Carlsberg Res. Commun. Vol. 42, p. 35-43

THE LOCALIZATION OF ECERIFERUM LOCI IN BARLEY. IV. THREE POINT TESTS OF GENES ON CHROMOSOME 7 IN BARLEY

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Key words: Hordeum vulgare, erectoides, laxatum, variegated, dearistatum, map of ten genes

Eleven three point tests are reported for chromosome 7 in barley. The tests were analysed in the F_3 generation. The results permit the construction of a map for the ten genes studied.

Earlier work with translocation tester sets and two point tests has shown the following genes to be located on chromosome 7: the eceriferum genes *cer-i, cer-t, cer-w, cer-zj* and *cer-zp,* the erectoides genes *ert-g* and *ert-n,* the *laxatum* gene *lax-a,* the *variegated* gene *va* and the *dearistatum* gene *ari-c* (4, 12, 13, 14, 10, 11, 16). In order to map these genes on the chromosome eleven independent three point tests involving these ten loci have been made.

All mutant markers used are recessive and have generally well expressed morphological characters. *Eceriferum* denotes organ specific changes in the waxcoating, *erectoides* dense ears, *laxatum* lax ears, *variegated* yellow stripes on leaves, and *dearistatum* short awns. In each of the eleven three point tests the genes are combined in such a way that all 27 possible F_2 genotypes can be distinguished by progeny analysis in F_3. Between 780 and 1759 F_2 plants have been analysed per test cross, and only F_2 progenies with normal segregation ratios were used for the F_3 analysis. Environmental influences on crossover frequencies have been minimised by growing the F_1 generation under standard conditions in the phytotron (2). The resulting map is presented in Figure 1.

2. MATERIALS AND METHODS

The following mutants have been used as markers: *cer-i*^{16} (7), *cer-t*^{22}(7), *cer-zj*^{78}(8), *cer-zp*^{313} (8), *cer-w*^{48}(8), *ert-g*^{24} (9), *ert-n*^{51} (9), *lax-a*^{4} (10), *ari-e*^{1} (10) in Bonus background and *va* (16) in Montcalm background. From crosses involving these mutants (4, 12, 13, 14) the following double mutant lines have been isolated:

cer-t^{22} *cer-zj*^{78}, *ari-e*^{1} *cer-zj*^{78}, *lax-a*^{4} *cer-zj*^{78}, *cer-w*^{48} *ert-g*^{24}, *cer-t*^{22} *cer-zp*^{313}, *cer-i*^{16} *cer-zp*^{313}, *lax-a*^{4} *cer-i*^{16}, *lax-a*^{4} *ert-g*^{24}. Each of these double

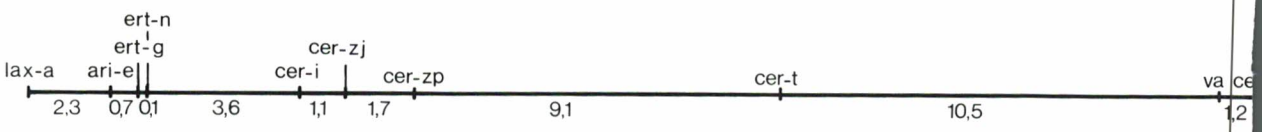

Figure 1. Sequence of ten genes on chromosome 7.

mutant lines was crossed with one or more markers. The combinations in the eleven three point tests are given in Table I, where the linked markers in coupling phase from the double mutant lines are designated as m and c. The marker of the other parent which then is present in the F_1 in repulsion phase is designated as r. As an example the three point test number 11 (Table 1) is written out in extension with the following formula:

$$P: \frac{lax\text{-}a\ ert\text{-}g\ Cer\text{-}t}{lax\text{-}a\ ert\text{-}g\ Cer\text{-}t} \times \frac{Lax\text{-}a\ Ert\text{-}g\ cer\text{-}t}{Lax\text{-}a\ Ert\text{-}g\ cer\text{-}t} \quad \text{or} \quad \frac{mcR}{mcR} \times \frac{MCr}{MCr}$$

