doi:10.14720/aas.2022.118.4.2234 Original research article / izvirni znanstveni članek

Combining ability for morphological and nutritional traits in a diallel cross of tomato (*Solanum lycopersicum* L.)

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Received June 04, 2021; accepted November 14, 2022.
Delo je prispelo 4. junij 2021, sprejeto 14. november 2022

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Abstract: Tomato (*Solanum lycopersicum* L.) is one of the most important vegetable crops grown in Nigeria, either for fresh market or industrial purposes, necessitating the development of a robust tomato breeding programme aimed at maximizing genetic improvement on economically important traits. In this study, the combining ability, nature of gene action, heterosis, and heritability for morphological, nutritional, and physicochemical parameters of tomato were examined in five tomato parents and ten F_1 offsprings, generated with a 5 × 5 half diallel mating design in the greenhouse in 2017. The field evaluation was conducted at the Teaching and Research Farm of Ladoke Akintola University of Technology, Ogbomoso, Nigeria during the cropping season of 2018 using a randomized complete block design with three replications. Analysis of variance for combing ability revealed that both additive and nonadditive gene actions contributed to the fundamental genetic mechanism underlying the inheritance of the measured traits. The top two general combiner parents were UC-OP and Ib-local. Furthermore, the best tomato hybrid specific combiners were FDT$_4$ × UC-OP, FDT$_2$ × Ib-local and UC-OP × Ib-local which involved one parent having a high general combining ability effect for fruit yield and the other having other desirable traits. These hybrids may be further utilized in tomato breeding programmes.

Key words: combining ability; gene action; heritability; heterosis; hybrid; tomato; variation

Kombinacijske zmožnosti za morfološke in hranilne lastnosti paradižnika (*Solanum lycopersicum* L.) pri dialelnem križanju

Izvleček: Paradižnik (*Solanum lycopersicum* L.) je ena najpomembnejših vrtnin, ki se goji v Nigeriji za svežo porabo ali za industrijske namene. Za maksimiranje pridelave je potrebno razviti robustne žlahtniteljske programe, v katerih bi izboljšali njegove genetske in ekonomske lastnosti. V raziskavi je bila preverjena kombinacijska zmožnost delovanja genov, heteroze in dedovanja za morfološke, hranilne in fizikalno-kemijske lastnosti petih starševskih genotipov paradižnika in desetih F_1 potomcev, pridobljenih v 5 x 5 polovičnem dialelnem križanju v rastlinjaku leta 2017. Ovrednotenje v poljskem poskusu je bilo izvedeno na Teaching and Research Farm of Ladoke Akintola University of Technology, Ogbomoso, Nigeria v rastni sezoni 2018 v popolnem naključnem bločnem poskusu s tremi ponovitvami. Analiza variance za kombinacijske zmožnosti je pokazala, da je aditivno in neaditivno delovanje genov prispevalo k osnovnim mehanizmom dedovanja merjenih lastnosti. Dva najboljša starša za komibiniranje lastnosti sta bila ‘UC-OP’ in ‘Ib-local’. Najboljša križanja za kombiniranje lastnosti so bila ‘FDT$_4$’ × ‘UC-OP’, ‘FDT$_2$’ × ‘Ib-local’ in ‘UC-OP’ × ‘Ib-local’, ki so vsebovala starše z velikimi splošnimi kombinacijskimi lastnostmi za pridelek plodov in druge zaželjene lastnosti. Ti hibridi bi lahko bili uporabljeni v nadaljnih žlahtiteljskih programih paradižnika.

Ključne besede: kombinacijska zmožnost; delovanje genov; sposobnost dedovanja; heteroza; hibrid; paradižnik; spremenljivost

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1 INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is one of Nigeria's most important vegetable crops, second only to onions, due to its high consumption, and is well adapted to a variety of climatic conditions, soil types, and altitudes (Osei et al., 2010). Tomatoes make an important contribution to human health and welfare because they are high in ascorbic acids (Vitamin C), minerals (calcium, phosphorus, and iron), and antioxidants (lycopene and β-carotene), which lower the risk of lung, breast, and prostate cancers (Willcox et al., 2003; Palozza et al., 2011; Rai et al., 2012). As a result, breeding programmes prioritize the nutritional and physico-chemical properties of tomato fruit (Panthee et al., 2015; Acharya et al., 2018). Tomato yield is a complex character that is affected by numerous factors. It is critical to note that, due to the geometric progression of human population and the rapid rate of urbanization, which is reducing cultivable land and increasing demand for tomato, breeding for high yield alone is insufficient to meet the demands of consumers and end-users. In Nigeria, there is still a significant gap in the development of high yielding and nutritive tomato hybrids. Several biotic and abiotic stresses are major impediments to the successful adoption and cultivation of improved tomato varieties (Soresa et al., 2020). The Nigerian tomato market is currently saturated with mixtures of diverse cultivar that are unable to meet the numerous demands. Consequently, it has become critical to assess the genetic potential of locally available tomato cultivars for their efficient utilization and further improvement.

In spite of the relatively high cost of hybrid seeds it has proven to be a successful approach for vegetable improvement (Kaushik & Dhaliwal, 2018) and usually characterized by high yield and homogeneity. Therefore, to obtain worthwhile information on the genetic makeup of cultivars useful as parental line in hybrid combination, the combining ability is primarily valuable (Sprague & Tatum, 1942). General combining ability (GCA) and specific combining ability (SCA) distinguishes between the average performance of parents in crosses (GCA) and the deviation of individual crosses from the average of the parents (SCA). Additionally, GCA basically involves additive gene action while SCA provides genetic information on the crosses, hence elucidates the existing nonadditive gene action which offers good choice for exploitation of heterosis (Ahmad et al., 2009; Senapati & Kumar 2015). The diallel mating design approach used in the expression of combining ability of lines provides information on the nature and magnitude of gene actions involved in the expression of quantitative and qualitative traits and helps to identify superior parents for hybrid development. Therefore, involving combining ability as a technique in the analysis and understanding of the genetic potential of parents and their hybrids is one of such possible ways in addressing tomato farmers' and consumers demands. Furthermore, diallel mating designs are useful in estimating genetic parameters, which contributes to a better understanding of the mechanism used to predict genetic progress when parental lines are chosen based on their own performance (Falconer, 1989).

Previous studies have used the diallel mating design to generate information on genetic parameters; GCA estimates (Patil et al., 2013; Singh et al., 2014; Kumar et al., 2018), identification of superior cross combinations with SCA estimates (de Souza et al., 2012; Yadav et al., 2013; Saleem et al., 2013a), heterosis relative to mid parents with potence ratio (THI, 2009; Shende et al., 2012; Agarwal et al., 2014) and heritability in broad and/or narrow sense (Osekita & Ademiluyi, 2014; Mohamed et al., 2018; Kumar et al., 2018) for diverse morphological traits in F_1 tomato hybrids. Results obtained from their studies provided essential information on gene actions controlling the inheritance of traits and crosses that can be utilized for developing high yielding tomato hybrid as well as for exploiting hybrid vigour.

Therefore, this experiment was carried out to determine general and specific combining abilities effects, nature of gene action, relationships between traits, and to estimate heritability, heterosis and the mean performance for qualitative and quantitative traits of tomato cultivars crossed in a half diallel mating design.

2 MATERIALS AND METHODS

The study was conducted at the Teaching and Research Farm of Ladoke Akintola University of Technology (LAUTECH), Ogbomoso, Nigeria and the soils are characterized as alfisol. The Global Positioning System coordinates of the experimental site was 8°10′ North, 4°10′ East, with an altitude of 341 m above sea level. The experimental site falls into the derived savanna agro-ecology of Nigeria, with annual mean rainfall of 1,100 mm and daily temperature ranges from 28–30 °C.

