (1916) and ENGLEDOW (1920) as a case of monohybrid with the long-hair character dominant.

Letting $L\,l$ denote the pair of factors concerned in this case, table 4 indicates independent assortment between the $L\,l$ pair and the $A\,a^s\,a^f$ series. The populations in which the two dominants have entered from

<div align="center">TABLE 4</div>

NUMBER OF CULTURE	PARENTAL COMBINATIONS	F₂ CLASSES			
		La^s	La^f	la^s	la^f
22216	la^f and La^s	28	6	13	0
22219	la^f and La^s	21	9	7	4
23219	la^f and La^s	117	37	37	10
22224	La^s and la^f	16	4	6	0
23224	La^s and la^f	52	12	13	9
22228	La^s and la^f	94	40	41	13
23228	La^s and la^f	54	19	19	7
22221	La^f and la^s	9	3	1	1
23221	La^f and la^s	49	15	14	6
140×136	La^s and la^f	68	16	19	9
23236		LA	La^f	lA	la^f
23236	Laf and lA	128	62	38	19
		LA	La^s	lA	la^s
22217	La^s and lA	34	25	17	8
23217	La^s and lA	183	52	51	17
22218	lA and La^s	7	5	2	1
Total.........		860	305	278	104

<div align="center">For independent assortment, $\chi^2=1.94$; P=0.586</div>

one side and the two recessives from the other, give totals of 450 : 143 : 155 : 52, while the populations in which each side has contributed one dominant and one recessive give totals of 410 : 162 : 123 : 52. Thus there can be no objection that the summation of the two groups of populations has obscured a linkage relation.

<div align="center">CROSSES INVOLVING $L\,l$, $A\,a^s\,a^f$ AND $N\,n$</div>

In most cultivated varieties of barley the caryopsis is adherent to the lemma and palea at maturity, but many races exist in which the caryopsis

remains free. The distinction is due to a single factor difference with the adherent (hulled) condition completely or partially dominant over the free (naked) condition (BIFFEN 1907, etc.). Using $N\,n$ to denote the pair of factors concerned, table 5 indicates independent assortment between $L\,l$, $A\,a^s\,a^f$ and $N\,n$.

TABLE 5

CULTURE	PARENTAL COMBINA-TIONS	F2 CLASSES							
		La^sN	La^sn	La^fN	La^fn	la^sN	la^sn	la^fN	la^fn
22221	La^fn and la^sN	3	6	1	2	0	1	1	0
23221	La^fn and la^sN	38	11	12	3	10	4	3	3
		LAN	LAn	La^fN	La^fn	lAN	lAn	la^fN	la^fn
23236	La^fn and lAN	98	26	45	11	27	10	13	8
Total		139	43	58	16	37	15	17	11

For independent assortment, $\chi^2 = 11.54$; $P = 0.118$

CROSS INVOLVING $L\,l$, $S\,s$, $N\,n$ AND $A\,a^s$.

The $L\,l$ pair, besides having effect on the rachilla as mentioned before, also determines the nature of pubescence of the outer glumes in a similar way. But the extent of the pubescence of the outer glumes is determined by another factor pair identified from the following cross, which also yields results concerning its relations with $A\,a^s$, $L\,l$ and $N\,n$.

Number 154 has the genetic constitution[3] $L\,L\,a^s\,a^s\,N\,N$, with the pubescence of the outer glumes restricted to the central ridge; number 025 has the genetic constitution $llAANN$, with the major portion of the outer glumes covered by short hairs. On crossing No. 154 ♀ with No. 025 ♂ the F_1 plants possessed outer glumes in a heavily haired condition not found in either parent. The distribution of the F_2 plants with respect to hairiness is as follows:

237 plants,—outer glumes heavily haired and rachilla long-haired;

  77 plants,—central ridge of outer glumes haired and rachilla long-haired;

[3] The lateral floret of this strain is much less well developed than that of the typical $H.$ *distichon*. The breeding results reveal that it has the formula a^sa^s, the modification being due to genetic factors lying outside the locus of the triple-allelomorph series.

72 plants,—outer glumes covered with short hairs and rachilla short-
haired;

21 plants,—central ridge of outer glumes haired and rachilla short-
haired.

The actual distribution fits closely with the typical dihybrid ratio.
Thus, if we denote the factor pair affecting the extent of pubescence on the
outer glumes by Ss, No. 154 had the formula $LLss$, No. 025 had the
formula $llSS$, and F_1 had the formula $LlSs$. S is only partially dominant
over its allelomorph in the spreading effect, while ss restricts the hair to
the central ridge.

The distribution with respect to all four pairs of contrasting characters
is as follows:

$LSNA$	147	$lSNA$	44
$LSNa^s$	58	$lSNa^s$	18
$LSnA$	26	$lSnA$	6
$LSna^s$	6	$lSna^s$	4
$LsNA$	36	$lsNA$	12
$LsNa^s$	8	$lsNa^s$	2
$LsnA$	28	$lsnA$	6
$Lsna^s$	5	$lsna^s$	1

If we disregard the Nn pair for the moment, it can be seen that the
remaining factors are assorted in conformity with the typical Mendelian
trihybrid ratio. The trihybrid distribution is as follows:

LSA	173	
LSa^s	64	
LsA	64	For independent assortment
Lsa^s	13	$\chi^2 = 6.85$; P $= 0.445$
lSA	50	
lSa^s	22	
lsA	18	
lsa^s	3	

The relation between Ss and Nn is represented by the distribution 267
SN : 42 Sn : 58 sN : 40 sn, which clearly indicates linkage. The linkage
value is calculated by Professor CLAUSEN's method, in table 6. The size
of χ^2 is somewhat too large. The disturbing element is due to the large
deviation from the 3 N : 1 n ratio, which is 3.36 times the probable error.
This is merely an extreme case that occasionally happens in random
sampling without invalidating the monohybrid nature of hulled versus
naked. This statement finds confirmation in the F_3 data.

