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Selfing revealed positive values than backcrossing for yield and yield enhancing traits among tomato segregating populations generated from *Solanum lycopersicum* × *S. pimpinellifolium* crosses under tropical humid climate

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Abstract

The objectives of this study were to assess phenotypic variability among F_3 and BC_1F_2 tomato populations, and apply genotype by yield*trait (GYT) biplots for population and line selection based on multiple traits. Four diverse cultivated parents ('CLN2498D' and 'CLN2417H' from Ethiopia; 'UC Dan INDIA' and 'Tima' from Nigeria), and wild parent 'LA2093' were used to generate 276 potential breeding lines. The lines were categorized into eight populations ('Pop_1_W/H1', 'Pop_2_W/H2', 'Pop_3_W/D1', 'Pop_4_W/D2', 'Pop_5_W/T1', 'Pop_6_W/T2', 'Pop_7_W/U1', and 'Pop_8_W/U2'), and evaluated twice in the field using 19 × 15 alpha-lattice design with two replicates. Significant differences were observed among lines

and populations for all yield enhancing traits. 'Pop_1_W/H1', 'pop_4_W/D2' and 'pop_6_W/T2' expressed the highest genetic divergence for plant height, number of leaves, total flower and fruit number, and fruit weight. GYT biplots revealed that all yield*trait interactions had a positive correlation with each other. F_3 populations, 'Pop_5_W/T1' and 'pop_1_W/H1' exhibited the best performance for majority of the yield*trait combinations. Hierarchical clustering on principal components (HCPC) revealed overlapping lines (70.58% of Cluster D lines) and (54.05% of Cluster U lines) from the two F_3 populations. In BC_1F_2 population, 32.35% of the 34 original lines of Cluster D and 48.48% of Cluster T lines overlapped between Clusters D and T, while 18.18% of Cluster T lines and 8.82% of Cluster H lines were transgressive between Clusters T and H. Transgressive segregants '0210U1', '0211U1', and '0171T1' of selfed population using multivariate analysis were believed to represent potential sources of novel genetic variation for future tomato breeding.

Keywords: *Solanum pimpinellifolium*, genotype by yield*trait biplot, humid environment, multi-traits, tomato population improvement, superiority index

1. Introduction

Tomato (*Solanum lycopersicum*) is the world's second most important vegetable crop after potato (FAOSTAT 2020). Its global production has increased by over 54% between 2000 and 2014 (FAO 2017). In 2019, 182 million metric tons of tomato was produced which was valued at about US $95 billion (FAOSTAT 2020). The increase in tomato fruit production hinges on the use of improved and high yielding cultivars (Wang et al. 2020).

However, the consistent increase in world production over the years has not adequately satisfied the global tomato fruit demand. Asfaw (2021) observed a supply gap in tomato fruit demand.

Atugwu et al. (2019) attributed this scarcity to environmental limitations placed on the most available high premium cultivars by the humid environmental conditions. Tomato leaf size, fruit yields and fruit quality are reduced drastically at lower vapor pressure deficit or higher humidity. There is also significant increase in flower and fruit abortion, high disease occurrence and rapid fruit decay both in field and after harvest under high humidity conditions (Uguru and Atugwu 2000).

The challenge in terms of yield loss, reduced productivity and susceptibility of tomato to both biotic and abiotic stress factors caused by high humidity of the production environment is increasingly drawing attention of the stakeholders in tomato research and production. For instance, Xu (2007) reported significant yield loss in tomato grown under high air humidity, which was suspected to be a result of lower photosynthesis-related activities and lower photosynthetic capacity evident under such growing condition compared to tomato exposed to low humidity. Alam et al. (2010) observed extreme sensitivity of tomato to hot as well as humid environments, which affected yield and other physiological processes negatively.

In tackling new challenges, breeders have relied on wild relatives of plant for novel gene donor. Among the wild relatives of tomato, *Solanum pimpinellifolium* stands out as a good gene donor. This is due to its large genetic variability, high compatibility, excellent growth architecture, good fruit organoleptic qualities, prolonged fruit shelf life, profuse flowering and fruiting, and high adaptability to humid environment (Miller and Tanksely 1990; Foolad 2007; Rodriguez et al. 2006; Rodriguez et al. 2010; Schwarz et al. 2014; Grandillo et al. 2013; Celik et al. 2017; Piosik et al. 2019; Wang et al. 2020).

74 *S. pimpinellifolium* played a vital role in the development of heat-tolerant tomato varieties in
75 Taiwan (Ebert and Chou 2015). In Nigeria, it showed better responses to high humidity
76 compared to the cultivated elite tomatoes (Atugwu and Uguru 2012). Among many benefits of
77 gene introgression from *S. pimpinellifolium* is the increased fruit number, which is a major
78 contributory attribute to yield, in addition to resilience to high humidity (Wang et al. 2020).
79 These inherent benefits in *S. pimpinellifolium* is the motivation in selecting one of its lines
80 'LA2093' to improve tomato for increased yield and adaptability to the humid tropical climes.

81 Evaluation of different population means performance of derived progenies at early segregating
82 generations as an approach to improve most economic traits especially yield and fruit quality
83 traits for selection have recently been reported in tomato (Finzi et al. 2020; Gomes et al. 2021).
84 Selection of any of such populations for improvement would be dependent on performance of the
85 populations across the multiple traits. However, a major challenge has been the difficulty of
86 knowing which statistical tool, preferably multivariate, is most suitable for evaluating multiplex
87 traits in either germplasm or breeding populations of crops.

88 Genotype selection or population improvement based on multiplex traits raises a lot of concern
89 in plant breeding. Genotype by yield*trait (GYT) biplot analysis is a novel tool with high
90 efficiency compared to other statistical tools (Yan and Frégeau-Reid 2018). The GYT biplot
91 positions genotypes or populations in hierarchy based on their levels in yield combination with
92 other target traits whether polygenic, monogenic or oligogenic other than yield, and expresses
93 trait profiles, which is their strengths and weaknesses. This is as opposed to the existing methods
94 which only concentrate efforts on genotype evaluation by their levels in individual traits
95 (Mohammadi 2019).

The objectives of this research are; (i) to assess the phenotypic variation in yield enhancing traits in tomato using segregating lines to identify novel sources of improved performance, and (ii) select population (s) among F_3 and BC_1F_2 populations, based on yield and other target traits using GYT biplots analyses in a humid environment.

2. Materials and Methods

2.1 Experimental sites description

The present study was conducted at research field of the Department of Horticulture and Plant Sciences, Jimma University, Ethiopia during the 2020/2021 and 2021/2022 cropping seasons. Jimma is classified as warm to cold-environment locally known as "Weyna Dega" (Abdela et al. 2017), suitable for agriculture, with high degree of humidity, located on latitude 07º4′N, longitude 36º50′E and altitude 1,710 m above the sea level in the south west, Oromia region of Ethiopia. The monthly weather conditions of Jimma during the experiment seasons are presented in Figures 1 and 2. Jimma is mainly covered with black, gray and red colored plastic clay soils (Alemineh et al. 2020).

2.2 Genetic materials

A total of 276 potential breeding lines generated from four parental lines - elite parents of cultivated tomato (*S. lycopersicum*) and wild parent 'LA2093' of *S. pimpinellifolium* from California's C.M. Rick Tomato Genetic Resource Center were used for this trial. The domesticated cultivars were morphologically diverse in terms of superiority and weakness in the traits studied. The four elite lines - 'CLN2498D' (D) and 'CLN2714H' (H) from Ethiopia and 'UC Dan INDIA' (U) and 'Tima' (T) from Nigeria were used.

117 ‘CLN2498D’ and ‘UC Dan INDIA’ were superior performing parents based on fruit yield and
118 shape/size of fruits (round and large) but had fewer number of fruits and susceptive of the humid
119 condition of the growing environment whereas ‘CLN2714H’ and ‘Tima’ were poor performers
120 in terms of fruit number production, fruit yield, having elongated medium fruit size, and longer
121 floral and fruit phenology. The wild parent (W) ‘LA2093’ was commonly used as pollen donor
122 to the four cultivated materials (females) using a bi-parental mating design by hand pollination
123 according to Ozores-Hampton (2014). According to Wang et al. (2020) ‘LA2093’ has prolonged
124 shelf life, an early flowering and maturing variety, quantitative disease resistant and relatively
125 resilient to humid environmental condition. It possesses enormous genetic potentials, having
126 desirable alleles for breeding choice tomato cultivars with appreciable economic qualitative and
127 quantitative traits performance.

128 Four F_1 crosses, *viz*., ‘H × W’, ‘T × W’, ‘D × W’, and ‘U × W’ were obtained. Then two
129 different crosses were done. Firstly, the F_1 materials realized from each cross were crossed back
130 to the recurrent parents to obtain BC_1. The BC_1 was also selfed to obtain BC_1F_2 and $BC_1F_{2:3}$
131 progenies, and secondly, the F_1 population selfed to produce F_2. The F_2 of each cross was selfed
132 to produce F_3. A total of eight populations were developed: four F_3 populations and four BC_1F_2
133 populations. The following populations were coded as presented in Table 1.

134 **2.3 Field management and experimental design**

135 The plant materials were evaluated using an alpha lattice experimental design with two
136 replicates. Each replicate contained 19 blocks whereas each block contained 15 plots. The
137 tomato seeds were first planted in plastic seed trays filled with sterilized top soil mixed with well
138 cured poultry manures and river sand in the ratio of 3: 2: 1, respectively by volume with the use

of a head pan. At 24 days after seedling emergence with the appearance of 4-5 true leaves, uniform vigorous seedlings were transplanted to the field.

Each plot occupied by a particular genotype of each cross whether $F_{3:4}$ or $BC_1F_{2:3}$ consisted of three rows of plant (30 plants/ plot) in an area of 1.5m × 5m with 0.5m × 0.5m inter-intra row spacing. A distance of 1m and 0.5m alleys were ensured between blocks and plots, respectively. Poultry droppings at the rate of 10 metric tons per hectare were worked into the soil within each replicate 16 days before seedlings were transplanted. Cultural practices such as weed control, irrigation, fertilizer (DAP-Di Ammonium Phosphate), fungicide (Ridomil-Mancozeb and Metalaxyl-M), staking, pruning, and insecticide (Karate-Lambda-Cyhalothrin 5% EC) were applied as suggested by Osei et al. (2010).

2.4 Data collection

Data were taken on 10 plants of each genotype in each replicate all from inner plants of each plot eluding border plants. The following morphological traits were measured and recorded at 9 week after transplanting during which the genotypes were expected to have completed vegetative process as recommended by AVRDC guideline (Dinssa et al. 2015).

Plant height (PH cm) was measured from the plant base to the shoot tip. Number of leaves (NL), primary branches (NBp), secondary branches (NBs), and nodes (NN) were counted. Phenological traits included; number of days to first anthesis (DFA), 50% anthesis (D50A), first fruit emergence (DFFE), 50% fruit set (D50FS), and first fruit ripening (DFFR) were taken from the day of transplantation of seedlings. Fruit shelf-life traits included: number of days to first fruit spoilage (D1stFSp) and 100% fruit spoilage (D100FSp) stored under room temperature according to Arah et al. (2015).

161 The room temperature ranged from 18ºC to 23ºC while the relative humidity was from 84% to
162 91% throughout the shelf life duration. Total number of flowers per plant (TNFlPP) and total
163 number of fruits per plant (TNFrPP) were counted. Fruits were cut crosswise to count number of
164 locules per fruit (NLPF). The total number of mature fruits showing ripening initiation at second
165 harvest was weighed with electronic weighing balance and the fruit weight per plant (FWPP g)
166 recorded. The total fruit yield per hectare (TFYPH t/h) was estimated as described by Dinssa et
167 al. (2015).

