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Full Length Research Paper

Generation Mean Analysis for Yield and Yield Related Traits in Five Tomato Genotypes in Kenya

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Running Head: Inheritance of Yield and Yield Related Traits

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Abstract

The study aimed to determine inheritance of tomato yield and yield related traits in Kenya. Six generations were developed. Experiment was conducted in a split-plot design with crosses as main plots and generations as subplot at two sites. The six generations in all crosses performed better at Kabete compared to Mwea site. Significant yield increase of ≥18.11% per plant was registered in F_1 and F_2 generationsin comparison to parental genotypes. Cross Roma VF x AVTO1429 had the highest yield of 5.59 and 5.39kg plant^{-1}in F_2 and F_1 generations, respectively. Highly significant additive, dominance, additive x additive, dominance x dominance and additive x dominance effects were noted in total soluble sugars and number of fruits per plant while significant dominant and additive x additive interaction effects were noted in fruit firmness and fruit width traits. BC_1P_2 of cross Roma VF x Valoria select had the highest TSS Brix of 4.00%. $P_{2,}$ F_1 and F_2 hybrids and BC_1P_2 of cross Roma VF x Valoria select had the highest number of fruits. The importance of gene effects for inheritance was in additive and dominance-additive portions of genetic traits expressions which implied that the traits were inherited.

Keywords: Generation mean, inheritance, tomato, yield traits, additive, dominance.

INTRODUCTION

Demand for tomato with quality fruits and diverse agronomic traits influences tomato production systems by Kenyan growers[1]. The increase in demand for tomato from growers and consumers has elicited the need to improve the existing cultivars to mitigate the gap[2]. Examples of existing tomato cultivars grown in Kenya are Riogrande, Cal J, Roma VF, UC82, Danny select, Valoria select and Eden select among others[3].

Tomato constitutes 7% of total horticulture produce in Kenya and 14% of the entire vegetable produce[2]. Tomato is cultivated on 0.4 million hectares in Kenya, which produces about 280, 000 tonnes annually with an average value of 151 million USD[4]. However, from 2016 to 2018, a decrease of 30% in tomato production against an increasing demand of 300,000 tonnes has been reported[5]. In addition, tomato consumption per capita has increased by more than 41.7% in same period[6]. The decline in tomato productivity has led to increase in tomato prices making them unaffordable and therefore, Kenya has resulted to importation of over 27, 000 tonnes from Ethiopia and Tanzania[5].

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Tomato improvement programs needs to incorporate specific morphological and phenological traits such as determinate growth habit, fruit set, and pedicel condition as well as fruit quality traits such as low pH, high soluble solids, total solids, and firmness among others[7]. According to Edson and Akyoo[8], desirable yield traits such as high yields, firmness and large fruit size are essential parameters contributing to productivity and profitability of tomato growers. Furthermore, these traits provide consumer satisfaction, quality raw materials for the processing industry and enhance competitiveness of tomato crop in the horticultural sector[8]. However, tomato technologies, innovations and management practices (TIMPS) are scanty in Kenya and in most African countries[9]. In addition, breeding programs in Kenya have only focused on cereals, root crops, beverage crops and pulses and hence no tomato breeding programme initiated by public or private company[1]. Moreover, the only tomato breeding program in East African region is the World Vegetable Centre Regional Program, formerly Asian Vegetable Research and Development Centre (AVRDC) program based in Tanzania[10]. Therefore, tomato varieties such as Cal J, Proster F_1, Kentom F_1, M-82, Kilele F_1 and Roma VF grown in the country are largely imported from abroad and very expensive[2]. Furthermore, imported tomato seeds are hardly affordable and accessible by small-scale growers and the varieties are susceptible to diseases and pests such as bacterial wilt and *Tuta absoluta* and abiotic stress such as tolerance to heat stress[9].

Majority of Kenyan farmers are interested in growing tomato varieties with increased yields and resistance to pest and diseases[1]. Improved tomato cultivars especially hybrids are more productive because of commonly reported fruit yield heterosis of 20 to 50%[11,13]. This make farmers interested in growing F_1 varieties. Moreover, hybrids exhibit other advantages such as early maturity, resistance to pests and diseases, higher growth vigour that help overcome abiotic stresses like drought and large sized fruits of high quality[12]. Despite the advantages, the hybrid tomatoes varieties grown by farmers in Kenya are not adapted to different agro-ecological zones across the country[13]. This therefore means demand-led breeding of locally adapted improved varieties especially hybrids with market preferred traits are desirable[13].

