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# The modification of a common wheat-*Thinopyrum distichum* translocated chromosome with a locus homoeoallelic to *Lr19*

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**Summary.** The 'Chinese Spring' *ph1b* and *ph2b* mutants, as well as the nulli 5B tetra 5D stock were utilized in an attempt to effect homoeologous chromatin exchange between the 'Indis' chromosome translocation [derived from *Thinopyrum distichum* (Thunb.) Löve] and chromosome arm 7DL of common wheat. A homoeoallele of *Lr19* and linked genes for yellow flour-pigmentation were utilized as markers. Seven selections with recombinations involving the foreign, translocated segment were recovered. Four of these had white endosperms and were leaf-rust resistant. The remaining lines were leaf-rust resistant and had levels of endosperm pigmentation intermediate to those of 'Indis' and 'Chinese Spring'. The recombined translocation segments coding for white endosperm are no longer associated with chromosome 7D. The original translocated segment may, therefore, not be fully homoeologous to 7DL. The recombinants with white endosperm also lack the stem-rust resitance gene *Sr25*, but retained the segregation distorter locus, *Sd-1*. However, it seems as though an enhancer locus (or loci) of *Sd-1* had been lost.

**Key words:** *Triticum aestivum* – Intergeneric gene transfer – Allosyndetic recombination

## Introduction

Many beneficial traits, such as disease and insect resistance, have been transferred from *Thinopyrum* Löve (previously *Agropyron* and *Elytrigia*) to wheat (Pienaar 1990). By backcrossing the *Triticum aestivum* cv. 'Inia 66'/*Thinopyrum distichum* (Thunb.) Löve amphiploid (2n = 70) to 'Inia 66', Pienaar (1981, 1983) obtained fertile partial amphiploids with 2n = 56. Following a further backcross to 'Inia 66', plants with 2n = 49 were produced. From the $B_2F_3$, two plants with resistance to prevailing leaf- and stem-rust races were selected (Pienaar et al. 1985), giving rise to the germplasm line 'Indis' (2n = 42). Marais et al. (1988) and Marais and Marais (1990) found that 'Indis' has a heterologous chromosome 7D pair in which most or all of the long arm has been exchanged for a *Th. distichum* segment.

The alien segment in 'Indis' appears to be homoeologous to the *Lr19*-bearing translocated segment derived from *Thinopyrum ponticum* by Sharma and Knott in 1966, and to 7DL of common wheat (Marais 1991). The introgressed genes include a highly effective leaf-rust resistance homoeoallele(s), *Lr19d*, a less effective stem-rust resistance homoeoallele (*Sr25d*) and probably two genes for yellow endosperm-pigmentation (alleles *Y-1d* and *Y-2d*) (Marais 1991). The leaf-rust resistance and yellow-pigment loci appear to be loosely linked. The two translocations produce novel, but identical, WSP-D1 bands (henceforth referred to as WSP-D1c) and both have null alleles at the *Ep-D1* and *α-Amy-D2* loci. Both chromosome translocations cause distortion of segregation ratios (Zhang and Dvořák 1990; Marais 1990). The segregation distortion factor of the *Th. ponticum*-derived segment was found to be situated proximally to the *Lr19* locus, and was designated *Sd-1* by Zhang and Dvořák (1990). In the present study, the allelic form of *Sd-1* in 'Indis' is designated *Sd-1d*.

Since the translocated segment and the normal wheat arm 7DL do not recombine during meiosis, the introgressed genes are inherited as a large linkage block (Marais and Marais 1990). Unfortunately, the linked yellow-pigment genes preclude the commercial utilization of the very promising leaf-rust resistance gene(s).

A substantial degree of homoeology may exist between the *Lr19*-carrying chromosome arm of *Thinopy-*

*rum* and 7DL of common wheat. Sears (1973) reported the successful transfer of *Lr19* to wheat by means of induced homoeologous recombination between wheat chromosome 7D and *Th. ponticum* (= *Agropyron elongatum*, 2n = 10x = 70) chromosome 7Ag. Twelve transfers were found among 138 offspring of nulli-5B, tri-5D, mono-7Ag, mono-7D plants. Kibirige-Sebunya and Knott (1983) used both the 'Chinese Spring' nulli-5B tetra-5D and *ph1b* stocks to induce homoeologous pairing in plants monosomic for chromosomes 7D of wheat and a different group 7 chromosome ($7e1_2$) of *Th. ponticum*. Recombinant wheat chromosomes carrying genes for stem-rust resistance from *Th. ponticum* were recovered at relatively high frequencies.