TABLE 6

PHENOTYPE	OBSERVED FREQUENCY	CALCULATED FREQUENCY INDEPENDENT ASSORTMENT	OBSERVED MINUS CALCULATED		BALANCED LINKAGE RATIO
SN	267	228.9375	38.0625	228.9375+31.3125	=260.25
Sn	42	76.3125	−34.3125	76.3125−31.3125	= 45.00
sN	58	76.3125	−38.3125	76.3125−31.3125	= 45.00
sn	40	25.4375	14.5625	25.4375+31.3125	= 56.75
Total	407		125.2500 ÷ 4 = 31.3125		

$$\text{Percent of crossing over} = 100 \left(1 - 2\sqrt{\frac{56.75}{407}}\right) = 25.32 \pm 1.73$$

For the calculated linkage relation, $\chi^2 = 9.05$; P $= 0.029$

Table 7 gives the distribution of characters in the fifty F_3 populations of this cross. When all the F_3 populations in which there is segregation with respect to the adherence of the caryopsis are summarized, the distribution is 635 hulled : 228 naked, which is a fairly close agreement with theoretical expectation.

Table 8 gives the distribution in the eleven F_3 populations grown from the F_2 plants heterozygous for both S and N. It is probable in this case that cultures 23295, 23313, and 23289 are cases of reversed linkage, while in the remaining eight cultures the original linkage relation is exhibited. The eight cultures together give a distribution of 171 SN : 36 Sn : 30 sN : 41 sn. The crossover value calculated for this distribution is 27.54 ± 2.05 percent. The three cases of reversed linkage give a total distribution of 54 SN : 31 Sn : 20 sN : 3 sn. The crossover value calculated from this distribution is 23.58 ± 5.68 percent. Both of these crossover values do not differ significantly from the value determined from the F_2 data, which is 25.32 percent.

DENSITY OF THE SPIKE IN RELATION TO $L\,l$, $S\,s$, $N\,n$, $A\,a^s$

Linkage between the factor concerned in the adherence of the caryopsis and a factor for density with a gametic ratio of "5 : 1" has been reported by UBISCH (1921). MIYAKE and IMAI (1922) report the linkage of Nn with two factors for density with crossover values 13 percent and 23 percent, respectively. To determine the relation between density and the other characters dealt with in the cross 154 × 025, measurements have been taken on the ten internodes above the first node giving rise to a good central spikelet. The best spike is chosen for measurement in each plant.

TABLE 7

F_1 DISTRIBUTION

CULTURE NUMBER	CHARACTER OF F_1 PARENT	LSNA	LSNa	LSnA	LSna	LsNA	LsNa	LsnA	Lsna	lSNA	lSNa	lSnA	lSna	lsNA	lsNa	lsnA	lsna
23270	LSNA	12	5	5	1												
23293	"	18	5				1			5	1						
23294	"	21	7	11		5				1	2						
23295	"	17		5	1	8						3	1	1	1	3	
23296	"	9	1			3		2		2	2						
23298	"	27	12	4	1			3				1					
23299	"	22	6	5	3		2			3	1	1		1		1	
23301	"	14	2	2				2		3		2					
23302	"	16				4				5							
23303	"	13	7	5						4	2						
23304	"	15	5			5				7							
23307	"	25	4	9		4	1			2							
23310	"	10		3		1				2							
23313	"	10	3	6				4		3	1	1		3		1	
23316	"	19								7		4		1		2	
23318	"	24								7		3					
23271	LSNa		20								4						
23274	"		14		5						4		4				
23275	"		13		2		3		2	1*	8						
23276	"		34				7										
23277	"		22		5						6		1				
23279	"		29				9										
23282	"		26		3		6		7								
23285	"		20		3		1		3		7		2				1
23287	"		17		3		3		4		3				2		
23288	"		31								11						

TABLE 7 (continued)

CULTURE NUMBER	CHARACTER OF F1 PARENT	F2 DISTRIBUTION															
		LSNA	*LSNa*	*LSnA*	*LSna*	*LsNA*	*LsNa*	*LsnA*	*Lsna*	*lSNA*	*lSNa*	*lSnA*	*lSna*	*lsNA*	*lsNa*	*lsnA*	*lsna*
23290	*LSnA*			13	5			6	2			8	1			4	
23309	"			9				1				3					
23312	"			28				8									
23317	"			29				7									
23268	*LsNA*					11	1	5	3					5		1	2
23269	"					12	4	8	2	2*				4	1	2	
23311	"					13	5							8	2		
23273	*LsNa*						14		11						5		3
23283	"						21		6								
23286	"						13		2						5		
23291	*LsnA*							15	1							3	1
23292	"							14								7	
23315	"							32									
23278	*Lsna*								31								
23280	"								22								5
23289	*lSNA*									13	7	4	3	4	2		
23297	"									16	5			11	3		
23300	"									26	6	9					
23305	"									25	6	5	1				
23314	"									32							
23281	*lSNa*										16		2		2		9
23284	"												8		2		
23306	*lsNA*													21	6	6	3

*Probably result of natural crossing.

