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Segregation distortion of isozyme loci in cherimoya (*Annona cherimola* Mill)

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Abstract The allelic segregation of 13 isozyme loci in hand-fertilized heterozygous cherimoya trees (*Annona cherimola* Mill.) has been studied. We analyzed 63 locus × progeny combinations and found non-Mendelian segregation in 12 cases. The sequential Bonferroni method revealed only eight cases of non-Mendelian segregation; these have been investigated with several chi-square tests to discover what processes were involved. Gametic selection appears to be the main contributor, although zygotic selection seems also to play a part.

Key words Segregation distortion · *Annona* · Cherimoya · Isozyme · Gametic selection · Zygotic selection

Introduction

Distorted segregation ratios at some loci have been found in most plants where large numbers of markers have been analysed. Torres (1990), in his review of isozymes in fruit trees, comments that statistically significant single-gene segregation distortion is very common in fruit trees and other woody plants but that the origin of this phenomenon is as yet unclear.

Among intraspecific crosses, segregation distortion has been observed at RFLP or isozymic loci in several cultivated plants, such as maize (Edwards et al. 1987), lettuce (Landry et al. 1987), rice (McCouch et al. 1988), chick-pea (Kazan et al., 1993), lentil (Muehlbauer et al. 1989), pea (Weeden and Marx 1984), bean (Koenig and Gepts 1989), sunflower (Kahler and Lay 1985), camellia (Wendel and Parks 1982) and grape (Weeden et al. 1988).

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There may be various causes for non-Mendelian segregation, which may be produced by factors affecting all steps from chromosome disjunction through to seed maturation. Several studies have demonstrated that the segregation distortion of isozyme and other molecular markers may be produced by lethal genes, or other linked loci, which affect the viability of the markers (Grant 1975; Zamir and Tadmor 1986; Bradshaw and Stettler 1994). Certation or competition between pollen grains (Hornaza and Herrero 1992), self-incompatibility mechanisms (Savolainen et al. 1992), or the presence of segregation distorters (Lyttle 1991) may be other mechanisms involved in segregation distortion. As Bradshaw and Stettler (1994) noted, differences in life history and mating systems among taxa showing segregation distortion may provide many different mechanisms capable of producing skewed inheritance ratios.

The cherimoya tree is a semi-deciduous fruit tree of Andean origin and is cultivated in several subtropical zones in the world; for example, California and southern Spain. The fruit of this tree is a valuable crop but its cultivation involves problems, such as protogyny (Thompson 1970), which render self-pollination difficult, although incompatibility as such has not been described in this crop. Cherimoya has been the subject of several genetic studies aimed at distinguishing between cultivars by using isozyme techniques (Ellstrand and Lee 1987; Pascual et al. 1993), studying its flower biology (Khan et al. 1991), and obtaining a genetic linkage map (Lee and Ellstrand 1987).

Molecular markers usually segregate in a predictable way as dominant or co-dominant, but it is necessary to study the inheritance of these markers to confirm the precise mode involved. Deviations from expected segregation ratios may influence the development of breeding programs based on the selection of molecular markers. The success of these breeding programs is highly dependent upon the knowledge of these distorting markers and their control capacity.

In this paper we report on an analysis of the behaviour of 13 polymorphic isozyme genes showing non-

Mendelian segregation, due to several causes, in eight of them.

Material and methods

For the genetic analysis of isozyme gene segregation in cherimoya (*Annona cherimola* Mill) we used progeny seeds from fruit produced by hand self-fertilizing 14 different cultivars from the subtropical tree collection of the Estación Experimental "La Mayora" (CSIC. Málaga, Spain). Table 1 shows the denominations, abbreviations and genotypes for 14 polymorphic loci in the 14 cultivars analyzed.

About 50 mg of secondary endosperm from each seed was homogenised with 150 µl Tris-HCl extraction buffer (Soltis et al. 1983) in a refrigerated mortar, maintaining temperatures close to 4 °C. The extract was absorbed on to 5 × 11-mm paper wicks (Whatman n°3) and loaded in a horizontal starch gel [10% starch, 60 starch Sigma Chemical Co.: 40 starch hydrolyzed in our laboratory following the method of Moretti et al. (1957)].

The gel/electrode buffers and the gel running conditions were as described in Pascual et al. (1993).

