Genetic control of morphological traits in tomato fruits

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ABSTRACT

This study was carried out to investigate the inheritance of the tomato fruit shape and other morphological traits in a single (biparental) cross among Nemadoro and Stevens cultivars.The F_1, F_2 and backcross to both parents generations were obtained and evaluated along with the parental lines in a randomized complete block design with four replications. Mean and variance estimates of genetic parameters were obtained using the models proposed by Mather and Jinks (1982). Genes controlling morphological tomato fruit traits predominantly showed additive effects, but partial dominance was also often displayed. The narrow sense heritability estimate for fruit shape, evaluated by the length/diameter ratio, was 50.18%. The narrow sense heritability at the individual plant level for average fruit weight and number of loculi were high, 67.08% and 87.46%, respectively, indicating favorable conditions for selecting these traits. The additive dominant model was adequate to explain the inheritance of fruit length, pericarp thickness, fruit length/diameter ratio and average locule weight.

KEY WORDS: *Lycopersicon esculentum* Mill, breeding, heritability, locule, average, weight, shape.

INTRODUCTION

Most economically important traits in tomato are quantitative inherited and, consequently, highly affected by the environment. Therefore, studies to improve knowledge of the genes controlling these traits are very relevant for planning efficient breeding programs (Khattra et al., 1990). The progress of these programs may depend on a greater understanding of genetic control mechanisms.

Many morphological traits in tomato, especially those directed to the Brazilian table, are important, but highly complex. The preference for the 'Santa Cruz' type is deeply rooted in the Brazilian eating habits, and its market share in Brazil reached nearly 95% after the 1960s. The Kada, Miguel Pereira, Angela Hiper, Angela Gigante I-5100 and Santa Clara cultivars were the latest released in this group during that period, and tended to produce increasingly larger fruits, while maintaining the basic shape of the 'Santa Cruz' type (Nagai, 1985). The tendency to maintain the 'Santa Cruz' shape for decades might have resulted from the fact that these cultivars are widely adapted to the climatic conditions of several regions in Brazil. Among the commercial traits are fruit size and shape, good conditions for transport and packing and fruit firmness (Filgueira, 2000). The trend seems to continue today in the newest cultivars of this group, which have presented large fruits like such as the Angela Gigante I-1500 and Santa Clara cultivars. These cultivars, although still showing characteristics inherent in the 'Santa Cruz' group, are predominantly trilocular (Asgrow do Brazil, 1981; Nagai, 1985) instead of bilocular.

The Brazilian production of tomato for ´in natura´ consumption went through great technological changes, specially after the introduction of the long life tomato in on the market in 1988. This type has increased its share in the "in natura" tomato market to an estimated 70% today (Della Vecchia and Kock, 2000).This change is probably due to the high post-harvest conservation ability of these cultivars. Yet producers continue to prefer the `Santa Cruz´ type considering the characteristics that have kept it on the market for many decades.

According to Gontijo et al. (1983), parental lines with high average fruit weight, with three to four loculi per fruit, and with the characteristic shape of the 'Santa Cruz´ cultivar group should be selected to start a tomato breeding program for the Brazilian market. Morphological traits such as fruit shape and size have been some of the most challenging problems for the F1 hybrid production in Brazil due to market demand, which favors the 'Santa Cruz´ type. Maluf (1990) emphasized the importance of fruit size among the traits of economic relevance for table tomato breeding programs in Brazil.

Other economically important traits are the number of loculi and fruit average weight (Powers,1941). In Brazil, the market demand for characteristic fruit shape and size (average weight) has limited F1 hybrid production. The rounded shape of these hybrids precludes their classification as a multilocular or salad type. This situation clearly establishes the need for a specific breeding program to develop parental lines for the 'Santa Cruz′ type hybrid production. Knowledge of these traits inheritance is needed prior to developing such a program.

Many studies on tomato fruit size inheritance have seldom showed positive heterosis. In general, fruit size in the F1 generation is smaller than the arithmetical mean of the parents (Larson and Currence, 1944; Fogle and Currence,1950; Powers, 1952; Maluf et al., 1982b). Few studies on the genetic control of tomato plant traits, such as shape, size or others, have been carried out in Brazil. Consequently, studies to increase knowledge of the interrelationships between average fruit weight, number of loculi and average weight per locule were considered of great importance, when fruit size gain is required (Melo et al.,1988). Powers (1950) reported that the increase in fruit size may be due to the recombination between a greater number of loculi per fruit with greater weight per locule.The number of loculi was considered important to average fruit weight determination (Rick and Butler,1956).