TABLE 8

CULTURE NUMBER	SN	Sn	sN	sn
23295	17	11	8	2
23296	14	10	5	6
23302	21	4	5	3
23313	17	13	6	1
23316	26	7	3	6
23275	21	2	3	2
23282	26	3	6	7
23285	27	5	3	4
23287	20	3	3	4
23289	20	7	6	0
23281	16	2	2	9

From measurement of ten individuals in each case, No. 154 had a mean length of 42.2 mm, while No. 025 had a mean length of 30.7 mm. The length of the first ten internodes in the F_1 was 37 mm. The distribution of density in F_2 is given in table 9. Some plants have been left out because they did not have good spikes for measurement of density.

As no extensive measurements have been made on the P_1 and F_3 populations, it is not possible to get a definite notion of the number of density factors concerned here. As to the relation of density with the other factors concerned in this cross, the inequality of the mean density values of the contrasting classes appears to be significant in the cases of N versus n and S versus s. If this correlation is due to a single factor in the SN linkage group, that factor should lie nearer to S than to N. In the absence of more extensive data, it is fruitless to speculate further.

THE INTERRELATIONS BETWEEN N n, K k AND A a^s a^f

HAYES and GARBER (1921) report the results of experiments conducted at the MINNESOTA AGRICULTURAL EXPERIMENT STATION, indicating the independent assortment between the factors affecting the contrasting characters:

$(K\ k)$ Hooded versus awned,
$(B\ b)$ Black versus white,
$(N\ n)$ Hulled versus naked,
$(a^s\ a^f)$ Two-rowed versus six-rowed.

The independent assortment between Nn and a^sa^f has found confirmation in the foregoing cross. In crossing No. 038 ♀ of the genetic constitu-

tion, $NNkk$, by No. 100 ♂, of the genetic constitution, $nnKK$, the F_2 distribution is 166 NK : 64 Nk : 53 nK : 25 nk. In crossing No. 165 ♀, of the genetic constitution, $a^f a^f KK$, by No. 108 ♂, of the genetic constitution, $AAkk$, the F_2 distribution is 72 AK : 21 Ak : 22 $a^f K$: 12 $a^f k$. Simple inspection indicates the absence of significant correlation in the $Nk \times nK$ cross, while in the $Ak \times a^f K$ cross, the appearance of negative correlation needs no special comment except that data from actual cases of independent assortment may display with equal frequency apparent negative or positive correlation.

The F_2 results from crossing No. 173 ♀, of the genetic constitution $nnKKa^f a^f$, with No. 141 ♂ of the genetic constitution $NNkka^s a^s$, are as follows:

	22235	23235	Total	
NKa^s	46	63	109	
NKa^f	13	12	25	
Nka^s	10	7	17	
Nka^f	2	3	5	For independent assortment
nKa^s	9	18	27	
nKa^f	3	6	9	$\chi^2 = 19.42$; P $= 0.007$
nka^s	1	3	4	
nka^f	1	0	1	

The wide departure from the typical trihybrid distribution is primarily due to the great deviation from the 3 K : 1 k ratio (170 K : 27 k). Sixteen F_2 plants were carried to the F_3 generation. Two of these were awned and bred true. Of the 14 hooded plants, 6 bred true, and 8 segregated into hooded and awned with the summary ratio of 150 hooded : 38 awned. The F_3 tests thus indicate that these contrasting characters of the terminal appendage of the lemma are due to a single factor difference here, as has been found elsewhere. A great part of the discrepancy was probably due to the occurrence of selective elimination in the F_2 population grown in 1923, in which only about half of the seeds sown produced heads.

The discrepancy in the 3 K : 1 k ratio being primarily responsible for the large size of χ^2 in the above test, the typical trihybrid ratio is still good so far as the interrelations between the three pairs of factors are concerned. Thus, though the results from this cross can not be taken as a demonstration, it is, nevertheless, in conformity with the other experiments indicating independent assortment between Nn, Kk and $Aa^s a^f$.

TABLE 9

LENGTH OF TEN BASAL INTERNODES IN MILLIMETERS

	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	MEAN IN MM	DIFFERENCE IN MEANS
N	1	2	2	10	7	21	15	24	21	15	22	18	8	12	11	11	4	5	2	3	3	·	2	1	3	1	·	36.81±.22	2.01±.47
n	·	·	·	2	·	2	2	1	1	6	11	2	5	9	2	4	2	2	3	·	·	·	1	·	·	·	1	38.82±.42	
S	1	2	2	12	7	22	13	24	19	18	27	13	8	13	8	10	3	6	2	2	·	·	3	1	2	1	1	36.51±.22	3.07±.47
s	·	·	·	·	·	1	4	1	3	3	6	7	5	8	5	5	3	1	3	1	3	·	·	·	1	·	·	39.58±.41	
L	·	1	1	8	6	18	11	20	19	15	23	17	10	19	10	13	6	6	3	3	3	·	3	·	3	·	1	37.44±.22	1.24±.47
l	1	1	1	4	1	5	6	5	3	6	10	3	3	2	3	2	·	1	2	·	·	·	·	1	·	·	1	36.20±.42	
A	1	2	1	8	5	17	12	14	19	17	26	16	11	16	12	10	3	6	5	2	3	·	3	1	2	1	1	37.41±.22	.93±.40
a	1	2	1	4	2	6	5	11	3	4	7	4	2	5	1	5	3	1	·	1	·	·	·	1	1	1	1	36.48±.33	
Total	1	2	2	12	7	23	17	25	22	21	33	20	13	21	13	15	6	7	5	3	3	c	3	1	3	1	1	37.09±.19	

