

# GENETIC STUDIES IN BARLEY—III. LINKAGE RELATIONS OF SOME PLANT CHARACTERS

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In previous communications, Murty and Jain (1959, 1960) reported the mode of inheritance of various plant characters. The present paper describes the linkage relations of these characters.

At present, six out of the seven possible linkage groups in barley are well established. Recent work by Kramer, Veyl and Hanson (1954) indicates that the groups formerly designated as III and VII should be considered as one. The literature on the linkage relationships in barley have been extensively reviewed by Robertson, Wiebe and Immer (1941), Robertson, Wiebe and Shands (1947, 1955) and Smith (1951).

## MATERIALS AND METHODS

The linkage relations of the following characters were studied in the  $F_2$ ,  $F_3$  and  $B_1$  generations in five crosses, *viz.*, E.B. 171  $\times$  E.B. 417, E.B. 177  $\times$  E.B. 417, K. 251  $\times$  E.B. 438, K. 251  $\times$  E.B. 132 and C. 138-2  $\times$  E.B. 132. The following symbols used for these characters are those recommended by Robertson *et al.* (1941, 1947, 1955). The asterisks indicate characters, for which recommended symbols do not appear to be available.

Non-six row <i>vs</i> six row	(V v)
Long <i>vs</i> short outer glume awns	(E e)
Normal green <i>vs</i> Virescent seedlings	(Y y, Yc yc)
Purple <i>vs</i> white leaf sheath	(Pr pr)
Hooded <i>vs</i> awned lemma	(K k)
Black <i>vs</i> white lemma and pericarp	(B b)
Semi spreading <i>vs</i> erect type of early growth habit	(Eh eh)*
Broad <i>vs</i> narrow leaves	(Brl brl)*
Early <i>vs</i> late heading date	(Ea ea, Ea <sub>2</sub> , ea <sub>2</sub> , Ea <sub>3</sub> ea <sub>3</sub> )

The association between various factor pairs was tested by  $\chi^2$  test for independence by the general contingency method. Whenever linkage was suspected the recombination value was calculated by the product method in the  $F_2$  and by the maximum likelihood method in the  $F_3$ .

## RESULTS

### A. Analysis of $F_2$ data:

(a) *Detection of linkage.*—In order to find out if there was any linkage between the various character pairs mentioned above, the joint segregation of two qualitative characters of each cross at a time were subjected to  $\chi^2$  test and that of a quantitative and a qualitative character to 't' test for independence. The results are summarized in tables 1 and 2 respectively.

TABLE 1  
*X*<sup>2</sup> test for independence between various character pairs from the *F*<sub>2</sub> data

Cross	Total number of plants					<i>X</i> <sup>2</sup>	P Value
	AB	Ab	aB	ab	Total		
<b>V v, Pr pr (3 : 1) (3 : 1)</b>							
E.B. 171 × E.B. 417	.. 375	29	36	90	530	227.72	<0.01
E.B. 177 × E.B. 417	.. 351	18	23	90	482	278.148	<0.01
K. 251 × E.B. 438	.. 243	30	21	61	355	132.97	<0.01
<b>V v, Yc yc (3 : 1) (3 : 1)</b>							
E.B. 171 × E.B. 417	.. 384	30	123	8	545	0.198	0.70-0.50
E.B. 177 × E.B. 417	.. 357	10	112	6	485	1.564	0.30-0.20
<b>V v, K k (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 132	.. 315	132	115	47	609	0.015	0.95-0.90
C. 138-2 × E.B. 132	.. 377	104	109	25	615	0.557	0.50-0.30
<b>V v, B b (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 132	.. 337	110	127	35	609	0.592	0.50-0.30
C. 138-2 × E.B. 132	.. 360	121	102	32	615	0.091	0.80-0.70
<b>V v, Eh eh (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 438	.. 204	72	56	28	360	1.688	0.20-0.10
<b>V v, Brl brl (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 438	.. 206	75	68	15	364	2.555	0.20-0.10
<b>E e, Pr pr (3 : 1) (3 : 1)</b>							
E.B. 171 × E.B. 417	.. 287	100	123	20	530	7.380	<0.01
E.B. 177 × E.B. 417	.. 292	77	81	27	471	1.496	0.30-0.20
K. 251 × E.B. 438	.. 189	80	76	16	361	5.348	0.05-0.02
<b>E e, Yc yc (3 : 1) (3 : 1)</b>							
E.B. 171 × E.B. 417	.. 357	27	135	9	528	0.101	0.80-0.70
E.B. 177 × E.B. 417	.. 353	12	106	4	475	0.030	0.90-0.80
<b>E e, K k (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 132	.. 312	138	118	41	609	1.347	0.30-0.20
C. 138-2 × E.B. 132	.. 341	90	145	39	615	0.008	0.95-0.90
<b>E e, B b (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 132	.. 343	107	121	38	609	0.001	0.98-0.95
C. 138-2 × E.B. 132	.. 332	101	130	52	615	1.605	0.30-0.20
<b>E e, Eh eh (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 438	.. 191	80	70	19	360	2.601	0.20-0.10
<b>E e, Brl brl (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 438	.. 207	64	67	25	363	0.468	0.50-0.30

