African Crop Science Journal, Vol. 30, No. 4, pp. 441 - 453
ISSN 1021-9730/2022 $4.00

DOI: https://dx.doi.org/10.4314/acsj.v30i4.4

ANALYSIS OF TOMATO AGRONOMIC TRAITS USING GENERATION MEAN

F.K. KATHIMBA, P.M. KIMANI, R.D. NARLA and L.M. KIRIIKA[1]

Department of Plant Science and Crop Protection, University of Nairobi, P. O. Box 29053-00625, Nairobi, Kenya
[1]Department of Horticulture and Food Security, Jomo Kenyatta University of Agriculture and Technology, P. O. Box 6200-00620, Nairobi, Kenya
Corresponding author: francisgath@gmail.com

(*Received 29 July 2022; accepted 2 September 2022*)

ABSTRACT

Information on inheritance of agronomic traits and lack of tomato (*Solanum lycopersicum* L.) a robust breeding programme in Kenya, has led to dependency on imported tomato varieties. The objective of this study was to assess the inheritance of growth attributes of tomato lines in Kenya and identify cross family with great potential for further breeding. Six generations; namely P1, P2, F1, F2, BC1P1 and BC1P2, were developed from five parental lines. A split-plot design with crosses as main plots and generations as subplots was used in two sites (Kabete Field Station and Mwea Research Station), located in Kenya. Cross Roma VF x AVTO1424 and Roma VF x AVTO1314 were the earliest (33 days) to reach 50% flowering; while BC1P2, of Roma VF (38 days) was the latest to flower. Mwea Station had plants with the tallest plants, with a mean height of 62 cm at 50% flowering, compared to Kabete Station with a mean height of 48 cm. A significant increase (>10%) in plant height was registered in F_1 generations compared to parental lines. Plant height at maturity across the environments ranged from 82 cm for shorter parent, Roma VF, to 120 cm for taller offspring BC1P1. Significant genotype x environment interactions were observed in Roma VF x AVTO1314 and Roma VF x AVTO1429 for days to 50% flowering, plant height, and number of trusses per plant. The importance of gene effects for agronomic trait inheritance was in additive and dominance-additive portions, which implied that traits were inherited.

Key Words: Additive, dominance, *Solanum lycopersicum*

RÉSUMÉ

Les informations sur l'hérédité des traits agronomiques et le manque de tomate (*Solanum lycopersicum* L.), un programme de sélection robuste au Kenya, ont conduit à une dépendance vis-à-vis des variétés de tomates importées. L'objectif de cette étude était d'évaluer l'hérédité des attributs de croissance des lignées de tomates au Kenya et d'identifier les familles croisées avec un grand potentiel de sélection. Six générations ; à savoir P1, P2, F1, F2, BC1P1 et BC1P2, ont été développés à partir de cinq lignées parentales. Une conception en parcelles divisées avec des croisements comme parcelles

principales et des générations comme sous-parcelles a été utilisée dans deux sites (Kabete Field Station et Mwea Research Station), situés au Kenya. Les croisements Roma VF x AVTO1424 et Roma VF x AVTO1314 ont été les plus précoces (33 jours) à atteindre 50 % de floraison ; tandis que BC1P2, de Roma VF (38 jours) était la dernière à fleurir. Mwea Research Station avait des plantes avec les plantes les plus hautes, avec une hauteur moyenne de 62 cm à 50 % de floraison, par rapport à Kabete Field Station avec une hauteur moyenne de 48 cm. Une augmentation significative (> 10%) de la hauteur des plantes a été enregistrée dans les générations F_1 par rapport aux lignées parentales. La hauteur des plantes à maturité dans tous les environnements variait de 82 cm pour le parent plus court, Roma VF, à 120 cm pour la progéniture plus grande BC1P1. Des interactions génotype x environnement significatives ont été observées chez Roma VF x AVTO1314 et Roma VF x AVTO1429 pour les jours jusqu'à 50 % de floraison, la hauteur de la plante et le nombre de fermes par plante. L'importance des effets des gènes pour l'hérédité des traits agronomiques était dans les portions additives et dominance-additifs, ce qui impliquait que les traits étaient hérités.

Mots Clés : Additif, dominance, *Solanum lycopersicum*

INTRODUCTION

Tomato (*Solanum lycopersicum* L.) represents 7% of the horticulture and 14% of vegetables produced in Kenya (Ochilo *et al.,* 2019). Demand for quality tomato fruits and diversity in agronomic traits by Kenyan consumers and growers continues to increase, hence the need to improve the existing cultivars to respond to the demand (Agong *et al.,* 2001). A major drop in tomato production (30%) was registered against increased increase consumption of more than 41.7% per *capita* (KNBS, 2019). Tomato productivity decline in Kenya has led to price fluctuations, in turn causing purchase of more than 27, 000 metric tonnes from neighbouring countries (Mwangi *et al.,* 2020).