Although genetics has greatly contributed to the tomato plant breeding progress in the last fifty years, new studies are required on quantitative traits, especially those related to fruit morphology. Little information is available on the fruit shape trait, especially on its genetic control, when compared with other traits such as total yield per plant, number of fruit per plant and average fruit weight.

Biparental crosses and their derived populations were used to investigate the genetic control of shape and other important morphological traits of tomato fruits, such as number of loculi per fruit, firmness, average fruit weight, thickness, length and fruit cross diameter.

The present study was carried out to provide information about these traits for the Brazilian breeding programs.

MATERIAL AND METHODS

The 'Nemadoro′ and 'Stevens′ tomato cultivars were used as parents in a single (biparental) cross to obtain the F_1, F_2, BC_1 and BC_2 generations under greenhouse conditions in 1992. The generations were assessed under field conditions at the Ijaci Experimental Station MG, from April to June 1993. The parental cultivars characteristics: Stevens was introduced from South Africa and has determined growth habit and rounded, firm, multilocular and good quality fruits (Stevens et al., 1992); Nemadoro is a cultivar for industrial processing that has determined growth habit and yields firm, two loculi and square-oblong shaped fruits that resembles the 'Santa Cruz′ type (Pessoa et al., 1988). The six generations were obtained from plants cultivated in 20-liter pots containing substrate prepared with two parts of sieved soil and one part of organic compost. Twenty plants of each parent were cultivated in a greenhouse to obtain the F_1 generation. The crosses were obtained by controlled manual pollination. Pollen was collected from the Stevens cultivar (male parent) and the Nemadoro cultivar plants were later emasculated and used as the female parent. The other generations were obtained from the second semester of 1992 onwards by selfing and backcrossing the F_1 generation to P_1 and P_2 to obtain the F_2, RC_{11} and RC_{12}, respectively. At this stage, the plants were individually tutored in the greenhouse and all the management practices necessary for a good crop were carried out. Seeds from the plant generations used for the assessment of the morphological traits of the tomato fruits were sowed on 'Speedling′ type trays containing 128 cells, which were filled with 50% burnt rice husk and 50% organic ′Plantcell' substrate. The trays were kept throughout this phase of seedling production in half open germinators specially designed for this purpose, suspended 40 cm above the soil on iron supports. Sowing was carried out on April 16 and transplantation on April 23 of 1993. Seedlings were daily watered daily and preventively sprayed twice a week to maintain a satisfactory phytosanitary condition.

Seedlings were field transplanted 30 days after sowing in 1.0 m spaced rows, keeping 0.50 m between plants. Field soil rows were fertilized with chicken manure at two liters per linear meter and formulated (4-14-8 NPK) mineral fertilizer, at 300g per linear meter. Side-dressing fertilizations were weekly carried out weekly, the first before earth up with ammonia sulfate at 30 g per plant. Each plant was individually tutored on a 1.5 m tall wooden tutor. They were later tied with plastic strings . The plant lateral shoots that appeared on the leaf axles were eliminated .As the plants had determined growth the shoot removal was only done until the formation of the second bunch.

Conventional spray irrigation was used.

The experiment was carried out at the Ijaci Experimental Station, MG, from April to June 1993 in a six treatment randomized complete block design with four replications. The experiment was designed to estimate the components of means and variances of parents, F_1, F_2 and backcross generations (Mather and Jinks, 1982, 1984; Cavalli, 1952; Rowe and Alexander, 1980; Warner, 1952). The plots had a fixed number of 20 plants from each generation and special care was taken to maintain the number of plants from each population: 80 from the P_1, P_2 and F_1 generations, 400 from the F_2 generation and 240 plants from each backcross. Each complete experimental block was made up of one 20 plant plot from each of the P_1, P_2, F_1 generations, five plots from the F_2 generation and three plots from each of the back crosses, in a total of 14 randomized plots per block.