Staining assays for acid phosphatase (ACPH), alcohol dehydrogenase (ADH), Diaphorase (DIA), glutamate dehydrogenase (GDH), glutamate oxalaceate transaminase (GOT), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), malic enzyme (ME), phosphoglucose isomerase (PGI), phosphoglucose mutase (PGM), 6-phosphogluconate dehydrogenase (6PGDH), shikimate dehydrogenase (SKDH), superoxide dismutase (SOD) and triose phosphate isomerase (TPI) were prepared as described by Soltis et al. (1983) and Wang and Szmidt (1989) with minor modifications (Perfectti 1995). Beauchamp and Fridovich's (1971) method was followed to stain for SOD activity.

The loci were named according to the mobility of their electromorphs, with numbers reflecting their relative advance in the electrophoretic gel, as proposed by Lee and Ellstrand (1987) and Pascual et al. (1993). A similar system was used for alleles.

Segregation analyses were made on seed data (equivalent to an F_2) using the computer program Linkage-1 (Suiter et al. 1983).

The observed segregations for each locus were tested against the expected Mendelian ratio (1:2:1) for the progeny of a heterozygous individual. The sequential Bonferroni method (Rice 1989; Palmer 1994) was applied in order to avoid type-I errors deriving from the large number of tests. If no adjustment is made for the number of tests performed, then the probability of a type-I error increases concomitantly with the number of tests in the group (Rice 1989).

With cases appearing to show non-Mendelian segregation, we carried out three chi-square tests. The first such test (χ^2g) is to reveal whether the two alleles (p and q) appear in the same frequency (H_0); if H_0 is rejected it might indicate the existence of gametic or zygotic selection (Westphal and Wricke 1991), thus implying selection against one allele or one homozygous genotype. The second test ($\chi^2 z$) analyses whether, on taking p and q experimental frequencies, the genotypes observed result from the random union of gametes (H_0) (Pham et al. 1990), thus suggesting, when significant, the possibility of zygotic selection, assortative mating or fertilization. The third test (χ^2h) analyses whether half of the offspring are heterozygotes (H_0), and provides information about whether segregation is Mendelian in at least one sex. The sequential Bonferroni method was also applied to these tests.

Results

Genetic control of the isozymes analysed

With the exception of GDH, the remaining 13 isozymic systems analyzed displayed clear banding patterns, which may be explained by the existence of 23 loci. GDH showed weak activity and only after staining for more than 6 h, did it display a pattern with two activity zones, very similar to that described by Ratajczak et al. (1988) in *Lupinus*. Nevertheless, due to the poor activity of this enzyme in cherimoya we have not been able to analyze this electrophoretic system.

The genetic control of ACPH, ADH, DIA, GOT, IDH, MDH, 6PGDH, PGI, SKDH, SOD and TPI has been reported elsewhere (Ellstrand and Lee 1987; Lee and Ellstrand 1987; Pascual et al. 1993; Perfectti 1995).

ME has been described previously in cherimoya as an isozymic system with a single monomorphic gene in Spanish cultivars (Pascual et al. 1983). Upon analysis, however, a second allele, labelled 2, appears in cultivars C3te, CU, PE and SP78 from Peru, B2 from Bolivia, and CH and SA from California. Heterozygous individuals showed a pattern consisting of two bands, coinciding with those which appeared in homozygous individuals for each of these alleles. This suggests that cherimoya ME has a monomeric structure, similar to that reported by Gaur and Slinkard (1990) in *Cicer*.

Ellstrand and Lee (1987) reported two PGM genes in *A. cherimola*; *Pgm-1* being monomorphic in all their cultivars. However, these authors do not explain the existence of individuals with four bands for PGM activity (i.e. cultivar Bonita). Our analysis has revealed the presence of two polymorphic PGM genes in cherimoya. The electromorphs belonging to the gene *Pgm-1* are the most-anodal and cathodal and thus occupy flanking positions outside the two electromorphs encoded by *Pgm-2*.

SOD in cherimoya shows a band pattern with five activity zones (Perfectti 1995), but only the most anodal zones (SOD-4 and SOD-5) showed sufficient resolution to be used for genetic analysis. SOD-4 is encoded by the monomorphic gene *Sod-4*. Because the SOD-5 zone only appears in leaves we have not analyzed its segregation.

Got-3, *Idh-1*, *Mdh-2*, *Pgi-2*, *Skd-2*, *Acp-2*, *Dia-1*, *Sod-4*, and *6Pgd-2* appeared as monomorphic genes in the cultivars studied. The *6Pgd-1* gene described by Ellstrand and Lee (1987) showed no activity with the electrophoretic techniques used in our study.