The objective of the present study was to induce homoeologous recombination between the differential segment of 'Indis' and wheat chromosome arm 7DL in the absence of either *Ph1* or *Ph2*. The use of the translocated chromosome, which has a normal 7DS arm, may result in a higher incidence of recombination than did the use of the complete *Thinopyrum* chromosome in the studies of Sears (1973) and Kibirige-Sebunya and Knott (1983). The derived progenies were screened for recombinants involving the pigment loci and *Lr19* only. Such recombinants would hopefully be directly utilizable in breeding programmes or could be employed in further attempts to replace additional undesirable chromatin.

## Materials and methods

The 'Chinese Spring' monosomes, nulli 5B tetra 5D stock, and *ph1b* and *ph2b* mutants were all obtained from the late Professor ER Sears, Department of Agronomy, University of Missouri-Columbia, Columbia 65211, USA. Utilizing these, translocation heterozygotes which were deficient for either *Ph2* or *Ph1* were derived from the following crosses.

(1) (Monosomic $F_1$: 'Chinese Spring monosome 3D'/'Indis')// 'Chinese Spring $ph_2b$ mutant',
(2) (Monosomic $F_1$: 'Chinese Spring monosome 5B'/'Indis')// 'Chinese Spring *ph1b* mutant', and
(3) (Monosomic $F_1$: 'Chinese Spring monosome 5B'/'Indis')// 'Chinese Spring nulli 5B tetra 5D'.

Plants with 41 chromosomes (probably *Ph* deficient) and resistant to leaf-rust race 3SA132 (translocation heterozygotes) were selected from each cross. Clones of the presumably *Ph*-deficient selections from cross 1 were lost due to a greenhouse failure, so that tests to confirm the absence of *Ph2* could not be carried out. The selections from cross 2 were pollinated with *Aegilops variabilis* to test for homoeologous pairing. Only five of the eight combinations produced male-fertile progeny. In all instances a high level of homoeologous pairing was evident during metaphase-I in PMCs of the hybrids. C-banding (Giraldez et al. 1979) of root tip cells from four of 11 plants derived from cross 3, confirmed the absence of chromosome 5B.

The *Ph*-deficient translocation heterozygotes selected from crosses 1, 2 and 3 were pollinated with the white endosperm, leaf-rust susceptible tester 'Inia 66', and the resulting progenies were designated 87M70, 88M22 and 88M93, respectively. Resistant $F_1$ plants from these crosses were raised, and their $F_2$ tested for flour colour. Method 14-50 of the American Association of Cereal Chemists (AACC 1976) was slightly modified for this purpose (Marais 1991). Seedling leaf-rust resistance was assessed using race 3SA132. 'Inia 66' seedlings develop a type 4 reaction when inoculated with this race whereas 'Indis' seedlings develop a fleck reaction.

Resistant plants from families which appeared to include recombinants, were grown for confirmatory tests and to obtain translocation homozygotes. Eventually, seed samples from homozygous translocation recombinants were milled on a 'Quadrumat Junior' mill and the flour used for pigment determinations utilizing the unmodified method 14-50 of the AACC (1976). Polymorphisms produced by the recombinants for marker loci on chromosome 7DL were also studied. Separation by isoelectric focusing of endopeptidases, alpha-amylases and WSP-1 proteins was done as described by Marais and Marais (1990) and Marais (1991).

In order to determine whether the recombination events involved chromosome 7D, the four white-endosperm recombinants were crossed to 'Chinese Spring' monosomics for chromosome 7D. Monosomic $F_1$ plants were grown and the $F_2$ segregation ratios were studied. *Sd-1d* is known to elicit only a mild response in crosses with 'Chinese Spring' (Marais 1990) and was not expected to confound the results. The recombinants with white endosperms were also crossed to a plant monotelodisomic for 7DL. Resistant monotelodisomic $F_1$ plants were selected for the purpose of studying their meiotic behaviour and doing telocentric mapping (Sears 1962) of the marker genes (which were expected to be located on chromosome 7D). The telosome used was confirmed to be 7DL by C-banding and by pollinating the monotelodisomic plants with 'Indis'. Monotelodisomic $F_1$ kernels were then used to carry out endopeptidase determinations. Since 'Indis' does not produce an *Ep-D1* product, the presence of EP-D1a on a zymogram will reflect the presence of 7DL.