Tomato fruit morphological traits were assessed in individual plants. The first ten fruits were harvested based on an established color uniformity pattern. Fruits were wrapped in plastic bags and labeled according to each plant code. They were later taken to an experimental facility for weighing and measuring. Fruits were counted and weighed (ten fruits/plant), and scores were given to the protuberances (prominence of the stylus scar) on the fruit of some plants. Scores varied from 0 to 3, where zero was attributed to genotypes with no protuberance and 1, 2 and 3 to genotypes with up to 1mm, 2mm and 3mm long protuberances, respectively. The same ten fruits from each plant were measured for longitudinal length (C) and transversal diameter(D) on a custom made graduated scale and evaluated for firmness in a texture meter. The fruits were then cut and the pericarp thickness was measured with a pachymeter and the number of loculi counted. All these measurements were recorded on a spreadsheet for each plant in the experiment. Fruit shape was determined by a ratio established between length and diameter. Ratios greater than one defined the 'Santa Cruz´ type and ratios smaller than one defined the Salada (rounded) type.The average weight per locule was obtained by dividing the average fruit weight by the average number of loculi in each material. When all the data were collected, an analysis of variance was performed for each individual trait based on the P_1, P_2, F_1, F_2, RC_{11} and RC_{21} generations means.

The genetic components of the means were estimated by a joint scaling test designed by Cavalli (1952), quoted by Rowe and Alexander (1980), which also tested the model goodness of fit . Models of increasing complexity were successively fitted to the data, as suggested by Hayman (1958) and Mather and Jinks (1971). In some cases the **m, [a],** and **[d]** model was adequate to estimate the genetic components but, in other situations where epistasis was present , the **m, [a], [d], [i], [j]** and **[l]** model was needed, where **m** is the mean, **a** is the contribution of the homozygous loci, **d** the contribution of the heterozygous loci, **i** the epistatic interaction of the additive/additive type; **j** the interaction of the additive/dominant type, and **l** the dominant/dominant interaction.

The genetic variance components and associated errors were estimated according to the methodology of Mather and Jinks (1982, 1984), adapted by Vello (1985). The broad sense (h^2a) and narrow sense (h^2r) heritabilities and respective standard errors were estimated following the scheme proposed by Warner (1952). The weighted least squares method was used to test the model goodness of fit (Rowe and Alexander, 1980).

RESULTS

Significant differences among the generations means were observed for fruit longitudinal length (C), transversal diameter (D), number of loculi per fruit (NL), fruit pericarp thickness (PE), fruit firmness (FF), fruit shape (C/D), prominence of the stylus scar (protuberance – BI) and average weight per locule (PML). However, no significant difference for average fruit weight (PMF) was detected.

Additive effects predominated in the control of the morphological traits although partial dominance was also observed for all traits. The additive-dominant model was adequate to explain the variability of the generation means for fruit longitudinal length (C), fruit pulp thickness, fruit shape (C/D) and average weight per locule (Table 1). Dominance in these cases decreased increased trait expression. Among these traits, only the average weight per locule and its genetic control mechanisms have received attention from researchers (Power 1941; Fogle and Currence, 1950; Powers et al., 1950). The effects of dominance (d) and homozygote x homozygote type epistasis (i) helped reducing the expression of the number of loculi per fruit (although dominance was positive), average weight per fruit and fruit transversal diameter (Table 1).

The variance analysis detected a predominance of additive effects and the presence of partial dominance, as indicated by the average degree of dominance. Variance due to dominant effects of the genes was

Table 1. Mean genetic components estimated for the tomato fruit traits using the generations derived from the cross between the Nemadoro x Stevens cultivars, Lavras, UFLA, 1995.

Model Parameters/ Morphological traits	m	a	d	i	j	l
Longitudinal Length (C)	6.080±0.027	0.714±0.024	-0.4139±0.0518	X	X	X
Transversal diameter (D)	6.0009±0.099	0.4129±0.0238	-0.5014±0.1613	-0.5266±0.101	X	X
Number of loculi per fruit	3.3497±0.117	0.68901±0.027	-0.3342±0.1675	-0.5909±0.122	X	X
Fruit pericarp thickness	0.6875±0.004	0.1107±0.0036	-0.0048±0.0085	X	X	X
Fruit firmness	9.0258±0.234	0.1907±0.1145	-1.0777±0.3733	-0.3279±0.253	0.703±0.32	X
Average fruit weight	125.882±3.806	5.7405±1.1188	-26.683±5.7929	-24.086±4.058	X	X
Fruit shape (C/D)	1.118±0.00427	0.2083±0.004	-0.1294±0.0088	X	X	X
Average weight per locule	39.7975±0.4573	7.9686±0.4057	-6.7409±0.883	X	X	X

also detected in the genetic control of this trait, but in reduced magnitude (Table 2).

