GENETIC RESISTANCE TO DDT IN *HORDEUM*

I. LINKAGE STUDIES IN DIPLOID BARLEY

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1. INTRODUCTION

THE application of DDT to susceptible genotypes of *Hordeum* causes marked chlorosis, and even death (Hayes, 1959, 1960). Hayes (1960), and Wiebe and Hayes (1960) found that resistance was controlled by a single recessive gene *ddt*. In a series of related analogues of DDT, Wiebe (1964), and Upshall and Goodwin (1964) showed that the configuration of the molecule was more important than its chemical composition in conferring phytocidal activity. Upshall and Goodwin (1964) concluded from their investigations that the toxic effect of DDT on a susceptible genotype was due to its gaining access to a functional lipoprotein in the chloroplast by penetrating the covering membrane; in resistant genotypes, DDT is adsorbed on the chloroplast, but presumably, does not penetrate the chloroplast membrane.

The present investigations were designed to locate the *ddt* locus on one of the seven linkage groups of barley (*Hordeum sativum* Jess.). The nomenclature adopted for the chromosomes and linkage groups is that described by Ramage, Burnham and Hagberg (1961).

2. MATERIALS AND METHODS

Two series of crosses were investigated: the first involved crosses of parents with contrasting genetic markers, and the second a set of crosses between normal parents and a series of translocation stocks.

(i) *Genetic markers*

A summary of the information regarding the genetic markers with their linkage group and symbol designation is given in table 1.

All the genetic marker stocks were DDT susceptible and were crossed with Cb 763 (Proctor), which is DDT resistant. All the genetic markers used were known to be simply inherited and distributed amongst the seven linkage groups.

(ii) *Translocation stocks*

The second series of crosses was made between normal cultivars, either the DDT resistant Cb 763 (Proctor) or the susceptible Cb 545 (Rika), and seven homozygous interchange stocks with contrasting DDT reaction. These stocks contain translocations which involve each of the seven chromosomes, and were provided by Dr R. T. Ramage, University of Arizona, Tucson. In an F_2 population, derived from a cross of a normal genotype with a reciprocal translocation stock, a ratio of 1 normal : 2 heterozygous translocations : 1 homozygous translocation is expected. Since normal and

homozygous translocation stocks both have normal fertility, and genotypes heterozygous for translocations show signs of sterility (referred to as semisterility), a phenotypic ratio of 1 fertile : 1 semisterile is expected in the F_2 generation. After a series of comparisons of parents (0-6 per cent. sterility) and F_1 hybrids (18-40 per cent. sterility) 10 per cent. ovule sterility was selected as the point of differentiation between normal and semisterile individuals.

All the F_1 hybrids containing the genetic markers and translocations were produced in the glasshouse during the summer and grown under supplementary light in the following winter. F_2 plants were sown in 3 inch whalehide pots and transplanted to a bird-proof nursery.

TABLE 1

Summary of genetic characters with their linkage groups and gene symbol designations used in linkage tests with the Ddtddt *gene*

W.P.B.S. Accession No.†	Linkage group and chromosome number	Character pair	Gene symbols
Cb 822	1	Green *vs* chlorina seedlings	$F_c f_c$
Cb 823		Normal *vs* brachytic	*Brbr*
Cb 819, Cb 820, Cb 823		Covered *vs* naked caryopsis	*Nn*
Cb 868	2	Awn *vs* awnless	*Lklk*
Cb 854		Normal *vs* orange seedlings	*Oror*
Cb 820, Cb 822, Cb 823		Six row *vs* two row	*Vv*
Cb 819	3	Green *vs* white seedlings	$A_n a_n$
Cb 820		Normal *vs* streaked seedling	*Stst*
Cb 861		Normal *vs* " Uzu "	*Uzuz*
Cb 822	4	Hooded *vs* awned	*Kk*
Cb 870		Green *vs* glossy seedlings-2	$Gl_2 gl_2$
Cb 819	5	Black *vs* white lemma and pericarp	*Bb*
Cb 869		Normal *vs* third outer glume	*Trdtrd*
Cb 865	6	Normal *vs* orange lemma	*Oo*
Cb 865	7	Rough *vs* smooth awn	*Rr*
Cb 867		Short *vs* long basal internode	*Lblb*

† Stocks Cb 819-823 supplied by Dr D. W. Robertson, Colorado State University. Stocks Cb 861-87c supplied by Dr A. Hagberg, Svalöf, Sweden.

