Hindawi
International Journal of Agronomy
Volume 2023, Article ID 3003355, 17 pages
https://doi.org/10.1155/2023/3003355

Research Article

Hybrid Vigor and Heritability Estimates in Tomato Crosses Involving *Solanum lycopersicum* × *S. pimpinellifolium* under Cool Tropical Monsoon Climate

Chikezie Onuora Ene,[1,2] **Wosene Gebreselassie Abtew**,[1] **Happiness Ogba Oselebe**,[3] **Friday Ugadu Ozi**,[3] **Onwuchekwa Ogah**,[4] **Emeka Chibuzor Okechukwu**,[5,6] **and Uchechukwu Paschal Chukwudi**[6]

[1]*Department of Horticulture and Plant Sciences, Jimma University, Jimma, Ethiopia*
[2]*Department of Agriculture, Alex Ekwueme Federal University Ndufu-Alike, Abakaliki, Nigeria*
[3]*Department of Crop Production and Landscape Management, Ebonyi State University, Abakaliki, Nigeria*
[4]*Department of Applied Biology, Ebonyi State University, Abakaliki, Nigeria*
[5]*University of Worcester, School of Science and the Environment, Henwick Grove, Worcester WR26AJ, UK*
[6]*Department of Crop Science, University of Nigeria, Nsukka, Enugu State, Nigeria*

Correspondence should be addressed to Chikezie Onuora Ene; enechike17@gmail.com

Received 23 September 2022; Revised 10 January 2023; Accepted 11 January 2023; Published 25 January 2023

Academic Editor: Maria Serrano

High humidity is a major constraint to increased tomato fruit production in a cool tropical monsoon climate. However, the genetic variation observed in *Solanum pimpinellifolium* makes it a good gene donor for breeding tomato cultivars capable of thriving under high humidity. The objective of this study was to estimate heterosis, heritability for higher yield, and to assess the adaptability of the genotypes to humid conditions. Genotypes were raised from five morphologically divergent parents, viz., wild parent (*W*)–"LA2093," "CLN2498D" (*D*), "CLN2417H" (*H*), "Tima" (*T*), and "UC Dan INDIA" (*U*). The F_1s were generated by biparental mating design using "LA2093" as a common pollen donor that was selfed to produce F_2s and backcrossed to both parents to obtain BC_1s and BC_2s. The trial was laid out in a randomized complete block design with three replicates. Data were collected on selected yield-influencing traits and analyzed. "$D \times W$" and "$U \times W$" hybrids showed significant positive better parent heterosis for fruit weight per plant (30.4% and 35.5%) and total fruit yield (48.6% and 26.9%), respectively. The additive variance was higher than dominance variance for all the traits, including total fruit yield in all hybrids *viz*., "$H \times W$," "$D \times W$," "$T \times W$," and "$U \times W$." High narrow sense heritability estimate of ≥60% was observed in "$D \times W$" and "$U \times W$" hybrids for the majority of the floral and fruit traits including total fruit yield. This makes the improvement of "$D \times W$" and "$U \times W$" hybrids by direct selection advantageous. Hence, the adoption of selection for the affected traits in subsequent tomato breeding programs would enhance fruit yield and adaptability to humid environments.

1. Introduction

Solanum pimpinellifolium is a close relative of *Solanum lycopersicon* with no known cross-compatible challenge [1–3]. *S. pimpinellifolium* genome has been known to possess more desirable than undesirable alleles for better varieties development as compared to other wild species [4–6]. Atugwu and Uguru [7] reported that most cultivated tomatoes performed poorly for some quantitative traits under high humidity as compared to *S. pimpinellifolium.*

Despite the several breakthroughs in tomato fruit improvement through traditional and molecular breeding, still, many known cultivars find humid environments unfavorable. In such environments, yield is reduced due to high flower abortion rates, disease incidence, and rapid post-harvest fruit decay [8, 9].

In spite of its small fruit cherries, *S. pimpinellifolium* is believed to possess the required attributes for improving tomato yield and quality performance due to its prolific fruiting nature, early flowering, fruit maturity, disease resistance ability, good growth architecture, high cross-compatibility with the cultivated species, high adaptive nature under humid environment and higher fruit shelf life [2]. Earlier studies on interspecific hybrids involving *S. lycopersicum* and *S. pimpinellifolium* centered majorly on qualitatively inherited traits such as vertical or specific disease resistance [10], fruit color and fruit shape [11], organoleptic qualities such as flavor, sweetness, and texture [12], and lycopene content [13]. However, genetic exploitation of the variation in *S. pimpinellifolium* for the development of cultivars with improved fruit yield and tolerance to humid environments has not received attention [14, 15].

High heterosis in hybrid crops are often linked with high productivity, and better opportunity to express desirable lines in the subsequent generations than those with low heterosis [16, 17]. Previous studies have implicated increased genetic distance among parental lines as being pivotal for increased heterosis [18–20]. When the hybridization is interspecific rather than intraspecific, there are even higher chances of transferring desired traits and obtaining the expected genetic recombination in the next generation [21].

Parents chosen for planned hybridization to estimate either heterosis or heritability, or both, are considered on account of their ability to give rise to superior progenies with transferable traits rather than on their performance standing alone [22]. This means that parents with outstanding performance in any trait may not transfer such performance to the next generation unless the trait is heritable. Breeding in self-pollinated crops is constrained by a narrow genetic base due to inbreeding [23]. Hence, Atugwu and Uguru [7] recommended interspecific hybridization for self-pollinated crops.

The objective of this study was to exploit heterosis and estimate the heritability of the main quantitative traits controlling fruit yield in tomato interspecific hybrids in humid ecology to assess adaptability and identify genotype (s) that could be good substitutes for the already existing unproductive ones to meet global fruit demand.

2. Materials and Methods

2.1. Description of Study Environment. The field trial was carried out in the Department of Horticulture and Plant Sciences, Jimma University, Ethiopia, during the 2020/2021 and 2021/2022 cropping seasons from November to April, taking a total duration of 18 weeks in each season. Jimma is an environment with a cool tropical monsoon climate located on latitude 07°4′N, longitude 36°50′E, and altitude 1,710 m above sea level in the southwest Oromia region of Ethiopia. The monthly weather conditions of Jimma during the experiment seasons are presented in Figures 1 and 2. According to soil classification by Sorsa et al. [24], Jimma is covered with majorly black, gray, and red colored plastic clay soils.

2.2. Plant Materials. The genetic material used was four parental lines of cultivated tomato (*S. lycopersicum*) and accession of *S. pimpinellifolium* (wild parent)-“LA2093,” C.M. Rick Tomato Genetic Resources Center (TGRC). The domesticated accessions were four morphologically diverse materials. Two divergent parents included; “CLN2498D” (*D*) and “CLN2714H” (*H*) sourced from Ethiopia as well as “UC Dan INDIA” (*U*) and “Tima” (*T*) from Nigeria were used as characterized by Ene et al. [25] in terms of superiority and weakness in the quantitative traits. “CLN2498D” and “UC Dan INDIA” were superior performing parents in terms of fruit size (round and large) and fruit yield but had fewer fruit numbers and lacked resilience to humid environmental conditions whereas “CLN2714H” and “Tima” were the weaker performers in terms of fruit yield, fruit number; had elongated medium fruit size, and took longer days to achieve the phenological traits. The wild parent (*W*) was used as a pollen donor to pollinate the four cultivated materials (females) using a biparental mating design by hand pollination as described by Ozores-Hampton [26]. According to Wang et al. [27], “LA2093” has a prolonged shelf life, early flowering and maturing, is quantitative disease resistant, and relatively adapted to humid monsoon climate in addition to profuse fruit number production but produced circular cherries. Four F_1 crosses, viz., “$H \times W$,” “$T \times W$,” “$D \times W$,” and “$U \times W$” were obtained. The F_1 materials were crossed back to the recurrent (cultivated) and donor (wild) parents to obtain their backcrosses (BC_1 and BC_2), respectively, and at the same time selfed to produce F_2. A pictorial description of the floral parts (style, stigma, and ovary), and fruits of the tomato parents and their progenies in each cross, including F_1, BC_1 (F_1 backcrossed to recurrent parent), BC_2 (F_1 backcrossed to donor parent), and their F_2 hybrids in varying sizes and shapes are presented in Figures 3 to 7. The parental lines, F_1 hybrids and their backcrosses as well as the F_2 segregating populations were evaluated for floral and fruit traits.

2.3. Experimental Design and Cultural Practices. Tomato seedlings were raised on plastic seed trays filled with sterilized soil mixed with well-cured poultry manure and river sand in a ratio of 3 : 2 : 1, respectively. After 24 days of seedling emergence at about 4-5 leaves stage, uniform vigorous seedlings were transplanted to the field and laid out in a randomized complete block design with three replicates. Each plot occupied by a particular parent or F_1 genotype of each cross consisted of two rows of plants (20 plants/plot) in an area of $1\,\mathrm{m} \times 5\,\mathrm{m}$ with $50\,\mathrm{cm} \times 50\,\mathrm{cm}$ inter-intra-row spacing. However, each of the backcrosses (BC_1 and BC_2) or F_2 genotypes of each cross consisted of six rows of plants (60 plants/plot) in an area of $3\,\mathrm{m} \times 5\,\mathrm{m}$ with similar spacing. A distance of 1 m and 0.5 m alleys were maintained between blocks and plots, respectively. Poultry manure was added at the rate of 10 metric tons per hectare in the soil within each block before two weeks of transplantation.

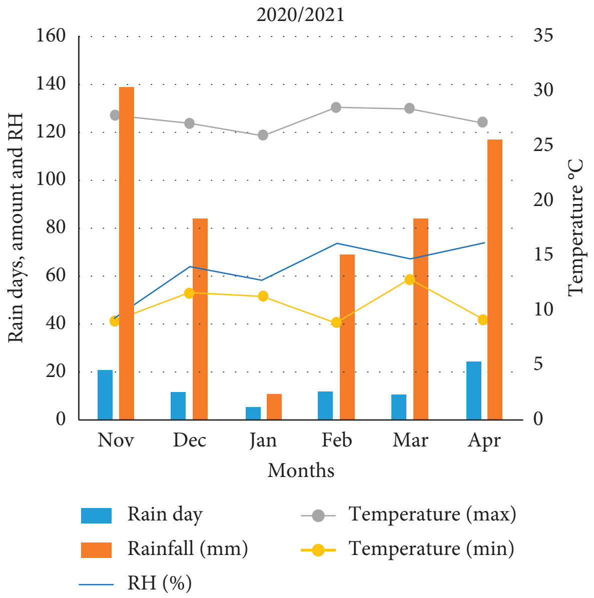

Figure 1: Monthly weather conditions of Jimma during the 2020/2021 experiment season.

Recommended agronomic practices such as irrigation, weed control, fertilizer (DAP-Di Ammonium Phosphate), fungicide (Ridomil-Mancozeb and Metalaxyl-M), staking, pruning, and insecticide (Karate-Lambda-Cyhalothrin 5% EC) was applied as described by Osei et al. [28].

3. Data Collection

Data were collected from 5 plants among the parents, 5 plants among the F_1s, 20 plants among the BC_1s and BC_2s, and 35 plants among the F_2 segregating progenies in each replicate of each plot. Floral traits measured were; the number of days to first anthesis and number of days to 50% anthesis from the day of transplantation of seedlings, number of flowers per truss, the total number of flowers per plant, and number of aborted flowers per plant, while flower length (mm), flower width (mm), style length (mm), style diameter (mm), stigma length (mm), and stigma diameter (mm) were measured using a Moticam with Motic Image Plus 2.0 software. The Moticam captured the floral parts and with the scale reference tools measured the flower parts in micrometer (μm) which was later converted to millimeter (mm). Ovary length (mm) and ovary diameter (mm) were measured using an ocular micrometer fitted in a microscope eyepiece which has a rule scale also calibrated in micrometer (μm). Conversion to mm was also performed afterwards. The ovary area (mm^2) and ovary perimeter (mm) were measured according to Nnungu and Uguru [29]. All the floral traits apart from the phenological traits were measured at 90 to 100% flower anthesis.

