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GENETIC ANALYSIS OF COMPONENTS OF FRUIT SIZE AND SHAPE IN A DIALLEL CROSS OF TOMATO CULTIVARS

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ABSTRACT

Traits related to fruit size and shape (average fruit weight = FW, number of locules per fruit = LF, average weight per locule = WL; fruit length/diameter ratio = FR) were studied in a partial complete diallel cross of six tomato (*Lycopersicon esculentum* Mill.) cultivars: 1. Euromech; 2. Flora-Dade; 3. Rio Grande; 4. Royal Chico; 5. UC-82; 6. VF-65-433. In cultivars 1, 3 and 5, fruit are barrel-shaped (FR values around 1.10-1.20); in cultivar 2, deep-oblate (FR = 0.88); in cultivar 4, pear-shaped (FR = 1.41); and in cultivar 6, cylindrical (FR = 1.99). Diallel analysis of Gardner and Eberhart (Biometrics 22: 439-452, 1966) demonstrated that the variety effects were more important than heterosis effects for the four traits under consideration. The predominantly additive nature of the genetic effects was the cause of high correlations found between hybrid and parental means in all cases. Jinks and Hayman's approach to diallel analysis indicates that partial dominance is involved in the expression of WL and FR. Partially dominant alleles act in the direction of smaller WL and FR. Genotypic correlations among the traits were generally low (except between FW and LF), indicating that genetic progress could be obtained for both larger FW and higher FR. The results indicate that F_1 hybrids with barrel-shaped fruit can be obtained from parents such as Flora-Dade only if the other parent has an FR value around 2.0.

INTRODUCTION

Fruit size and shape are important attributes in fresh market tomatoes. In the Brazilian market, the predominant horticultural type is the so-called "Santa Cruz"

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group. This includes a wide range of cultivars with indeterminate growth habit and essentially barrel-shaped bi- to trilocular fruit, from the original Santa Cruz (with bilocular fruit of 70-80 g) to the most recent ones (Angelá Gigante I-5100 and Santa Clara, with a much higher fruit weight and with a higher proportion of trilocular fruit) (Gontijo *et al.*, 1983; Mello *et al.*, 1988). Multilocular tomatoes, varying in number of locules from four to 10 or more, with very large round or deep oblate fruit are also grown on a limited scale.

Number of locules per fruit and average weight per locule are related to fruit weight (Powers, 1945, 1950; Rick and Butler, 1956; Gontijo *et al.*, 1983). Powers (1945) concluded that the relationship between number of locules and locule weight is such that increments in fruit weight could be attained by simultaneous selection for larger number of locules per fruit and for a higher weight per locule. Powers (1950) studied the inheritance of weight per locule in a three-parent diallel cross, and indicated that the trait is polygenically controlled. Rick and Butler (1956) concluded that both number of locules per fruit and fruit weight are complex traits, greatly influenced by environment.

The majority of studies of inheritance of fruit size in tomatoes indicate that there is hardly ever heterosis for this trait, and that fruit size in the hybrids is usually smaller than the parental arithmetic mean (Larson and Currence, 1944; Fogle and Currence, 1950; Powers, 1952; Maluf *et al.*, 1982; Melo, 1988). The hybrid vigor often detected for yield can usually be accounted for by the increase in the number of fruit rather than by increased fruit size (Rick and Butler, 1956).

Components of fruit size and shape such as number of locules per fruit, average weight per locule and fruit length/diameter ratio are important concerns when breeding fresh market tomatoes. In a diallel cross studied by Miranda (1978) and Maluf *et al.* (1983), the largest values of heterosis for yield were found in hybrids among contrasting parental genotypes, namely between bilocular cultivars of the Santa Cruz group and multilocular round-fruited cultivars; unfortunately, these hybrids had no commercial value, because their commercialization in the Santa Cruz class was precluded by fruit shape, and in the multilocular class by fruit size, as imposed by the complex relationship between those traits (Dias, 1960; Cheng, 1972; Maluf *et al.*, 1983; Melo, 1988; Mello *et al.*, 1988). On the other hand, desirable barrel-shaped fruit can be obtained in a hybrid between two cultivars in the Santa Cruz type, but heterosis is usually negligible and fruit size is inferior to that of the larger fruited parent (Melo, 1988).