CROSS INVOLVING Bb, Ll, $a^s a^f$

In crossing No. 127 ♀, of the genetic constitution $bbll a^f a^f$, with No. 171 ♂, of the genetic constitution $BBLL a^s a^s$, the F_2 distribution is as follows:

<div style="text-align:center">

23 BLa^s
4 BLa^f
8 Bla^s
5 bLa^s
2 bLa^f
5 bla^s

</div>

With respect to the goodness of fit of this distribution to the typical trihybrid ratio, $\chi^2 = 8.48$ and $P = 0.295$. Thus, mathematically, the deviation is not excessive. But the distribution of 27 BL : 8 Bl : 7 bL : 5 bl suggests linkage. For the independent assortment between Bb and Ll, $\chi^2 = 1.90$ and $P = 0.595$. For linkage between Bb and Ll with the calculated crossover value of 39.40 ± 6.47, $\chi^2 = 0.93$. Thus, further evidence is needed for decision as to the existence of linkage.

The three F_3 populations in which segregation has taken place both with respect to Bb and Ll are given in table 10. All the three populations included in table 10 appear to exhibit the original linkage relation. The crossover value calculated from summary ratio of the three populations is 40.48 ± 4.72. The close agreement between the results of the F_2 and F_3 can be taken as a strong evidence for the assumed linkage relation.

TABLE 10

CULTURE NUMBER	BL	Bl	bL	bl
23263	18	5	2	2
23264	22	6	11	4
23266	15	1	4	1
Total	55	12	17	7

CROSS INVOLVING Bb, Rr, Ll AND Ss

The smooth-awn character of barley, in which the awn is smooth at its lower portion where the teeth are particularly strong in the common varieties, have been found by HARLAN (1920) to behave as a simple Mendelian recessive. The factor pair determining rough- and smooth-awned characters is here denoted by Rr. Strain No. 135 ♀, of the genetic

TABLE 11

F₂ DISTRIBUTION

CULTURE NUMBER	CHARACTER OF F₁ PARENT	*BRLS*	*BRLs*	*BRlS*	*BRls*	*BrLS*	*BrLs*	*BrlS*	*Brls*	*bRLS*	*bRLs*	*bRlS*	*bRls*	*brLS*	*brLs*	*brlS*	*brls*
23476	*BRLS*	15		6		3		2									
23477	"	9	4	4	1	1				5				1			
23479	"	18	3	5	1	2	2	1		6	2						
23480	"	21	4						1	5	4			1		1	
23482	"	8	4	2	1	1	2	1		1	1			3			
23486	"	5	4	4		5								1	1		
23491	"	8	2			7	2			12					1		
23493	"	11				2	2			1				4		1	
23500	"	13	4	1		7				2		2					
23506	"	14	4	4		2	1		2	2	5			2			
23510	"	11		9	1												
23517	"	10	4	4		1				2		1					
23518	"	18		4	2												1
23526	"	5		2		1	1	1		2		3		2			
23530	"	9	2	2		3			2	3		2			1		
23536	"	12	2	5		4			1	6		1					
23538	"	4	4	4		2	4	1	1	2		2	2				
23539	"	9	4	3		7	2	2									
23540	"	21	7	8	1												
23492	*BRLs*		16		6						6		2				
23508	"		13		9												
23528	"		17				6				9						
23581	"		4		6		4				3		3				

TABLE 11 (continued)

CULTURE NUMBER	CHARACTER OF F₂ PARENT	F₃ DISTRIBUTION															
		$BRLS$	$BRLs$	$BRlS$	$BRls$	$BrLS$	$BrLs$	$BrlS$	$Brls$	$bRLS$	$bRLs$	$bRlS$	$bRls$	$brLS$	$brLs$	$brlS$	$brls$
23484	$BRlS$			24	13							9					
23489	"			19								6					
23502	"			15	8							6	2				
23505	"			10	3				4			7	2				
23515	"			18	6			1									
23516	"			27	4							8					
23522	"			19									1				
23525	$BRls$			12	5			2				2				2	
23527	"			22								1					
23532	"			20								5					
23533	"			7													
23483	$BRls$				17								4				2
23487	"				19				3				11				
23496	"				27								12				
23481	$PrLS$					12	9							2	3		
23501	"					5	5	2	3					4	3		1
23509	"					10		2						5			
23511	"					14	7							9	3		
23520	"					21	11										
23521	"					6	4	5						6			
23524	"					12	2	6	2						2	1	
23529	"					15											
23537	"					10	5								1		1

