Full Length Research Paper

Tracking fruit size increase in recombinants obtained from an interspecific cross between cultivated tomato (*Solanum esculentum)* and wild tomato relative *(S. pimpinellifolium)*

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The present study was conducted to track the progress in fruit size increment in inter-specific tomato hybrids from F_1 to F_{12} generation. Selection was imposed at every generation and the incremental rate in single fruit size from one generation to another was obtained using relative performance difference (RPD) between successive generations. Increase in fruit size was vivid at every generation and there were discernable evidence to show that the inheritance of fruit size was under polygenic control. The fruit size incremental rate was slow from F_1 to F_7. Thereafter, the increase became more rapid and attained a peak at the F_9 generation. The fruit size increase from F_{10} to F_{12} generation was remarkably low with the relative performance difference not exceeding 22%. The correlation studies showed non - significant relationship between fruit size and fresh fruit yield at the early generations. The association between the two traits was positive and significant at the advanced generations. The implications of these on tomato improvement have been discussed.

Key words: Tomato, fruit size, interspecific cross, *Solanum esculentum, Solanum pimpinellifolium.*

INTRODUCTION

Large fruit size is a desirable horticultural characteristic in tomato improvement and an important feature in crop breeding. Large fruits are highly sought after and they attract higher premium in both local and urban markets. The overall yield of tomato is largely influenced by the number and weight of the fruits. The wild species, *Solanum pimpinellifolium* harbors numerous desirable horticultural and agronomic characteristics, including disease resistance (Tanksley et al., 1996) and abiotic stress tolerance (Chen and Foolad, 1998), but produces very small fruits. Easily grown under field conditions, the wild tomato relative is compatible with the genetically well-understood *Solanum esculentum* (Grandillo and Tanksely, 1996a, b; Miller and Tanksely, 1990; Palmer and Zamir, 1982; Warnock, 1988). Preliminary field crosses and cytological studies of Uguru and Atugwu (2001) have shown that it is possible to produce hybrids between cultivated tomato 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. The close phylogenetic relationships between the two species have enhanced inter-specific hybridizat-ion between them. A great amount of genetic variability for fruit size exists in tomato species and varieties (Powers, 1951). Fruit size is a volumetric trait that is determined as the product of diameter, height and depth (Powers, 1951). Uguru and Onwubiko (2002) observed that

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inheritance of fruit size was controlled by multiplicative gene action involving several genes. Most tomato fruit traits are quantitatively inherited. A large member of QTLs have been identified in tomato that are associated with fruit development, size, shape, colour, ripening, organoleptic quality and yield (Causse et al., 2001, 2002; Van der Knaap and Tanksley, 2001, 2003; Nesbitt and Tanksley, 2001; Saliba-Colombani et al., 2001; Fulton et al., 2002; Liu et al., 2002; Van der Knaap et al., 2002; Frary et al., 2003; Barrero and Tanksley, 2004; Semel et al., 2006). Molecular mapping studies have revealed the presence of dozens of QTLs for fruit size in tomato, some of which with very large effects (Chen et al., 1999). But to date, definitive studies on the trend of fruit size increment in interspecific hybrids have not been done. The present study was initiated therefore, to evaluate fruit size increment in the segregating populations of interspecific cross between *S. esculentum* and *S. pimpinellifollium*.

MATERIALS AND METHODS

The materials used in this study comprised one cultivated tomato variety, roma and a wild tomato relative *S. pimpinellifolium*. The experiments were carried out in the Department of Crop Science Research Farm, University of Nigeria, Nsukka from 2001 to 2008. Crosses were made using the Wild tomato (W) as the pollen parent and the Roma (R) as the seed parent (Roma × Wild). Seedlings of the two parents were raised in nursery boxes filled with sterilized soil, well cured poultry manure and river sand at a ratio of 3: 2: 1. Seedlings were transplanted into poly bags at 4 weeks after planting. Crosses were made using a pair of sharp forceps, magnifying glass, dissecting pins and scissors. Pollination was effected artificially on emasculated young flower buds before anthesis. The successful crosses were tagged. The F_1 hybrids were planted to generate the F_2 population.

Selection started from the F_2 generation with 5% selection intensity. The selected plants were allowed to random mate at every generation from F_2 to F_{12}. The selection in every generation was based on individual plant performance. The fruits of the selected plants were harvested and weighed individually with a digital weighing balance to obtain the single fruit weights.

Statistical analysis

Statistical analysis was done to determine the means and standard deviation, variance and frequency distribution using the SPSS software computer package version 10.0. Inter- generation differences were estimated using a relative performance differential analogous to single parent heterosis (SPH). Thus, progress in F_2 relative to the F_1 generation ($RPD_{2,1}$) and in F_3 relative to F_1 generation ($RPD_{3,1}$) in that order up to F_{12} generation were calculated as outlined:

$RPD_{s,p} = 100 (G_s - G_p/G_p)$

Where:

RPD = Relative Performance Difference
G_S = Succeeding generation
G_p = Preceding generation

Correlations were computed to examine inter- character relationships between single fruit weight and number of fruits and fresh fruit yield per plant.

