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HETEROSIS AND COMBINING ABILITY FOR RELATED TRAITS IN TOMATO

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ABSTRACT

Tomato (*Solanum lycopersicum* L.) yields have continued to plummet in Kenya due to biotic stresses and reliance on low yielding varieties. This study aimed at determining heterosis and combining ability for fruit yield and yield components among tomato genotypes and select F_1 hybrids combining high fruit yield and other market demanded traits under Kenyan conditions. Ten parental genotypes and their 45 F_1 hybrids were studied using 10×10 half diallel mating design, excluding the reciprocals and the self's. The experiment was set up in Kiambu and Kirinyaga Counties in Kenya. Out of 45 F_1 hybrids evaluated, 89% had reduced (negative heterosis) days to 50% flowering and 11% days to maturity, compared to their better parents. Higher heterosis (-9%) was recorded on days to flowering in AVTO1429 x Cal J VF) and -5% for maturity in Roma VF x AVTO1314. All the F_1 hybrids had positive heterosis for number of trusses per plant and fruit yield. F_1 hybrid AVTO1429 x AVTO1314 had the highest positive heterosis of 114.39% for fruit weight per plant yield. The results showed high significant difference among the ten genotypes for general and specific combining ability effects (male x female) for all the traits evaluated. There was additive and non-additive gene action for the traits, which are important aspects in developing a tomato breeding programme.

Key Words: Gene action, heterosis, *Solanum lycopersicum,* trusses

RÉSUMÉ

Les rendements de la tomate (*Solanum lycopersicum* L.) ont continué de chuter au Kenya en raison des stress biotiques et de la dépendance aux variétés qui donnent le faible rendement. Cette étude visait à déterminer l'hétérosis et à combiner la capacité de rendement en fruits et les composants de rendement parmi les génotypes de tomates et sélectionner des hybrides F1 combinant un rendement élevé en fruits et d'autres caractéristiques demandées par le marché dans les conditions kenyanes. Dix génotypes parentaux et leurs 45 hybrides F1 ont été étudiés à l'aide d'un plan d'accouplement 10 × 10 demi-diallèle, à l'exclusion de la sélection récurrente réciproque et autofécondation. L'expérience a été mise en place dans les comtés de Kiambu et Kirinyaga au Kenya. Les 89 % de 45 hybrides F1 évalués avaient des jours réduits (hétérosis négatif) à 50 % de floraison et 11 % de jours jusqu'à maturité, par rapport à leurs meilleurs parents. Une hétérosis plus élevée (-9 %) a été enregistrée sur les jours précédant la floraison chez AVTO1429 x Cal J VF) et -5 % pour la maturité chez Roma VF x AVTO1314. Tous les hybrides F1 avaient une hétérosis positive pour le nombre de grappes par plante et le rendement en fruits. L'hybride F1 AVTO1429 x AVTO1314 présentait l'hétérosis positive la plus élevée de 114,39 % pour le rendement en poids de fruit par plante. Les résultats ont montré une différence significative élevée entre les dix génotypes pour les effets de capacité de combinaison généraux et spécifiques (mâle x femelle) pour tous les traits évalués. Il y avait une action génique additive et non additive pour les traits qui sont des aspects importants dans le développement d'un programme de sélection de tomates.

Mots Clés : action des gènes, hétérosis, *Solanum lycopersicum*

INTRODUCTION

Plant breeding presents a huge potential for improvement of the productivity of tomatoes (*Solanum lycopersicum* L.) in eastern Africa under the increasingly stressful environmental conditions. Presence of adequate information on heterosis is a pre-requisite for breeding tomato and other crop hybrids (Brajendra *et al.,* 2012).

Heterosis in tomatoes is mainly exhibited through hastened growth and development, early maturity, increased vigour, higher yields and resistance to biotic and abiotic stresses; but in some circumstances it can also result in lateness to maturity (Fufa *et al.,* 2009; Gul *et al.,* 2011). Unfortunately, heterosis levels of local tomato varieties, which is a pre-requisite for the development of new disease resistant hybrid varieties, is not known in countries such as Kenya (Kenneth, 2016).

Combining ability in breeding means the relative ability of a genotype to transmit or transfer genetic superiority to its offsprings when crossed with other individuals (Costa *et al*., 2018). Combining ability provides valuable information to breeders on the genetic potential of parental lines and development of hybrid varieties (Troyer, 2006). It also provides information on gene effects, which can also be used in developing an effective breeding strategy (Costa *et al.,* 2018). Tomato yields reportedly declined from 20 t ha^{-1} since 2012 to 18.7 t ha^{-1} in 2017 (FAO, 2017); and this was associated mainly with the use of outdated low yielding varieties that are sensitive to biotic and abiotic stresses (Sigei *et al.,* 2014). Kenya's tomato seed development programme is generally weak; hence, commercial farmers rely on expensive imported seed which is often ill-adapted to local conditions (Mwangi *et al.,* 2020). In some cases, farmers grow tomato from their locally selected seeds, such as Valoria FS and Danny FS, based on resistance to major diseases such as bacterial wilt (reports not validated). Most of these selections lack better attributes associated with fruit yields and yield quality (Ochilo *et al.,* 2019).

Tomato breeding has received little research attention in Kenya, hence, there is scanty documented research information on the crop to inform policy and development programmes (Munyi and De Jonge, 2015). Thus, understanding of heterosis and combining ability for yield and yield related traits in local and introduced tomato lines; and their F_1 hybrids is critical in designing hybrid tomato breeding programmes appropriate for Kenyan circumstances (Tamta *et al.,* 2018). The objective of this study was to determine heterosis and combining ability for fruit yield and yield components in tomato genotypes under Kenyan conditions.

MATERIALS AND METHODS

Experimental site. The experiment was conducted in 2018 at two sites, namely Kabete Field Station, University of Nairobi in Kiambu

County and at Mwea Research Station of Kenya Agricultural and Livestock Research Organisation (KALRO) in Kirinyaga County. Kabete Field Station in agro-ecological zone (AEZ) III lies on latitude 01°15'S, longitude 036°44'E. The Station is located at 1820 m above sea level (m.a.s.l.). It experiences bimodal rainfall of 1059 mm per year, and temperature range of 12.3 to 22.5 °C. Mwea Research Station, Kirinyaga County (AEZ II) lies on latitude 0 37'S and longitude 37 20' E at 1159 m.a.s.l. It experiences average rainfall of 850 mm annually, and temperature range of 15.6 to 28.6 °C (Lengai, 2016).