2.1 GENETIC MATERIALS

Five tomato cultivars with different traits, FDT_4 (P_1), FDT_2 (P_2), UC-OP (P_3), Ib-local (P_4) and Kerewa (P_5) representing the cultivars in the rain forest and derived savanna agro ecology of Nigeria were used in this study as the parental lines. Seeds of FDT_4 and FDT_2 were collected from the Federal University of Agriculture, Abeokuta (FUNAAB), Nigeria and seeds of UC-OP and Ib-local were collected from the National Horticultural Research Institute (NIHORT), Ibadan, Nigeria. Kerewa a popular commercial cultivar was collected on farmers' field in Ogbomoso (Table 1). In the first growing season (2017), the parental tomato cultivars were grown in a greenhouse to conduct all needed crosses by hand in all possible combinations excluding reciprocals. In the second growing season (2018), tomato plants were evaluated on field.

2.2 NURSERY OPERATIONS

In 2017 growing season, seeds of each parental line were sown in nursery bed and watered regularly for six weeks. The seedlings were transplanted into a 4.5 kg soil-filled pot mixed with organic fertilizer (0.3 kg of poultry manure) in the greenhouse at six weeks after sowing and each cultivar was represented by 15 pots. The pots were laid out to fit into a diallel mating design and staking was done to keep the plants erect for easy crossing. Hybridization commenced at 7 weeks after transplanting (WAT). To achieve effective pollination, each parent lines with matured flowers that were ready to open within 24 hours were emasculated and crossed using the half diallel mating design of Griffing (1956) method II to produce the F_1's consisting of single crosses and parental lines (selfing). The pollinated flowers were carefully covered with pollinating bags and tagged for identification. The fruits from all successful pollinations were harvested at maturity and the seeds were extracted, dried and labeled for evaluation. The mating design produced 15 genotypes consisting of 10 hybrid crosses and 5 parental lines from selfing.

2.3 TRIAL EVALUATION AND DATA COLLECTION

Each of the 15 genotypes was raised as seedlings in nursery beds for six weeks and regularly watered before being transplanted to the evaluation plots. The parents (5) and F_1's (10) were evaluated on the field at the Teaching and Research Farm of LAUTECH in 2018, using a randomized block plot design with three replications. Each genotype was transplanted on a 5 m by 7.5 m plot with a spacing of 1 m between plots and 0.5 m between plants on a plot. N.P.K (15-15-15) fertilizer was applied at the rate of 120 kg N ha^{-1} three WAT. All other cultural practices, and plant protection against weeds, diseases and insects, were performed as recommended for commercial tomato production. Data collection commenced at 6 WAT and continued till harvesting. Data were recorded on plant height (PH) and stem width (SW), number of leaves per plant (NLPP), number of days to 50 % flowering (DTF), number of secondary branches (NSB), number of cluster per plant (CLPP), number of flower per cluster (NFPC). All harvested fruits of each plant were counted and weighed to determine number of fruits per plant (NFP), and total fruits mass per plant (FWP) measured in gram. Average fruit mass was estimated by dividing the total mass of all harvested fruits per plant by their total number.

Samples of five random ripe fruits per plant were taken from all replications of each genotype to measure pericarp thickness (PCAP) in mm and number of locules per fruit (NLOBE).

2.4 NUTRITIONAL AND PHYSICOCHEMICAL ANALYSES

Tomato fruit juice of each genotype was extracted from five random red ripe fruits per plant taken from all replicates. The extracted juice was filtered through double-layered muslin cloth and used for estimating total soluble solids (TSS), which was measured using a hand refractometer (RA-130-KEM, Kyoto Electronics Manufacturing Co., Ltd., Kyoto, Japan). The readings were recorded as °Brix (0-32 °C) at room temperature. For determination of vitamin C (VIT C) measured in mg kg^{-1}, 10 ml of juice was diluted in 100 ml of distilled water and titrated with NaOH 0.1 N till pH 8.2. The solution was titrated with iodine (0.1 N) till changes in colour occur (IPGRI, 1996). To determine lycopene (LPEN) content (mg kg^{-1}), 5 ml of acetone-n-hexane mixture in the ratio 4:6 was added to 0.8 g of tomato pulp for each genotype. The mix was centrifuged at 5000 rpm for 5 min at 4 °C; the supernatant was extracted and placed in spectrophotometre (model 6400, Jenway) and scanned at 503 nm using the acetone-n-hexane mix as blank (Rosales et al., 2006). Lycopene content was quantified using an extinction coefficient ($E^{\%}$) of 3150. All analysis was done in triplicate for each sample.

2.5 STATISTICAL ANALYSES AND ESTIMATION OF GENETIC PARAMETERS

Analysis of Variance (ANOVA) was conducted and estimate of the combining ability of the genotypes were calculated using SAS (SAS institute, 2011) statistical package according to Griffing's (1956) method II, model II for half diallel analysis which assumes that the genotype and the replicate are both random variables.

Table 1: Description of genetic materials used in the diallel crosses

Genotype	Source	Characteristics	Fruit colour
FDT_4	Federal University of Agriculture, Abeokuta	Oblong fruit shape with two slight lobes	Orange
FDT_2	Federal University of Agriculture, Abeokuta	Rectangle fruit shape	Orange
UC-OP	National Horticultural Research Institute, Ibadan	Rectangle shape, open pollinated variety	Orange
Ib-local	National Horticultural Research Institute, Ibadan	Flat shaped fruit, average-sized with five lobes	Red and yellow
Kerewa	Ogbomoso	Oblong shape, average sized with three lobes.	Pink

The relative importance of general combining ability (GCA) compared to specific combining ability (SCA) was calculated according to Baker (1978). If the ratio is closer to 1, it indicates predominance of additive gene action and greater predictability of progeny performance based on GCA effects (Gurmu et al., 2018). Least square mean were computed and separated using Fisher's least significant difference (LSD) test ($p < 0.05$). Mid-parent heterosis was calculated for all measured traits using the formula of Mather & Jinks (1971) and the student *t*-statistics was used to determine the statistical difference of F_1 hybrid means and the mid-parent according to Wynne et al. (1970) and Kolawole et al. (2019). Potence ratio was calculated according to Smith (1952) to determine the degree of dominance. Complete dominance is indicated when relative potence of gene set = +1.0; while partial dominance is indicated when the relative potence of gene set is between (-1 and +1); over-dominance is considered when potence ratio exceeds +1, whereas, the value zero, indicates absence of dominance. The positive and negative signs indicate the direction of dominance of either parent. Narrow (h^2_{ns}) and broad (H^2_{bs}) sense heritabilities were determined according to Mather & Jinks (1971). Estimates of heritability were categorized as low = < 0.50, moderate = 0.50 and high = > 0.50, (Robinson et al., 1949). Phenotypic correlation coefficients were computed for all pairs of traits using the PROC CORR in SAS (SAS Institute, 2011).

3 RESULTS

3.1 ANALYSIS OF VARIANCE AND MEAN PERFORMANCE

There were highly significant ($p < 0.001$) differences in the mean squares of the tomato parental lines and hybrids for all morphological traits, nutritional and physicochemical parameter measured except for number of leaves per plant (Table 2).