TABLE 1—(Contd.)

Cross	Total Number of Plants					X <sup>2</sup>	P Value
	AB	Ab	aB	ab	Total		
<b>Pr pr, Eh eh (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 438	192	70	63	29	354	0.780	0.50-0.30
<b>Pr pr, Brl brl (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 438	201	68	73	18	360	1.131	0.30-0.20
<b>Pr pr, Yc yc (3 : 1) (3 : 1)</b>							
E.B. 171 × E.B. 417	398	41	104	20	563	..	..
E.B. 177 × E.B. 417	373	12	96	6	487	1.730	0.20-0.10
<b>K k, B b (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 132	334	96	130	49	609	1.817	0.20-0.10
C. 138-2 × E.B. 132	363	123	99	30	615	0.229	0.70-0.50
<b>Brl brl, Eh eh (3 : 1) (3 : 1)</b>							
K. 251 × E.B. 438	193	88	81	12	374	12.079	<0.01

TABLE 2

'T' test for independence between heading date and some qualitative characters in the F<sub>2</sub>

Character	Mean days taken for heading	Difference	't' = $\frac{D}{S.E.D}$	't' value at 5% level
<b>Ea<sub>3</sub> ea<sub>3</sub>, V v</b>				
Non-six-row (V)	95.3 ± 0.3293	0.7	1.06	1.959
Six-row (v)	94.6 ± 0.5382			
<b>Ea<sub>3</sub> ea<sub>3</sub>, Pr pr</b>				
Purple (Pr)	94.8 ± 0.2769	0.7	1.28	1.959
White (pr)	95.5 ± 0.5457			
<b>Ea<sub>3</sub> ea<sub>3</sub>, Ee</b>				
Long (E)	94.5 ± 0.3221	1.2	1.66	1.959
Short (e)	95.7 ± 0.5713			
<b>Ea<sub>3</sub> ea<sub>3</sub>, Brl brl</b>				
Broad (Brl)	95.0 ± 0.3323	0.5	0.76	1.959
Narrow (brl)	95.5 ± 0.4989			
<b>Ea<sub>3</sub> ea<sub>3</sub>, Eh eh</b>				
Semi-spreading (Eh)	95.8 ± 0.3402	3.0	4.8**	1.959
Erect (eh)	92.8 ± 0.5276			

\*\*Significant at 1 per cent level.

It would be seen that **V v** showed linkage with **Pr pr**. The loci **E e** and **Pr pr** themselves appeared to be linked in two crosses while they showed independent segregation in the third. **Eh eh** exhibited linked inheritance with **Brl brl** and **Ea<sub>3</sub> ea<sub>3</sub>**. All the other eighteen combinations studied showed that the concerned gene pairs were inherited independently of each other.

(b) *Estimation of linkage intensities.*—Whenever linkage was suspected, recombination value was worked out by the product method outlined by Immer (1930). The expected frequency distributions were calculated from the estimated cross-over values and compared with the observed values by subjecting the data to  $\chi^2$  analysis. The data showing linkage relations between various factor pairs are given in table 3.

