# THE LOCALIZATION OF ECERIFERUM LOCI IN BARLEY V. THREE POINT TESTS OF GENES ON CHROMOSOME 1 AND 3 IN BARLEY

by

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Five three point tests are reported for chromosome 1 and four three point tests for chromosome 3. The tests were analysed in the $F_3$ generation.

Maps for two regions on chromosome 1 comprising five and four genes respectively, can be constructed from the data obtained. The map spanning the distance *cer-f* to *ert-m* confirms previous results for this interval. As observed earlier, coefficients of coincidence larger than 1 corresponding to negative interference are found in this region of chromosome 1. It is suggested that the consistent occurrence of negative interference in this interval is due to its location close to the centromere. In the other region studied on chromosome 1 normal positive interference is observed.

On chromosome 3 a linkage map of the four markers analysed is presented. Positive interference is found in the three point tests of this region.

## 1. INTRODUCTION

In a previous paper (24) a linkage map comprising five barley genes on chromosome 1, namely eceriferum *cer-f*, albina $ac_2$, erectoides *ert-d*, *ert-a* and *ert-m* has been presented. In all three point tests involving these genes more double crossovers were observed than expected from the frequencies of crossover in each of the two intervals covered by the three markers. This result was surprising and I have therefore repeated these three tests and can confirm the occurrence of negative interference in this region of chromosome 1.

In order to investigate whether negative interference is a common characteristic for chromosome 1 markers in barley a different region on chromosome 1 has been studied by three point tests. The region contains the four genes virescent *yc*, chlorina *fc*, ecriferum *cer-a* and brachytic *br*. Normal positive interference was obtained in two three point tests involving these markers.

One region on chromosome 3 has been mapped with four three point tests involving

Figure 1. Sequence, distances and standard deviations based on the maximum likelihood method of calculation for the nine genes on chromosome 1.
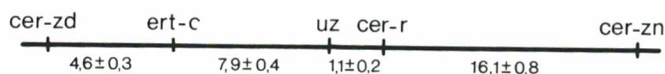
Figure 2. Sequence, distances and standard deviations based on the maximum likelihood methods of calculation for the five genes on chromosome 3.

five genes: eceriferum *cer-zd, cer-r* and *cer-zn,* erectoides *ert-c* and semibrachytic *uz.* Normal positive interference is found in this region. The maps derived are given in Figures 1 and 2.

## 2. MATERIALS AND METHODS

The mutants used as markers have been either induced in the cultivar Svalöf's Bonus or have been transferred by repeated back crossing into Bonus background by PERSON & HAGBERG (17). The following mutants have been employed:

| | | |
|---|---|---|
| albina | chromosome 1 | $ac_2$ (19) |
| erectoides | chromosome 1 | $ert$-$a^{23}$ (16, 8, 22) |
| erectoides | chromosome 1 | $ert$-$d^{33}$ (16) |
| erectoides | chromosome 1 | $ert$-$m^{40}$ (16) |
| eceriferum | chromosome 1 | $cer$-$f^9$ (11, 21) |
| eceriferum | chromosome 1 | $cer$-$a^1$ (11, 8) |
| brachytic | chromosome 1 | $br$ (18) |
| chlorina | chromosome 1 | $fc$ (19) |
| virescent | chromosome 1 | $yc$ (19) |
| semibrachytic | chromosome 3 | $uz$ (26) |
| erectoides | chromosome 3 | $ert$-$c^{39}$ (16) |
| eceriferum | chromosome 3 | $cer$-$r^{19}$ (11, 22) |
| eceriferum | chromosome 3 | $cer$-$zd^{67}$ (11, 8) |
| eceriferum | chromosome 3 | $cer$-$zn^{244}$ (12, 21, 22) |

Form crosses involving these mutants (21,22,23) the following double mutant lines have been isolated: $ert$-$a^{23}$ $cer$-$f^9$, $ert$-$d^{33}$ $cer$-$f^9$, $ert$-$m^{40}$ $cer$-$f^9$, $br$ $cer$-$a^1$, $uz$ $cer$-$r^{19}$, $ert$-$c^{39}$ $cer$-$zn^{244}$, $uz$ $cer$-$zn^{244}$, $ert$-$c^{39}$ $cer$-$r^{19}$. Each of these double mutant lines was crossed with one or more markers. The combinations in the nine 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. Crosses, growth of the material in the field or the phytotron (3) and analyses were carried out as described in the previous paper of this series (25).