168 **2.5 Statistical analysis**

169 Before computing the analysis of variance, test for homogeneity of residual variances was
170 carried out using F test where larger variance was divided by the smaller variance between the
171 two seasons, which suggested the two sets of data could be combined. Each population data
172 along parents was subjected to two-way analysis of variance (ANOVA) using R software (R
173 Core Team 2017) to analyze variance components.

174 Descriptive statistics and genetic parameters were done using the package "variability" in R as
175 recommended by Raj et al. (2020). The descriptive statistics were means, and ranges (minimum
176 and maximum), while the genetic parameters included genetic advance as percentage of mean
177 (GAM), genotypic coefficient of variation (GCV), phenotypic coefficient of variation (PCV);
178 broad sense heritability (h_{bs}) which was estimated as the ratio of genotypic variance (GV) to
179 phenotypic variance (PV). The GCV and PCV values were categorized as high (>20%), medium
180 (10–20%) and low (<10%) based on the recommendation of Burton and DeVane (1953). The
181 expected GAM (%) on 5% selection intensity were ranked as low (1 – 10%), intermediate (10 –
182 20%) and high (>20%) whereas broad sense heritability was categorized as low (0 – 30%),
183 intermediate (30 – 60%) and high (>60%) according to Khan et al. (2021). Comparison among

184 populations was based on these classified genetic parameters: GCV, PCV, h_{bs} and GAM using
185 graphs.

186 Data were further analyzed by the 'genotype by yield*traits (GYT)' biplots for the 'Tester
187 Vector' view showing relationship among yield-trait combinations, the 'Average Tester
188 Coordination' view ranking the genotypes based on their overall superiority and their strengths
189 and weaknesses, and 'which wins where' view or the polygon view highlighting genotypes with
190 outstanding profiles based on the genotype by yield*trait combined data, an option of GGE
191 biplot software version 6.3 (Yan 2001). We adopted the principle of GYT biplot analysis on the
192 various populations with 'each population mean' representing genotype of the GYT biplot
193 analysis.

194 From the original data (Supplemental Table S1), a GYT table was derived (Supplemental Table
195 S2), in which each column was a yield*trait combination. The method indicates that each trait
196 should either be multiplied or divided by total fruit yield according to the objectives of breeding.
197 To develop the GYT table, traits with favorable or desirable increased values (such as PH, NL,
198 NBp, NBs, NN, TNFlPP, TNFrPP, FWPP, D1stFSp, D100FSp, and NLPF) were multiplied with
199 yield using the multiplication operator ("*") whereas traits with favorable decreased values (the
200 phenological traits) were used to divide yield using the division operator ("/").

201 By this method, in the GYT table a larger value is always more desirable. A mean superiority
202 index (MSI) which involved all yield*trait combinations was also calculated based on the
203 standardized GYT table as described by (Yan and Frégeau-Reid 2018) using the formula as
204 follows:

205 $$P_{ij} = \frac{T_{ij} - \overline{T}_j}{S_j}$$

Where,

Pij is the standardized value of genotype *i* for yield-trait combination *j* in the standardized table, $\bar{T}ij$ is the original value of genotype *i* for yield-trait combination *j* in the GYT table (Supplemental Tables S2), *Tj* is the mean across genotypes for yield-trait combination *j*, and *Sj* is the standard deviation for yield-trait combination *j*. The biplots of GYT were based on singular value decomposition of trait-standardized data ("Scaling = 1, Centering = 2") and trait-focused singular value partition ("SVP = 2") according to Yan and Tinker (2005), for all the views employed in the present trial except the 'Average Tester Coordination' view which showed SVP = 1. Traits were regarded as 'tester' when using 'relation among testers' option. The 'Tester Vector' view of the GYT biplots showed associations among the yield-trait combinations. The 'Average Tester Coordination' view of the GYT biplots ranked the populations based on their overall superiority and their strengths and weaknesses. The 'which-won-where' view of the GYT biplots was used to highlight population with outstanding profiles.

Hierarchical clustering on principal components (HCPC) was done to group the genotypes based on the measured traits, and the results were visualized using the *fviz_cluster* functions of the R package *"factoextra"* for factor map (Kassambara and Mundt 2020).

3. Results

3.1 Genetic variability, heritability and genetic advance for quantitative traits

Despite the variations recorded in some weather elements for the two years, the test for homogeneity carried out on the tomato traits data suggested the performance of a combined analysis of variance. The result showed that genotypes within each population differed significantly for total fruit yield and other traits studied (P<0.001). The descriptive and genetic

parameters including h_{bs} and GAM of the traits in each population are summarized in Supplemental Tables S4a & S4b to S7a & S7b.

Comparing the parental lines, 'CLN2498D' was the highest for NLPF (7.22), FWPP (3093.2 g) and yield (64.03 t/h), followed by 'UC Dan INDIA' (6.48, 2955.1 g and 61.17 t/h, respectively) while the wild parent, 'LA2093' displayed the highest values for PH (160.06 cm), NL (191.48), NBp (12.53), NBs (45.72), NN (39.51), TNFlPP (511.78) and TNFrPP (496.25), highest days to observe the fruit firmness and expressed the least days to observed all the floral and fruit phenological traits. Variation of the populations from the better performing parent was also shown in this study. For instance, 'pop_1_W/H1' showed higher maximum values for PH (176.29 cm), TNFlPP (568.66), TNFrPP (534.15) and NLPF (7.35); 'pop_7_W/U1' for NL (195.96), NBp (14.53), NBs (47.81), and NN (43.34); 'pop_8_W/U2' for D1stFSp (27.24 days) and D100FSp (37.23 days) than those recorded in the better parents depending on trait.

'pop_5_W/T1' had the highest maximum value among the 8 populations for FWPP (2292.55g) and fruit yield (46.15 t/h), the least maximum values for DFFE (28.23 days), and DFFR (48.82 days); 'Pop_7_W/U1' for DFA (15.93 days), D50A (20.04 days) and D50FS (36.81 days) although the values were poorer than the better performing parents. Moreover, the mean values showed similar results trend with the maximum range descriptions except that among the populations, least D50FS (34.89 days) was recorded in 'pop_5_W/T1'.

All the 8 populations displayed low (<10%) GCV and PCV for the phenological traits: DFA, D50A, DFFE, D50FS and DFFR. High (>20%) GCV and PCV were shown in all the populations for PH. For NL, majority of the populations expressed medium to high GCV and PCV with the exception of 'pop_4_W/D2' and 'pop_8_W/U2'. Intermediate (10-20%) or high (>20%) GCV

and PCV were recorded for FWPP and NLPF in all populations except ‘pop_5_W/T1’ which showed low values for FWPP. All the populations displayed medium or high GCV and PCV values for NBp except ‘pop_8_W/U2’, whereas for NBs all the populations were low apart from ‘pop_1_W/H1’, ‘pop_5_W/T1’ and ‘pop_6_W/T2’.

‘Pop_3_W/D1’ and ‘pop_7_W/U1’ showed high GCV and PCV for NN; leaving the rest populations intermediate, whereas ‘pop_6_W/T2’ had low values. ‘Pop_3_W/D1’, ‘pop_4_W/D2’, ‘pop_7_W/U1’ showed intermediate GCV and PCV values for TNFlPP and TNFrPP while ‘pop_5_W/T1’ and ‘pop_6_W/T2’ could display similar category of GCV and PCV only for TNFrPP. For the two traits which tested fruit durability after harvest, D1stFSp and D100FSp, all the populations expressed medium or high GCV and PCV values with the exclusion of ‘pop_3_W/D1’ and ‘pop_4_W/D2’, although ‘pop_7_W/U1’ displayed medium GCV and PCV only for D100FSp. For fruit yield, ‘pop_2_W/H2’, ‘pop_3_W/D1’ and ‘pop_7_W/U1’ displayed moderate GCV and PCV values. The difference between the GCV and PCV values were negligible for all the traits in all populations.

All the populations exhibited very high magnitude of GV and PV for traits such as PH, NL, TNFlPP, TNFrPP, and FWPP. Among the populations, ‘pop_1_W/H1’ displayed in magnitude the highest GV and PV values for PH and NL; ‘pop_4_W/D2’ for TNFlPP and TNFrPP; and ‘pop_6_W/T2’ for FWPP. The variations that existed between the PV and GV for all the traits in all the populations were minimal.

High (>20%) GAM was displayed by all the populations for PH, NL, NBp, NN, and NLPF, except ‘pop_4_W/D2’ for NL (13.13%); ‘pop_6_W/T2’ for NN (16.20%) and ‘pop_8_W/U2’ for NL (13.18%) and NBp (15.42%) which showed intermediate values. For NBs, high GAM

were expressed by ‘pop_1_W/H1’, ‘pop_5_W/T1’ and ‘pop_6_W/T2’; intermediate by ‘pop_2_W/H2’, ‘pop_3_W/D1’ and ‘pop_7_W/U1’. GAM values for DFA and D50A were low (<10%) in ‘pop_1_W/H1’, ‘pop_4_W/D2’ and ‘pop_6_W/T2’ and moderate (10-20%) in ‘pop_3_W/D1’ and ‘pop_8_W/U2’. However, ‘pop_2_W/H2’ displayed moderate value for DFA whereas ‘pop_5_W/T1’ and ‘pop_7_W/U1’ exhibited similar class of GAM for D50A.

The expression of high GAM was observed in ‘pop_3_W/D1’, ‘pop_4_W/D2’, and ‘pop_7_W/U1’ for TNFlPP and TNFrPP leaving the rest with medium values for similar traits. All the populations showed low (<10%) GAM for traits such as: DFFE, D50FS, and DFFR except ‘pop_6_W/T2’ which displayed a weak intermediate value for DFFE. Apart from ‘pop_5_W/T1’ which expressed moderate GAM for FWPP, the rest populations showed high values with ‘pop_3_W/D1’ being the highest. For D1stFSp and D100FSp, high GAM were noted in ‘pop_1_W/H1’, ‘pop_2_W/H2’, ‘pop_5_W/T1’ and ‘pop_6_W/T2’; intermediate values were observed in ‘pop_3_W/D1’ and ‘pop_4_W/D2’; while ‘pop_7_W/U1’ displayed high GAM for D100FSp and moderate for D1stFSp. All the populations evaluated showed medium GAM for total fruit yield except ‘pop_2_W/H2’, ‘pop_3_W/D1’ and ‘pop_7_W/U1’ which displayed high values for the same trait.

High (>60%) broad sense heritability were found in all the populations for virtually all the traits studied. However, moderate (30-60%) heritability estimates were consistently observed for DFFR in all the populations except ‘pop_6_W/T2’ (63.20%) and ‘pop_5_W/T1’ (26.25%) which showed high and low (<30%) values, respectively for similar trait. ‘Pop_4_W/D2’ expressed intermediate heritability for DFFE (52.03%) and low value for D50FS (25.97%) leaving the rest populations with high values for the same traits. Moderate heritability estimate was recorded in ‘Pop_6_W/T2’ for D50A (50.50%) among all the populations. Figures 3 to 7 present graphs

which compared the 8 populations for each quantitative trait and concentrated only on the categorized genetic parameters such as genotypic coefficient of variation, phenotypic coefficient of variation, heritability estimates in broad sense and genetic advance as a percentage of mean.

3.2 Genotype by yield*trait (GYT) biplots using different views

The idea behind the involvement of different views of the GYT biplot was to allow the data to be investigated from different angles for better understanding of the relationship between populations and yield*trait combinations, superior population(s) as well as the yield*trait profiles of the populations. The total variation revealed by the PC1 and PC2 among the yield*traits combinations of these views/models was 97.5%.

3.2.1 Relationships among yield*trait combinations using the Tester Vector view of the GYT biplot

According to the Tester Vector view of the GYT biplot for the 8 populations, all yield*trait interactions had a positive correlation with each other as shown by the acute angles between their vectors (Figure 8). This may be due to the involvement of yield as a component of all yield*trait combinations. This vital feature of GYT biplot makes it unique when compared to GT biplot as genotypes or populations are easily ranked graphically and meaningfully based on their yield*trait combinations.