The parental plants were grown and crossed in the field. The F_1 plants were grown and selfed in the phytotron under continuous light. During the first 60 days the plants were kept with a diurnal cycle of 16 hrs at 15°C and 8 hrs at 10°C. The plants were matured for 30 days with a temperature cycle of 16 hrs at 25°C and 8 hrs at 20°C. The F_2 generation was grown and selfed in the field and classified for the markers according to the eight observable phenotype classes MCR, mCR, MCr, McR, mCr, Mcr mcR and mcr.

Table I

The gene combinations analysed in eleven three point tests. The letters m and c designate the markers which are in coupling; r designates the marker which is in repulsion with respect to m and c.

Test number	m	c	r
1	*cer-t*^{22}	*cer-zj*^{78}	*ert-n*^{51}
2	*ari-e*^{1}	*cer-zj*^{78}	*cer-t*^{22}
3	*lax-a*^{4}	*cer-zj*^{78}	*cer-t*^{22}
4	*lax-a*^{4}	*cer-zj*^{78}	*cer-t*^{22}
5	*cer-t*^{22}	*cer-zj*^{78}	*ert-g*^{24}
6	*cer-w*^{48}	*ert-g*^{24}	*cer-zj*^{78}
7	*cer-t*^{22}	*cer-zp*^{313}	*ert-g*^{24}
8	*cer-zp*^{313}	*cer-t*^{22}	*va*
9	*cer-i*^{16}	*cer-zp*^{313}	*va*
10	*lax-a*^{4}	*cer-i*^{16}	*va*
11	*lax-a*^{4}	*ert-g*^{24}	*cer-t*^{22}

After rejection of the F_2 families with abnormal segregations 23 grains from each F_2 plant were grown as F_3 for determination of the F_2 genotype. All 27 genotype classes can be distinguished in this way (Table II) unless a genotype is lethal or sterile. The latter was the case under the particular field conditions for *ert-n*^{51} in test number 1 involving *cer-t*^{22}, *cer-zj*^{78} and *ert-n*^{51}. The complete sterility of *ert-n*^{51} results in only 19 F_2 phenotype classes and the recombination frequencies were calculated in the same manner as earlier for three point tests involving a lethal gene (15). The crossover frequencies were calculated by the maximum likelihood method (1,3) as well as by the method used in earlier work for estimation of crossover classes from first principle (15). The latter is called here the approximate method. The maximum likelihood method for a three point test has been programmed for computer calculation using a Fischer score iteration.

3. RESULTS AND DISCUSSION

The observed number of plants in the 27 possible genotype classes of an F_2 generation are listed in Table II. The genotypes missing in test one are due to the total sterility of the plants homozygous for *ert-n*^{51} as explained under Materials and Methods. The origin of the genotypes for the different crosses is given in

Table II

Observed number of F_2 plants in 27 genotype classes from the eleven three point tests. Genotypes were determined in F_3.
M = wildtype allele; m = the mutant allele which is in coupling with c
C = wildtype allele; c = the mutant allele which is in coupling with m
R = wildtype allele; r = the mutant allele in repulsion to c and m