This implied the presence of considerable genetic variation which could be exploited in tomato breeding programme. The coefficient of variation (CV) showed good experimental precisions for most of the traits measured. The analysis of variance for combining ability partitioned genetic variation into GCA and SCA. General and specific combining abilities effects showed significant ($p < 0.001$) additive and nonadditive gene actions influencing all traits except for stem width and number of flower per cluster for GCA and number of leaves per plant, number of days to 50 % flowering and fruit mass per plant for SCA. The comparison between the genetic variance components showed higher values of GCA than those of SCA for 8 traits. The relative importance of GCA in comparison with SCA calculated based on Baker's Ratio ranged from 0.21 for number of flower per cluster to 0.93 for number of leaves per plant. The ratios were closer to unity for 9 traits out of 14, indicating the prevalence of additive gene action for plant height, number of leaves per plant, number of days to 50 % flowering, number of secondary branches, cluster per plant, pericarp thickness, number of locules per fruit, fruit mass per plant and vitamin C while nonadditive gene action was more important for stem width, number of flower per cluster, number of fruits per plant, lycopene and total soluble solid.

The mean performance of the 15 genotypes showed wide variabilities for seven of the traits measured and some hybrids had significantly higher vigour, yield and nutritional quality than the parental cultivars. The parental cultivar, Ib-local (P_4) was superior for 4 morphological traits such as stem width, cluster per plant, number of flower per cluster and fruit mass per plant (Table 3). Consequently, crosses involving Ib-local (P_4): FDT_4 × Ib-local, UC-OP × Ib-local and Ib-local × Kerewa had the highest mean value for number of fruits per plant, number of days to 50 % flowering, fruit mass per plant, cluster

Table 2: Mean squares, general and specific combining ability for morphological traits, nutritional and physicochemical parameters of five tomato parents and their 10 crosses

SOURCE OF VARIATION	df	PH (cm)	SW (mm)	NLPP	DTF	NSB	CLPP	NFPC
REPLICATION	2	0.07	0.01	580.96	0.47	0.07	1.49	0.16
GENOTYPE	14	3.83^{***}	0.01^{***}	1688.42	17.37^{***}	16.99^{***}	16.31^{***}	0.85^{*}
GCA	4	5.62^{***}	0.004	4221.20^{***}	38.49^{***}	18.82^{***}	20.44^{***}	0.15
SCA	10	3.11^{***}	0.012^{***}	675.31	8.92	16.26^{***}	14.65^{***}	1.13^{**}
ERROR	28	0.59	0.003	889.72	4.75	0.76	1.44	0.37
CV (%)		1.45	19.89	13.13	6.44	13.32	15.18	11.31
GCA/SCA		0.78	0.41	0.93	0.90	0.70	0.74	0.21
MEAN		52.88	0.31	227.16	33.87	6.53	7.91	5.38
MINIMUM		50.30	0.16	197.33	31.33	4.67	5.33	4.67
MAXIMUM		54.50	0.42	262.00	40.33	14.33	12.67	6.33

	df	NFP	PCAP (mm)	NLOBE	FMP (g)	LPEN (mg kg^{-1})	VIT C (mg kg^{-1})	TSS (°Brix)
REPLICATION	2	29.4	0.00	0.03	1024.21	0.12	0.03	0.01
GENOTYPE	14	452.00^{***}	0.02^{***}	2.82^{***}	2328.83^{*}	1836.91^{***}	4773.07^{***}	3.83^{***}
GCA	4	111.48^{**}	0.02^{***}	3.57^{***}	5191.15^{**}	664.32^{***}	5783.25^{***}	1.56^{***}
SCA	10	588.21^{***}	0.02^{***}	2.53^{***}	1183.91	2305.95^{***}	4368.99^{***}	4.74^{***}
ERROR	28	27.76	0.00	0.05	932.38	0.23	0.11	0.02
CV (%)		25.91	3.06	8.63	5.90	0.88	0.21	3.32
GCA/SCA		0.27	0.67	0.74	0.90	0.37	0.73	0.40
MEAN		20.33	0.55	2.67	517.47	54.05	160.23	4.61
MINIMUM		11.67	0.46	1.00	466.85	13.54	98.43	1.92
MAXIMUM		61.00	0.71	5.00	573.22	91.60	231.25	6.10

*, **, *** indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively
GCA = general combining ability; SCA = specific combining ability; CV = Coefficient of variation
PH = plant height; SW = stem width; NLPP = number of leaves per plant; DTF = number of days to 50 % flowering; NSB = number of secondary branches; CLPP = cluster per plant; NFPC = number of flower per cluster; NFP = number of fruits per plant; PCAP = pericarp thickness; NLOBE = number of locules per fruit; FMP = fruit mass per plant; LPEN= lycopene; VIT C = vitamin C; TSS= total soluble solid

per plant, tallest plant and stem width. The parental cultivar, UC-OP (P$_3$) was superior for only three morphological traits. It had the highest number of secondary branches, number of fruits per plant and the thickest pericarp. F$_1$ hybrids with UC-OP (P$_3$) as one of the parents (FDT$_2$ × UC-OP, UC-OP × Ib-local and UC-OP × Kerewa) had the thickest pericarp, the tallest plant and the highest fruit mass per plant. The parental cultivar, Kerewa (P$_5$) had the highest mean value for nutritional and physicochemical quality, but with the lowest mean values for most of the morphological traits. Although crosses made to Kerewa (P$_5$) which includes: FDT$_4$ × Kerewa, FDT$_2$ × Kerewa, UC-OP × Kerewa and Ib-local × Kerewa had the highest mean value for number of secondary branches, number of flower per cluster, vitamin C content, number of locules per fruit, cluster per plant, early flowering and stem width. The parental cultivar, FDT$_4$ (P$_1$) was the tallest with the earliest flowers. Crosses involving of FDT$_4$ (P$_1$) such as: FDT$_4$ × FDT$_2$, FDT$_4$ × Ib-local and FDT$_4$ × Kerewa; had the highest mean value for number of leaves per plant, number of fruits per plant, number of secondary branches and number of flower per cluster. The parental cultivar, FDT$_2$ (P$_2$) had highest mean value only for number of leaves per plant. However Crosses of FDT$_4$ × FDT$_2$, FDT$_2$ × UC-OP, FDT$_2$ × Kerewa and FDT$_2$ × Ib-local; had the highest number of leaves per plant and early flowering. The F$_1$ hybrids morphological traits, nutritional and physicochemical parameters mean val-

Table 3: Mean performance of parents and their hybrids for morphological traits, nutritional and physicochemical parameters