The fruit traits measured were; the number of days to first fruit emergence, the number of days to 50% fruit set, and the number of days to first fruit ripening. Fruit shelf life traits included the number of days to first fruit spoilage, the number of days to 50% fruit spoilage, and the number of days to 100% fruit spoilage when stored under room temperature based on fruits shriveling following the method of Arah et al. [30]. From each genotype, 5 fruits were taken randomly after the second harvest to measure fruit polar diameter (cm) and fruit equatorial diameter (cm) by using a vernier caliper. Fruits were cut crosswise to measure pericarp thickness (cm) by using a vernier caliper. The number of locules per fruit was counted alongside. The number of fruits per truss and the total number of fruits per plant were counted. The total number of mature fruits at the second harvest was weighed with an electronic weighing balance and the fruit weight per plant was recorded. The total fruit yield per hectare was estimated as described by Dinssa et al. [31].

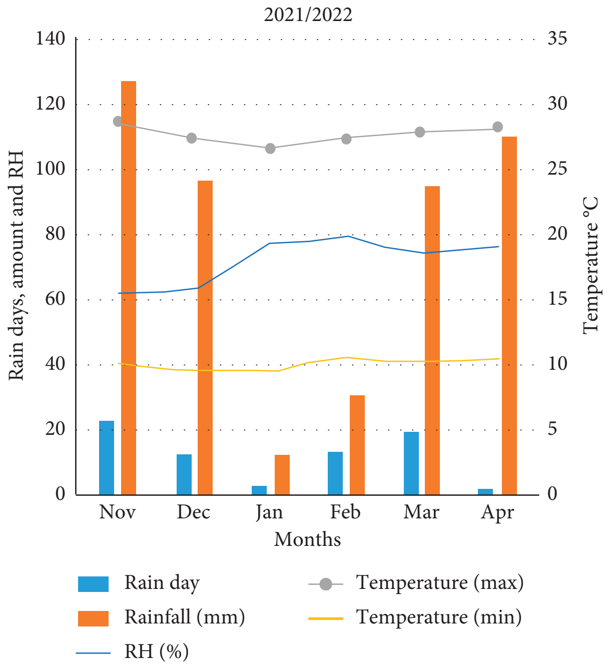

Figure 2: Monthly weather conditions of Jimma during the 2021/2022 experiment season.

3.1. Statistical Analysis

Before conducting the analysis of variance, the test for homogeneity of error variances was carried out using the F test where the larger variance was divided by the smaller variance between the two seasons, which suggested a combined analysis as recommended by Gomez and Gomez [32]. The data collected for quantitative traits from parents and F_1s crosses were subjected to two-way analysis of variance (ANOVA) using R software [33] to find the means of the crosses and parents. The significant means were separated using the F-LSD at 5% and 1% levels of probability. The same pooled data were used for genetic analysis.

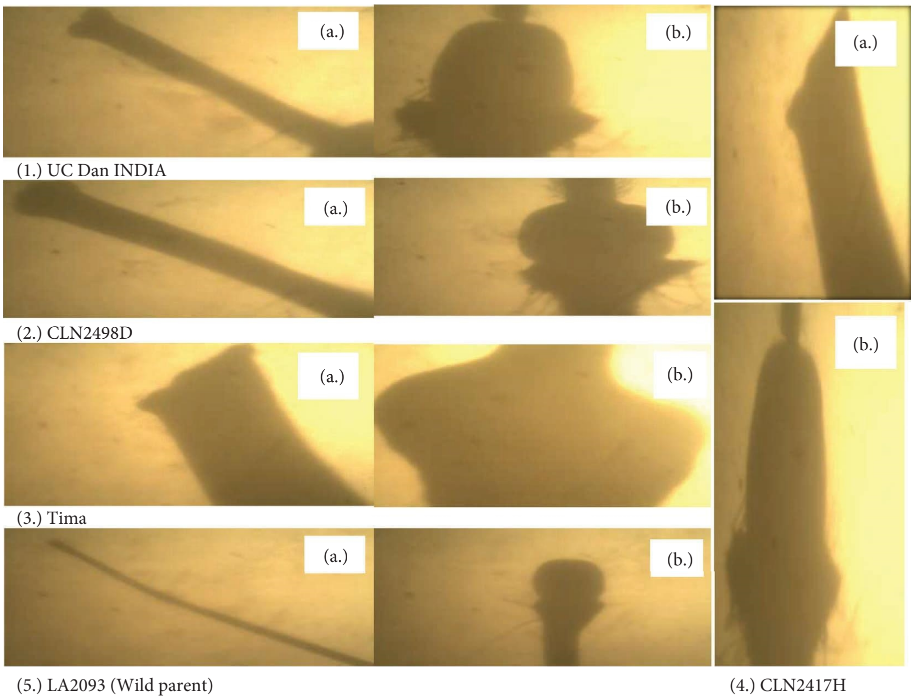

Figure 3: Tomato parents used in this work showing the variation relationship in size and shape of, (a) style and stigma, and (b) ovary.

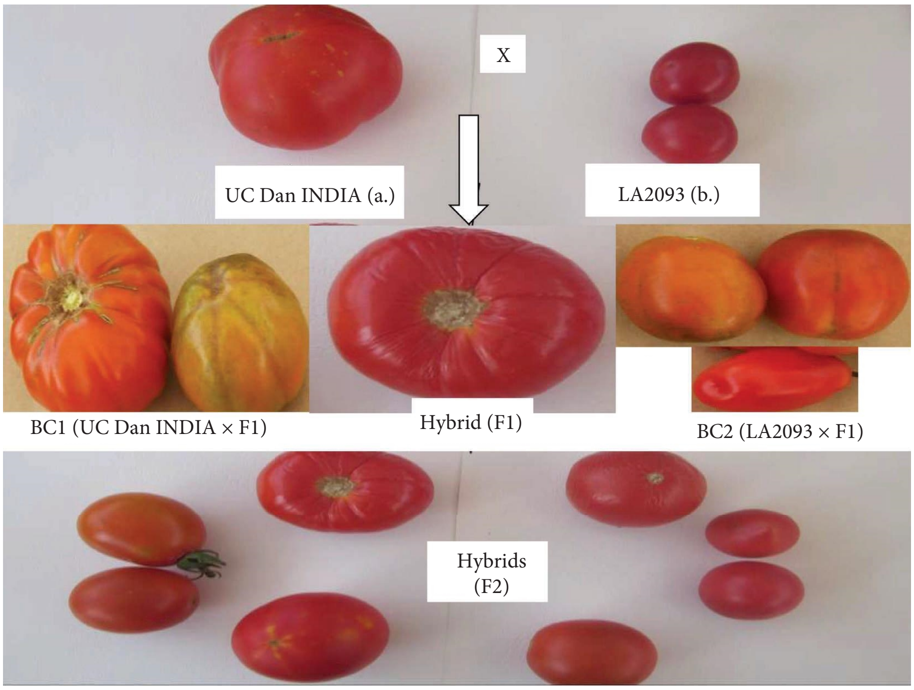

Figure 4: Tomato parents and their progenies. (a) Parent$_1$ (UC Dan INDIA), (b) Parent$_2$ (LA2093), hybrid F_1, BC$_1$ (F_1 backcrossed to UC Dan INDIA), BC$_2$ (F_1 backcrossed to LA2093), and their F_2 hybrids varied in size and shapes.

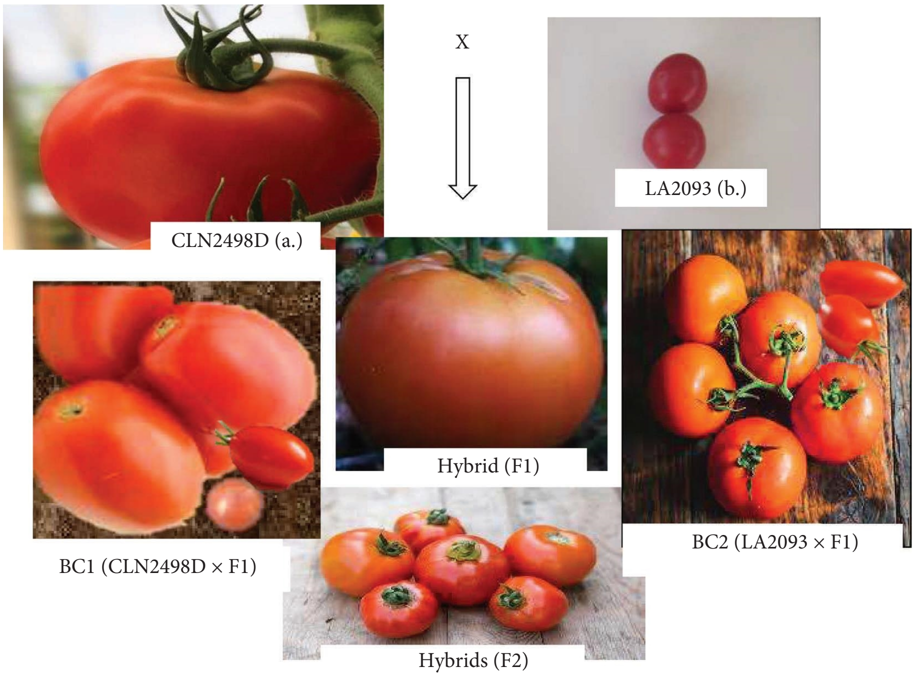

Figure 5: Tomato parents and their progenies. (a) Parent$_1$ (CLN2498D), (b) Parent$_2$ (LA2093), hybrid F_1, BC$_1$ (F_1 backcrossed to CLN2498D), BC$_2$ (F_1 backcrossed to LA2093), and their F_2 hybrids varied in size and shapes.

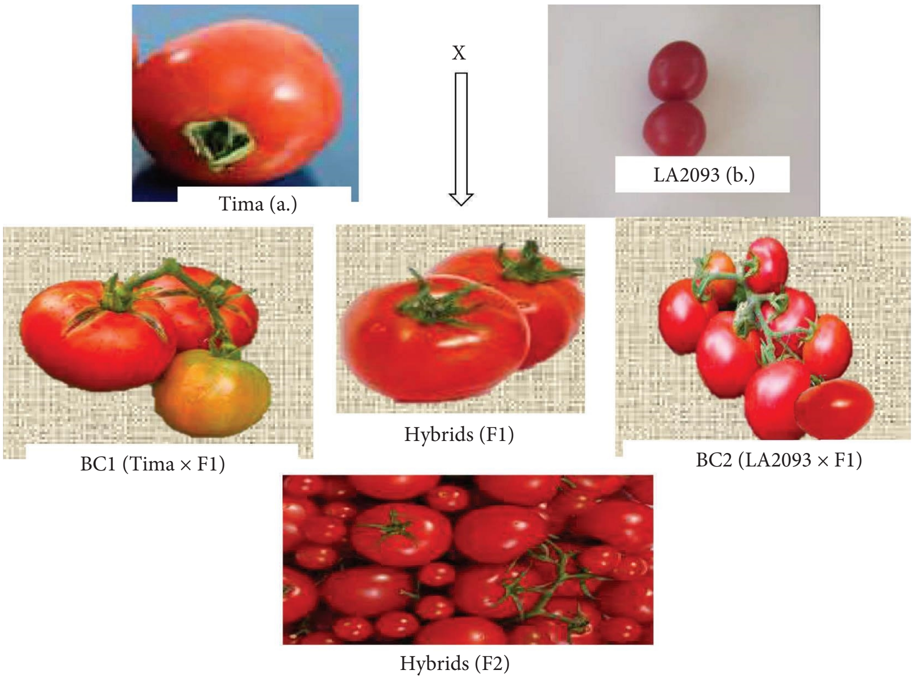

Figure 6: Tomato parents and their progenies. (a) Parent$_1$ (Tima), (b) Parent$_2$ (LA2093), hybrid F_1, BC$_1$ (F_1 backcrossed to Tima), BC$_2$ (F_1 backcrossed to LA2093), and their F_2 hybrids varied in size and shapes.

