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Genic heterozygosity maintained by chromosomal interchanges in rye

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Six different rye cultivars were electrophoretically analysed. Three of them showed chromosome polymorphism for reciprocal translocations at various frequencies, while the other three were chromosomally homogeneous. The cultivars were shown to be polymorphic for isozymes at the loci *Got*-3, *Pgm*-1, *Gpi*-1, *Acph*, *Mdh*-1 *and Mdh*-2*b*. The results obtained seem to indicate that the frequency of polymorphic loci, heterozygosity per locus and mean heterozygosity per cultivar are higher in those cultivars having chromosomal interchanges. In the "Ailés" cultivar, plants homozygous and heterozygous for interchanges were analysed, both in open- and self-pollination. The structural heterozygotes showed a higher genic heterozygosity mainly for the *Pgm*-1 and *Mdh*-2*b* loci. Possible explanations of this phenomenon are discussed.

INTRODUCTION

Structural heterozygosity for reciprocal translocations and inversions reduces the fertility of individuals due to the special chromosomal behaviour at meiosis. In the case of interchanges, unbalanced gametes can arise in an adjacent orientation of multivalents at Metaphase I. Various hypotheses have been proposed to explain the existence and maintenance of structural heterozygosity for interchanges that occur in many natural populations, especially in plants (Burnham, 1956). On the basis of the totally or partially suppressed crossing-over in interstitial segments (Burnham, 1962) it has been suggested that structural heterozygosity could be advantageous since it could serve as a mechanism for the possible establishment of coadapted gene complexes within the interstitial segments, and/or for preserving the genic heterozygosity in translocation heterozygotes through sucessive generations. Some authors have proposed that the selective advantage of genic heterozygosity occurs because relatively heterozygous individuals are better buffered against environmental fluctuations than those with low levels of heterozygosity (Lerner, 1954); while others have suggested an advantage due to the existence of new enzymatic forms in multimeric enzymes (Fincham, 1972; Clarke, 1979).

There are several pieces of evidence (for a review see Turelli and Ginzburg, 1983) for the existence of a positive correlation between the fitness increase and the heterozygosity. If there is a relationship between chromosomal and biochemical polymorphisms, it would be expected that populations showing chromosomal polymorphism would be, on average, more heterozygotic than those which do not.

The existence of an association between chromosomal rearrangements and electrophoretic alleles has been mainly analyzed in *Drosophila* inversions, and it has been demonstrated that the enzyme loci are in linkage disequilibrium with the inversions (reviewed in Ishii and Charlesworth, 1977; Hedrick *et al.*, 1978). In plants most of the information now available is obtained in the genus *Oenothera* (Levy and Levin, 1975; Levy and Winternheimer, 1977; Ellstrand and Levin, 1980) and more recently in *Isotoma* (James *et al.*, 1983).

The occurrence of interchange heterozygosity has been reported both in cultivated (Müntzing and Prakken, 1941; Akdik and Müntzing, 1949) and wild rye (Hrishi and Müntzing, 1960; Hrishi *et al.*, 1969) either at the inter- or intra-population levels (Candela *et al.*, 1979; Figueiras *et al.*, 1983).

The aim of this work is to analyse the existence of a possible relationship between chromosomal and isozymic polymorphism in different cultivars

of *Secale cereale* L. In one of them ("Ailés") the studied plants were obtained either by open- or self-pollination. This cultivar has been previously studied and showed the following charecteristics:

(a) A rather constant frequency (15-20 per cent) of structural heterozygotes for several generations (Candela *et al.*, 1982).
(b) Chromosomal polymorphism due to many different reciprocal translocations (Candela *et al.*, 1979). All the seven chromosomes of the haploid complement are involved in interchanges with similar frequency.
(c) Low frequency of translocated homozygotes, as can also be inferred from the high number of different translocations detected.

MATERIAL AND METHODS

At least 100 plants were electrophoretically analysed from each of six cultivars of *Secale cereale* L. ($2n = 14$) named Elbon (U.S.A.), JNK (Japan), Palencia (Spain), La Estrada (Spain), Mansilla (Spain) and Ailés (Spain). These can be considered as natural populations since artificial selection had never been carried out on them.

The cultivars Palencia, JNK and Elbon did not show chromosomal polymorphism: the frequency of structural heterozygosity (FSH) was 0·00. The remaining cultivars were polymorphic and the samples analysed in the present work, La Estrada (1978), Mansilla (1980) and Ailés (1979), showed a frequency of structural heterozygosity of 4·0 per cent, 9·8 per cent and 15·4 per cent, respectively (Candela *et al.*, 1982; Figueiras *et al.*, 1983; González-Jaén *et al.*, 1985). All the cultivars were reproduced in panmictic and homogeneous conditions in experimental fields.