**Table 1.** Results obtained following the pollination of *Ph*-deficient translocation heterozygotes with 'Inia 66'

| Translocation heterozygotes used as female parents: | | Cross number | Number of $F_1$ | | | Number of resistant recombinants |
|---|---|---|---|---|---|---|
| Number of plants | Condition at pairing control locus | | Seeds obtained | Plants resistant | Plants resistant, fertile | |
| 8 | $-, ph_2b$ | 87M70 | 2,019 | 952 | 540 | 1 |
| 9 | $-, ph_1b$ | 88M22 | 1,431 | 605 | 262 | 6 |
| 11 | $-, -$[a] | 88M93 | 887 | 427 | 143 | 0 |

[a] With reference to the *Ph1* locus

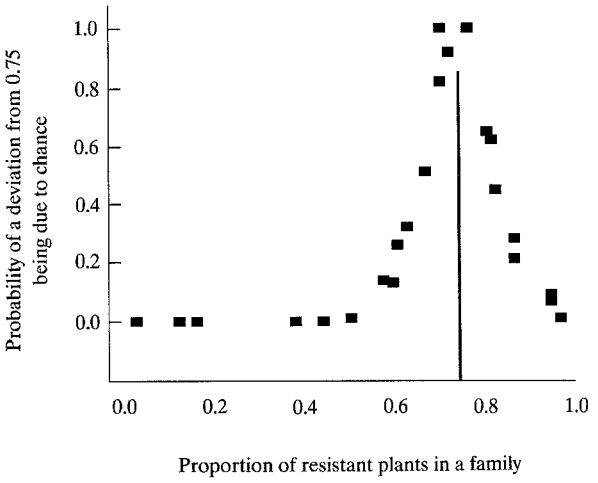


**Fig. 1.** Segregation of a recombined translocated chromosome (selection 87M70-63) in $F_4$ families derived from $F_3$ heterozygotes

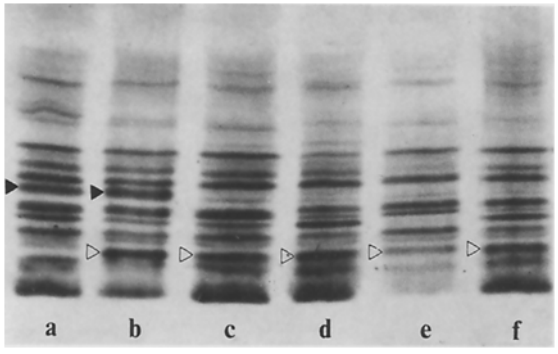


**Fig. 2.** WSP-1 polymorphisms of **a**, 'Indis'; **b**, 88M22-149; **c**, 'Inia 66'; **d**, 87M70-63; **e**, 88M22-157; and **f** 88M22-184. Plants **b** and **d–f** were translocation homozygotes. The positions of WSP-D1a (*open triangles*) and WSP-D1c (*solid triangles*) are indicated

## Results and discussion

The numbers of *Ph*-deficient translocation heterozygotes obtained in each of the three crossing strategies are given in Table 1. Also given, are statistics regarding the success rate of each attempt. Since no knowledge was available regarding the proximity of the marker genes, fairly large numbers of $F_1$ progeny were obtained. However, inviability and low fertility reduced the number of useable, resistant $F_1$ plants to only 16–27% of the total $F_1$ seeds. Sterility probably resulted both from genetic defects induced by the *Ph* deficiencies and the gametocidal effect of the translocated chromosome (Marais 1990). Preferential transmission of the translocated chromosome resulted in a higher level of yellow pigmentation in those $F_2$ bulks without recombined marker genes, and thus facilitated their removal.