RESULTS

The incremental rate of the fruits from F_1 to F_{12} is shown in Figure 1. Consistent progress was observed from F_1 to F_{12} except for the slight decline at the F_2 and F_{10} generations. The trend showed a gallop effect between F_7 and F_9 resulting in a steep slope. Thereafter, the incremental rate became gradual up to F_{12}. The mean values from F_9 to F_{12} exceeded the mean value of the cultivated tomato that is the main target for improvement.
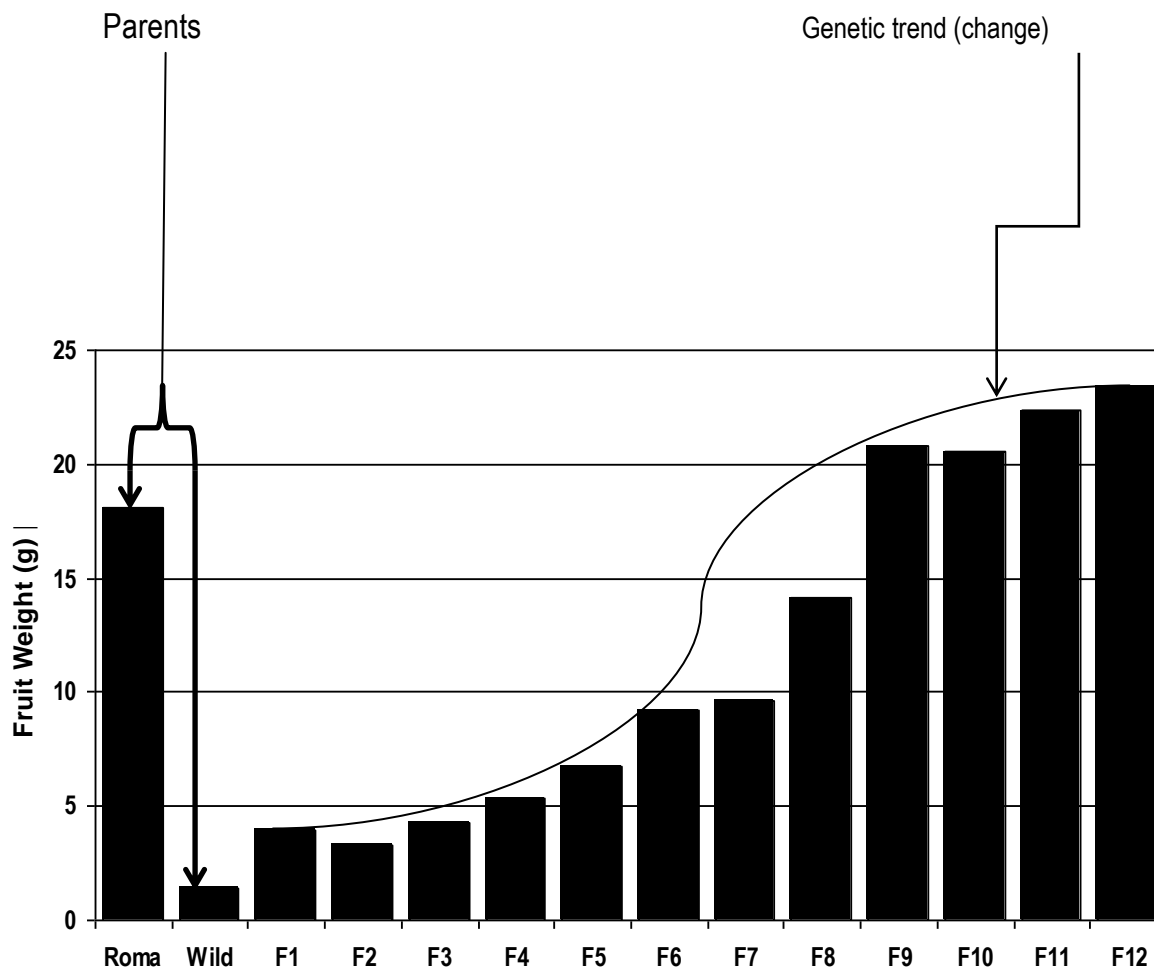
The frequency distribution of the parents and the progenies (F_1 to F_{12}) are shown in Figures 2 to 5. All the families including the parents showed continuous distribution with no evidence of segregation due to major gene effects. The frequency distribution of the wild parent is presented in Figure 2a. The fruit size ranged from 0.3 to 3.0 g. The spread around the mean showed that 95% of the population ranged from 0.53 to 2.27 g, an indication of extreme homogenous population. The very low variance of 0.177 g (Table 1) also reinforces homogeneity in the population. The results with respect to single fruit weight of the roma parent are presented in Figure 2b. The variation was more pronounced in the population of the roma variety (Table 1) than in the wild population as evidenced by the high variance recorded for the roma variety. The fruits ranged from 3.33 to 31.66 g with a mean of 18.09 g. The dispersion revealed that 95% of the fruits fell between 8.11 and 28.06 g with a greater proportion of large fruits.

The F_1 had a mean of 3.95 g as against the mid-point value of 9.73 g between the two homozygotes (Figure 4). The F_1 had a fruit weight range of 1 to 8.35 g. The phenotype of the F_1 overlapped with those of the wild parent. Only few fruits weighed above 8 g. Figure 2d show the frequency distribution of the F_2 population. Fruit size in F_2 ranged from 1 to 7.65 g with a mean of 3.28 g. The frequency distribution showed extreme skewness towards the small fruit size. There were no trasgressive segregants for large fruits in the F_2.

The distribution of the F_3 population showed fruits that ranged from 2 to 8.5 g with a mean of 4.33 g (Figure 3a). A standard deviation of 1.275 (Table 1) indicated that 95% of the population had fruits that ranged from 1.78 to 6.88 g. This revealed single fruit weight gain of 1.05 g over the mean of the F_2.

At the 4th filial generation, greater proportion of the fruits weighed 4 g and above (Figure 3b). There was strong evidence of transgressive segregation as some fruits were observed to be lying outside the range of 2 to 10 g.

Figure 3c shows the frequency distribution of the F_5 population. The distribution shows an upward shift in the mean fruit weight from 3.95 g in the F_1 generation to 6.76 g in the F_5 giving a mean weight gain of 2.81 g from F_1 to F_5 generation. There is an increase in the proportion of fruits that weighed more than 7 g. The F_6 generation also maintained a continuous distribution curve (Figure 3d). The least single fruit weight in this generation is 6 g.

Figure 1. Distribution of mean single fruit weight (g) of the parents and their progenies from F_1 - F_{12}.

Many of the fruits weighed above 9 g. The fruits at F_7 population ranged from 8 to 18 g (Figure 4a). Some fruits had mean fruit weight outside the range and weighed above 30 g. The dispersion indicated that 95% of the fruits fell within the range of 2.84 to 16. 36 g. There was obvious reduction in the number of fruits that weighed less than 10g at F_8 population (Figure 4b). The fruits that weighed up to 38 g were outside the 95% range. An increment of 4.3 g was obtained over the F_7 population was obtained.

