

INHERITANCE OF FRUIT SIZE IN LYCOPERSICON SPECIES

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ABSTRACT

The mode of inheritance of fruit size in crosses involving tomato (*Lycopersicon esculentum*) and its wild relative (*L. pimpinellifolium*) was investigated. Fruit size as determined by single fruit weights was inherited quantitatively. The frequency distributions of the parents and progenies approximated continuous variations thus implicating fruit size as a polygenic trait. It was difficult to explain the genetic components involved in the inheritance of fruit size with the additive dominance model. Results and the frequency distribution of the data provided convincing evidence that fruit size inheritance in tomato is governed by multiplicative gene action. Improvement of fruit size in this circumstance cannot be achieved through hybrid combinations that exploit heterosis or other breeding methods that emphasize the concentration of paternal and maternal genes. Rather, the backcross breeding method, using the cultivated tomato as the recurrent parent is recommended for upgrading the fruit size while still retaining some of the desirable attributes of the wild parent.

Key words: Tomato, fruit size, *Lycopersicon esculentum*, *Lycopersicon pimpinellifolium*

INTRODUCTION

Large fruit size is a desirable horticultural characteristic in tomato improvement and is still an important feature in crop breeding programmes. While a great amount of genetic variability for fruit size exists in tomato species and varieties (Powers, 1951; Atugwu, 2001; AVRDC, 1984) definitive studies on the inheritance of fruit size in tomato are rare. In a study of the relationship between fruit size and seed number in blackberry, Moore *et al* (1974) observed that fruit weights generally were intermediate between the parental clones but data were insufficient to draw valid conclusions on the inheritance. In raspberry, Toyama (1961) found evidence that dominance is important in the inheritance of fruit size with a partial dominance of light fruit size over heavy fruits. Frequency distribution indicated quantitative inheritance in fruit weight.

The wild tomato, *Lycopersicon pimpinellifolium*, has been accorded considerable attention as a useful material for the improvement of the domesticated tomato, *L. esculentum* (Foolad and Lin, 1999). However, the wild tomato possesses some undesirable horticultural characteristics principal among which is the small fruit size (Tanksley *et al*; 1996).

Easily grown under field conditions it is compatible with the genetically well-understood *L. esculentum* (Grandillo and Tanksky, 1996a, 1996b; Miller and Tanksley 1990; Palmer and Zamir, 1982; Rick 1982; Warnock, 1988) thus availing exceptional opportunities for enrich-

ing the germplasm of the *Lycopersicon* species for purposes of breeding and genetics. For a start, preliminary field crosses and cytological studies (Uguru and Atugwu, 2001) have shown that it is possible to produce hybrids between cultivated tomatoes and the wild relative by conventional breeding methods. The interspecific hybrids arising from these crosses have shown high level of pollen viability and fertility, a phenomenon that has permitted the furtherance of the new hybrids to higher generations. But since the wild tomato species is characterized by small fruit size and consumer preference is in favour of large fruits, it is important to investigate fruit size inheritance in crosses between the two species. This will serve as a prelude to the development of breeding strategies for improved fruit size. Peter and Rai (1980) reported a degree of dominance of 0.79 for equatorial perimeter of tomato indicating partial dominance to additive gene action in the inheritance of this fruit size determining parameter.

The purpose of the present study is to objectively and efficiently evaluate fruit size distribution in the parents, F₁ and segregating populations with a view to elucidating the genetic basis of inheritance of this important horticultural trait.

MATERIALS AND METHOD

The materials used in this study comprise two cultivated fresh market tomato varieties: Roma and Tropica and one wild tomato relative, *L. pimpinellifolium*. The Roma

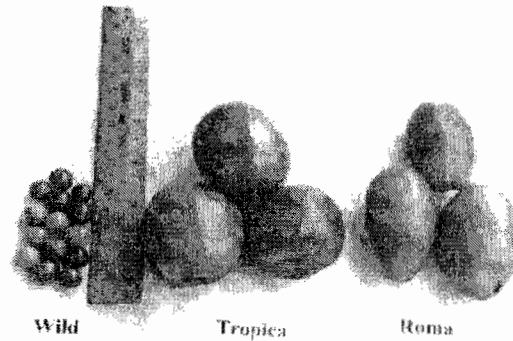


Plate 1. Fruit size of the three parents (Wild, Roma and Tropica).

Table 1: Record on the fruit sizes of the parents, F_1 , F_2 , and backcrosses showing the mean, range, standard deviation and sample size.