The result showed that the magnitudes of angles among yield*D1stFSp, yield*D100FSp and the rest yield*trait combinations were higher although all yield*trait combinations indicated high positive correlation. Among all populations, ‘pop_5_W/T1’ and ‘pop_1_W/H1’ had the largest values for yield*PH, yield*NN, yield*TNFlPP and yield*TNFrPP, although they had high proximity with several other yield*trait combinations.

3.2.2 Superiority vs. "weaknesses and strengths" of genotypes using the Average Tester Coordination view of the GYT biplot

Figure 9 represents the Average Tester Coordination view for the 8 tomato populations. This view of the GYT biplot showed the superiority ranking of the populations based on their yield*trait combinations. The single arrow line which passed through the biplot origin and the average yield*trait interactions is the average tester coordinate (ATC) whereas the small circle on the ATC showed the placement of the "average yield*trait combination," which was determined by the coordinates of all yield*trait combinations in the biplot. The double arrow blue line is the general population mean. It divided the plot into two parts which separated the populations based on their performance. The populations found on the side of the ATC arrow (right) showed better performance for the surrounding yield*traits combinations whereas those found at the opposite side (left) showed weak performance.

The best ranked population based on the yield*trait combinations was 'pop_5_W/T1' and was followed by 'pop_1_W/H1', 'pop_4_W/D2', and 'pop_6_W/T2'. In contrast, 'pop_2_W/H2', 'pop_7_W/U1', 'pop_3_W/D1', and 'pop_8_W/U2' were ranked the poorest based on their performance below the population mean for all the yield*trait combinations. Based on traits profiles of the populations, 'pop_5_W/T1', 'pop_1_W/H1', and 'pop_6_W/T2' appeared to be balanced for various yield*trait combinations; while 'pop_4_W/D2' was strong in the two shelf-life traits: D1stFSp and D100FSp in combination with yield but weak in TNFlPP, TNFrPP, PH, and NN. Despite populations general superiority or weakness stand, those placed below the ATC such as 'pop_5_W/T1', 'pop_1_W/H1', 'pop_6_W/T2', and 'pop_2_W/H2' tended to have relatively good levels of the traits below the ATC while having poor levels of the traits above the

ATC. The opposite is true for populations ('pop_7_W/U1', 'pop_3_W/D1', 'pop_8_W/U2' and 'pop_4_W/D2') placed above the ATC.

The weakness and strength of each population is presented in Supplemental Table S3. The best populations were 'pop_5_W/T1' and 'pop_1_W/H1' based on the magnitude of their mean values as expressed in the mean superiority index (MSI) table, in that order. Of these, 'pop_5_W/T1' did not have any negative value for all yield*traits combinations, while the second placed 'pop_1_W/H1' exhibited negative values for D1stFSp. Apart from these best performer populations mentioned which had positive MSI, the rest populations expressed negative values for MSI.

3.2.3 Genotypes performance on yield*trait combinations using which-won-where view of the GYT biplot

The result showed that 'pop_5_W/T1' accompanied by 'pop_1_W/H1' exhibited the best performance for a majority of the yield*trait combinations (Figure 10). The only yield*trait combination left out was yield*D1stFSp which projected 'pop_4_W/D2' as the best performer. However, 'pop_4_W/D2' and 'pop_5_W/T1' shared equal but leading performance for yield*D100FSp which appeared on the radiate line between the two populations. The result showed that these populations mentioned were the best in combining fruit yield with the other traits as observed in the present biplot.

3.3 Clustering pattern analysis for the quantitative traits in F_3 and BC_1F_2 populations

Clustering pattern analysis using hierarchical clustering on principal components (HCPC) classified the lines into four clusters in the two population types (Figures 11 and 13). However, transgressive segregation was observed for the studied traits in both F_3 and BC_1F_2.

There was significant structuring among the lines observed in F_3 composite populations. Among F_3 populations (Figure 11), clusters D and U which encompassed originally lines from crosses between 'CLN2498D × LA2093' and 'UC Dan INDIA × LA2093' contained transgressive or overlapping lines (70.58% of all D lines) and (54.05% of all U lines), respectively from the two populations. These two populations/clusters were characterized by less vigorous plants with lower performance in virtually all traits compared to clusters H and T (Figure 12; Supplemental Tables S4a, S5a, S6a, & S7a). Of the 37 lines of 'UC Dan INDIA × LA2093' cross (cluster U), two lines '0210U1' and '0211U1' were lone genotypes (outliers) whereas '0171T1' was the only lone genotype from 'Tima × LA2093' cross (cluster T 'pop_5_W/T1').

Similar trend was found between clusters H and T of 'CLN2417H × LA2093' and 'Tima × LA2093' crosses, respectively. 8.57% of all H lines and 30.30% of all T lines were found overlapping between clusters/populations H and T. Lines such as '0020H1' and '0035H1' of cluster H found their way expressly among lines of cluster T whereas '0144T1' of cluster T showed slight drifting into cluster H. The cluster description is found in Figure 11.

The mean of each F_3 population plotted in a boxplot analysis displayed significant differences for all the studied traits (Figure 12). Cluster H 'pop_1_W/H1' had the highest mean values for PH, TNFlPP, and TNFrPP; while cluster T 'pop_5_W/T1' had the highest for NB_prim, NB_sec, NN, FWPP, and fruit yield, the least DFFE, DFFR, also taking the shortest days to 100% fruits shriveling. Number of leaves, D1stFSp, and D100FSp implicated cluster/population U 'pop_7_W/U1' as the cluster with the highest mean values while having the least mean values for DFA and D50A. In contrast, Clusters D 'pop_3_W/D1' and U consistently showed lower performance comparatively for traits such as PH, NB_prim, NB_sec, NN, TNFlPP, TNFrPP, including fruit yield.

With respect to BC_1F_2 populations (Figure 13), lots of transgressive segregations were also observed. Three clusters, D, T and H showed profuse overlapping *viz*., clusters D and T, as well as clusters T and H. 32.35% of the 34 original lines of cluster D and 48.48% of all T lines overlapped between clusters D and T, while 18.18% of all T lines and 8.82% of all H lines were found transgressive between clusters T 'pop_6_W/T2' and H 'pop_2_W/H2'. Very negligible number of cluster U lines was found overlapped with cluster T. Apart from all the phenological traits, NBp and NBs where cluster U performed best, cluster T took leadership for the rest yield enhancing traits including yield itself (Supplemental Tables S4b, S5b, S6b, & S7b). There was significant population structuring among the lines observed in BC_1F_2 composite population used in this study.

Some lines were found elsewhere outside their original clusters. For instance, lines '0195T2' and '0194T2' of cluster T were found in clusters H and U, respectively; line '0055H2' of cluster H drifted into cluster T, line '0124D2' of cluster D fell into cluster H and '0272U2' of cluster U was found in cluster D. BC_1F_2 lines were generated through backcross to the recurrent parents. The description of the clusters D, H, T, and U of the BC_1F_2 population is found in Figure 12.

Using the boxplot analysis, the mean of each BC_1F_2 cluster group showed significant differences ($p < 0.05$) for all studied yield enhancing traits (Figure 14). Cluster H outperformed the rest clusters in mean values for PH, TNFlPP, and TNFrPP, although it took the longest days to achieve first anthsis, 50% anthesis, and 50% fruit set. Cluster U was consistent with the least mean values for DFA, D50A, D50_FS, and DFFE, except DFFR where cluster T showed the least mean value. Cluster U 'pop_8_W/U2' also had highest mean value for NB_sec. Cluster T 'pop_6_W/T2' had the highest mean values for NN, FWPP, NLPF, and fruit yield. Clusters D and U were comparatively higher for NL, NB_prim, D1stFSp, and D100FSp.

4. Discussion

4.1 Comparative analysis of variation among the selfed and backcrossed populations

Analysis of variance showed significant variation for virtually all traits studied, as well as wider ranges for most traits in all the 8 populations including the F_3 and BC_1F_2 population types. The highest maximum range and mean values among populations for various traits gave an indication that selection for PH, TNFlPP, TNFrPP, and NLPF will favor 'pop_1_W/H1'; NL, NBp, NBs, NN, least DFA, D50A and D50FS will enhance 'Pop_7_W/U1'; FWPP and fruit yield, least DFFE and DFFR will improve 'pop_5_W/T1' of selfed (F_3) populations, whereas selection for increased D1stFSp and D100FSp will favor the backcross population 'pop_8_W/U2'. Gomes et al. (2021) reported the presence of variability among the BC_1F_3 populations of Santa Cruz type dwarf tomato which supported the selection of tomatoes that stood out for agronomic and quality traits. De Oliveira et al. (2021) in another study reported genetic dissimilarities among 19 BC_1F_3 populations evaluated for agronomic and fruit quality traits. In the present study, evaluating F_3 and BC_1F_2 populations simultaneously opened up opportunity for comparison, of which the selfed populations showed better variability and yield trait increased performance. Atugwu and Uguru (2012) reported enormous variation and fruit size increase among early recombinants of a cross between cultivated species and *S. pimpinellifolium* accession. The high or medium to high GCV and PCV displayed for a majority of traits in one population or the other showed greater phenotypic and genotypic variability among the lines of the affected populations, hence, higher strength of the affected traits to make progress in selection. The opposite is the case for traits that expressed low GCV and PCV values. The narrow differences between PCV and GCV for all the traits in all populations showed less influence of the environment on the expression of these traits, suggesting the presence of high coefficient of additive genetic variance and hence,

indicated that direct selection would be effective and provides desirable output for improvement (Saleem et al. 2013). Furthermore, it reflects the potential for these affected traits to respond to selection pressure on affected segregating populations, a case of evolvability of the traits (Hill 2010). Evolvability expresses a trait's capacity to adapt to various selection pressures to which a population is subject (Cheung 2020). Heritability and genetic advance simultaneously give a more reliable gain from selection in a breeding program. High or moderate to high heritability followed by similar categories of genetic advance as percentage of mean for PH, NL, NBp, NLPF, FWPP, fruit shelf life traits, and total fruit yield observed in one population or the other indicated that the inheritance pattern in these traits were due to additive gene actions, which also showed the effectiveness of selection to improve the traits at F_{2-3} generation (Henareh 2015). The phenological traits *viz*., DFA, D50A, DFFE, D50FS, and DFFR, which expressed low values of genetic advance in a majority of the populations gave the traits a drawback for selection although the heritability for some were high or moderate to high. Low GAM indicated the involvement of non additive gene action in the inheritance of these traits, giving large scope for heterosis breeding as an improvement approach (Saravanan et al. 2019). Saravanan et al. (2019) reported high heritability combined with low genetic advance as a percentage of mean for days to 50 % flowering in tomato. Among the populations studied, 'pop_1_W/H1' followed by 'pop_4_W/D2' and 'pop_6_W/T2' expressed the highest genetic divergence for PH, NL, TNFlPP, TNFrPP, and FWPP based on their high magnitude of PV and GV. This revealed options or signs of future success for obtaining best fruit producing, humid tolerant tomato lines. Finzi et al. (2020) identified some tomato populations with the highest divergence and the most promising for development of inbred lines with improved fruit traits among the 12

452 BC_1F_2 populations of dwarf round tomatoes. Genetic dissimilarity was also reported in BC_1F_3
453 populations of saladette tomato (De Oliveira et al. 2021).