Generation means analysis had been widely adopted in assessing additive and dominance genetic effects and their interactions related to the expression of quantitative traits (Mather and Jinks, 1982). Generation mean analysis has been used to determine yield (Bhatt *et al.,* 2001), cold tolerance (Foolad and Lin, 2001), vitamin C and total soluble sugars (Bhatt *et al.,* 2001), and acyl sugar content (Resende *et al.,* 2002) in tomato. Morphological and agronomic traits such as plant height, number of trusses, days to 50% flowering and inter truss spacing, provide essential information for tomato breeding aimed at crop improvement (Valls, 2007). Huang *et al.* (2012) revealed that morphological and agronomic traits do not only provide consumer satisfaction and quality raw materials for the processing industry, but also enhance the competitiveness of tomato crop in the horticultural sector. However, in Kenya, there is minimum breeding programme undertaken by either public sector like KALRO or private companies such as Monsanto and Syngenta to back up production. This has led to limited availability of information on tomato breeding (Kenneth, 2016).

Improved tomato cultivars, especially hybrids are more productive because of the commonly reported fruit yield heterosis of 20 to 50% (Kumar *et al.,* 2017), which make farmers interested in growing F_1 varieties. Besides the high yields, hybrids exhibit other advantages such as early maturity, resistance to pests and diseases, growth vigour that help overcome abiotic stresses like drought and big fruit size of high quality (Goffar *et al.,* 2016).

It is worth mentioning that lack of varieties adapted to different agro-ecological zones across the country poses a challenge to farmers growing hybrid tomatoes (Goffar *et al.,* 2016). This, therefore, means that demand-led breeding of locally adapted improved varieties, especially hybrids with market preferred traits, coupled with within seed production, will ensure that these varieties are more easily accessible and affordable by farmers than the imported hybrid varieties

(Fufa *et al.,* 2009). The objective of this study was to assess the inheritance of growth attributes of tomato lines in Kenya and identifying cross family with great potential for further breeding.

METHODOLOGY

Experiment sites. A study was carried out from 2018 to 2019 during the long and short season, at Kabete Field Station and Mwea Research Station. Kabete Field Station is situated at 01°15'S; 036°44'E with and elevation of 1820 m above sea level (masl). It receives mean annual rainfall of 1059 mm in a bimodal pattern, and temperatures ranging from 12.3 to 22.5 °C. Soils are deep and well-drained humic nitisols with a pH range 5.0 to 5.4 (Lengai, 2016).

Mwea Research Station is located in the Agro-ecological zone II, situated at 0°41'S; 037°21'E and altitude 1247masl. It received mean annual rainfall of 973 mm also in a bimodal pattern. Temperatures range from 15.6 to 28.6 °C and soils are well drained Niti-rhodic ferrosols with a pH of about 5.1 (Kathimba *et al.,* 2022).

Experimental design. The experiment involved development of study populations and field evaluations of parental lines and their progenies. Study populations were generated between April and September, 2018 at Kabete Field Station. Hybridisation of five parental lines in 10 x 10 half diallel mating design, excluding reciprocals, was carried out from April-August 2018 and backcrosses to both parents from September-December 2018, also at Kabete Field Station, following a modified protocol of Griffing (1956).

Plant materials. The study used five tomato genotypes, i.e., three genotypes, namely AVT01424, AVT01429 and AVT01314 sourced from the World Vegetable Centre (AVRDC), a commercial variety Roma VF acquired from Continental Seeds Co. Limited and Valoria selection from farmers in Kirinyaga County. AVTO1429 is indeterminate, while AVTO1424 and AVTO1314 are semi-determinate, thus flower and mature early, making them suitable for open field cultivation (Fufa *et al.,* 2009). Commercial variety Roma VF is a determinate pure-line that flowers and matures early. Moreover, this variety is low yielding, requires staking, and lacks resistance to bacterial wilt (Kathimba *et al.,* 2022). Valoria selection is a determinate line preferred by farmers in Central Kenya, and also requires staking. Besides, this line is late flowering, late maturing and low yielding (Kathimba *et al.,* 2022).

Development of study populations. Four bi-parental crosses were developed using a half diallel mating design from Roma VF and AVTO1429, AVTAO1424, AVTO1314 and Valoria Select, giving F1 hybrids. The F1s' were backcrossed to both parents (BC1P1 and BC1P2) and also advanced to F2 at Kabete Field Station, during September - December, 2018; following a protocol by Sharma (1988). Six generations were developed for each cross; namely P1, P2, F1, F2, BC1P1 and BC1P2. Field trial evaluations were carried out at Kabete Field and Mwea Research Stations during the long rain season, April-August, 2019.

Evaluation of study populations. Seedlings were raised in germination trays with 204-cells (3.5 cm deep and 2.5 cm wide) containing peat moss as planting media, at Kabete Field Station on 6th March 2019. Trays were sown with one seed per cell and raised under a net-house. Seedlings were watered daily in hot weather (23-28 ^{o}C) and once on a two-day interval in cool weather (15.6-23 ^{o}C) to provide sufficient moisture for growth.

Seedlings having four true leaves were hardened by reducing watering to 25 days after sowing. Netting was removed to expose the seedling to sunlight to become stocky and sturdy. Seedlings were watered 12 hours before transplanting to the field. One-month-old seedlings, having pencil thickness, were then transplanted to open fields for evaluations at Kabete Field and Mwea Research Stations

on 8th April 2019. Transplanting was done early in the morning to reduce the transplanting shock; and watered immediately as described in KALRO (2016) manual.