Plants homozygous for the chlorina marker *fc* are of poor viability in mixed stands with phenotypically normal plants. Many chlorina plants die before heading and they were therefore in the $F_2$ rows tagged and counted at the three leaf stage as well as at harvest time. The surviving chlorina plants were sown separately in the $F_3$ generation to avoid competition with normal plants.

## 3. RESULTS AND DISCUSSION
### 3.1. Chromosome 1
The observed number of plants in the 18 viable genotype classes of the three point tests number 1 to 4 and in the 27 viable genotype classes in test number 5 are listed in Table II. In the latter

Table I

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

| Chromosome | Test number | m | c | r |
|---|---|---|---|---|
| 1 | 1 | $ert\text{-}d^{33}$ | $cer\text{-}f^9$ | $ac_2$ |
| 1 | 2 | $ert\text{-}m^{40}$ | $cer\text{-}f^9$ | $ac_2$ |
| 1 | 3 | $ert\text{-}a^{23}$ | $cer\text{-}f^9$ | $ac_2$ |
| 1 | 4 | $br$ | $cer\text{-}a^1$ | $yc$ |
| 1 | 5 | $br$ | $cer\text{-}a^1$ | $fc$ |
| 3 | 6 | $uz$ | $cer\text{-}r^{19}$ | $cer\text{-}zd^{67}$ |
| 3 | 7 | $cer\text{-}zn^{244}$ | $ert\text{-}c^{39}$ | $cer\text{-}zd^{67}$ |
| 3 | 8 | $uz$ | $cer\text{-}zn^{244}$ | $cer\text{-}zd^{67}$ |
| 3 | 9 | $cer\text{-}r^{19}$ | $ert\text{-}c^{39}$ | $cer\text{-}zd^{67}$ |

Table II

Observed number of $F_2$ plants in the 27 genotype classes from nine three point tests.
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

Figures in parenthesis under test 5 refer to the number of plants after correction for sublethality of the genotype fcfc.

| Genotype | Test number 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| 1 MmCcRr | 824 | 547 | 504 | 309 | 415 | 620 | 279 | 399 | 447 |
| 2 mmccRR | 409 | 270 | 248 | 127 | 197 | 297 | 118 | 189 | 217 |
| 3 MMCCrr | – | – | – | – | 153(205) | 300 | 125 | 185 | 222 |
| 4 MmCCrr | – | – | – | – | 34 (52) | 0 | 85 | 3 | 48 |
| 5 MmccRR | 17 | 83 | 48 | 45 | 58 | 0 | 81 | 1 | 44 |
| 6 MMCcRr | 18 | 83 | 46 | 48 | 59 | 2 | 86 | 7 | 46 |
| 7 mmCcRr | 23 | 81 | 48 | 40 | 56 | 3 | 88 | 6 | 43 |
| 8 mmccRr | 4 | 5 | 7 | 93 | 15 | 75 | 16 | 43 | 22 |
| 9 MMCCRr | 7 | 4 | 2 | 97 | 18 | 71 | 13 | 46 | 24 |
| 10 MmCcRR | 5 | 6 | 4 | 102 | 19 | 79 | 15 | 47 | 26 |
| 11 MmCcrr | – | – | – | – | 9 (14) | 72 | 13 | 43 | 24 |
| 12 MMCcrr | – | – | – | – | 1 (1) | 5 | 2 | 61 | 2 |
| 13 mmCcRR | 20 | 11 | 12 | 10 | 2 | 8 | 2 | 54 | 1 |
| 14 MmCCRr | 19 | 15 | 16 | 27 | 4 | 8 | 4 | 57 | 5 |
| 15 MmccRr | 22 | 13 | 14 | 26 | 4 | 7 | 6 | 55 | 3 |
| 16 MMCcRR | 0 | 0 | 0 | 16 | 2 | 0 | 3 | 0 | 2 |
| 17 mmCcrr | – | – | – | – | 1 (1) | 0 | 4 | 0 | 0 |
| 18 mmCCrr | – | – | – | – | 1 (2) | 0 | 14 | 0 | 0 |
| 19 MMccRR | 0 | 5 | 6 | 2 | 6 (0) | 0 | 17 | 0 | 3 |
| 20 mmccrr | – | – | – | – | 0 | 7 | 0 | 2 | 1 |
| 21 MMCCRR | 0 | 0 | 0 | 18 | 0 | 5 | 1 | 3 | 0 |
| 22 mmCCRr | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 23 MMccRr | 0 | 1 | 2 | 2 | 0 | 3 | 2 | 0 | 1 |
| 24 MmCCRR | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 5 | 0 |
| 25 Mmccrr | – | – | – | – | 0 (0) | 1 | 0 | 6 | 0 |
| 26 mmCCRR | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 3 | 0 |
| 27 MMccrr | – | – | – | – | 0 (0) | 0 | 0 | 2 | 0 |