454 **4.2 Tomato Selfed populations better than backcrossed populations**

455 The correlation coefficient between two particular traits is approximately equal to the cosine of
456 the angle across the space separating their vectors (Yan and Kang 2003). The positive correlation
457 witnessed virtually for all yield*trait combinations implied that yield combined with all the other
458 traits as indicated by the acute angles of their vectors in the biplot. Also, the long vector which
459 represents each of the yield*trait combination indicates very strong and high relationship among
460 the yield*trait combinations. These showed that one of the traits should be enough selection
461 criteria. A major advantage of relationship among yield*trait biplot view is its ability to identify
462 excessive traits, select fewer traits and reduce costs in traits measurement and management
463 without undermining experiment precision.

464 The trait profile experience showed excellent performance of selfed populations 'pop_5_W/T1'
465 and 'pop_1_W/H1' for yield*TNFlPP, yield*TNFrPP, yield*PH and yield*NN, although they
466 had high proximity with the other yield*trait combinations. Hence, these populations were
467 considered promising, each with specific positive yield*traits associations. Relationship among
468 yield*trait biplot view is not considered as the best to check trait profiles of the genotypes (Yan
469 and Frégeau-Reid 2018). However, becoming aware of the interrelationships among the
470 yield*trait combinations make it easier to take a well informed decision on any genetic material
471 for breeding programs, aimed at selecting trait of interest for improvement (Mendonça et al.
472 2018; De Oliveira et al. 2019; Kendal 2019).

The Average Tester (trait) Coordination view of GYT biplot is effective as genotypes are ranked on the account of their levels in combining yield with target traits, and simultaneously indicating the strengths and weaknesses of the genotypes (Yan and Frégeau-Reid 2018). The results also expressed the possibility of determining contrasting populations based on the yield*traits combinations for improving tomato breeding. In the present study, 'pop_5_W/T1', 'pop_1_W/H1', 'pop_4_W/D2', and 'pop_6_W/T2 ranked as the best in combination of some yield enhancing traits with fruit yield under cool tropical monsoon climatic conditions of Jimma, Ethiopia, which showed genetic gain in tomato breeding program. This was based on the magnitude of their mean values as expressed in the mean superiority index (MSI) table, which was evidence of the yield*trait profiles of the populations. Of these, 'pop_5_W/T1' did not have any negative value for all traits, which showed that this population had the best characteristic performance across multi-traits studied; while 'pop_1_W/H1' which followed 'pop_5_W/T1' based on MSI table exhibited negative value only for D1stFSp indicating that this population had low value for this traits among the best performers. The MSI ranked the tomato populations by means of all yield*traits studied, where high values of MSI showed the best performing population (s). Other studies have used MSI ranking to identify top performers, like Yan and Frégeau-Reid (2018) for Oat, Mohammadi (2019) for durum wheat, and Lance et al. (2020) for red spring wheat.

Using the polygon model, 'pop_5_W/T1' and 'pop_1_W/H1' also exhibited the best performance for a majority of the yield*trait combinations which showed they were the best in combining fruit yield with the rest traits in the humid ecology. 'pop_4_W/D2' together with 'pop_5_W/T1' having taken the longest time to achieve the initial and 100% fruit spoilage proved to possess more gene for fruit firmness from the wild parent 'LA2093' among the other

populations. The polygon view of genotype by yield*trait (GYT) biplot has recently been used to study yield*trait combination profiles of genotypes, genotype evaluation and selection for improvement in several crop species including oat (Yan and Frégeau-Reid, 2018; Yan et al. 2019), sesame (Boureima and Yaou 2019), durum wheat (Mohammadi 2019; Kendal 2019), cowpea (De Oliveira et al. 2019; Araújo et al. 2021), peanut (Mahmoud et al. 2020), cotton (Peixoto et al. 2022), and *Jatropha curcas* (Purwati et al. 2022).

4.3 Clustering pattern analysis

The clustering pattern was supported by the significant differences observed among selfed and backcrossed populations for all seventeen investigated traits. This variation registered among these tomato populations/clusters may be due to differences and similarities in genetic constitution of the genotypes. This is partly in agreement with the report of Kanneh et al. (2016b) who noted that variation observed among tomato interspecific genotypes was due to differences in genetic and environment conditions. Interspecific hybridization can mix genetic materials from two different species, which has proven to be an effective way to increase phenotypic variability (Wang et al. 2020). The significant structuring among the lines of F_3 and BC_1F_2 composite populations although with a bit of transgressive segregation and overlapping lines contradicts the findings of Yu et al. (2008) and Bajgain et al. (2016) who reported no significant population structure among the recombinant inbred lines of the nested association mapping population design. According to the authors, the lack of structure among the lines could be credited to the parents, which were diverse from each other. However, the population structure pattern observed in F_3 and BC_1F_2 composite populations in the present study followed the relatedness found among the recurrent parents in an earlier genetic characterization study

(Ene et al. 2022). The closeness in relationship among the recurrent parents could have contributed to the observed population structuring pattern among the lines.

The high percentage of overlapping lines observed between clusters D and U, as well as clusters H and T for the studied traits in F_3 populations indicated a level of close tie between the overlapping clusters. It could be suspected that the genetic distance between the parental lines that generated lines of these clusters that showed overlapping are similar. Ene et al. (2022) reported the grouping of the recurrent parents of clusters D (CLN2498D) and U (UC Dan INDIA) in the same cluster while those of clusters H (CLN2417H) and T (Tima) in the same cluster showing a level of relatedness. Although each cluster was of different interspecific cross, they were half sib progenies sharing a common parent (pollen donor-wild parent 'LA2093') from the initial cross. This established a level of relationship among the progenies altogether. Similar implication could be attributed to the same lines overlapping or drifting witnessed between clusters D and T, as well as clusters T and H of BC_1F_2 populations. Rieseberg et al. (1999) reported that transgressive segregation is favored by high genetic distance between the parental lines, preferably of different species.

The outliers '0210U1' and '0211U1' lines from cluster U; lines '0020H1' and '0035H1' of cluster H which found their way among lines of cluster T; and '0144T1' of cluster T which showed slight drifting into cluster H, revealed trangressive behavior of the segregating lines among selfed populations. A situation where little minority of recombinants are outliers relative to the range of parental phenotypes, and is commonly observed in plant breeding populations (Boyle et al. 2017). Whereas this phenomenon has been linked to complementary action of gene and epistasis, the biochemical, physiological, and molecular bases have not been fully understood (Pabuayon et al. 2021). Interspecific transgressive individuals have been argued to

541 represent a potential source of novel genetic variation in crop species as they can potentially
542 affect characters of adaptive significance (De Vicente and Tanksley 1993; Singh et al. 2018a;
543 Pabuayon et al. 2021).

544 Similar implication could be likened to the lines '0195T2' and '0194T2' of cluster T which
545 found their way into clusters H and U, respectively; line '0055H2' of cluster H which drifted into
546 cluster T, line '0124D2' of cluster D which fell into cluster H and '0272U2' of cluster U finding
547 its way into cluster D, among BC_1F_2 populations. De Vicente and Tanksley (1993) reported that
548 interspecific transgressive lines of tomato possessed characteristics that allowed them to occupy
549 new ecological niches where others could not or better competed in existing environments.
550 Epistatic interactions of parental alleles and complementary action of additive alleles are
551 regarded as being responsible for the superior or inferior attributes of transgressive segregants
552 (Dittrich-Reed and Fitzpatrick 2013).

553 Among selfed (F_3) populations, desirable performance appeared for PH, TNFlPP, and TNFrPP in
554 cluster H (pop_1_W/H1); NB_prim, NB_sec, NN, FWPP, fruit yield, early DFFE and DFFR in
555 cluster T ('pop_5_W/T1'); and NL, D1stFSp, and D100FSp in cluster U ('pop_7_W/U1'). For
556 BC_1F_2, desirable performance was observed in cluster U ('pop_8_W/U2') for early DFA, D50A,
557 D50_FS, and DFFE; cluster T (pop_6_W/T2) for NN, FWPP, NLPF, and fruit yield; clusters D
558 and U for NL, NB_prim, D1stFSp, and D100FSp. The findings suggested that improvement of
559 these traits through single plant selection would favor the genotypes of the respective clusters
560 and could be beneficial for future tomato breeding program, after verifying their consistencies
561 over different environments (Gonzalo et al. 2020). It further advocated that high yielding and
562 adaptable lines to high humidity could emerge from interspecific hybridization following single
563 plant selection (Gaur et al. 2008).

5. Conclusions

Genetic variability study revealed considerable dissimilarity among the lines within each population and between populations that would be useful for fruit yield improvement and adaptability to tropical humid climes. High or moderate to high heritability and high genetic advance as percentage of mean for PH, NL, NB_prim, NN, NLPF, TNFlPP, TNFrPP, FWPP, D1stFSp, D100FSp, and total fruit yield noticed in one population or the other indicated that their inheritance pattern were due to additive gene actions, which suggested selection as an effective improvement approach. Among the F_3 and BC_1F_2 populations, 'pop_1_W/H1', 'pop_4_W/D2' and 'pop_6_W/T2' which expressed the highest genetic divergence for PH, NL, TNFlPP, TNFrPP, and FWPP were most promising for development of inbred lines with improved fruit traits. Selection for increased post-harvest durability will favor 'pop_8_W/U2'.

Application of GYT biplots models in this study presents a novel approach to tomato population improvement based on multiplex traits. 'pop_5_W/T1' and 'pop_1_W/H1' of F_3 population, ranked the best in combining some yield enhancing traits with fruit yield, indicating genetic gain and showing adaptability to the growing environment. GYT biplots could help to conquer the general challenge of crop selection on multiple traits which has been a problem in plant breeding.

Clustering pattern showed significant differences among F_3 and BC_1F_2 populations for all studied traits. Cluster T ('pop_5_W/T1') among F_3 populations, and cluster T (pop_6_W/T2) among BC_1F_2 populations showed desirable performance for fruit weight and fruit yield, and of course any improvement program for fruit yield under humid condition would favor the genotypes of these clusters. Using multivariate analysis, transgressive segregants '0210U1', '0211U1', and

585 '0171T1' of selfed (F_3) population were observed. They are believed to represent a potential
586 source of novel genetic variation for future tomato breeding program.

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592 **Data Availability Statement**

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

595 **Competing Interests**

596 The authors declare that there are no conflicts of interest, financial or nonfinancial, directly or
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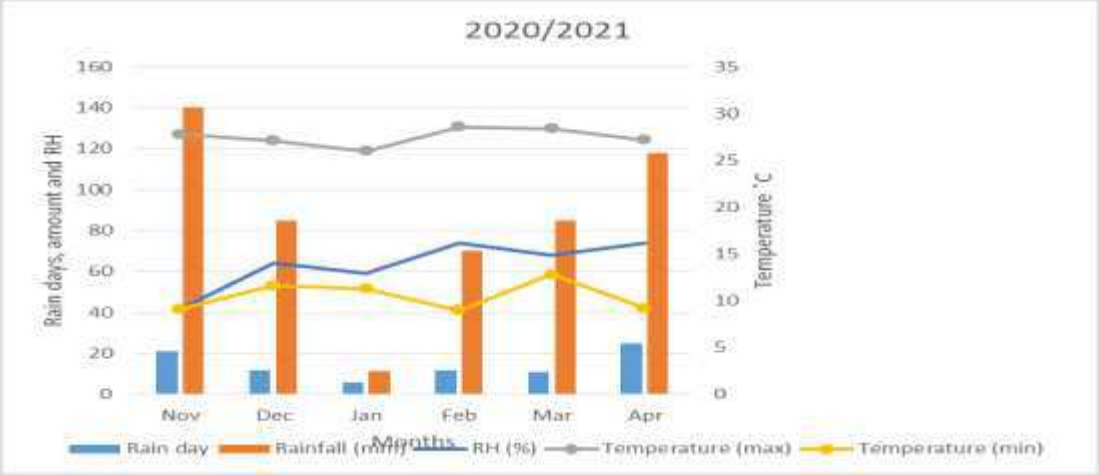
Table 1: Population naming description