Plant materials. The study used 10 tomato genotypes selected based on diversity of traits; which included three breeding accessions from the World Vegetable Centre (WVC) in Taiwan (AVT01424, AVT01429 and AVT01314); four commercial cultivars sourced from Continental Seeds Company Limited (Riogrande, Roma VF, Cal J VF and UC82); and three selections (Eden, Danny and Valoria) from farmers of Kirinyaga County. From these genotypes, 45 crosses were evolved in a 10×10 half diallel mating design, excluding the reciprocals and the self's (AVRDC, 2001).

Treatment layout. The ten genotypes were sown in germination trays containing peat moss as the planting media. Seedlings were transplanted after 28 days to a crossing block at Kabete Field Station, after attaining pencil thickness. The parental crossing plots consisted of two rows measuring 2.4 m long with 10 plants at spacing of 60 cm x 60 cm. Supplemental irrigation was provided with a drip system at intervals of 45 minutes. Diammonium phosphate (DAP) at 12 g plant^{-1} and of N: P: K (17% nitrogen: 17% phosphorus: 17% potassium) at 12 g plant^{-1} were applied during transplanting. Metalaxyl-M and propineb (700 g kg^{-1}) at the rate of 50 g in 20 litres water was applied to control Pythium, early and late blight. Imidaclopride+betacyfluthrine 100 plus 45 g l^{-1} at rate of 0.2 l ha^{-1} was applied every 7 days to control white flies. Thiamethoxam at 25 ml in 20 litres water per week was used to control leaf miners. Plots were kept weed free manually, twice, and seedlings were staked using sticks and sulti twine to provide support for the plant.

Preparation of female parent. Crosses were made manually using the standard procedure of hand emasculation and pollination. Emasculation was carried out when 2 to 3 flowers in an inflorescence were fully grown, but before flower petals opened. This was done with the aid of pointed forceps, following the protocol of AVRDC (2001). This was done from 8 to 11 a.m. when temperatures in the field ranged from 21-25 °C; and in the evening between 4 to 6 p.m. when temperature ranged from 15-20 °C. Isolation distance of 3 m was maintained between the male and female plants.

Pollen harvesting. Pollen was harvested using the modified electric tooth brush, manufactured by VegiBee-Garden pollinators (model VBP-02), using a pollen collection cap. Pollen was then transferred in a well labelled modified syringe holder, for pollinating the ready stigma. Pollination, which involved dipping the stigma into the pool of pollen in the pollen container, was carried out 2 to 3 days after anthesis, at a temperature range of 21 to 23 °C (Singh *et al.,* 2004).

Successful pollination was visualised within one week of pollination, by the enlargement of the fruit. Two sepals were removed after hybridisation for distinguishing hand-pollinated cluster from self's during fruit harvesting. Clusters were labelled with waterproof tags containing information of female, male and crossing date.

Fruit harvesting and seed extraction. Fruits were harvested manually upon turning red; and were placed in a woven net and clearly labelled with information. Eight fruits were hand-crushed in a pail containing 1 litre of water, and later transferred to a second pail also with 1 litre of water plus 10 ml of 0.6 M hydrochloric acid to remove mucilage surrounding the seeds. The pulp and acid mixture were stirred continuously after every 15 minutes, for 45 minutes; and the supernatant was drained.

The seeds were washed with distilled water to remove extra debris from the pulp, before being sun-dried for 3 days to a moisture content not exceeding 8%, following a modified protocol of Cheema *et al.* (2005). The dried seeds were packed in khaki paper envelopes before storage in a cool, well-ventilated and dry place. F_1 individuals were evaluated along with their parents for various horticultural traits, in a randomised complete block design, with three replicates; at both Kabete Field Station and Mwea Research Station.

Data collection. Data were recorded on days to 50% flowering, days to maturity, number of trusses per plant, fruit shape index, fruit yield per plant and subsequently per hectare; and total soluble solids. The International Plant Genetic Resources Institute (IPGRI) system for evaluation of tomatoes was used in data collection (IPGRI, 2003). Duration to 50% flowering was determined as the duration from planting to the day when half the plants in a plot had at least one flower. Duration to 50% maturity was determined as number of days taken from transplanting to at least 50% ripening of fruits per plant indicated by the red colour on tomato fruit.

Tomato fruit shape index (FSI) was calculated as a ratio of the equatorial diameter and polar diameter (Lindstrom, 1925). Shape was determined as: Approximately FSI of 1.00 is round fruit, 0.75 oblate fruit and e"1.15 ovate shape. Number of trusses were determined by counting the trusses per plant from the main stems of six plants and calculating their mean per tomato genotype.

Fruit weight per plant was determined by weighing a random sample using electronic weighing balance model AG64-100 (Wagtech International, New York).Total soluble solids, TSS (^{o} Brix) was determined from juice of each fruit from six random plants per plot at mature green and red stage. Tomato fruit juice was squeezed in 250 ml beaker, followed by filtration through a Whatman filter paper (No 1). The juice filtrate was dispensed onto Erma handheld refractometer (model 28-62%, manufactured by Labline, in India) and the readings were recorded.