*Recombination in the absence of Ph2*

A single recombinant for the marker loci was found among the 540 resistance-carrying $F_2$ populations, a frequency of occurrence of 0.19% (Table 1). Recombinant translocation homozygotes from this population (87M70-63) were resistant to leaf rust, yet had white endosperms and, like 'Inia 66' and 'Chinese Spring', produced both the EP-D1a and α-AMY-D2a isozymes. Also, the recombinants no longer had stem-rust resistance or produced the WSP-D1c water-soluble protein associated with 'Indis', but did produce WSP-D1a, which is also produced by 'Inia 66' and 'Chinese Spring'. When $F_3$-derived $F_4$ populations (the progenitor of which was a heterozygous $F_2$ individual) were tested for leaf-rust resistance, 26 segregating populations were recovered. While some populations segregated in accordance with a 3:1 expectation, preferential transmission of either resistance or susceptibility was apparent in other populations (Fig. 1). Two $F_5$ populations were subsequently raised from heterozygotes selected from an $F_4$ population in which self-elimination apparently occurred. One $F_5$ family showed preferential transmission of leaf-rust resistance; in the second family susceptibility was preferentially transmitted [36 plants resistant: 27 plants susceptible ($\chi^2$ for deviation from a 3:1 ratio = 9.78, $P = 0.002$)]. The recombined chromosome therefore appears to have an altered gametocidal property, since the original 'Indis' translocation was always transmitted preferentially in the combinations tested thus far (Marais 1990).

*Recombination in the absence of Ph1*

From a total of 405 populations screened, six were identified as having recombinant translocated chromosomes. All recombinants resulted from the use of the *ph1b* mutant rather than the nulli 5B tetra 5D aneuploid. Three of the recombinants (88M22-149, 88M22-157 and 88M22-184) had white endosperms and expressed the *Ep-D1a* and *α-Amy-D2a* alleles. All three selections seem to have lost *Sr25*. While they were all highly resistant to leaf-rust race 3SA132, results obtained by Z.A. Pretorius (1991, personal communication) indicated that 88M22-184 is susceptible to some races of leaf-rust. Selections 88M22-157 and 88M22-184 produced WSP-D1a instead of the WSP-D1c produced by the original translocation. Selection 88M22-149, however, expressed both forms of WSP-D1 (Fig. 2). This may be indicative of an aberrant crossover event, or else of a structural difference between the normal chromosome 7DL of common wheat and the translocated chromosome. A segregating $F_3$ population was found among the 88M22-149 progeny in which preferential transmission of susceptibility apparently occurred. In this population 34 resistant: 32 susceptible plants were observed ($\chi^2$ for deviation from a 3:1 ratio = 18.2, $P = 0.00$). $F_1$ progeny from the first backcross

**Table 2.** The fertilities of $F_1$ monosomic plants, resulting from the pollination of 'Chinese Spring' monosome 7D plants with pollen from four recombined translocation homozygotes, and segregation of leaf-rust resistance in their respective $F_2$ progenies

| Recombined translocated chromosomes | $F_1$ monosomics | | Chromosome complement[a] | $F_2$ progeny | | |
|---|---|---|---|---|---|---|
| | Florets studied | Fertility (%) | | Resistant (R) | Susceptible (S) | Ratio (R:S)[b] |
| 87M70-63 | 642 | 83 | – | 159 | 13 | |
| | | | 40 | 1 | 1 | |
| | | | 41 | 24 | 3 | |
| | | | 42 | 9 | 0 | |
| | | | 43 | 1 | 0 | |
| | | | Total | 194 | 17 | 92:8 (0.00) |
| 88M22-149 | 280 | 19 | – | 32 | 20 | |
| | | | 40 | 0 | 1 | |
| | | | 40+t | 2 | 0 | |
| | | | 40+2t | 0 | 1 | |
| | | | 41 | 8 | 3 | |
| | | | 41+t | 3 | 1 | |
| | | | 42 | 5 | 4 | |
| | | | 42+t | 0 | 1 | |
| | | | 43 | 1 | 1 | |
| | | | 44 | 1 | 0 | |
| | | | Total | 52 | 32 | 62:38 (0.01) |
| 88M22-157 | 534 | 84 | – | 88 | 19 | |
| | | | 41 | 25 | 3 | |
| | | | 42 | 9 | 2 | |
| | | | 43 | 1 | 0 | |
| | | | Total | 123 | 24 | 84:16 (0.02) |
| 88M22-184 | 332 | 55 | – | 70 | 32 | |
| | | | 40+t | 4 | 1 | |
| | | | 41 | 15 | 1 | |
| | | | 41+t | 2 | 0 | |
| | | | 42 | 12 | 3 | |
| | | | Total | 103 | 37 | 74:26 (0.78) |

[a] t, unidentified telosome(s)
[b] The probabilities that the observed ratios deviate from 3:1 by chance, appear in brackets

of the recombinants to 'Inia 66' were all resistant, while a 1:1 ratio of resistant: susceptible was expected. Respectively 11 ($\chi^2=9.1$, $P=0.003$), 14 ($\chi^2=12.1$, $P=0.001$) and 16 ($\chi^2=14.1$, $P=0.0002$) seedlings were screened in each case. It would seem, therefore, that *Sd-1* was retained in all three recombinants.