Family	Mean	Range	Std. Dev.	N
Roma (A)	22.9	8.0 – 52.0	7.16	202
Wild (B)	1.57	0.11 – 3.0	0.57	317
Tropica (C)	25.7	5.0 – 95.0	15.30	115
A x B, F_1	2.88	1.25 – 4.75	0.74	72
B x C, F_1	4.1	0.5 – 11.5	1.12	53
A x B, F_2	3.60	3.0 – 14.5	3.20	450
B x C, F_2	3.70	0.30 – 12.3	1.72	165
(A x B) F_1 x A	7.3	0.41 – 22.0	4.22	132
(A x B) F_1 x B	1.42	0.75 – 4.50	0.53	62
(B x C) F_1 x C	12.0	4.0 – 34.0	7.16	129

and Tropica varieties enjoy wide popularity with growers and consumers in Nigeria mainly because of their large fruits and the relatively low water content of their pulp. The wild species is endowed with very tiny fruits (Plate 1).

Two crosses were made using the wild species as the pollen parent in the cross, Roma x wild and as the seed parent in the cross, wild x Tropica.

The experiments were carried out in the Crop Science research field, University of Nigeria Nsukka from 2000 to 2002. The F_1 generations of Roma x wild and wild x Tropica were from crosses made using a dissection probe needle for pollen transfer on plants raised in black polythene pots. Pollination was effected on buds emasculated mechanically one day before they were due for anthesis, and plants were tagged so as to indicate the parents crossed. The same method was applied between the F_1 and their parents to obtain the backcross generations.

The plant materials evaluated included the three parents, F_1 , F_2 and backcross progenies of the cross between Roma and wild, and the wild and Tropica. However, the progenies of the backcross of the F_1 (wild x Tropica) to the wild parent were destroyed in the

course of the experiment and are therefore not included in the result. Except for the F_1 progenies that were evaluated in pots, all plantings were done on raised beds.

Data on fruit size was collected from all plants in the parents, F_1 , and backcrosses when the plants had attained full maturity and the fruits were fully ripened. Because of the large plant population of the F_2 generation, samples were taken at random from the plots. Fruit size was determined by weighing single fruits using a sensitive balance and recorded in grammes.

Statistical analysis

Statistical Analysis to determine the means, standard deviation, variances, frequency distribution and skewness coefficients were done using the SPSS computer package version 10.5.

RESULTS

The fruits of the wild species are tiny, bead-like and round in shape in contrast to Roma with large oval-shaped fruits and Tropica with large spherical fruits (Plate 1).

The frequency distributions of the parents, F_1 ,

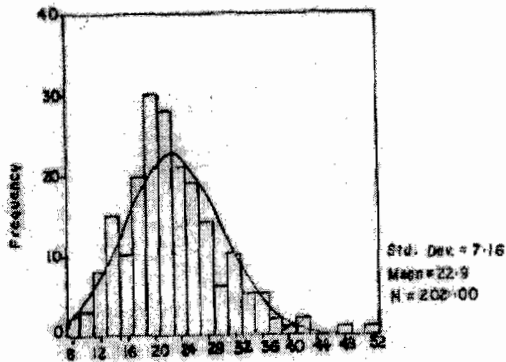


Fig. 1: Frequency distribution of fruit size in the Roma parent.

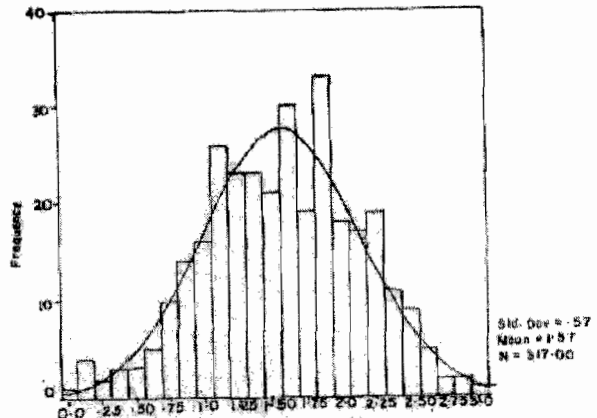


Fig. 2: Frequency distribution of fruit size in the wild parent.