One possible approach to breeding highly heterotic combinations in the Santa Cruz class would be to modify the shape of the round-shaped parent so as resemble that of the Santa Cruz parent, while retaining the combining ability between the two parents. This will probably include several generations of testing for combining ability during the process of breeding a barrel-shaped line to substitute the round-fruited one – an approach likely to be expensive and time consuming.

Another approach could be to obtain barrel-fruited F_1 hybrids from parents that are highly divergent in fruit shape, namely from combinations between round and cylindrical-fruited types. Combinations of such divergent parents are likely to be heterotic (Maluf *et al.,* 1983). Furthermore, deep oblate to round fruited cultivars with good horticultural quality are quite common. It remains to be determined what the ideal fruit/diameter ratio for the cylindrical-fruited parent should be. If a suitable line with cylindrical fruit can be identified or created through breeding, it would save considerable effort in testing for combining ability, which is usually the most expensive part of the breeding programme.

This paper reports on the genetic analysis of fruit size and shape components in a diallel cross of six tomato cultivars. These cultivars varied in shape from deep-oblate to cylindrical fruit, and included barrel-shaped types. We seek to determine what ideotype a breeding line should have in order to be useful as a parent in combination with round-fruited types for the production of F_1 hybrids in the barrel-shaped fruit category.

MATERIALS AND METHODS

Experimental material

Six inbred cultivars were chosen for the study: 1. Euromech; 2. Flora-Dade; 3. Rio Grande; 4. Royal Chico; 5. UC-82; 6. VF-65-433. These cultivars had determinate growth habit. All but Flora-Dade are used in Brazil primarily for processing, but Rio Grande has also been grown as a fresh market cultivar. Fruit shape is deep-oblate to globe in Flora-Dade, pear-shaped in Royal Chico, cylindrical in VF-65-433 and barrel-shaped in Euromech, Rio Grande and UC-82. The cultivars were crossed in all possible combinations. No distinction was made between reciprocal crosses. The six cultivars and their 15 F_1 hybrids thus obtained were used in the genetic analysis.

Experimental design

The 21 main treatments (six inbred cultivars and 15 F_1 hybrids) were field tested in the experimental farm of the Centro Nacional de Pesquisa de Hortaliças/ EMBRAPA in Brasília-DF, in a randomized complete block design with four replications, in the Fall-Winter season of 1982. Each block was subdivided in three sets. Each set within a block included seven different main treatments, plus five additional treatments (cultivars Earlystone, IPA-3, Peto-86, Rio Fuego and Roma-VF). The additional treatments were used in the adjustment of the main treatment least square means for every set, through the LSMEANS option of the SAS package (Statistical Analysis System Institute Inc., 1979). The LSMEANS estimates of the 21 main treatments were used in the diallel analysis.

Data collection

Thirty randomly chosen fruit were sampled per plot at the date of the first harvest. The following traits were measured on a plot basis:

– average fruit weight = FW
– average number of locules per fruit = LF
– average weight per locule = WL = FW/LF
– average fruit length = FL
– average fruit diameter = FD
– length/diameter ratio = FR = FL/FD

Diallel analysis

The traits FW, LF, WL and FR were analysed according to the randomized complete block design, and those showing significant treatment effects were analysed according to the procedure of Jinks-Hayman (Hayman, 1954a,b), when the following parameters were estimated:

D = variance component relative to additive gene action;

H_1 = variance component relative to dominant gene action;

H_2 = variance component relative to dominant gene action ($H_1 = H_2$ only when genes with positive and negative effects are present in equal frequencies);

F = genetic component relative to the frequencies of dominant and recessive alleles in the parental population ($F > 0$ if dominant alleles have higher frequencies than recessive alleles, and $F < 0$ if the reverse is true);

h^2 = variance component relative to dominant gene action (h^2 reflects the square of the difference between the mean of the n parental lines and the grand mean of the n^2 possible combinations in the diallel table);

E = experimental error variance.

In order to help in the interpretation, additional diallel analysis were performed by adjusting the parameters of the analyses of Gardner and Eberhart (1966). The components of the coefficients of correlation between cultivar and F_1 hybrid means were calculated as shown by Miranda Filho and Vencovsky (1978). The genotypic correlations among traits FW, LF, WL and FR were calculated according to Hallauer and Miranda Filho (1981).