The DDT reaction of F_2 phenotypes was obtained by applying a 0·2 per cent. aqueous emulsion of DDT (1,1,1,-trichloro 2,2-bis-(*p*-chlorophenyl) ethane) to a single leaf of each plant (Rana, 1965). The genetic constitution of the F_2 plants was checked by testing 20 F_3 seedlings from each F_2 plant. The most pronounced symptoms of DDT chlorosis on susceptible plants were apparent 2 weeks after application; resistant plants showed no sign of chlorosis.

Tests for goodness of fit of observed to theoretical ratios were made by the use of χ^2. The test for heterogeneity was that described by Mather (1951). Where irregularities in the behaviour of individual characters occurred in a dihybrid ratio, the observed frequencies were compared with theoretical frequencies calculated by the use of contingency tables, also outlined by Mather (*loc. cit.*).

Linkage intensities were calculated from the tables provided by Joachim (1947). These tables enabled the standard error and recombination percentage to be computed from F_2 data, using the product method.

TABLE 2

Tests for independent segregation in F_2 *populations of* Ddtddt *and three genetic markers located in linkage group 1*

Cb 763 crossed with	Genotypes tested				F_2 phenotypes				Total	χ^2	P
	X	*x*	*Y*	*y*	*XY*	*Xy*	*xY*	*xy*			
Cb 822	F_c	f_c	*Ddt*	*ddt* O	421	150	151	59	781	3·41	0·20-0·50
				E	439·3	146·4	146·4	48·8			
Cb 823	*Br*	*br*	*Ddt*	*ddt* O	1454	438	495	156	2543	4·30	0·20-0·50
				E	1430·5	476·8	476·8	158·9			
Cb 823	*N*	*n*	*Ddt*	*ddt* O	415	164	139	57	775	5·17	0·10-0·20
				E	435·6	145·2	145·2	48·2			
Cb 819	*N*	*n*	*Ddt*	*ddt* O	306	116	131	48	601	9·01	0·02-0·05
				E	338·1	112·7	112·7	37·5			
Cb 820	*N*	*n*	*Ddt*	*ddt* O	47	27	19	6	99	5·24	0·10-0·20
				E	55·7	18·5	18·5	6·2			
Total for 3 crosses	*N*	*n*	*Ddt*	*ddt* O	768	307	289	111	1475	12·34	<0·01
				E	829·8	276·6	276·6	92·2			

O = observed frequency.
E = expected frequency.
χ^2 test for heterogeneity of *Nn* and *Ddtddt* = 7·08 (6 d.f.)
(P = 0·20-0·50)

3. RESULTS

(i) *Tests for linkage with genetic markers*

The results of the linkage tests for each group are presented separately, similar analytical methods were applied throughout, but they are reported in detail only for Group 1.

The three characters chlorina (f_c), brachytic (*br*) and naked (*n*) have been located in Group 1. The observed ratios, and those expected if the genetic markers and *Ddtddt* were inherited independently (9:3:3:1 ratio), are given in table 2 with the χ^2 and probability values.

The χ^2 and probability values for linkage of F_c f_c with *Ddtddt* ($\chi^2 = 3{\cdot}41$; P = 0·20-0·50) and *Brbr* with *Ddtddt* ($\chi^2 = 4{\cdot}30$; P = 0·20-0·50) indicate that they are independent. The factor *Nn* was studied in three crosses; in two of these crosses, Cb 763 × Cb 820 and Cb 763 × Cb 823, the probability for independence was low but not significant (P = 0·10-0·20). In the remaining cross, Cb 763 × Cb 819, there was a significant deviation (P = 0·02-0·05) of the observed from the expected ratio of 9:3:3:1. The combined data from all three crosses for *Nn* also depart significantly (P = <0·01) from the expected ratio, the heterogeneity test indicating that the disturbance of the observed segregation from the expected was similar in all three families.