Generation mean analysis (GMA) is a simple technique for characterizing gene effects for a polygenic character which determines the presence or absence of non-allelic interaction[14]. The greatest advantage of GMA is that it provides the estimation of epistatic gene effects namely additive x additive, additive x dominance and dominance x dominance involved in the expression of quantitative traits such as yield and yield related traits[14]. Apart from yield, the method has been used successfully for research on mode of inheritance patterns of numerous tomato traits; such as days to flowering and maturity[12], plant height[15], total soluble sugars[16], among others. Inheritance of tomato resistance to late blight caused by *Phytophthora infestans* has been studied by generation mean analysis[17]. The findings reported involvement of incomplete dominance of ph-2 gene. Generation means have been used to analyse inheritance of resistance to *Ralstonia pseudosolanacearum* in tomato which has been reported to involve two major genes with segregation independent of additive effects only, plus polygene with additive and dominance effects[18]. The model has also been used for similar research on quantitative traits in many crops such as yield inheritance pattern of grass pea (*Lathyrus sativus*L.)[19] and runner beans[20]. The aim of this study was to determine the inheritance of yield attributes of tomato genotype and identifying the cross family with great potential for further breeding.

MATERIAL AND METHODS

Experimental sites

Experiments were conducted at Kabete Field Station and Mwea Research Station from 2018 to 2019. Kabete Field Station is agro-ecological zone (AEZ) III, located at 01°15'S; 036°44'E in Kiambu County which is an elevation of 1820m above sea level (asl). It has a bimodal rainfall of 1059 mm per year distributed in two seasons which are the long rain (March to May) and short rains (October to December). Temperature ranges from 12.3 to 22.5°C and soils are humic nitisols that are deep and well-drained with a pH of 5.4[21].

Mwea Research Station is located at 0°41'S; 037°21'E in Kirinyaga County and an elevation of 1247 masl, which is agro-ecological zone II. The area has a bimodal rainfall regime of 973 mm annually with long rain from March to May and short rains from October to December. Temperature ranges from 15.6 to 28.6°C and soils are Niti-rhodic ferrasols with a pH of 5.1[22].

Plant materials

Five tomato genotypes were used in this study. They included three breeding genotypes from the World Vegetable Centre (AVRDC) in Taiwan namely; AVTO1424, AVTO1429 and AVTO1314, one commercial variety known as Roma VF sourced from Continental Seeds Company Limited and one selection from farmers in Kirinyaga County, Valoria select. Roma VF is a pure-line with market demanded traits such as oval shaped fruits, long shelf life and marketable firm fruit. However, the variety lacks genes for resistance to bacterial wilt disease which affect its productivity in many farmer's fields in Central Kenya especially at Mwea, Kirinyaga County[23]. AVTO1424, AVTO1429 and AVTO1314 are genotypes with gene for resistance to bacterial wilt[24]. AVTO1424 is semi-determinate line with oblong shaped, medium to large fruits.

The fruit has deep red internal colour due to crimson gene (ogc) which increases lycopene content[24]. AVTO1429 is indeterminate line with round, large fruits[24]. AVTO1314 is semi-determinate line with round, medium sized fruits[24]. However, the performance of these lines in Kenya is not known.Valoria selection is determinate line that is high yielding with oblong and firm fruits selected by farmers in Central Kenya. Growers claim it is resistant to bacterial wilt but this has not been verified.

Development of Study populations

Four bi-parental crosses were made between Roma VF and AVTO1429, AVTO1424, AVTO1314 and Valoria Select to come up with F_1 hybrids in April-August season, 2018. The F_1's was backcrossed to both parents to come up with BC_1P_1 and BC_1P_2 and were also advanced to F_2 at Kabete Field Station during September-December, 2018. Six generations were generated for each cross: P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2 following a modified procedure of Kosev and Vasileva[19]. The generations were evaluated in field trials at Kabete Field Station and Mwea Research Station.

Evaluation of study populations

Experimental layout

Seedlings were raised in germination trays containing peat moss as planting media at Kabete Field Station on 6th March, 2019. The trays had 204-cells (3.5 cm deep and 2.5 cm wide) and were obtained from Amiran Kenya Limited. One seed was sown per cell and trays were placed on benches in a net-house. Seedlings were watered daily in hot weather and once every two days when the weather was cool to provide sufficient moisture for growth.

Seedlings were hardened 25 days after sowing when they had 4 true leaves by slightly reducing the water supply. In addition, the netting was removed to expose the seedling to strong sunlight so that they are stocky and sturdy. Seedlings were watered 12 hours before transplanting in the field. One month old seedlings were transplanted to evaluation sites in open field at Kabete Field and Mwea Research Stations on 8th April, 2019 after attaining pencil thickness. Transplanting was done early in the morning to reduce the transplanting shock and plants were watered immediately after, following a protocol by KALRO[25]. The land was prepared by deep ploughing (45cm) the fields to improve the soil structure, water holding capacity and to achieve a fine tilth. Regular ridges that were 30 cm high and 25 cm wide were made to raise the beds.

The trial design was split-plot with the four crosses as main plots and the six generations as subplot. The whole experiment was replicated three times. The main plot measured 36x54 meters with eighteen subplots each measuring 2x3 meters. Each subplot had four rows with five plants per row and therefore 20 plants per plot. Number of plants per plot varied with generations. 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 Kosev and Vasileva[19].