Heterosis was estimated by the relative performance of the F_1 hybrids expressed as a percentage high or lower performance of the new F_1 hybrid compared to the better parent (Virmani *et al.,* 1997) *viz*:

$$BPH = \frac{F1-BP}{BP} \times 100 \quad \text{.............. Equation 1}$$

Where:

BPH = Better parent heterosis; F_1 = mean performance of a single cross; and BP = mean performance of the better parent

Statistical analysis. Data collected were subjected to analysis of variance (ANOVA) using GenStat 15th edition. Significant means were separated using Fisher's protected Least Significant Difference (LSD) test at P< 0.05.Genetic analyses that involved a diallel analysis to determine General Combining Ability, Specific Combining Ability, variances and effects, relative importance of GCA/SCA and interaction of GCA and SCA with environments were conducted using genetic design tool in AGD-R (Analysis of Genetic Design with R) version 5.0, with genotypes as the fixed factors (Francisco *et al.,* 2018). The means were separated using the Least Significance Differences (LSD) at <0.05. Estimation of variance components was developed on the expectation's values from the analysis of variance for combining ability (Equation 2).

$$gi = \frac{Xi}{tr} - \frac{X}{ltr}$$ .... Equation 2

Where:

gi = General combining ability effect of ith line, Xi = Total of ith line overall including replications and X = Total of all hybrid combinations.

Estimation of SCA effects was as elaborated in Equation 3.

$$Sij = \frac{Xij}{r} - \frac{Xi}{trl} - \frac{Xj}{rl} + \frac{X}{tr}$$ ....Equation 3

Where:

Sij = Specific combining ability of the ith line and jth parent cross, Xij = Total (ij)th combination for all replications

Overall performance of the male and female in the diallel design was equated to their respective general combining abilities (GCA) and their interactions equated to their respective specific combining abilities (SCA).

RESULTS AND DISCUSSION

Heterosis for yield and yield related attributes. Results of heterosis and combining ability for fruit yields revealed significant differences among the genotypes for all the yield traits (Tables 1-3). Results further revealed additive and non-additive gene actions. Additive gene action represents the proportion of genotypic value that is transmitted from parent to the progeny; while non-additive gene action represents the different proportion of dominance that results from gene interaction (Mishra *et al.,* 2017; Rakha and Sabry, 2019).Analysis of variance for GCA/SCA effects revealed additive gene action for days to 50% flowering, days to maturity, number of trusses per plant, total soluble sugars, fruit firmness and tomato yield. It is apparent that the magnitude of heterosis was improved compared to parental material. This was illustrated because the best performing hybrids (Eden select x Cal J, Roma VF x AVTO1429, AVTO1429 x Valoria select and Cal J x Danny select) had higher heterosis percentage for yield traits, exceeding the currently used commercial varieties. It may be possible to developed crosses into improved commercial hybrids to either supplement or replace existing hybrids.

Days to flowering and fruit maturity. Up to 89% of F_1 hybrids reduced days to flowering and maturity compared to their better parents (Table 1). F_1 hybrids which showed heterosis for earliest flowering and maturity, were AVTO1424 x AVTO1314 (-13.11%), followed by Cal J x AVTO1314 (-12.61%) and UC82 x Valoria select (-3.99%). On the other hand. AVTO1429 x UC82 (19.96%), followed by Cal J x Danny select (16.60%) and AVTO1424 x Danny select (16.60%) were the latest flowering and maturing F_1 hybrids, compared to the better parents. Negative heterosis is desirable for days to 50% flowering and maturity because it implies earliness in the hybrid progeny.

A cross between early x early maturing parents led to generation of early maturing progeny, as observed in AVTO1424 x AVTO1314 (Table 1). This was because additive gene action was dominant in the inheritance of this trait in the F_1 progeny. In addition, a cross between late and early maturing parents generated early maturing F_1 hybrids as observed in Cal J x AVTO1314. This shows that the early maturing parent exhibited complete dominance over the late maturing parent.Similar findings were observed by Brajendra *et al.* (2012) in Manipur, India after crossing parental lines in a 7 x 7 half diallel. They reported negative heterosis of -5.65% for days to maturity in the progeny. Similarly, a study by Kumari and Sharma (2011) revealed a maximum significant negative heterosis over the better parents for days to first flowering and maturity in tomato. Only two cross combinations, EC-521041 x

TABLE 1. Heterosis for days to 50% flowering, maturity, number of trusses per plant, fruit shape index, soluble sugars, yield per plant and per ha grown in two environments in Kenya