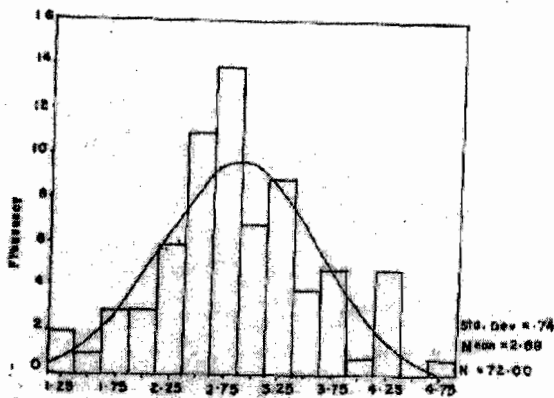


Fig. 3: Frequency distribution of fruit size in the F_1 Roma x w

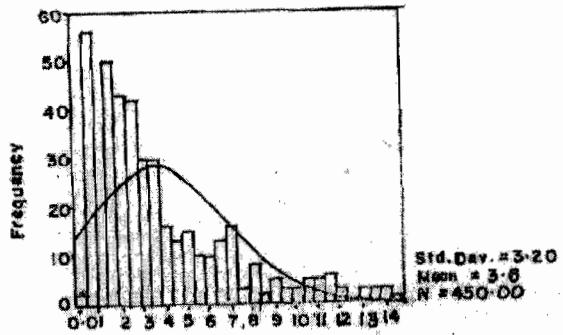


Fig. 4: Frequency distribution of fruit size in F_2 generation of Roma x wild.

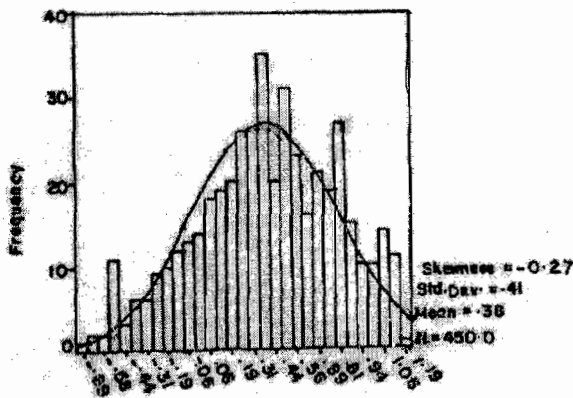


Fig. 5: Fruit size distribution of F_2 (Roma x wild) in a logarithmic scale

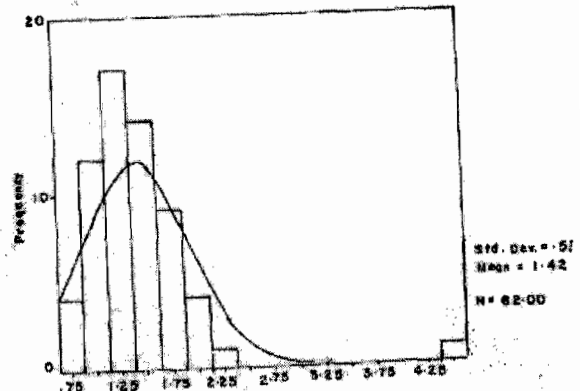


Fig. 6: Frequency distribution of fruit size in the backcross, Roma x wild x wild.

F₂ and backcrosses are shown in figures 1 to 7 in Roma x wild and figures 8 to 12 in wild x Tropica. All the families including the parents showed continuous distribution with no evidence of segregation due to major gene effects.

Roma x wild

The two parents, Roma and wild differed considerably in fruit size. Variation was more pronounced in the population of the Roma variety ($\delta^2 = 51.26$) than in the population of the wild parent ($\delta^2 = 0.32$). In Roma, fruit size ranged from 8.0g to 52.0g with a mean of 22.9g. The spread around the mean indicates that 95% of the entire population had fruits ranging from 8.57g to 37.23g with a greater proportion of the fruits being large (Fig. 1). Fruit size in the wild species ranged from 0.11g to 3.0g (Table 1). The spread around the mean (Fig. 2) is indicative of the existence of an extreme homogeneous population as 95% of the fruits ranged from 0.43g to 2.71g. The very low variance of 0.32 also reinforces homogeneity in the population. The frequency distribution of the wild parent is a perfect fit to a normal curve.

The frequency distributions for fruit size of F₁ and F₂ plants are shown in Figures 3 and 4. Fruit size in the F₁ population ranged from 1.25 to 4.75g with a mean of 2.88g (Table 1). A standard deviation value of 0.74 (Fig. 3) indicates that 95% of the population had fruit size ranging from 1.4g to 4.36g.