Genotype \ Test number	1	2	3	4	5	6	7	8	9	10	11
1 Mm Cc Rr	477	611	418	386	588	379	639	513	581	344	293
2 mm cc RR	225	306	208	186	285	178	309	243	268	144	146
3 MM CC rr	–	298	202	189	279	172	317	251	275	148	139
4 Mm CC rr	–	43	47	40	76	97	65	42	13	26	12
5 Mm cc RR	61	52	38	36	71	99	61	50	19	31	13
6 MM Cc Rr	59	45	41	36	66	101	65	42	15	31	7
7 mm Cc Rr	54	50	46	40	71	97	61	43	19	27	8
8 mm cc Rr	27	88	60	50	32	2	37	56	124	102	42
9 MM CC Rr	23	85	58	51	27	1	40	54	133	106	35
10 Mm Cc RR	26	89	59	55	35	7	40	51	129	104	43
11 Mm Cc rr	–	82	62	49	30	11	46	53	120	107	37
12 MM Cc rr	–	1	0	0	3	23	4	3	5	4	0
13 mm Cc RR	1	2	0	0	2	26	5	1	3	2	0
14 Mm CC Rr	6	10	6	7	8	21	6	8	8	15	1
15 Mm cc Rr	1	10	8	6	5	26	9	11	7	12	0
16 MM Cc RR	2	8	7	5	4	1	3	5	3	11	0
17 mm Cc rr	–	5	8	3	2	0	4	6	1	10	0
18 mm CC rr	–	1	2	2	5	12	2	1	0	0	0
19 MM cc RR	2	1	1	2	3	16	2	2	0	1	0
20 mm cc rr	–	6	4	3	1	0	2	3	14	16	2
21 MM CC RR	0	6	2	5	1	0	2	2	17	19	2
22 mm CC Rr	0	0	0	0	0	7	0	0	0	0	0
23 MM cc Rr	1	0	0	0	0	5	0	0	0	0	0
24 Mm CC RR	0	0	0	0	0	0	0	0	0	0	0
25 Mm cc rr	–	0	0	0	0	0	0	0	0	0	0
26 mm CC RR	0	0	0	0	0	1	0	0	0	0	0
27 MM cc rr	–	0	0	0	0	0	0	0	0	0	0

Table III. From this table it can be seen if a particular genotype is the result of fertilization by two non-crossover gametes, by one non-crossover gamete with one crossover gamete, by two crossover gametes and so on. The order of the three loci in each three point test is derived unambigously from Tables II and III. For instance in the tests 1-5 or 7-11 genotypes 12 to 15 are less frequent than genotypes 4 to 7 and 8 to 11. This implies that the former have arisen by more than one crossover and that therefore marker c lies between marker m and r. The derived order of the genes is presented in Figure 2.

The recombination frequencies between the markers as calculated by the maximum likelihood method are given in Figure 2 and the crossover frequencies determined by the approximate method are given in Table IV. The distances as found by the two methods are compared in Table V, where it can be seen that both methods give very similar values. The distance between *cer-t* and *cer-zj* has been measured in five different tests to values ranging between 10·5 centimorgan and 12·2 centimorgan. This attests to the uniformity of the present three point tests. Likewise the distance between *cer-t* and *ert-g* has been determined three times resulting in distances of 11·3, 13·8 and 14·9 centimorgan. Using the test numbers 5 and 7 a more accurate measure is obtained for this gene distance by adding the recombination frequencies found with the intermediate markers *cer-zj* and *cer-zp* respectively. Since the

Table III

Origin of the genotypes listed in Table II.
P = parental non-crossover gamete; I = gamete with crossover in region I; II = gamete with crossover in region II; I + II = double crossover gamete. In test number 1-5, 7-11 corresponds region I to m-c and region II to c-r, where in test 6 region I corresponds to m-r and region II to c-r.

Genotypes 1-5, 7-11	in test 6	
1	1	P × P or I × I or II × II or I + II × I + II
2	2	P × P
3	3	P × P
4	4	P × I
5	5	P × I
6	6	P × I or I + II × II
7	7	P × I or I + II × II
8	12	P × II
9	13	P × II
10	14	P × II or I + II × I
11	15	P × II or I + II × I
12	8	P × I + II
13	9	P × I + II
14	10	P × I + II or I × II
15	11	P × I + II or I × II
16	22	I × II
17	23	I × II
18	18	I × I
19	19	I × I
20	26	II × II
21	27	II × II
22	16	I + II × I
23	17	I + II × I
24	24	I + II × II
25	25	I + II × II
26	20	I + II × I + II
27	21	I + II × I + II

Table IV

Distances obtained from the estimated frequencies for the various genotypes as derived from first principle according to the approximate method (15).