Crosses	Days to 50% flowering (%)	Better parent (d)	Days to maturity (%)	Better parent (d)	Number of trusses plant^{-1} (%)	Better parent (no.)	Fruit shape index (%)	Better parent	Total soluble sugars (% Brix)	Better parent (%)	Yield plant^{-1} (kg) (%)	Better parent	Yield ha^{-1} (kg) (%)	Better parent
Eden select x Roma VF	-3.03	38.67	8.63	93.44	186.36	4.41	13.19	0.73	-0.35	4.84	3.10	2.22	3.10	44,465
Eden select x AVTO1429	-5.34	38.56	7.37	93.44	302.24	3.67	20.51	0.84	2.32	5.05	22.64	1.92	22.61	38,348
Eden select x Cal JVF	-6.90	38.67	1.13	93.44	249.60	3.67	-4.59	0.84	-3.44	4.99	23.21	1.92	23.16	38,348
Eden select x AVTO1424	-3.89	38.67	7.37	93.44	267.33	3.67	14.89	0.84	-4.57	4.83	61.03	1.92	61.02	38,348
Eden select x Danny select	-6.09	36.56	7.64	87.33	178.42	4.94	3.68	0.84	-10.08	5.31	0	2.64	0.02	52,851
Eden select x AVTO1314	-7.21	38.44	-0.29	93.44	187.86	4.79	32.70	0.84	4.61	4.90	26.55	1.92	26.51	38,348
Eden select x UC82	-3.07	36.11	9.94	84.89	243.06	3.67	1.90	0.84	0.35	4.55	31.81	2.04	31.80	40,797
Eden select x Valoria select	-0.87	38.67	10.05	93.44	206.19	3.88	4.75	0.84	-6.10	4.79	0.29	2.79	0.29	55,740
Eden select x Riogrande	-1.30	38.67	9.51	93.44	217.00	3.69	-5.19	0.87	-10.37	5.13	-4.55	2.29	-4.51	45,711
Roma VF x AVTO1429	-8.80	38.56	5.69	94.78	238.55	4.41	20.23	0.73	-11.19	5.05	41.57	2.22	41.56	44,465
Roma VF x Cal JVF	-6.45	40.44	4.22	98.67	194.76	4.41	14.18	0.73	8.03	4.99	11.34	2.22	11.34	44,465
Roma VF x AVTO1424	-4.34	38.33	6.29	95.33	308.67	4.41	20.31	0.73	3.51	4.84	17.72	2.22	17.70	44,465
Roma VF x Danny select	-0.16	36.56	13.94	87.33	189.36	4.94	13.41	0.73	-9.95	5.31	-7.49	2.64	-7.47	52,851
Roma VF x AVTO1314	-6.35	38.44	2.35	96.56	253.07	4.41	42.35	0.73	-2.28	4.90	11.61	2.22	11.62	44,465
Roma VF x UC82	-3.07	36.11	15.24	84.89	293.77	4.79	14.49	0.73	-5.31	4.84	51.24	2.22	51.23	44,465
Roma VF x Valoria select	-8.92	40.44	4.90	98.67	197.25	4.41	19.63	0.73	-0.68	4.84	-0.97	2.79	-0.98	55,740
Roma VF x Riogrande	-5.21	40.44	2.70	98.67	211.32	4.41	11.47	0.73	-0.23	5.13	14.39	2.29	14.40	45,711
AVTO1429 x Cal JVF	-1.89	38.56	6.21	94.78	214.73	4.41	13.12	0.88	3.60	5.05	51.14	1.84	51.12	36,721
AVTO1429 xAVTO1424	-4.77	38.33	6.74	94.78	269.33	3.42	14.02	0.90	-3.47	5.05	77.61	1.02	77.63	20,457
AVTO1429 x Danny select	2.11	36.56	18.32	87.33	186.52	4.94	24.68	0.93	-7.27	5.31	3.93	2.64	3.96	52,851
AVTO1429 x AVTO1314	-0.71	38.44	-0.06	96.56	339.08	3.40	3.90	1.16	-8.32	5.05	114.39	1.05	114.44	20,977
AVTO1429 x UC82	0.62	36.11	19.96	84.89	156.53	4.79	22.24	0.87	-1.39	5.05	27.01	2.04	27.03	40,797
AVTO1429 x Valoria select	-3.61	38.56	7.09	94.78	282.22	3.88	26.84	0.87	-5.01	5.05	-9.08	2.79	-8	55,740
AVTO1429 x Riogrande	-3.61	38.56	6.56	94.78	182.62	3.69	23.12	0.87	- 10.61	5.13	-9.84	2.29	-9.81	45,711
Cal JVF x AVTO1424	0.01	38.33	5.51	94.78	283.84	3.49	3.48	0.88	-8.09	4.99	66.01	1.84	66.02	36,721
Cal JVF x Danny select	-0.62	36.56	16.60	87.33	146.20	4.94	3.39	0.88	-4.82	5.31	7.79	2.64	7.80	52,851

TABLE 1. Contd.

Crosses	Days to 50% flowering (%)	Better parent (d)	Days to maturity (%)	Better parent (d)	Number of trusses plant^{-1} (%)	Better parent (no.)	Fruit shape index (%)	Better parent	Total soluble sugars (% Brix)	Better parent (%)	Yield plant^{-1} (kg) (%)	Better parent	Yield ha^{-1} (kg) (%)	Better parent
Cal JVF x AVTO1314	-3.75	38.44	-12.61	94.78	359.18	3.49	27.17	0.88	-6.31	5.31	33.28	1.84	33.28	36,721
Cal JVF x UC82	3.85	36.11	12.50	84.89	166.56	4.79	1.22	0.87	0.82	4.99	3.53	2.04	3.54	40,797
Cal JVF x Valoria select	-8.13	41.00	2.34	94.78	192.01	3.88	2.24	0.87	6.73	4.99	-1.11	2.79	-1.12	55,740
Cal JVF x Riogrande	-5.36	41.56	6.21	94.78	170.98	3.69	-1.58	0.87	6.20	5.13	-6.47	2.29	-6.47	45,711
AVTO1424 x Danny select	-0.62	36.56	16.60	87.33	204.15	4.94	4.14	0.90	-16.92	5.31	-13.96	2.64	-13.94	52,851
AVTO1424 x AVTO1314	-6.95	38.33	-13.11	95.33	276.06	3.42	31.85	0.90	-2.28	4.90	88.37	1.05	88.41	20,977
AVTO1424 x UC82	-7.69	36.11	15.24	84.89	225.88	4.79	4.56	0.87	-11.99	4.83	48.53	2.04	48.55	40,797
AVTO1424 x Valoria select	-2.60	38.33	6.29	95.33	237.11	3.88	3.05	0.87	-2.46	4.83	-11.12	2.79	-11.12	55,740
AVTO1424 x Riogrande	-5.21	38.33	3.15	95.33	265.46	3.69	5.72	0.87	-9.09	5.13	6.78	2.29	6.82	45,711
Danny select x AVTO1314	-2.44	36.56	12.99	87.33	193.82	4.94	21.54	0.93	-8.85	5.31	-14.26	2.64	-14.25	52,851
Danny select x UC82	-4.92	36.11	13.88	84.89	207.40	4.94	1.87	0.87	-5.84	5.31	2.16	2.64	2.18	52,851
Danny select x Valoria select	-5.63	36.56	8.78	87.33	162.01	4.94	2.72	0.87	-3.54	5.31	7.07	2.79	7.07	55,740
Danny select x Riogrande	0.29	36.56	11.45	87.33	163.42	4.94	-0.37	0.87	-5.24	5.31	-1.93	2.64	-1.91	52,851
AVTO1314 x UC82	-6.77	36.11	9.75	84.89	246.15	4.79	26.81	0.87	-8.81	4.90	24.85	2.04	24.88	40,797
AVTO1314 x Valoria select	-6.78	38.44	1.49	96.56	268.81	3.88	26.80	0.87	-0.35	4.90	-7.25	2.79	-7.26	55,740
AVTO1314 x Riogrande	-2.01	38.44	0.46	96.56	275.26	3.88	24.92	0.87	2.26	5.13	-21.83	2.29	-21.81	45,711
UC82 x Valoria select	-1.23	36.11	-3.99	84.89	204.16	4.79	3.43	0.87	-1.82	4.79	6.17	2.79	6.19	55,740
UC82 x Riogrande	-5.38	36.11	8.96	84.89	163.21	4.79	1.08	0.87	-4.17	5.13	2.27	2.29	2.29	45,711
Valoria select x Riogrande	-4.07	41.00	5.39	96.78	249.48	3.88	-5.34	0.87	-7.88	5.13	-9.44	2.79	-9.44	55,740