Several structural homozygotes (SHm) and heterozygotes (SHt) from the Ailés 1 sample were reproduced by open pollination; 446 plants (sample 2) from the total offspring obtained were classified as SHm and SHt according to their chromosomal configuration observed at Metaphase I (7II or 1IV+5II, respectively) and electrophoretically analysed. Forty plants (sample 3) out of the total SHt from sample 2 were reproduced by selfing, giving rise to the first inbred generation, named sample 4. These plants were also analysed both electrophoretically and cytologically. A scheme describing the relationship between the different samples is shown in fig. 1.

Electrophoresis was carried out for the isozymatic systems: Glutamate oxaloacetate transaminase (GOT, EC 2.6.1.1), Phosphoglucomutase (PGM, EC 2.7.5.1), Glucose phosphate isomerase (GPI, EC 5.3.1.9), Acid and Alkaline phosphatases (ACPH and ALK, EC 3.1.3.2), Malate dehydrogenase (MDH, EC 1.1.1.37.), Leaf peroxidases (PER, EC 1.11.1.7.), Esterases (EST, EC 3.1.1.2.), Aminopeptidase (AMP, EC 3.4.11.1.) and Indophenol oxidase (IPO, EC 1.9.3.1.) following the protocols of Pérez de la Vega and Allard (1984) and Figueiras *et al.* (1985). The loci which showed variant alleles (see figs. 2 and 3 for nomenclature of alleles and genotypes) involve all the chromosome pairs with the exception of 5*R* and 6*R* chromosomes (table 1). Plantlets from the homogeneous species *Secale vavilovii* were used as a standard in all the gels.

RESULTS

In all the six cultivars seven activity zones belonging to six isozymic systems were invariant (GOT-1 and GOT-2, GPI-2, ALK-1, PER-5, AMP and IPO). Neither ALK-3, ALK-4, MDH-3, PER or EST were considered because they have a poor resolution in many cases, show null alleles or there are some doubts about their genetic control. Therefore, only five enzymatic systems were analysed corresponding to six different loci: *GOT*-3, *Pgm*-1, *Gpi*-1, *Acph*, *Mdh*-1 and *Mdh*-2*b*. The genetic con-

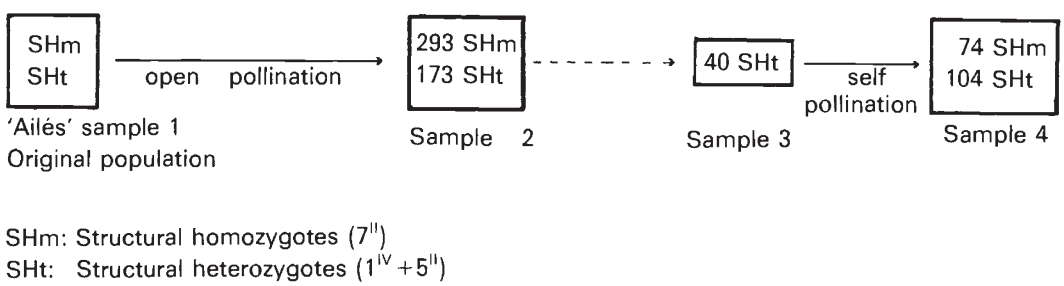

Figure 1 Origin of the four samples of Ailés cultivar.