RESULTS AND DISCUSSION

Table I describes the six inbred cultivars and their F_1 hybrids with respect to FW, LF, WL and FR. Flora-Dade, a cultivar with round to deep oblate fruit, is the only parental inbred with an FR ratio smaller than 1 (FR = 0.88); it also differs markedly from the other five inbreds in its larger fruit weight and larger number of locules per fruit (LF = 4.90, contrasting with LF < 2.70 for the other inbreds). Euromech, Rio Grande and UC-82 are basically cultivars with barrel-shaped fruit with FR ranging from 1.08 to 1.18; they resemble the fresh market cultivars of the Santa Cruz class in fruit shape, and the larger fruited Rio Grande is indeed used for that purpose.

Table I - Separation among treatment means in a partial complete diallel cross of six tomato cultivars.

Treatment	Treatment means[x]			
	Average fruit weight	No. locules per fruit	Average weight per locule	Length/Diameter ratio
Cultivars:				
1. Euromech	52.3 g	2.64 ed	19.9 e	1.08 fg
2. Flora-Dade	109.7 a	4.90 a	22.8 cde	0.88 h
3. Rio Grande	69.3 cdefg	2.12 e	32.8 abc	1.18 ef
4. Royal Chico	82.6 bcd	2.27 e	36.4 a	1.41 cd
5. UC-82	50.4 g	2.49 e	20.4 ed	1.14 ef
6. VF-65-433	66.7 defg	2.21 e	30.4 abcd	1.99 a
Hybrids:				
1 x 2	82.9 bcd	3.41 bcd	24.4 bcde	0.93 gh
1 x 3	61.9 defg	2.38 e	26.0 bcde	1.16 ef
1 x 4	64.0 defg	2.62 ed	24.6 bcde	1.21 ef
1 x 5	48.8 g	2.54 e	19.3 e	1.03 fgh
1 x 6	54.6 fg	2.46 e	22.2 ed	1.47 bc
2 x 3	90.9 abc	3.69 b	24.6 bcde	0.95 gh
2 x 4	94.7 ab	3.91 b	24.4 bcde	0.93 gh
2 x 5	80.2 bcde	3.55 bc	22.7 cde	0.92 gh
2 x 6	76.8 bcdef	3.42 bcd	22.3 ed	1.15 ef
3 x 4	82.4 bcd	2.50 e	33.3 ab	1.25 ed
3 x 5	59.2 efg	2.33 e	25.6 bcde	1.18 ef
3 x 6	64.6 defg	2.39 e	27.2 abcde	1.54 bc
4 x 5	59.0 efg	2.77 cde	22.8 cde	1.18 ef
4 x 6	69.7 cdefg	2.41 e	28.7 abcde	1.60 b
5 x 6	52.7 g	2.29 e	23.1 cde	1.43 bc

[x] Mean separation by Tukey's Studentized Range Test (alpha = 0.05).

Royal Chico, with pear-shaped fruit, has a significantly higher FR ratio (FR = 1.41) than the former cultivars, but significantly lower than that of VF-65-433 (FR = 1.99), which bears cylindrical fruit.

Knowledge of the predominant modes of gene action could clarify whether a hybrid's fruit size and shape can be adequately predicted from its parental inbreds. The diallel analysis of Jinks-Hayman (Hayman, 1954a,b) was used in the study of the modes of inheritance of FW, LF, WL and FR, and the variance components and genetic parameter estimates obtained are shown in Tables II and III. The genetic analyses according to the analysis of variance of Gardner and Eberhart (1966) are shown in Table IV.

Table II - Variance components for traits related to fruit size and shape in a partial complete diallel cross of six tomato cultivars.