Environments were Kabete 2018 long rain seasons, and at Mwea during 2018 long rain season

TABLE 2. General combining ability effects of 10 tomato parental genotypes for yield traits

Genotypes	Mean squares								
	Days to 50% flowering	Days to maturity	Trusses per plant	Fruit length (cm)	Fruit diameter	Fruit shape index (FSI) (cm)	Total soluble sugar (Brix %)	Average fruit weight (g)	Yield per plant (kg)
Eden select	-0.10	-0.12	-0.79	2.86*	0.34	-0.04	-0.20	-13.62	0.00
Roma VF	0.50*	2.28*	1.96*	0.99*	-3.99	-0.09	0.01	-32.33	0.16*
AVTO1429	0.23	1.50	0.36	-1.25	5.89*	0.14*	0.04	-1.50	-0.20
Cal J	0.83*	-0.50	-1.12	-0.25	-2.09	-0.04	0.22*	-28.31	0.00
AVTO1424	0.14	1.47*	0.23	-0.01	-0.17	-0.01	-0.14	-20.39	-0.13
Danny select	-0.79	-0.90	0.18	-0.61	-0.93	-0.01	0.10*	-26.42	0.19*
AVTO1314	-0.18	-2.04	0.23	-3.88	4.51*	0.17*	0.02	-11.46	-0.32
UC82	-1.56	-4.28	0.66	-1.38	-2.69	-0.03	-0.15	-33.60	0.12*
Valoria select	0.30	1.15	-0.36	0.88	-0.37	-0.03	-0.01	187.37*	0.29*
Riogrande	0.64*	1.44*	-1.35	2.65*	-0.50	-0.06	0.11*	-19.74	-0.11

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

TABLE 3. Specific combining ability (SCA) effects of 45F_1 tomato hybrids for agronomic and yield traits

Crosses	Mean squares								
	Days to 50% flowering	Days to maturity	Trusses per plant	Fruit length (cm)	Fruit diameter (cm)	Fruit shape index (FSI)	Total soluble sugar (Brix %)	Average fruit weight (g)	Yield per plant (kg)
Eden select x Roma VF	0.33	3.79	-4.05**	1.46	2.14	0.02	0.16	25.66	-0.30**
Eden select x AVTO1429	-0.74	3.40	-0.32	0.88	0.01	-0.02	0.48**	18.19	0.11
Eden select x Cal JVF	-1.34	0.83	-2.90	-0.77	-6.02**	-0.11**	-0.41**	1.48	0.75**
Eden select x AVTO1424	-1.34	-0.44	-0.78	1.61	-1.89**	-0.06**	-0.05	21.85	-0.07
Eden select x Danny select	-0.27	5.49	-3.36	0.39	1.51	0.02	0.32**	25.81	-0.12
Eden select x AVTO1314	-1.51	4.11	-0.87	0.73	-1.89**	-0.05	0.12	14.17	0.54
Eden select x UC82	0.35	3.43	-1.47	-1.54	2.40	0.07**	0.11	20.92	0.78**
Eden select x Valoria select	-0.74	2.02	0.32**	-2.05	0.00	0.03	0.30**	20.79	0.15
Eden select x Riogrande	0.35	2.63	-3.46	1.05	-1.67	-0.05**	0.13	39.81**	-0.30**
Roma VF x AVTO1429	-0.24	3.47	-1.21	0.32	0.66	0.01	-0.33**	21.86	0.74**
Roma VF x Cal JVF	-1.38	-0.53	-1.16	0.68	-0.29	-0.02	0.03	20.11	0.02
Roma VF x AVTO1424	0.02	2.56	-3.36	2.80	1.62	-0.02	-0.18	26.24**	-0.34**
Roma VF x Danny select	2.12**	7.18**	-1.90	-2.31	1.18	0.08**	-0.07	17.78	0.32
Roma VF x AVTO1314	-0.31	7.68**	-2.41	-0.58	0.01	0.01	-0.12	18.47	0.23
Roma VF x UC82	0.55	5.37	-0.90	-1.75	-1.45	0.00	-0.39**	14.32	-0.22
Roma VF x Valoria select	-0.83	-0.23	-1.17	-2.75	0.26	0.05**	0.47**	16.94	0.30
Roma VFx Riogrande	-1.26	3.04	-2.14	-2.33	-0.77	0.02	-0.08	15.99	0.20
AVTO1429 x Cal JVF	1.51**	1.48	-1.17	0.08	-2.98**	-0.04	-0.27	15.78	0.33
AVTO1429 xAVTO1424	-0.92	-10.19**	1.41**	-2.90	-1.09	0.04	-0.11	13.15	0.33
AVTO1429 x Danny select	-0.90	3.68	-3.11	-1.55	1.85	0.08**	0.07	25.67	-0.02
AVTO1429 x AVTO1314	-0.13	4.55	-1.41	-0.25	0.83	0.02	-0.13	25.22	-0.04
AVTO1429 x UC82	-0.28	2.18	-2.79	1.12	0.32	-0.01	0.07	23.67	0.13
AVTO1429 x Valoria select	-0.05	4.27	0.72**	1.06	1.78	0.01	-0.13	26.80**	0.65**

TTABLE 3. Contd.