A split-plot design with four families as main plots and the six generations as subplots, replicated three times, was established. The main plots had a configuration of 36 m x 54 m, with 18 subplots of 2 m x 3 m. Each subplot had four rows, each having five plants. The number of plants per plot varied with generations from 20 to 200 plants because segregating a population requires more plants to allow definitive evaluation of the traits. The segregating F_2 and backcross populations were assigned more rows than the non-segregating F_1 and parental populations as follows; 40 rows with 200 plants for F_2 generation, 20 rows with 100 plants for backcross generations and 4 rows with 20 plants for each non-segregating population (P_1, P_2 and F_1) following a modified procedure of Checa *et al.* (2006).

Crop management. The crop was maintained weed-free by hand-weeding at 2-3 weeks intervals; and mainly rain-fed and supplemented with drip irrigation. Di-ammonium phosphate (DAP) fertilisers (18: 46: 0) and N: P: K (17: 17: 17) were each applied at the rate of 12 g plant^{-1} during transplanting. The plants were top-dressed with calcium ammonium nitrate (CAN) at the rate of 5 g plant^{-1} when they were 25 cm tall, and 10 g plant^{-1} at 55 days after transplanting. Fertiliser application was to ensure nutrient levels did not limit proper crop growth (KALRO, 2016).

Metalaxyl-M and Propineb (700 g kg^{-1}) at the rate of 50 g per 20 litres of water was applied at an interval of two weeks, to manage early and late blights. Imidacloprid (100 g l^{-1}) and betacyfluthrine (45 g l^{-1}) were applied at the rate of 1.5 litres ha^{-1} and Thiamethoxam at the rate of 8 g per 20 litres of water were used to control aphids, whiteflies and leaf miners during the crop growth cycle.

Data collection. Data on 50 F_1 plants, 50 plants of each parent in a cross, 300 plants of each backcross, and 600 plants of the F_2 generation were collected following Sharma's (1988) protocol. Parameters assessed included height of plant, duration to 50% flowering, inter truss spacing and the number of trusses per plant.

Plant height was measured at 50% flowering and at physiological maturity from soil base up to main stem of the plant, using a measuring tape. The number of days to 50% flowering was determined when half of plants in a plot had one flower. The number of trusses per plant was assessed from a random sample of six plants per plot, and averaged at the harvesting stage. Inter truss spacing was determined using a measuring tape, as the distance between two trusses. Six random plants were taken as a representative sample per plot and averaged.

Data analysis. Data for agronomic traits for each generation and cross comparison were subjected to analysis of variance (ANOVA) using GenStat software 15th edition. Means were separated using Tukey's procedure for multiple comparisons ($P<0.05$), following a protocol of Checa *et al.* (2006).

The significantly different variables showed by orthogonal contrasts between parents P_1 and P_2 were further subjected to generation mean analysis (GMA) to establish if the respective traits are quantitatively or qualitatively inherited, using the methodology proposed by Checa *et al.* (2006). Segregation ratios were subjected to chi-square tests to establish goodness-of-fit for observed ratios. The outcome was compared with the observed results to determine differences due to chance or other traits using Equation 1.

$$\text{Chi-square} = (\text{Observed} - \text{Expected})^2/\text{Expected} \quad \text{Equation 1}$$

Hence, $x^2 = \Sigma [(O-E)^2 / E]$

Where:

x^2 = Chi-square, O = Observed and E = Expected

Analysis of generation means. Analysis of generation means followed the approach of Sharma (1988) as follows, *viz*:

(i) Development of generation means. This was calculated by summing the number of observations for a trait in each generation and dividing it by the total number (n) of sampled plant i.e. $\bar{X}$ =T/n.

(ii) Calculating the variance and variance of mean for each generation. Variance for each generation = Σ SS/ (n-1) and Variance of mean for each generation was $\bar{V}$=V/n. Epistasis affects the estimation of additive and dominance components of variance. Scaling tests were used to determine epistatic effects for traits studied and appropriate model for genetic analysis. Four scales A, B, C, D were used to determine the presence of an additive, and dominance effects, and additive x additive and additive x dominance interactions. Computation of the scales was achieved as:

A= $P^_1$ +$F^_1$-2B^C_1, B=$P^_2$+$F^_1$-2B^C_2, C=$P^_1$+$P^_2$+2 $F^_1$-4 $F^_2$ and D=2$F^_2$-B^C_1-B^C_2 ..... Equation 2

Where:

A= additive x dominance (P_1), B= additive x dominance (P_2); C= dominance x dominance; D=additive x additive. Test for significance of each scale was carried out using the equation:

t (A) = A/SE (A) ……...…… Equation 3

Where:

A = additive x dominance (P_1) and SE = Standard error. This was done for each scaling test. Significance of even one of the 4 scales showed the presence of epistasis, therefore necessitated analysis of components of means. Analysis of components of means in crosses with epistasis was conducted using 6-parameters model since backcrosses were used following a procedure of (Sharma, 1988).

RESULTS

Time to 50% flowering. The six generations of cross Roma VF x AVTO1429 and Roma VF x AVTO1424 had no significant difference (P<0.05) in all sites (Table 1). Significant differences were, however, observed in cross Roma VF x AVTO1314 and Roma VF x Valoria select at (P<0.05). Cross Roma VF x AVTO1424 and Roma VF x AVTO1314 had an equal mean of 33 days; while Roma VF x AVTO1429 and Roma VF x Valoria select had a mean of 34 and 35, respectively (Table 2). Despite the marginal differences in Roma VF x AVTO1314 six generations, the F_1 hybrid reached flowering within 32 days; whereas P_1 (Roma VF) reached flowering three days later (35 days). Similarly, F_1 hybrid in cross Roma VF x Valoria select flowered within 34 days, which was significantly different from BC1P2, that flowered within 38 days (Table 2). Both Kabete and Mwea Stations showed marginal differences in the days to 50% flowering in all the crosses (P<0.05).