Crop Management

The crop was hand-weeded after every 2-3 weeks to maintain weed free field. The crop was mainly rain fed but supplemental irrigation using drips was provided as needed. Di-ammonium phosphate fertilizer (DAP 18:46:0) and N.P.K (17:17:17) at the rate of 12 g plant^{-1} was applied during transplanting. The plants were top dressed with calcium ammonium nitrate (CAN) at the rate of 100kg/ha when plants were 25 cm high and 200kg/ha 55days after transplanting. Fertilizer application was to ensure adequate nutrient levels for the crop to prevent deficiency disorders[25]. Metalaxyl-M and Propineb (700g/kg) at the rate of 50g/20 litres water was alternated every two weeks to control early and late blight. Imidaclopride (100 g l^{-1}), betacyfluthrine (45g l^{-1}) at rate of 0.2 l ha^{-1}, and Thiamethoxam at the rate of 8g / 20 litres water was used to control aphids, whiteflies, and leaf miners during the crop growth cycle.

Data collection

Data was collected on a total of 50 F_1 plants, 50 plants of each parent in a cross, 300 plants of each backcross and 600 plants for the F_2 generation following a modified protocol of [26]. In the field trials, data was collected on the following traits: total soluble sugar content, fruit firmness, fruit yield, number of fruits per plant, fruit length and width.

Fruit brix was evaluated as the average total soluble solute measure of mature red fruit using a handheld refractometer (model 28- 62%, manufactured by Labline, in India) harvested at mature green and red stage. Fruit firmness was measured as the average firmness of mature red fruits measured using digital handheld penetrometer (Lutron electronic Fruit Hardness Tester model FR 5105, from Taiwan). Fruit yield was measured as the total weight in kilograms of the fruits harvested per plant expressed as kg ha^{-1}. Weighing was by electronic weighing balance (model AG64-100, Wagtech International, New York). Number of fruits per plant was determined by counting the total fruits harvested in each of the six randomly tagged plants per plot. Tomato fruit length and width was measured as the equatorial diameter and polar diameter, respectively using a tape measure[27].

Data analysis

Analysis of variance (ANOVA) to establish significant differences among the generations for each trait, and to compare crosses was conducted separately for each of the population using Genstat software 15th edition. Mean separation was carried out using Tukey's procedure for multiple comparison ($P \leq 0.05$), following a protocol by Kathimba *et al.*[13]. Those variables that showed significant differences by orthogonal contrasts between parents P_1 and P_2 were subjected to generation mean analysis (GMA) to determine traits that were quantitatively or qualitatively inherited using the methodology proposed by Kathimba *et al.*[13]. 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 whether the differences are because of chance or other traits hence: Chi-square= (Observed-Expected) ^{2} /Expected which is expressed as; $x^2= \sum [(O-E)^2/ E]$. The calculated chi-square value was used to determine *P* (probability) value from chi-square table. If *P* value obtained <5%, the variation between the segregating ratios was influenced by other traits but if *P* value >5% the variation was due to chance and within the acceptable deviation[28].

Generation mean analysis

Calculation of generation mean analysis followed the approach of Sharma[26]as follows:

Development of generation means, calculated by summing the number of observations for a trait in each generation and dividing by the total number (n) of sampled plant ($\dddot{\bar{X}}$=T/n). Variance for each generation was calculated using formula (=∑ SS/ (n-1)) and mean variance of each generation ($\bar{V}$=V/n).

Epistasis affect estimation of additive and dominance components of variance. Therefore, Scaling tests were used to determine if there were epistatic effects for traits studied and to determine the appropriate model for genetic analyses. Four scales A, B, C, D were used to determine presence of additive, dominance, and the type of interaction effects. Computation of the scales was achieved as: $A= \overline{P}_1 + \overline{F}_1 - 2\overline{BC}_1$, $B=\overline{P}_2+\overline{F}_1-2\overline{BC}_2$, $C=\overline{P}_1+\overline{P}_2+2\overline{F}_1-4\overline{F}_2$, $D=2\overline{F}_2-\overline{BC}_1-\overline{BC}_2$, 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), Where: A= additive x dominance (P_1) and SE= Standard error). This was done for each scaling tests. Significant differences of even one of the 4 scales meant epistasis was present and necessitated analysis of components of means. Analysis of components of means in crosses where epistasis was present was conducted using 6-parameters model since backcrosses were used following the procedure of Sharma[26].

RESULTS

Highly significant differences across the six generations of all the crosses except Roma VF x Valoria select at ($P \leq 0.05$) were noted in total soluble sugars, number of fruits per plant, yield per plant and fruit width (Table 1). Highly significant differences at ($P \leq 0.05$) were observed in all traits except fruit width across the two environments (Kabete and Mwea sites) in cross Roma VF x Valoria select.

Highly significant differences at ($P \leq 0.01$) were recorded for number of fruits per plant, yield per plant and fruit length across the two environments in all the crosses. Highly significant interaction between the generation x environment was noted in cross Roma VF x AVTO1429 for number of fruits per plant at ($P \leq 0.01$) and in cross Roma VF x AVTO1314 for fruit firmness at ($P \leq 0.05$).

The scaling tests were significantly different at ($P \leq 0.01$) in cross Roma VF x AVTO1429 only (Table 2). Total soluble sugar, fruit firmness and fruit width traits showed significantly high dominant effects (scaling test B) while number of fruits per plant showed additive effects (scaling test A) at ($P \leq 0.01$).