Genotype	PH (cm)	SW (mm)	NLPP	DTF	NSB	CLPP	NFPC	NFP	PCAP (mm)	NLOBE	FMP (g)	LPEN	VIT C	TSS (°Brix)
Parents														
FDT_4 (P_1)	53.03	0.32	209.33	31.33	5.00	5.33	5.67	11.67	5.20	2.10	487.51	24.19	184.74	5.34
FDT_2 (P_2)	50.30	0.27	217.67	34.00	5.33	5.33	5.00	12.67	4.80	1.00	499.26	88.75	166.64	1.92
UC-OP (P_3)	52.87	0.35	206.67	33.33	5.67	5.33	5.67	61.00	5.30	2.00	494.29	14.26	204.18	5.10
Ib-local (P_4)	52.07	0.42	207.67	34.00	4.67	8.00	6.00	15.67	4.80	5.00	518.02	51.78	127.54	4.22
Kerewa (P_5)	51.03	0.20	201.00	34.67	5.33	6.00	4.67	14.33	5.20	2.83	466.85	91.60	231.25	5.82
Mean	51.86	0.31	208.47	33.47	5.20	6.00	5.40	23.07	5.06	2.59	493.18	54.11	182.87	4.48
Crosses														
P_1×P_2	53.33	0.30	262.00	33.33	6.00	8.00	5.00	16.67	5.30	2.33	517.67	57.75	110.69	5.32
P_1×P_3	53.13	0.31	259.33	33.33	6.00	11.00	6.00	17.33	6.10	2.00	516.16	42.73	164.67	3.69
P_1×P_4	54.07	0.23	250.00	33.67	5.67	9.67	5.33	33.33	5.60	3.17	570.95	83.40	176.45	5.25
P_1×P_5	52.70	0.31	257.33	31.67	14.33	8.67	6.33	15.00	6.60	3.10	512.35	54.51	98.43	4.81
P_2×P_3	53.00	0.37	253.00	32.33	7.67	8.33	5.00	15.67	7.10	2.00	518.69	57.39	123.66	6.10
P_2×P_4	52.87	0.16	223.00	33.33	5.00	11.00	4.67	17.33	5.20	2.00	509.04	76.12	188.44	4.81
P_2×P_5	53.40	0.33	216.67	31.33	6.00	6.33	5.00	18.67	4.60	3.00	524.84	37.50	200.43	3.83
P_3×P_4	54.50	0.29	197.33	40.33	6.00	7.00	5.00	18.33	5.80	2.33	573.22	55.43	115.13	2.84
P_3×P_5	54.40	0.34	240.33	38.00	8.33	6.00	6.00	19.33	4.90	4.00	515.43	13.54	131.07	5.26
P_4×P_5	52.47	0.38	206.00	33.33	7.00	12.67	5.33	18.00	6.30	3.20	537.75	61.75	180.17	4.82
Mean	53.39	0.30	236.50	34.07	7.20	8.87	5.37	18.97	5.75	2.71	529.61	54.01	148.91	4.67
LSD (0.05)	1.28	0.10	49.89	3.65	1.46	2.01	1.02	8.81	0.30	0.39	51.07	0.80	0.55	0.26

PH = plant height; SW = stem width; NLPP = number of leaves per plant; DTF = number of days to 50 % flowering; NSB = number of secondary branches; CLPP = cluster per plant; NFPC = number of flower per cluster; NFP = number of fruits per plant; PCAP = pericarp thickness; NLOBE = number of locules per fruit; FMP = fruit mass per plant; LPEN= lycopene (mg kg^{-1}); VIT C = vitamin C (mg kg^{-1}); TSS= total soluble solid ues tended to be either more than their respective mid-or better parental values with few exceptions.

3.2 ESTIMATES OF GENERAL AND SPECIFIC COMBINING ABILITIES EFFECTS

The estimates of GCA effects varied among the five parental cultivar and they all showed good general combining abilities for diverse traits. The parental cultivars FDT$_4$ with highly significant ($p < 0.001$) and positive GCA effects was considered as good general combiner only for fruit vitamin C content (Table 4). Although, two other parents viz. Kerewa and UC-OP showed highly significant ($p < 0.001$) and positive GCA effect for this trait as well.

Moreover, for number of flower per cluster, UC-OP parental cultivar showed highly significant ($p < 0.001$) and positive GCA effect. Similarly, parental cultivar FDT$_2$ showed highly significant ($p < 0.001$) and positive GCA effect for number of leaves per plant and fruit lycopene content. The parental cultivar Ib-local showed highly significant ($p < 0.001$) and positive GCA effect for plant height, fruit mass per plant and fruit lycopene content. Parental cultivar Kerewa showed highly significant ($p < 0.001$) and positive GCA effects for number of secondary branches, cluster per plant and total soluble solid. On the other hand, considering number of days to 50 % flowering, UC-OP parental cultivar with significant ($p < 0.05$) and negative GCA effects was considered as good general combiner because desirable GCA effects for this trait must be negative for the development of early tomato hybrid. Likewise, parental cultivars UC-OP, FDT$_2$ and FDT$_4$ with significant ($p < 0.001$) and negative GCA effects for number of locules per fruit were considered as good general combiners. This is because a minimal number of fruit locules are desired for attractive shape and ease of processing in tomato.

Table 4: Estimates of the GCA effects of five tomato parents for morphological traits, nutritional and physicochemical parameters

	Parents				
TRAITS	FDT$_4$	FDT$_2$	UC-OP	Ib-local	Kerewa
PH (cm)	-0.70^{***}	-0.06	0.14	0.73^{***}	-0.11
SW (mm)	0.01	-0.02	0.01	-0.01	0.01
NLPP	-15.90^{**}	20.77^{***}	6.96	-6.75	-5.09
DTF	-0.65	-0.55	-1.03^{*}	2.35^{***}	-0.12
NSB	-1.17^{***}	0.59^{***}	-0.17	-0.50^{**}	1.26^{***}
CLPP	-1.73^{***}	0.46	0.41	0.17	0.70^{**}
NFPC	0.06	0.06	-0.13	-0.04	0.06
NFP	0.71	-1.48	3.38^{***}	0.05	-2.67^{**}
PCAP (mm)	-0.04^{***}	0.01^{**}	0.03^{***}	-0.02^{***}	0.01^{***}
NLOBE	-0.14^{***}	-0.30^{***}	-0.43^{***}	0.40^{***}	0.47^{***}
FMP (g)	-21.63^{***}	4.18	-3.30	22.15^{***}	-1.41
LPEN (mg kg^{-1})	-4.22^{***}	8.66^{***}	-5.56^{***}	1.63^{***}	-0.52^{***}
VIT C (mg kg^{-1})	19.67^{***}	-19.12^{***}	6.24^{***}	-15.38^{***}	8.59^{***}
TSS (^{o}Brix)	0.01	-0.19^{***}	0.28^{***}	-0.35^{***}	0.24^{***}

*, **, *** indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively

PH = plant height; SW = stem width; NLPP = number of leaves per plant; DTF = number of days to 50 % flowering; NSB = number of secondary branches; CLPP = cluster per plant; NFPC = number of flower per cluster; NFP = number of fruits per plant; PCAP = pericarp thickness; NLOBE = number of locules per fruit; FMP = fruit mass per plant; LPEN= lycopene; VIT C = vitamin C; TSS= total soluble solid

None of the SCA effects were significant for number of leaves per plant and fruit mass per plant (Table 5). For plant height only the cross between Ib-local × Kerewa had positive and significant ($p < 0.01$) SCA effect. Likewise, only FDT$_4$ × Ib-local had positive and highly significant ($p < 0.001$) SCA effect for stem width, only the F$_1$ hybrid (FDT$_2$ × UC-OP) had positive and significant ($p < 0.05$) SCA effect for number of flower per cluster and only FDT$_4$ × UC-OP had positive and highly significant ($p < 0.001$) SCA effect for number of fruits per plant. Also, from the 10 F$_1$ hybrids, two crosses (FDT$_2$ × Kerewa and Ib-local × Kerewa) exhibited positive and highly significant ($p < 0.001$) SCA effects for number of secondary branches and the former reflected higher positive values for SCA effect. Similarly, the crosses between FDT$_4$ × Kerewa and FDT$_2$ × Kerewa had positive and highly significant ($p < 0.001$) SCA effect for pericarp thickness and the later reflected higher positive values for SCA effect. For cluster per plant, three crosses (FDT$_4$ × Ib-local, FDT$_2$ × UC-OP and UC-OP × Ib-local) showed positive and significant ($p < 0.001$) SCA effects whereas, the later reflected the highest positive values for SCA effect. The crosses FDT$_4$ × FDT$_2$, FDT$_4$ × Kerewa, UC-OP × Ib-local and Ib-local × Kerewa exhibited negative and highly significant ($p < 0.001$) SCA effects for number of locules per fruit but FDT$_4$ × FDT$_2$ had the highest negative value for SCA effect. Five out of the ten F$_1$ hybrids reflected positive and highly significant ($p < 0.001$) SCA effects for nutritional and physicochemical parameters. With respect to fruit lycopene content the best hybrid combination was found to be the cross FDT$_4$ × FDT$_2$, which gave the highest positive value for SCA effect. Comparing the estimated SCA effects for all crosses, the cross between FDT$_2$ × Ib-local could be considered as the best hybrid combination for vitamin C and total soluble solid since; it showed the highest and highly significant ($p < 0.001$) positive values for the SCA effects.