Crosses	Mean squares								
	Days to 50% flowering	Days to maturity	Trusses per plant	Fruit length (cm)	Fruit diameter (cm)	Fruit shape index (FSI)	Total soluble sugar (Brix %)	Average fruit weight (g)	Yield per plant (kg)
AVTO1429 x Riogrande	1.22	9.05**	-4.24**	-1.03	-0.95	0.00	0.24	8.50	0.24
Cal JVF x AVTO1424	1.12	4.72	-2.28	1.48	1.22	0.00	0.11	21.25	-0.44**
Cal JVF x Danny select	-2.02	5.08	-0.79	0.12	-0.15	-0.01	-0.31**	18.11	0.60**
Cal JVF x AVTO1314	-0.76	6.29**	-1.17	0.63	-0.80	-0.03	0.20	20.73	-0.04
Cal JVF x UC82	-1.20	3.93	0.18**	-0.35	0.09	0.02	-0.25	23.64	0.31
Cal JVF x Valoria select	0.85	6.24	-2.47	-1.08	-0.72	0.01	-0.14	-190.77**	0.06
Cal JVF x Riogrande	0.42	4.51	-4.00**	-2.60	0.26	0.05**	-0.04	-188.71**	-0.13
AVTO1424 x Danny select	-0.98	3.29	-0.66	-1.44	0.43	0.04	-0.08	-184.81	0.00
AVTO1424 x AVTO1314	-0.91	0.79	-2.69	1.60	1.56	0.00	0.28**	-185.13	0.03
AVTO1424 x UC82	0.45	3.15	-2.28	0.82	-0.46	-0.02	0.02	-188.13	-0.13
AVTO1424 x Valoria select	-1.78**	-0.81	-2.39	0.44	-0.81	-0.03	0.19	-189.73**	0.07
AVTO1424 x Riogrande	-1.06	3.33	-1.06	0.34	1.03	0.01	0.04	-185.04	0.17
Danny select x AVTO1314	-0.19	-10.94**	-1.24	-0.21	0.04	0.00	0.01	-186.60	0.11
Danny select x UC82	1.52**	5.45	-1.65	2.78	0.64	-0.03	-0.16	24.04	-0.14
Danny select x Valoria select	0.76	2.05	-2.39	-1.01	0.13	0.02	0.15	20.23	0.13
Danny select x Riogrande	-1.15	2.49	-4.06**	-1.69	0.76	0.04	-0.41**	23.59	-0.06
AVTO1314 x UC82	1.26	4.16	-3.02	-0.70	-0.71	0.00	0.27**	17.23	-0.18
AVTO1314 x Valoria select	-1.71**	-0.14	-0.88	-1.05	0.57	0.03	-0.15	21.47	0.24
AVTO1314 x Riogrande	-0.28	1.23	-1.33	1.01	-0.03	-0.02	-0.03	20.37	0.08
UC82 x Valoria select	0.60	2.04	0.18**	-0.94	0.99	0.02	0.27**	26.25**	-0.22
UC82 x Riogrande	-2.19**	-0.23	-2.21	-0.70	0.27	0.01	0.10	18.13	-0.10
Valoria select x Riogrande	1.62**	3.84	-0.23	-1.37	-3.67**	-0.05**	-0.22	-196.15**	-0.09

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

Solan Vajr (-6.56%) and EC-538146 x Solan Vajr (-8.41%), showed significant negative heterosis over better parents. Early flowering and maturity in tomato are important traits, desired for consideration in designing a tomato breeding programme. Speedy tomato improvement in Kenya can be brought about by exploiting heterosis for earliness observed in this study.

Number of trusses per plant. All the F_1 hybrids had significant increases in the number of trusses per plant, compared to their better parents (Table 1). F_1 hybrids with the highest heterosis for number of trusses per plant (> 300%) were Cal J x AVTO1314 (359.18%), AVTO1429 x AVTO1314 (339.08%), Roma VF x AVTO1424 (308.67) and Eden select x AVTO1429 (302.24%). In contrast, the lowest heterosis was recorded in Cal J x Danny select (146.20%), AVTO1429 x UC82 (156.53%) and Danny select x Valoria select (162.01%). A cross between parents with medium number of trusses per plant, led to generation of F_1 hybrid Cal J x AVTO1424 with a higher number of trusses per plant. Additive gene action was dominant in the inheritance of this trait in the F_1 progeny. Therefore, positive heterosis for higher number of trusses is desired because they are associated with tomato yields and, hence high crop productivity.

These findings are in agreement with those of Amaefula *et al*. (2014), who reported better parent heterosis for the number of trusses per plant. The study followed hybridisation of three parental lines (Petomech, Grosso and Insulata) and wild parent (*Lycopersicon pimpinellifolium*) in Nigeria using 4 x 4 diallel. They reported better parent heterosis of 14.56% for number of trusses per plant. Similarly, Singh and Asati (2011) reported the highest heterotic effects over better parents, exhibited by crosses Type-1 x KT-15 (70.06%) and H-24 x KT-15 (43.84%) for number of trusses per plant.

Fruit shape index (FSI). Heterosis showed that 11% of F_1 hybrids had negative values between -0.37 and -5.34%, which indicated elongated fruit shape; while 89% of F_1 hybrids had positive heterosis percentage that indicated pronounced fruit shape (Table 1).Fruit shape index ranged from –5.34% for Valoria select x Riogrande, to 42.35% for Roma VF x AVTO1314. F_1 hybrids with the most elongated fruit shape were Valoria select x Riogrande (-5.34%), Eden select x Riogrande (-5.19%) and Eden select x Cal J (-4.59%).Crosses with pronounced round fruit shape included Roma VF x AVTO1314 (42.35%), Eden select x AVTO1314 (32.70%), AVTO1424 x AVTO1314 (31.85%) and Cal J x AVTO1314 (27.17%).Fruit shape index is an important trait in the selection of tomato fruits for market. Kenyan consumers prefer elongated fruits because round fruit are perceived to have shorter shelf life (Kenneth, 2016). Fruit shape index is influenced by the fruit length and diameter. A study conducted by Gul *et al.* (2011) recorded significantly better parent heterosis for the fruit length and fruit diameter of 32.7 and 15.5%, respectively. This was after conducting a study using 8 x 8 diallel, excluding reciprocals in Islamabad, Pakistan. Ahmad *et al.* (2011) also reported that about 50% combinations from 10 crosses that exhibited significant positive heterosis for fruit length and diameter, which determines the FSI over the better parent and this conforms to the findings of the current study. Comparable findings to those of the present study were reported by Rakha and Sabry (2019) in a study to classify the best combiner parents and cross combinations for developing accomplished hybrids for yield and quality components in tomato using half diallel test in Egypt. They reported FSI increase compared to the better parent as indicated by 14.29% heterosis. This implies that FSI is a desirable indicator for elongated and pronounced fruits. The five F_1 hybrids with elongated fruit shape have potential for further development to varieties preferred by Kenyan consumers.