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**Table III**

Origin of the genetypes 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 1-3, region I corresponds to c-r, and region II to r-m. In tests 4-5, 7, 9 region I corresponds to c-r, and region II to c-m. In test 6, 8 region I corresponds to r-m and region II to m-c.

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

test plants homozygous for *fc* are sublethal as mentioned under Materials and Methods. Only 205 of the 275 chlorina plants in the $F_2$ reached maturity and could be tested in $F_3$. Assuming equal lethality in all nine *fcfc* genotypes the distribution of the 275 chlorina plants can be calculated and is given in parenthesis.

The genotypes listed in Table II result from various combinations of non-crossover gametes, gametes carrying one crossover and gametes carrying two crossovers as tabulated in Table III. As genotypes resulting from non-crossover gametes with gametes carrying a double crossover (P × I + II) are less frequent than genotypes resulting from a fertilization between non-crossover gametes and single crossover gametes (P × I, P × II) the order of the three markers involved in each three point test can be derived from Tables II and III. The result is graphically presented in Figure 3, which also contains the recombination frequencies determined by the approximate method. Good agreement is obtained with the distances reported earlier (24). The interval between *cer-f* and $ac_2$ averages here 2,8 centimorgan versus 2,3 in (24). The distance $ac_2$ to *ert-d* with 2.8 compares to 2.5, that of $ac_2$ to *ert-m* with 13.3 to 12.8 and the interval $ac_2$ to *ert-a* with 9.4 to 8.5 centimorgan. In these three tests the frequency of observed double crossovers is consistently higher than the expectation (Table IV) leading to coefficients of
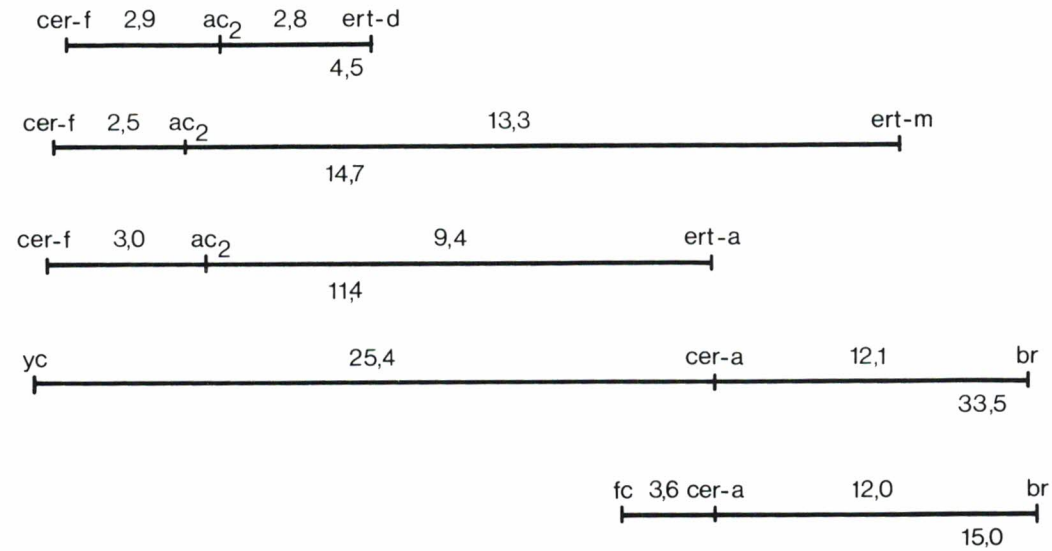
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cer-f   2,9   ac₂   2,8   ert-d