The endosperm pigmentation of the three remaining recombinants (88M22-42, 88M22-98 and 88M22-103) was intermediate to those of 'Indis' and 'Chinese Spring'. All three lines had stem-rust resistance, and produced the endopeptidase and WSP polymorphisms of 'Indis'. Regarding α-AMY-D2, two of the lines produced no product, whereas 88M22-42 produced α-AMY-D2a.

### *The segregation and meiotic pairing behaviour of the recombined translocation chromosomes coding for white endosperm*

In order to determine whether the leaf-rust resistance gene is still associated with chromosome 7D, the recombinants that produced white endosperm were crossed as male parents to 'Chinese Spring' monosome 7D plants. The fertilities of monosomic $F_1$ plants, as well as the root tip chromosome numbers and leaf-rust resistances of their $F_2$s, were recorded (Table 2). If the recombined translocation segments were still associated with chromosome 7D, the susceptible $F_2$ plants should have been nullisomics for 7D. As is evident from Table 2, this was not the case. It appears, therefore, that all recombination events resulting in recombinants with white endosperm, caused relocation of *Lr19d* to a different chromosome(s). The results also suggested varying levels of segregation distortion in the $F_1$, ranging from none (cross involving 88M22-184) to the preferential transmission of either resistance (crosses involving 87M70-63 and 88M22-157) or susceptibility (cross involving 88M22-149).

Telosomes frequently occurred in the progenies of the monosomic plants in which susceptibility was preferentially (88M22-149) or normally (88M22-184) transmitted. In these $F_2$s the frequencies of plants with telo-

**Table 3.** Meiotic chromosome pairing in monotelodisomic plants, heterozygous for a recombined translocated chromosome, and having a normal 7DL telosome

| Recombined translocated chromosome | Number of PMCs studied | Average number of meiotic configurations per PMC | | | | |
|---|---|---|---|---|---|---|
| | | I[t] | I | II | III | IV |
| 87M70-63 | 27 | 0.00 | 1.15 | 20.15 | 0.04 | 0.11 |
| 88M22-149 | 10 | 0.00 | 1.90 | 19.20 | 0.30 | 0.20 |
| 88M22-157 | 26 | 0.12 | 0.42 | 20.54 | 0.08 | 0.04 |
| 88M22-184 | 25 | 0.04 | 0.52 | 20.48 | 0.00 | 0.12 |

**Table 4.** Root tip chromosome numbers and leaf-rust resistance data for $F_1$ progenies, derived from the pollination of two wheat cultivars with pollen from plants which were monotelodisomic 7DL, and heterozygous for a single, recombined translocated chromosome

| Female parent | Male parent having 7DL and a single, recombined translocated chromosome from: | Chromosome complement of the $F_1$ | Number of $F_1$ plants: | | |
|---|---|---|---|---|---|
| | | | Resistant | Susceptible | P[a] |
| 'Inia 66' | 87M70-63 | 41+t | 5 | 1 | |
| | | 42 | 48 | 47 | |
| | | Total | 53 | 48 | 0.69 |
| 'Inia 66' | 88M22-149 | 41 | 0 | 1 | |
| | | 41+t | 0 | 1 | |
| | | 41+t[b] | 0 | 10 | |
| | | 41+2t[b] | 0 | 1 | |
| | | 42 | 1 | 31 | |
| | | 42+t | 0 | 1 | |
| | | 42+t[b] | 1 | 3 | |
| | | 43 | 1 | 2 | |
| | | Total | 3 | 50 | 0.00 |
| 'Chinese Spring' | 88M22-157 | 41+t | 2 | 5 | |
| | | 42 | 41 | 49 | |
| | | 43 | 1 | 0 | |
| | | Total | 44 | 54 | 0.36 |
| 'Chinese Spring' | 88M22-184 | 41 | 2 | 1 | |
| | | 41+t | 5 | 5 | |
| | | 42 | 42 | 44 | |
| | | 42+t | 0 | 1 | |
| | | 43 | 0 | 1 | |
| | | Total | 49 | 52 | 0.84 |

[a] P, probability that the observed ratios deviate from 1:1 by chance

[b] An unidentified telosome(s)

somes were respectively 25% and 18% (Table 2). The telosomes are of unknown origin and are probably the products of the modified gametocidal interactions.