Broad and narrow sense heritabilities at the individual level of moderate magnitudes were detected for longitudinal fruit length. However, they had associated errors of only 16% and 27%, respectively, indicating relative reliability in the transmission of genotypic superiority to future generations. The broad sense heritability for the transversal fruit diameter was very low (8.17%), with an associated error greater than the estimated, indicating that special care should be taken in selecting superior genotypes .The heritability obtained in the narrow sense was moderate (48.9%) with a smaller associated error (26.9%), showing that the environmental and non-additive genetic effects are preponderant for its expression. According to Vello and Vencovsky (1978), when these estimates have large associated errors, their practical use should be approached cautiously. However, reliable practical use could be made for the number of loculi per fruit trait due to its high broad (80.86%) and narrow sense (87.46%) heritabilities associated to small errors of 5.0% and 10.48%, respectively. Similarly, high heritability associated to small errors were observed for average fruit weight for both broad (56.46% and 10.20%, respectively) and narrow (67.08% and 18.02%, respectively) senses.

Selection for average weight per locule may be difficult due to the presence of non-additive gene action and large environmental effects. Results showed a low broad sense heritability value of 32.99% for the trait associated with an error of 25.10% indicating, therefore, low precision. A moderate narrow sense heritability value (45.01%) was obtained associated with a very large error (32.74%), again indicating low precision.

For pericarp thickness and fruit firmness traits, the narrow sense heritability values were low, 22.95% and 38.34%, associated to large errors of 73.48% and 39.40%, respectively. Similarly, the broad sense heritability value for fruit firmness was low (11.32%) and associated with a very large error (86.73%). These results indicated that selection for thick pericarp and firm fruit type is not likely to be efficient. Similar difficulty is faced when selecting for fruit shape due to the trait moderate narrow sense heritability value (50.18%), associated to a large error (31.60%).

The results showed that, in general, tomato fruits which are both large and 'Santa Cruz´ type are difficult to obtain. A larger number of loculi may favor fruits with greater weight, but can hinder the appearance of a 'Santa Cruz´ type of fruit with greater pericarp thickness, fruit firmness and prominent stylus scar (protuberance).

Regarding the estimates obtained for the number of genes or gene blocks, it should be pointed out that they were based on assumptions, and should be interpreted with caution . They indicated, however, that working with number of loculi trait (n = 4.39) should be easier than working with fruit firmness (n = 13.48), where the number of genes is greater and reflects the greater complexity of its use in breeding programs.

DISCUSSION

Gontijo et al. (1983) suggested that an increase in the average weight of tomato plant fruits of the 'Santa Cruz´ type would be easier to obtain by increasing the number of loculi rather than by increasing the

Table 2. Estimates of additive (s^2_A), dominance (s^2_D) and environmental variances (s^2_E), broad (h^2a) and narrow (h^2r) sense heritabilities, mean degree of dominance (gmd) and probable number of genes (n) for the tomato fruit traits. Lavras, UFLA, 1995.

Morphological traits	σ^2_A	σ^2_D	σ^2_E	h^2_r	gmd	n
Longitudinal Length (C)	0.150	-0.024[1/]	0.134	0.528±0.14	0.62	6.73
Transversal diameter (D)	0.281	-0.255[1/]	0.293	0.489±0.10	0.34	6.80
Number of loculi per fruit	1.435	-0.565[1/]	0.205	0.874±0.09	0.55	4.39
Fruit pericarp thickness	0.0011	-0.0012[1/]	0.0038	0.229±0.16	0.11	14.7
Fruit firmness	1.2154	-0.9658[1/]	1.9542	0.383±0.15	------	13.4
Average fruit weight	692.904	-269.27[1/]	340.02	0.670±0.12	------	8.49
Fruit shape (C/D)	0.0072	0.00284	0.004	0.501±0.15	0.88	8.70
Average weight per locule	34.169	-13.618[1/]	41.74	0.450±0.14	0.84	10.0