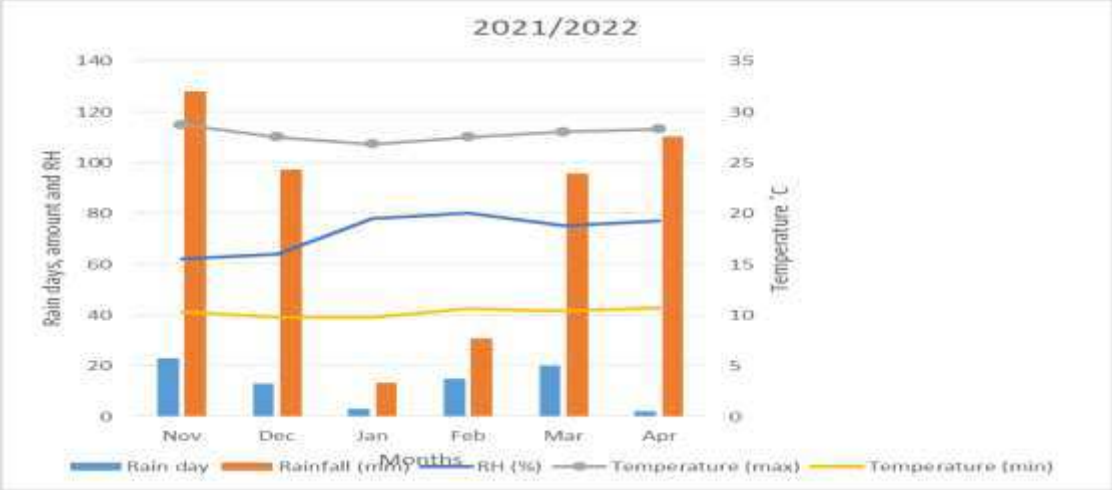
No.	Code	Description/ pedigree
1.	Pop_1_W/H1 (F_3 Cluster H)	F_3 population developed by selfing F_2 hybrids of a cross between 'CLN2714H' (H) and 'LA2093' (W)
2.	Pop_2_W/H2 (BC_1F_2 Cluster H)	BC_1F_2 population developed by selfing backcross to the recurrent parent (BC_1) from a cross between 'CLN2714H' (H) and 'LA2093' (W); H = recurrent parent
3.	Pop_3_W/D1 (F_3 Cluster D)	F_3 population developed by selfing F_2 hybrids of a cross between 'CLN2498D' (D) and 'LA2093' (W)
4.	Pop_4_W/D2 (BC_1F_2 Cluster D)	BC_1F_2 population developed by selfing backcross to the recurrent parent (BC_1) from a cross between 'CLN2498D' (D) and 'LA2093' (W); D = recurrent parent

5.	Pop_5_W/T1 (F_3 Cluster T)	F_3 population developed by selfing F_2 hybrids of a cross between 'Tima' (T) and 'LA2093' (W)
6.	Pop_6_W/T2 (BC_1F_2 Cluster T)	BC_1F_2 population developed by selfing backcross to the recurrent parent (BC_1) from a cross between 'Tima' (T) and 'LA2093' (W); T = recurrent parent
7.	Pop_7_W/U1 (F_3 Cluster U)	F_3 population developed by selfing F_2 hybrids of a cross between 'UC Dan INDIA' (U) and 'LA2093' (W)
8.	Pop_8_W/U2 (BC_1F_2 Cluster U)	BC_1F_2 population developed by selfing backcross to the recurrent parent (BC_1) from a cross between 'UC Dan INDIA' (U) and 'LA2093' (W); U = recurrent parent



807

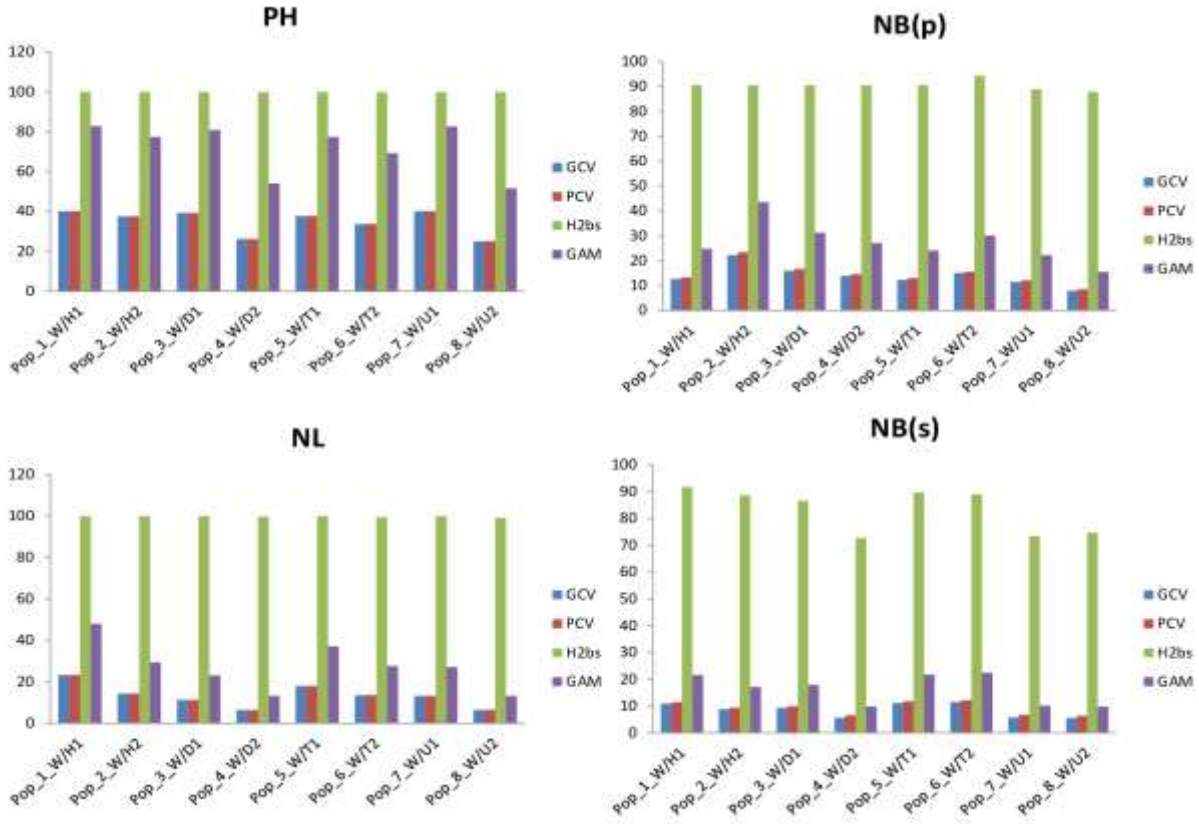
808 **Figure 1:** Monthly weather conditions of Jimma during the 2020/2021 experiment season



809

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

811



812 **Figure 3:** Genetic variation, broad sense heritability and genetic advance among tomato populations for
813 plant height (PH), number of primary branches (NBp), number of leaves (NL) and number of secondary
814 branches (NBs)

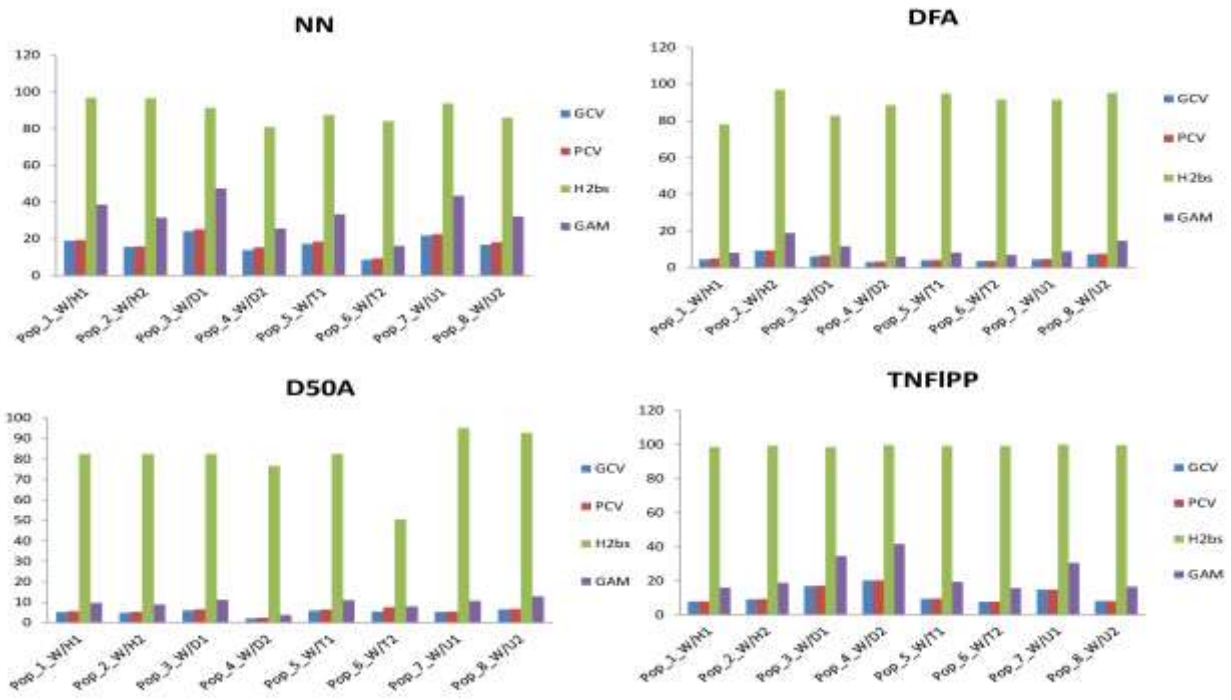


Figure 4: Genetic variation, broad sense heritability and genetic advance among tomato populations for number of nodes (NN), days to first anthesis (DFA), days to 50% anthesis (D50A) and total number of flower per plant (TNFlPP)

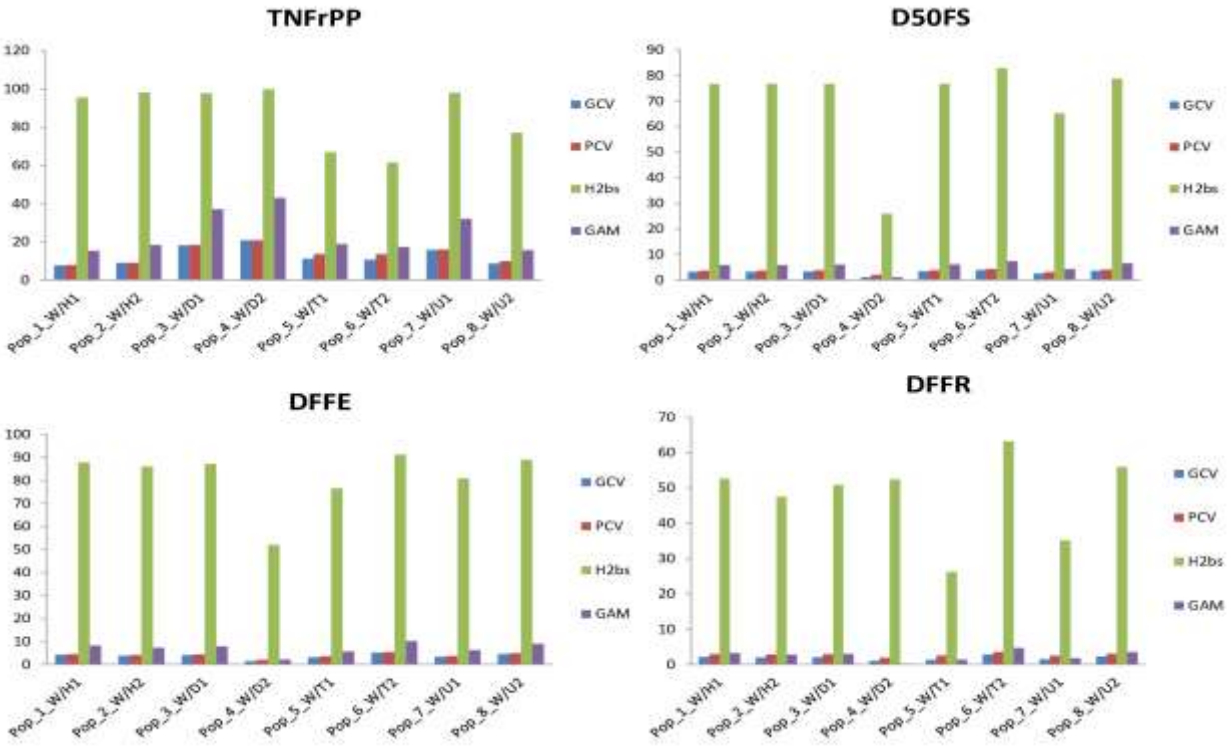


Figure 5: Genetic variation, broad sense heritability and genetic advance among tomato populations for

total number of fruit per plant (TNFrPP), days to 50% fruit set (D50FS), days to first fruit emergence (DFFE) and days to first fruit ripening (DFFR)