Segregation analysis

Adh-1. The segregation of *Adh-1* was studied in the offspring of eight cultivars which were heterozygotic for this gene (Table 2). Seven cultivars showed Mendelian segregation (1:2:1), but in cultivar SP78 the offspring had an excess of homozygotes for allele 2.

Got-1. On analysing the segregation of this gene in seven heterozygotic cultivars (Table 1) we observed a significant deviation from Mendelian expectations only in the offspring of cultivar Peru Seed 24, which showed a severe deficiency of homozygotes for the slowest allele (Table 2).

Got-2. All three cultivars analysed (MA, PE and SA) showed Mendelian segregation for this gene.

Table 1 Genotypes for 14 polymorphic loci in 14 cherimoya cultivars

Cultivar (abbreviation)	Genotype													
	Adh-1	*Got-1*	*Got-2*	*Idh-2*	*Mdh-1*	*Me-1*	*Pgi-1*	*Pgm-1*	*Pgm-2*	*Skd-1*	*Sod-5*	*Tpi-1*	*Tpi-2*	*Tpi-3*
Bolivia seedling #2 (B2)	12	13	12	22	11	22	66	12	12	22	22	12	22	12
Bolivia seedling #3 (B3)	11	13	11	22	11	11	66	12	12	22	22	22	22	11
Bonita (BO)	12	33	22	22	12	22	46	12	12	22	22	11	22	12
Chiuna 3 temprana (C3te)	22	33	22	24	12	12	65	11	11	22	22	11	22	22
Chaffey Riverside (CH)	12	33	22	44	12	12	44	11	11	22	12	11	12	22
Cumbe (CU)	22	33	22	24	12	12	56	11	11	22	22	11	22	22
Fino de Jete (FI)	12	24	22	22	11	11	44	11	12	12	22	11	11	12
Manteca (MA)	12	24	12	22	11	11	25	11	12	22	22	11	11	11
Selección Perú 78 (SP78)	12	23	22	24	11	12	44	11	11	22	12	11	12	12
Pinchudo (PC)	12	24	22	24	12	11	44	11	12	12	22	12	12	12
Peru seed 24 (PE)	12	23	12	24	13	12	44	11	11	22	22	11	12	22
Salmon (SA)	22	34	12	22	13	12	44	11	12	22	22	11	22	22
Serena (SE)	12	34	22	22	11	11	44	11	12	12	22	11	11	12
White (WH)	12	23	22	12	11	11	46	12	11	22	22	12	22	12

Table 2 Chi-square analysis of the segregation of 13 polymorphic isozyme loci in self-fertilised cultivars of cherimoya

Locus	Cultivar	Genotype	Observed segregation			χ^2	P	P'[d]
			SS[a]	SF[b]	FF[c]			
Adh-1	SP78	12	17	39	52	31.019	< 0.0001	< 0.001
	WH	12	11	46	22	4.446	0.108	ns[e]
	PC	12	6	15	12	2.455	0.293	ns
	CH	12	16	23	18	2.226	0.323	ns
	MA	12	18	26	19	1.952	0.377	ns
	BO	12	15	21	14	1.320	0.517	ns
	PE	12	35	59	27	1.132	0.568	ns
	SE	12	20	31	19	0.943	0.624	ns
Got-1	PE	23	7	42	25	10.108	0.006	0.042
	MA	24	22	37	10	4.536	0.104	ns
	WH	23	22	48	34	3.385	0.184	ns
	SA	34	8	8	3	3.105	0.212	ns
	PC	24	9	12	5	1.385	0.500	ns
	B3	13	4	9	7	1.100	0.577	ns
	SE	34	14	37	18	0.826	0.662	ns
Got-2	SA	12	3	3	4	1.800	0.407	ns
	PE	12	23	55	27	0.543	0.762	ns
	MA	12	16	36	15	0.403	0.818	ns
Idh-2	CU	24	27	45	33	2.829	0.243	ns
	WH	12	13	39	18	1.629	0.443	ns
	C3te	24	7	12	10	1.483	0.476	ns
	PE	24	29	64	38	1.305	0.521	ns
	PC	24	9	15	10	0.529	0.767	ns
	SP78	24	28	52	27	0.103	0.950	ns
Mdh-1	CH	12	25	28	7	11.067	0.004	0.028
	CU	12	26	60	19	3.076	0.215	ns
	PE	12	35	74	25	2.955	0.228	ns
	BO	12	10	30	10	2.000	0.368	ns
	SA	13	5	16	7	0.857	0.651	ns
	PC	12	11	23	15	0.837	0.658	ns
	C3te	12	9	13	7	0.586	0.746	ns
Me-1	PE	12	45	49	36	9.123	0.010	0.060 (ns)
	CU	12	34	51	20	3.819	0.148	ns
	CH	12	20	24	15	2.898	0.235	ns
	C3te	12	7	12	10	1.483	0.476	ns
	SP78	12	26	50	32	1.259	0.533	ns
	SA	12	7	10	6	0.478	0.787	ns
Pgi-1	C3te	56	4	12	8	1.333	0.513	ns
	BO	46	11	23	16	1.320	0.517	ns
	MA	25	21	34	15	1.086	0.581	ns
	WH	46	29	50	26	0.410	0.815	ns