Test number	1	2	3	4	5	6	7	8	9	10	11
Total number of gametes	1930	3598	2554	2302	3188	2564	3438	2880	3508	2520	1560
Crossovers in region I	196	234	213	189	340	543	299	223	93	173	41
Crossovers in region II	87	428	292	258	156	134	210	268	657	613	174
Crossovers in I + II (double)	4	6	0	0	10	8	18	8	16	12	0
Crossover frequency in region I in %	10.2	6.4	8.3	8.2	10.7	21.2	8.7	7.7	2.7	6.9	2.6
Crossover frequency in region II in %	4.5	11.9	11.4	11.2	4.9	5.2	6.1	9.3	18.7	24.3	11.2
Double crossovers, expected	0.0046	0.0076	0.0095	0.0092	0.0052	0.0110	0.0053	0.0072	0.0051	0.0168	0.0029
Double crossovers, observed	0.0021	0.0017	0.0000	0.0000	0.0031	0.0031	0.0052	0.0028	0.0046	0.0048	0.0000

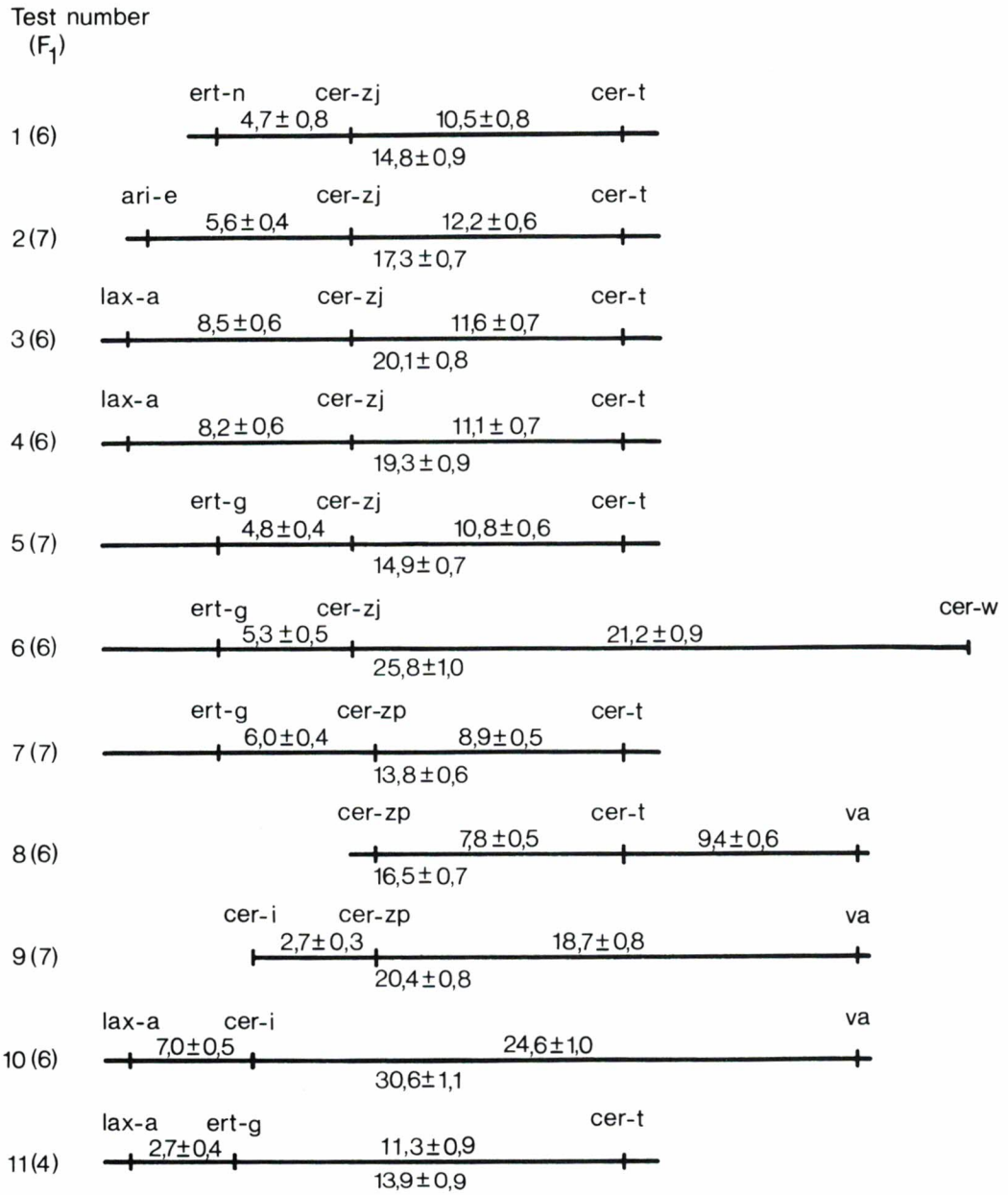

Figure 2. Distances and standard deviations based on the maximum likelihood method of calculation. The numbers in parenthesis designate the number of F_1 plants i.e. F_2 families analyzed.

double crossovers are detected with the aid of the intermediate markers the distances increase from 14·9 to 15·6 and from 13·8 to 14·9 centimorgan. The map distance from *lax-a* to *cer-t* has been determined in tests 3, 4, 11 with crossover frequencies of 20·1, 19·3 and 13·9 centimorgans. In all three tests no double crossovers were found and the distance thus remains the same if the intermediate marker is used for map distance calculation.

Table V

Comparison of distances found by two methods of calculation.

Test number	Region I		Region II	
	Computer method	Approx. method	Computer method	Approx. method
1	10.5 %	10.2 %	4.7 %	4.5 %
2	5.6 %	6.4 %	12.2 %	11.9 %
3	8.5 %	8.3 %	11.6 %	11.4 %
4	8.2 %	8.3 %	11.1 %	11.2 %
5	10.8 %	10.7 %	4.8 %	4.9 %
6	21.1 %	21.1 %	5.3 %	5.6 %
7	8.9 %	8.7 %	6.0 %	6.1 %
8	7.8 %	7.7 %	9.4 %	8.3 %
9	2.7 %	2.7 %	18.7 %	18.7 %