To test the nature of the disturbance from the expected 9:3:3:1 ratio, the deviations of the *Ddtddt* and *Nn* factors from an expected 3:1 ratio, were examined separately. χ^2 values for each family and for the combined data are given in table 3.

The heterogeneity test shows that, averaged over all the crosses, *Ddtddt* did not segregate according to a 3:1 ratio and that the three families were consistent in giving an excess of resistant plants. The χ^2 value for the *Nn* factor suggested that there might be some deviation from a 3:1 ratio (P = 0·05-0·10), but the data of the individual χ^2 values for each family indicated that only the progeny from Cb 763 × Cb 819 deviated markedly from a 3:1 ratio.

Since the segregation of the *Ddtddt* factor deviated from a 3:1 ratio in this series of crosses, the χ^2 for independence was calculated in a 2 × 2 contingency table. The expected frequencies of the four phenotypic classes, using the observed ratio of 2·5 DDT susceptible: 1 DDT resistant, and 2·7 covered: 1 naked, and assuming no linkage, were:

Frequency	*Ddt N*	*Ddt n*	*ddt N*	*ddt n*
Expected	771·8	283·8	306·4	113·5
Observed	768	307	289	111

This provides a χ^2 value of 0·121 (1 d.f.) with a probability value between 0·50-0·95, indicating an absence of any linkage of *Ddtddt* with *Nn*. A summary of the results from similar tests for independence of *ddt* with markers in all seven linkage groups is given in table 4.

TABLE 3

Segregation for the factor Ddtddt *and* Nn *and* χ^2 *values for the deviation of observed from expected 3:1 ratios*

Cb 763 crossed with	Phenotypes		χ^2	P 1 d.f.	Phenotypes		χ^2	P 1 d.f.
	DDT Susc. (*Ddt*)	DDT Res. (*ddt*)			Covered (*N*)	Naked (*n*)		
Cb 819	437	164	1·68	0·20-0·50	422	179	7·33	<0·01
Cb 820	66	33	3·67	0·05-0·10	74	25	0·00	0·50-0·95
Cb 823	554	221	5·11	0·01-0·02	579	196	0·04	0·50-0·95
Total for 3 crosses	1057	418	8·77	<0·01	1075	400	3·53	0·05-0·10

Heterogeneity test

	χ^2	DDT reaction		Covered *vs* naked		P
		d.f.	P	χ^2	d.f.	
Deviation	8·77	1	<0·01	3·53	1	0·05-0·10
Heterogeneity	1·69	2	0·30-0·50	3·84	2	0·10-0·20
Total	10·46	3		7·37	3	

TABLE 4

Summary of tests for independent segregation in F_2 populations of Ddt ddt *and genetic markers located in the seven linkage groups of barley*