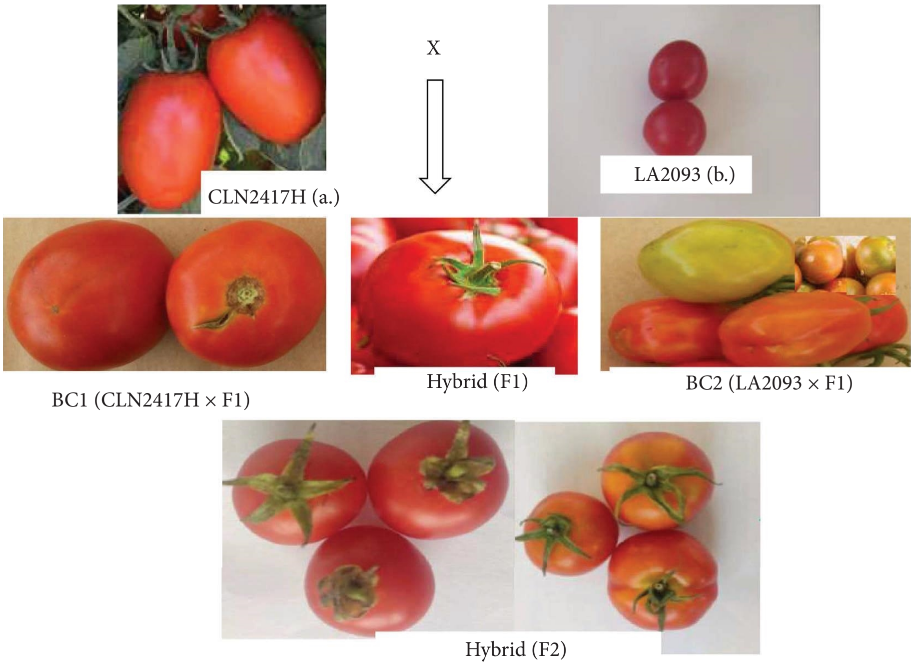

Figure 7: Tomato parents and their progenies. (a) Parent$_1$ (CLN2417H), (b) Parent$_2$ (LA2093), hybrid F_1, BC$_1$ (F_1 backcrossed to CLN2417H), BC$_2$ (F_1 backcrossed to LA2093), and their F_2 hybrids varied in size and shape.

3.2. Genetic Analysis. Heterosis was calculated according to Allard [34].

$$\text{Heterosis over Better Parent}\,(\%) = \frac{\overline{F}_1 - \overline{\text{BP}}}{\overline{\text{BP}}} \times \frac{100}{\mathbf{1}},$$
$$\text{Heterosis over the Mid Parent}\,(\%) = \frac{\overline{F}_1 - \overline{\text{MP}}}{\overline{\text{MP}}} \times \frac{100}{\mathbf{1}}, \tag{1}$$

where $\overline{\text{BP}}$ = mean of better parent value; $\overline{\text{MP}}$ = mean of midparent value; and $\overline{F}_1$ = mean of F_1s value.

Test of significance for BP heterosis was performed as described by Kumar et al. [35]:

$$\text{CD} = \mathbf{SE_d} \times \mathbf{t},$$
$$\mathbf{SE_d} = \pm\sqrt{\left(\frac{\mathbf{2EMS}}{r}\right)}. \tag{2}$$

The test of significance for MP heterosis was determined following the "t" test suggested by Wynne et al. [36]:

$$\mathbf{MP\,(t)} = \pm\frac{\overline{\mathbf{F}}_\mathbf{1} - \overline{\mathbf{MP}}}{\mathbf{SE_d}},$$
$$\mathbf{SE_d} = \pm\sqrt{\left(\frac{\mathbf{3EMS}}{\mathbf{2r}}\right)}, \tag{3}$$

where $\mathbf{SE_d}$ = standard error of difference; CD = critical Difference; $t = t$ tabulated at 5% and 1% probability; and r = number of replications; MP = midparent; EMS = error mean square as analyzed in ANOVA involving $F1$s and parents; 2 and 3 = constants.

The estimate of the genetic variance (additive and dominance) as well as environment for floral and fruit traits of tomato were determined using the variance estimate method as described by Mather and Jinks [37] and Acquaah [38].

$$\sigma_e^2 = \frac{P_1 + P_2 + F_1}{3},$$
$$\sigma_a^2 = 2F_2 - \text{BC}_1 + \text{BC}_2);$$
$$\sigma_d^2 = \frac{((\text{BC}_1 + \text{BC}_2 - F_2 - (P_1 + P_2 + F_1))}{3}; \tag{4}$$
$$\sigma_p^2 = \sigma_e^2 + \sigma_a^2 + \sigma_d^2;$$
$$\sigma_g^2 = \sigma_a^2 + \sigma_d^2.$$

Broad and narrow-sense heritability was estimated using the method proposed by Warner [39] as follows and presented in graphs:

$$H_{bs} = \frac{\sigma_g^2}{\sigma_p^2} \times 100,$$
$$H_{ns} = \frac{\sigma_a^2}{\sigma_p^2} \times 100. \tag{5}$$

Where σ_e^2 = environmental variance; σ_a^2 additive variance; σ_d^2 = dominance variance; σ_p^2 = phenotypic variance; σ_g^2 = genotypic variance; H_{bs} = broad sense heritability; and H_{ns} = narrow sense heritability.

The variances of the tomato parental lines, F_1, F_2, BC_1, and BC_2 population were used to determine the additive variance, dominance variance, genotypic variance, phenotypic variance, environmental variance, and estimated heritability presented in the Supplemental Tables S1 to S4.

4. Results

4.1. Weather Description. The mean monthly rainfall, relative humidity, rain days, and temperatures (minimum and maximum) in Jimma during the trials (2020/2021 and 2021/2022) are presented in Figures 1 and 2. The analysis of the meteorological data showed variations in the minimum and maximum temperatures, amount of rainfall, rain days, and relative humidity in different years. In the first year and second years the highest rainfall was observed in November with 140.4 mm and 128.0 mm, followed by April with 118.0 mm and 110.3 mm, respectively. The quantity of rainfall was lowest in January (11.3 mm and 13.3 mm) in the two years. The highest number of rainy days was noticed in April (25 days) in the first season and November (23 days) in the second experiment. The highest relative humidity was recorded in February (80%), followed by January (78%), April (77%), and March (75%), all in the second year, whereas in the first year of the experiment, January and April shared the highest (74%) relative humidity. November in both years exhibited the lowest relative humidity recorded. During the two experimental years, the maximum temperature range of 26°C to 28.7°C and a minimum temperature range of 9°C to 12.8°C were recorded. In the first year, February and March recorded the highest maximum (28.6°C) and minimum (12.8°C) temperatures, while in the second year, November and April showed the highest maximum (28.7°C) and minimum (10.7°C) temperatures.

4.2. Evaluation of Heterosis. Among the parents, "CLN2498D" showed comparatively lower DFA, D50A, and NAFlPP; higher FL, FW, OD, OA, OP, and SgD (Tables 1 and 2). The number of flowers per truss and the number of flowers per plant projected the wild parent as the better parent. For SlL and OL, "CLN2498D" and "UC Dan INDIA" shared higher but similar values comparatively.

Among the hybrids, "$D \times W$" and "$U \times W$" had the least DFA and D50 A, respectively, although statistically similar ($P \geq 0.05, 0.01$). "$U \times W$" and "$D \times W$" which showed higher NFlPT, TNFlPP, FL, and FW also had the least NAFlPP. The style length of the hybrids varied from 0.3 cm as found in "$T \times W$" to 1.0 cm in "$D \times W$." "$D \times W$" and "$U \times W$" hybrids consistently shared similar and higher performance for SlD, OL, OD, OA, OP, and SgD, whereas SgL was shared between all hybrids except "$T \times W$" (Tables 1 and 2).

Table 3 displays the estimates of BP and MP heterosis for the floral traits of the tomato interspecific hybrids. Results showed significant positive BP heterosis for the NAFlPP, SlL, OD, OA, OP, SgL, and SgD in all crosses. Significant BP heterosis in the undesirable direction was recorded for the NFlPT as well as the TNFlPP in all crosses. Crosses such as "$H \times W$" and "$T \times W$" expressed significant and positive BP heterosis for DFA and D50 A but significant and negative for FlW. "$D \times W$" and "$U \times W$" crosses expressed a significant and positive BP heterotic effect for SlD. Of the 4 crosses, significant and positive BP heterosis was observed for OL only in "$D \times W$." Not even a single cross displayed significant BP heterosis for FlL, although "$H \times W$" and "$T \times W$" were negative while "$D \times W$" and "$U \times W$" were positive. Similarly, "$D \times W$" and "$U \times W$" expressed nonsignificant and negative BP heterosis for DFA and D50A and positive for FlW. "$H \times W$" and "$T \times W$" hybrids expressed nonsignificant negative and positive BP heterosis, respectively, for SlD. The magnitude of better parent heterosis varied from −82.5% recorded for the TNFlPP in "$T \times W$" to 149.0% found in "$D \times W$" for OA.

Significant and negative relative heterosis was exhibited by the 4 crosses for the TNFlPP. Of the 4 hybrids, significant negative MP heterosis was exhibited by "$D \times W$" and "$U \times W$" for FlL, FlW, and SlL. "$T \times W$" and "$U \times W$" hybrids expressed significant and positive MP heterosis for SlD. Of the 4 hybrids, significant negative MP heterosis was found in "$T \times W$" for the NFlPT and positive for the NAFlPP. For OD, significant and negative MP heterosis was exhibited by "$D \times W$," while for the OP, significant and positive heterosis was recorded in "$H \times W$." "$H \times W$" and "$T \times W$" hybrids expressed significant and positive MP heterotic effect for OA while "$D \times W$" expressed significant and negative heterosis for similar traits. "$H \times W$" and "$D \times W$" expressed significant positive and negative MP heterosis, respectively, for SgL. For SgD, "$D \times W$" and "$T \times W$" hybrids expressed significant negative and positive MP heterosis, respectively. Not even a single hybrid displayed significant and negative MP heterosis for DFA and D50A. A similar result was recorded for OL but this time of negative MP heterosis. The magnitude of MP heterosis ranged from −67.6% found in "$T \times W$" for the TNFlPP to 58.6% recorded for OA in "$H \times W$."

Among parental lines, shorter DFFE, D50FS, and higher FPD, FED, and total fruit yield were expressed by "CLN2498D" (Tables 4 and 5). Least days to first fruit ripening and a higher number of fruits per plant, the number of days to initial sign of fruit spoilage, 50% fruit spoilage, and 100% fruit spoilage were exhibited by "LA2093" (wild parent). Higher performance for NFrPT, FWPP, and NLPF were observed in "UC Dan INDIA" while fruits with the highest pericarp thickness were found in "CLN2498D" and "UC Dan INDIA."

"$D \times W$" showed comparatively among hybrids, lower DFFE, D50FS, DFFR, higher FPT, and total fruit yield. Maximum NFrPT, TNFrPP, FWPP, FPD, FED, and NLPF were observed in "$U \times W$." For fruit shelf life traits, "$H \times W$" took the longest number of days to witness the initial fruit shriveling, 50% and 100% shriveling.

The estimates of BP and MP heterosis for the fruit-related traits of tomatoes are shown in Table 6. The results indicated that all hybrids expressed significant positive BP heterosis for DFFR and significant negative BP heterosis for

Table 1: Mean performance of parental lines and F_1 hybrids for the floral traits of tomato.