Similarly, fruit firmness trait showed significantly high additive x additive interaction effects (scaling test C) while fruit length showed additive x dominant interaction effects (Scaling test D) at ($P \leq 0.01$). Therefore, further analysis using a 6-parameter model was carried out since cross Roma VF x AVTO1429 showed epistasis and backcross were used (Table 3).

Total soluble sugars (Brix)

Total soluble sugars (TSS) across the two environments in cross Roma VF x AVTO1429 ranged from 3.05% Brix of parent P_1 (AVTO1429)to 3.45% Brix offspring, BC_1P_1 while in cross Roma VF x AVTO1424, TSS rangedfrom 3.14% Brix of offspring, $BC_1P_1$to 3.38% Brix of parent, Roma VF (Table 1).

Similarly, TSS in cross Roma VF x AVTO1314 ranged from 3.41% Brix of offspring, F_1 to 3.64% Brix of parent, AVTO1314 while in cross Roma VF x Valoria select, TSS varied from 3.45% Brix for P_1 (Valoria select) to 3.77% Brix of offspring, BC_1P_2.F_1 hybrids of cross Roma VF x AVTO1429 at Mwea Research Station had the lowest TSS Brix of 2.85% while BC_1P_2 of cross Roma VF x Valoria select at Kabete Research Station had the highest at 4.00%.

Scaling tests showed non-significant additive x dominance interaction of -0.59ns; presence of additive x dominance interaction represented by -0.12**; non-significant dominance x dominance interaction of -0.61 and non-significant additive x additive interaction of -0.05 (Table 2). Results showed that the combined gene effects represented by 4.69 was higher than the interaction components at 1.53 put together (Table 3).

Table 1: Mean performance of parental genotypes in the 4 crosses for Total soluble sugars, Fruit Firmness, No. of fruits per plant, Yield per plant, Fruit length and width evaluated at Kabete and Mwea in 2018.