Table 2 (Continued)

Locus	Cultivar	Genotype	Observed segregation			χ^2	P	P'[d]
			SS[a]	SF[b]	FF[c]			
Pgm-1	WH	12	54	47	31	18.955	0.0001	< 0.001
	B2	12	26	51	18	1.863	0.394	ns
	B3	12	7	8	5	1.200	0.549	ns
	BO	12	12	21	12	0.200	0.905	ns
Pgm-2	PC	12	23	8	3	33.059	< 0.0001	< 0.001
	SE	12	30	25	15	12.143	0.002	0.012
	SA	12	10	7	3	6.700	0.035	0.175 (ns)
	BO	12	15	15	14	5.178	0.075	ns
	B2	12	30	45	20	2.368	0.306	ns
	MA	12	20	34	16	0.514	0.773	ns
	B3	12	6	9	5	0.300	0.861	ns
Skd-1	FI	12	0	18	8	8.769	0.013	0.039
	PC	12	6	12	14	6.000	0.050	0.100 (ns)
	SE	12	18	36	16	0.171	0.918	ns
Tpi-1	PC	12	15	16	10	3.195	0.202	ns
	WH	12	33	51	21	2.829	0.243	ns
Tpi-2	CH	12	26	20	9	14.600	0.001	0.004
	PE	12	27	28	22	6.377	0.041	0.123 (ns)
	PC	12	12	14	8	2.000	0.368	ns
	SP78	12	28	48	32	1.630	0.443	ns
Tpi-3	WH	12	16	21	17	2.704	0.259	ns
	SE	12	12	18	8	0.947	0.623	ns

[a] SS: homozygotes for the slowest allele
[b] FF: homozygotes for the faster allele
[c] SF: heterozygotes
[d] P': probability after used Bonferroni's method
[e] ns: non-significant

Idh-2. We found Mendelian segregation in all six cultivars analyzed, independently of the allelic pairs involved (alleles 2 and 4 or alleles 1 and 2).

Mdh-1. We analyzed the offspring of seven cultivars (Table 2). The cultivar Chaffey Riverside showed a significant deficiency in allele 2 with regard to Mendelian proportions. The remaining six showed Mendelian segregation.

Me-1. Out of six segregations studied (Table 2) the cultivar Peru Seed 24 was the only one showing non-Mendelian segregation, with a slight deficiency in allele 2.

Pgi-1. A 1:2:1 segregation appeared in all four cultivars studied.

PGM. Non-Mendelian segregations appeared in both *Pgm-1* and *Pgm-2* genes. Cultivar WH (Table 2) showed a clear deviation in the allelic segregation of gene *Pgm-1* with regard to Mendelian proportions, with an excess in allele 1. In B2, B3 and BO cultivars, however, segregation was Mendelian in this gene. Out of the seven cultivars analysed for the segregation of *Pgm-2* we found three cultivars (PC, SA and SE) with different distortion levels in their segregation, but always with a deficiency in allele 2.

Skd-1. We did not find SS homozygotes among the offspring of the cultivar Fino de Jete (Table 2). These was also a slight deficiency in allele 1 in cultivar Pinchudo.

TPI. Segregations were Mendelian in *Tpi-1* and *Tpi-3*. In *Tpi-2*, however, we found non-Mendelian segregation in two of the four cultivars analysed. The cultivar Chaffey Riverside showed a clear deficit in allele 2 (Table 2) and Peru seed 24 showed a slight deficit in heterozygotes.

On the whole, significant (acceptance level: 0.05) deviations with respect to expected Mendelian proportions appeared in 12 out of 63 gene × cultivar combinations. With this acceptance level it might be expected that 5% of the non-Mendelian segregations were caused by chance. In cherimoya we actually found 19%, a clearly higher frequency than the expected percentage. A non-parametric technique to detect false H_0 is the sequential Bonferroni technique (Rice 1989). When we applied this technique to our data (Table 3) we obtained significant results in 8 out of 12 cases, which means that 12.7% of the total number of segregations analysed were non-Mendelian.