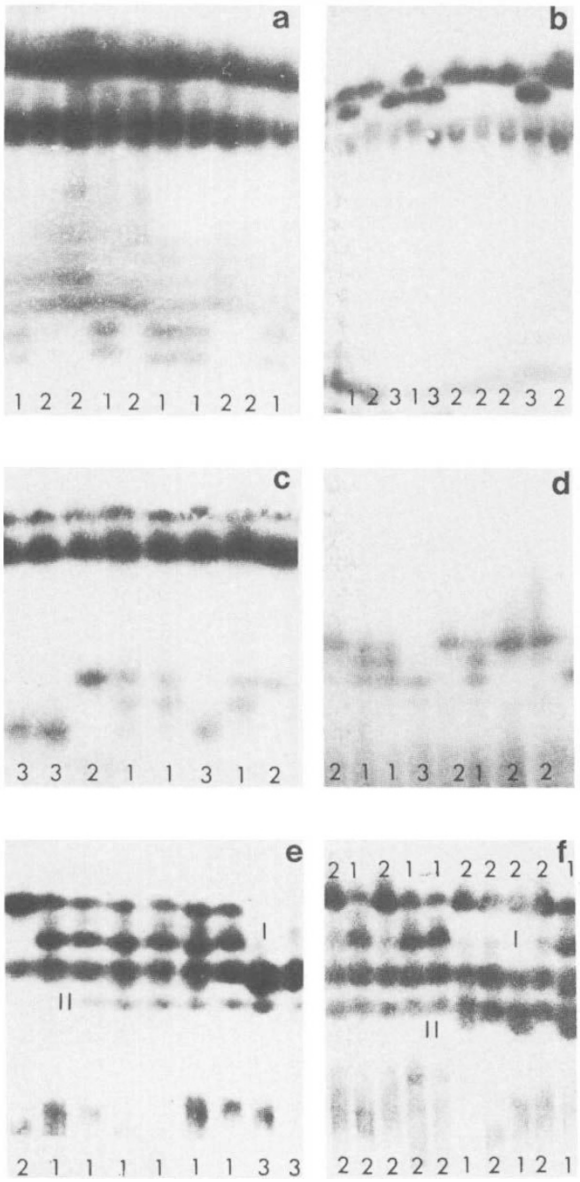

Figure 2 Zymogram phenotypes of the isozyme systems that showed variability in the rye cultivars examined. (a) Glucose phosphate isomerase: 1, heterozygote 13; 2, homozygote 11. (b) Phosphoglucomutase: 1, heterozygote 12; 2, homozygote 22; 3, homozygote 11. (c) Glutamate oxaloacetate transaminase: 1, heterozygote 12; 2, homozygote 11; 3, homozygote 22. (d) Acid phosphatase: 1, heterozygote 12; 2, homozygote 11; 3, homozygote 22. (e) Malate dehydrogenase zone I (the fastest migrating zone): 1, heterozygote 13; 2, homozygote 11; 3, homozygote 33. Malate dehydrogenase zone II (the slowest migrating zone): all the slots were homozygotes 11. (f) Malate dehydrogenase zone I: 1, heterozygote 13; 2, homozygote 11. Malate dehydrogenase zone II: 1, heterozygote 12; 2, homozygote 11.

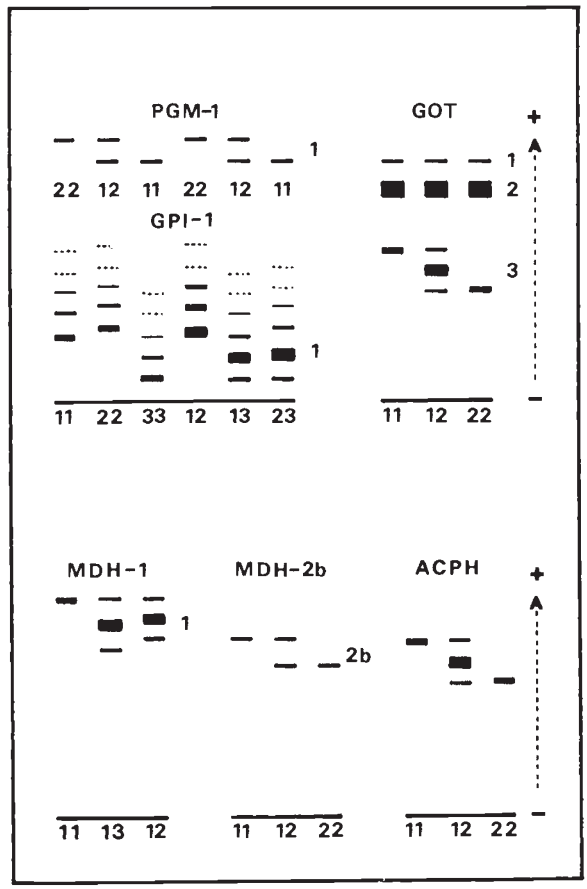

Figure 3 Zymogram phenotypes of the polymorphic isozyme systems Phosphoglucomutase (PGM, monomer), Glucosephosphate isomerase (GPI, dimer), Glutamate oxaloacetate transaminase (GOT, dimer), Malate dehydrogenase (MDH-1, dimer and MDH-2, monomer) and acid phosphatase (ACPH, dimer). The genotypes are shown below the zymograms and the different activity zones are indicated on the right side. The non-polymorphic isozyme systems (AMP, IPO) and the systems that present nul alleles (L-PER, EST, ALK) are not in the figure. Samples derived from 12-day-old seedling leaves.

trol of these enzymatic system has been described by Peréz de la Vega and Allard (1985) and Figueiras *et al.* (1985).