The F_9 population showed discernable skewness towards the right implicating large fruit sizes (Figure 4c). The proportion of the fruits that attained 20 g and above was large and very few fruits weighed less than 10 g. An increment of 6.32 g over the mean weight of the F_8 generation was attained. At the F_{10} generation, 10 g was the least single fruit weight. A good number of the fruits weighed up to 38.33 g (Figure 4d). The spread around the mean showed that 95% of the population ranged from 7.66 to 35.06 g. The incremental rate declined to 1.08 from the 4.3 g of the F_8 gain over the F_7 and 6.32 g of the F_9 gain over F_8 population.

The distribution of F_{11} population was similar to that of the F_{10}. The spread around the mean showed that 95% of population ranged from 9.11 to 35.21 g. An insignificant number of fruits weighed less than 15 g (Figure 5a).The rate of increment however declined to 0.8 g.
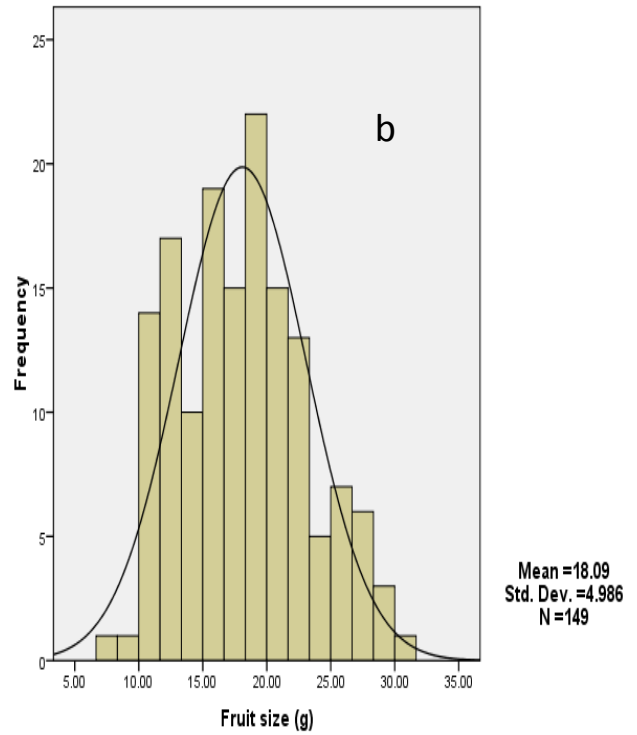
Figure 5b shows the frequency distribution of the F_{12} generation. The fruits ranged from 11.66 to 40 g. The spread around the mean showed that 95% of population ranged from 12.64 to 36.84 g. There was a remarkable evidence of a reduction in the proportion of the small fruits in the F_{12} generation.