Linkage group tested	Cb 763 crossed with	Genotypes tested				F_2 phenotypes				Total	Deviations from expected (9:3:3:1) ratio		Deviations from expected in 2×2 contingency table	
		X	*x*	*Y*	*y*	*XY*	*Xy*	*xY*	*xy*		χ^2	P	χ^2	P
1	Cb 822	*Fc*	*fc*	*Ddt*	*ddt*	421	150	151	59	781	3·41	0·20-0·50		
	Cb 823	*Br*	*br*	*Ddt*	*ddt*	1454	438	495	156	2543	4·30	0·20-0·50		
	Cb 823, Cb 819, Cb 820	*N*	*n*	*Ddt*	*ddt*	768	307	289	111	1475	12·34	>0·01	0·121	0·50-0·95
2	Cb 854	*Or*	*or*	*Ddt*	*ddt*	117	37	37	15	206	0·49	0·50-0·95		
	Cb 868	*Lk*	*lk*	*Ddt*	*ddt*	94	29	33	10	166	0·28	0·95-0·99		
	Cb 820, Cb 823, Cb 822	*V*	*v*	*Ddt*	*ddt*	900	349	292	114	1655	8·01	0·02-0·05	0·10	0·50-0·95
3	Cb 820	*St*	*st*	*Ddt*	*ddt*	421	127	166	54	768	6·40	0·05-0·10	0·185	0·95-0·99
	Cb 861	*Uz*	*uz*	*Ddt*	*ddt*	189	51	67	26	333	3·74	0·20-0·50		
	Cb 819†	A_n	a_n	*Ddt*	*ddt*	443	163	...	...	606	1·16	0·50-0·95		
4	Cb 822	*K*	*k*	*Ddt*	*ddt*	427	149	145	60	781	2·97	0·20-0·50		
	Cb 870	Gl_2	gl_2	*Ddt*	*ddt*	184	56	57	15	312	1·60	0·50-0·95		
5	Cb 819	*B*	*b*	*Ddt*	*ddt*	325	123	116	42	606	2·01	0·50-0·95		
	Cb 869	*Trd*	*trd*	*Ddt*	*ddt*	105	32	33	10	180	2·04	0·50-0·95		
6	Cb 875	*O*	*o*	*Ddt*	*ddt*	69	33	20	8	130	4·07	0·20-0·95		
7	Cb 865	*R*	*r*	*Ddt*	*ddt*	72	34	17	7	130	6·21	0·05-0·10	0·087	0·50-0·95
	Cb 867	*Lb*	*lb*	*Ddt*	*ddt*	113	34	57	21	225	11·28	0·01-0·02	0·30	0·50-0·95

χ^2 for heterogeneity of *Nn* and *Ddt ddt* = 7·08 (6 d.f.) P = 0·20-0·50.
χ^2 for heterogeneity of *Vv* and *Ddt ddt* = 7·69 (6 d.f.) P = 0·20-0·50.
† Expected ratio 3 *XY*:1 *Xy*.

Whenever there was a significant deviation from the expected 9:3:3:1 ratio, the data were re-tested after adjustment for any deviations of the individual segregation from an expected 3:1 ratio. None of the χ^2 values calculated on this basis were significant.

The factor a_n located in group 3 is a recessive lethal and consequently 25 per cent. of each population is lost. Progeny tests yielded information which enabled the genetic constitution of the F_2 plants to be inferred:

Cross	Genotypes tested				F_2 genotypes (Expected 6:3:2:1)				Total	χ^2	P
	X	*x*	*Y*	*y*	*XxY*	*XXY*	*Xxy*	*XXy*			
Cb 819 × Cb 763	A_n	a_n	*Ddt*	*ddt*	O 279 E 303·0	164 151·5	104 101·0	59 50·5	606	3·86	0·20-0·50

Thus it would appear from the results presented in table 4 that there is a complete lack of association between the *ddt* locus and any of the markers listed in table 1.

(ii) *Tests for linkage in translocation stocks*

A summary of the results of F_2 segregations in crosses between 7 translocation stocks and normal stocks of contrasting DDT reaction is presented in table 5. The F_2 progeny of three crosses involving *T*1-6*a*, *T*3-7*a* and *T*4-5*a* were grown in both 1963 and 1964, since analysis of F_3 data from these three crosses in 1963 did not fit the expected ratios.