Generation	Total soluble sugars (Brix %)			Fruit Firmness(Nmm^{-1})			Number of fruits per plant			Yield per plant (kg)			Fruit length (mm)			Fruit width (mm)		
	Kabete	Mwea	Mean	Kabete	Mwea	Mean	Kabete	Mwea	Mean	Kabete	Mwea	Mean	Kabete	Mwea	Mean	Kabete	Mwea	Mean
Cross 1 (Roma VF x AVTO1429)																		
P_1	3.14	3.39	3.27	65.11	56.16	60.63	92	41	66	4.07	1.38	2.73	56.66	43.9	50.28	53.37	50.66	52.01
P_2	3.51	3.08	3.29	58.99	54.22	56.61	111	42	76	4.89	1.54	3.21	55.68	44.48	50.08	44.18	49.05	46.61
F_1	3.25	2.85	3.05	60.32	52.19	56.26	115	48	81	5.39	2.22	3.81	54.12	42.58	48.35	49.65	46.45	48.05
F_2	3.44	3.19	3.32	57.93	50.64	54.29	105	45	75	5.59	2.15	3.87	53.66	44.70	49.18	47.84	45.74	46.79
BC_1P_1	3.62	3.28	3.45	64.07	51.25	57.66	115	56	86	5.03	2.15	3.59	52.38	45.95	49.17	55.53	50.53	53.03
BC_1P_2	3.30	3.17	3.23	59.20	52.25	55.72	107	44	75	5.20	2.16	3.68	55.62	44.79	50.21	45.48	48.94	47.21
Mean	3.38	3.16	3.27	60.94	52.79	56.86	107.3	45.9	76.6	5.03	1.93	3.48	54.69	44.4	49.54	49.34	48.56	48.95
CV (%)			6			7.6			15.4			10.1			5.3			8.1
LSD (5%)			0.6			10.66			19.18			0.99			5.31			12.26
Cross 2 (Roma VF x AVTO1424)																		
P_1	3.13	3.34	3.24	68.29	55.46	61.88	79	16	48	4.41	1.53	2.97	56.07	46.47	51.27	50.93	52.09	51.51
P_2	3.32	3.45	3.38	55.98	50.65	53.31	84	45	65	4.91	1.76	3.33	55.50	46.93	51.21	45.03	49.17	47.10
F_1	3.35	2.99	3.17	62.19	52.62	57.41	105	31	68	4.92	2.30	3.61	53.46	46.91	50.18	49.43	50.19	49.81
F_2	3.27	3.19	3.23	63.21	58.97	61.09	80	27	54	4.84	1.92	3.38	54.26	47.01	50.64	48.37	49.08	48.73
BC_1P_1	3.21	3.07	3.14	64.83	57.74	61.29	64	17	40	5.26	1.93	3.59	54.62	45.58	50.10	50.55	50.77	50.66
BC_1P_2	3.33	3.17	3.25	51.24	55.52	53.38	96	38	67	5.15	2.37	3.76	52.66	46.60	49.63	45.74	49.89	47.81
Mean	3.27	3.2	3.23	60.96	55.16	58.06	84.8	28.9	56.8	4.91	1.97	3.44	54.43	46.58	50.51	48.34	50.2	49.27
CV (%)			9.6			6.6			28.7			8.6			3			4.1
LSD (5%)			0.85			6.1			28.47			0.85			2.46			3.99
Cross 3(Roma VF x AVTO1314)																		
P_1	3.75	3.54	3.64	59.76	48.75	54.26	82	32	57	4.39	0.85	2.62	53.00	45.60	49.30	53.22	53.12	53.17
P_2	3.83	3.23	3.53	64.99	51.66	58.33	105	42	73	4.95	1.91	3.43	55.00	45.20	50.10	51.21	46.69	48.95
F_1	3.69	3.12	3.41	56.70	56.31	56.50	117	54	85	5.34	1.61	3.47	62.40	43.90	53.20	47.44	50.38	48.91
F_2	3.57	3.47	3.52	61.24	55.43	58.33	103	44	73	4.72	1.43	3.08	50.70	45.70	48.20	52.02	51.14	51.58
BC_1P_1	3.68	3.49	3.59	60.21	53.42	56.81	105	39	72	4.72	1.09	2.90	51.00	44.70	47.90	56.68	52.51	54.6
BC_1P_2	3.84	3.22	3.53	60.54	55.12	57.83	120	55	87	5.25	1.99	3.62	49.50	44.90	47.20	49.66	50.55	50.11
Mean	3.73	3.35	3.54	60.57	53.45	57.01	105.3	44.1	74.7	4.9	1.48	3.19	53.6	45	49.3	51.7	50.73	51.22
CV (%)			6.4			5.7			15.9			10.9			15.7			8
LSD (5%)			0.81			15.3			22.84			1.85			12.57			6.93
Cross 4 (Roma VF x Valoria FS)																		
P_1	3.71	3.20	3.45	58.19	52.47	55.33	75	35	55	4.64	1.73	3.18	53.74	43.87	48.80	47.53	44.37	45.95
P_2	3.65	3.34	3.50	58.74	55.67	57.20	117	33	75	4.89	1.85	3.37	55.78	44.82	50.30	45.26	47.44	46.35
F_1	3.66	3.50	3.58	54.48	54.42	54.45	132	53	92	5.15	2.01	3.58	53.74	42.98	48.36	50.01	46.33	48.17
F_2	3.74	3.43	3.59	53.30	51.49	52.40	151	65	108	4.76	2.04	3.40	52.81	43.03	47.92	48.00	45.41	46.70
BC_1P_1	3.70	3.23	3.47	58.29	52.32	55.30	97	45	71	4.89	2.28	3.58	54.05	44.43	49.24	45.79	46.09	45.94
BC_1P_2	4.00	3.55	3.77	52.32	47.10	49.71	131	49	90	5.17	1.84	3.50	53.69	44.59	49.14	46.90	45.11	46.00
Mean	3.74	3.38	3.56	55.89	52.25	54.07	117	46.5	81.7	4.91	1.96	3.44	53.97	43.95	48.96	47.25	45.79	46.52
CV (%)			5.6			8.5			12.5			12.1			4.7			5.7
LSD (5%)			0.32			7.16			16.71			1.18			5.1			11.55

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

Table 2: Scaling tests for generations in tomato for different yield and yield related traits in cross Roma VF x AVTO1429

Scales	**Total soluble sugars (% Brix)**	**Fruit firmness(Nmm^{-1})**	**Number of fruits per plant**	**Yield per plant (kg)**	**Fruit length (mm)**	**Fruit width (mm)**
A= $(\bar{P}_1 + \bar{F}_1 - 2\overline{BC}_1)$	-0.589	1.57	5.8**	-0.642	0.29	-6
B= $(\bar{P}_2 + \bar{F}_1 - 2\overline{BC}_2)$	-0.124**	1.43**	-12.5	-0.342	-1.99	0.24**
C= $(\bar{P}_1 + \bar{P}_2 + 2\bar{F}_1 - 4\bar{F}_2)$	-0.609	12.6**	-118.7	-1.914	0.34	7.56
D= $(2\bar{F}_2 - \overline{BC}_1 - \overline{BC}_2)$	-0.052	-4.80	56	0.465	-1.02**	-6.66

A=additive effects; B=dominance effects; C=additive x additive interaction effects; D=additive x dominance interaction effects. *, ** Significant at 5 and 1 percent probability levels, respectively.