The results of the genetic progress (Table 2) revealed low incremental rate of the fruit size at the early generations (F_1 to F_3) and a consistent increase as the generations advanced. A retrogression of -17% was observed in the F_2 generation over the F_1 generation. There was consistent single fruit size increment from F_3 to F_{12} generations. F_3 had 9% increases over the F_1; F_4 gained 35% over the F_1; F_5 gained 71% over the F_1 and F_6 gained 133% over the F_1. They continued in that order up to the F_{12} which gained 526% over the F_1 generation. Then F_3 over F_2 was 32.01%, F_4 over F_2 was 63.4%, F_5
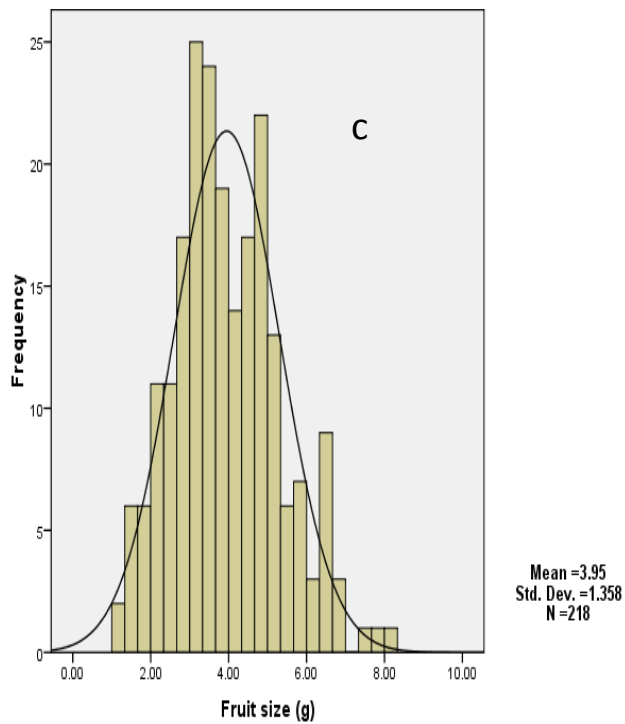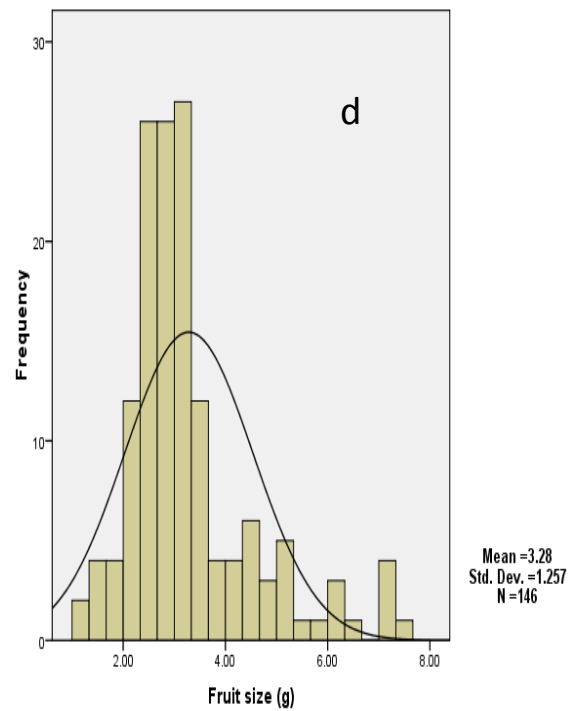
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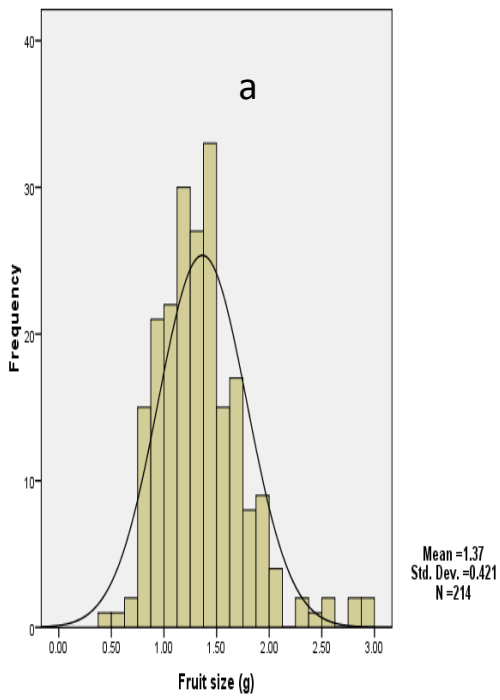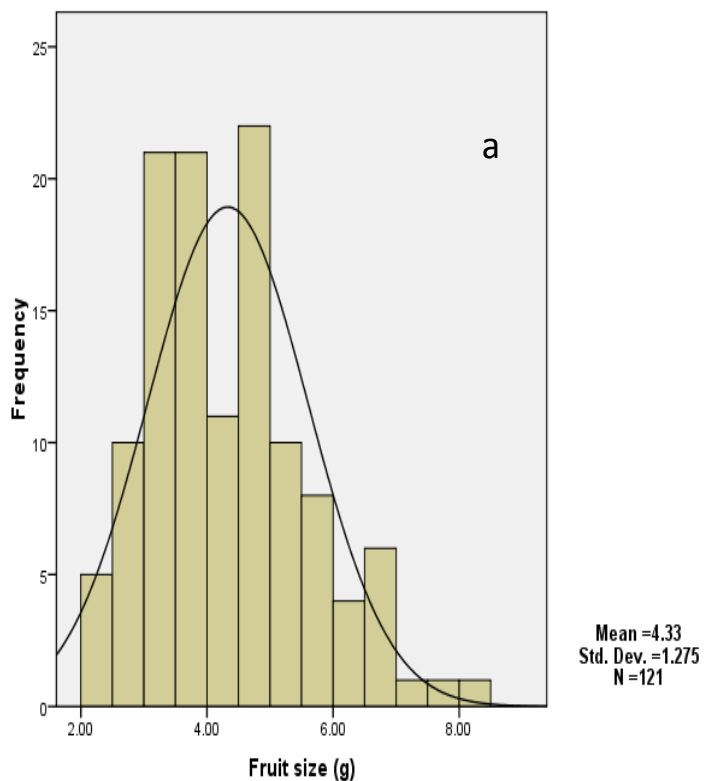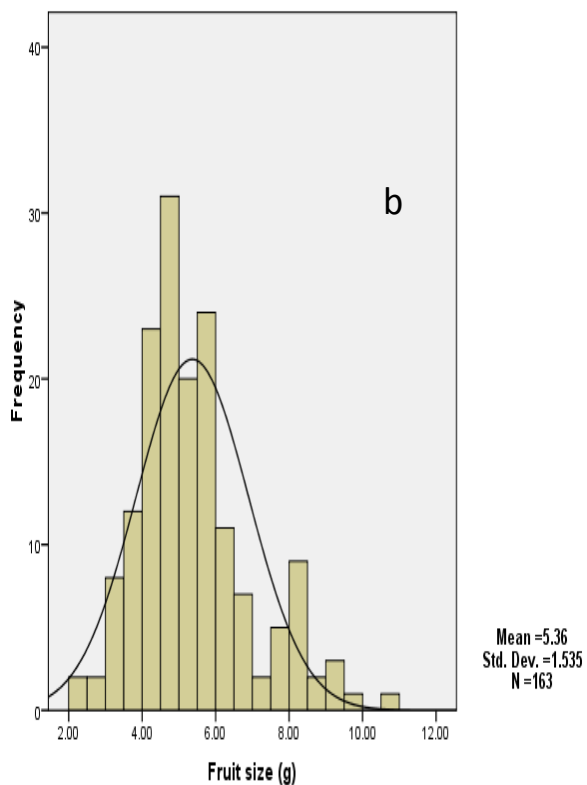
Roma

Figure 2. Frequency distribution of wild (a), Roma (b), F_1 (c) and F_2 (d) of the cross Roma x Wild (R X W) with respect to fruit size.

F₃   F₄

Figure 3. Frequency distribution of F₃ (a), F4 (b), F₅ (c) and F₆ (d) of the cross Roma x Wild (R × W) with respect to fruit size.