Metaphase-I pairing of chromosome 7D from each of the four recombinants with white endosperm and 7DL was also studied. The results are summarized in Table 3 and are indicative of very normal pairing. The regular occurrence of unpaired chromosomes and the incidence of multivalents in the material probably resulted largely from abnormalities induced in the *Ph*-deficient ancestors or, alternatively, can be explained by the observation of R. de V. Pienaar (1991, personal communication) that the 'Inia 66' and 'Chinese Spring' chromosome complements differ by one, or possibly two, reciprocal translocations.

The monotelo 7DL disomic translocation heterozygotes utilized in the meiotic study were also used to pollinate susceptible tester plants with white endosperms ('Inia 66' and 'Chinese Spring'). Data on the leaf-rust resistance and chromosome numbers of the $F_1$ progeny obtained, are summarized in Table 4. The majority of the progeny either had a euploid chromosome complement or were monotelodisomic. As would be expected, the male transmission frequency of 7DL was very low (7.5%). A telosome(s) other than 7DL also occurred at a relatively high rate (28.3%) in the progeny of the cross involving 88M22-149. While the *Lr19* locus appeared to segregate independently of this telosome(s), its unusual transmission/induction rate may relate to the actions of a relocated *Sd-1* locus. The results of the cross involving 88M22-149 were also extraordinary in the sense that 94% of the progeny were susceptible. This would imply a very strong suicidal tendency of the translocated chromosome in the genetic background of the male parent. Regarding the remaining combinations, approximately one half of the progeny from each were susceptible, which would confirm that the translocation segregated independently of the 7D centromere in each cross.

*The nature of the recombined translocated chromosomes*

Earlier results (Marais 1991), suggested the following linear sequence on the 'Indis' translocated chromosome for some of the markers used, centromere, *Lr19*, *Wsp-D1*, *Y-1* and *Y-2*. Thus, in the recombinants with white endosperm, terminal sections of the translocated chromosome were probably lost. Since the latter recombinants show preferential transmission of resistance in some backgrounds, the *Sd-1* locus is likely to be situated close to, or proximal to, the leaf-rust resistance gene. Recent results obtained by Zhang and Dvořák (1990) showed the *Sd-1* locus to be situated between the centromere and *Lr19* on the *Th. ponticum*-derived translocated chromosome. The original 'Indis' translocated chromosome was always transmitted preferentially (Marais 1991). However, in the present study, three of the recombined forms with white endosperm showed preferential transmission, normal transmission or self-elimination. Normal transmission or self-elimination appeared to be associated with a high incidence of newly formed telosomes. It is very unlikely that the suicidal effect is merely the result of an interaction of *Sd-1d* with a rare combination of 'Chinese Spring' and 'Inia 66' background genes. Rather

it would seem that recombination affected an area of the translocation which contains an enhancer locus or loci of *Sd-1*, that normally prevents self-elimination. Since the gametocidal response to the presence of *Sd-1d* is under multichromosomal control (unpublished data), specific combinations of 'Chinese Spring' and 'Inia 66' chromosomes probably interact with *Sd-1d* and an enhancer(s) to produce a particular effect.

The recovery of recombinants with partially white endosperm is in accord with previous results (Marais 1991) which suggested the presence of at least two yellow-pigment loci on the translocated chromosome. *Sr25* appears to be located between *Lr19* and *Y-2*. The *α-Amy-D2* locus maps close to (10 recombination units from) the centromere on 7DL of common wheat, whereas the *Ep-D1* locus segregates independently of the centromere and *α-Amy-D2* (Chao et al. 1989). Both the *Ep-D1a* an *α-Amy-D2a* alleles were recovered in all the exchanges resulting in recombinants with white flour, whereas the *α-Amy-D2a* allele occurred in one of the recombinants with partially white flour.

The relocation of *Lr19* to a different chromosome probably resulted in the introduction of a normal chromosome 7D that pairs regularly with the 7DL telosome, and normally expresses the *α-Amy-D2* and *Ep-D1* loci. The relocation events would have required the occurrence of double exchanges. The expected infrequent occurrence of these exchanges, as well as the choice of marker genes, may account for the relatively low frequency of recombinants recovered as compared to the results of Sears (1973) and Kibirige-Sebunya and Knott (1983).

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