Cultivar analyses

The allelic frequencies and the frequency of polymorphic loci for the six cultivars analyzed are shown in tables 2 and 3, respectively. Two criteria have been used to classify a locus as polymorphic: (a) if the frequency of the most frequent allele is 0·95 or less, and (b) if this frequency is 0·99 or less.

Table 1 Chromosomal location of isozyme structural genes in *Secale cereale* cv. Imperial, cv. King II and cv. Dakold

Enzymes	Genes	Chromosome or chromosome arm of genome R*	References
Glucosephosphate isomerase 1[a]	*Gpi*-1	1*p*	Hart (1979), Chojecki and Gale (1982)
Malate dehydrogenase-1[a]	*Mdh*-1	2*q*	Figueiras *et al.* (1985)
Glutamate oxaloacetate transaminase-3[a]	*Got*-3	3(*q*?)	Hart (1975), Tang and Hart (1975)
Malate dehydrogenase-2	*Mdh-2b*	3(*q*?)	Salinas and Benito (1985*a*)
Phosphoglucomutase-1	*Pgm*-1	4*p*	Salinas and Benito (1985*b*)
Acid phosphatase[a]	*Acph*	7*p*	Salinas and Benito (1984*a*)

* Rye chromosome nomenclature according to Sybenga (1983).
p = short arm; *q* = long arm; *q*? = chromosome arm assigned by homoeology with hexaploid wheat.
[a] Dimeric enzymes.

Table 2 Allelic frequencies of the six polymorphic loci analysed

		Cultivar					
		Without interchange polymorphism			With interchange polymorphism		
Locus	Allele	Elbon	JNK	Palencia	La Estrada	Mansilla	Ailés 1
Got-3	1	0·668	0·705	0·782	0·800	0·921	0·773
	2	0·332	0·295	0·218	0·200	0·079	0·227
Pgm-1	1	0·958	0·955	0·836	0·908	0·887	0·877
	2	0·042	0·045	0·164	0·092	0·113	0·123
Gpi-1	1	0·963	0·600	0·714	0·825	0·657	0·777
	2	0·014	0·195	0·194	0·150	0·274	0·137
	3	0·023	0·205	0·092	0·025	0·069	0·086
Acph	1	0·986	0·935	0·996	0·917	1·000	0·950
	2	0·014	0·065	0·004	0·083	0·000	0·050
Mdh-1	1	1·000	1·000	0·996	0·950	0·990	0·977
	3	0·000	0·000	0·004	0·050	0·010	0·023
Mdh-2b	1	0·977	1·000	0·933	0·942	0·917	0·900
	2	0·023	0·000	0·067	0·058	0·083	0·100
No. of plants analysed		107	100	119	120	102	110

In general, the loci *Mdh*-1 and *Acph* are the less polymorphic followed by *Mdh-2b*, in the six cultivars (table 2). It can be observed that the cultivars which carry translocations are more polymorphic by both criteria of classification (table 3). This difference is more clearly seen when the means for both the cultivars without translocations and those with translocations are compared. The frequency of rare alleles was also higher in chromosomally polymorphic cultivars than in monomorphic; these data have not been taken in account in this work.

The data on the heterozygosity per locus and mean heterozygosity per cultivar and the FSH in each cultivar are shown in table 4. Heterozygosity values were obtained directly from the observed genotypic frequencies. When a given locus was not in Hardy-Weinberg equilibrium (following Nei's method, 1975) it is marked with an asterisk in table 4.

Although the mean heterozygosity differences between both groups of cultivars (with or without interchanges) are not statistically significant, as a general trend, the mean heterozygosity is higher in cultivars carrying chromosomal interchanges (table 4); and it is confirmed by the existence of a significant positive correlation between FSH and the mean heterozygosity per cultivar. The

Table 3 Percentage of polymorphic loci in the cultivars analysed. Two different criteria were used to define a locus as polymorphic: (a) when the most frequent allele is present at a frequency of 0·95 as a maximum, (b) when the most frequent allele is present at a frequency of 0·99 as a maximum

Cultivar	0·95 (%)	0·99 (%)
Elbon	1/6 (16·67)	5/6 (83·33)
JNK	3/6 (50·00)	4/6 (66·67)
Palencia	4/6 (66·67)	4/6 (66·67)
Mean (Without interchange polymorphism)	44·45 ± 14·70	72·22 ± 5·55
La Estrada	6/6 (100·00)	6/6 (100·00)
Mansilla	4/6 (66·67)	5/6 (83·33)
Ailés 1	4/6 (66·67)	6/6 (100·00)
Mean (With interchange polymorphism)	77·78 ± 11·11	94·44 ± 5·56

correlation and regression coefficients calculated were $r = +0{\cdot}873$ and $b = 0{\cdot}421$, which are both statistically significant ($t_{4\text{-df}} = 3{\cdot}58$, $0{\cdot}5 > p > 0{\cdot}01$).