Several kind of processes, mainly gametic or zygotic selection, have been proposed to explain these anomalous segregations (Zamir and Tadmor 1986), which are very frequently found in trees (Torres 1990). In an attempt to investigate the kind of processes involved, we carried out three χ^2 tests. These tests grouped the non-Mendelian segregations into three categories (Table 3):

(1) Distortion characterized by a clear deviation from the expected frequencies for each allele (i.e. χ^2g significant but χ^2z and χ^2h non-significant). This

Table 3 Chi-square analysis of non-Mendelian segregations

Locus	Cultivar	X^2g			X^2z			X^2h			
		X^2	P	P'[a]	X^2	P	P'	X^2	P	P'	
Mdh-1	CH	10.800	0.001	< 0.006	0.039	0.843	ns	0.267	0.605	ns	
Tpi-2	CH	10.509	0.001	< 0.006	2.111	0.146	ns	4.091	0.043	ns	Gametic selection
Got-1	PE	8.757	0.003	0.012	3.156	0.076	ns	1.351	0.245	ns	in one sex
Pgm-2	SE	6.429	0.011	0.022	4.422	0.036	ns	5.714	0.017	ns	
Pgm-2	PC	23.529	< 0.001	< 0.008	2.674	0.102	ns	9.529	0.002	0.014	Gametic selection
Adh-1	SP78	22.685	< 0.001	< 0.008	4.024	0.045	ns	8.333	0.004	0.023	in both sex
Pgm-1	WH	8.015	0.005	0.014	9.310	0.002	0.018	10.939	0.001	0.007	
Skd-1	FI	4.923	0.027	0.027	7.287	0.007	0.048	3.846	0.050	ns	Zygotic selection

[a] P': probability after used Bonferroni's method
[b] ns: non-significant

type of distortion presumably implies some kind of gametic selection in a single sex, most probably pollen selection because the mobile gamete is the male gamete. *Got-1* in Pe, *Mdh-1* and *Tpi-2* in CH, and *Pgm-2* in SE showed this pattern.

(2) Distortion characterized by showing significant χ^2g and χ^2h, which may be interpreted as being produced by gametic selection in both sexes. *Adh-1* in SP78 and *Pgm-2* in PC both behave in this way.

(3) Distortion showing significant χ^2g and χ^2z, which presumably implies some kind of zygotic selection. *Pgm-1* in WH and *Skd-1* in FI can be included in this category.

Discussion

Our results provide new data concerning the inheritance of enzyme systems and the segregation distortion of isoenzyme loci. This data, together with the loci described by Lee and Ellstrand (1987), increases to 28 the number of isozymic loci described in cherimoya.

We have observed that the 13 non-monomorphic genes usually show Mendelian segregation but that some loci in some cultivars gave significant segregation distortion. These anomalous segregations involve 19% of the genes × progeny studied, a much higher frequency than that we should expect by chance (5%). Upon applying the sequential Bonferroni method the segregation distortion level decreased to 12.7%.

Distortion in the segregation of individual genes is quite common in fruit-bearing trees and in woody plants in general (Torres 1990). It has also been observed in other cultivated plants (e.g. Zamir and Tadmor 1986; Weeden et al. 1988; Muehlbauer et al. 1989; Koenig and Gepts 1989; Gaur and Slinkar 1990; Kazan et al. 1993). Van Heemstra et al. (1991) found 6% aberrant segregations in cranberry, which could be considered a product of chance at the 5% significance level. In *Cuphea*, Krueger and Knapp (1990) found distortion in 8 out of 58 segregations analysed. In *Citrus* about 29% and up to 37% of the markers show some kind of segregation distortion according to Durham et al. (1992). In hazel, Rovira et al. (1993) found non-Mendelian segregation in 10 out of 46 cases (22%). Zamir and Tadmor (1986) showed that 13% of the genes of *Lens*, *Capsicum* and *Lycopersicum* did not segregate in a Mendelian way in intraspecific crosses, which increased to 54% in the case of interspecific crosses.

In cherimoya, on the basis of analyzing offspring produced by self-fertilization, Lee and Ellstrand (1987) reported that the offspring of the cultivars Ott and Spain showed a segregation distortion in the genes *Pgi-1* and *Mpi* respectively.