The population homozygous for small fruit size had a mean of 1.57g and one from which the mid-giant fruit size alleles are entirely absent had a mean fruit size of 22.9g. The F₁ heterozygote had a mean of 2.88g as against the mid-parent value of 12.24g between the two homozygotes. Thus the parameter "d" measuring the departure of each homozygote from the mid-parental value would be 10.66g and 'h' measuring the departure of the heterozygote from the mid-parent is -9.30. Though negative 'h' is still within the range delimited by the fruit size-beltling gene. The phenotypes of the heterozygote overlapped with values of the wild parent in contrast to the values of the Roma parent where there was no such overlap. The F₂ values varied between the parental limits with no discrete classes. Fruit size in F₂ ranged from 3.0g to 14.5g with a mean of 3.6g (Table 1). The frequency distribution showed extreme skewness in favour of the small fruits (Fig. 4). There were no transgressive segregants for large fruits. A logarithmic transformation of the F₂ gave a distribution that approximated a normal probability curve (Fig. 5) with a skewness coefficient ($sk = -0.27$) that is very close to zero. Similar to the F₂ population, the frequency distribution of the backcross populations were asymmetrical and biased towards the small-fruited wild parent. The backcross to the wild parent showed great tendency towards the small-fruited wild parent (Fig. 6). The progeny mean fell well below the mid-parental value. Plants with large fruits were obtained in a very low frequency in the backcross to the large fruited Roma parent (Fig. 7). Although the mean fruit size appreciated to 7.3g, the

distribution was more or less biased towards the small fruit size. Fruit size ranged from 0.41g to 22g with a mean of 7.3g. The spread around the mean indicates that many of the plants had large fruits with some weighing up to 22.0g.

Wild x Tropica

The results obtained from the cross, wild x Tropica were nearly similar to those from the cross, Roma x wild. Fruit size in Tropica ranged from 5.0g to 95.0g with a mean of 25.7g (Table 1). A standard deviation value of 15.30g indicates that a great proportion of the fruits weighed more than 25.7g (Fig. 8).

The frequency distribution of the F₁ population approximated a normal curve (Fig. 9) with a mean less than the mid-parent value. The wild parent had a mean fruit size of 1.57g; the Tropica 25.7g and the mid-parental value is 13.64g. Similar to the result obtained in the Roma x wild cross, 'h' has a negative value of -9.54.

The frequency distribution of the F₂ population approximated a normal curve that is however asymmetrical with a slight bias in favour of the small fruit size (Fig. 10). Fruit size ranged from 0.30g to 12.3g with a mean of 3.70g. The spread around the mean indicates that 95% of the fruits fell within a range of 0.26 and 7.14g. There were no transgressive segregants for both small and large fruits among the F₂ progenies. The transformation of the F₂ data from the arithmetic scale to the logarithmic scale produced a distribution (Fig. 11) with a skewness coefficient that is close to zero ($sk = -0.66$). The highest percentage of large fruited progenies were found in the backcross, Wild x Tropica x Tropica. The population averaged fruit of 12.0g and there were no segregants with fruit size comparable to those homozygous for small fruit size. The frequency distribution showed discernable skewness in favour of small fruit size (Fig. 12)

Table 2 shows the variances and means of the segregating populations. The mean and variance appear to be correlated as they both increased proportionately (i.e. as the means increased, so do variances).

DISCUSSION

The observed pattern of variation, with fruit size appearing to be controlled by several genes and with a picture of dominance of small fruit size over the large ones is in accord with findings in crops like blackberry (Caldwell and Moore 1982) and raspberry (Moore *et al.* 1974). The frequency distributions of the parents and progenies approximated continuous variations thus implicating fruit size as a polygenic trait. This is further validated by the wide range in fruit size in the various families. In the two crosses, Roma x wild and wild x Tropica, the F₁ means were close to the mean fruit weight of the wild parent. The heterozygotes could not contribute meaningfully to the increase in fruit size following the miniaturizing effects of the small fruits of the wild parent. Consequently, the frequency distribution was skewed towards the small-fruited wild parent. There were no