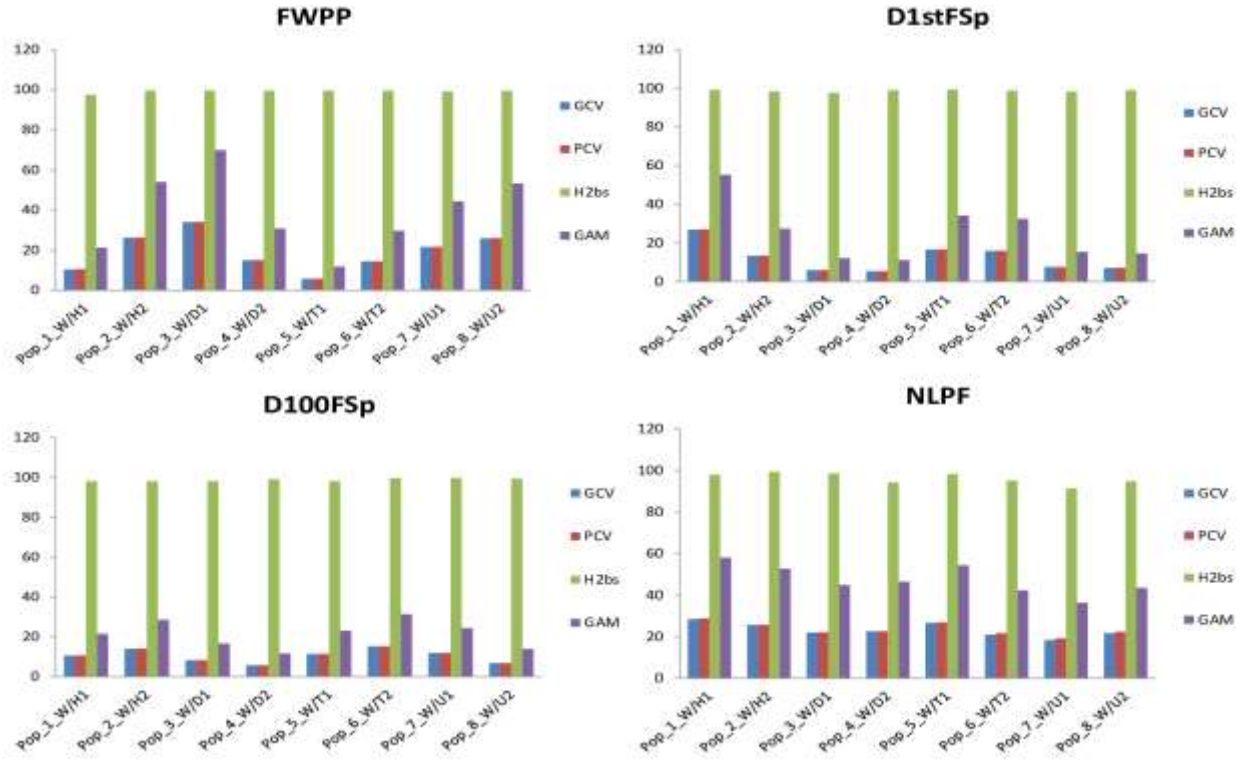


Figure 6: Genetic variation, broad sense heritability and genetic advance among tomato populations for fruit weight per plant (FWPP), days to first fruit spoilage (D1stFSp), days to 100% fruit spoilage (D100FSp) and number of locules per fruit (NLPF)

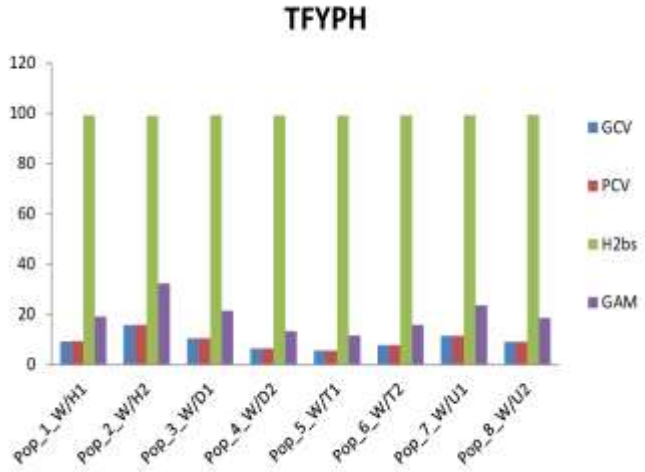
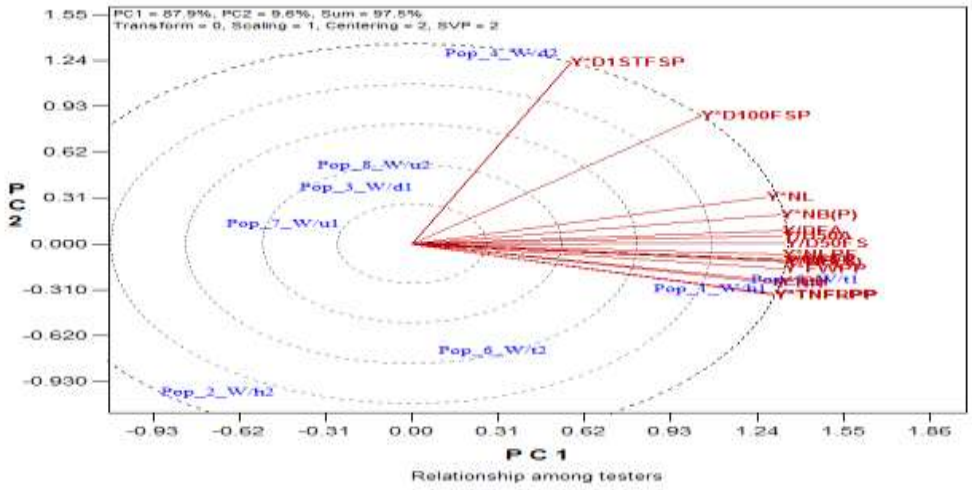
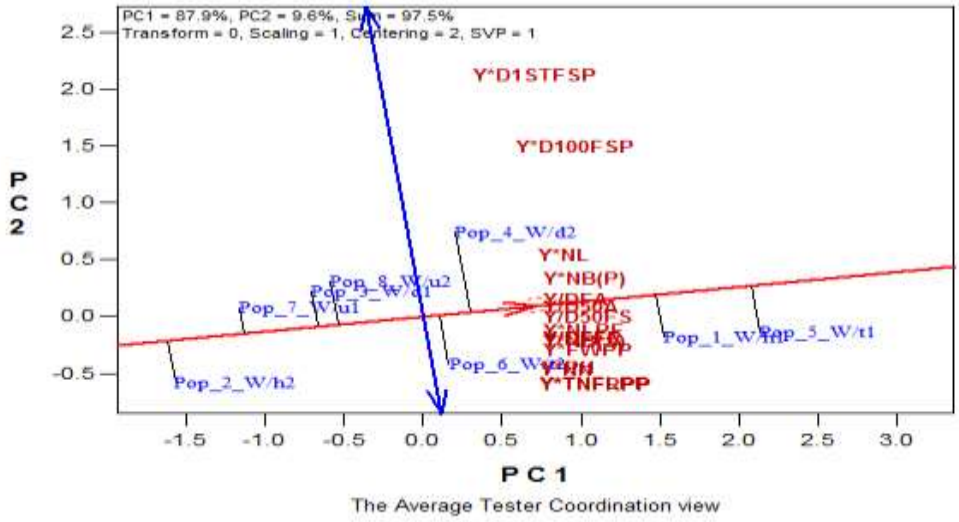


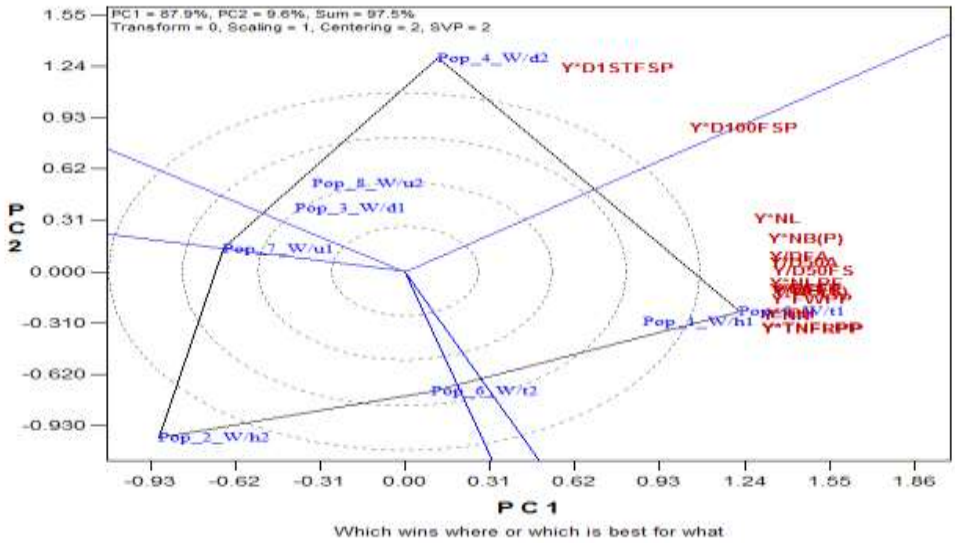
Figure 7: Genetic variation, broad sense heritability and genetic advance among tomato populations for total fruit yield per hectare



Figures 8: The Tester Vector view showing relationship among testers/traits of genotype by yield*trait (GYT) biplot of 8 populations based on yield*traits combinations; PH (cm): Plant height, NL: Number of leaves, NB(p): Number of primary branches, NB(s): Number of secondary branches, NN: Number of nodes (at 9 week after transplanting), DFA: Days to first anthesis, D50A: Days to 50% anthesis, TNFlPP: Total number of flower per plant, TNFrPP: Total number of fruit per plant, FWPP (g): Fruit weight per plant, DFFE: Days to first fruit emergence, D50FS: Days to 50% fruit set, DFFR: Days to first fruit ripening, D1stFSp: Day to initial fruit spoilage after harvest, D100FSp: Days to 100% fruit spoilage after harvest, NLPF: Number of locule per fruit, Y (t/h): Total fruit yield per hectare, Pop_1_W/H1 (F_3 of 'H × W'), Pop_2_W/H2 (BC_1F_2 of 'H × W'), Pop_3_W/D1 (F_3 of 'D × W'), Pop_4_W/D2 (BC_1F_2 of 'D × W'), Pop_5_W/T1 (F_3 of 'T × W'), Pop_6_W/T2 (BC_1F_2 of 'T × W'), Pop_7_W/U1 (F_3 of 'U × W'), Pop_8_W/U2 (BC_1F_2 of 'U × W')