TABLE 3

*Phenotypic distribution of F<sub>2</sub> population for different characters, from barley crosses in which linkage was suspected, with percentage recombination for each cross, as calculated by the product method*

Cross	Total number of plants					X <sup>2</sup>	P value
	AB	Ab	aB	ab	Total		
<b>V v, Pr pr</b>							
(i) <i>E.B. 171 × E.B. 417 (Coupling phase)</i>							
F <sub>2</sub> observed	.. 375	29	36	90	530		
Expected							
(11.8 ± 1.50%)	.. 368.07	29.43	29.43	103.07		3.621	0.50-0.30
(ii) <i>E.B. 177 × E.B. 417 (Coupling phase)</i>							
F <sub>2</sub> observed	.. 351	18	23	90	482		
Expected							
(9.2 ± 1.38%)	.. 340.34	21.16	21.16	99.34		1.840	0.70-0.50
(iii) <i>K. 251 × E.B. 438 (Coupling phase)</i>							
F <sub>2</sub> observed	.. 243	30	21	61	355		
Expected							
(15.3 ± 2.09%)	.. 241.17	25.08	25.08	63.67		1.755	0.70-0.50
<b>E e, Pr pr</b>							
(i) <i>E.B. 171 × E.B. 417 (Repulsion phase)</i>							
F <sub>2</sub> observed	.. 287	100	123	20	530		
Expected							
(39.2 ± 3.63%)	.. 285.35	112.15	112.15	20.35		2.436	0.50-0.30
(ii) <i>K. 251 × E.B. 438 (Repulsion phase)</i>							
F <sub>2</sub> observed	.. 189	80	76	16	361		
Expected							
(40.2 ± 3.48%)	.. 194.98	75.62	75.62	14.58		0.5773	0.95-0.90
<b>Brl brl, Eh eh</b>							
(iii) <i>K. 251 × E.B. 438 (Repulsion phase)</i>							
F <sub>2</sub> observed	.. 193	88	81	12	374		
Expected							
(34.5 ± 4.52%)	.. 198.13	82.37	82.37	11.13		0.608	0.90-0.80

It will be seen that the cross-over values between **v-pr**, worked out in the three crosses, ranged from 9.2 per cent. to 15.3 per cent. The linkage intensities between **e-pr**, in the two crosses were 39.2 per cent. and 40.2 per cent. The gene **eh** showed linkage with **brl** at a distance of 34.5 per cent. cross-over value. It also showed a significant association with **ea<sub>3</sub>**.

#### B. Analysis of back-cross data

The association between the factor pairs **V v K k**, **V v B b**, **K k B b** and **V v Pr pr** was studied from the backcross data. The results are set out in table 4.

TABLE 4

*X<sup>2</sup> test for independence between various characters from the test cross data*

Cross	Total number of plants					X <sup>2</sup>	P value
	AB	Ab	aB	ab	Total		
<b>V v, K k</b>							
(K. 251 × E.B. 132) F <sub>1</sub> × K. 251							
Observed	..	22	30	25	25	102	
Expected	..	25.5	25.5	25.5	25.5		1.284 0.80-0.70
(1 : 1 : 1 : 1)	..	25.5	25.5	25.5	25.5		
<b>V v, B b</b>							
(K. 251 × E.B. 132) F <sub>1</sub> × K. 251							
Observed	..	28	24	19	31	102	
Expected	..	25.5	25.5	25.5	25.5		3.177 0.50-0.30
(1 : 1 : 1 : 1)	..	25.5	25.5	25.5	25.5		
<b>K k, B b</b>							
(K. 251 × E.B. 132) F <sub>1</sub> × K. 251							
Observed	..	21	26	26	29	102	
Expected	..	25.5	25.5	25.5	25.5		1.284 0.90-0.70
(1 : 1 : 1 : 1)	..	25.5	25.5	25.5	25.5		
<b>V v, Pr pr</b>							
(E.B. 171 × E.B. 417) F <sub>1</sub> × E.B. 171							
Observed	..	7	1	2	9	19	
Expected	..	4.75	4.75	4.75	4.75		9.38 0.05-0.02
(1 : 1 : 1 : 1)	..	4.75	4.75	4.75	4.75		

There was no linkage between the loci studied in the back cross, (K. 251 × E.B. 132) × K. 251. In the other backcross, (E.B. 171 × E.B. 417) × E.B. 171, **V v** and **Pr pr** appeared to be linked with a recombination value of 15.8 per cent (Table 5).