TABLE 11 (continued)

CULTURE NUMBER	CHARACTER OF F₁ PARENT	BRLS	BRLs	BRlS	BRls	BrLS	BrLs	BrlS	Brls	bRLS	bRLs	bRlS	bRls	brLS	brLs	brlS	brls
		F₂ DISTRIBUTION															
23478	BrLs	.	.	.	.	.	19	.	10	.	.	.	.	.	.	.	.
23490	"	.	.	.	.	.	19	.	.	.	.	.	.	.	4	.	.
23485	bRLS	.	.	.	.	.	.	.	.	4	2	8	1	4	3	.	.
23495	"	.	.	.	.	.	.	.	.	14	.	7	.	5	.	3	.
23497	"	.	.	.	.	.	.	.	.	13	.	2	.	.	.	2	.
23503	"	.	.	.	.	.	.	.	.	18	.	9	.	8	.	.	.
23512	"	.	.	.	.	.	.	.	.	18	3	9	1	.	.	.	.
23513	"	.	.	.	.	.	.	.	.	11	.	3	.	4	.	.	.
23534	"	.	.	.	.	.	.	.	.	13	2	3	1	.	.	.	.
23507	bRLs	.	.	.	.	.	.	.	.	.	17	.	4	.	9	.	.
23504	"	.	.	.	.	.	.	.	.	.	16	.	2	.	8	.	.
23488	bRlS	.	.	.	.	.	.	.	.	.	.	18	1	.	.	5	7
23494	"	.	.	.	.	.	.	.	.	.	.	22	.	.	.	.	.
23498	"	.	.	.	.	.	.	.	.	.	.	21	6	.	.	5	1
23499	"	.	.	.	.	.	.	.	.	.	.	17	4	.	.	4	1
23519	"	.	.	.	.	.	.	.	.	.	.	19	10	.	.	.	.
23523	"	.	.	.	.	.	.	.	.	.	.	17	4	.	.	2	6
23535	bRls	.	.	.	.	.	.	.	.	.	.	.	18	.	.	.	8

constitution *bbllRRSS*, was crossed with No. 174 ♂, of the genetic con-
stitution *BBLLrrss*. The F_2 distribution is as follows:

28 *BRLS*	10 *bRLS*
8 *BRLs*	2 *bRLs*
15 *BRlS*	8 *bRlS*
4 *BRls*	1 *bRls*
15 *BrLS*	2 *brLS*
5 *BrLs*	1 *brLs*

Thus, no class with *rl* is present and the relation between *Rr* and *Ll* is
represented by the distribution 48 *RL* : 28 *Rl* : 23 *rL* : 0 *rl*. If no other
evidence were available, this distribution would favor the notion that a
single factor is responsible for both the dominant rough-awn character
and the recessive short-hair character, and its allelomorph is responsible
for both the recessive smooth-awn character and the dominant long-hair
character. That this is not the case will be seen from the F_3 results.

The distribution with respect to *Bb* and *Ll* is 56 *BL* : 19 *Bl* : 15 *bL* : 9 *bl*.
Assuming that linkage exists between *Bb* and *Ll*, as indicated by the
previous cross, the crossover value is 44.04 ± 4.74 percent. For the cal-
culated linkage relation, $\chi^2 = 0.70$; for independent assortment, $\chi^2 = 1.97$.

The relation between *Bb* and *Rr* is represented by the distribution
55 *BR* : 20 *Br* : 21 *bR* : 3 *br*. The crossover value calculated from this
distribution is 41.48 ± 5.45 percent. The χ^2 values for the calculated
linkage relation and for independent assortment are 0.42 and 2.09,
respectively.

Table 11 contains the results from 64 F_3 populations grown from the F_2
plants of this cross.

The F_3 populations which are the progenies of the F_2 plants heterozy-
gous for both *R* and *L* are assembled in table 12. The F_3 results leave no
doubt that *Rr* and *Ll* are entirely different factor pairs. In fact, the
repulsion has been very much weakened. The crossover value calculated
from the summary of the thirteen populations showing repulsion (158
RL : 63 *Rl* : 88 *rL* : 9 *rl*) is 28.70 ± 3.43 percent. The summary of the
seven populations showing coupling (132 *RL* : 34 *Rl* : 24 *rL* : 13 *rl*) gives
a crossing over value of 34.54 ± 2.89 percent. Whether the great dis-
crepancy between the linkage intensities exhibited by the F_2 and F_3
populations is primarily due to environmental influence or to recombina-
tion of genetic factors that modify the frequency of crossing over is
difficult to ascertain. Whatever little evidence we have is in favor of the
latter explanation; for the close agreement of the two crossover values
between *Bb* and *Ll* obtained from the F_2 and F_3 data of the cross No. 127 ✕

No. 171 indicates the probable ineffectiveness of ordinary environmental changes in the field in inducing great variations in the frequency of crossing over in barley, while the great variations in linkage intensities exhibited by the different F_3 populations, which will be evident when the other relations have been considered, are best explained by the recombination of genetic factors modifying the frequency of crossing over.