		DFA	D50A	NFlPT	TNFlPP	NAFlPP	FlL	FlW
		Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
Parents								
W		22.5 ± 2.2	27.9 ± 2.2	11.6 ± 0.3	484.2 ± 7.1	7.7 ± 1.7	0.4 ± 0.1	0.1 ± 0.02
H		30.3 ± 2.0	35.6 ± 2.0	6.5 ± 0.3	47.1 ± 2.1	12.7 ± 0.9	0.5 ± 0.1	0.2 ± 0.02
D		19.3 ± 1.9	23.8 ± 2.0	10.4 ± 0.7	87.1 ± 1.8	7.9 ± 0.4	0.9 ± 0.04	0.4 ± 0.1
T		28.9 ± 1.3	33.3 ± 2.3	5.9 ± 0.6	40.6 ± 2.7	14.7 ± 1.2	0.5 ± 0.1	0.2 ± 0.03
U		23.2 ± 1.9	27.5 ± 2.3	10.3 ± 0.3	93.1 ± 2.0	12.6 ± 1.4	0.7 ± 0.1	0.4 ± 0.1
F_1hybrids								
$H\times W$		28.4 ± 2.7	32.5 ± 2.2	4.9 ± 0.5	50.5 ± 1.6	11.2 ± 1.0	0.6 ± 0.1	0.1 ± 0.01
$D\times W$		19.9 ± 1.8	25.7 ± 1.8	10.8 ± 0.3	101.2 ± 1.6	8.1 ± 0.8	1.0 ± 0.1	0.3 ± 0.1
$T\times W$		24.3 ± 1.4	31.5 ± 0.5	5.2 ± 0.4	39.8 ± 1.5	8.8 ± 0.4	0.6 ± 0.1	0.1 ± 0.1
$U\times W$		20.9 ± 1.8	23.9 ± 2.0	11.1 ± 0.4	104.9 ± 2.1	8.1 ± 0.4	0.9 ± 0.03	0.3 ± 0.1
LSD	0.05	2.6	1.9	1.2	6.9	2.0	0.3	0.09
	0.01	3.4	2.4	1.7	9.3	2.7	0.4	0.1

W: wild parent (“LA2093”); *H*: CLN2714H; *D*: CLN2498D; *T*: Tima; *U*: UC dan INDIA; DFA: days to first anthesis; D50A: days to 50% anthesis; NFlPT: number of flowers per truss; TNFlPP: total number of flowers per plant; NAFlPP: number of aborted flowers per plant; FlL (mm): flower length; FlW (mm): flower width; LSD: least significant difference; SE: standard error of a mean.

Table 2: Mean performance of parental lines and F_1 hybrids for the floral traits of tomato (Cont’d).

		SlL	SlD	OL	OD	OA	OP	SgL	SgD
		Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
Parents									
W		0.2 ± 0.02	0.1 ± 0.01	0.1 ± 0.01	0.01 ± 0.01	0.01 ± 0.00	0.2 ± 0.02	0.05 ± 0.01	0.1 ± 0.01
H		0.4 ± 0.1	0.1 ± 0.02	0.1 ± 0.00	0.1 ± 0.01	0.01 ± 0.00	0.2 ± 0.02	0.1 ± 0.02	0.1 ± 0.02
D		0.9 ± 0.1	0.1 ± 0.02	0.2 ± 0.03	0.2 ± 0.02	0.03 ± 0.01	0.6 ± 0.1	0.1 ± 0.02	0.2 ± 0.02
T		0.4 ± 0.1	0.1 ± 0.01	0.1 ± 0.02	0.1 ± 0.01	0.01 ± 0.00	0.3 ± 0.4	0.05 ± 0.01	0.1 ± 0.01
U		0.9 ± 0.1	0.1 ± 0.01	0.2 ± 0.02	0.1 ± 0.02	0.02 ± 0.00	0.4 ± 0.1	0.1 ± 0.02	0.1 ± 0.02
F_1hybrids									
$H\times W$		0.5 ± 0.1	0.1 ± 0.00	0.1 ± 0.02	0.12 ± 0.03	0.01 ± 0.01	0.4 ± 0.1	0.1 ± 0.02	0.1 ± 0.02
$D\times W$		1.0 ± 0.05	0.1 ± 0.02	0.2 ± 0.03	0.3 ± 0.03	0.04 ± 0.01	0.7 ± 0.1	0.1 ± 0.02	0.3 ± 0.02
$T\times W$		0.6 ± 0.02	0.1 ± 0.00	0.1 ± 0.03	0.12 ± 0.02	0.02 ± 0.00	0.4 ± 0.1	0.06 ± 0.01	0.1 ± 0.01
$U\times W$		1.1 ± 0.1	0.1 ± 0.03	0.2 ± 0.02	0.2 ± 0.03	0.03 ± 0.01	0.6 ± 0.1	0.1 ± 0.02	0.2 ± 0.02
LSD	0.05	0.1	0.02	0.2	0.2	0.1	Ns	0.02	0.02
	0.01	0.1	0.03	0.2	0.2	0.1	Ns	0.02	0.03

W: wild parent (“LA2093”); *H*: CLN2714H; *D*: CLN2498D; *T*: Tima; *U*: UC dan INDIA; SlL (mm): style length; SlD (mm): style diameter; OL (mm): ovary length; OD (mm): ovary diameter; OA (mm^2): ovary area; OP (mm): ovary perimeter; SgD (mm): stigma diameter; SgL (mm): stigma length; LSD: least significant difference; SE: standard error of a mean.

Table 3: Estimates of the better parent (BP) and midparent (MP) heterosis for the floral traits of F_1 hybrids of tomatoes.

Crosses	Heterosis	DFA (%)	D50A (%)	NFlPT (%)	TNFl PP (%)	NAFl PP (%)	FlL (%)	FlW (%)	SlL (%)	SlD (%)	OL (%)	OD (%)	OA (%)	OP (%)	SgL (%)	SgD (%)
$H\times W$	BP	26.2*	24.8*	−39.2*	−81.2*	61.1*	−4.1	−36.8*	14.0*	−17.1	−25.0	4.7*	30.3*	23.9*	28.0*	37.8*
$D\times W$	BP	−4.4	−1.8	−26.6*	−73.8*	17.1*	1.8	8.4	52.5**	22.4*	44.8*	17.5*	149.0*	57.1*	32.1*	70.9*
$T\times W$	BP	22.7*	18.2*	−48.5*	−82.5*	83.4*	−5.1	−31.6*	13.1*	2.6	−25.0	16.0*	69.8*	28.0*	25.9*	37.7*
$U\times W$	BP	−3.8	−1.8	−23.5*	−72.6*	60.1*	7.7	8.4	49.2*	42.1*	25.0	37.3*	88.0*	38.2*	46.6*	86.6*
$H\times W$	MP	7.6	9.5	−22.3	−65.7*	21.8	−13.7	−30.1	−15.0	−24.1	−8.5	−19.9	58.6*	29.7*	3.0*	−9.9
$D\times W$	MP	3.0	6.0	−14.3	−55.5*	8.0	−35.3*	−33.2*	−36.9*	−13.1	−9.2	−39.0*	−30.1*	−11.1	−27.2*	−16.7*
$T\times W$	MP	7.4	7.8	−31.7*	−67.6*	26.4*	−12.3	−17.7	−13.0	19.1*	−8.9	−8.2	15.7*	12.3	−10.6	5.8*
$U\times W$	MP	5.1	6.1	−11.7	−54.1*	21.8	−34.4*	−32.2*	−35.3*	17.4*	−4.8	−7.6	−10.1	−0.5	−3.0	−6.1

W: wild parent (“LA2093”); *H*: CLN2714H; *D*: CLN2498D; *T*: Tima; *U*: UC dan INDIA; DFA: days to first anthesis; D50A: days to 50% anthesis; NFlPT: number of flowers per truss; TNFlPP: total number of flowers per plant; NAFlPP: number of aborted flowers per plant; FlL (mm): flower length; FlW (mm): flower width; SlL (mm): style length; SlD (mm): style diameter; OL (mm): ovary length; OD (mm): ovary diameter; OA (mm^2): ovary area; OP (mm): ovary perimeter; SgD (mm): stigma diameter; SgL (mm): stigma length; *: significant at 5% level of significance; **: significant at 1% level of significance.

the TNFrPP. Significant and positive BP heterosis was exhibited by “$H\times W$” and “$T\times W$” for DFFE, whereas for D50FS, only “$H\times W$” of all hybrids expressed significant and similar heterotic direction. Of the 4 hybrids evaluated for NFrPT and D50FrSp, “$H\times W$” and “$T\times W$” showed significant negative BP heterosis, while for FWPP, FPD, and

Table 4: Mean performance of parental lines and F_1 hybrids for the fruit traits of tomato.

		DFFE Mean ± SE	D50FS Mean ± SE	DFFR Mean ± SE	NFrPT Mean ± SE	TNFrPP Mean ± SE	FWPP Mean ± SE
Parents							
W		31.3 ± 1.6	41.0 ± 1.6	50.7 ± 1.4	11.1 ± 0.3	466.3 ± 4.4	313.7 ± 3.8
H		43.4 ± 1.6	47.0 ± 1.9	69.9 ± 2.2	4.8 ± 0.2	43.4 ± 1.6	295.1 ± 4.3
D		22.6 ± 0.7	28.5 ± 1.2	52.4 ± 1.6	9.8 ± 0.5	78.0 ± 3.5	1823.8 ± 20.1
T		33.8 ± 1.4	41.0 ± 1.2	60.9 ± 1.3	5.2 ± 0.2	34.1 ± 2.9	383.2 ± 11.4
U		28.0 ± 0.8	36.3 ± 1.2	53.3 ± 2.1	11.7 ± 0.3	80.2 ± 1.5	2456.1 ± 63.6
F_1hybrids							
H × *W*		37.8 ± 0.8	44.9 ± 1.5	53.6 ± 1.4	4.6 ± 0.8	38.3 ± 1.6	286.5 ± 6.2
D × *W*		28.6 ± 1.1	36.2 ± 1.1	54.7 ± 0.7	9.8 ± 0.8	94.2 ± 2.0	1987.6 ± 71.2
T × *W*		33.9 ± 1.1	40.8 ± 1.5	52.9 ± 1.5	4.5 ± 0.5	55.4 ± 1.7	330.9 ± 6.0
U × *W*		29.6 ± 0.5	36.8 ± 1.7	56.6 ± 1.3	10.5 ± 0.5	99.3 ± 4.8	2507.9 ± 39.1
LSD	0.05	1.9	2.6	2.8	1.1	6.9	78.7
	0.01	2.5	3.4	3.8	1.5	9.2	105.4

W: wild parent ("LA2093"); *H*: CLN2714H; *D*: CLN2498D; *T*: Tima; *U*: UC dan INDIA; DFFE: days to first fruit emergence; D50FS: days to 50% fruit set; DFFR: days to first fruit ripening; NFrPT: number of fruits per truss; TNFrPP: total number of fruits per plant; FWPP (g): fruit weight per plant; LSD: least significant difference; SE: standard error of a mean.

Table 5: Mean performance of parental lines and F_1 hybrids for the fruit traits of tomato (Cont'd).

		FPD Mean ± SE	FED Mean ± SE	NLPF Mean ± SE	D1stFrSp Mean ± SE	D50FrSp Mean ± SE	D100FrSp Mean ± SE	FPT Mean ± SE	TFY Mean ± SE
Parents									
W		3.5 ± 0.3	3.2 ± 0.2	2.6 ± 0.1	17.7 ± 0.3	25.5 ± 1.2	33.7 ± 1.3	2.7 ± 0.02	10.6 ± 0.9
H		6.5 ± 0.5	4.5 ± 0.1	3.5 ± 0.04	11.8 ± 0.3	18.0 ± 1.3	25.5 ± 1.3	4.5 ± 0.5	14.0 ± 0.7
D		10.4 ± 0.1	7.2 ± 0.2	4.8 ± 0.5	12.2 ± 1.0	19.3 ± 0.7	24.0 ± 1.5	5.1 ± 0.5	31.9 ± 1.2
T		7.5 ± 0.2	4.2 ± 0.1	3.1 ± 0.1	8.3 ± 0.1	13.9 ± 0.9	19.5 ± 1.0	3.4 ± 0.1	17.9 ± 0.4
U		9.9 ± 0.3	6.1 ± 0.6	5.5 ± 0.6	14.3 ± 1.0	19.5 ± 1.4	28.4 ± 2.9	5.1 ± 0.5	30.6 ± 1.9
F_1hybrids									
H × *W*		6.2 ± 0.3	4.4 ± 0.3	3.1 ± 0.1	13.3 ± 1.0	20.1 ± 1.1	27.2 ± 3.1	4.1 ± 0.2	9.1 ± 0.5
D × *W*		10.6 ± 0.2	8.1 ± 0.3	5.4 ± 0.1	14.0 ± 0.7	20.9 ± 1.8	26.4 ± 1.6	5.5 ± 0.2	35.3 ± 2.5
T × *W*		8.5 ± 0.2	4.1 ± 0.3	2.7 ± 0.2	12.0 ± 1.0	18.9 ± 1.1	25.3 ± 1.8	2.4 ± 0.1	12.5 ± 0.7
U × *W*		10.7 ± 0.2	7.5 ± 0.2	6.4 ± 0.2	15.0 ± 0.8	21.8 ± 1.1	26.1 ± 1.3	5.4 ± 0.1	32.3 ± 1.7
LSD	0.05	0.6	0.6	0.6	1.7	2.6	4.6	0.5	2.6
	0.01	0.8	0.7	0.8	2.3	3.5	6.1	0.7	3.4

W: wild parent ("LA2093"); *H*: CLN2714H; *D*: CLN2498D; *T*: Tima; *U*: UC dan INDIA; FPD (cm): fruit polar diameter; FED (cm): fruit equatorial diameter; NLPF: number of locules per fruit; D1stFrSp: number of days to first fruit spoilage; D50FrSp: number of days to 50% fruit spoilage; D100FrSp: number of days to 100% fruit spoilage; FPT (cm): fruit pericarp thickness; TFY (t/ha): total fruit yield per hectare; LSD: least significant difference; SE: standard error of a mean.

fruit yield, "*D* × *W*" and "*U* × *W*" exhibited significant positive BP heterosis. Of the 4 hybrids studied, only the "*D* × *W*" hybrid showed significant positive BP heterosis for FED. For the NLPF, significant positive better-parent heterosis was found in "*D* × *W*" and "*T* × *W*," while for D100FrSp, similar hybrids expressed significant negative BP heterosis. Significant and negative BP heterosis was recorded in 3 hybrids except for "*U* × *W*" for the days to the initial sign of fruit spoilage, whereas for FPT, significant and positive heterobeltiosis was exhibited by "*H* × *W*," "*D* × *W*" and "*U* × *W*" hybrids. Based on the magnitude, BP heterosis varied from −82.5% displayed by "*T* × *W*" for the TNFrPP to 48.6% recorded in "*D* × *W*" for total fruit yield.