|— — — — — — —|— — — — —|
                4,5

cer-f   2,5   ac₂                    13,3                         ert-m

|— — —|— — — — — — — — — — — — — — — — — — — — — — —|
            14,7

cer-f   3,0   ac₂              9,4                    ert-a

|— — —|— — — — — — — — — — — — — — — — —|
           11,4

yc                    25,4                          cer-a    12,1        br

|— — — — — — — — — — — — — — — — — —|— — — — — — —|
                                            33,5

                              fc  3,6 cer-a          12,0          br

                              |—|— — — — — — — — —|
                                      15,0

Figure 3. Distances on chromosome 1 based on the approximate method.

**Table IV**

**Distances obtained from the estimated frequencies for the various genotypes as derived from the first principle according to the approximate method (14).**

| Test number | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| Total number of gametes | 2736 | 2248 | 1914 | 1932 | 2260 | 3120 | 1948 | 2436 | 2362 |
| Crossovers in region I | 77 | 55 | 57 | 461 | 80 | 351 | 84 | 228 | 114 |
| Crossovers in region II | 74 | 283 | 181 | 235 | 271 | 34 | 493 | 279 | 214 |
| Crossovers in I + II (double) | 22 | 18 | 18 | 24 | 6 | 0 | 12 | 10 | 8 |
| Crossover frequency in region I in % | 2.8 | 2.6 | 3.0 | 23.9 | 3.5 | 11.3 | 4.3 | 9.4 | 4.8 |
| Crossover frequency in region II in % | 2.7 | 12.6 | 9.5 | 12.2 | 12.0 | 1.1 | 25.3 | 11.5 | 9.1 |
| Double crossovers, expected | 0.0008 | 0.0031 | 0.0028 | 0.0290 | 0.0042 | 0.0012 | 0.0109 | 0.0107 | 0.0044 |
| Double crossovers, observed | 0.0080 | 0.0080 | 0.0094 | 0.0124 | 0.0027 | 0.0000 | 0.0062 | 0.0041 | 0.0034 |

coincidence between 2.6 amd 10.5 (Table V) confirming the strong negative interference for this region.

The first case of negative interference has been reported for the centromere region of chromosome 3 in Drosophila melanogaster by MORGAN, STURTEVANT & BRIDGES (2,13). These authors also noted that coincidence values change with the chromosomal region studied and noted that in the second and third chromosomes the coincidence values are highest near the mid-points (centromeres) and