Table 5: Estimates of the SCA effects involving morphological traits, nutritional and physicochemical parameters of 10 tomato crosses derived from a 5 × 5 half diallel

CROSS	PH (cm)	SW (mm)	NLPP	DTF	NSB	CLPP	NFPC
FDT$_4$ × FDT$_2$	-1.82***	-0.03	-14.37	1.33	-0.62	-1.30*	-0.49
FDT$_4$ × UC-OP	0.55	0.03	-11.56	1.14	0.48	-1.25*	0.37
FDT$_4$ × Ib-local	-0.84*	0.12***	3.16	-1.57	-0.19	1.65**	0.60
FDT$_4$ × Kerewa	0.54	-0.13***	8.79	0.33	-0.48	0.02	-0.65*
FDT$_2$ × UC-OP	0.17	0.01	4.44	1.05	-0.95*	2.22***	0.70*
FDT$_2$ × Ib-local	0.51	-0.04	8.83	-2.00	-0.95*	1.13	-0.06
FDT$_2$ × Kerewa	0.56	0.03	7.79	-0.95	4.24***	-1.22*	0.35
UC-OP × Ib-local	-0.89*	-0.14***	-4.37	-1.86	-0.86	2.51***	-0.54
UC-OP × Kerewa	0.33	0.05	-0.44	-0.86	-0.14	-3.08***	-0.41
Ib-local × Kerewa	1.06**	0.05	8.70	3.67**	1.52***	-4.03***	0.30

	NFP	PCAP (mm)	NLOBE	FMP (g)	LPEN (mg kg^{-1})	VIT C (mg kg^{-1})	TSS (°Brix)
FDT$_4$ × FDT$_2$	-6.90***	-0.04***	-1.23***	-0.76	30.27***	5.85***	-2.51***
FDT$_4$ × UC-OP	36.57***	-0.02*	-0.10	1.75	-30.02***	18.04***	0.20*
FDT$_4$ × Ib-local	-5.43*	-0.02**	2.07***	0.02	0.32	-36.99***	-0.05
FDT$_4$ × Kerewa	-14.14***	0.04***	-0.46***	-14.30	20.86***	27.92***	1.66***
FDT$_2$ × UC-OP	-0.71	0.02	0.06	-2.19	-14.42***	17.32***	-1.01***
FDT$_2$ × Ib-local	-4.90	0.01	0.39***	27.15	19.06***	50.71***	1.18***
FDT$_2$ × Kerewa	-1.90	0.05***	0.52***	-16.04	-21.29***	-62.58***	1.24***
UC-OP × Ib-local	-6.43*	-0.05***	-0.64***	-27.28	26.00***	37.35***	0.27***
UC-OP × Kerewa	-13.81***	-0.04***	0.48***	19.90	3.98***	-23.67***	-0.38***
Ib-local × Kerewa	-0.48	-0.003	-0.68***	-11.34	-43.51***	-36.72***	-0.32***

*, **, *** indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively
PH = plant height; SW = stem width; NLPP = number of leaves per plant; DTF = number of days to 50 % flowering; NSB = number of secondary branches; CLPP = cluster per plant; NFPC = number of flower per cluster; NFP = number of fruits per plant; PCAP = pericarp thickness; NLOBE = number of locules per fruit; FMP = fruit mass per plant; LPEN= lycopene; VIT C = vitamin C; TSS= total soluble solid

3.3 BROAD-SENSE (H^2) AND NARROW-SENSE (h^2) HERITABILITIES ESTIMATES

Broad sense heritability estimates ranged from 0.28 for number of leaves per plant to 1.00 for lycopene and vitamin C (Table 6). The estimates were high for plant height, stem width, number of secondary branches, cluster per plant, number of fruits per plant, pericarp thickness, lycopene, vitamin C and total soluble solid, indicating low environmental influence. The remaining five traits had low broad sense heritability estimates. Narrow sense heritability estimates ranged from 0.04 for number of secondary branches to 0.50 for pericarp thickness.

The estimates were relatively low for number of leaves per plant, number of secondary branches, cluster per plant, number of flower per cluster and vitamin C whereas, stem width, number of days to 50 % flowering, pericarp thickness, lycopene and total soluble solid had moderate narrow sense heritability estimates, suggesting their importance in enhancing selection.

3.4 HETEROSIS AND POTENCE RATIO ESTIMATES OF TOMATO F_1 HYBRIDS

All the traits showed either or both significant positive or negative heterosis in different crosses, thereby reflecting that the parental cultivars are genetically diverse for traits measured except for number of secondary branches and pericarp thickness (Table 7). Mid-parent heterosis estimates for plant height were significant and positive for the ten tomato F_1 hybrids, and the highest (5.4 %) was observed for FDT$_2$ × Kerewa. The potence ratios for plant height ranged from 0.7 to 7.5, with nine crosses indicating overdominance and one indicating partial dominance in the inheritance of this trait. Simi-

Table 6: Narrow and broad sense heritability for morphological traits, nutritional and physicochemical parameters of tomato

Traits	Narrow-sense Heritability	Broad-sense Heritability
PH (cm)	0.14	0.66
SW (mm)	0.21	0.57
NLPP	0.08	0.28
DTF	0.25	0.49
NSB	0.04	0.88
CLPP	0.08	0.77
NFPC	0.09	0.42
NFP	0.15	0.87
PCAP (mm)	0.50	0.95
NLOBE	0.10	0.33
FMP (g)	0.13	0.33
LPEN (mg kg^{-1})	0.22	1.00
VIT C (mg kg^{-1})	0.09	1.00
TSS (°Brix)	0.25	0.99

PH = plant height; SW = stem width; NLPP = number of leaves per plant; DTF = number of days to 50 % flowering; NSB = number of secondary branches; CLPP = cluster per plant; NFPC = number of flower per cluster; NFP = number of fruits per plant; PCAP = pericarp thickness; NLOBE = number of locules per fruit; FMP = fruit mass per plant; LPEN= lycopene; VIT C = vitamin C; TSS= total soluble solid

larly, fruit mass per plant reflected desirable positive mid parent heterosis for the ten tomato F_1 hybrids, and the highest (13.7 %) was observed for FDT_4 × Ib-local. The potence ratios for fruit mass per plant ranged from -8.8 to 3.4 with nine crosses indicating overdominance and one cross combination (FDT_2 × Ib-local) indicating no dominance in the inheritance of this trait. For number of leaves per plant, a positive heterosis is desirable and was estimated for nine F_1 hybrids, and the highest (25.7 %) was observed for FDT_4 × UC-OP. These results were also confirmed by potence ratios, which had positive/negative values, indicating the presence of partial to over dominance effects. Regarding number of leaves per plant, 9 F_1 hybrids exhibited significant positive heterosis over mid parent and only the cross between UC-OP × Ib-local had significant negative heterosis but was also the only hybrid with significant positive heterosis over mid parent for cluster per plant. The potence ratios for number of leaves per plant ranged from -11.6 to 49.8 with eight crosses indicating overdominance and two indicating partial dominance in the inheritance of this trait whereas, the potence ratios for cluster per plant indicates partial dominance. For number of days to 50 % flowering, a negative heterosis is desirable and was estimated for half of the tomato F_1 hybrids, and the lowest (-8.7 %) was observed for FDT_2 × Kerewa indicating earliness, supported by the potence ratios signifying partial to over dominance effects. The estimates of heterosis, relative to mid parental values reflected significant mid parent heterosis but with only negative signs, on five and four tomato F_1 hybrids for number of flower per cluster and number of fruits per plant respectively, indicating the presence of the various degree of recessiveness involved in the inheritance of the two traits. This result was also confirmed by the potence ratios, which appeared with negative values for most of the hybrids. The range of significant mid parent heterosis in the desired direction for nutritional parameters varied from 2.3 to 28.1 % with the maximum (11.4 %) for lycopene content being found in FDT_2 × UC-OP while the best hybrid for tomato vitamin C content was FDT_2 × Ib-local with mid parent heterosis estimate of 28.1 %. These results were further confirmed with the potence ratios which were majorly described by partial to over dominance effects.