In 1963 progeny involving five translocation stocks failed to fit ($P = 0{\cdot}05$) the expected ratio of 3 DDT susceptible semisterile: 3 DDT susceptible fertile: 1 DDT resistant semisterile: 1 DDT resistant fertile. In four of these five crosses there were deviations from the expected ratios for either *Ddt* segregating or semisterility, but in the fifth cross (involving *T*3-7*a*) neither character deviated significantly from the expected, and yet there was an overall deviation from the expected 3:3:1:1 ratio. The χ^2 for independence was obtained by subtracting from the χ^2 for joint segregation the two χ^2 values for the loci segregating individually. The non-significant χ^2 values for linkage of *Ddtddt* with semisterility indicate that the gene was independent of the points of interchange in six translocations, but for the cross involving *T*3-7*a* the χ^2 value (15·34) was highly significant, indicating that the *Ddt* gene was linked with the points of interchange in this translocation stock. The results from the 1964 tests confirm this point.

The χ^2 values from the other two translocations containing chromosomes 3 and 7, *T*2-3*d* and *T*6-7*b*, did not give any sign of linkage.

(iii) *Predictions regarding the position of the* ddt *locus*

All the available information regarding the genetical and cytological maps of the seven chromosomes of barley has been presented by

TABLE 5

Summary of tests for linkage between the Ddtddt *gene and the break point in F_2 populations from crosses of normal with interchange stocks*

Translocation† × normal (*N*) *Ddt* or *ddt*	F_2 phenotypes††				Total	χ^2 and probabilities for			
	Ddt S	*Ddt* F	*ddt* S	*ddt* F		Joint segregation 3:3:1:1	*Ddt*:*ddt* 3:1	F:S 1:1	Independence
1963									
*T*1-5*a*×*N Ddt*	83	122	26	33	264	9·40 0·02-0·05	0·99 0·20-0·50	8·02 0·01	0·39 0·50-0·95
*T*1-6*a*×*N ddt*	111	93	53	36	293	9·94 0·01-0·02	4·52 0·02-0·05	4·18 0·02-0·05	1·24 0·20-0·50
*T*2-3*d*×*N ddt*	89	92	40	58	279	19·92 <0·01	17·24 <0·01	1·58 0·20-0·50	1·10 0·20-0·50
*T*2-4*a*×*N ddt*	99	116	36	26	277	3·85 0·20-0·50	1·01 0·20-0·50	0·18 0·50-0·95	2·66 0·10-0·20
*T*3-7*a*×*N ddt*	129	80	28	50	287	18·61 <0·01	0·73 0·20-0·50	2·54 0·10-0·20	15·34 <0·01
*T*4-5*a*×*N ddt*	97	102	34	32	265	0·18 0·95-0·99	0·01 0·50-0·95	0·04 0·50-0·95	0·13 0·50-0·95
*T*6-7*b*×*N Ddt*	134	89	47	24	294	16·47 <0·01	0·36 0·50-0·95	15·72 <0·01	0·39 0·50-0·95
1964									
*T*1-6*a*×*N ddt*	187	162	59	51	459	2·63 0·10-0·20	0·26 0·50-0·95	2·37 0·10-0·20	0·0 0·99
*T*3-7*a*×*N ddt*	190	145	31	89	455	35·96 <0·01	0·46 0·50-0·95	0·38 0·50-0·95	35·12 <0·01
*T*4-5*a*×*N ddt*	176	157	67	51	451	3·45 0·20-0·50	0·32 0·50-0·95	2·71 0·10-0·20	0·42 0·50-0·95

† Nomenclature according to Ramage *et al.* (1961) †† S:semisterile. F:Fertile (normal) plants.

Nilan (1964). From these maps it is clear that the characters used in this investigation are located in each of the 7 chromosomes. *br*, f_c and *n* on 1, *Lk*, *v* and *or* on 2, a_n, *uz*, and *st* on 3, *K* and gl_2 on 4 provide markers in both arms of these chromosomes. But *trd* and *B* provide markers only in the short arm of chromosome 5, while *o* in chromosome 6 is near the centromere and *R* and *lb* are both located in the long arm of chromosome 7 (Robertson *et al.*, 1955). Since there is no evidence of any linkage with the genetic markers investigated, it is highly probable that *ddt* is not located on chromosome 1, 2, 3 or 4. On the other hand, since any two loci separated by more than 50 crossover units appear in inheritance to be independent, it is clear that if the *ddt* gene is located in the long arm of chromosome 5, or in the extremity of either arm of 6, or the short arm of 7, it would be possible to miss any association with the characters used in this investigation. However, Hayes (unpublished) has evidence that *ddt* is independent of the genes responsible for mildew resistance from *H. spontaneum* which are located in the long arm of chromosome 5 (Moseman, 1964).