10	7.0 %	6.9 %	24.6 %	24.3 %
11	2.7 %	2.6 %	11.3 %	11.2 %

The following distances have been measured twice: *cer-zp* to *cer-t* with 7·8 and 8·9 centimorgan; *lax-a* to *cer-zj* with 8·5 and 8·2 centimorgan; *ert-g* to *cer-zj* with 4·8 and 5·3 centimorgan; *cer-zp* to *va* with 18·7 and 17·2 centimorgan; and *cer-i* to *va* with 24·6 and 21·4 centimorgan. Thus, on the whole good reproducibility of individual linkage values has been obtained in this material.

From these linkage values the map in Figure 1 can be constructed. No inconsistencies were met with in arranging the 10 genes in the order given. All map distances of Figure 2 have been weighted with the procedure described by JENSEN and HELMS JØRGENSEN (5). It should however be pointed out that the order of *ari-e, ert-g* and *ert-n* is not proven by a three point test. This is also the case for the order *cer-i, cer-zj, cer-zp* and the order *va, cer-w.*

Coefficients of coincidence (γ) have also been calculated by two methods. One uses the relationship $p_3 = p_2\text{-}2\gamma p_1 p_2$ in which p_3 is the recombination frequency of the two most distant loci, whereas p_1 and p_2 are the recombination frequencies in region I and II respectively. The other method estimates the observed double crossovers from first principles (Table IV) and devides their frequency with the expected number of crossovers. The values obtained are presented in Table VI. No significant differences are apparent between the two types of estimates. In all three point tests positive interference is observable. In tests 3, 4 and 11 no double crossovers happened to be directly observed which results in coefficients of coincidence of zero. Negative interference as has been found for certain markers of chromosome 1 (15) has not been observed here.