Table 3: Test of significance for the scaling tests of cross Roma VF x AVTO1429 on all yield and yield related traits

Scale	**Fruit length (mm)**		**Scale**	**Fruit width (mm)**		**Scale**	**Fruit firmness**	
	Standard error	**t(scale/SE)**		**Standard error**	**t(scale/SE)**		**Standard error**	**t(scale/SE)**
A=-1.32	1.35	-0.98	A=2.24	1.27	1.77	A=-0.82	1.68	-0.49
B=0.38	1.52	0.25	B=2.52	1.27	1.98**	B=12.23	1.67	7.35**
C=4.4	2.32	1.90	C=1.84	2.06	0.89	C=11.83	2.42	4.90**
D=-2.54	1.03	-2.46**	D=1.46	0.88	1.65	D=-0.21	1.14	-0.18

Continuation of table 3

Scale	**Total soluble sugars (% Brix)**		**Scale**	**Number of fruits per plant**		**Scale**	**Yield per plant (kg)**	
	Standard error	**t(scale/SE)**		**Standard error**	**t(scale/SE)**		**Standard error**	**t(scale/SE)**
A=0.095	0.08	1.20	A=-23.7	7.99	-2.97**	A=-0.4	0.36	-1.12
B=-0.47	0.07	-6.34**	B=7.1	10.01	0.71	B=-0.061	0.4	-0.15
C=-0.24	0.13	-1.83	C=4.6	17.06	0.27	C=0.10	0.62	0.17
D=-0.07	0.06	-1.16	D=-10.6	7.52	-1.41	D=-0.28	0.27	-1.03

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

Number of fruits per plant

Results showed that parents in all the crosses had significantly higher fruit number per plant ranging from 75 to 117 fruits at Kabete site as compared to Mwea site that ranged from 16 to 45 fruits. Parental genotypes AVTO1429, AVTO1424 and AVTO1314 had the highest number of fruits in all the crosses (Table 1). Similarly, F_1 hybrids had higher fruit number per plant at Kabete site which ranged from 105 to 132 fruits than the range of 31 to 54 fruits at Mwea site for all the crosses. This trend of results was also observed in F_2 hybrids with fruit number ranging from 80 to 151 fruits at Kabete site and 27 to 65 fruits at Mwea site for all the crosses. Results for F_1 and F_2 hybrids were consistent across the crosses. Significant increase in number of fruits per plant in comparison to parental genotypes was registered in F_1 and F_2 generation of all crosses. $P_{2,}$ F_1 and F_2 hybrids and BC_1P_2 of cross Roma VF x Valoria select had the highest number of fruits. The number of fruits per plant across the two environments ranged from 55 fruits of parent P_1 (AVTO1429) to 108 fruits of F_2 in cross Roma VF x AVTO1429 and from 57 fruits of parent P_1 (AVTO1424) to 87.20 fruits of BC_1P_2 in cross Roma VF x AVTO1424. Similarly, in cross Roma VF x AVTO1314, the number of fruits per plant across the two environments ranged from 48 fruits of parent P_1 (AVTO1314) to 68 fruits of F_1 while in cross Roma VF x Valoria select, they varied from 66 fruits of parent P_1 (Valoria select) to 86 fruits of BC_1P_1.
Scaling test showed presence of additive x dominance interaction represented by 5.8**; non-significant additive x dominance interaction of -12.5; non-significant dominance x dominance interaction illustrated by -118.7 and non-significant additive x additive interaction indicated by 56 (Table 2). Results showed that the combined gene effects represented by -9.55 was lower than the interaction components put together, indicated by -4.93 (Table 3).

Yield per plant (kg)

Results showed that parents in all the crosses had higher yield per plant at Kabete site which ranged from 4.07 to 4.95kg compared to Mwea site that ranged from 0.85 to 1.91kg. Parental genotypes AVTO1429, AVTO1424 and AVTO1314 had the highest yields in all the crosses (Table 1). Similarly, F_1 hybrids had higher yield per plant at Kabete site which was between 4.92 and 5.39kg compared to Mwea site that ranged from 1.61 to 2.30kg for all the crosses. F_2 hybrids had similar trend in yield per plant. Yields at Kabete site ranged from 4.72 to 5.59kg and the yield at Mwea site was between 1.43 and 2.15kg for all the crosses. Results for F_1 and F_2 hybrids were consistent across the crosses. Significant yield increase per plant in comparison to parental genotypes was registered in F_1 and F_2 generation of all crosses. $P_{2,}$ F_1 and F_2 hybrids and BC_1P_2 of cross Roma VF x AVTO1429 had the highest yields. Yield per plant across the two environments in cross Roma VF x AVTO1429 varied from 2.73kg of parent P_1 (AVTO1429) to 3.87kg of F_2 and from 2.97kg of parent P_1 (AVTO1424) to 3.76kg of BC_1P_2 in cross Roma VF x AVTO1424. Similarly, in cross Roma VF x AVTO1314, yield per plant varied from 2.62kg of parent P_1 (AVTO1314) to 3.62kg of BC_1P_2 and from 3.18kg of parent P_1 (Valoria select) to 3.58kg of BC_1P_1 and F_1 in cross Roma VF x Valoria select. Scaling tests showed non-significant additive x dominance interaction (-0.64); non-significant additive x dominance interaction (-0.34); non-significant dominance x dominance interaction (-1.91) and non-significant additive x additive interaction (0.47) (Table 2).