F₇

F₈

F₉

F₁₀

Figure 4. Frequency distribution of F₇ (a), F₈ (b), F₉ (c) and F₁₀ (d) of the cross Roma x Wild (R × W) with respect to fruit size.
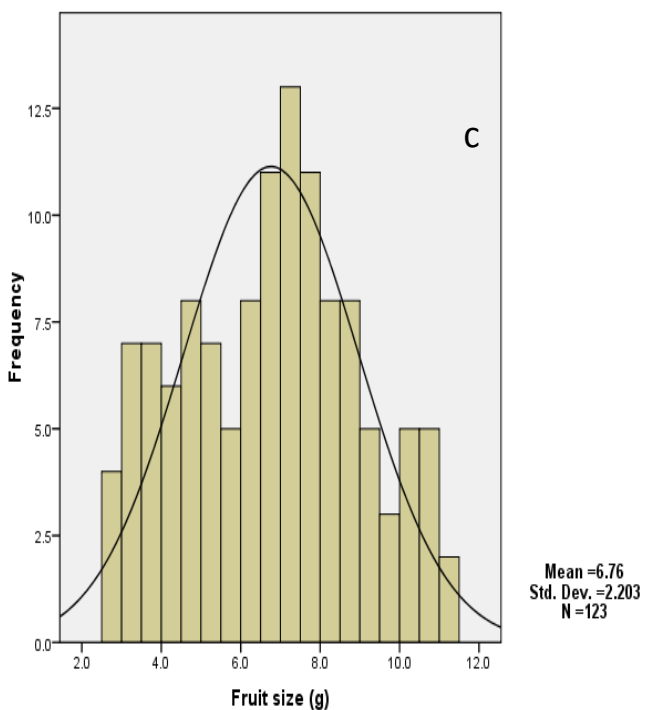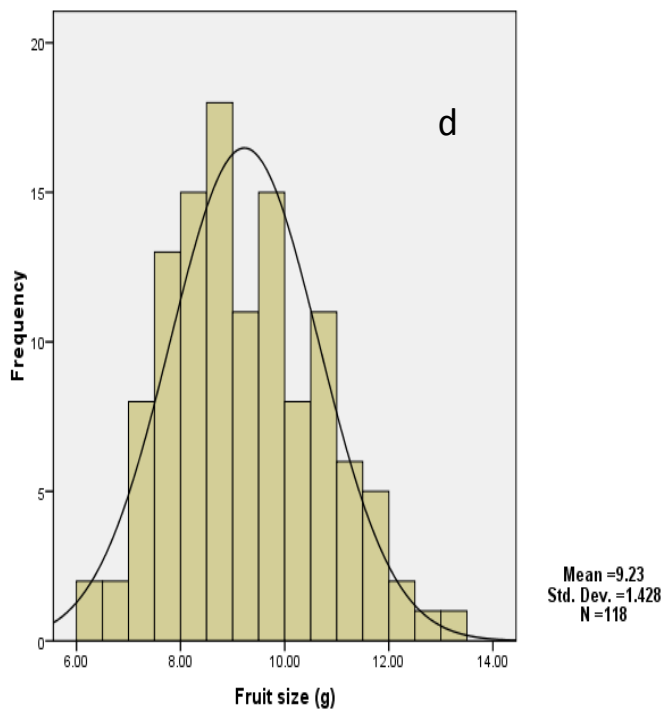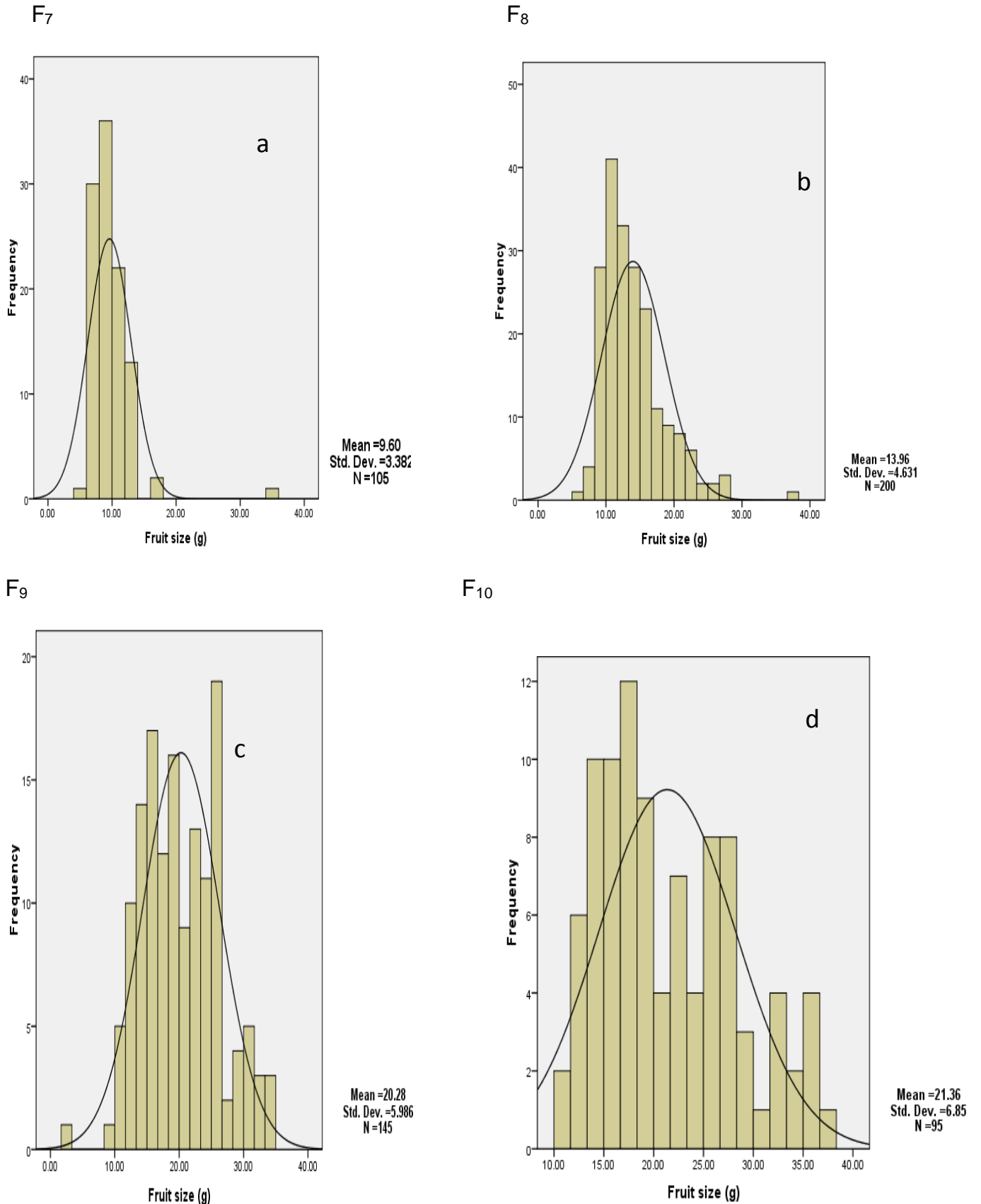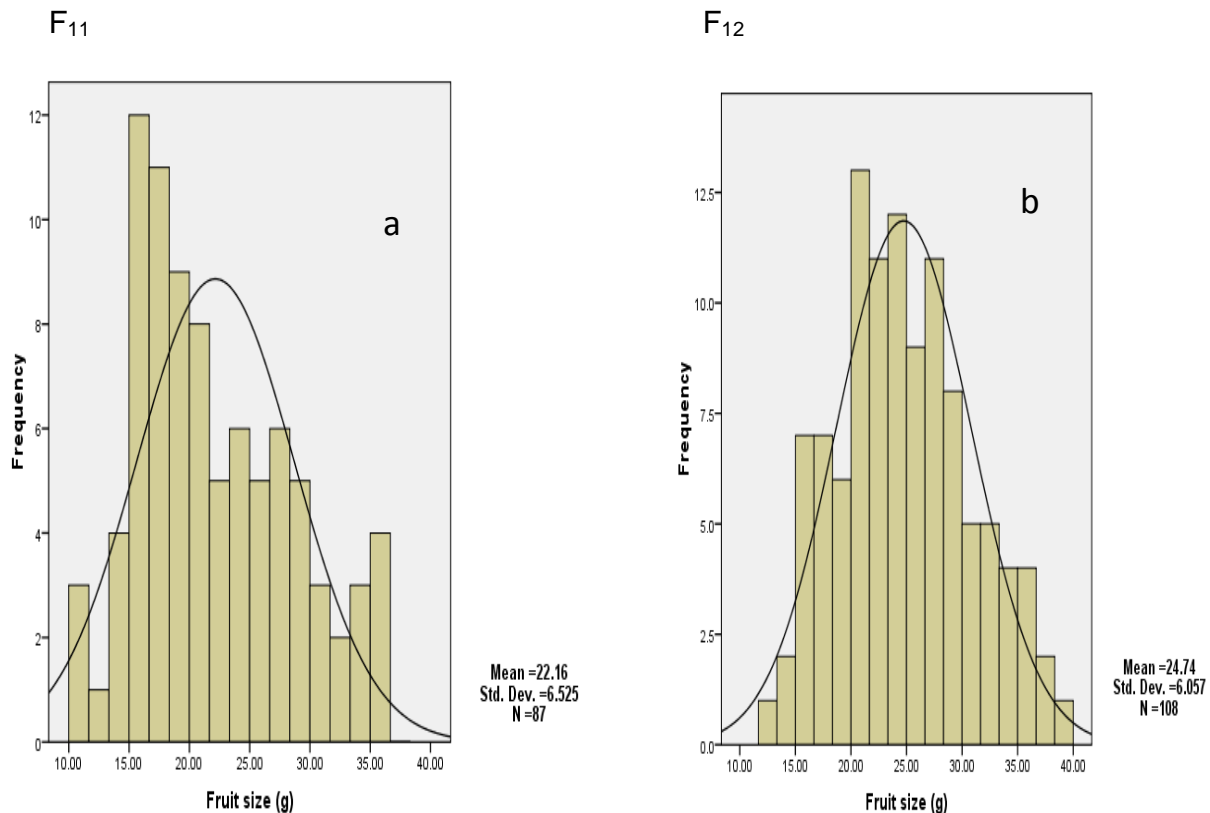
F_{11} F_{12}