TABLE 12

CULTURE NUMBER	RL	Rl	rL	rl
23476	15	6	3	2
23477	18	5	2	0
23479	21	6	4	1
23482	21	3	4	3
23506	25	4	3	3
23530	12	4	3	1
23536	20	6	5	3
Total coupling	132	34	24	13
23486	11	4	8	0
23500	15	3	11	1
23517	12	5	3	0
23526	7	4	2	0
23538	8	6	8	0
23539	13	3	9	3
23531	10	4	6	0
23485	6	9	7	0
23495	14	7	5	3
23503	18	9	8	2
23513	11	3	4	0
23507	17	4	9	0
23504	16	2	8	0
Total repulsion	158	63	88	9

The F_3 populations grown from the F_2 plants heterozygous for both B and R are assembled in table 13. The summary proportion for all the populations showing the original linkage relation (144 BR : 55 Br : 73 bR : 12 br) gives a crossover value of 31.40 ± 3.56 percent. The summary proportion for all the populations showing the reversed linkage (101 BR : 23 Br : 21 bR : 16 br) gives a crossover value of 32.26 ± 6.61 percent. The close agreement between the two values argues for the correctness of the classification as to the real genetic constitution of the F_2 parents. The degree of repulsion has been considerably increased in comparison with the F_2 data.

TABLE 13

CULTURE NUMBER	BR	Br	bR	br
Coupling				
23477	18	1	5	1
23486	13	5	2	3
23493	13	4	1	1
23500	14	7	4	5
23517	14	1	3	2
23525	12	2	2	2
23484	17	3	4	2
Total coupling	101	23	21	16
Repulsion				
23482	15	5	9	2
23491	12	9	12	2
23506	22	6	7	0
23526	7	2	5	0
23530	11	4	5	0
23536	19	6	7	2
23538	10	8	4	2
23528	17	6	9	3
23531	10	4	6	0
23515	21	5	9	1
Total repulsion	144	55	73	12

TABLE 14

CULTURE NUMBER	BL	Bl	bL	bl
23477	14	5	6	0
23482	15	5	10	1
23486	14	4	5	0
23500	20	1	6	3
23506	21	7	7	0
23517	11	4	4	1
23526	7	2	2	3
23530	12	3	3	2
23536	18	7	7	2
23538	12	6	4	2
23492	16	6	6	2
23531	8	6	3	3
23501	10	5	7	1
23509	10	2	6	0
23524	14	7	8	2
Total	202	70	84	22

The F_3 populations grown from the F_2 plants heterozygous for both B and L are assembled in table 14. If all these populations are summed up, the proportion is 202 BL : 70 Bl : 84 bL : 22 bl, which is in the form of repulsion instead of coupling. This is, however, not unexpected, as, besides the low intensity of linkage and the considerable size of its probable error, populations with the reversed linkage relation may be present in excess of their normal proportion as a consequence of ordinary fluctuation.[4] No attempt is made to classify the populations in this case, as too much uncertainty is involved here.

CONCLUSION REGARDING THE *BRL* GROUP

Considering all the evidence that has been presented, it is certain that Bb, Rr, and Ll lie in the same linkage group. The most probable sequence is BRL. The distance between R and L is probably considerably shorter than that between B and R, though on account of the great differences in crossover values between F_2 and F_3 results, the assignment of definite distances must await more extensive experiments.

In this connection it may be noted that COLLIN and TROUARD-RIOLLE (1923) claim to have found dissociation of characters in F_1 resulting from crossing a black smooth-awned barley with a white rough-awned barley. The following is quoted verbatim from their original paper.

"Les types les plus curieux, en F_1, sont épis dont les grains restent noirs, mais d'un noir très attenué, tandis que les barbes sont tout blanches et parfaitment lisses; la form lisses à grain blancs recherchée par l'agriculture, fait complètement défaut en F_1 et n'apparaita qu'en F_2 dans la descendance des épis noir rugueux. . . . . Tous les grains provenant d'épis lisses, que soit la teint des barbes, ont donné en F_2 des épis lisses, gris ou noir, comme si la dissociation était accomplié des F_1."

The rough-awned forms are reported to segregate in F_2 into all the nine possible combinations of black, gray and white color, with rough, smooth, and smooth-rough awn, but no numerical data are given.

It is interesting to note that all the F_1 smooth-awned spikes are reported to have black or gray kernels and give no white spikes in F_2. It seems that these investigators did not appreciate the developmental differences in the characters under consideration, when they attach genetic significance to

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[4] Denoting the amount of crossing over by c, the coefficient of the F_2 gametes with recombined linked factors is $\dfrac{c-c^2}{1-2c-2c^2}$, which is intermediate between c and 0.5, the value for independent assortment, (between $1-c$ and 0.5 if c ever exceeds 0.5). The value expressed by this formula approximates the value calculated from the summary F_3 distribution when a large number of equal-sized F_3 populations are dealt with.

the differences among spikes of the same plant. As the progenies of all the "rough" spikes are lumped together in an ambiguous manner, I seriously doubt whether their "rough" spikes of plants bearing other smooth spikes were really rough. I believe that the supposed F_1 segregants merely represent failures in the intended pollinations, which were probably due to faulty technique, allowing self-pollination to occur (the occurrence of parthenogenesis has never been reported in barley and therefore can scarcely be considered an available interpretation).