Variance component	Estimates (± Std. Error)			
	Average fruit weight	No. locules per fruit	Average weight per locule	Length/Diameter ratio
D	448.0 (±20.3)	1.120 (±0.068)	42.56 (±3.04)	0.1502 (±0.0031)
F	-105.4^x (±48.8)	0.265 (±0.164)	12.41 (±7.32)	0.0156 (±0.0074)
H_1	- 62.7^x (±59.4)	0.084 (±0.199)	3.18 (±8.92)	0.0195 (±0.0090)
H_2	- 39.7^x (±51.7)	0.030 (±0.174)	5.80 (±7.77)	0.0142 (±0.0078)
h^2	9.4 (±30.5)	-0.018^x (±0.102)	13.64 (±4.58)	0.0193 (±0.0046)
E	71.6 (±8.6)	0.104 (±0.029)	14.97 (±1.30)	0.0045 (±0.0013)
$(D - H_1)$	510.7 (±25.7)	1.036 (±0.086)	39.38 (±3.85)	0.1307 (±0.0039)

^{x} Negative estimates that are not significantly different from zero at alpha = 0.05.

The estimates of Jinks-Hayman's variance components D, H_1 and H_2 indicate that additive genetic effects are more important than dominance effects in the expression of all traits under consideration: in all cases the estimate of D was significantly diferent from zero (as indicated by the low standard deviations), as opposed to the estimates of H_1 and H_2. Furthermore, the estimates of $(D-H_1)$ are also significantly different from zero, indicating that the additive variance component is significantly larger than dominance variance component, in all cases.

The lack of precision in the estimates of the average degree of dominance, minimum number of genes with dominance, ratio of number of dominant to number

Table III - Parameters obtained from analysis of traits related to fruit size and shape in a partial complete diallel cross of six tomato cultivars.

Parameter	Estimates			
	Average fruit weight	No. locules per fruit	Average weight per locule	Length/Diameter ratio
Average degree of dominance	–[x]	0.27	0.27	0.36
Minimum number of genes with dominance	–[x]	–[x]	2.35	1.35
Ratio of # dominant to # recessive alleles	–[x]	2.52	3.29	1.34
Product of mean frequencies of + and – loci with dominance	–[x]	0.09	0.46	0.18
Coefficient of correlation between (Wr + Vr) and Yr	0.338[ns]	0.546[ns]	0.869*	0.939**
Regression of Wr on Vr:				
– slope	0.654[y]	0.590[y]	0.851[z]	0.987[z]
– intercept	135.2	0.311	0.845	0.030
– coeff. of correlation	0.715[ns]	0.753[ns]	0.972**	0.985**

[ns] Not significantly different from zero by the t test at alpha = 0.05.

*, ** Significantly different from zero by the t test at alpha = 0.05 and alpha = 0.01, respectively.

[x] Estimates could not be obtained, due to negative estimates of parameters D, H_1, H_2 or h^2.

[y] Not significantly different from zero or from unity by the t test at alpha = 0.05.

[z] Significantly different from zero by the t test (alpha = 0.01), but not significantly different from unity (alpha = 0.05).

of recessive alleles and/or product of mean frequencies of positive and negative loci for FW and LF (Table III) are probably a reflection of an entirely additive gene action in the expression of these traits. This explanation is corroborated by the results of Gardner and Eberhart's analysis of variance in Table IV, indicating no significant effects of heterosis for either FW or LF, and by the estimates of the mean components in Table V, where the estimates of the heterosis components for these traits are negligible when compared to the variety effects. The absence of dominance effects in

Table IV - Gardner and Eberhart's Type II analysis of variance for a diallel cross among six tomato cultivars.

Source of variation	d.f.	Mean squares: Average fruit weight	No. locules per fruit	Average weight per locule	Length/Diameter ratio
Blocks	3	153.500^{ns}	0.145550^{ns}	15.8562^{ns}	0.0031277^{ns}
Treatments	20	1062.579**	2.049328**	83.6559**	0.3025637**
Varieties	5	4085.315**	7.885889**	266.7446**	1.1404584**
Heterosis	15	54.996^{ns}	0.103805^{ns}	22.6271^{ns}	0.0232655**
- average	1	94.031^{ns}	0.089905^{ns}	94.7930*	0.1180648**
- variety	5	67.214^{ns}	0.169757^{ns}	19.4605^{ns}	0.0286193**
- specific	9	43.871^{ns}	0.068709^{ns}	16.3678^{ns}	0.0097579*
Residual	60	71.562	0.104330	14.9763	0.0044619

^{ns}Not significant by the F test at alpha = 0.05.