TABLE 5

Phenotypic distribution with percentage recombination, of  $B_1$  population for **V v, Pr pr** from the back-cross (*E.B.* 171  $\times$  *E.B.* 417)  $F_1 \times E.B.$  171

Material	Total number of plants					$X^2$	P Value
	AB	Ab	aB	ab	Total		
Observed ..	7	1	2	9	19		
Expected (15.8 $\pm$ 8.41%) ..	6.83	2.67	2.67	6.83		1.532	0.70-0.50

### C. Analysis of $F_3$ data

(a) *Detection of linkage.*—The linkage relationship between various factor pairs was studied in the different crosses from the  $F_3$  data. In all, nineteen character combinations were studied in this generation. The observed frequencies for various genotypes, with the  $\chi^2$  test for independence are given in table 6.

TABLE 6

$X^2$  test for independence between genes for various characters, from  $F_3$  data

Material	Total number of families										$X^2$	P value
	AA BB	Aa BB	AA Bb	Aa Bb	AA bb	Aa bb	aa BB	aa Bb	aa bb	Total		
<b>Vv, Pr pr (1:2:1) (1:2:1)</b>												
<i>E.B.</i> 171 $\times$ <i>E.B.</i> 417 ..	17	13	3	29	0	4	1	6	26	99	79.38	<0.001
<i>E.B.</i> 177 $\times$ <i>E.B.</i> 417 ..	23	7	4	29	1	5	2	10	17	98	65.10	<0.001
<b>Vv, Yc yc (1:2:1) (1:2)</b>												
<i>E.B.</i> 171 $\times$ <i>E.B.</i> 417 ..	9	17	11	29	..	..	10	23	..	99	1.17	0.70-0.50
<i>E.B.</i> 177 $\times$ <i>E.B.</i> 417 ..	11	17	17	23	..	..	11	19	..	98	0.26	0.90-0.80
<b>Vv, K k (1:2:1) (1:2:1)</b>												
<i>K.</i> 251 $\times$ <i>E.B.</i> 132 ..	10	8	12	22	3	10	9	9	7	90	5.42	0.30-0.20
<i>C.</i> 138-2 $\times$ <i>E.B.</i> 132 ..	5	10	5	25	4	12	4	10	5	80	1.86	0.80-0.70
<b>Vv, B b (1:2:1) (1:2:1)</b>												
<i>K.</i> 251 $\times$ <i>E.B.</i> 132 ..	5	8	11	24	9	8	8	12	5	90	5.17	0.30-0.20
<i>C.</i> 138-2 $\times$ <i>E.B.</i> 132 ..	3	18	7	22	4	7	5	11	3	80	2.81	0.70-0.50
<b>Vv, Eh eh (1:2:1) (1:2:1)</b>												
<i>K.</i> 251 $\times$ <i>E.B.</i> 438 ..	1	2	5	10	1	7	5	8	0	39	6.71	0.20-0.10
<b>Vv, Brl brl (1:2:1) (1:2:1)</b>												
<i>K.</i> 251 $\times$ <i>E.B.</i> 438 ..	3	13	10	18	3	11	4	10	8	80	3.32	0.70-0.50
<b>Vv, Ea<sub>3</sub> ea<sub>3</sub> (1:2:1) (1:2:1)</b>												
<i>K.</i> 251 $\times$ <i>E.B.</i> 438 ..	1	2	5	10	1	7	5	8	0	39	6.71	0.20-0.10

TABLE 6—(Contd.)