Table VI

The coefficient of coincidence found in the eleven three point tests.

Test number	Coefficient of coincidence γ $\gamma = \frac{p_1 + p_2 - p_3}{2p_1 p_2}$	estimation method from the first principle
1	0.44	0.46
2	0.37	0.22
3	0.01	0.00
4	0.00	0.00
5	0.66	0.60
6	0.30	0.28
7	0.98	0.98
8	0.51	0.39
9	0.98	0.90
10	0.30	0.29
11	0.02	0.00

Some of the map distances analysed in the present report have been previously determined by two point tests in F_2 or F_3 generations. A summary of these earlier data is compiled in Table VII and compared to the dis-

Table VII

Recombination frequencies and standard deviations (S.D.) from the present three point tests compared with earlier results from two point tests. Distances in italics were obtained by summation of distances determined with intermediate marker. Data in paranthesis are from materials with abnormal segregation ratios.

	This work	Earlier work			
	Recombination frequency and S. D.	Recombination frequency and S. D.	Number of plants	Generation	Reference
lax-a–ert-g	*2.7 ± 0.4*	0	460	F_2	(10)
lax-a–cer-i	7.0 ± 0.5	1.5 ± 0.5	329	F_3	(14)
lax-a–cer-zj	8.4 ± 0.6	(3.0 ± 0.6)	369	F_3	(14)
lax-a–cer-zp	*9.4 ± 0.4*	6.0 ± 1.2	182	F_3	(14)
ari-e–cer-i	*4.5 ± 0.6*	5.6 ± 1.3	152	F_3	(14)
ert-g–cer-i	*3.8 ± 0.4*	1.7 ± 0.7	181	F_3	(13)
ert-g–cer-zj	5.1 ± 0.5	5.3 ± 0.8	399	F_3	(13)
ert-g–cer-zp	6.0 ± 0.4	7.8 ± 1.2	263	F_3	(14)
ert-g–cer-t	14.2 ± 0.6	13.3 ± 1.9	177	F_3	(13)
ert-n–cer-zj	4.7 ± 0.8	(0.4 ± 0.3)	234	F_3	(14)
cer-i–cer-zj	*1.1 ± 0.4*	(4.6 ± 1.1)	183	F_3	(14)
cer-i–cer-zp	2.7 ± 0.3	(4.6 ± 1.1)	197	F_3	(14)
cer-i–va	*23.0 ± 0.6*	36.0 ± 4.0	472	F_3	(13)
cer-zj–cer-t	*11.2 ± 0.3*	(18.2 ± 1.8)	286	F_3	(13)
cer-zj–va	*20.6 ± 0.6*	(33.0 ± 4.0)	479	F_2	(13)
cer-zj–cer-w	21.2 ± 0.9	41.0 ± 3.0	819	F_2	(14)
cer-zp–cer-t	8.4 ± 0.5	10.0 ± 5.0	446	F_2	(14)
cer-zp–va	17.8 ± 0.8	18.0 ± 4.0	529	F_2	(14)
cer-zp–cer-w	*20.5 ± 1.4*	21.0 ± 3.0	857	F_2	(14)
va–cer-w	*1.5 ± 1.5*	(10.0 ± 4.0)	540	F_2	(14)