There was a genotype by environment interaction for cross Roma VF x AVTO1314 and Roma VF x Valoria select for the two environments (P<0.01), but none in cross Roma VF x AVTO1429 and Roma VF x AVTO1424. All the scaling tests showed significant differences (P<0.01) in cross Roma VF x AVTO1429. From the scaling tests, significant interactions in additive x additive (1.76**) and additive x dominance (-2.04**) were recorded (Table 3). Significant additive

TABLE 1. Mean squares for plant height at 50% flowering at Kabete and Mwea, 2019

Source	Df	Mean squares for plant height at 50% flowering			
		Cross 1 (Roma VF x AVTO1429)	Cross 2 (Roma VF x AVTO1424)	Cross 3 (Roma VF x AVTO1314)	Cross 4 (Roma VF x Valoria select)
Replication	2	826.97	446.12	200.62	639.67
Environments[ß]	1	1848.12	2136.13*	2560.76**	1062.71
Residual	2	179.77	70.07	27.69	183.44
Generations	5	118.35**	97.08**	46.41	48.52
Environment. Generations	5	45.67	64.82*	22.46	20.00**
Residual	35	21.41	17.64	28.95	9.08

[ß]Environments were Kabete and Mwea long seasons, 2018. *, ** Significant at 5 and 1 percent probability levels, respectively

(-0.08**) and dominance (-0.63**) effects were also recorded for cross Roma VF x AVTO1429 (Table 3). Therefore, further analysis using the 6-parameter model was carried out since backcrosses were used. Roma VF x AVTO1429 showed presence of epistasis. Results showed that a combined gene effect of 3.6 was higher than the interaction components of 2.29 put together (Table 4).

Plant height at 50% flowering. Plant height varied significantly in the six generation, for crosses Roma VF x AVTO1429, Roma VF x AVTO1424 and Roma VF x Valoria select; but not in the six-generation of cross Roma VF x AVTO1314 (Table 1). Plant height also showed highly significant differences between Kabete Field and Mwea Research Stations; in crosses Roma VF x AVTO1424 at (P<0.05) and Roma VF x AVTO1314 at (P<0.01). With the exception of cross Roma VF x AVTO1424 having significant variations at (P<0.05) for interactions between the genotypes and each of the two environments, all the other crosses had none.

Results showed that for all generation in the four crosses, Mwea Research Station had the taller plants at 50% flowering than Kabete Field Station. Except for the six generations of cross Roma VF x AVTO1424, the rest of the crosses had no significant difference (P<0.05) for plant height at 50% flowering (Table 1). Both P_2 in Roma VF x AVTO1429 and Roma VF x AVTO1424 had short plant height at 50% flowering; whereas the tallest were BC1P1 and P_1 with 67.04 and 59.60 cm, respectively (Table 2). Besides, a significant increase (>10%) in plant height at 50% flowering was recorded in F_1 generation of all crosses, compared to parental genotypes. Hybrid Roma VF x AVTO1429 had the tallest plants (63.76 cm); while F_2 hybrids in all the crosses had shorter plants at Kabete Field Station ranging from 41.55 to 52.68 cm, than at Mwea Research Station which ranged from 53.37 to 68.58 cm (Table 2).

The scaling tests showed significant differences at (P<0.01) in cross Roma VF x AVTO1429 (Table 3). The scaling tests showed additive effects of -9.76**; dominance effect of -5.58**; and additive x additive interaction effects of -0.8** (Table 3). Therefore, further analysis using a 6-parameter model was carried out since backcrosses were used. Roma VF x AVTO1429 showed presence of epistasis. Results showed that a combined gene effect of 10.85 was higher than the interaction components of 0.85 put together (Table 4).

TABLE 2. Mean performance of parental accessions in the 4 crosses for days to 50% flowering, Plant height at 50% flowering, plant height at maturity, inter truss spacing and No. of trusses per plant evaluated at Kabete and Mwea in 2018