Total soluble sugar (Brix). Heterosis for total soluble sugars ranged from -16.92 to 8.03%, and 24% of the F_1 hybrids had increased soluble sugar compared to better parents (Table 1). Crosses with higher soluble sugars than better parent included Roma VF x Cal J (8.03%), Roma VF x AVTO1424 (3.51%), AVTO1429 x Cal J (3.6%), Cal J x Valoria select (6.73%) and Cal J x Riogrande (6.20%). F_1 hybrids with the lowest total soluble sugars were AVTO1424 x Danny select (-16.92%), AVTO1424 x UC82 (-11.99%) and Roma VF x AVTO1429 (-11.19%). Total soluble sugar is a measure of % brix of soluble solutes in a tomato fruit (Kumar *et al.*, 2017). Higher soluble sugars are desirable in tomato processing industry; while lower solutes are desired in freshly consumed or table tomatoes (Ahmad *et al.*, 2011). A cross between parents with higher total soluble sugar led to generation of F_1 hybrid Cal J x Riogrande with higher soluble sugar of 5.45%Brix. This indicates that the additive gene action was dominant in the inheritance of this trait in the F_1 progeny. Significant positive heterosis of 33.33 % of total soluble solids was reported by Kumar *et al.* (2006) in three crosses in India, namely ArkaMeghali x Punjab Chhuhara, Arka Saurabh x ArkaAbha and Arka Saurabh x Punjab Chhuhara. Similarly, Ahmad *et al.* (2011) reported that 15 F_1s out 21 crosses showed significant positive heterosis ranging 3.93% to 31.89%. Rakha and Sabry (2019) also reported highly significant negative heterosis in most crosses between both mid and high parent. Kumar *et al.* (2017) also reported findings that support this study that the range of heterosis per cent for total soluble solids varied from -15.44 (P_4 x P_6) to 7.45% (P_5 x P_7) similar to findings herein.The study revealed that 5 F_1 hybrids had high total soluble sugar content of between 4.61 and 8.03. High total soluble solids (4-8^o Brix) are the main desirable quality component for nutritional and processing purpose. Based on the present study results, the hybrids have potential for development into tomato cultivar to be used in processing industries.

Yield per plant. Better parent heterosis for yield showed that 69% of F_1 hybrids had increased yield per plant over the better parents; while 31% had reduced yields (Table 1).The high proportion of F_1 hybrids (69%) that demonstrated positive heterosis, is good news for tomato production in Kenya because it signifies high productivity per unit area, with genotypic improvement. Heterosis for yield per plant ranged from 114.39% for AVTO1429 x AVTO1314 to -21.83% recorded in AVTO1314 x Riogrande. A cross between parents with higher yield per plant led to generation of F_1 hybrid with higher yield per plant as shown by Roma VF x UC82 with 3.36 kg. Additive gene action was dominant in the inheritance of this trait in the F_1 progeny. High positive heterosis is desired because it signifies high productivity per unit area. Negative heterosis, on the other hand, symbolises lower yields and not desirable by many growers because high yield is a major factor in a breeding programme.Similar findings were documented by Rana *et al.* (2005) in a study on heterosis for yield and quality traits on 30 F_1 tomato hybrids after crossing six parents (LE 79-5, EC 191538, BWR 5, EC 191536, Hawaii 7998 and BT-18). Results showed better parent heterosis of 264.91 % for marketable yields by the F_1 hybrid from cross EC 191538 × LE 79-5 and 117.46% for BWR 5 × Hawaii 7998. Positive heterosis for fruit yield was also reported by Singh and Sastry (2011) after they crossed 10 genetically diverse tomato varieties in New Delhi in all possible combinations, excluding reciprocals. The cross Sel 7 x BSS 368 exhibited better parent heterosis for fruit yield per plant (45.89%), plant height (-38%) and average fruit weight (62.70%). Kumur *et al.* (2017) reported that crosses P_4 x P_7, P_5 x P_7 and P_1 x P_7 were the best heterotic combinations as they exhibited significant heterosis percentage for yield per plant over the standard parent. These high yielding F_1 hybrids expressed heterosis of 60.80, 25.80 and 23.13%, respectively.

Results implied that low yielding varieties with other desirable traits such as early maturity and high soluble sugars had potential for improvement by incorporating high yielding varieties in a breeding programme.

General Combining Ability effects. General combining ability for tomato genotypes UC82 (-1.56), Dannyselect (-0.79), AVTO1314 (-0.18) and Eden select (-0.10) showed negative GCA for days to 50% flowering, signifying genotypes with early flowering (Table 2). Similarly, the highest negative GCA effects for days to maturity were exhibited by parental line UC82 (-4.28), AVTO1314 (-2.04), Danny select (-0.90), Cal J (-0.50) and Eden select (-0.12) signifying early maturity. This suggests that these genotypes are early flowering and maturing, and good combiners for earliness. Therefore, these genotypes may be useful donors in hybridisation programmes for generating promising combinations of early flowering and maturing tomato. Similar findings were reported by Saleem *et al*. (2013) that parental line B23 and B24 showed desirable GCA effects for days to maturity, with GCA values of -0.93 and -1.23, respectively. Previous studies in India reported good combiners for yield, early flowering and maturity traits in tomatoes (Brajendra *et al.,* 2012; Tamta *et al.,* 2018).

Parental genotypes, Eden select (2.86), Riogrande (2.65) and Roma VF (0.99), recorded positive GCA for the polar diameter (fruit length), suggesting that their potential for use in breeding varieties with elongated or saladette fruits. Parental lines AVTO1429 (-1.25) and AVTO1314 (-3.88) showed negative GCA effects; signifying round shaped fruits. Similarly, parental genotypes AVTO1314 (0.17) and AVTO1429 (0.14) contributed positive GCA effects for fruit shape index, signifying more round fruit shape; while negative GCA effects which signified genotypes with more elongated fruit shape were exhibited by Riogrande (-0.06), Eden select (-0.04), Roma VF (-0.09), Cal J (-0.04), UC82 (-0.03) and Valoria select (-0.03). Comparable findings by Saleem *et al.* (2013) reported that parental line B25 that had higher GCA effects for fruit length had a positive GCA value of 0.42.