tances obtained in the three point tests. Of the twenty map distances considered seven give good agreement between the present and the earlier determinations. From the earlier work seven map distances are given in parenthesis, because they include data from F_2 families with abnormal segregation ratios and have therefore to be considered less accurate. Abnormal segregation ratios are relatively frequent in barley and can in most cases by traced down to gametic selection. Of the residual six distances those between *lax-a* to *ert-g*, *cer-i* to *va*, *cer-zj* to *cer-w*, had been determined by F_2 analysis only which gives less accurate data for instance due to miss-classification. The large discrepancy between the earlier and present determinations of crossover frequency between *lax-a* and *cer-i* remains unexplained at present. The larger frequency for the *lax-a* to *cer-zp* distance in the present work as compared to the earlier analysis is at least in part explained by its determination with the aid of an intermediate marker. Likewise the larger distance between *ert-g* and *cer-i* in the present work as compared to earlier data probably results from its indirect computation.

It has been mentioned in the Introduction that F_2 families with abnormal segregation ratios were not analysed further. In addition the segregation of the individual F_2 families which were analysed in the F_3 have been tested by χ^2 analysis for homogeneity before being accepted in the calculations of the crossover frequencies given in Figure 2. This is illustrated in Table VIII for three point test number 2, which is based on seven F_1 plants giving the seven F_2 families 2.1-2.7. Clearly family 2.7 deviates drastically in crossover frequency both for region I (*ari-e* to *cer-zj*) and region II (*cer-zj* to *cer-t*). This family is therefore rejected. For the χ^2-comparison in region I the total crossing over frequency of families 2·1 to 2·6 has been used as expected values (last line in Table VIII). For region II the expected value comprises families 2·1 to 2·6 (last line in Table VIII) as well as all families measuring the crossover frequency be-

Table VIII

Recombination frequency and χ^2 for three point test number 2.

Test number	Recombination frequency in region		χ^2 for region	
	I	II	I	II
2.1	5.6 ± 1.0	10.3 ± 1.4	0.0	0.0
2.2	5.7 ± 1.1	9.2 ± 1.4		
2.3	6.3 ± 1.1	12.4 ± 1.6	0.4	1.6
2.4	6.1 ± 1.1	10.9 ± 1.5	0.2	0.1
2.2 + 2.5	5.1 ± 0.7	10.3 ± 1.0	0.5	0.0
2.6	5.7 ± 1.0	11.3 ± 1.4	0.0	0.4
2.7	12.7 ± 1.6	17.8 ± 1.9	17.0	13.3
2	5.6 ± 0.4	12.5 ± 0.6	0.0	4.5

tween *cer-zj* to *cer-t* in three point tests 1, 3, 4 and 5. The computer program used cannot handle cases, in which the combined recombination frequencies in region I and II ($p_1 + p_2$) are less than the recombination frequencies between the two most distant markers (p_3). This happens to be the case with family 2·5, which therefore has been combined with the smallest family in the test namely 2.2. In the other three point tests one family each had to be rejected in test number 8 and 10 because of χ^2-values of 18, 12 and 13. After these 3 rejections the three point tests were satisfactory to the criteria used by JENSEN & HELMS JØRGENSEN (5) for consistent mapping.

One way of testing the reliability of the classification is offered by the approximate method applied by SØGAARD (15). The observed frequency distribution of the 27 genotypes in a three point test can be compared with the distribution expected from first principle. An example is given for test number 10 in Table IX with excellent agreement between the two distributions.

Crosses to translocations with a breakage point in the long arm of chromosome 7 give close linkage with most of the eceriferum genes on chromosome 7 (4, 13, 14) indicating these genes to be on the long arm. Whereas crossover between *cer-t, cer-zj, cer-zp* or *cer-t* and the translocations studied was not observed, more than 10% crossover occurred in crosses with *cer-w* (SØGAARD, unpublished). Such large crossover values are believed to indicate a location distally to the translocation breakage point

Table IX

The comparison between the observed and expected phenotype classes in three point test number 10.