Crosses	Generation	Days to 50% flowering			Plant height at 50% flowering (cm)			Plant height at maturity			Inter truss spacing (cm)			No. of trusses per plant		
		Kabete	Mwea	Mean	Kabete	Mwea	Mean	Kabete	Mwea	Mean	Kabete	Mwea	Mean	Kabete	Mwea	Mean
Cross Roma VF x AVTO1429	P1	33	35	34	56.35	64.76	60.56	84.2	86.5	85.3	16.03	18.43	17.23	18	19	18
	P2	34	35	34	47.54	59.75	53.64	82.5	81.9	82.2	19.05	17.73	18.39	18	20	19
	F_1	33	32	32	54.18	73.33	63.76	95.1	91.6	93.4	17.08	19.21	18.37	21	23	22
	F_2	33	33	33	52.68	68.58	60.63	104.1	95.8	99.9	16.93	19.8	18.15	23	26	24
	BC_1P_1	33	35	34	62.74	71.35	67.04	134.1	105	119.5	17.76	20.58	19.17	21	22	22
	BC_1P_2	33	34	34	50.64	72.34	61.49	97.5	104.5	101	16.35	21.47	18.91	20	22	21
	Mean	33.12	34.04	34	54.02	68.35	61.19	99.6	94.2	96.9	17.2	19.54	18.37	20.14	22.03	21.08
	CV (%)			3.4			7.6			8.6			14.4			10
	LSD (5%)			2.48			14.59			28.25			6.78			4.06
Cross Roma VF x AVTO1424	P1	34	34	34	47.37	71.83	59.6	84	85.5	84.7	15.73	17.24	16.49	17	20	18
	P2	34	35	35	43.11	55.56	49.33	78.5	73.3	75.9	13.23	14.67	13.95	17	21	19
	F_1	33	32	33	50	68.73	59.37	82.4	90.4	86.4	15.33	19.11	17.22	19	23	21
	F_2	32	33	33	46.02	59.95	52.98	95	79	87	14.32	15.86	15.09	18	20	19
	BC_1P_1	34	35	34	51.59	56.67	54.13	83.5	93.1	88.3	15.28	19.31	17.3	18	20	19
	BC_1P_2	33	34	34	44.05	61.83	52.94	81.8	81.1	81.4	15.22	16.32	15.77	18	21	19
	Mean	33.44	33.96	33.7	47.02	62.43	54.72	84.2	83.7	83.9	14.85	17.08	15.97	17.78	20.89	19.34
	CV (%)			3.3			7.7			17.4			8.7			11.1
	LSD (5%)			2.4			9.52			22.74			3.82			5.02

TABLE 2. Contd.

Crosses	Generation	Days to 50% flowering			Plant height at 50% flowering (cm)			Plant height at maturity			Inter truss spacing (cm)			No. of trusses per plant		
		Kabete	Mwea	Mean	Kabete	Mwea	Mean	Kabete	Mwea	Mean	Kabete	Mwea	Mean	Kabete	Mwea	Mean
Cross Roma VF x AVTO1314	P1	35	36	35	47.92	58.73	53.33	83.3	91	87.2	15.3	20.25	17.78	17	20	18
	P2	33	35	34	49.05	67.3	58.17	74.9	83.2	79	14.49	16.36	15.42	17	20	18
	F_1	33	30	32	47.38	69.21	58.29	76.9	84.7	80.8	13.94	18.04	15.99	21	21	21
	F_2	33	34	34	42.85	59.76	51.3	68.7	73.6	71.1	14.83	15.79	15.31	17	20	18
	BC_1P_1	34	34	34	49.32	63.61	56.46	79.6	85.2	82.4	15.97	17.52	16.74	17	21	19
	BC_1P_2	34	33	33	46.7	65.81	56.25	81.7	89.7	85.7	13.97	16.62	15.29	18	20	19
	Mean	33.79	33.6	33.69	47.2	64.07	55.64	77.5	84.6	81	14.75	17.43	16.09	17.73	20.1	18.91
	CV (%)			3.4			9.7			7.7			8.2			5.9
	LSD (5%)			1.82			9.11			9.78			2.27			4.28
Cross Roma VF x Valoria FS	P1	34	36	35	41.08	57.06	49.07	75.86	68.68	72.27	15.7	14.27	14.98	17	18	17
	P2	34	37	35	43.24	55.56	49.4	72.52	81	76.76	15.47	15.08	15.27	16	20	18
	F_1	33	36	34	49.87	60	54.94	71.33	77.95	74.64	14.04	15.96	15	17	20	18
	F_2	34	36	35	41.55	53.57	47.56	79.16	75.29	77.23	15.23	15.6	15.41	17	20	18
	BC_1P_1	33	36	35	44.48	54.33	49.4	75.71	75.83	75.77	14.05	14.78	14.42	19	20	19
	BC_1P_2	34	41	38	44.41	49.33	46.87	77.6	80.17	78.88	13.56	15.47	14.52	18	20	19
	Mean	33.66	36.92	35.29	44.11	54.97	49.54	75.36	76.49	75.93	14.67	15.19	14.93	17.26	19.53	18.4
	CV (%)			3.8			6.1			4.6			8.7			8.7
	LSD (5%)			3.17			15.78			6.43			2.08			2.61

LSD = Least significant differences of means at P<0.05), CV = Coefficient of variation. Environments were Kabete and Mwea long rains, 2018

TABLE 3. Scaling tests for generations in tomato for different growth traits in cross (Roma VF x AVTO1429) that showed significance

Scales	Days to 50% flowering	Plant height at 50% flowering (cm)	Plant height at maturity	Inter truss spacing (cm)	No. of trusses per plant
A= ($P^_1$ +$F^_1$-2B^C_1)	-0.08**	-9.76**	-60.3ns	-2.74ns	-2.61**
B= ($P^_2$+$F^_1$-2B^C_2)	-0.63**	-5.58**	-26.4ns	-1.06ns	-1.66ns
C= ($P^_1$+$P^_2$+2 $F^_1$-4 $F^_2$)	1.76**	-0.8**	-45.3ns	-0.24ns	-16.21ns
D= ($2F^_2$-B^C_1-B^C_2)	-2.04**	-7.27ns	-20.7ns	-1.78**	5.97ns