Figure 5. Frequency distribution of F_{11} (a) and F_{12} (b) of the cross Roma x Wild (R X W) with respect to fruit size.

Table 1. Mean single fruit weight (g), standard deviation and range of the parents and their progenies with respect to single fruit weight.

Family	Mean	N	Standard deviation	Range
Wild	1.37	214	0.421	0.375 - 3.00
Roma	18.09	149	4.986	3.33 - 31.66
FI	3.95	218	1.358	1.00 - 8.33
F2	3.28	146	1.257	1 .00 - 7.65
F3	4.33	121	1.275	2.00 - 8.50
F4	5.36	163	1.535	2.00 - 11.00
F5	6.76	123	2.203	2.5 - 11.50
F6	9.23	118	1.428	6.00 - 13.5
F7	9.60	123	3.382	4.00 - 18.00
F8	13.96	200	4.631	5.00 - 28.33
F9	20.28	145	5.986	9.67 - 35.00
F10	21.36	95	6.85	10.00 - 38.33
F11	22.16	87	6.525	10.00 - 36.66
F12	24.74	108	6.057	11.66 - 40.00

over F_2 was 106%, F_6 over F_2 was 181.4% and F_{12} over F_2 was 654.3%.The correlation coefficients between single fruit weight, fresh fruit weight and number of fruits per plant are presented in Table 3. The results revealed that the association of fresh fruit weight and single fruit

yield were positive and significant in all the advanced generations (F_7 to F_{12}). The relationships between number of fruits per plant and single fruit weight were negative at F_2, F_3, F_4, F_7, F_9, F_{11} and F_{12} generations; and positive at F_1, F_5, F_6 and F_8 generations. Significant and

Table 2. Genetic progress (%) from (generation to generation) for fruit size increment.

F_1	Dev.	F_2	Dev.	F_3	Dev.	F_4	Dev.	F_5	Dev.	F_6	Dev	F_7	Dev.	F_8	Dev.	F_9	Dev	F_{10}	Dev	F_{11}	Dev.
$RPD_{2,1}$	-17	$RPD_{3,2}$	32.01	$RPD_{4,3}$	23.78	$RPD_{5,4}$	25.75	$RPD_{6,5}$	36.53	$RPD_{7,6}$	4.0	$RPD_{8,7}$	45.42	$RPD_{9,8}$	45.3	$RPD_{10,9}$	5.33	$RPD_{11,10}$	3.75	$RPD_{12,11}$	11.64
$RPD_{3,1}$	9.62	$RPD_{4,2}$	63.41	$RPD_{5,3}$	56.12	$RPD_{6,4}$	72.20	$RPD_{7,5}$	42.01	$RPD_{8,6}$	51.2	$RPD_{9,7}$	111.3	$RPD_{10,8}$	53.01	$RPD_{11,9}$	9.27	$RPD_{12,10}$	15.8		
$RPD_{4,1}$	35.69	$RPD_{5,2}$	106.1	$RPD_{6,3}$	113.2	$RPD_{7,4}$	79.10	$RPD_{8,5}$	106.5	$RPD_{9,6}$	119..7	$RPD_{10,7}$	122.5	$RPD_{11,8}$	58.7	$RPD_{12,9}$	21.99				
$RPD_{5,1}$	71.13	$RPD_{6,2}$	181.4	$RPD_{7,3}$	121.7	$RPD_{8,4}$	160.4	$RPD_{9,5}$	200	$RPD_{10,6}$	131.4	$RPD_{11,7}$	139.6	$RPD_{12,8}$	77.22						
$RPD_{6,1}$	133.67	$RPD_{7,2}$	192.7	$RPD_{8,3}$	222.4	$RPD_{9,4}$	278.5	$RPD_{10,5}$	215.9	$RPD_{11,6}$	140.1	$RPD_{12,7}$	157.7								
$RPD_{7,1}$	143.03	$RPD_{8,2}$	325.6	$RPD_{9,3}$	368.4	$RPD_{10,4}$	298.5	$RPD_{11,5}$	227.8	$RPD_{12,6}$	168.0										
$RPD_{8,1}$	253.42	$RPD_{9,2}$	518.3	$RPD_{10,3}$	339.3	$RPD_{11,4}$	313	$RPD_{12,5}$	265.9												
$RPD_{9,1}$	413.41	$RPD_{10,2}$	551.2	$RPD_{11,3}$	411.8	$RPD_{12,4}$	361.6														
$RPD_{10,1}$	440.75	$RPD_{11,2}$	575.6	$RPD_{12,3}$	471.4																
$RPD_{11,1}$	461.01	$RPD_{12,2}$	654.3																		
$RPD_{12,1}$	526.3																				