Isozymic polymorphism in SHm and SHt Ailés plants of sample 2

In order to know if SHm and SHt contribution to the total genic heterozygosity values was different, a sample of SHm and SHt plants from the Ailés cultivar was electrophoretically analysed. Tables 5 and 6 show the allelic frequencies, the heterozygosity per locus and mean heterozygosity values, respectively, for both SHm and SHt plants. The values were calculated as in the preceding section.

Mean heterozygosity is similar in both SHm and SHt. However, there are significant differences for some of the loci analysed when the heterozygosity per locus in both plant types are compared, *i.e.*, SHm heterozygosity is higher than that of the SHt for the *Got*-3 locus, while the situation is the reverse for *Pgm*-1 and *Mdh*-2*b* (table 6).

On the other hand, SHm and SHt plants were compared with respect to the number of heterozygous loci per individual (up to a maximum of five loci). The percentage of homozygous plants for all the loci analysed was similar (24·57 per cent and 20·23 per cent for SHm and SHt, respectively), and the frequency of heterozygotes for one locus was higher in SHm than in SHt plants (60·18 per cent versus 50·72 per cent).

Inbreeding effect in SHt plants

The importance of structural heterozygosity as a mechanism for preserving the genic heterozygosity under inbreeding was examined in plants from the Ailés cultivar. The allelic frequencies, the heterozygosity per locus and the mean heterozygosity of 40 SHt plants (sample 3) and their progenies obtained by selfing (sample 4) are summarised in tables 5 and 6.

Most of the analysed loci are not in Hardy-Weinberg equilibrium, which can be attributed to the conditions in which plants were reproduced. Heterozygosity per locus and the mean heterozygosity values generally decreased in the first selfing generation (table 6). However, the pattern of decrease is different for SHm and SHt for some of the loci analysed. SHt heterozygosity is higher than that of the SHm for the *Pgm*-1, *Gpi*-1 and *Mdh*-2*b* loci. These differences are of the same type as those found in Ailés sample 2.

Table 4 Estimated values of heterozygosity of the six polymorphic loci analysed

	Cultivar							
	Without interchange polymorphism				With interchange polymorphism			
Locus	Elbon	JNK	Palencia	$\bar{x}$	La Estrada	Mansilla	Ailés 1	$\bar{x}$
Got-3	0·458	0·130*	0·286	0·291 ± 0·085	0·267	0·160	0·363	0·263 ± 0·059
Pgm-1	0·084	0·050	0·177*	0·104 ± 0·038	0·150	0·206	0·246	0·201 ± 0·028
Gpi-1	0·028	0·400*	0·219*	0·216 ± 0·107	0·217	0·333*	0·227*	0·254 ± 0·037
Acph	0·009	0·110	0·008	0·042 ± 0·034	0·133	0·000	0·100	0·078 ± 0·040
Mdh-1	0·000	0·000	0·008	0·003 ± 0·003	0·033	0·020	0·046	0·033 ± 0·008
Mdh-2*b*	0·047	0·000	0·135	0·061 ± 0·040	0·127	0·147	0·164	0·146 ± 0·011
Mean heterozygosity	0·104 ± 0·072	0·115 ± 0·061	0·139 ± 0·046	0·120 ± 0·045	0·155 ± 0·033	0·149 ± 0·041	0·191 ± 0·46	0·163 ± 0·038
FSH	0·00	0·00	0·00		4·00	9·80	15·38	

* Population not in equilibrium for this locus (Nei, 1975).
FSH: Frequency of structural heterozygosity.