As these several studies indicate, this phenomenon has been widely reported in the literature but its causes remain obscure. Grant (1975) and Torres et al. (1986) suggest that a deficiency in some genotype is not in itself lethal, but rather that this deficiency may be linked to other factors which result in lethality at some stage of development. Zamir and Tadmor (1986) indicate that these factors may be subject to selection in pre- and post-zygotic periods of reproduction. Alternative explanations have also been proposed. Tadmor et al. (1987) have suggested that linkage between markers and translocation break-points of some chromosomes could explain the distortion in segregation. Koenig and Gepts (1989), however, propose the preferential fertilization and elimination of certain zygotes as an explanatory mechanism. Vaillancourt and Slinkard (1992) have put the anomalous segregation down to the preferential elimination of certain chromosomes, which produces distortion in the segregation for loci located in these chromosomes. Linkage to self-incompatibility loci may also cause distortion (Abe et al. 1993). Certation and selective processes at the pollen level in general have been proposed as inductor phenomena in these anomalous segregations (Hornaza and Herrero 1992).

Our analyses (Table 3) have allowed us distinguish between different possible mechanisms for segregation distortion. As shown in the table, all anomalous segregations showed rejection of H_0, where $p = q = 0.5$ (see χ^2g column). A similar result was obtained in a study of 30

loci in rice, where Pham et al. (1990) found that 18 genes showed non-Mendelian segregations in 12 offspring and almost none produced the two types of gametes in equal frequency, despite the fact that genotypic frequencies fitted those expected. The anomalous segregations in cherimoya can be explained in the main by two types of selection: gametic selection and zygotic selection.

Gametic selection might be caused by deleterious factors (bound to isozymic loci) expressed during gamete development and/or functioning. This may occur either in both sexes (type-2 segregations in Table 3) or else in only one sex (type-1 segregations in Table 3), most likely the male sex which is the active one. The latter class could also be observed if phenomena such as certation played a role. As a whole, these types of segregations account for 75% of the observed non-Mendelian behaviour in cherimoya.

Zygotic selection was apparent in several segregations (type-3 in Table 3), which seemed to imply selection against certain diploid genotypes. This was the case with *Skd-1* in cultivar FI, the segregation of which was similar to that of a lethal gene in homozygosis (2:1 segregation). The larger or smaller linkage between the lethal gene and the isozyme marker will imply that the effects in the segregation of the marker will be more or less apparent.

Several authors (Hendrick and Muona 1990; Fu and Ritland 1994 a) have developed methods to detect recessive genes which affect viability and are found linked to some such markers as RFLPs or isozymes. Starting from the non-Mendelian segregations of the marker in a cross between heterozygotes we may calculate the values of C (the amount of recombination between the loci) and s (the factor by which viability of a genotype is affected), but a large sample size is necessary compared to the sample required to detect non-Mendelian segregation (Fu and Ritland 1994b). Fu and Ritland (1994b) have made a study involving the inclusion of h (an index of the degree of dominance of the lethal allele in heterozygotes) into the analysis of deviation from Mendelian segregation, in which they developed a graphic method to determine the values of h and therefore the kind of dominance. When the graphic method of Fu and Ritland (1994b) was applied to the anomalous segregations found in cherimoya, all appeared as cases of selection against particular zygotes, with values of h varying from complete recessivity to underdominance ($1 < h \leq 1/s$). Without a more detailed analysis it is impossible to discriminate between gametic and zygotic selection with some values of h. The χ^2 tests used in the present report can be used as additional criteria to eliminate the possibility of gametic selection, because the observed non-Mendelian segregation could always have been produced by some kind of zygotic selection. It would be very useful, whenever possible, to test allele frequencies in the gamete pool, to ascertain whether these are the major source of segregation distortion.

Most of the genotypes that appeared less frequently than expected in the non-Mendelian segregations were homozygotes for alleles appearing very infrequently in a collection of the 210 cultivars studied (unpublished data). This would indicate that these markers may be linked to lethal genes.

In some plants, such as rice (McCouch et al. 1988), *Brassica* (Landry et al. 1991) or alfalfa (Echt et al. 1993), it has been found that genes that show distortion in segregation are generally grouped in the genome. In cherimoya, however, the seven loci which showed some type of aberrant segregation were distributed throughout several linkge groups with no clear grouping pattern (unpublished data).

In summary, phenomena such as the genetic linkage to deleterious factors which prevent the development of some gametes, pollen competition, and linkage to lethal genes, could well explain the anomalous segregations found in cherimoya.

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