*, ** Significant at 5 and 1 percent probability levels, respectively

Plant height at maturity. Plant height at maturity demonstrated significant differences (P<0.01) across the six generations of crosses Roma VF x AVTO1429 and Roma VF x AVTO1314 (Table 1). These variations (P<0.01) were recorded at both Kabete and Mwea Stations. Significant interactions between the two sites and the genotypes for crosses Roma VF x AVTO1429 (P<0.05) and Roma VF x Valoria select (P<0.01) were observed (Table 1). Results showed that plant height at maturity for parents in all the crosses ranged from 72.27 to 91.00 cm, with Roma VF as the shortest parent recording <83 cm in all cross (Table 2). Similarly, F_1 hybrids in all the crosses had plant heights ranging from 71.33 to 95.10 cm at both study stations. Also, the F_2 hybrids had similar height at maturity that ranged from 71.10 to 104.10 cm in all crosses, at both study stations. Results for F_1 and F_2 hybrids were high across the crosses. Plant height at maturity across the two environments ranged from 82.20 cm, recorded in parent Roma VF to 119.50 cm recorded in offspring, BC1P1 (Table 2).

Due to insignificant differences (P<0.01) in additive x additive and additive x dominance interaction and additive effects and dominance effects (Table 3), further analysis of components of means was not necessary. However, analysis of component of mean was carried out using a 6-parameter model since backcrosses were used. Results showed a combined gene effect of 13.93, which was significantly higher than the interaction components (Table 4).

Inter truss spacing. Inter truss spacing across the two study stations ranged from 17.23 cm for parent P (AVTO1429) of cross Roma VF x AVTO1429, to 19.17 cm offspring F1 x BC1P1 (Table 2). For cross Roma VF x AVTO1424, the range was from 13.95 cm for parent P, (Roma VF) to 17.30 cm for offspring, F1 x BC1P1; while cross Roma VF x AVTO1314 ranged from 15.29 cm for offspring, BC1P2, to 17.78 cm for parent (AVTO1314). The inter truss spacing across the two study stations for cross Roma VF x Valoria select ranged from 14.42 cm for offspring, BC1P1 to 15.41 cm offspring, BC1P2, (Table 2). Results showed that all the scaling tests had no significant differences at (P>0.01) for all the crosses (Table 3). However, significant differences in additive x dominance interaction at (P<0.01) for cross Roma VF x AVTO1429 were recorded. The scaling test showed presence of additive x additive interaction, represented by -1.78** (Table 3). Therefore, further analysis using a 6-parameter model was carried out since backcrosses were used. Cross Roma VF x AVTO1429 showed epistasis. Results showed that the combined gene effects (3.0) were

TABLE 4. Gene effects on cross Roma VF x AVTO1429 for all the evaluated traits using a 6-parameter model

Gene effects/ Components	at df.	Plant height at maturity			Plant height at 50% flowering (cm)			Days to 50% flowering			Number of trusses per plant			Inter truss spacing (cm)		
		Expectation/ Estimate	Standard error	t (gene effect/ SE)	Expectation/ Estimate	Standard error	t (gene effect/ SE)	Expectation/ Estimate	Standard error	t (gene effect/ SE)	Expectation/ Estimate	Standard error	t (gene effect/ SE)	Expectation/ Estimate	Standard error	t (gene effect/ SE)
Mean	629	99.9	1.43	69.69**	60.63	0.64	94.49**	32.87	0.13	247.74**	24.41	0.34	70.83**	18.15	0.24	76.054**
Additive effect	502	18.5	3.15	5.87**	5.55	1.38	4.03**	0.26	0.28	0.91ns	0.27	0.6	0.45ns	0.26	0.58	0.45ns
Dominance effect	1,506.00	51.05	6.34	8.06**	21.2	3.11	6.82**	2.28	0.85	2.69**	-8.28	1.96	-4.21**	4.12	1.61	2.55**
Add. x Add. Interaction	1,131.00	41.4	8.52	4.86**	14.54	3.76	3.86**	4.08	0.78	5.24**	-11.94	1.83	-6.52**	3.56	1.5	2.38ns
Add. Dom. Interaction	52	33.9	6.78	5.00**	4.18	3.12	1.34ns	1.06	0.69	1.54ns	0.95	1.39	0.68ns	1.68	1.36	1.23ns
Dom. x Dom. Interaction	1,381.00	-128.1	14.52	-8.82**	-29.88	6.88	-4.35**	-6.4	1.43	-4.49**	7.67	3.12	2.46ns	-7.36	2.77	2.65**

lower than the interaction components (6.26) put together (Table 4).

Truss number per plant. Significant difference across the six generations of cross Roma VF x AVTO1429 and Roma VF x AVTO1314 for this trait (P<0.01) were recorded (Table 1). Interactions between each of the two study stations and the genotypes in all the crosses except Roma VF x Valoria select were significantly different (P<0.05). Number of trusses plant^{-1} across the two study stations ranged from 18 trusses for parent P•(AVTO1429) of cross Roma VF x AVTO1429 to 24 trusses in offspring F, and from 18 trusses for parent P (AVTO1424) of cross Roma VF x AVTO1424 to 21 trusses in offspring F_1 (Table 2). Similarly, the number of trusses per plant across the two environments ranged from 18 trusses for parent P, (Roma VF) of cross Roma VF x AVTO1314 to 21 trusses in offspring F_1 and from 17 trusses for parent P (Valoria select) of cross Roma VF x Valoria select to 19 trusses in offspring BC1P1.