Material	Total number of families									X <sup>2</sup>	P value	
	AA BB	Aa BB	AA Bb	Aa Bb	AA bb	Aa bb	aa BB	aa Bb	aa bb			Total
<b>E e, Pr pr (1:2:1) (1:2:1)</b>												
E.B. 171 × E.B. 417 ..	3	14	16	18	15	9	14	4	6	99	21.43	<0.001
E.B. 177 × E.B. 417 ..	10	13	8	22	7	10	7	9	5	91	1.64	0.90-0.80
<b>E e, Yc yc (1:2:1) (1:2)</b>												
E.B. 171 × E.B. 417 ..	9	17	11	29	..	..	10	23	..	99	1.18	0.50-0.30
E.B. 177 × E.B. 417 ..	13	17	12	28	..	..	6	15	..	91	3.61	0.20-0.10
<b>E e, Kk (1:2:1) (1:2:1)</b>												
K. 251 × E.B. 132 ..	6	14	9	22	7	8	7	11	5	89	1.57	0.90-0.80
C. 138-2 × E.B. 132 ..	5	6	4	24	6	12	7	13	3	80	7.16	0.20-0.10
<b>E e, Bb (1:2:1) (1:2:1)</b>												
K. 251 × E.B. 132 ..	6	8	13	23	3	13	7	10	6	89	3.18	0.70-0.50
C. 138-2 × E.B. 132 ..	4	15	6	19	5	8	7	15	1	80	6.36	0.20-0.10
<b>E e, Eh eh (1:2:1) (1:2:1)</b>												
K. 251 × E.B. 438 ..	3	3	4	12	3	4	2	7	1	39	2.48	0.70-0.50
<b>E e, Brl brl (1:2:1) (1:2:1)</b>												
K. 251 × E.B. 438 ..	7	6	10	22	8	10	7	6	4	80	5.15	0.30-0.20
<b>E e, Ea<sub>3</sub> ea<sub>3</sub> (1:2:1) (1:2:1)</b>												
K. 251 × E.B. 438 ..	6	15	17	16	2	7	5	7	5	80	6.22	0.20-0.10
<b>Pr pr, Yc yc (1:2:1) (1:2)</b>												
E.B. 171 × E.B. 417 ..	16	12	15	26	..	..	8	22	..	99	84.71	0.10-0.05
E.B. 177 × E.B. 417 ..	14	14	18	29	..	..	11	12	..	98	2.53	0.30-0.20
<b>Kk, Bb (1:2:1) (1:2:1)</b>												
K. 251 × E.B. 132 ..	8	6	11	28	8	9	7	8	5	90	6.56	0.20-0.10
C. 138-2 × E.B. 132 ..	5	11	13	19	8	10	2	9	3	80	1.87	0.80-0.70
<b>Ea<sub>3</sub> ea<sub>3</sub>, Brl brl (1:2:1) (1:2:1)</b>												
K. 251 × E.B. 438 ..	8	14	6	20	6	4	4	14	4	80	7.27	0.20-0.10
<b>Ea<sub>3</sub> ea<sub>3</sub>, Eh eh (1:2:1) (1:2:1)</b>												
K. 251 × E.B. 438 ..	1	4	9	11	6	3	3	2	0	39	9.31	Just 0.05
<b>Brl brl, Eh eh (1:2:1) (1:2:1)</b>												
K. 251 × E.B. 438 ..	3	1	2	14	3	2	5	6	3	39	9.99	0.05-0.02

The  $F_3$  data supplied added information concerning the apparent linkage or independence of the various character combinations. The results obtained in this generation were similar to those obtained in the  $F_2$  generation.

It will be seen from Table 6 that there was an indication of linkage between factor pairs **V v**, **Pr pr** in two crosses; between **E e**, **Pr pr** in one of the two crosses and between **Eh eh**, **Ea<sub>3</sub> ea<sub>3</sub>** and between **Brl brl**, **Eh eh**. The other factor combinations showed independent segregation.

(b) *Estimation of linkage intensities.*—In the crosses where there was an indication of linkage, the recombination values were worked out by the maximum likelihood method for the doubly dominant  $F_2$  phenotypes, classified into genotypes in the  $F_3$ . The equation to be maximized by differentiation with respect to 'p' from doubly dominant  $F_2$ s (AB), is given by Kramer and Burnham (1947).

The linkage intensities for the different character combinations in various crosses, as worked out from the  $F_3$  data, are set out in table 7.

TABLE 7

*Values of p calculated by the maximum likelihood method from the  $F_3$  data, together with their standard errors*

Source of data	Percentage recombination
<b>V v, Pr pr</b>	
E.B. 171 × E.B. 417 .. ..	20.0 ± 5.12
E.B. 177 × E.B. 417 .. ..	13.5 ± 4.06
<b>E e, Pr pr</b>	
E.B. 171 × E.B. 417 .. ..	43.5 ± 10.01
<b>Brl brl, Eh eh</b>	
K. 251 × E.B. 438 .. ..	43.0 ± 15.96
<b>Ea<sub>3</sub> ea<sub>3</sub>, Eh eh</b>	
K. 251 × E.B. 438 .. ..	38.0 ± 12.53

It will be seen from Table 7 that the linkage between the genes **V v**, **Pr pr** was 20.0 per cent. in the cross E. 171 × E.B. 417 and 13.5 per cent. in the cross E.B. 177 × E.B. 417. The genes **E e**, **Pr pr** were linked with a cross-over value of 43.5 per cent. The genes **Brl brl** showed linkage with **Eh eh** with a cross-over value of 43.0 per cent. and with **Ea<sub>3</sub> ea<sub>3</sub>** with a cross-over value of 38.0 per cent.