Table V

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

| Test number | Coefficient of coincidence and standard deviation found by maximum likelihood method | found by estimation method from the first principle |
|---|---|---|
| 1 | $7.3 \pm 1.6$ | 10.5 |
| 2 | $1.7 \pm 0.5$ | 2.6 |
| 3 | $1.9 \pm 0.6$ | 3.4 |
| 4 | $0.7 \pm 0.1$ | 0.4 |
| 5 | $0.7 \pm 0.3$ | 0.6 |
| 6 | $0.3 \pm 0.4$ | 0.0 |
| 7 | $0.5 \pm 0.2$ | 0.6 |
| 8 | $0.3 \pm 0.1$ | 0.4 |
| 9 | $0.9 \pm 0.3$ | 0.8 |

fall off rapidly and symmetrically on each side. In the acrocentric X chromosome on the other hand the highest coincidence values were not found close to the contromere but again in the middle portion of the chromosome. M. M. GREEN (9) has reinvestigated and confirmed the occurrence of negative interference in the centromere region of chromosome 3 in Drosophila with coincidence values ranging from 1.5 to 2.8. Considerable higher negative interference (10.5) was obtained for the cer-f, $ac_2$, ert-d three point test in barley. As noted earlier (24) the coincidence value drops, but remains above 1 when the crossover distance in region II increases from 2.8 to 13.3 centimorgan ($ac_2$ to ert-a and $ac_2$ to ert-m).

The gene $ac_2$ is placed on the short arm of chromosome 1 by TSUCHIYA & SINGH (28) by means of telotrisomics analyses and considered to be close to the contromere because of absent crossover with translocation break points in the short arm (5). Gene ert-m has been placed by PERSSON (15) to the short arm of chromosome 1 with the aid of translocations. There is thus some evidence that the region cer-f-$ac_2$-ert-d is close to the contromere which suggest that the negative interference in this region in barley is comparable to the phenomenon in Drosophila.

The other two three point tests on chromosome 1 in barley (Fig. 3, Tables III, IV, V) permit the ordering of the four markers yc, fc, cer-a and br in agreement with the map

derived from two-point tests. Positive interference is found in this chromosome region. The maps of the two regions with distances calculated by the maximum likelihood method (1,4) and weighted by the procedure of JENSEN & HELMS JØRGENSEN (10) are presented in Figure 1. The region yc to br is in the short arm of chromosome 1. The markers fc, cer-a and br have been placed in the short arm by means of telotrisomics (27) with br most distal (7). Definitive information on the location of yc relative to ert-m is not available but the distances obtained by two point tests, which are collected in Table VI all support a location of yc between ert-m and fc. The recombination frequencies of the intervals ert-a to yc, ert-a to cer-a, ert-m to cer-a, ert-a to yc and $ac_2$ to cer-a give roughly a range of 1 to 16 per cent crossover between ert-m and yc.

3.2 Chromosome 3

The results of the three point tests are presented in Figure 4 with the crossover values obtained by the approximate method. The sequence of the genes has to be as depicted in Figure 2, but the distance between cer-r and cer-zn will have to be redetermined as the distances between cer-zd and cer-zn in three point tests number 7 and 8 cannot be satisfactorily reconciled. Coincidence values are less than one indicating positive interference (Table V). Comparison of the distances determined here