3.5 PHENOTYPIC CORRELATIONS BETWEEN TRAITS

Fruit mass per plant was significant ($p < 0.01$) and positively correlated with plant height (r = 0.46), number of days to 50 % flowering (r = 0.34) and cluster per plant (0.34) (Table 8). Number of flower per cluster had a significant ($p < 0.01$) positive association with stem width (r = 0.45) and number of secondary branches (r = 0.38).

A positive and significant ($p < 0.01$) correlation was observed between number of secondary branches and number of leaves per plant (r = 0.39). Number of locules per fruit also showed significant ($p < 0.05$) and positive correlation with stem width (r = 0.30) and number of flower per cluster (r = 0.33). On the other hand, correlation between the nutritional parameters and morphological traits were significant ($p < 0.01$) but negative, with correlation coefficient ranging from -0.30 to -0.51.

4 DISCUSSION

The significant variation among the tomato parental lines and their F_1 hybrids for all traits except number of leaves per plant shows inherent variability among the parental cultivars which support the report of Saleem et al. (2013b) and Kumar et al. (2018). These variations allowed combining ability analysis (Singh & Chaudhary, 1977). Considering all the traits measured in this study,

Table 7:Estimates of percent mid-parent heterosis and potence ratios for morphological traits, nutritional and physicochemical parameters of 10 tomato crosses

	Crosses									
	FDT$_4$ × FDT$_2$		FDT$_4$ × UC-OP		FDT$_4$ × Ib-local		FDT$_4$ × Kerewa		FDT$_2$ × UC-OP	
	Parameters									
TRAITS	MPH (%)	Potence ratio	MPH (%)	Potence ratio	MPH (%)	Potence ratio	MPH (%)	Potence ratio	MPH (%)	Potence ratio
PH (cm)	3.2**	1.2	0.3**	2.2	2.9**	3.1	1.3**	0.7	2.8**	1.1
SW (mm)	-0.6	-0.1	-7.4	1.7	-37.5**	2.8	20.5	0.8	18.1	1.4
NLPP	22.7**	-11.6	24.7**	38.5	19.9**	49.8	25.4**	12.5	19.3**	-7.4
DTF	2.0**	-0.5	3.1**	-1.0	3.1**	-0.8	-4.0**	0.8	-4.0**	4.0
NSB	16.1	-5.0	12.5	-2.0	17.2	5.0	177.4	-55.0	39.4	13.0
CLPP	50.0	0.0	106.3	0.0	45.0	-2.3	52.9	-9.0	56.3	0.0
NFPC	-6.3**	-1.0	5.9	0.0	-8.6**	3.0	22.6	2.3	-6.3**	-1.0
NFP	36.9	-9.0	-52.3**	0.8	143.9	-9.8	15.4	-1.5	-57.5**	-0.9
PCAP (mm)	5.9	1.5	15.8	-25.0	12.0	2.6	27.6	43.0	39.5	8.6
NLOBE	50.5	1.4	-2.4	-1.0	-10.8**	0.3	25.7	-1.7	33.3	1.0
FMP (g)	4.9**	-4.1	5.2**	-7.5	13.7**	-4.5	7.4**	3.4	4.4**	-8.8
LPEN (mg kg^{-1})	2.3**	-0.1	122.3	4.7	119.6	-3.3	-5.9**	0.1	11.4**	-0.2
VIT C (mg kg^{-1})	-37.0**	-7.2	-15.3**	3.1	13.0**	0.7	-52.7**	4.7	-33.3**	-3.3
TSS (^{o}Brix)	46.7	1.0	-29.3**	-12.7	9.9	0.9	-13.8**	3.2	74.0	1.6
	Crosses									
	FDT$_2$ × Ib-local		FDT$_2$ × Kerewa		UC-OP × Ib-local		UC-OP × Kerewa		Ib-local × Kerewa	
	Parameters									
TRAITS	MPH (%)	Potence ratio	MPH (%)	Potence ratio	MPH (%)	Potence ratio	MPH (%)	Potence ratio	MPH (%)	Potence ratio
PH (cm)	3.3**	1.9	5.4**	7.5	3.9**	5.1	4.7**	2.7	1.8**	1.8
SW (mm)	-54.1**	-2.5	39.0	-2.4	-26.2*	2.9	23.6	0.8	21.5	0.6
NLPP	4.9**	-2.1	3.5**	-0.9	-4.8**	19.7	17.9**	12.9	0.8**	0.5
DTF	-2.0**	0.0	-8.7**	-9.0	19.8**	-20.0	11.8**	-6.0	-2.9**	3.0
NSB	0.0**	0.0	12.5	0.0	16.1	1.7	51.5	17.0	40.0	-6.0
CLPP	65.0	3.3	11.8	2.0	5.0**	-0.3	5.9	-1.0	81.0	5.7
NFPC	-15.2**	-1.7	3.5	-1.0	-14.3**	5.0	16.1	1.7	0.0	0.0
NFP	22.4	2.1	38.3	6.2	-52.2**	-0.9	-48.7**	-0.80	20.0	4.5
PCAP (mm)	9.0	-13.0	-7.3	-2.2	15.2	2.9	-7.0	-5.5	26.9	-6.7
NLOBE	-33.3**	-0.5	56.5	1.2	-33.3**	0.8	65.5	-3.8	-18.3**	-0.7
FMP (g)	0.1**	0.0	8.7**	-2.6	13.3**	-5.7	7.3**	2.5	9.2**	1.8
LPEN (mg kg^{-1})	8.3**	-0.3	-58.4**	-37.1	67.9	-1.2	-74.4**	1.0	-13.9**	0.5
VIT C (mg kg^{-1})	28.1**	-2.1	0.8**	0.1	-30.6**	-1.3	-39.8**	6.4	0.4**	-0.0
TSS (^{o}Brix)	56.9	1.5	-1.0	-0.0	-39.0**	-4.1	-3.7	0.6	-3.9	0.3

MPH = Mid-parent heterosis

*, **Significantly different from mid-parent at 0.05 and 0.01 probability levels, respectively, using *t*-test

Table 8: Pearson's correlation coefficients (r) between tomato morphological traits and nutritional parameters