Genotype	Observed	Expected
1	344	337.9
2	144	149.3
3	148	149.3
4	26	28.3
5	31	28.3
6	31	29.1
7	27	29.1
8	102	104.6
9	106	104.6
10	104	104.8
11	107	104.8
12	4	2.2
13	2	2.2
14	15	12.1
15	12	12.1
16	11	9.9
17	10	9.9
18	0	1.3
19	1	1.3
20	16	18.3
21	19	18.3
22	0	0.2
23	0	0.2
24	0	0.8
25	0	0.8
26	0	0.0
27	0	0.0

(6). This would place the other *cer* loci into the interstitial segment of the translocations and would orient the linkage map of Figure 1 with *lax-a* nearest to the centromere.

ACKNOWLEDGEMENTS

I thank Professor DITER von WETTSTEIN for critical reading of the manuscript and the late Professor OVE FRYDENBERG and lic. agro. JENS JENSEN for provision of the computer program to calculate the maximum likelihood estimates and for extensive discussion. I am also indebted to the personnel of the Phytotron at the Royal College of Forestry, Stockholm, for growing the plants.

REFERENCES

1. BAILEY, N.T.J.: Introduction to the mathematical theory of genetic linkage. Clarendon Press, Oxford, pp.1-298 (1961)
2. DORMLING, I., Å. GUSTAFSSON & D. von WETTSTEIN: Phytotron cultivation of Bonus barley: The control of maturation and grain quality. Hereditas 63, 415-428 (1969)
3. ELANDT-JOHNSON, R. C.: Probability models and statistical methods in genetics. John Wiley and Sons, New York, pp. 1-592 (1971)
4. FESTER, T. & B. SØGAARD: The localization of eceriferum loci of barley. Hereditas 61, 327-337 (1969)
5. JENSEN, J. & J. Helms JØRGENSEN: The barley chromosome 5 linkage map I. Literature survey and map estimation procedure. Hereditas 80, 5-16 (1975)
6. KRAMER, H. H. & B. A. S. BLANDER: Orientating linkage maps on the chromosomes of barley. Crop.Sci. 1, 339-342 (1961)
7. LUNDQVIST, U. & D. von WETTSTEIN: Induction of eceriferum mutants in barley by ionizing radiation and chemical mutagens. Hereditas 48, 342-362 (1962)
8. LUNDQVIST, U., P. von WETTSTEIN-KNOWLES & D. von WETTSTEIN: Induction of eceriferum mutants in barley by ionizing radiation and chemical mutagens. II. Hereditas 59, 473-504 (1968)
9. PERSSON, G. & A. HAGBERG: Induced variation in quantitative character in barley. Morphology and cytogenetics of erectoides mutants. Hereditas 61, 115-178 (1968)
10. PERSSON, G.: An attempt to find suitable genetic markers for dense ear loci in barley I. Hereditas 62, 25-96 (1969)
11. PERSSON, G.: An attempt to find suitable genetic markers for dense ear loci in barley II. Hereditas 63, 1-28 (1969)
12. SØGAARD, B.: The localization of eceriferum loci in barley. II. Cand. scient. thesis, Copenhagen Univ., pp.1-28 (1970)
13. SØGAARD, B.: Linkage studies on eceriferum mutants in barley. Barley Genetic Newsletter 1, 41-47 (1971)
14. SØGAARD, B.: Continued linkage studies on eceriferum mutants in barly. Barley Genetics Newsletter 3, 57-61 (1973)
15. SØGAARD, B.: The localization of eceriferum loci in barley. III. Three-point tests of genes on chromosome 1 in barley. Hereditas 41, 41-48 (1974)
16. WALKER, G. W. R., J. DIETRICH, R. MILLER & K. KASHA: Recent barley mutants and their linkages. II. Genetic data for further mutants. Can. J. Genet. Cytol. 5, 200-219 (1963)