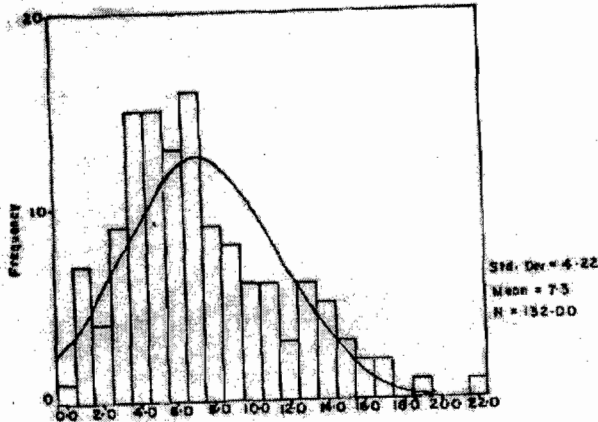


Fig. 7. Frequency distribution of fruit size in the backcross, Roma x wild x Roma

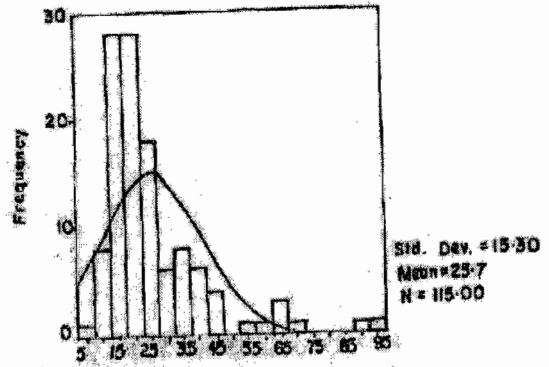


Fig. 8. Frequency distribution of fruit size in the parent, Tropica

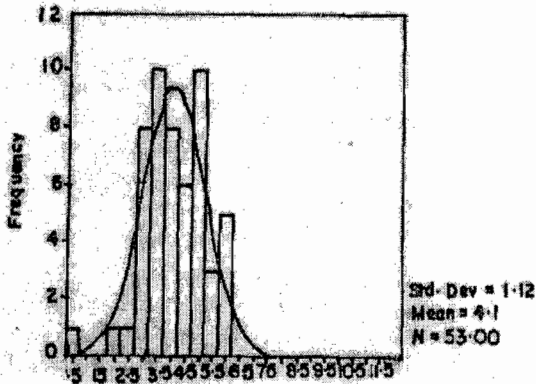


Fig. 9. Frequency distribution of fruit size in F_1 generation of wild x Tropica

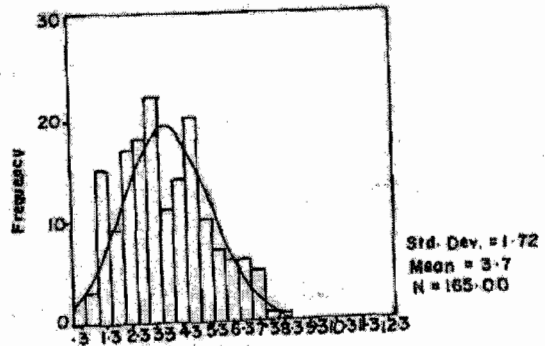


Fig. 10. Frequency distribution of fruit size in F_2 generation of wild x Tropica

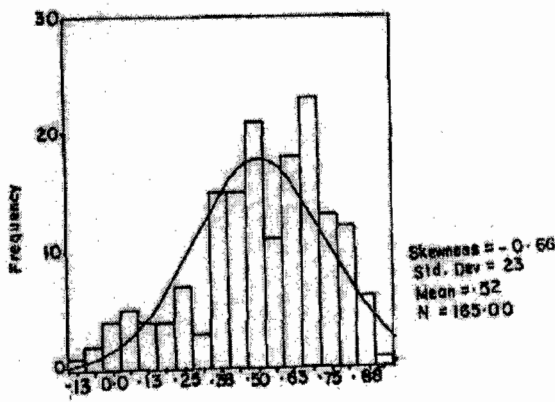


Fig. 11. Fruit size distribution of F_2 (wild x Tropica) in a logarithmic scale

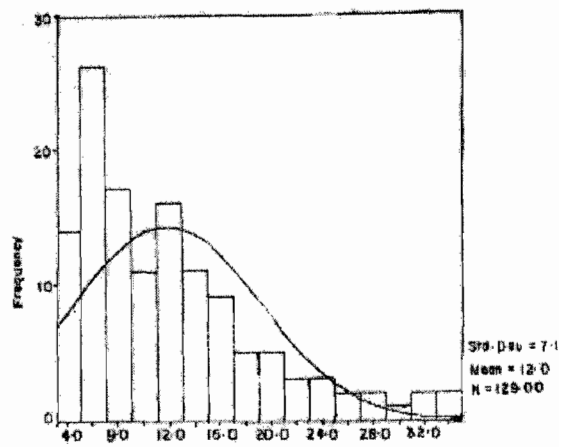


Fig. 12. Frequency distribution of fruit size in the backcross, wild x Tropica x Tropica