All hybrids exhibited significant negative MP heterosis for the TNFrPP. Of 4 hybrids examined, "*D* × *W*" and "*U* × *W*" consistently expressed significant and negative MP heterotic effects for FWPP, FED, NLPF, FPT, and fruit yield. All hybrids except "*U* × *W*" showed significant MP heterosis for DFFE. For D50FS, significant and positive MP heterosis was manifested only by "*D* × *W*." Significant positive MP heterosis was shown by "*H* × *W*" and "*T* × *W*" for DFFR, whereas for the NFrPT the same hybrids exhibited significant negative MP heterosis. Of the 4 hybrids evaluated for FPD, 3 showed significant negative MP heterosis. "*T* × *W*" of all hybrids consistently maintained significant and negative MP heterosis for all shelf life-related traits such as days to first, 50%, and 100% fruit spoilage. The magnitude of MP heterosis varied from −69.3% manifested by "*U* × *W*" for FWPP to 17.6% found in "*D* × *W*" for D50FS.

4.3. Variance Components and Heritability Estimates. The total variance was decomposed into additive, dominance, and environmental components, while estimates of heritability were computed for different crosses.

Results showed that additive variance had higher values than the dominance variance in all crosses for all floral traits

Table 6: Estimates of the better parent (BP) and midparent (MP) heterosis for the fruit traits of F_1 hybrids of tomatoes.

Crosses	Heterosis	DFFE (%)	D50 FS (%)	DFFR (%)	NFrPT (%)	TNFr PP (%)	FWPP (%)	FPD (%)	FED (%)	NLPF (%)	D1st FrSp (%)	D50 FrSp (%)	D100 FrSp (%)	FPT (%)	TFY (%)
$H \times W$	BP	37.5*	14.7*	35.5*	−56.9*	−78.3*	−5.2	3.8	0.8	1.4	−32.2*	−28.6**	−23.1	2.4*	2.3
$D \times W$	BP	−3.1	−0.3	12.3*	−11.3	−75.6*	30.4*	9.2*	6.5*	8.3*	−29.9*	−22.2	−26.7*	2.0*	48.6*
$T \times W$	BP	21.4*	5.0	18.4*	−50.1*	−82.5*	1.0	4.2	0.1	7.2*	−49.6*	−43.2**	−39.0*	1.4	3.8
$U \times W$	BP	−0.6	−1.0	10.4*	−10.9	−75.0*	35.5*	13.9*	3.0	2.5	−18.8	−21.7	−14.9	2.5*	26.9*
$H \times W$	MP	15.1*	6.9	14.0*	−39.8*	−60.4*	−2.3	−26.8	−16.8	−16.5	−18.7	−16.2	−12.5	−23.3	−12.2
$D \times W$	MP	12.4*	17.6*	3.8	−1.9	−58.8*	−61.7*	−44.8*	−34.7*	−24.3*	−17.1	−11.3	−14.3	−29.1*	−56.7*
$T \times W$	MP	15.0*	4.6	7.6*	−31.8*	−67.4*	−9.1	−33.1*	−13.5	−5.1	−31.3*	−26.4*	−22.7*	−11.1	−22.9
$U \times W$	MP	3.7	5.1	3.4	−2.2	−57.4*	−69.3*	−39.9*	−29.3*	−35.5*	−10.1	−11.3	−7.6	−29.5*	−62.3*

W: wild parent ("LA2093"); *H*: CLN2714H; *D*: CLN2498D; *T*: Tima; *U*: UC dan INDIA; DFFE: days to first fruit emergence; D50FS: days to 50% fruit set; DFFR: days to first fruit ripening; NFrPT: number of fruits per truss; TNFrPP: total number of fruits per plant; FWPP (g): fruit weight per plant; FPD (cm): fruit polar diameter; FED (cm): fruit equatorial diameter; NLPF: number of locules per fruit; D1stFrSp: number of days to first fruit spoilage; D50FrSp: number of days to 50% fruit spoilage; D100FrSp: number of days to 100% fruit spoilage; FPT (cm): fruit pericarp thickness; TFY (t/ha): total fruit yield per hectare; *, significant at 5% level of significance; **, significant at 1% level of significance.

(Supplemental Tables S1 and S2). The total number of flowers per plant produced the highest variance components in magnitude in all hybrids. All hybrids showed a low magnitude of dominance and environmental variances for all floral traits. Phenotypic variance ranged from 0.0001 in "*U* × *W*" for OA to 20,938.41 in "*T* × *W*" for the TNFlPP. Broad and narrow sense heritability differed tremendously for all flower-related traits in all the hybrids with broad sense heritability higher. Broad sense heritability ranged from 28.98% in "*T* × *W*" for FlL to 94.90% in "*D* × *W*" for OP. Flower length recorded in "*H* × *W*" (45.29%) and "*T* × *W*" (28.98%) indicated moderate and low broad sense heritability, respectively (Figures 8 and 9). Narrow sense heritability varied from 27.50% expressed in "*T* × *W*" for FlL to 69.05% recorded in "*D* × *W*" for the TNFlPP. Most of the flower-related traits showed moderate to high narrow sense heritability. Flower length indicated low narrow sense heritability in "*H* × *W*" (34.82%) and "*T* × *W*" (27.50%) hybrids.

The variance components are presented in Supplemental Tables S3 and S4, while heritability estimates in a broad and narrow sense for all fruit traits are shown in Figures 10 and 11. The magnitude of dominance variance is less than the additive variance for all fruit-related traits reviewed. Wide variations were observed for both genetic components with the least additive and dominance variances of 0.04 and 0.01, respectively, recorded in "*H* × *W*" for the NLPF. Fruit weight per plant from "*U* × *W*," on the other hand,, gave the highest additive and dominance variances of 423,210.15 and 144,197.66, respectively. The low magnitude of dominance and environmental variances for all fruit traits were expressed in all hybrids. Variance due to phenotype ranged from 0.09 in "*H* × *W*" for the NLPF to 588,127.76 for FWPP in "*U* × *W*." Large variation was observed between heritability in the broad sense and narrow sense for all fruit traits in all hybrids, with broad sense indicating higher values comparatively. Very high (≥80%) heritability estimates in a broad sense were expressed for most fruit traits among the crosses. The least broad sense heritability of 62.70% for the NLPF in "*H* × *W*" was observed, whereas the NFrPT from the same hybrid gave the highest broad sense heritability of 97.18%. Narrow sense heritability was moderate to high for most fruit traits ranging from 50.04% recorded for NLPF in "*H* × *W*" to 72.54% in "*D* × *W*" for the TNFrPP.

5. Discussion

Significant positive BP heterosis for NAFlPP, SlL, OD, OA, OP, SgL, and SgD was exhibited by all hybrids, which showed that these hybrids outperformed the better parent. However, the advantage or disadvantage of the BP heterosis depends on the trait. For instance, the positive BP heterosis for the number of aborted flowers implied low flower retention in the affected hybrids compared to the better parent, "LA2093." In this case, there would be a reduction of fruit yield in the hybrids, which is disadvantageous. However, for traits such as SlL, OD, OP, SgL, and SgD having positive BP heterosis would be advantageous as they improved yield in hybrids compared to the better parents, the recurrent parents (Table 2).

Significant positive MP heterosis recorded for SlD, NAFlPP, SgD, OP, SgL, and OA showed that the hybrids performed higher than the parents' mean performance, which is an advantage except for the number of aborted flowers. Significant positive BP and MP heterosis indicated the predominance of nonadditive gene actions or most likely overdominance in the genetic control of these traits [40]. Significant negative BP heterosis recorded for the NFlPT, TNFlPP, and FlW indicated poor performance in all the crosses compared to the better parent (Table 1). Similar implications could be attributed to the significant negative heterosis over midparent values for TNFlPP, FlL, FlW, SlL, NFlPT, OD, OA, and SgD. It further indicated the presence of additive gene effects in the affected crosses.

The result disagrees with the findings of Gul et al. [41], who reported positive significant BP and MP heterosis for flower number per cluster although in intraspecific hybrids. However, Amaefula et al. [42] observed negative BP heterosis for similar floral traits in interspecific hybrids as in the present study. Nnungu and Uguru [29] reported positive BP and MP heterosis for the style length and flower length but negative for flower width, style diameter, and stigma diameter in all six interspecific hybrids. Bhattarai et al. [43] reported significant positive heterosis for stigma length in most crosses. They also reported that tomato floral traits such as flower length and width, style length and diameter, stigma length and diameter, ovary length, ovary diameter, and ovary area had been found to show enormous influence on the fruit development pattern including fruit size/weight, which has a direct effect on fruit yield.

The positive significant BP heterosis for DFA and D50A suggested longer days to express these traits than it took the better parent. Although nonsignificant, the positive heterosis over midparents for similar traits also implied higher longevity in the expression of these phenological traits more than experienced in the parents' mean performance. This contradicted the report of Powers and Lyon [44] that tomato F_1 hybrids are usually earlier in flower appearance than the earliest parent or midparent. Singh et al. [45] reported that heterosis is not always manifest early in the reproductive process. Kanneh et al. [46] reported negative MP heterosis in tomatoes for days to flowering. Negative BP and MP heterosis for days to 50% flowering was also reported in most hybrids by Javed et al. [47]. Negative BP heterosis for days to first anthesis and 50% anthesis indicated earliness in the flower reproductive process in the affected hybrids, which translated to higher fruit yield comparatively. Burdick [48] associated early flowering with higher fruit yield in cultivated tomatoes.

Significant positive heterosis over a better parent for DFFR shown by all hybrids suggested longer days to express this trait than the better parents. Similar implications applied to DFFE and D50FS in the affected hybrids. Significant positive MP heterosis observed for DFFE, D50FS, and DFFR indicated longer days to observe these traits in these hybrids than the average performance of the parents.