#### D. Combined linkage intensity values

The linkage intensities for different factor pairs obtained from different sources, viz.,  $B_1$ ,  $F_2$  and  $F_3$  generations, and from various crosses, were combined and an average p value worked out. Fisher's method of scoring (1946) was adopted to test the

homogeneity of the group of linkage intensities to be combined. When the data were considered homogeneous, the average *p* value was obtained by approximating the combined *p* value by weighting each separate recombination value by appropriate use of the amount of information furnished by each source of data.

The recombination percentages obtained from various sources of data, their test for homogeneity and the average *p* value, as determined from all the data combined, are summarized in table 8.

TABLE 8

*X*<sup>2</sup> test for homogeneity of different *p* values from various sources and the average weighted *P* values

Source of material	Percentage recom- bination			<i>X</i> <sup>2</sup> for homoge- neity	D.F.	<i>P</i> value from <i>X</i> <sup>2</sup> for homo- geneity	Average percentage recombina- tion by weigh- ting
	<i>F</i> <sub>2</sub>	<i>F</i> <sub>3</sub>	<i>B</i> <sub>1</sub>				
<b>V v, Pr pr</b>							
E.B. 171 × E.B. 417 ..	11.8	20.0	15.8				
E.B. 177 × E.B. 417 ..	9.2	13.5	..	7.72	5	0.20-0.10	11.74±0.3
K. 251 × E.B. 438 ..	15.3	..	..				
<b>E e, Pr pr</b>							
E.B. 171 × E.B. 417 ..	39.2	43.5	..				
K. 251 × E.B. 438 ..	40.2	..	..	0.109	2	0.95-0.90	39.88±2.59
<b>Brl brl, Eh eh</b>							
K. 251 × E.B. 438 ..	34.5	43.0	..	1.674	1	0.20-0.10	35.12±4.32
<b>Ea<sub>3</sub> ea<sub>3</sub>, Eh eh</b>							
K. 251 × E.B. 438 ..	Corre- lated	38.0	..	..	..	..	38.0±12.53

## DISCUSSION

The work done by previous workers indicates that the factors **V v**, **E e**, **Pr pr**, **B b** and **K k** are located in linkage groups I, I, I, II and IV respectively (Ubisch, 1919; Miyake and Imai, 1929; Robertson, 1929; Buckley, 1930; Daane, 1931 and others). The factors for normal *vs* virescent seedlings have been located in two linkage groups, I and VII and have been designated as **Y y** and **Yc yc** respectively (Robertson *et al.* 1941). In the present study, the normal *vs* virescent seedling character did not show any linkage with **V v**, **E e** and **Pr pr**, reported to be located in linkage group I. The factor controlling virescence of E.B. 171 and E.B. 177 is, therefore, likely to be located in linkage group VII. This, however, needs confirmation by studying the relationship of this factor with the marker genes of group VII.

The fact that the factors **V v**, **E e** and **Pr pr** are located in the linkage group I, as observed by a number of other workers, is confirmed by the results obtained in the

present study. These factors appeared to be linked with each other, the cross-over values between **v-pr**, and **e-pr** being 11.74 per cent. and 39.9 per cent. respectively. Between **v-pr**, Robertson (1933) calculated the recombination value to be 9.0 per cent. Woodward (1957) reported this value to be 16.0 per cent. Between **v-e**, the recombination values reported by different workers were 26.6 per cent. (Robertson, Immer, Wiebe and Stevenson, 1944), 24.7 per cent. (Bose, Aziz and Bhatnagar, 1937), 28.0 per cent. (Immer and Henderson, 1943), and 26.7 per cent. (Swenson and Wells, 1944). Woodward (1957) studied five crosses with regard to these factor pairs and found that in four crosses the linkage values ranged from 26.5 to 27.0 per cent., while in the fifth cross there was no linkage between these characters. In the present study also such a situation has been met with. The reasons for such a discrepancy are, however, not quite clear from the data available in this study, though several reasons have been suggested (Woodward, 1957). The information on the linkage relationship between the factors **e-pr** does not seem to be reported in the literature so far.