*, **Significant by the F test at alpha = 0.05 and alpha = 0.01, respectively.

the expression of FW and LF, as also shown by the non-significance for heterosis in the analysis of variance, can account for the high coefficients of correlation between hybrid and parental means (Table VI), and also for the lack of significant coefficients of correlation between Wr and Vr (Table III) for these traits. It must be pointed out, however, that the high correlation between parental and hybrid means does not always indicate a lack of fominance effects; in fact, such a high correlation may occur when the component for average heterosis is significant and the other components of heterosis (i.e., varietal and specific heterosis) are non-significant, as shown by Miranda Filho and Vencovsky (1978).

In contrast to FW and LF, some degree of dominance appears to play a role in the expression of WL and FR, as indicated by the significantly larger than zero estimates obtained for the h^2 component (Table II), and by the significant heterosis effects detected in Gardner and Eberhart's analysis (Table IV). An average degree of dominance of 0.27 was estimated for WL, and of 0.36 for FR. For both WL and FR, the coefficients of correlation between (Wr + Vr) and Yr (Table III) indicate that dominant alleles appear to have negative metric effects: alleles that are dominant tend to decrease average weight per locule and to produce smaller length/diameter ratios. The non-additive gene action is responsible for a lower correlation between hybrid

Table V - Analysis of a diallel cross among six tomato cultivars: Mean components for type II analysis of Eberhart and Gardner (1966).

Component	Estimates			
	Average fruit weight	No. locules per fruit	Average weight per locule	Length/Diameter ratio
u	71.8	2.77	27.1	1.28
Variety effects:				
v_1	-19.5	-0.13	-7.3	-0.20
v_2	37.8	2.13	-4.3	-0.40
v_3	-2.5	-0.65	5.7	-0.10
v_4	10.7	-0.50	9.3	0.13
v_5	-21.4	-0.29	-6.7	-0.14
v_6	-5.1	-0.56	3.3	0.71
Average heterosis:				
h	-2.3	0.07	-2.4	-0.08
Variety heterosis:				
h_1	0.9	-0.13	1.8	0.06
h_2	0.6	-0.13	0.8	-0.08
h_3	4.1	0.09	0.4	0.07
h_4	0.2	0.24	-2.1	-0.02
h_5	-1.1	-0.04	0.7	0.02
h_6	-4.7	-0.03	-1.7	-0.05
Specific heterosis:				
s_{1x2}	2.7	-0.17	2.8	0.05
s_{1x3}	-1.6	-0.02	-0.2	-0.01
s_{1x4}	-2.2	-0.02	-0.9	0.07
s_{1x5}	0.0	0.08	-1.0	-0.06
s_{1x6}	1.1	0.13	-0.7	0.02
s_{2x3}	-0.9	0.14	-2.0	0.03
s_{2x4}	0.1	0.13	-1.6	-0.04
s_{2x5}	3.0	-0.04	1.8	0.06
s_{2x6}	-4.9	-0.05	-1.1	-0.07
s_{3x4}	4.4	-0.10	2.8	-0.02
s_{3x5}	-1.2	-0.10	0.2	0.02
s_{3x6}	-0.5	0.09	-0.8	0.01
s_{4x5}	-4.1	0.11	-1.9	0.00
s_{4x6}	1.9	-0.11	1.5	0.06
s_{5x6}	2.3	-0.05	1.0	-0.01

Table VI - Components of the coefficient of correlation (r) between hybrid and parental means, according to Miranda Filho and Vencovsky (1978).

Component	Estimates			
	Average fruit weight	No. locules per fruit	Average weight per locule	Length/Diameter ratio
Var (v)	484.5	1.128	48.81	0.1506
Cov (v,h)	8.9	- 0.081	- 8.95	- 0.0058
Var (h)	8.4	0.021	2.43	0.0036
Var (s)	11.0	0.017	4.09	0.0024
r (with 13 d.f.)	0.953	0.948	0.806	0.937

and parental means for WL than for the other traits (Table VI). These dominance deviations, even though highly significant for FR (Table IV), are not large enough to decrease the correlation between hybrid and parental means for this trait (Table VI); however, since small variations of FR are easily perceived by the human eye and affect dramatically the commercial acceptability of a hybrid, the deviations due to heterosis effects (Table V) cannot be ignored.