Parental lines, Cal J (0.22), Riogrande (0.11) and Danny select (0.10), had positive GCA effects for total soluble sugars (Table 2). Total soluble sugars are important quality parameters for fresh consumption and processing tomatoes because they directly influence tomato taste and flavour (Ahmad *et al*., 2011). A similar finding with a high positive value (6.33) for total soluble sugars was recorded in parental line Super Marmand (P_2) (El-Gabry *et al.,* 2014). Tomatoes for processing require a minimum Brix of 4.5, which compares with an acceptable range of 3.5 to 5.5 in fresh tomatoes (Kumar *et al*., 2017).

All the parents met minimum Brix criteria (more than 4.5%Brix), except for Eden select that had 4.0% Brix. In addition, all the F_1 hybrids, except AVTO1424 x UC82 and AVTO1424 x Danny select, had soluble sugar content of more than 4.5% Brix. Parental genotype Valoria select (187.37) contributed positive GCA effects for fruit weight (Table 2) signifying genotypes with highest average fruit weight. This shows the value of these genotypes in cross combination for developing tomato genotypes with bigger fruit size. Among the parental genotypes, Valoria select (0.29), Danny select (0.19), Roma VF (0.16) and UC82 (0.12) contributed positive GCA effects for yield per plant, signifying genotypes with highest yield per plant. Therefore, these parents have potential to be incorporate in an improvement programme for yield increase. El-Gabry *et al.* (2014) reported comparable finding that the best combiner with the highest positive value of GCA effects were the parental cultivars Super Strain-B for total yield per plant (0.10) and Edkawy for fruit weight (11.32) that had positive GCA. Similar findings have been reported by Saleem *et al.* (2013) that the parent B24 was attractive for fruit weight and fruit length with positive GCA values of 2.07 and 0.17, respectively.

Specific Combining Ability effects. Hybrids AVTO1429 x Riogrande, Roma VF x AVTO1314, Roma VF x Danny select and Cal J x AVTO1314 were specific combiners for days to maturity (Table 3). Most F_1 hybrids (89%) originated from parents with high positive GCA effects for days to maturity. Some of the hybrids (11%) originated from the crosses between high GCA x low GCA; while others originated from high GCA x high GCA. Negative SCA effects for days to maturity was recorded in the hybrids from cross-combination Danny select x AVTO1314 and AVTO1429 x AVTO1424, suggesting that these are late maturing hybrids. Early maturity observed in the hybrids with high x low GCA combination could be attributed to the interaction between positive allele from good combiner and negative allele in poor combiner. The hybrids from crosses with high x high GCA combination that were also early maturing, could be attributed to the interaction between positive allele from both parents with positive GCA associated with additive x additive allele interaction.

Hybrids of Eden select x AVTO1429, Roma VF x Valoria select, Eden select x Danny select, Eden select x Valoria select, AVTO1424 x AVTO1314, AVTO1314 x UC82, and UC82 x Valoria select were specific combiners for total soluble sugars (Table 3). Some of the hybrids originated from the crosses with low GCA x low GCA and others low GCA x high GCA. These results are consistent with the findings reported by Pandey *et al*. (2006), who observed that best cross combinations involved good x poor general combiners for fruits per plant, pericarp thickness, total soluble solids and total yield per plant; poor x good general combiners for titrable acidity and early yield per plant and poor x poor general combiners for fruit length. This suggests that better cross combinations are not always obtained between good general combiners. Variations of SCA and GCA effects indicated the former variance to be greater than GCA variance; implying dominance of non-additive gene action for total soluble solids as reported by Mondal *et al*. (2009). Combining ability analysis is an important technique used to understand the genetic potential of parents and their hybrids; and provides information on gene effects to help us in formulating an effective breeding strategy. From this study, it may be concluded that cross combinations that were specific combiners for yield traits could be included for further testing for exploitation of hybrid vigour in tomato.

Hybrids Eden select x Cal J, Roma x AVTO1429, AVTO1429 x Valoria select and Cal J x Danny select were more specific combiners for yield per plant (Table 3). Some of the hybrids originated from parental genotypes with low GCA effect x low GCA effects; while others from high GCA effects x low GCA effects. This is attributed to allelic interactions between low combiners x good combiners for the yield per plant. Similar finding on interactions of positive SCA effects were reported by Dhaliwal *et al*. (2004). In the present study, negative SCA effects for yield per plant were recorded on the crosses Cal J x AVTO1424, Roma VF x AVTO1424, Eden select x Riogrande and Eden select x Roma VF implying that the cross combinations were poor for yield trait. Parental genotypes with high or high x low GCA effects reflected positive SCA effects for fruit yield and were found to be the best genotypes for development of segregating F_2 populations for further breeding.

CONCLUSION

This study has shown that parental genotype with good general combining ability for tomato fruit yields (positive GCA effects) are poor specific combiners as exhibited in cross Roma VF x Eden select that reflected negative SCA effects. However, parental genotypes with high or high x low GCA effects reflected positive SCA effects for fruit yield and are the best genotypes for development of segregating F_2 populations for further breeding. In addition, cross-combinations of Eden select x AVTO1429, Roma VF x Valoria select, Eden select x Danny select, Eden select x Valoria select, AVTO1424 x AVTO1314, AVTO1314 x UC82 and UC82 x Valoria select that had high total soluble content could be used in developing varieties with high total soluble content (%Brix) that are demanded by processing industries. Lack of significant SCA effects shown by some crosses for various traits could be because of unfavourable genetic combinations of the parents and agronomic characters.From this experiment, Eden select x Cal J, Roma VF x AVTO1429, AVTO1429 x Valoria select and Cal J x Danny select have potential that could be used in developing varieties with high yield potential.

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