Data from the crosses involving the seven translocation stocks indicate quite clearly that the *ddt* locus is linked with the break-point in translocation stock *T*3-7*a* (table 5). It was not possible to decide from the data of the translocation stocks alone, whether *ddt* was located on chromosome 3 or 7, since neither *T*2-3*d* nor *T*6-7*b* showed any sign of linkage with *ddt*. However, by considering the data from the genetic markers and translocations, it was possible to infer that *ddt* was located in the short arm of chromosome 7.

To test the validity of this inferenc , a further series of translocation stocks with break-points located in cl.romosome 7, was obtained from Dr R. T. Ramage. These were crossed with normal parents having a contrasting DDT reaction; the F_2 segregates from these crosses were grown and studied in 1965. A summary of the linkage data from all crosses involving chromosome 7 is given in table 6, along with the calculated degree of recombination and standard errors.

Accepting the break positions given by Burnham and Hagberg (1956), Ramage, Burnham and Hagberg (1961), and Ramage and Suneson (1961), the most probable location of *ddt* in relation to the break-points and the marker genes studied, is illustrated in fig. 1.

According to Ramage and Suneson (1961) the break-point of *T*6-7*b* is located in the long arm and *T*6-7*a* probably in, or near, the centromere. *T*1-7*a* is broken in the short arm and, according to our results, *ddt* is estimated to be 7 crossover units away, but it is not possible to decide whether it is on the proximal or distal side. *T*4-7*b* and *T*1-7*c* are broken in the satellite region. Ramage and Suneson (*loc. cit.*) proposed that the break-point of *T*3-7*a* was located in the short arm of chromosome 7, however, Kasha and Burnham (1965) were of the opinion that the break was in the long arm relatively near the centromere; our results confirm this latter view, since the break of *T*6-7*a* in or near the centromere has a recombination value of $0{\cdot}11 \pm 0{\cdot}033$ with

TABLE 6

F_2 phenotypic frequencies for determining the degree of recombination in crosses containing translocations involving chromosome 7 and normal stocks

Cross	Source of F_2 information	Observed F_2 frequency					Per cent. Recombination	S.E.±
		Ddt, S. a	*Ddt*, F. b	*ddt*, S. c	*ddt*, F. d	Total		
T3-7a × *N ddt*	1963	129	80	28	50	287	0·19	±0·039
T3-7a × *N ddt*	1964	190	145	31	89	455	0·16	±0·027
T3-7a × *N ddt*	Combined	319	225	59	139	742	0·17	±0·022
T6-7b × *N Ddt*	1963	134	89	47	24	294	Independent	
T6-7a × *N Ddt*	1965	97	62	10	36	205	0·11	±0·033
T4-7b × *N Ddt*	1965	112	47	20	42	221	0·13	±0·034
T1-7a × *N ddt*	1965	130	61	8	46	245	0·07	±0·021
T1-7c × *N ddt*	1965	101	69	18	22	210	0·27	±0·063

ddt, compared with 0·17±0·022 for the break of *T*3-7*a*. This location of the *ddt* gene would explain its lack of association with any of the genetic markers tested and with the break of *T*6-7*b*.