Table 5 Allelic frequencies in the six polymorphic loci analysed of structural homozygous and heterozygous Ailés plants (open- and self-pollination were considered)

		Sample 2		Sample 3	Sample 4		
Locus	Allele	SHm	SHt	SHt	Total	SHm	SHt
Got-3	1	0·790	0·858	0·712	0·683	0·723	0·654
	2	0·210	0·142	0·288	0·317	0·277	0·346
Pgm-1	1	0·853	0·798	0·662	0·764	0·764	0·764
	2	0·147	0·202	0·338	0·236	0·236	0·236
Gpi-1	1	0·696	0·665	0·450	0·441	0·358	0·500
	2	0·161	0·220	0·400	0·419	0·480	0·375
	3	0·143	0·115	0·150	0·140	0·162	0·125
Acph	1	0·981	0·983	1·000	1·000	1·000	1·000
	2	0·019	0·017	0·000	0·000	0·000	0·000
Mdh-1	1	0·968	0·971	0·950	0·969	0·953	0·981
	2	0·030	0·012	0·000	0·000	0·000	0·000
	3	0·002	0·017	0·050	0·031	0·047	0·019
Mdh-2b	1	0·932	0·870	0·750	0·829	0·838	0·822
	2	0·068	0·130	0·250	0·171	0·162	0·178
No. of plants analysed		293	173	40	178	74	104

SHm = Structural homozygotes.
SHt = Structural heterozygotes.

Table 6 Estimated values of heterozygosity in the six polymorphic loci analysed of structural homozygous and heterozygous Ailés plants (open- and self-pollination were considered)

	Sample 2		Sample 3		Sample 4	
Locus	SHm	SHt	SHt	Total	SHm	SHt
Got-3	0·317	0·237	0·475	0·309	0·311	0·308
Pgm-1	0·253	0·358	0·525	0·191	0·149	0·221
Gpi-1	0·348*	0·393*	0·700	0·337	0·297	0·365
Acph	0·024	0·035	0·000	0·000	0·000	0·000
Mdh-1	0·065	0·058	0·100	0·051	0·068	0·039
Mdh-2b	0·123	0·225	0·500	0·264	0·189	0·317
Mean heterozygosity	0·188 ± 0·056	0·218 ± 0·060	0·383 ± 0·111	0·192 ± 0·057	0·169 ± 0·050	0·208 ± 0·063

* Population not in equilibrium for this locus (Nei, 1975).
SHm = Structural homozygotes.
SHt = Structural heterozygotes.

DISCUSSION

Our observations show a higher genetic variability in the rye cultivars carrying structural heterozygosity for reciprocal translocations as a result of both a higher number of polymorphic loci (table 3) and a higher genic heterozygosity (table 4). We have not found any difference in reproductive behaviour between the six cultivars analysed, so that this cannot explain the difference. The existence of a positive correlation between the structural heterozygote frequencies and the mean heterozygosity is consistent with the existence of an association between chromosomal and genetic polymorphisms.

Comparison of genic heterozygosity between homozygous and heterozygous structural plants of the Ailés cultivar and in the first inbred generation (table 6) indicates that the structural heterozygosity for reciprocal translocations may keep the genic heterozygosity in those loci linked to the translocations. However, this could only be so if the less frequent alleles were located on the translocated chromosomes. Moreover this mechanism would

increase in efficiency with increase in linkage between the loci and the translocation points. For a locus not linked with the translocation the distribution of genic heterozygotes among structural heterozygous and homozygous plants will be at random.

Following this reasoning, we could propose that the loci *Got*-3, *Pgm*-1 *and Mdh*-2*b* are linked with translocations present in the Ailés cultivar, since genic heterozygotes for these loci are not equally frequent in structural homozygotes and heterozygotes. Studies now in progress on some of the interchanges isolated from these samples support this conclusion. *Got*-3 and *Mdh*-2*b* loci are linked with, at least, two different interchanges. One of these involves 3R and 1R chromosomes, being the *Got*-3 locus in the translocated segment and the *Mdh*-2*b* in the interstitial segment. The translocated chromosome carries allele 1 for both loci (Figueiras *et al.*, 1985). The other interchange involves 3R and 4R chromosome pairs. Both loci appear to be totally linked to it, allele 1 for *Got*-3 and allele 2 for *Mdh*-2*b* loci being on the translocated chromosome. Moreover, allele 2 for *Pgm*-1 is totally linked to two heterozygotes carrying interchanges which involve 4R and 5R chromosome pairs. Other of the interchanges analyzed which involves 1R chromosomes, is partially associated with allele 3 for *Gpi*-1 locus.

If the genic heterozygosity for certain loci had a selective advantage, the structural heterozygotes would be favoured by the natural selection. This could explain the correlation between the structural and genic heterozygosities found, and also the maintenance of the chromosomal polymorphism for reciprocal translocation.

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