The factors **eh-brl** and **eh-ea<sub>3</sub>** showed linkage with cross-over values of 35.12 per cent. and 38.0 per cent. respectively, while **ea<sub>3</sub>** and **brl** appeared to show independent inheritance from each other. These data, therefore, suggest that the order of these three genes is **ea<sub>3</sub>-eh-brl**. Information on the linkage relationships of these genes are being reported for the first time. These genes were found to be inherited independently of the factors on chromosome I.

Factors for heading date have been located in three linkage groups, *viz.* I, IV and V and have been designated as **Ea ea**, **Ea<sub>2</sub> ea<sub>2</sub>** and **Ea<sub>3</sub> ea<sub>3</sub>** respectively (Griffie, 1925; Neatby, 1929 and Robertson *et al.*, 1947). In the present study, heading date did not show any linkage with **V v**, **E e** and **Pr pr** of group I. This, therefore, suggests that the factor **Ea ea** does not operate in controlling the expression of heading date in the cross under study. The factor controlling this character in this cross may, therefore, be located in linkage group IV or V. The factor controlling semi-spreading *vs* erect type of early growth habit (**Eh eh**) does not seem to have been studied previously although information is available on the factors controlling spring *vs* winter habit. Three independent factors, *viz.*, **Sh sh**, **Sh<sub>2</sub> sh<sub>2</sub>** and **Sh<sub>3</sub> sh<sub>3</sub>**, have been reported to control the expression of this character. Takahashi and Yasuda (1956) showed that the factor pair **Sh<sub>2</sub> sh<sub>2</sub>** is linked with **R r** for awn barbing and **S s** for rachilla hairs in the order **Sh<sub>2</sub>-r-s**, in linkage group V. Walker, Kasha and Miller (1958) have reported that the factor for broad leaves is linked with the factor controlling long *vs* short-haired rachilla (**S s**) in linkage group V. If it is considered that the factor controlling the leaf shape (**Brl brl**) in the cross under study is the same as that reported by Walker *et al.* (1958) and is located on chromosome V, then the factors for heading date and early growth habit can be located on chromosome V, as they show linkage with the factor for leaf shape, their order of arrangement being **ea<sub>3</sub>-eh-brl**. However, the assumption that these genes lie on chromosome V needs further confirmation by studying their relationship with other marker genes in linkage group V.

#### SUMMARY

Linkage relationships between twenty-two character combinations were studied in the different crosses of barley in the F<sub>2</sub>, F<sub>3</sub> and B<sub>1</sub> generations.

The factors controlling the expression of normal *vs*. virescent seedlings (**Yc yc**), hoods *vs*. awns (**K k**), black *vs*. white lemma and pericarp (**B b**), broad *vs*. narrow leaves (**Brl brl**) and heading date (**Ea<sub>3</sub> ea<sub>3</sub>**) showed independent inheritance from the factors for non-six row *vs*. six row (**V v**) and long *vs*. short outer glume awns (**E e**). The factors **Eh eh**, **Brl brl**, **Ea<sub>3</sub> ea<sub>3</sub>** and **Yc yc** were inherited independently of **Pr pr** (purple *vs*. white leaf sheath). The factor **K k** also showed independent inheritance from **B b** factor.

It appears that the factors **V**, **e** and **pr** belong to linkage group I, the cross-over values among **v-pr** and **e-pr**, being  $11.74 \pm 0.87$  per cent and  $39.88 \pm 2.69$  per cent respectively.

The cross-over values between the genes **eh-brl**, **eh-ea<sub>3</sub>** were  $35.12 \pm 4.32$  per cent. and  $38.0 \pm 12.53$  per cent. respectively, while **ea<sub>3</sub>** and **brl** appeared to show independent inheritance. The order of these genes, therefore, appears to be **ea<sub>3</sub>-eh-brl**; none of these genes showed any linkage with marker genes in linkage group I. The possibility of these genes belonging to linkage group V is discussed.

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