RPD = Relative performance different. Dev. = Deviation.

Table 3. Correlation analysis between single fruit weight, number of fruits per plant and fresh fruit yield.

Generation (S)	Number of fruits/plant	Fresh fruit yield/plant
F1	0.001	-0.174
F2	-0.271	0.142
F3	-0.404	-0.015
F4	-0.187	-0.266
F5	0.416	0.133
F6	0.450*	0.442
F7	-0.075	0.451*
F8	0.299	0.512*
F9	-0.382	0.548**
F10	0.201	0.551**
F11	-0.393	0.502*
F12	-0.435*	0.491*

*= Significant, **= highly significant.

positive correlation between single fruit weight and the number of fruits per plant was observed only at the F_6 generation.

DISCUSSION

The first QTLs to be implicated in the increment of fruit size in tomato fruit weight (fw) is 2.2 (Alpert et al., 1995; Farry et al., 2000). By crossing a wild and a cultivated tomato, mutations in about six

QTLs seem to have been responsible for transforming the small berries of wild tomato to the extremely large fruits associated with the present day cultivars (Tanksley, 2004). The findings of the present study appears to be at variance with this proposition as fruit size increase appears to be associated with pyramiding of alleles for fruit size after several cycles of selection rather than mutation. Except for the slight drop at the F_{10}, the incremental rate of single fruit weight was consistent from one generation to another among the segregating populations. This resulted to a near perfect ogive curve which is suggestive of continuous gain in fruit size with selection. The decline at F_2 from the F_1 validates strong heterotic effect of the F_1 over the F_2 population in fruit size inheritance.

The frequency distribution of the parents and progenies showed continuous variation thus, suggesting fruit size in tomato as a polygenic trait. This is further validated by the wide range in the fruit size distribution in all the generations. A picture of dominance of the small fruit size over the large ones at the early generations (F_1 and F_2) is in agreement with the findings in crops like raspberry (Toyama,1961) and blackberry (Caldwell and Moore, 1982). The skewness towards the small fruits of the wild parent in the F_2 is an indication that the frequency of the alleles contributing to small fruit size was very high at the early generations (Uguru and Onwubiko, 2002). Evidence abound in literature that crops have been improved using various selection methods (Allard, 1960; Casali and Tigchelar, 1975; Miller et al., 1991). The results obtained in the present study agree with the reports as can be discerned from the sigmoid growth pattern in the increase in fruit size from the first filial generation (F_1) to the F_{12} generation. The rate of fruit size increment was minimal from F_1 to F_5 with a mean difference of 2.81 g. The rate increased rapidly from F_5 to F_9 with a mean difference of 13.52 g and less rapidly from F_9 to F_{12} with a mean difference of 4.46 g. This trend provides a strong evidence of additive gene action in the inheritance of fruit size in tomato. Allelic accumulation appears to have made major contributions to fruit size increment. The fruits at the early generations had fewer fruit size determining alleles as implicated by the minimal initial incremental rate from the F_1 to F_5 generation. The period of perceptible incremental rate in fruit size coincided with the period of maximum allelic accumulation (F_6 to F_9). After the F_9 generation there were indications of exhaustion of the number of fruit size determining alleles as the incremental rate dropped considerably. The similarity in the mean values of the F_9, F_{10}, F_{11} and F_{12} populations suggests homogeneity among the descendants and selection beyond these generations would not be meaningful.

In addition to fruit size increment over the F_{12} generation, correlations between the traits and number of fruits and weight of fresh fruit weight per plant were also determined. As expected, most of the correlation values between single fruit weight and fruit numbers were negative. This relationship can be explained from yield plasticity view point (that is the fewer the number of fruits, the larger the individual fruit size and conversely, the more the number of fruits the smaller the size of the individual fruits). Both traits are interrelated and trade-offs exist between them. This means that improving individual fruit size would lead to a decline in the number of fruits per plant. Any breeding process aimed at improving both traits must therefore, strike a balance between them as both traits are important determinants of yield and the eventual returns to investment. The relationship between single fruit weight and fresh fruit yield per plant conveyed the most interesting result. Single fruit weight had significant and positive association with fresh fruit yield at the advance generations (F_7 to F_{12}). This contrasted with the association observed between the two traits at the early generations (F_1 to F_6) where the correlation values were mostly negative and non significant. Two deductions can be made from these observations. The first is that selection for simultaneous improvement of both traits is only reliable at the advanced generations. Secondly, the selections for improved fruit size at the early generations were effective as they resulted in the accumulation of alleles for fruit size increment over time.