	PH (cm)	SW (mm)	NLPP	DTF	NSB	CLPP	NFPC	NFP	NLOBE	FMP (g)	LPEN (mg kg^{-1})
SW	0.10										
NLPP	0.26	-0.08									
DTF	0.11	-0.13	-0.18								
NSB	0.11	0.18	0.39^{**}	-0.08							
CLPP	0.12	-0.11	0.29^{*}	-0.06	0.11						
NFPC	0.10	0.45^{***}	0.14	-0.09	0.38^{**}	0.01					
NFP	0.13	0.07	-0.17	0.06	-0.15	-0.12	0.09				
NLOBE	0.18	0.30^{*}	-0.06	0.15	0.16	0.13	0.33^{*}	-0.06			
FWP	0.46^{***}	0.09	0.17	0.34^{*}	0.10	0.34^{*}	0.00	-0.01	0.15		
LPEN	-0.44^{***}	-0.47^{***}	0.00	-0.01	-0.13	0.28	-0.42^{***}	-0.33^{*}	-0.19	0.07	
VIT C	-0.30^{*}	-0.30^{*}	-0.35^{*}	-0.22	-0.51^{***}	-0.10	-0.28	0.28	-0.21	-0.30^{*}	0.13

*, **, *** indicates significance at 0.05, 0.01, and 0.001 probability levels, respectively
PH = plant height; SW = stem width; NLPP = number of leaves per plant; DTF = number of days to 50 % flowering; NSB = number of secondary branches; CLPP = cluster per plant; NFPC = number of flower per cluster; NFP = number of fruits per plant; NLOBE = number of locules per fruit; FMP = fruit mass per plant; LPEN= lycopene; VIT C = vitamin C (mg kg^{-1})

the significant differences exhibited by GCA variance for number of leaves per plant, number of days to 50 % flowering and fruit mass per plant implies that only these three traits are controlled solely by additive gene action and the decision to improve those traits would be effective in early generations (Avdikos et al., 2021). The preponderance of additive variance in expression of morphological traits has been reported by Singh et al. (2010), Farzane et al. (2012), Shalaby (2013) and Vekariya et al. (2019). On the other hand, the exclusive significance of SCA variance for stem width and number of flower per cluster showed supremacy of nonadditive gene action the main cause of heterosis (Burdick, 1954) in the inheritance of these traits in agreement with the reports of (Govindarasu et al., 1981; Shankar et al., 2013).

The significance of both GCA and SCA variances for plant height, number of secondary branches, cluster per plant; number of fruits per plant, pericarp thickness, number of locules per fruit, lycopene, vitamin C and total soluble solid indicate the joint role of both additive and non-additive gene action which corroborate the report of Singh et al. (2010), Kumar et al. (2018) and Dufera et al. (2018). The magnitudes of GCA variances were higher than those of SCA variance for seven traits. Also, the ratio of GCA: SCA was greater than unity for those traits, indicating the preponderance of additive gene action in their inheritance (Christie & Shattuck, 1992). This is in agreement with Bakers' predictability ratio as the ratios for these traits were greater than 0.50. Therefore, selection for these traits could be an effective breeding approach in tomato improvement programmes. In addition, since GCA variances are higher than SCA variances, early generation selection of genotypes based on those traits becomes more efficient and promising hybrids can be identified (Smith et al., 2008). Conversely, the magnitude of SCA variances were higher than those of GCA variance for stem width, number of flower per cluster, number of fruits per plant, lycopene and total soluble solid as reported earlier (Farzane et al., 2012; Shende et al., 2012; de Souza et al., 2012; Yadav et al., 2013). Besides, the bakers' ratios were below 0.50 for these traits indicating the preponderance of nonadditive gene action in their inheritance (Christie & Shattuck, 1992). Thus, hybrid vigour can be exploited considering these traits in a tomato breeding programme but selection of superior genotypes may be delayed till later generations when the genes are fixed in the homozygous lines (Geleta & Labuschagne, 2006).

Out of the 14 traits measured, the overall parental mean value were significantly lower than the hybrids mean value for number of leaves per plant, number of secondary branches, cluster per plant, number of fruits per plant, fruit mass per plant and vitamin C which revealed an overall improvement in those traits through hybridization. It is important to mention that the parental lines and their offspring had similar gene for plant height which varied only by 2.9 %, as they both displayed the determinate growth habit. Additionally, the observed high number of leaves per plant was mainly because the data was collected at maturity which corroborates the report of Ibitoye et al. (2000). On the other hand, Ngosong et al. (2017) reported between 15 and 30 leaves per plant but at three weeks after planting which implies that the stage of plant maturity determines the number of leaves. Thakur et al. (2017) and Vieira et al. (2019) previously described pericarp mean thickness for ripe tomatoes ranging between 4.1mm and 7.6mm, correlating with the value obtained in this study. The wide range for vitamin C observed in this study was in consonance with the report of Rivero et al. (2022) who reported 115.7 to 178.5 mg kg^{-1} in tomato cultivars commercialized in Cuba. With the exception of stem width, comparing the mean performance of the ten F_1 hybrids and their parental cultivar for other measured traits shows that more than eight of the hybrids tended to be either higher than their respective lower parent or deviated towards the higher parent. Superiority reflected by these hybrids was in agreement with the report of Pradeepkumar et al. (2001) and Hannan et al. (2007).

The estimations of general and specific combining abilities provided information on the breeding potential of the five tomato parents and their F_1 crosses. In crop improvement programmes, an astute selection of parental lines promotes a well-planned hybridization programme, and a parent with higher positive significant GCA effects (depending on the desired direction per trait) is considered a good general combiner. The estimates of significant GCA effects in the desired direction shows the reflection of the parental cultivars potential to transfer the traits to their progeny (Gayosso-Barragán et al., 2019). The parental cultivar UC-OP had the most significant GCA effects, with 5 traits in the desired direction, followed by FDT_2 and Kerewa with 4 traits each. By ranking the five parents according to the GCA effects, only Ib-local can be identified as promising general combiners for fruit mass per plant and plant height. Likewise, only FDT_2 was identified as general combiner for number of leaves per plant. Also, only Kerewa was superior general combiners for secondary branches and cluster per plant and UC-OP combines well for early flowering, number of fruits per plant and number of locules per fruit. Considering more than a parent with significant GCA effects in the desired direction for some traits; the parental cultivars FDT_2 and Ib-local seems to be better general combiners for lycopene. The parental cultivars, FDT_4, Kerewa and UC-OP were promising general combiners for vitamin C, Kerewa and UC-OP were identified as superior general combiners for total soluble solid while FDT_2, UC-OP and Kerewa are good combiner for pericarp thickness which makes them suitable for industrial use. These two parents (FDT_2 and FDT_4) also combine well for number of locules per fruit. Hence, the five parents were general combiners for diverse traits. Parents with high GCA effects for multiple traits could be used in breeding programmes to develop tomatoes with different combinations of traits because favourable additive genes would have accumulated (Bahari et al., 2012). Previous studies have reported significantly positive GCA effects for number of branches per plant (Singh and Nandapuri, 1974), number of fruits per plant (Dharmatti, 1996), plant height (Patil, 2013), fruit mass (Singh et al., 2014) and total soluble solid (Kumar et al., 2018) in tomato in spite of the different parents and environments used in their studies.

High and positive SCA effect estimates reveal the best combiner among the parental cultivars for the development of hybrids with specific target traits (Peña et al., 1998).