Results showed that all the scaling tests had no significant differences at (P>0.01) for all the crosses (Table 3). However, for cross Roma VF x AVTO1429 the scaling test for additive effects (A) was significant (P<0.01). Scaling test also showed evidence of additive x dominance interaction of -2.61** (Table 3). Therefore, further analysis using a 6-parameter model was carried out since backcrosses were used. Roma VF x AVTO1429 showed epistasis. Results showed that the combined gene effects of -3.76 were lower than the interaction components of -3.16 put together (Table 4).

DISCUSSION

The parents in each cross were contrasting for all the traits evaluated. The offspring derived from the cross-combination Roma VF x AVTO1429 were earlier flowering and maturing, taller, had greater inter truss spacing and number of trusses per plant compared to other crosses and the better parent AVTO1429. This

was because additive gene action was dominant in the inheritance of these traits.

Time to 50% flowering. A cross between late and early maturing parents leads to generation of early maturing hybrids because early maturing parents exhibit complete dominance over the late maturing parent (Goffar *et al.,* 2016). Early flowering and maturity in tomato are important traits desired for designing a tomato breeding programme. Duration to flowering and maturity was controlled by dominance gene effects (2.69**) additive x additive (5.24**) and dominance x dominance interactions (-4.49**). The six-parameter model was adopted because one cross (Roma VF x AVTO1429) showed epistasis and backcrosses were used. These results were comparable with Goffar *et al.* (2016) findings after crossing a 9 x 9 half diallel in Gazipur, Bangladesh. They recorded that epistasis, which is the non-allelic gene interaction was observed on days to 50% flowering. In addition, dominant gene effects were noted in expression of flowers/cluster and locules number.

Plant height at 50% flowering and maturity. Plant height was controlled by main gene effects and their interactions. Scaling tests showed significant additive effects of -9.76**; dominance effect of -5.58**; and additive x additive interaction effects of -0.8**. This implied that plant height was inherited in the offspring. Similar findings were confirmed (Goffar *et al.,* 2016). Findings of Gul *et al.* (2011) also reported significant fully adequate additive-dominance gene action for plant height and fruits number plant^{-1}. However, studies by Tasisa *et al.* (2017) failed to establish the additive-dominance gene effects in Ethiopia. From their experiment additive-dominance, gene interactions were evident in tomato fruit shape index and acidity that can be titrated. The reason for the observed additive-dominance gene effects in most traits studied was a failure to identify parents with far contrasting traits. The parents used were Marglobe, Roma VF and Esthete. Evaluation of genetic inheritance in Shaanix, China by Thainukul *et al.* (2017) using the six generations showed significant gene effects of all plant characters that included; number of days to 50% flowering, number of branches, flowers and fruits per cluster, height of plant and average weight of fruit.

Inter truss spacing. Inter truss spacing was controlled by the dominance gene effects and the dominance x dominance interaction components. Similar studies were conducted by Sun *et al.* (2019) to determine the length of internode using multi-generation joint analysis and polygene model. Results demonstrated that major genes influence internode length and needs early selection in the pedigree selection.

Truss number per plant. The number of trusses plant^{-1} was controlled by major dominance gene and the additive x additive interaction of polygenes. Similar studies were conducted by Goffar *et al.* (2016) to evaluate the inheritance of yield traits and related traits in tomato. The deduction was that genetic gene effects are important in the plant characters, mainly the additive and dominant components.

CONCLUSION

Desirable agronomic traits of tomato such as days to flowering, maturity, plant height, inter truss spacing and number of trusses per plant despite being influenced by many genes, environment contributes to their expression significantly. For the four crosses; Roma VF x AVTO1429, Roma VF x AVTO1424, Roma VF x AVTO1314 and Roma VF x Valoria select, significant traits that contribute most to desirable yields include number of days to 50% flowering, height of plant height, truss number and inter truss and they are influenced by the environment. Earliest flowering and maturing offspring were recorded in the the F1 hybrid

from cross Roma VF x AVTO1429. Offspring with the highest plant height was the backcross of cross F_1 x AVTO1429 BC1P1. The offspring's derived from the cross-combination Roma VF x AVTO1429 had highest inter truss spacing and number of trusses per plant. F1, F2 and BC1P1 performed better in all traits evaluated than the better parent. This study also found importance of gene effects for agronomic trait inheritance was in additive and dominance-additive portions which implied that the traits were inherited. Contribution of both parents in the subsequent generations (offspring) is vital in developing a breeding program for a particular trait

ACKNOWLEDGEMENT

The authors are grateful to Continental Seeds Company for providing financial support for this work and University of Nairobi for giving physical facilities to carry out this research work.

REFERENCES

Agong, S.G., Schittenhelm, S. and Freidt, W. 2001. Genotypic variation of Kenya tomato (*Lycopersicum esculentum* L.) germplasm. *Bioline International* 6(1):13-17.

Bhatt, R.P., Biswas, B.R. and Kumar, N. 2001. Heterosis, combining ability and genetics for vitamin C, total soluble solids and yield in tomato (*Lycopersicon esculentum*) at 1700 m altitude. *Journal of Agricultural Science* 137:71-75.