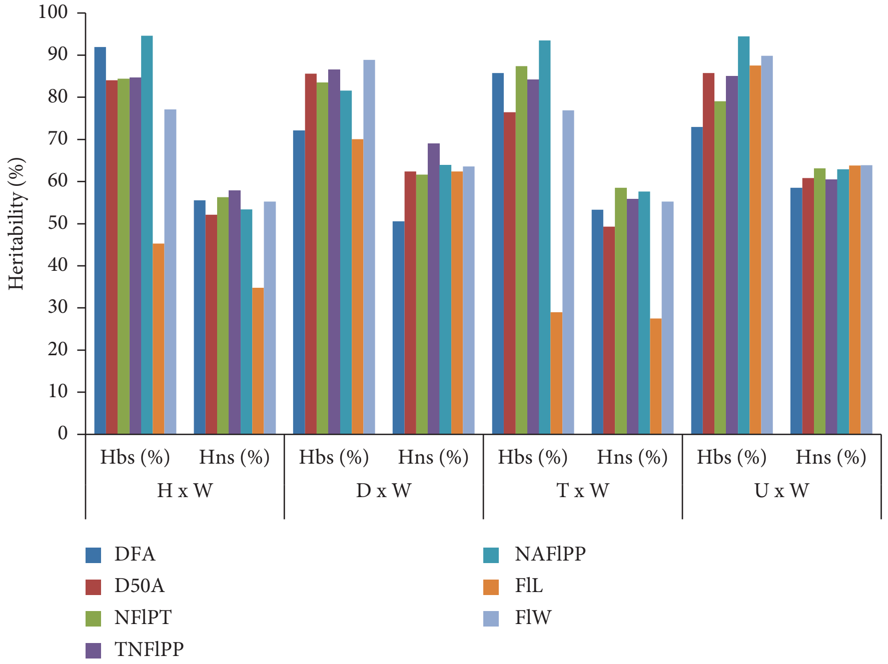

Figure 8: Estimates of the broad and narrow sense heritability for the floral traits viz., DFA: days to first anthesis, D50A: days to 50% anthesis, NFlPT: number of flowers per truss, TNFlPP: total number of flowers per plant, NAFlPP: number of aborted flowers per plant, FlL (mm): flower length, FlW (mm): flower width. *W*: wild parent ("LA2093"), *H*: CLN2714H, *D*: CLN2498D, *T*: Tima, *U*: UC dan INDIA, Hbs (%): heritability in broad sense, and Hns (%): heritability in narrow sense.

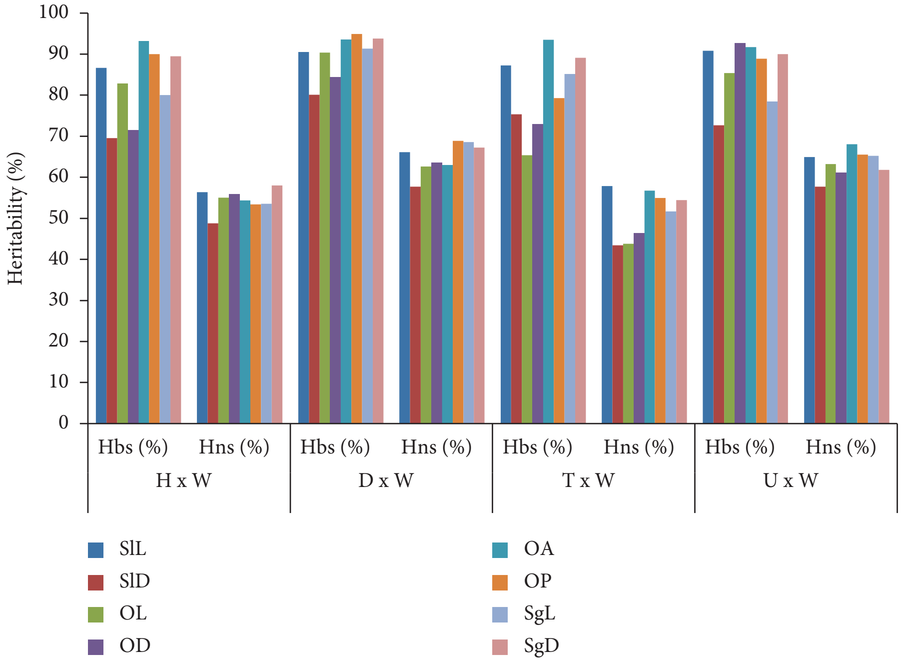

Figure 9: Estimates of the broad and narrow sense heritability for the floral traits viz., SlL (mm): style length, SlD (mm): style diameter, OL (mm): ovary length, OD (mm): ovary diameter, OA (mm^2): ovary area, OP (mm): ovary perimeter, SgD (mm): stigma diameter, SgL (mm): stigma length, *W*: wild parent ("LA2093"), *H*: CLN2714H, *D*: CLN2498D, *T*: Tima, *U*: UC dan INDIA, Hbs (%): heritability in broad sense, and Hns (%): heritability in narrow sense.

Liu et al. [20] reported that tomato F_1 hybrids are usually earlier in fruit setting and production than the earliest parents are. Kanneh et al. [46] reported negative MP heterosis in tomatoes for days to fruit maturity. With an extended duration of the vegetative stage, flowering, and fruiting time tend to deviate in F_1 but for what reason is still

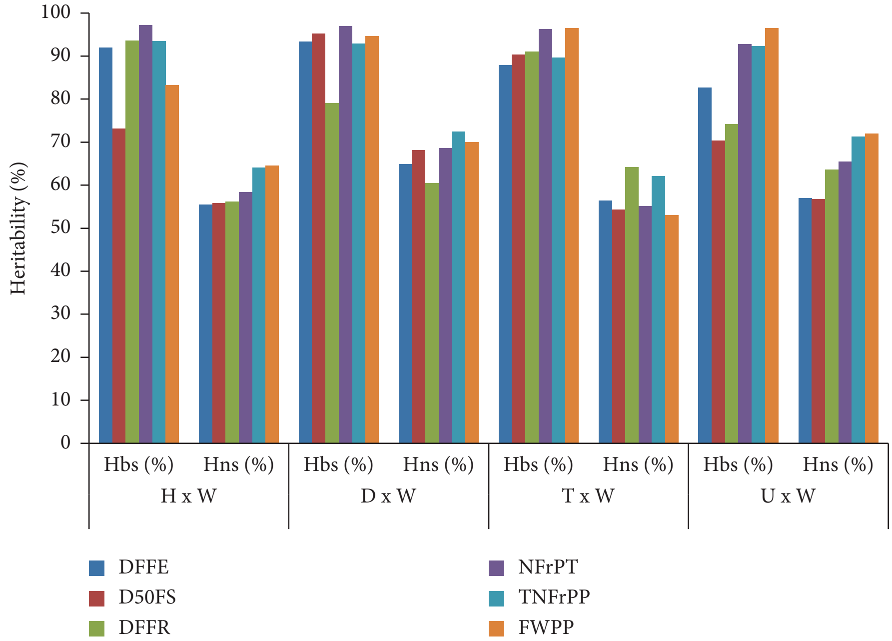

Figure 10: Estimates of the broad and narrow sense heritability for the fruit traits viz., DFFE: days to first fruit emergence; D50FS: days to 50% fruit set; DFFR: days to first fruit ripening; NFrPT: number of fruits per truss; TNFrPP: total number of fruits per plant; FWPP (g): Fruit weight per plant, *W*: wild parent ("LA2093"), *H*:CLN2714H, *D*: CLN2498D, *T*: Tima, *U*: UC dan INDIA, Hbs (%): heritability in broad sense, and Hns (%): heritability in narrow sense.

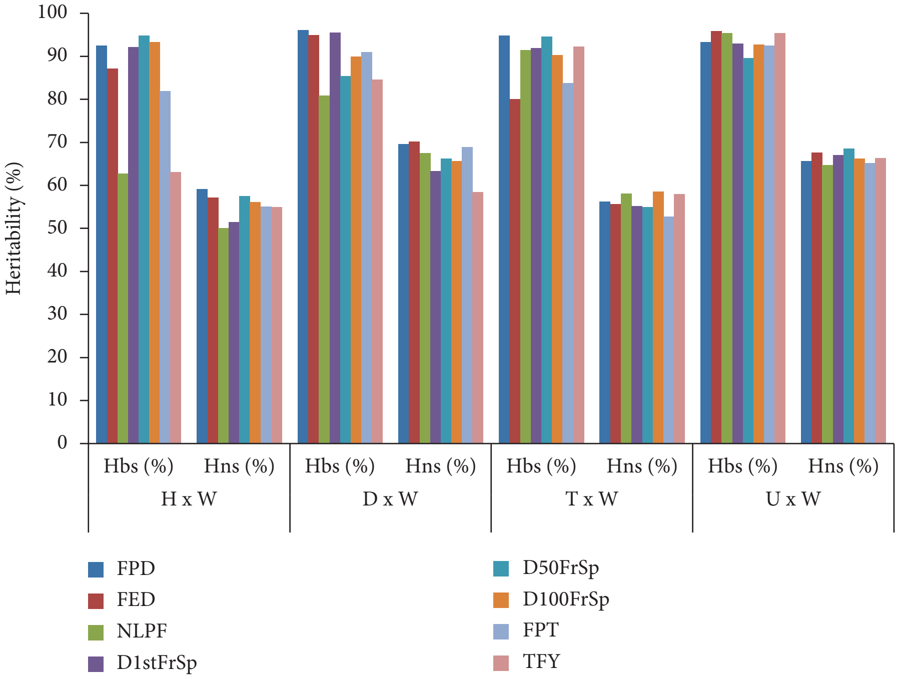

Figure 11: Estimates of the broad and narrow sense heritability for the fruit traits viz., FPD (cm): fruit polar diameter, FED (cm): fruit equatorial diameter, NLPF: number of locules per fruit, D1stFrSp: number of days to first fruit spoilage, D50FrSp: number of days to 50% fruit spoilage, D100FrSp: number of days to 100% fruit spoilage, FPT (cm): fruit pericarp thickness, TFY (t/ha): total fruit yield per hectare, *W*: wild parent ("LA2093"), *H*: CLN2714H, *D*: CLN2498D, *T*: Tima, *U*: UC dan INDIA, Hbs (%): heritability in broad sense, and Hns (%): heritability in narrow sense.

not understood [40]. Genetic and epigenetic reprogramming of genes in hybrids due to the switching of two parents' chromosomes has been linked to one of the justifications for positive heterobeltiosis for delayed flowering and fruiting [49].

Significant negative BP and MP heterosis for D1stFrSp, D50FrSp, and D100FrSp in one hybrid or the other implied earliness in the spoilage of the harvested fruits, compared to those of the better parent and the average performance of the parents. This opposed an earlier finding by Pratta et al. [50] that a cross between *S. pimpinellifolium* with *S. lycopersicum* yielded hybrid fruits with longer shelf life. Hence, the hybrids in the present study may require subsequent backcrosses with the wild parent, being the better parent to achieve a longer shelf life, or crossed with a tester variety that carries recessive mutant allele such as rin, nor or alc, responsible for high shelf life in tomato [51].

Significant positive BP heterosis expressed in various hybrids for FWPP, FPD, FED, NLPF, FPT, and fruit yield suggested that these hybrids performed higher than the recurrent parents which were the better parents for these fruit traits. These hybrids were consistent within the two seasons of evaluation. Due to the presence of dominance gene effects for these traits, exploitation of heterosis by heterosis breeding may be effective for improvement at a higher degree of these fruit-related traits including yield in the F_1 population. Therefore, these hybrids should be given special attention for tomato yield improvement especially in a humid clime as the present result deviated from the normal expected poor fruit traits performance in F_1 when the wild cherry is crossed with cultivated tomato. Kumar et al. [52] reported similar heterosis direction over better parent for fruit pericarp thickness and fruit yield, whereas the negative BP heterosis reported for the number of locules per fruit opposed that of the present trial.

Significant negative BP heterosis manifested for TNFrPP and NFrPT suggested the activity of additive genes indicating undesirability for these traits in the affected F_1 crosses. Shende et al. [53] reported contradicting directions of heterobeltiosis for similar traits although from intraspecific hybrids. However, Amaefula et al. [42] reported negative BP heterosis for similar traits and even more yield traits in both interspecific and intraspecific hybrids of tomatoes. Rakha and Sabry [54] also reported negative BP heterosis for fruit number per plant among all tomato hybrids evaluated. Significant negative MP heterotic effect for TNFrPP, FWPP, FED, NLPF, FPT, NFrPT, FPD, and fruit yield exhibited by one hybrid or the other suggested hybrid performance below that of the parents' mean. This also showed the presence of additive gene actions in the affected crosses.