Table 2: Means and variances of the segregating populations

Family	Roma x Wild		Wild x Tropica	
	Mean	Variance	Mean	Variance
F ₂	3.6	10.24	3.70	2.96
B ₁	1.42	0.28	-	-
B ₂	7.3	17.81	12	51.26

plants with large fruits in the backcross to the wild parent. But the percentage of large-fruited plants recovered was slightly increased by backcrossing the F₁ to the large fruited domesticated parents, a situation that may have arisen from a mild shift in gene frequency in favour of the large fruited parent. This would have some implications for selection on individual plant basis. On the average however, the mean fruit size of the backcross was still less than the least class value of the domesticated parent thereby reinforcing the overwhelming masking effects of alleles for small fruit size over those for large ones. That the minimum class value of the large fruited domesticated parent was not attained in any of the hybrid populations tends to suggest that the alleles for small fruit size maintained a ceiling that presumably moderated the incremental swelling of the fruits in subsequent generations.

Under additive gene action, the F₁ mean is expected to fall half way between the means of the two parental combinations (Brewbaker 1964; Mather and Jinks, 1977). But the observations were different in the inheritance of fruit size in tomatoes as the F₁ mean approximated the geometric mean, which is similar to the mean of the wild parent. This coupled with the extreme skewness of the F₂ and backcross populations towards the small-fruited wild parent would tend to implicate dominance of alleles for small fruit size over the alleles for large fruit size. This proposition is however invalidated by a number of observations. First, the segregating populations did not follow a normal probability distribution. Secondly, the mean values of the segregating generations are not centrally located and the upper tail of the curves approached zero much more slowly than did the lower tail. Thirdly, the skewed distribution of the F₂ generations approximated normal distributions after transforming the data to the logarithmic scale. The skewness coefficient of the transformed data for Roma x wild ($sk = -0.27$) and for wild x Tropica ($sk = -0.66$) closely approached zero thus indicating normality. By this transformation, the measurement of the phenotype is replaced by its logarithm. The multiplicative action of the alleles are removed and each allele makes its own independent contributions to the phenotype.

The F₁ means of the two populations (Roma x wild and wild x Tropica) approximate the geometric rather than the arithmetic mean between the parental values. The geometric mean of the cross, Roma x wild is 5.996 giving a geometric series of 1.57, 5.996 and 22.9

that increased by a multiplicative increment of 3.82. This closely resembles the values of 1.57, 2.88 and 22.9 found experimentally; but contrasts the 1.57, 12.24 and 22.9 that would have been obtained if the genes had acted additively. By the same reasoning, the geometric mean of wild x Tropica is 6.352 giving a geometric series of 1.57, 6.352 and 25.7 that increased by a multiplicative increment of 4.05. This closely resembles the values of 1.57, 4.10 and 25.7 found experimentally but contrasts with 1.57, 13.64 and 25.7 which would have been the case if the trait were to be arithmetically additive.

The asymmetrical curves coupled with the correlated means and variances, and the bias nature of the F₁ and F₂ means towards the mean of the small fruited wild parent and the conversion of the skewed distribution to normal distributions through logarithmic transformation provide convincing evidence that fruit size inheritance in tomato is governed by multiplicative gene action. The joint effects of the alleles governing fruit size is the product and not the sum of their individual actions. Fruit size is a volumetric trait that is determined as the product of diameter, height and depth (Powers, 1951). The alleles belittling fruit size act to multiply, by some constant factor, the effect of the genotype upon the trait. This provides some explanations why gene recombination at the segregating populations did not favour the production of fruits that are comparable to the mean weights of the two domesticated tomato varieties.

CONCLUSION

Apparently from the foregoing, it is impossible to explain the genetic components involved in the inheritance of fruit size in tomato with the additive-dominance model. Improvement of fruit size in tomato cannot therefore be achieved through hybrid combinations that exploit heterosis or other breeding methods that emphasize the concentration of paternal and maternal genes. In the light of such peculiarities, the backcross breeding method, using the cultivated tomato as the recurrent parent is recommended. The recurrence of the large fruited parent will upgrade the mean level of the next generation and enhance responsiveness of fruit size to selection.

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