Table VI

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

| | This work | Earlier work | | | |
|---|---|---|---|---|---|
| | Recombination frequency and S.D. | Recombination frequency and S.D. | Generation | n | References |
| Chromosome 1: | | | | | |
| cer-f - ac₂ | 2.8 ± 0.2 | (4.7 ± 1.0) | F₃ | 224 | (26) |
| cer-f - ert-d | 5.5 ± 0.4 | (2.4 ± 0.7) | F₃ | 229 | (26) |
| cer-f - ert-a | 12.5 ± 0.8 | 12 ± 3 | F₂ | 793 | (26) |
| cer-f - ert-m | 15.2 ± 2.8 | 13.3 ± 1.8 | F₃ | 208 | (26) |
| cer-f - yc | | 17.0 ± 1.5 | F₃ | 315 | (26) |
| cer-a - br | 12.1 ± 0.5 | 12.9 ± 2.1 | F₃ | 124 | (26) |
| cer-a - fc | 3.6 ± 0.4 | 3.5 ± 0.9 | F₃ | 187 | (26) |
| cer-a - yc | 25.4 ± 1.4 | 24.4 ± 1.6 | F₃ | 346 | (26) |
| cer-a - ac₂ | | 39.9 ± 2.0 | F₃ | 339 | (26) |
| cer-a - ert-a | | 36 ± 3 | F₂ | 817 | (26) |
| cer-a - ert-m | | 36.1 ± 2.4 | F₃ | 201 | (26) |
| cer-a - ert-d | | 45 ± 3 | F₂ | 644 | (26) |
| ert-a - yc | | 20.4 ± 1.8 | F₂ | 647 | (14) |
| ert-a - ert-m | 3.9 ± 2.8 | 17.2 ± 4.4 | F₂ | 476 | (15) |
| ert-d - yc | | 0 | F₂ | 438 | (15) |
| ert-d - fc | | free | F₂ | 414 | (15) |
| ert-d - ac₂ | 2.7 ± 0.3 | 1.2 ± 0.7 | F₂ | 145 | (15) |
| ert-d - br | | free | F₂ | 521 | (15) |
| ert-d - yc | | 24.6 ± 2.8 | F₂ | 302 | (15) |
| br - yc | 37.5 ± 1.5 | 35.5 ± 4.2 | F₂ | 228 | (15) |
| Chromosome 3: | | | | | |
| cer-zd - ert-c | 4.6 ± 0.3 | (0    ) | F₂ | 418 | (25) |
| cer-zd - uz | 10.8 ± 0.4 | (4.6 ± 0.6) | F₃ | 87 | (25) |
| cer-r - cer-zd | 13.9 ± 0.4 | 13.5 ± 1.7 | F₃ | 316 | (25) |
| cer-r - ert-c | 9.0 ± 0.4 | 9.1 ± 1.9 | F₃ | 126 | (25) |
| cer-r - uz | 1.1 ± 0.2 | 0.9 ± 0.7 | F₃ | 112 | (25) |
| cer-zn - ert-c | 19.1 ± 0.9 | 24 ± 3 | F₂ | 1036 | (25) |
| cer-zn - uz | 11.9 ± 0.7 | 12 ± 3 | F₂ | 914 | (25) |

cer-zd        12,4  uz    cer-r
├─────────────────┼──────┤
      11,3          1,1

cer-zd    ert-c  30,9                          cer-zn
├────────┼───────────────────────────────────┤
    4,3                    25,3

cer-zd        20,0  uz        cer-zn
├─────────────────┼──────────┤
      9,4               11,6

cer-zd    ert-c  13,2      cer-r
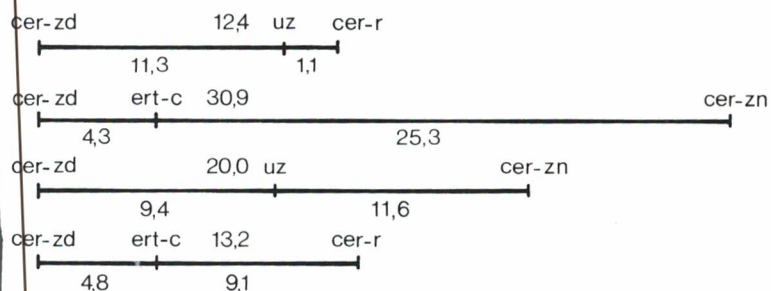├────────┼─────────────────┤
    4,8          9,1

Figure 4. Distances on chromosome 3 based on the approximate method.

with earlier results (Table VI) reveal acceptable agreement.

There has been conciderable uncertainty about the assignment of genes on chromosome 3 to its short or long arm. Thus, *uz* has been transferred from the short arm to the long arm (6,15) and back again to the short arm (20). The distance *uz* and *ert-c* can roughly be calculated from the data given by ESLICK & McPROUND (6) to 10% and is in agreement with the data in Figure 2. The genes *uz* and *cer-zn* are considered to be located in the short arm of the chromosome with *cer-zn* as the most distal marker (20).

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