ACKNOWLEDGEMENT

REFERENCES

Allard RW (1960). Pedigree Method of Plant breeding. Principles of Plant Breeding. John Wiley and Sons Inc. New York, pp 115-116.
Alpert KB, Grandillo S, Tanksley SD (1995). *fw 2. 2* a major QTL controlling fruit weight is common to both red- and green-fruited tomato species. Theort. Appl. Genet., 91:994- 1000.
Barrero LS, Tanksley SD (2004). Evaluating the genetic basis of multiple locule fruit in a broad cross section of tomato cultivars. Theor. Appl. Genet., 109, 669-679.
Caldwell JD, Moore JN (1982). Inheritance of fruit size in the cultivated tetraploid blackberry (Rubus (Tourn.) *L. subgenus* Eubatus. J. Amer. Soc. Hort. Sci., 107(4): 628-33.
Casali VWD, Tigchelar EC (1975). Compared simulation studies comparing pedigree, bulk and single seed decent selection in self-pollinated populated populations. J. Am.. Sci., 364-367.
Causse MV, Saliba-Colombani, Lesschaevel I, Buret M (2001). Genetic analysis of organoleptic quality in fresh market tomato. 2. Mapping QTLs for sensory attributes.Theor. Appl. Genet., 102, 273-283.
Causse M, Saliba-Colombani V, Lecomte L, Duffe P, Rousselle P, Buret M (2002). QTL analysis of fruit quality in fresh market tomato: a few chromosome regions control the variation of sensory and instrumental traits. J. Exp. Bot., 53, 2089-2098.
Chen FQ, Foolad MR (1998). A molecular linkage map of tomato based on a cross molecular map of tomato. Genome, 42:94 -103.
Chen FQ, Foolad MR, Hyman J, St Clair DA, Beelaman RB (1999). Maping of QTLs for lycopene and other fruit traits in a *Lycopersicon esculentum x L. pimpinellifolium* cross and comparison of QTLs across tomato species. Mol. Breed., 5(3): 283-299.
Foolad MR, Lin GY (1999). Genetic potential for salt tolerance during

germination is *Lycopersicon* species. Hortscience, 32:296-300.

Frary A, Doganlar S, Frampton A, Fulton T, Uhlig J, Yates H, Tanksley S (2003). Fine mapping of quantitative trait loci for improved fruit characteristics from *Lycopersicon chmielewskii* chromosome 1. Genome, 46, 235-243.

Fulton TM, Bucheli P, Voirol E, Lopez J, Petiard V, Tanksley SD (2002). Quantitative trait loci (QTL) affecting sugars, organic acids and other biochemical properties possibly contributing to flavor identified in four advanced backcross populations Euphytica, 127, 163-177.

Grandillo S, Tanksley SD (1996a). QTL analysis of horticultural traits differentiating the cultivated Tomato from the closely related species, *Lycopersicon pimpinellifolium*. Thoer. Appl. Genet., 92: 935-951.

Grandillo S, Tanksley SD (1996b). Genetic analysis of RELPs, GATA microsatellites and RAPDs in a Cross between *L. esculentum* and *L. pimpinellfolium.* Thoer. Appl. Genet., 92:957-965.

Liu J, Van Eck J, Cong B, Tanksley SD (2002). A new class of regulatory genes underlying the cause of pear-shaped tomato fruit. Proc. Natl. Acad. Sci. USA, 99: 13302-13306.

Miller JC, Tanksely SD (1990). RELP analysis of phylogenetic relationships and genetic variation in the genus *Lycopersicon.* Theor. Appl. Genet., 80: 437-448. Web of Science.

Miller EP, Sherman WB, Topp BL (1991). Fruit size increase in melting vs. non melting peaches. Proc. Fla. State. Hort. Soc., 104: 9-12.

Nesbitt TC, Tanksley SD (2001). *fw2.2* directly affects the size of developing tomato fruit, with secondary effects on fruit number and photosynthate distribution. Plant Physiol., 127, 575-583.

Palmer JD, Zamir D (1982). Chloroplast DNA evolution and phylogenic relationships in *Lycopersicon* Species. Proc. Natl. Acad. Sci., 79: 5006-5010.

Powers L (1951). Gene analysis by the partioning method when interactions of genes are involved. Bot. Gaz., 113: 1-23.

Saliba-Colombani V, Causse M, Langlois D, Philouze J, Buret M (2001). Genetic analysis of organoleptic quality in fresh market tomato. 1. Mapping QTLs physical and chemical traits. Theor. Appl. Genet., 102, 259-272.

Semel Y, Nissenbaum J, Menda N, Zinder M, Krieger U, Issman N, Pleban T, Lippman Z, Gur A, Zamir D (2006). Over dominant quantitative trait Loci for yield and fitness in tomato. Proc. Natl. Acad. Sci. USA, 103, 12981-12986.

Tanksley SD (2004). The genetic, development and molecular base of fruit size and shape variation in tomato. The Plant Cell, 16: S181-S189.

Tanksley SD, Grandillo ST, Fulton M, Zamir D, EshedY, Lopez J, Beck BT (1996). Advance backcross QTL analysis in a cross between an elite processing line of tomato and its wild relative *L. pimpinellifolium*. Theor. Appl. Genet., 92: 213-223.

Toyama TK (1961). The breeding behavior of selected varieties of the raspberry especially with Respect to certain fruit characters which may be related seediness. Diss. Abstr., 22: 384.

Uguru MI, Atugwu AI (2001). Comparative study on the somatic chromosome number, yield and disease incidence of cultivated tomatoes and their wild relative. Agro-Science, 1(2): 52-58.

Uguru MI, Onwubiko CN (2002). Inheritance of fruit size in *Lycopersicon* species. Agro-Science, 3(1): 13-19.

Van der Knaap E, Tanksley S (2001). Identification and characterization of a novel locus controlling early fruit development in tomato. Theor. Appl. Genet., 103: 353-358.

Van der Knaap E, Lippman ZB, Tanksley S (2002). Extremely elongated tomato fruit controlled by four loci with epistatic interactions. Theor. Appl. Genet., 104: 241-247.

Van der Knaap E, Tanksley S (2003). The making of a bell pepper-shaped tomato fruit: Identification of loci controlling fruit morphology in Yellow Stuffer tomato. Theor. Appl. Genet., 107: 139-147.

Warnock SJ (1988). A review of taxonomy and phylogeny of the genus, *Lycopersicon*. Hortscience, 23: 669-671.