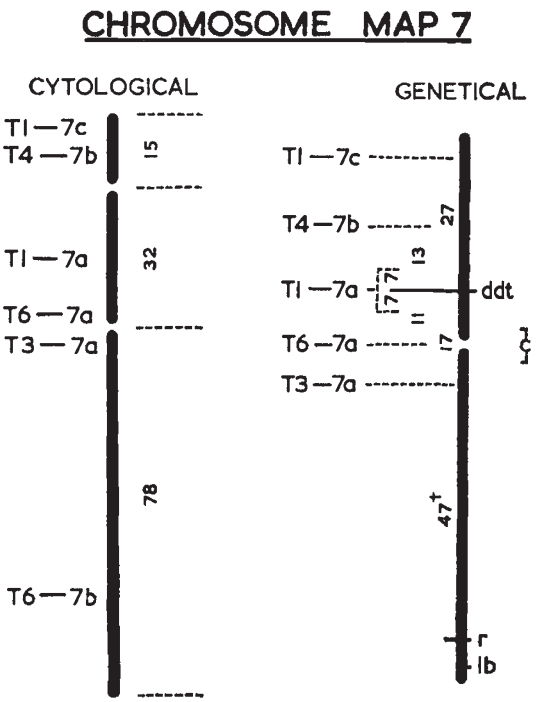

FIG. 1.†—Cytological and genetical maps of chromosome 7.

† (according to Kramer and Blander, 1961).

4. DISCUSSION

Previous studies (Hayes, 1959, 1960; Wiebe and Hayes, 1960) have indicated that DDT resistance in barley is controlled by a single recessive gene *ddt*. The results of this investigation confirm this conclusion, but in progeny segregating for covered *versus* naked (*Nn*), and two-row *versus* six-row (*Vv*), there proved to be an excess of DDT resistant genotypes. The χ^2 test for homogeneity showed that in each case this bias was consistent in three different crosses, however, there does not appear to be any genetic reason for the excess of resistant genotypes in these particular hybrids.

Some difficulty was experienced in classifying segregates from crosses of normal and translocation stocks since the degree of ovule sterility varied considerably both within and between crosses.

Nilan (1964) indicated that the variation in sterility could be due to the nature of the interchange and the manner of chromosome segregation from the interchange complex. The degree of sterility in an individual plant can be affected by the environment as well as by

the frequency of crossing over between the centromere and the point of interchange. Ramage (1964) suggested that the lower-than-expected degree of sterility from the single interchange heterozygotes in barley is probably due to a high frequency of alternate disjunction from the interchange complex, which leads to a reduced recovery of cross-overs in regions included in the interstitial segments *i.e.* the regions between the centromere and the translocation break-point. Thus the actual distance, as measured by normal genetic markers, is likely to exceed the estimate obtained by using stocks with break-points on the distal side of the *ddt* locus.

This investigation has demonstrated the value of translocations or chromosomal interchange break-points as genetic markers for mapping those segments of the chromosome which do not, as yet, have any easily identifiable loci. Locating *Ddtddt* on the short arm of chromosome 7 provides a convenient genetic marker for further studies on the linkage relationships of factors in group 7, which is not as yet endowed with a large number of easily identified markers.

5. SUMMARY

1. Results from numerous hybrid progenies confirmed that resistance to DDT chlorosis in barley was due to a single recessive gene *ddt*.

2. Sixteen well known genetic markers, involving all seven linkage groups, were used in inheritance studies, but they failed to show any linkage with *ddt*.

3. Crosses involving seven translocation stocks which included all seven chromosomes revealed a linkage of $0{\cdot}17 \pm 0{\cdot}022$ with the break-point in *T*3-7*a*. No association was detected with *ddt* and the break-points in *T*2-3*d* and *T*6-7*b*.

4. Further crosses involving four translocation stocks with break-points in the short arm of chromosome 7 confirmed that *ddt* is located in that arm with recombination values of $0{\cdot}07 \pm 0{\cdot}021$, $0{\cdot}11 \pm 0{\cdot}033$, $0{\cdot}13 \pm 0{\cdot}034$, $0{\cdot}27 \pm 0{\cdot}063$, with the break-points in *T*1-7*a*, *T*6-7*a*, *T*4-7*b* and *T*1-7*c* respectively.

6. REFERENCES

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