Other traits

Fruit firmness ranged from 49.71 $Nmm^{-1}$of BC_1P_2 in cross Roma VF x Valoria select to 61.88 $Nmm^{-1}$of P_1 (Roma VF). Cross Roma VF x AVTO1429 had the highest fruit firmness among the crosses. Fruit length at Kabete ranged from 49.5mm of BC_1P_2 in cross Roma VF x AVTO1314 to 64.40mm of F_1 hybrid in Roma VF x AVTO1314 while at Mwea site the length ranged from 42.58mm of F_1 hybrid in cross Roma VF x AVTO1429 to 46.93mm of P_2 (AVTO1424). The results revealed that cross Roma VF x AVTO1424 had the highest fruit length which signified that the fruits were more elongated in shape as compared to other crosses. Similarly, fruit width ranged from 44.18mm of P_2 (AVTO1429) to 56.68mm of BC_1P_1 in cross Roma VF x AVTO1314 at Kabete while at Mwea site the width ranged from 44.37mm of P_1 (Roma VF) to 53.12mm of F_1hybrid in cross Roma VF x AVTO1314. This signified that cross Roma VF x AVTO1314 had more pronounced fruits as compared to other crosses.
High significance in the scaling tests of cross Roma VF x AVTO1429 revealed that there was additive x dominance interaction effects represented by -2.46** for fruit length, dominance effects (1.98**) for width and additive x dominance interaction effects (4.90**) for fruit firmness at ($P \leq 0.01$)(Table 2). Dominant gene effects were lower at 6.20** than additive gene effects at 9.45** for fruit width trait. In addition, additive x additive gene component of 7.54** had higher values in comparison to dominant x dominant gene effects of -5.94 (Table 5).

DISCUSSION

Yield per plant is among the most important tomato traits in developing a breeding program.Yield and yield related traits are the most complex trait governed by polygenic gene that have specific interactions[35, 36]. This therefore, makes breeding with an aim to increase yields more difficult. The nature of gene action involved in the inheritance of various characters are very important to decide any breeding methodology for crop improvement[35].

Table 4. Gene effects for the cross Roma VF x AVTO1429 onTotal soluble sugars, number of fruits per plant and fruit firmness using 6 parameter model.

Gene effects / Components	at df.	Total soluble sugars (% Brix)			Fruit firmness			Number of fruits per plant		
		Expectation / Estimate	Standard error	t(gene effect/SE)	Expectation / Estimate	Standard error	t(gene effect/SE)	Expectation / Estimate	Standard error	t(gene effect/SE)
ḿ (Mean)	629	3.32	0.02	143.48**	54.29	0.36	148.99**	108.2	3.05	35.53**
d̂ (additive effect)	502	0.22	0.04	5.67**	1.94	0.87	2.22	-19	4.41	-4.31**
ĥ (dominance effect)	1506	-0.13	0.13	-0.98	7.24	2.47	2.93**	-84.85	16.19	-5.24**
î (Add. x Add. interaction)	1131	0.1	0.12	0.87	9.6	2.27	4.22**	-112	15.04	-7.45**
ĵ (Add. Dom. interaction)	752	0.47	0.1	4.74**	-0.14	2.1	-0.07	-18.3	10.35	-1.77
l̂ Dom. x Dom. Interaction	1381	-0.82	0.2	-4.08**	-6.6	4.24	-1.56	105.3	24.55	4.29**

Environments were Kabete and Mwea longrain season, 2018. *, ** Significant at 5 and 1 percent probability levels, respectively.

Table 5: Gene effects for the cross Roma VF x AVTO1429 on yield per plant, fruit length and width using 6 parameter model

Gene effects / Components	at df.	Yield per plant (kg)			Fruit length (mm)			Fruit width (mm)		
		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	3.87	0.1	38.75**	49.18	0.38	130.74**	46.79	0.32	147.94**
additive effect	502	-0.09	0.19	-0.49	-1.04	0.71	-1.46	5.82	0.62	9.45**
dominance effect	1506	-0.09	0.6	-0.15	0.21	2.25	0.093	12.06	1.94	6.20**
Add. x Add. interaction	1131	-0.93	0.55	-1.69	2.04	2.07	0.99	13.32	1.77	7.54**
Add. Dom. interaction	752	0.3	0.45	0.66	-2.28	1.77	-1.29	6.24	1.51	4.13**
Dom. x Dom. interaction	1381	-0.05	0.98	-0.06	-3.74	3.67	-1.02	-19.08	3.21	-5.94**

Environments were Kabete and Mwea long rainseason, 2018. *, ** Significant at 5 and 1 percent probability levels, respectively.