[1/] Only narrow sense heritabilities were estimated due to the presence of negative dominance values. Negative estimates of the dominance variance were taken as zero to obtain the other parameter estimates.

average weight per locule. The data in this study corroborated those of these authors, who also reported on the adequacy of the additive-partial dominance model to explain variability of traits. However, for traits such as fruit transversal diameter (D), number of loculi per fruit, average fruit weight and fruit firmness, the additive-dominance model was not adequate, and a more complex model including epistatic effects was needed. Most studies, however, reported only a partial dominance towards lower number of loculi per fruit (Rick and Butler, 1956; Miranda et al., 1982). In addition, the results from this work are not in line with those obtained by Miranda et al. (1982) for the number of loculi per fruit and those of Maluf et al. (1982a) for average fruit weight, who did not detected epistasis. Larson and Currence (1944), Fogle and Currence (1950), Powers, (1952) and Maluf et al. (1982a, 1982b) also reported partial dominance controlling average fruit weight. The model including epistatic effects was necessary to explain the genetic variability of fruit firmness means.

Powers (1939); Peirce and Currence (1959) and Khalf-Allah and Peirce (1963) suggested that the average fruit weight and number of loculi traits are highly heritable. Previous studies have shown that average fruit weight and number of loculi contributed directly to fruit size and were to a certain extent indicators of fruit size (Mac Arthur and Butler, 1938; Powers, 1939; Mac Arthur and Butler, 1938).

CONCLUSIONS

The inheritance of transversal diameter, longitudinal length of fruits, number of loculi, scar prominence, fruit pericarp thickness, fruits firmness, average fruit weight, C/D ratio (shape) and average weight per loculi show partial dominance in a predominantly additive model, although epistatic effects also occur. The estimated value of the narrow sense heritability coefficients, at the individual plant level, suggests that it is possible to accocomplish an efficient selection for average fruit weight and number of loculi per fruit. On the other hand the narrow sense heritability coefficient for fruit shape characteristic was 50.18% with an error of 31.60% indicating a drop in precision. In this situation, the expression of this character depends as heavily on the genetic additive effects as on the non additive, suggesting certain difficulty in the selection process. In this case, the model verifies the adaptation of the additive-dominant to explain the longitudinal length of fruits, fruit pericarp thickness, C/D ratio and average weight per loculi. However for the transversal diameter, number of loculi and average fruit weight, the adaptation of the model includes epistatic effects on the additive x additive type in the control of these characters. For these reasons, it can be concluded that to obtain an increase in the average weight of tomato fruits, selection for an increased number of loculi per fruit must be prioritized. It also can be observed that there is a considerable difficulty in obtaining tomato fruits that simultaneously introduce large fruits with the Santa Cruz shape, since a larger number of loculi can favor fruits with larger weight. This increase in number per loculi can damage the shape of the "Santa Cruz" type, as well as pericarp thickness, fruit and prominence firmness of the estilar scar.

RESUMO

Controle genético de características morfológicas em frutos de tomate

Este estudo foi realizado para estudar a herança do formato de fruto de tomate e outras características morfológicas de um simples cruzamento biparental entre a cultivar Nemadoro e Stevens. As gerações F_1, F_2 e os retrocruzamentos para ambas as gerações dos pais foram obtidas e avaliadas junto com as linhagens parentais em um delineamento experimental de blocos casualizados, com quatro repetições.As estimativas dos parâmetros genéticos foram obtidas utilizando-se os componentes de média e variância segundo o modelo proposto por Mather e Jinks (1982).Os genes que controlam as características morfológicas do fruto de tomate se mostraram predominantemente com efeito aditivo,mas foi mostrado também a dominância parcial.A estimativa da herdabilidade no sentido restrito para formato de fruto, avaliada pela razão comprimento/diâmetro, foi de 50.18%.A estimativa da herdabilidade restrita para o nível individual de plantas, para peso de fruto e número médio de lóculos por fruto foi de 67.08% e 87.46%, respectivamente, indicando condições favoráveis para seleção para estas características.O modelo aditivo-dominante foi adequado para explicar a herança de comprimento de fruto, a espessura da polpa do fruto, a relação comprimento/diâmetro e o peso médio por lóculo.

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