The absence of dominant gene action for FW agrees with results of Maluf *et al.* (1982) for this trait in a diallel with another set of tomato cultivars. In contrast, the absence of dominant gene action for LF contrasts with results of Miranda *et al.* (1982): these authors, working with the same diallel as Maluf *et al.* (1982), found the trait to be controlled essentially by one locus, with partial dominance for the allele that controls smaller number of locules. The partial dominance in WL agrees with results found by Gontijo *et al.* (1983), but contrasts with these results in the direction of the dominance effects: our results indicate partial dominance in the direction of smaller WL, while the opposite is indicated by Gontijo *et al.* (1983).

The modes of inhertiance of FW, LF, WL and FR have important implications for the breeding of fresh market tomatoes. It is clear that F_1 hybrids with barrel-shaped fruit (FR ratios between 1.10 and 1.20) can be obtained not only from crosses between cultivars convergent in fruit shape (e.g. Euromech, Rio Grande and UC-82), but also in crosses between divergent cultivars (e.g. Flora-Dade x VF-65-433). The latter alternative, which envolves divergent parents, is more likely to yield heterotic F_1 hybrids. Furthermore, since multilocular tomatoes are often large fruited and FW is inherited additively, it should be easy to obtain fairly large barrel-shaped fruit in their F_1 hybrids, provided that fruit size is not too small in the second parent. In fact, the F_1 hybrid Flora-Dade x VF-65-433 produced heavier fruit than the barrel-shaped cultivars Euromech, UC-82 and Rio Grande, even though in the latter case the differences were not statistically significant (Table I).

Our results can help to determine what ideotype a breeding line should have in order to be useful as a parent in combination with round-fruited types for the production of F_1 hybrids in the barrel-shaped fruit category. It should be ideally a cultivar or line with cylindrical fruit with two to three locules, and with large WL. Since the round-fruited counterparts would have FR around 0.90 and the putative hybrids 1.10 to 1.20, it follows from the existance of partial dominance in the direction of lower FR ratios that the line with cyclindrical fruit should have an FR ratio around 2.00. The genotypic correlations among traits FW, LF, WL and FR (Table VII) are generally low enough to permit the selection for this ideotype to be effective.

Table VII - Genotypic correlation coefficients (r_G) among traits related to fruit size and shape in a partial complete diallel cross of six tomato cultivars.

Traits	Estimates of r_G			
	Average fruit weight	No. locules per fruit	Average weight per locule	Length/Diameter ratio
Average fruit weight	1.000			
No. locules per fruit	0.828	1.000		
Average weight per locule	0.238	-0.227	1.000	
Length/Diameter ratio	-0.391	-0.676	0.497	1.000

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RESUMO

Peso médio de fruto, número médio de lóculos por fruto, peso médio por lóculo e relação comprimento/diâmetro de frutos (FR) foram estudados em um cruzamento dialélico parcial completo entre seis cultivares de tomate: 1. Euromech; 2. Flora-Dade; 3. Rio Grande; 4. Royal Chico; 5. UC-82; 6. VF-65-433. As cultivares 1, 3 e 5 tem formato de barril (FR em torno de 1.10 a 1.20); a cultivar 2 é de frutos arredondados (FR = 0.88), a 4 é de frutos piriformes (FR = 1.41) e a 6 de frutos cilíndricos (FR = 1.99). A análise dialélica segundo o modelo de Gardner e Eberhart (Biometrics 22: 439-452, 1966) mostrou que, para todas as características analisadas,

o efeito de variedades foi mais importante do que os efeitos de heterose. Houve alta correlação entre as médias dos híbridos e as médias dos respectivos pais em todos os casos, evidenciando a predominância dos efeitos genéticos aditivos. A análise dialélica de Jinks-Hayman indica dominância incompleta para peso médio por lóculo e para relação comprimento/diâmetro. Alelos dominantes agem no sentido de diminuir o peso médio por lóculo e a relação comprimento/diâmetro dos frutos. As correlações genotípicas entre as características analisadas foram geralmente baixas (exceto entre peso médio de fruto e número de lóculos por fruto), indicando a possibilidade de progresso genético simultâneo tanto para maior tamanho de frutos quanto para maior FR. Os resultados demonstram que a obtenção de híbridos F_1 com formato de fruto do tipo Santa Cruz a partir de genitor de frutos arredondados como Flora-Dade somente é possível quando o outro parental tiver FR em torno de 2.0.

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