A six-parameter model was adopted as most suitable for data analysis of P_1, P_2, F, F_2 and backcrosses of the four crosses studied. This was because one cross (Roma VF x AVTO1429) showed epistasis and backcrosses were used. The six parameters in this model were; Mean, additive effects, dominance effects, Additive x Additive interaction, Additive x Dominance interaction and Dominance x Dominance interaction[35]. Comparable studies have been reported on the use of six parameter model for generation mean analysis[37]. The parents in each cross were contrasting for all the traits evaluated. All the offspring derived from the cross-combination Roma VF x AVTO1429 had higher yield per plant compared to the better parent (Roma VF) as indicated by Table 1. Offspring with the smallest yield per plant were backcross (BC_1P_1), of F_1 x Roma VF followed by BC_1P_2. It is reported that for most traits, the mean of BC_1 and BC_2 are less than the means of F_1 and F_2 population due to higher percentage of heterosis in F_1 and evolution of transgressive segregants in F_2 population[39]. Heterosis for yield per plant was 18.7%. The combined gene effects were higher than the interaction components put together as shown by Table 4. However, results revealed that there was no significance in both additive and dominance gene effects on yield in this study. Similarly, Dagade *et al.*[35] reported that fruit yield trait showed low heritability indicating non additive gene action. This suggests exploitation of heterosis breeding in F_1 and selection of desirable segregants in further generation. The results were contrary to the findings of Goffar *et al*. [12] who used a 9x9 half diallel design to study inheritance of yield and yield components in tomato. In their study, yield was attributed to additive-dominance genetic model. Similarly, Jasmina *et al.*[29], reported both additive and dominance gene effects on yield with prevalence of dominance gene action.

Three offspring derived from the cross-combination Roma VF x AVTO1429 had higher number of fruits per plant compared to the better parent (Roma VF). Combined gene effects were lower than the interaction components put together. Number of fruits per plant were controlled by additive and dominant gene effects together with interactions from the polygenes, additive x additive and the additive x dominance effects (Table 4). Studies by Thainukul *et al*. [30] on six generations from cross-combination X604-1(P_1) and TTD302A (P_2) revealed important influence of additive and dominant gene effects in fruits traits and yields in tomato. Similar findings of additive gene effects and additive x dominance interaction effects have been confirmed for number of fruits per plant by Jasmina *et al.*[29] and Hidayatullah *et al.*[31]. Gul *et al.*[32] also reported significant adequate additive dominance model for number of fruits per plant. These findings support the current study.

Two offspring derived from the cross-combination Roma VF x AVTO1429 had higher total soluble sugars compared to the better parent (AVTO1429) (Table 1). Offspring with the smallest total soluble sugars were backcross (F_1 x Roma VF BC_1P_2), followed by F_1. The combined gene effects were higher than the interaction components put together (Table 2). Heterosis for total soluble sugars was -7.3% and the trait were controlled by major dominant genes and interactions of additive and dominance effects. Similar results were documented by Akhtar and Hazra[33] in their study undertaken in West Bengal, India. The study was on the nature of gene action for fruit quality characters of tomato using a 7x7 half diallel design and six generations per cross population. Heterotic breeding is the most practicable approach in improvement of yield components when non-additive gene effect is more prominent than additive gene effects[36, 40].

The test of significance for the scaling tests in cross Roma VF x AVTO1429 revealed that dominant gene effects were lower than additive gene effects for fruit width trait. In addition, the additive x additive gene component had higher values in comparison to dominant x dominant gene component. Dominant effects had higher values than additive effects for fruit length and additive x dominance interaction effects were higher than dominant x dominant effects (Table 5). The presence or absence of epistasis can be detected by the analysis of generation means using the scaling test[37]. This test measures epistasis accurately whether it is complimentary (additive x additive) or duplicate (additive x dominance) and (dominance x dominance) at the digenic level[37]. Fruit firmness was controlled by additive x dominance interaction effects. The results revealed that the traits were governed by duplicate epistasis. Similar findings were reported by Somraj *et al.*[14] who reported higher additive gene effects and additive x additive gene component for fruit width trait and higher dominant effects for fruit length. Studies by Tasisa *et al.*[15]also reported that additive-dominance gene interactions were noted in tomato fruit shape index and acidity that can be titrated. The reason for the reported additive and dominance gene effects in most traits studied was the failure to identify parents with contrasting traits. Similarly, Desalegn *et al*.[38] reported additive gene action being more prominent in controlling yields per plant, number of fruits, fruits length, fruit diameter and fruit weight. Aisyah *et al.*[34] also reported that the ratio of components of genetic variance revealed the predominant role of non-additive gene actions in controlling total yield, number of locules and pericarp thickness.

CONCLUSION

Understanding the gene effects is important in estimating the contribution of major gene and polygenes for selection of high-yielding tomato genotypes. However, this is complicated due to occurrence of duplicate epistasis for yield and yield related traits. Contribution of both parents in the subsequent generations (offspring) is vital in developing a breeding program for a particular trait. Significant yield increase per plant in comparison to parental genotypes was registered in F_1 and F_2 generation of all crosses. In addition, P_2, F_1 and F_2 hybrids and BC_1P_2 of cross Roma VF x AVTO1429 had the highest yields and fruit firmness. Therefore, cross family Roma VF x AVTO1429 has great potential for further breeding.

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Author's Contribution

All the authors jointly designed the experiments. FKK conducted the experiment, performed data analysis, and drafted the manuscript with inputs from all the authors. PMK, RDN and LMK supervised the experiments and reviewed the manuscript. All authors read and approved the final manuscript.

Abbreviations

AVRDC: World Vegetable Centre; g: grams; l: litres; ha: Hectares; t: tonnes; AEZ: Agro-ecological zones; asl: Above Sea Level; m: meters

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Availability of data and materials

The data used and analysed during this study is available from the corresponding author on request.

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests

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