Powers [55] reported that hybrids from the cross between *S. pimpinellifolium* and *S. lycopersicum* usually have smaller fruit traits performance than the parental arithmetic mean. Gul et al. [41] observed positive and significant BP and MP heterosis for fruit traits such as fruit number per cluster, fruit weight, fruit polar diameter, fruit equatorial diameter, and fruit yield, although the materials were raised from similar species. The direction of heterosis, whether positive or negative, depends on the nature of the genetic variation of a particular plant species [56]. The number of fruits per truss and the total number of fruit per plant are of great significance for the improvement of fruit yield in tomatoes [57, 58]. Improvement of fruit yield is possible in interspecific hybrids with positive and significant BP and MP heterosis for yield-enhancing traits. Hybrid vigour can easily be observed for tomato fruit yield through an increased number of fruits per plant rather than by increased floral and fruit size traits [29, 59, 60]. Garg and Cheema [61] reported that fruit number played a greater role than fruit weight in improving the marketable yield of tomato hybrids.

Heterosis relationships can be complex, and hence, there is a need to establish heterotic groups or pools based on parental genetic divergence in tomatoes just like it has been achieved with rice [62], maize [63, 64], winter cabbage [65], and other crops to help breeders conduct research on heterosis. The hypothesis footing of the heterotic group and division, heterosis model, and heterosis pattern validation is the utilization of heterosis. This would definitely help to improve the breeding efficiency of tomatoes as well as speed up the progress of the breeding effect [66]. Recently, Jin et al. [67] tried to establish and obtain a heterosis group division for tomatoes.

Heritability tries to make a prediction of the progress of selection based on magnitude. In the present trial, the magnitude of additive variance found to be higher than the dominance variance for all reviewed floral and fruit traits showed the importance of the additive gene effects, which is in agreement with the moderate to high narrow sense heritability for these traits. Hence, breeding methods based on direct selection, pedigree selection, single-seed descent, and backcross should be used for the improvement of the affected traits. Vekariya et al. [68] reported additive genetic variation predomination in most of the quantitative traits of tomatoes. Amaefula et al. [42] reported higher dominance variance for most of the traits examined, which contradicts the results of the present study. Ajay et al. [69] reported that additive variance, despite being a major factor, is not usually the best measure of the inheritance of a character. Therefore, the possibility of having a trait highly affected by a gene may still show a relatively low additive variance. The predominance of additive variance tries to reveal the existence of variation between homozygotes at a particular locus with the positive and negative signs of alleles distributed between parents involved in the crossing. For instance, Mather [70] and Robinson et al. [71] concluded that negative dominance variance could have arisen due to errors in sampling as well as environmental interactions.

The higher phenotypic variance than the genotypic variance for all affected traits showed an interaction of the traits with the environment. For the floral and fruit-related traits studied, all crosses showed a low magnitude of dominance and environmental variances, revealing higher estimates of broad and narrow-sense heritability. A similar result has been reported by Rakha and Sabry [54]. The high broad sense heritability estimates recorded in virtually all crosses for a majority of the floral and fruit traits showed that the scope of genetic improvement of these traits is most likely through selection. The moderate to high narrow sense heritability (45–72.54%) for all traits except for flower length observed in "$H \times W$" and "$T \times W$" crosses, style diameter, and ovary length found in "$T \times W$" with values ≤45% revealed the importance of an appreciable additive (fixable) gene effect which was responsible for the genetic variation in these hybrids. In the improvement of self-pollinated plants, additive variation is of immense benefit and encourages the effective selection of individuals with desirable traits from F_2 highly segregating populations, as the gain from the selection will solely rely on gametic variation [39]. As a result, improvement methods such as gametic selection, single-seed descent, backcross, pure line selection, pedigree, and bulk breeding are suggested for the advancement of segregating populations [72, 73]. Causse et al. [74] had earlier reported such additive variations for some fruit quality traits in crosses between large-fruited (cultivated) and wild tomato (cherry fruit) lines.

6. Conclusions

The crosses "$D \times W$" and "$U \times W$" exhibited a high level of heterosis for yield and yield component traits. These crosses can be used to improve tomato humid tolerance directly through heterosis breeding. For the other crosses, heterosis breeding, along with early generation selection for yield-component traits, can be used to improve humid tolerance along with yield. The recurrent cultivars "CLN2498D" or "UC Dan INDIA" obviously proved to be good donors of alleles for the improvement of fruit size in tomatoes in humid climate. The additive variance was found higher in magnitude than dominance variance indicating high narrow sense heritability for the majority of the traits studied. This suggested that direct selection starting from the F_2 segregating population as the best improvement approach is apt.

Data Availability

All data sets generated during and/or analyzed to support the findings of this study are phenotypic data and can be made available from the corresponding author upon request.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

Acknowledgments

The authors are grateful to the Ethiopian Agricultural Research Institute-Melkassa Agricultural Research Center, Ethiopia; National Horticultural Research Institute-Ibadan, Nigeria and C.M. Rick Tomato Genetic Resources Center, Department of Vegetable Crops, University of California, for providing us with the planting materials. This work was supported financially by the European Union Commission under the GENEs Project–with Grant (2016-2988/001-001) (an Intra-Africa Academic Mobility Scheme). This work is part of the Ph.D. research for C. O. Ene. The funder has no role in study design, collection of data and formal analysis, publication decision, or manuscript preparation.

Supplementary Materials

Supplemental Table S1: estimates of the variance components, broad and narrow sense heritability of the F_1 hybrids of tomato for the floral traits. Supplemental Table S2: estimates of the variance components, broad and narrow sense heritability of the F_1 hybrids of tomato for the floral traits (cont'd). Supplemental Table S3: estimates of the variance components, broad and narrow sense heritability of F_1 hybrids of tomato for the fruit traits. Supplemental Table S4: estimates of the variance components, broad and narrow sense heritability of F_1 hybrids of tomato for the fruit traits (cont'd). (*Supplementary Materials*)

References

[1] S. Grandillo, P. Termolino, and E. Van der Knaap, "Molecular mapping of complex traits in tomato," in *Genetics, Genomics, and Breeding of Tomato*, B. E. Liedl, J. A. Labate, J. R. Stommel, A. Slade, and C. Kole, Eds., pp. 150–227, CRC Press; Science Pub, Boca Raton, FL, USA, 2013.

[2] D. Schwarz, A. J. Thompson, and H.-P. Kläring, "Guidelines to use tomato in experiments with a controlled environment," *Frontiers of Plant Science*, vol. 5, pp. 625–716, 2014.

[3] L. Piosik, M. Ruta-Piosik, M. Zenkteler, and E. Zenkteler, "Development of interspecific hybrids between Solanum lycopersicum L. and S. sisymbriifolium Lam. via embryo calli," *Euphytica*, vol. 215, no. 2, p. 31, 2019.

[4] I. Celik, N. Gurbuz, A. T. Uncu, A. Frary, and S. Doganlar, "Genome-wide SNP discovery and QTL mapping for fruit quality traits in inbred backcross lines (IBLs) of Solanum pimpinellifolium L. using genotyping by sequencing," *BMC Genomics*, vol. 18, p. 1, 2017.

[5] L. Ramachandran, D. S. Parihar, and R. Pinnamaneni, "Clinical evaluation of efficacy of modified mucogingival flap technique with connective tissue graft in management of multiple adjacent class iii gingival recessions," *Int. j. recent sci. res.*, vol. 8, no. 4, pp. 16518–16522, 2017.

[6] J. Chand, R. Ahmad, M. Shahzad et al., "Expression of antioxidant genes can increase cold resistance in tomato (Solanum lycopersicum L.)," *Pakistan Journal of Botany*, vol. 53, no. 2, pp. 447–453, 2021.

[7] A. I. Atugwu and M. I. Uguru, "Tracking fruit size increase in recombinants obtained from an interspecific cross between cultivated tomato (Solanum esculentum L.) and wild tomato relative (S. pimpinellifolium L.)," *J. Plant Breed. Crop Sci.*-vol. 4, pp. 62–71, 2012.

[8] D. M. Asfaw, "Analysis of technical efficiency of smallholder tomato producers in Asaita district, Afar National Regional State, Ethiopia," *PLoS One*, vol. 16, no. 9, Article ID e0257366, 2021.

[9] A. Ohwofasa, S. Perveen, T. A. Khan, B. Ijaz, and T. Yasmin, "In silico promoter characterization of PR genes and expression analysis in transgenic tomato plants expressing OsRGLP1," *Pakistan Journal of Botany*, vol. 53, no. 5, pp. 1707–1716, 2021.

[10] V. Khanna, V. K. Khanna, W. Tyagi, M. Rai, and N. T. Meetei, "Wide hybridization and embryo-rescue for crop improvement in Solanum," *Agrotechnology*, vol. 1, no. 11, p. 004, 2013.

[11] W. Barrantes, G. Lopez-Casado, S. Garcia-Martinez et al., "Exploring new alleles involved in tomato fruit quality in an introgression line library of Solanum pimpinellifolium L," *Frontiers of Plant Science*, vol. 7, p. 1172, 2016.

[12] R. E. Voorrips, W. Verkerke, R. Finkers, R. Jongerius, and J. Kanne, "Inheritance of taste components in tomato," *Acta Physiologiae Plantarum*, vol. 22, no. 3, pp. 259–261, 2000.

[13] M. P. Kinkade and M. R. Foolad, "Validation and fine mapping of lyc12.1, a QTL for increased tomato fruit lycopene content," *Theoretical and Applied Genetics*, vol. 126, no. 8, pp. 2163–2175, 2013.

[14] M. R. Foolad, "Genome mapping and molecular breeding of tomato," *International Journal of Plant Genomics*, vol. 2007, p. 52, Article ID 64358, 2007.

[15] P. Gramazio, L. Pereira-Dias, S. Vilanova et al., "Morphoagronomic characterization and whole-genome resequencing of eight highly diverse wild and weedy S. pimpinellifolium and S. lycopersicum var. cerasiforme accessions used for the first interspecific tomato MAGIC population," *Horticulture Research*, vol. 7, no. 1, p. 174, 2020.

[16] A. Sharif, A. Bakhsh, M. Arshad, A. M. Haqqani, and S. Najma, "Identification of genetically superior hybrids in chickpea (Cicer arietinum L.)," *Pakistan Journal of Botany*, vol. 33, pp. 403–409, 2001.

[17] M. A. T. Ayenan, A. Danquah, P. Hanson, I. K. Asante, and E. Y. Danquah, "Identification of new sources of heat tolerance in cultivated and wild tomatoes," *Euphytica*, vol. 217, no. 3, pp. 33–16, 2021.

[18] O. P. Meena and V. Bahadur, "Breeding potential of indeterminate tomato (Solanum lycopersicum L.) accessions using D2 analysis," *SABRAO J. Breed. Genet*, vol. 47, no. 1, pp. 49–59, 2015.

[19] C. O. Ene, P. E. Ogbonna, C. U. Agbo, and U. P. Chukwudi, "Heterosis and combining ability in cucumber (Cucumis sativus L.)," *Information Processing in Agriculture*, vol. 6, no. 1, pp. 150–157, 2019.

[20] Z. Liu, J. Jiang, A. Ren et al., "Heterosis and combining ability analysis of fruit yield, early maturity, and quality in tomato," *Agronomy*, vol. 11, no. 4, p. 807, 2021.

[21] M. Thirupathi Reddy, K. Hari Babu, M. Ganesh, H. Begum, J. Dilipbabu, and R. S. Krishna Reddy, "Gene action and combining ability of yield and its components for late kharif season in okra (Abelmoschus esculentus (L.) Moench)," *Chilean Journal of Agricultural Research*, vol. 73, no. 1, pp. 9–16, 2013.

[22] C. Riedelsheimer, A. Czedik-Eysenberg, C. Grieder et al., "Genomic and metabolic prediction of complex heterotic traits in hybrid maize," *Nature Genetics*, vol. 44, no. 2, pp. 217–220, 2012.

[23] Y. H. Park, M. A. West, D. A. St Clair, and D. A. Clair, "Evolution of AFLPs for germplasm finger printing and assessment of genetic diversity in cultivars of tomato (Lycopersicon esculentum," *L) Genome.*, vol. 47, no. 3, pp. 510–518, 2004.