Figures 9: The Average Tester Coordination view of genotype by yield*trait (GYT) biplot involving 8 populations based on multi-trait; PH (cm): Plant height, NL: Number of leaves, NB(p): Number of primary branches, NB(s): Number of secondary branches, NN: Number of nodes (at 9 week after transplanting), DFA: Days to first anthesis, D50A: Days to 50% anthesis, TNFlPP: Total number of flower per plant, TNFrPP: Total number of fruit per plant, FWPP (g): Fruit weight per plant, DFFE: Days to first fruit emergence, D50FS: Days to 50% fruit set, DFFR: Days to first fruit ripening, D1stFSp: Day to initial fruit spoilage after harvest, D100FSp: Days to 100% fruit spoilage after harvest, NLPF: Number of locule per fruit, Y (t/h): Total fruit yield per hectare, Pop_1_W/H1 (F_3 of 'H × W'), Pop_2_W/H2 (BC_1F_2 of 'H × W'), Pop_3_W/D1 (F_3 of 'D × W'), Pop_4_W/D2 (BC_1F_2 of 'D × W'), Pop_5_W/T1 (F_3 of 'T × W'), Pop_6_W/T2 (BC_1F_2 of 'T × W'), Pop_7_W/U1 (F_3 of 'U × W'), Pop_8_W/U2 (BC_1F_2 of 'U × W')



Figures 10: The which-won-where view of genotype by yield*trait (GYT) biplot involving 8 populations based on multi-traits; PH (cm): Plant height, NL: Number of leaves, NB(p): Number of primary branches, NB(s): Number of secondary branches, NN: Number of nodes (at 9 week after transplanting), DFA: Days to first anthesis, D50A: Days to 50% anthesis, TNFlPP: Total number of flower per plant, TNFrPP: Total number of fruit per plant, FWPP (g): Fruit weight per plant, DFFE: Days to first fruit emergence, D50FS: Days to 50% fruit set, DFFR: Days to first fruit ripening, D1stFSp: Day to initial fruit spoilage after harvest, D100FSp: Days to 100% fruit spoilage after harvest, NLPF: Number of locule per fruit, Y (t/h): Total fruit yield per hectare, Pop_1_W/H1 (F_3 of 'H × W'), Pop_2_W/H2 (BC_1F_2 of 'H × W'), Pop_3_W/D1 (F_3 of 'D × W'), Pop_4_W/D2 (BC_1F_2 of 'D × W'), Pop_5_W/T1 (F_3 of 'T × W'), Pop_6_W/T2 (BC_1F_2 of 'T × W'), Pop_7_W/U1 (F_3 of 'U × W'), Pop_8_W/U2 (BC_1F_2 of 'U × W')

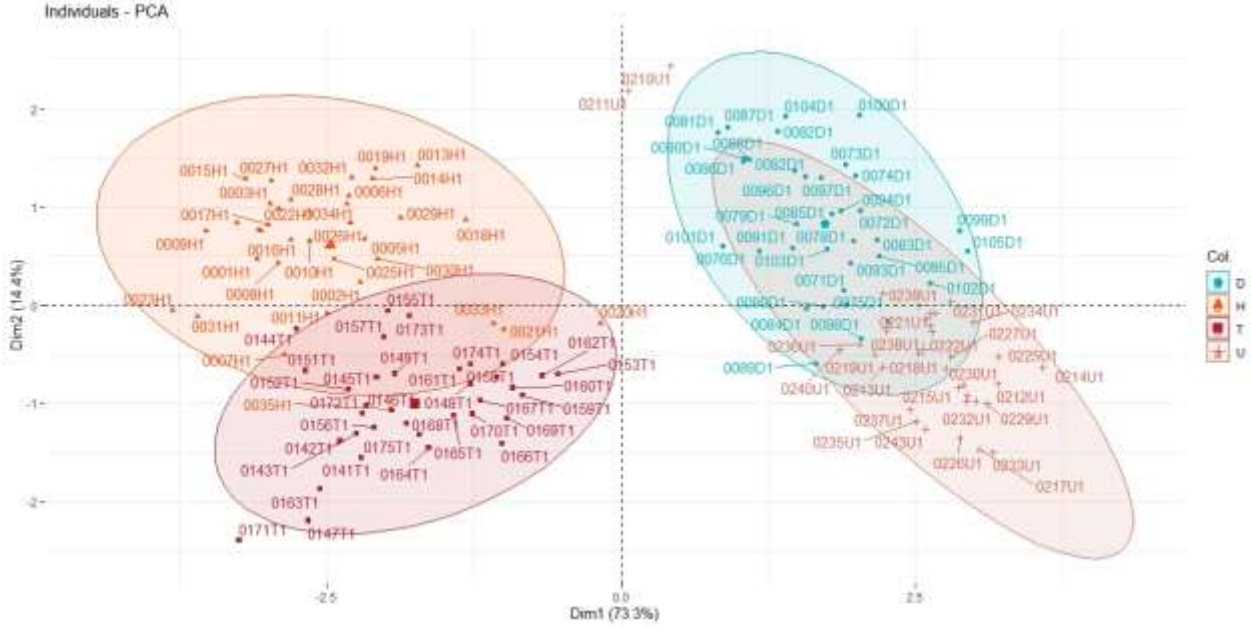
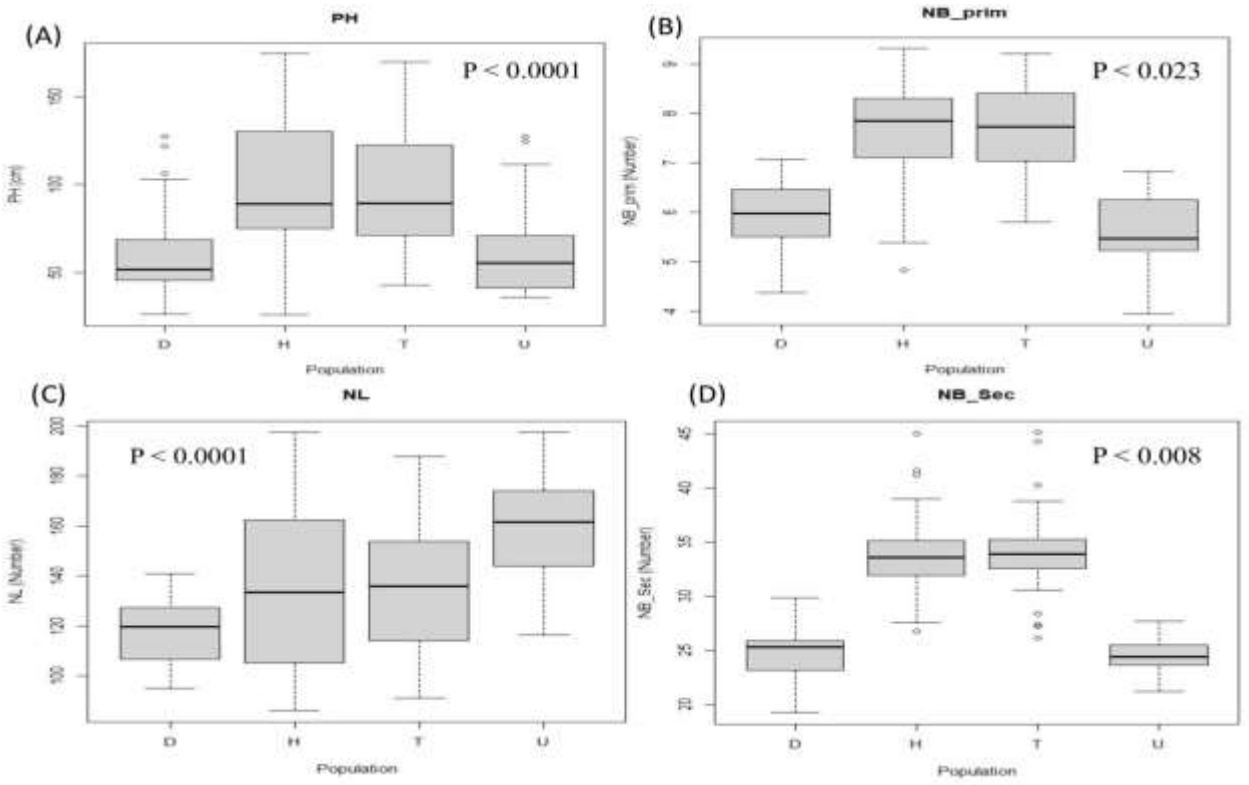
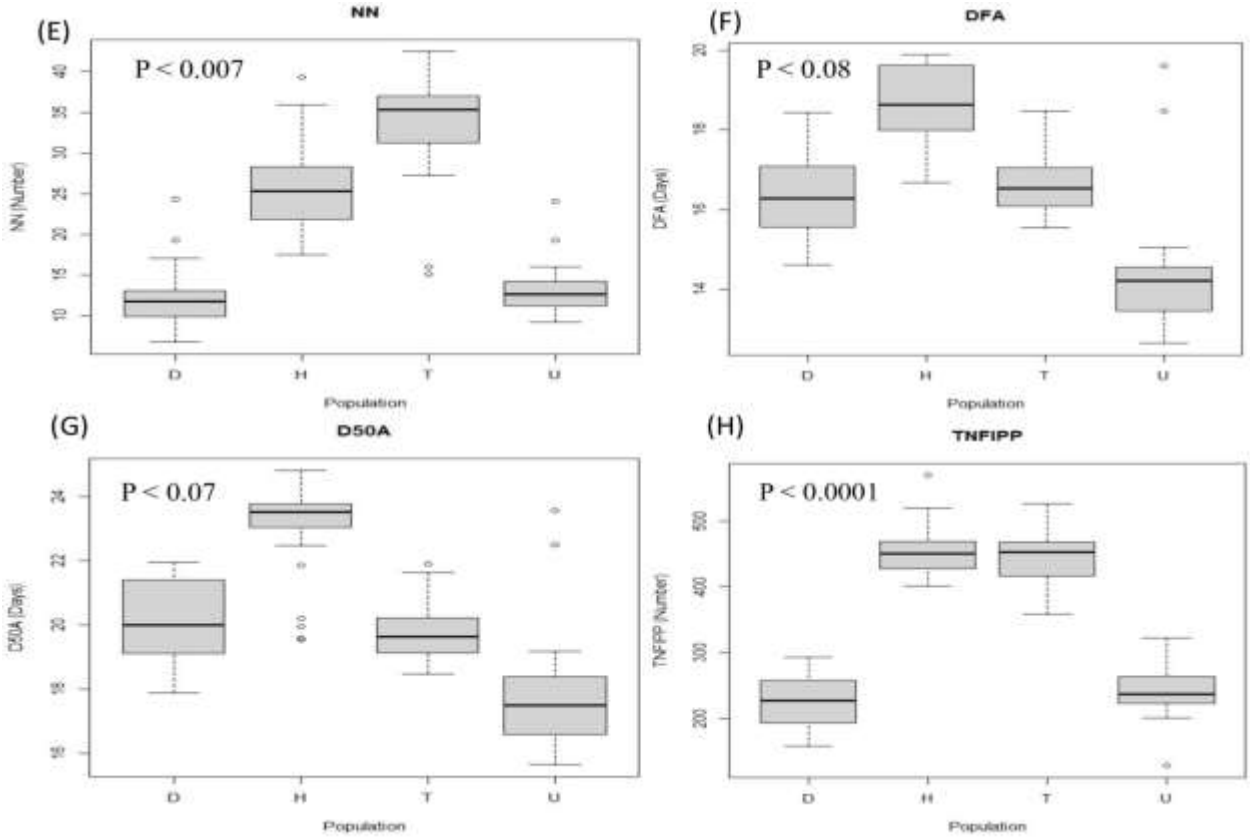