Checa, O., Ceballos, H. and Blair, M.W. 2006. Generation mean analysis of climbing ability in common beans (*Phaseolus vulgaris* L.). *Journal of Hereditry* 97(5):456-465.

Foolad, M.R. and Lin, G.Y. 2001. Genetic analysis of cold tolerance during vegetative growth in tomato, *Lycopersicon esculentum* Mill. *Euphytica* 122:105-111.

Fufa, F., Hanson, P., Dagnoko, S. and Dhaliwal, M. 2009. AVRDC - The world vegetable centre tomato breeding in sub-Saharan Africa: Lessons from the past, present work and future prospects. *In: I All African Horticulture Congress* 911: 87-98.

Goffar, M.A., Ahmed, A. and Halim, G.M.A. 2016. Inheritance mechanism of yield and yield components in tomato. *Bangladesh Journal of Agricultural Research* 41(2): 335-344.

Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel system. *Australian Journal of Biological Sciences* 9:463-493.

Gul, R., Rahman, H.U., Khalil, I.H., Shah, S.M.A. and Ghafoor, A. 2011. Estimate or heterosis in tomato (*Solanum lycopersicum* L.). *Bangladesh Journal of Agricultural Research* 36(3):521-527.

Huang, X.H., Zhao, Y., Wei, X.H., Li, C.Y., Wang, A., Zhao, Q., Li, W.J., Guo, Y.L., Deng, L.W., Zhu, C.R., Fan, D.L., Lu, Y.Q., Weng, Q.J., Liu, K.Y., Zhou, T.Y., Jing, Y.F., Si, L.Z., Dong, G.J., Huang, T., Lu, T.T., Feng, Q., Qian, Q., Li, J.Y. and Han, B. 2012. Genome-wide association study of flowering time and grain yield traits in a worldwide collection of rice germplasm. *Nature Review Genetics Journal* 44 (1): U32-U53.

KALRO. 2016. Kenya Agricultural and Livestock Research Organisation. Tomato Production Manual, Fruits and vegetables technical handbook. Retrieved from http:// www.kalro.org. Accessed on July 27, 2020.

Kathimba, F.K., Kimani, P.K., Narla, R.D. and Kiriika, L.M. 2022. Heterosis and combining ability for related traits in tomato. *African Crop Science Journal* 30(1):109-125.

Kenneth, T.O. 2016. Agro-morphological and nutritional characterization of tomato landraces (*Lycopersicon species*) in Africa. Masters of Science thesis, University of Nairobi, Kenya. 127pp.

KNBS. 2019. Kenya National Bureau of Statistics. Kenya's Facts and Figures.

Retrieved from: http://www.knbs.or.ke/news.pdf. (Accessed on June 11, 2020).

Kumar, P., Singh, N. and Singh, P.K. 2017. A study on heterosis in tomato (*Solanum lycopersicum* L.) for yield and its component traits. *International Journal of Current Microbiology and Applied Science* 6(7):1318-1325.

Lengai, G.W.M. 2016. Efficacy of plant extracts and antagonistic fungi as alternatives to synthetic pesticides in management of tomato pests and diseases. Doctoral dissertation, University of Nairobi, Kenya. 99pp.

Mather, K. and Jinks, I.L. 1982. Biometrical Genetics. Third Edition. Champan and Hall, London. 69pp.

Mwangi, T.M., Ndirangu, S.N. and Isaboke, H.N. 2020. Technical efficiency in tomato production among smallholder farmers in Kirinyaga County, Kenya. *African Journal of Agricultural Research*1 6(5):667-677.

Ochilo, W.N., Nyamasyo, G.N., Kilalo, D., Otieno, W., Otipa, M., Chege, F., Karanja, T. and Lingeera, E.K. 2019. Characterization and production constraints of smallholder tomato production in Kenya. *Scientific African* 2:e00014.

Resende, J.T.V., Maluf, W.R., Das Graças, C.M., Nelson, D.L. and Faria, M.V. 2002. Inheritance of acyl sugar contents in tomatoes derived from an interspecific cross with the wild tomato, *Lycopersicon pennellii* and their effect on spider mite repellence. *Genetics and Molecular Research* 1:106-116.

Sharma, J.R. 1988. Statistical and Biometrical Techniques in Plant Breeding. New Age International publishers, New Delhi, Mumbai, India. 432pp.

Sun, X.R., Liu, L., Zhi, X.N., Bai, J.R., Cui, Y.N., Shu, J.S. and Li, J.M. 2019. Genetic analysis of tomato internode length via mixed major gene plus polygene inheritance model. *Scientia Horticulturae* 246:759-764.

Tasisa, J., Mohammed, W., Hussien, S. and Kumar, V. 2017. Heterosis for some physiological traits in tomato (*Solanum lycopersicum* L.) hybrids in East Hararghe, Ethiopia. *World Applied Science Journal* 35(11):2300-2307.

Thainukul, N., Sakdarueakrot, S. and Yan, L. 2017. The evaluation of genetic inheritance, heritability and correlations coefficient of mutant tomato. *School Journal of Agriculture and Veterinary Science* 4(5):209-213.

Valls, J.F.M. 2007. Characterization of plant genetic resources. In: Nass, L.L. (Ed.), Plant genetic resources. *Brasilia: Embrapa Genetic Resources and Biotechnology* 1:281-305.