[24] A. Sorsa, S. Senadheera, and Y. Birru, "Engineering characterization of subgrade soils of Jimma town, Ethiopia, for roadway design," *Geosciences*, vol. 10, no. 3, p. 94, 2020.

[25] C. O. Ene, W. G. Abtew, H. O. Oselebe, F. U. Ozi, and U. N. Ikeogu, "Genetic characterization and quantitative trait relationship using multivariate techniques reveal diversity among tomato germplasms," *Food Sciences and Nutrition*, vol. 10, no. 7, pp. 2426–2442, 2022.

[26] M. Ozores-Hampton, *Hand Pollination of Tomato for Breeding and Seed Production*, UF/IFAS Southwest Florida Research and Education Center, Immokalee, FL, USA, 2014, http://edis.ifas.ufl.edu.

[27] X. Wang, L. Gao, C. Jiao et al., "Genome of Solanum pimpinellifolium provides insights into structural variants during tomato breeding," *Nature Communications*, vol. 11, no. 1, p. 5817, 2020.

[28] M. K. Osei, R. Akromah, S. L. Shilh, and S. K. Green, "Evaluation of some tomato germplasm for resistance to tomato yellow leaf curls virus disease (TYLCV) in Ghana," *Asp. Appl.*, vol. 96, pp. 315–323, 2010.

[29] S. I. Nnungu and M. I. Uguru, "Expression of heterosis in floral traits and fruit size in tomato (Solanum lycopersicum L.) hybrids," *Agro-Science - Journal of Tropical Agriculture, Food, Environment and Extension*, vol. 13, pp. 24–29, 2014.

[30] I. K. Arah, H. Amaglo, E. K. Kumah, and H. Ofori, "Preharvest and postharvest factors affecting the quality and shelf life of harvested tomatoes: a mini review," *International Journal of Agronomy*, vol. 2015, Article ID 478041, 6 pages, 2015.

[31] F. F. Dinssa, O. Mbwambo, J. Macharia, A. Aloyce, and O. Shilla, "Protocols for fruit, leafy and bulb-type vegetable cultivar testing," AVRDC – The World Vegetable Center, Shanhua, Taiwan, 2015.

[32] K. A. Gomez and A. A. Gomez, *Statistical Procedures for Agricultural Research*, p. 657, 2nd edition, An international rice research institute book. A Wiley-interscience Publication. John Wiley & Sons, New York, NY, USA, 1983.

[33] R. R Core Team, *A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria, 2017, http://www.R-project.org/.

[34] R. W. Allard, *Principles of Plant Breeding*, John Wiley & Sons, New York, NY, USA, 1960.

[35] A. Kumar, V. K. Mishra, R. P. Vyas, and V. Singh, "Heterosis and combining ability analysis in bread wheat (Triticum aestivum L.)," *J. Plant Breed. Crop Sci.*, vol. 3, pp. 209–217, 2011.

[36] J. C. Wynne, D. A. Emery, and P. W. Rice, "Combining ability estimation in F_1 Arachis hypogea hybrid," *Crop Science*, vol. 10, no. 6, pp. 713–715, 1970.

[37] K. Mather and J. L. Jinks, *Introduction to Biometrical Genetics*, pp. 249–252, Chapman and Hall Limited, London, UK, 1971.

[38] G. Acquaah, *Principles of Plant Genetics and Breeding*, Blackwell Publishing, Oxford, UK, 2007.

[39] J. N. Warner, "A method for estimating heritability," *Agronomy Journal*, vol. 44, no. 8, pp. 427–430, 1952.

[40] C. R. Mistry, K. B. Kathiria, S. Sabolu, and S. Kumar, "Heterosis and inbreeding depression for fruit yield attributing traits in Eggplant," *Current Plant Biology*, vol. 16, pp. 27–31, 2018.

[41] R. Gul, H.-U. Rahman, I. H. Khalil, S. M. A. Shah, and A. Ghafoor, "Heterosis for flower and fruit traits in tomato (Lycopersicon esculentum Mill.)," *African Journal of Biotechnology*, vol. 9, pp. 4144–4151, 2010.

[42] C. Amaefula, C. U. Agbo, and G. E. Nwofia, "Hybrid vigour and genetic control of some quantitative traits of tomato (Solanum lycopersicum L.)," *Open Journal of Genetics*, vol. 04, no. 01, pp. 30–39, 2014.

[43] U. Bhattarai, A. Sharma, R. Das, and P. Talukdar, "Genetic analysis of yield and yield-attributing traits for high temperature resistance in tomato," *International Journal of Vegetable Science*, vol. 22, no. 6, pp. 585–597, 2016.

[44] L. Powers and C. B. Lyon, "Inheritance studies on duration of developmental stages in crosses with the genus Lycopersicon," *Journal of Agricultural Research*, vol. 63, pp. 129–148, 1941.

[45] P. R. Singh, C. Karak, P. P Mohapatra, B. A. Kumar, and P. Hazra, “Manifestation of heterosis in bittergourd,” *International Journal of Current Microbiology and Applied Sciences*, vol. 7, no. 10, pp. 1376–1385, 2018.

[46] S. M. Kanneh, M. K. Osei, R. Akromah, and M. Frimpong, “Estimate of heterosis in early generations of tomato (Solanum lycopersicum L.),” *Agricultural and Food Science Journal of Ghana*, vol. 9, pp. 704–716, 2016.

[47] A. Javed, N. N. Nawab, S. Gohar et al., “Genetic analysis and heterotic studies in tomato (Solanum lycopersicum L.) hybrids for fruit yield and its related traits,” *SABRAO Journal of Breeding and Genetics*, vol. 54, no. 3, pp. 492–501, 2022.

[48] A. B. Burdick, “Genetics of heterosis for earliness in the tomato,” *Genetics*, vol. 39, no. 4, pp. 488–505, 1954.

[49] Z. J. Chen, “Genomic and epigenetic insights into the molecular bases of heterosis,” *Nature Reviews Genetics*, vol. 14, no. 7, pp. 471–482, 2013.

[50] G. R. Pratta, G. R. Rodriguez, R. Zorzoli, E. M. Valle, and L. A. Picardi, “Phenotypic and molecular characterization of selected tomato recombinant inbred lines derived from the cross Solanum lycopersicum x S. pimpinellifolium,” *Journal of Genetics*, vol. 90, no. 2, pp. 229–237, 2011.

[51] S. Kumar, P. H. R. Gowda, and N. M. Mallikarjuna, “Evaluation of selected F6 tomato lines for extended shelf life,” *SABRAO J. Breed. Genet.*vol. 47, no. 4, pp. 326–334, 2015a.

[52] V. Kumar, S. K. Jindal, M. S. Dhaliwal, and O. P. Meena, “Hybrid development for resistance to late blight and root knot nematodes in tomato (Solanum lycopersicum L.),” *SABRAO J. Breed. Genet.*vol. 47, no. 4, pp. 340–354, 2015b.

[53] V. D. Shende, T. Seth, S. Mukherjee, and A. Chattopadhyay, “Breeding tomato (Solanum lycopersicum L.) for higher productivity and better processing qualities,” *SABRAO J. Breed. Genet.*vol. 44, no. 2, pp. 302–321, 2012.

[54] M. K. Rakha and S. A. Sabry, “Heterosis, nature of gene action for yield and its components in tomato (Lycopersicon esculentum Mill.),” *Middle East Journal of Agriculture Research*, vol. 8, pp. 1040–1053, 2019.

[55] L. Powers, L. Ames, *Gene Recombination and Heterosis*, Heterosis and J. W. Gowen, Eds., State University Press, East Lansing, Michigan, 1952.

[56] E. A. Lee, M. J. Ash, and B. Good, “Re-examining the relationship between degree of relatedness, genetic effects, and heterosis in maize,” *Crop Science*, vol. 47, no. 2, pp. 629–635, 2007.

[57] S. Ahmad, A. K. M. Quamruzzaman, and M. R. Islam, “Estimate of heterosis in tomato (Solanum lycopersicum L.),” *Bangladesh Journal of Agricultural Research*, vol. 36, no. 3, pp. 521–527, 1970.

[58] S. H. Shah, S. Ali, S. Muhammad et al., “Influence of pH of co-cultivation medium, claforan® concentration, co-cultivation period, pre-selection duration and selection regime on tomato transformation,” *Pakistan Journal of Botany*, vol. 54, no. 3, pp. 855–863, 2022.

[59] C. Rick and L. Butler, “Cytogenetics of the tomato,” *Advances in Genetics*, vol. 8, pp. 267–382, 1956.

[60] L. Cui, Y. Wang, K. Cao, and Z. Zou, “Overexpression of the ATP synthase β subunit gene enhanced the ability of tomato (Solanum lycopersicum L.) plantlets to resist low temperatures,” *Pakistan Journal of Botany*, vol. 54, no. 3, pp. 879–885, 2022.

[61] N. Garg and D. S. Cheema, “Seeds of tomato (Solanum lycopersicum L) hybrids incorporating rin, nor, or alc alleles exhibit heterosis for yield and quality traits,” *Journal of New Seeds*, vol. 11, no. 3, pp. 250–261, 2010.

[62] W. Yingheng, C. Qiuhua, X. Hongguang et al., “Determination of heterotic groups and heterosis analysis of yield performance in indica rice,” *Rice Science*, vol. 25, no. 5, pp. 261–269, 2018.

[63] M. G. Kanyamasoro, J. Karungi, G. Asea, and P. Gibson, “Determination of the heterotic groups of maize inbred lines and the inheritance of their resistance to the maize weevil,” *African Crop Science Journal*, vol. 20, pp. 99–104, 2012.

[64] O. A. Oyetunde, B. Badu-Apraku, O. J. Ariyo, and C. O. Alake, “Efficiencies of heterotic grouping methods for classifying early maturing maize inbred lines,” *Agronomy*, vol. 10, no. 8, p. 1198, 2020.

[65] X. Li, H. Yu, Z. Li et al., “Heterotic group classification of 63 inbred lines and hybrid purity identification by using ssr markers in winter cabbage (Brassica oleracea L. var. capitata),” *Horticultural Plant Journal*, vol. 4, pp. 158–164, 2018.

[66] W. B. Suwarno, K. V. Pixley, N. Palacios-Rojas, S. M. Kaeppler, and R. Babu, “Formation of heterotic groups and understanding genetic effects in a provitamin a biofortified maize breeding program,” *Crop Science*, vol. 54, no. 1, pp. 14–24, 2014.

[67] L. Jin, L. P. Zhao, Y. L. Wang et al., “Combining ability and division of heterosis group in tomato,” *Jiangsu Journal of Agricultural Sciences*, vol. 35, pp. 667–675, 2019.

[68] T. A. Vekariya, G. U. Kulkarni, D. M. Vekaria, A. P. Dedaniya, and J. T. Memon, “Combining ability analysis for yield and its components in tomato (Solanum lycopersicum L.),” *Acta Scientific Agriculture*, vol. 3, no. 7, pp. 185–191, 2019.

[69] B. C. Ajay, B. N. Gnanesh, K. N. Ganapathy et al., “Genetic analysis of yield and quantitative traits in pigeon pea (Cajanus cajan L. Mill sp),” *Euphytica*, vol. 186, no. 3, pp. 705–714, 2012.

[70] K. Mather, *Biometrica Genetics: The Study of Continuous Variation*, Dover publication, Inc, New York, NY, USA, 1949.

[71] H. F. Robinson, R. E. Comstock, and P. H. Harvey, “Genetic variance in open pollinated varieties of corn,” *Genetics*, vol. 40, no. 1, pp. 45–60, 1955.

[72] R. Bernardo, “On the effectiveness of early generation selection in self-pollinated crops,” *Crop Sci*, vol. 43, no. 4, pp. 1558–1560, 2003.

[73] Z. Effah, M. K. Osei, R. Akromah, and M. Frimpong, “Hybridisation between cherry tomato (small fry) and Petomech for shortened fruit maturation, size and earliness,” *Afr. Crop Sci. J.*vol. 25, no. 1, pp. 25–32, 2017.

[74] M. Causse, M. Buret, K. Robini, and P. Verschave, “Inheritance of nutritional and sensory quality traits in fresh market tomato and relation to consumer preferences,” *Journal of Food Science*, vol. 68, no. 7, pp. 2342–2350, 2003.