All the hybrid combinations were found to be good specific combiners for a minimum of two traits, indicating the significant role of nonadditive gene action in the inheritance of these traits. Tomato is a self-pollinated crop; hence SCA effect may not contribute much to improvement of traits but cross combinations with SCA in the desired direction coupled with good GCA may be utilized in breeding programmes (Wamm et al., 2010; Rewale et al., 2003). In this study, all cross combinations showed at least one desirable SCA effect, and none of the hybrids showed significant SCA effects for all traits. Tomato F_1 hybrids viz. UC-OP × Ib-local was the best specific combiners with the highest number of traits. The cross combinations between FDT_4 × FDT_2, FDT_4 × UC-OP, FDT_4 × Kerewa and UC-OP × Ib-local exhibited highly significant positive SCA effects for some morphological traits, nutritional and physicochemical parameters. According to Singh & Narayanan (1993) SCA effect refers to non-additive gene action which has positive relationship with heterosis. Therefore, hybrids FDT_4 × UC-OP, FDT_2 × Ib-local and UC-OP × Ib-local which involves one parent with a high GCA effect for number of fruits per plant and fruit mass per plant may be considered useful for the improvement of fruit yield, lycopene, vitamin C and total soluble solid and heterosis breeding may be recommended (Saleem et al., 2013a). These hybrids would be expected to produce segregants of a fixable nature in segregating generations through the simple pedigree method (Pandiarana et al., 2015).

Heritability estimates indicate the reliability with which traits can be passed down from one generation to the next. Estimates of broad-sense heritability were high for most of the traits measured indicating that the variation observed for those traits are genetically determined and the effect of environment on them were low, hence selection based on phenotypic expression will be efficient for genetic improvement of these traits. Moreover, selection for these traits at early segregating generation could lead to selection of elite genotypes (Bozokalfa et al., 2010). The broad-sense heritability estimates obtained in this study are in agreement with earlier reports (Haydar et al., 2007; Sanjeev, 2010; Osekita & Ademiluyi, 2014; Kumar et al., 2018; Mohamed et al., 2018). Low narrow-sense heritability estimates for plant height, number of leaves per plant, number of secondary branches, cluster per plant, number of flower per cluster, number of fruits per plant, number of locules per fruit, fruit mass and vitamin C showed that they are primarily controlled by non-additive genes, and that selection for these traits may be ineffective.

The nature and magnitude of heterosis estimates help in the identification of promising hybrids (Pandiarana et al., 2015). The entire cross combinations were prominent for displaying highly significant heterosis over mid parent for only plant height and fruit mass per plant with the presence of various degrees of over dominance effects indicating the inherent genetic diversity between the parental cultivars and the newly developed hybrids that can be exploited through selection. This corroborates the report of previous researcher who found positive and significant heterosis for plant height and fruit mass per plant (Mageswari et al., 1999; Kurian et al., 2006; Shende et al., 2012; Agarwal et al., 2014). Thus, the best hybrid for plant height was FDT_2 × Kerewa (5.4 %) and superior hybrids for fruit mass per plant were FDT_4 × Ib-local (13.7 %) and UC-OP × Ib-local. Number of leaves per plant had mostly significant positive heterosis over mid parent with partial to over dominance effects. Out of 10 tomato F_1's, only one cross (UC-OP × Ib-local) expressed significant and positive heterosis with partial dominance for cluster per plant. The fewer the number of tomato locules the better for proper shape, firmness, processing, concentrations of solids and ascorbic acid (Dundi & Madalageri, 1991; Thamburaj, 1998). Heterosis in the negative direction with partial dominance effect with cross combinations FDT_2 × Ib-local and UC-OP × Ib-local (-33.3 %) are desirable hybrids for number locules per fruit. Considering the nutritional parameters, high lycopene and vitamin C are essential in the development of quality tomato because they add value to processed products as quality requirements desired by the consumers. Positive mid-parent heterosis estimates on few F_1 hybrids for lycopene and vitamin C found in this study were higher than the report of Pandiarana et al. (2015). These results were further confirmed with the potence ratios indicating partial to over dominance effects in the inheritance these parameters. Previous studies have reported significant positive heterosis for lycopene (YongFei et al., 1998), vitamin C (Makesh, 2002) and significant negative heterosis for number of locules per fruit (Sekhar et al., 2010). Early flowering in tomato is a desirable character; therefore negative heterosis is preferred over positive heterosis. Half of the cross combinations displayed significant negative heterosis over mid parent and the hybrids; FDT_2 × Kerewa depicted maximum significant negative heterosis. These results were strongly supported by the potence ratios, with two crosses each indicating partial to over-dominance effects, coupled with one cross combination signifying no dominance in the inheritance of this trait. Significant negative heterosis estimates were observed in the hybrids for number of fruits per plant and number of flower per cluster contrary to previous reports of Hannan et al. (2007). Various degrees of dominance were involved in the inheritance of the morphological and nutritional traits of tomato measured in this study and the negative values of potence ratio illustrated the presence of various degrees of recessiveness. Based on the significant percent mid parent heterosis estimate there is a potential to develop hybrids that are taller, early flowering, with fewer lobes, more number of leaves per plant, increased fruit mass per plant, higher lycopene and vitamin C content. In agreement with these findings, previous studies have reported significant performance of tomato hybrids above the parental lines (Singh et al., 2006; Dar et al., 2011; Singh et al., 2014; Pandey et al., 2015; Senapati & Kumar 2015).

Correlations between traits are critical in improving the efficiency of breeding programmes and assisting with appropriate selection indices (Nzuve et al., 2014). The positive relationship between fruit mass per plant, plant height, number of days to 50 % flowering, and cluster per plant is desirable, and it suggests that selecting taller tomato plants may result in larger fruits due to the stem reserve mobilization mechanism (Al-Tabbal & Al-Fraihat, 2012). Also, late flowering selection results in higher fruit yield and an increased number of tomato fruits due to a higher number of clusters per plant. Furthermore, the correlation between the number of flowers per cluster and the stem width and number of secondary branches, as well as the correlation between the number of leaves per plant and the number of secondary branches, show that traits with similar physiology were correlated and may be used for indirect selection. The relationship between the number of locules per fruit and stem width and the number of flowers per cluster suggests that selecting for a wider stem and flower cluster improves the capacity to support tomato fruits with many locules.

According to Mitchel et al. (1991) and Agong et al. (1997) nutritional and physicochemical properties are used as criteria to judge the organoleptic and processing qualities of tomato. Highly significant and negative correlations found between morphological traits and lycopene and even vitamin C corroborate the report of Agong et al. (2001) indicating that breeding programme would have to compromise some morphological traits to obtain better quality, particularly when nutrition is included as objectives in breeding programmes. On the contrary, Kaushik & Dhaliwal (2018) reported lack of significant correlations between morphological traits and biochemical traits.

5 CONCLUSION

The half diallel analysis technique revealed the relative breeding potential of the parental cultivars and superior good combiner parents. The results from this study clarifies the nature and magnitude of gene action involved in the inheritance of the traits measured, provided information on the genetic worth of parental lines and possibility of selecting superior hybrids for further exploitation. The combining ability study confirms the presence of high variation among the genotypes with the preponderance of both additive and nonadditive gene actions influencing the inheritance of morphological traits, nutritional and physicochemical parameters measured. Parental line Ib-local was identified as potential donor for plant height, fruit mass, fruit lycopene content and UC-OP was superior for earliness, fruits per plant, number of locules per fruit, fruit vitamin C content. These two parents may be useful in tomato improvement programmes. Three promising hybrids (FDT_4 × UC-OP, FDT_2 × Ib-local and UC-OP × Ib-local) were selected on the basis of involvement of one parent with a high GCA effect for number of fruits per plant and fruit mass per plant, relevance of SCA effects and heterosis. These cross combinations may be considered useful for the improvement of fruit yield, lycopene, vitamin C and total soluble solid contents. The selected superior tomato hybrid may be released as varieties to growers for commercial cultivation. The findings of this study could be used to determine the best approach for tomato improvement in a breeding programme.

This manuscript is part of M.Sc thesis of Olajoju Lola Oladokun mentored by Charity Onye Aremu.

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