THE FACTORS FOR GLUME WIDTH AND THEIR RELATIONS

In crossing No. 140 ♀ with No. 136♂, both of which possess the normal narrow outer glumes, the F_1 plants are like the parental forms with respect to this character. In the F_2, forms appeared in which the two outermost glumes (or sometimes the two central outer glumes) are widened and with awns more elongated. The proportion is 91 narrow : 21 wide, which is in perfect agreement with the 13 : 3 ratio. Evidently one of the parents must carry both the dominant factor for wide and the dominant factor for inhibition of the same character, while the other parent carries both of the recessives.

Besides this hidden difference, the two parents differ in two other obvious respects, 140 being of the LLa^sa^s type and 136 of the lla^fa^f type. The F_2 distribution with respect to all these characters is given below:

Narrow	La^s	54
Narrow	La^f	13
Narrow	la^s	17
Narrow	la^f	7
Wide	La^s_f	14
Wide	La^f	3
Wide	la^s	2
Wide	la^f	2
Total		112

For independent assortment, $\chi^2 = 3.35$; $P = 0.848$

Twelve F_3 populations were grown and examined for the character of the outer glume. The results are given in table 15. As a whole these F_3 results conform with the expectation. If more wide F_2 plants had been grown, we would find two-thirds of them exhibiting the 3 wide : 1 narrow ratio in F_3.

TABLE 15

NUMBER OF CULTURE	CHARACTER OF F₂ PARENT	F₃ DISTRIBUTION	
		Narrow	Wide
23419	Narrow	15	1
23420	Narrow	13	3
23421	Narrow	20	0
23422	Narrow	25	0
23423	Wide	0	32
23424	Narrow	25	7
23425	Narrow	37	0
23426	Wide	0	34
23427	Narrow	31	0
23428	Narrow	37	5
23429	Narrow	25	0
23430	Narrow	29	6

In crossing No. 125 ♀, which was short-haired and narrow, with No. 213♂, which was long-haired and wide, the F_1 is long-haired and narrow and the F_2 distribution is as follows:

Narrow L,   169
Narrow l,   52
Wide L,   53
Wide l,   12

Total   286

Though the outermost glumes of No. 213 do not exceed those of the normal forms conspicuously in width, many F_2 plants with conspicuously wide outer glumes are found in this cross as in the previous cross. Evidently one or more modifying factors affecting the width are at work, but their exact nature has not been determined.

Numbers 125 and 136 are from the same origin and probably identical strains. Hence, it may be assumed that they both have the genetic constitution $IIWW$, W standing for wide, and I, for inhibitor of wide.

Thus it appears that:

No. 213 has the constitution $iiWW$;

No. 140 has the constitution $iiww$.

TSCHERMAK (1919) mentions the wide glume character as a simple Mendelian recessive. Probably he has dealt with the factor pair Ii. SCHIEMANN (1921) reports the occurrence of wide plants in the F_2 of a cross between two narrow forms and discusses the origin and variability of the anomaly at some length. The proportion of wide plants which she

secured in the F_2 was too small to fit in the 13 : 3 scheme. As about 50 percent of her F_2 plants failed to ripen, due to segregation in rate of growth and in winter hardiness, there may have been selective elimination of the wide forms on account of linkage with some of the growth factors.

A variety of *H. vulgare*, No. 203, has all the outer glumes glabrous, very wide, and possessing awns as long and coarse as those of the lemmas. To distinguish it from No. 213, which has only slightly widened outermost glumes with short fine awns, this strain is called "extended."

In crossing No. 136 ♀ (*IIWWee*) with No. 203♂ (*EE*), the monohybrid distribution, 54 extended : 117 intermediate : 59 normal, has been secured in F_2. Evidently *I* does not inhibit the effect of *E* as it inhibits the effect of *W*. The relation between *E* and *W* has not been determined, as the attempt to cross No. 203 with No. 213 was not successful.

The cross between No. 151 ♀ (*eeBBa^{s}a$_s$*) and No. 203♂ (*EEbba^{f}a^f*) gives the following F_2 distribution.

BEa^s	84	
BEa^f	26	
Bea^s	35	
Bea^f	7	For independent assortment,
bEa^s	25	$\chi^2 = 5.24$; P $= 0.631$
bEa^f	12	
bea^s	11	
bea^f	1	
Total	201	

Though the distribution agrees well with expectation in case of a typical trihybrid, the proportion 109 Ea^s : 38 Ea^f : 46 ea^s : 8 ea^f suggests the existence of linkage. The calculated crossover value is 40.52 ± 3.93 percent. Besides, the distribution 119 Ba^s : 33 Ba^f : 36 ba^s : 13 ba^f gives a crossover value of 44.02 ± 3.32 percent; the distribution 110 BE : 42 Be : 37 bE : 12be gives a crossover value of 46.26 ± 3.71 percent. In each of the three cases, χ^2 for the calculated linkage intensity is less than 1.

It is probable that linkage actually exists between *Ee* and $a^s a^f$, as the calculated crossover value differs from fifty percent by 2.4 times the probable error of the former. χ^2 for independent assortment between *Ee* and $a^s a^f$ is 3.64, setting the value of P at 0.309. While this deviation can not be considered as significant by itself, the probability of linkage is increased by the fact that χ^2 for the assumed linkage intensity is less than 1.

The evidence presented in previous sections concerning linkage between *Bb* and *Ll* and independent assortment between *Ll* and $Aa^s a^f$ is against

the assumption that all the three factors involved in this cross lie in the same linkage group. Moreover, the calculated linkage intensities between Bb and $a^s a^f$ and between Bb and Ee are not significant in comparison with their probable errors, and χ^2 for independent assortment in each of these cases is small.

If the three factors really belong to the same linkage group with the sequence BEA, then it must be assumed, if the theory of linear arrangement of genes is applicable here, that B and A are very far apart from each other and that the direct crossover value of 46. 26 percent represents a distance probably exceeding one-hundred units, as a considerable amount of double crossing over may be expected between B and E and between E and A. Similar assumption must then also be made for a previous cross (No. 127 $\times$ No. 171) involving L, B and A, where the sequence for the hypothetical group is LBA and the distance between L and A must be extremely long. This consideration is further indication that the BEA group (whose establishment would lead to the establishment of the $LRBEA$ group) is highly improbable.

CROSS INVOLVING Aa^f AND Mm

A new variety of $H.$ $vulgare$ with branching inflorescence and greatly increased number of nodes has been described by the writer (HOR 1922). This character has been determined by HARLAN and POPE (1922) to behave as a simple Mendelian recessive. No. 156 ♀, a variety of $H.$ $deficiens$ with normal growth form $(AAMM)$, was crossed to No. 205♂, the six-rowed, many-noded, branching barley $(a^f a^f mm)$. The F_2 distribution is as follows, 123 AM : 43 Am : 39 $a^f M$: 15 $a^f m$.

Independent assortment is indicated, as this is a close fit to the typical dihybrid distribution, χ^2 being less than 1.

DISCUSSION

UBISCH (1916) has found the factor concerned in fertility,[5] Z, to be linked with G, one of the factors concerned in the barbing of the inner pair of nerves of the lemma, with a gametic ratio of "5 : 1." He also found (UBISCH 1919, 1921) L(main factor concerned in density), A (main factor for awn length), and S (factor for hulllessness) to lie in the same linkage group. The crossover values[6] which he has obtained for LA, AS and LS

[5] As no uniform symbols have been adopted, the original symbols as used by the different investigators are given with the original definitions.

[6] These values have been calculated by UBISCH from the nearest gametic ratio of n : 1, where n is an integer, and thus are not exact.

are 20 percent, 14.3 percent and 16.7 percent, respectively. He mentions the inapplicability of the theory of the linear arrangement of genes in this case; but since these values have not been derived from the same cross, it is probable that the discrepancy is due to different genetic factors modifying the frequency of crossing over, if the identities of his L, S and A in the different crosses are granted.

MIYAKE and IMAI (1922) report the establishment of two linkage groups, which are given below:

Group I

$\quad$ Nn, $\quad$ hulled *versus* naked,

$\quad$ L_1l_1, $\\$ L_2l_2, $\quad$ concerned in density,

$\quad$ A_1a_1, $\quad$ one of the factor pairs concerned in awn length,

$\quad$ C_1c_1, $\quad$ one of the factors concerned in hooded *versus* awned.

Group II

$\quad$ Uu, $\quad$ tall and slender *versus* short and stout,

$\quad$ A_2a_2, $\quad$ one of the factor pairs concerned in awn length,

$\quad$ Ii, $\quad$ awnless *versus* awned lateral floret,

$\quad$ Dd, $\quad$ two-rowed *versus* six-rowed,

$\quad$ P_1p_1, $\quad$ one of the factor pairs concerned in purple *versus* colorless kernel.

It does not seem to the writer that these two groups have been established beyond doubt with respect to all the factors therein included. The existence of L_2 as distinct from L_1 has been inferred by these investigators from the difference of 10 percent in the value of crossing over with N. Since the crossover values have been obtained from different crosses there is the possibility here too that the difference is due to different genetic factors affecting the frequency of crossing over. As these investigators report no measurements, it is difficult to appreciate the identities of the two density and four awn-length factors (two of which are not included in either of the two groups) assumed by them. Dd and Ii, which they have put in the same linkage group, evidently represent the two effects of the $a^s a^f$ pair of the $A a^s a^f$ series discussed in this paper.

The group I of MIYAKE and IMAI is the same as the LSA group of UBISCH and the NS group determined in this study.

The group II of MIYAKE and IMAI is the same as the ZG group of UBISCH and the probable group EA in this study.

The group BRL determined in this study is probably independent of either of the above two groups.

Whether the linkage between white No. 3 and *chlorina* forms of barley found by NILSSON-EHLE (1922) constitutes an additional group or belongs to one of the three above groups is not known.

SUMMARY

Ten factor pairs and one triple-allelomorph series have been dealt with, and evidence has been presented for linkage or independent assortment among them.

Two linkage groups have been definitely established in this study. One of these groups includes the factors concerned in the color of the kernel, the texture of the awn, and the length of hair on the rachilla. The other group includes the factors concerned in the adherence of the lemma to the caryopsis and the extent of pubescence on the outer glume. Linkage probably exists between the factors concerned in the fertility of the lateral floret and the extension of the outer glume, which constitute a separate group from the other two.

A study of the distribution of the density of the spike in an F_2 population indicates the probability of one or more density factors lying in the second of the above-mentioned groups, which is in agreement with the findings in previous works.

The linkage groups of barley which have thus far been determined by different investigators have been brought together in the discussion.

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