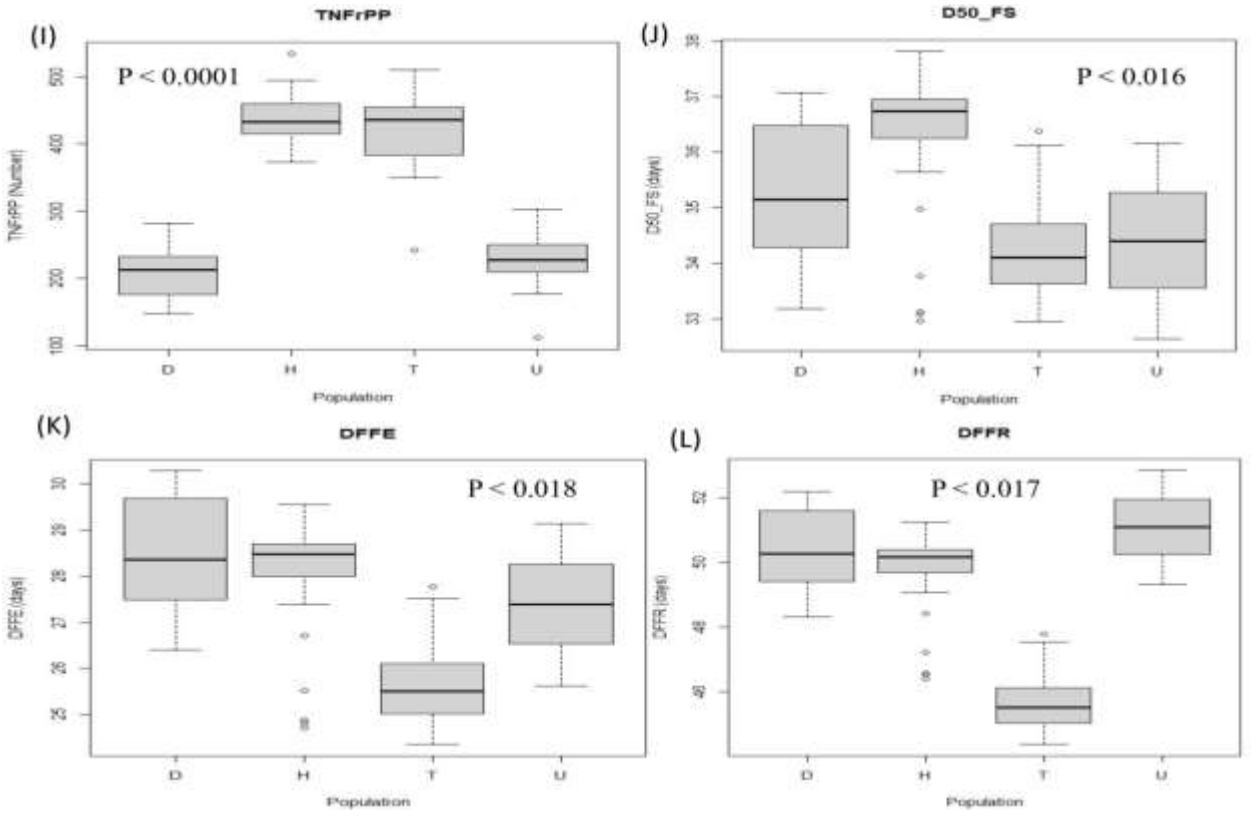
Figure 11: Factor map showing the clustering pattern of 139 F_3 lines of 4 biparental populations of tomato based on the hierarchical clustering on principal components analysis (HCPC). Cluster D: 'pop_3_W/D1' (n = 34), Cluster H: 'pop_1_W/H1' (n = 35), Cluster T: 'pop_5_W/T1' (n = 33), and Cluster U: 'pop_7_W/U1' (n = 37).


(A)
PH
P < 0.0001
PH (cm)
Population
D
H
T
U
(B)
NB_prim
P < 0.023
NB_prim (Number)
(C)
NL
P < 0.0001
NL (Number)
(D)
NB_Sec
P < 0.008
NB_Sec (Number)

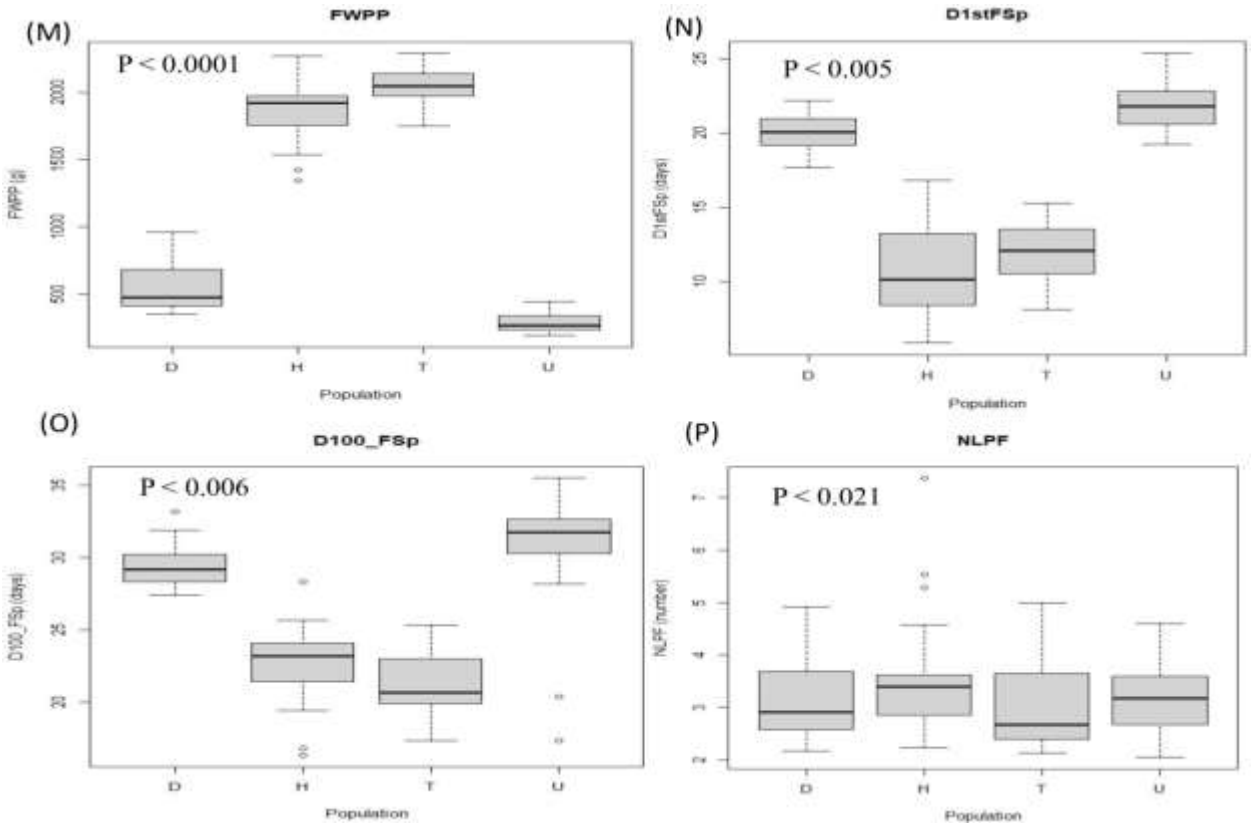
869


(E)
NN
P < 0.007
NN (Number)
(F)
DFA
P < 0.08
DFA (Days)
(G)
D50A
P < 0.07
D50A (Days)
(H)
TNFIPP
P < 0.0001
TNFIPP (Number)
Population

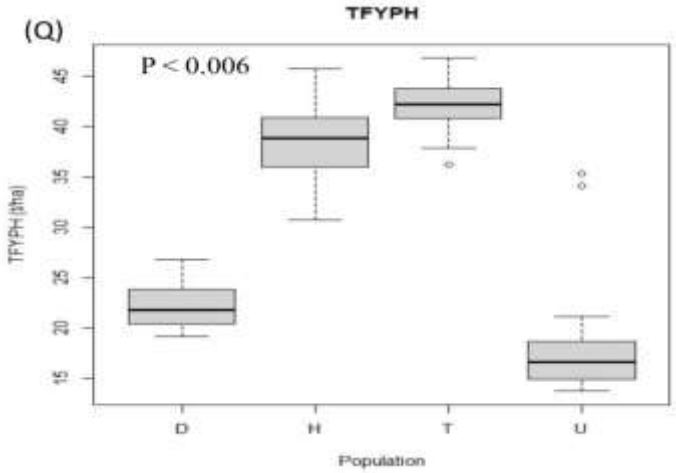
870


(I)
TNFrPP
P < 0.0001
TNFrPP (Number)
Population
D
H
T
U
(J)
D50_FS
P < 0.016
D50_FS (days)
Population
(K)
DFFE
P < 0.018
DFFE (days)
Population
(L)
DFFR
P < 0.017
DFFR (days)
Population

871

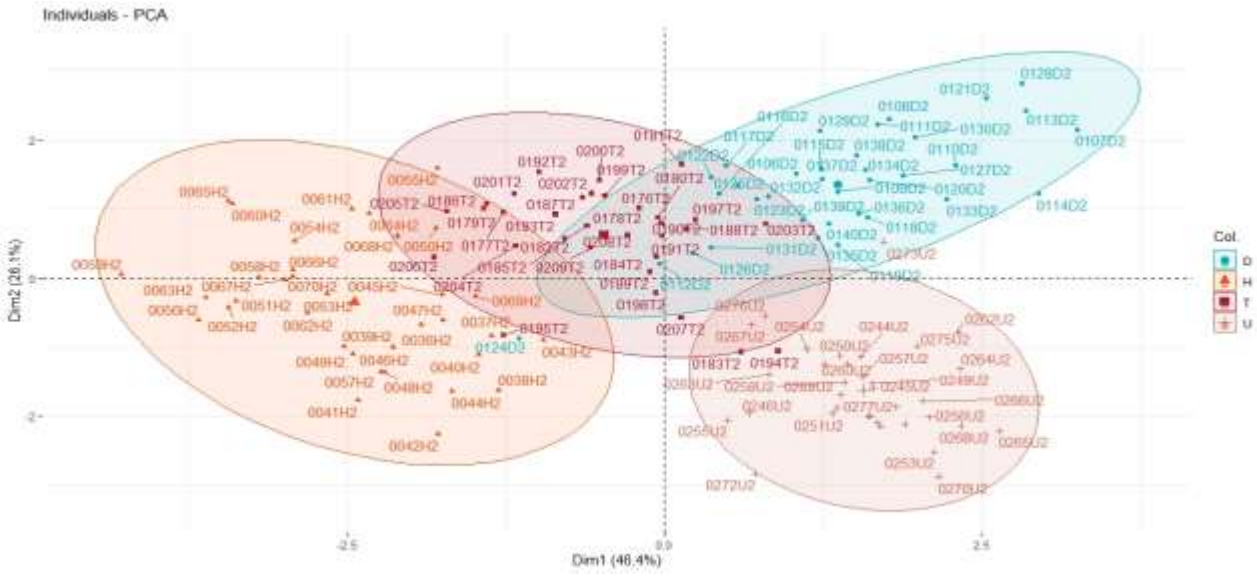

(M)
FWPP
P < 0.0001
FWPP (g)
Population
(N)
D1stFSp
P < 0.005
D1stFSp (days)
Population
(O)
D100_FSp
P < 0.006
D100_FSp (days)
Population
(P)
NLPF
P < 0.021
NLPF (number)
Population

872



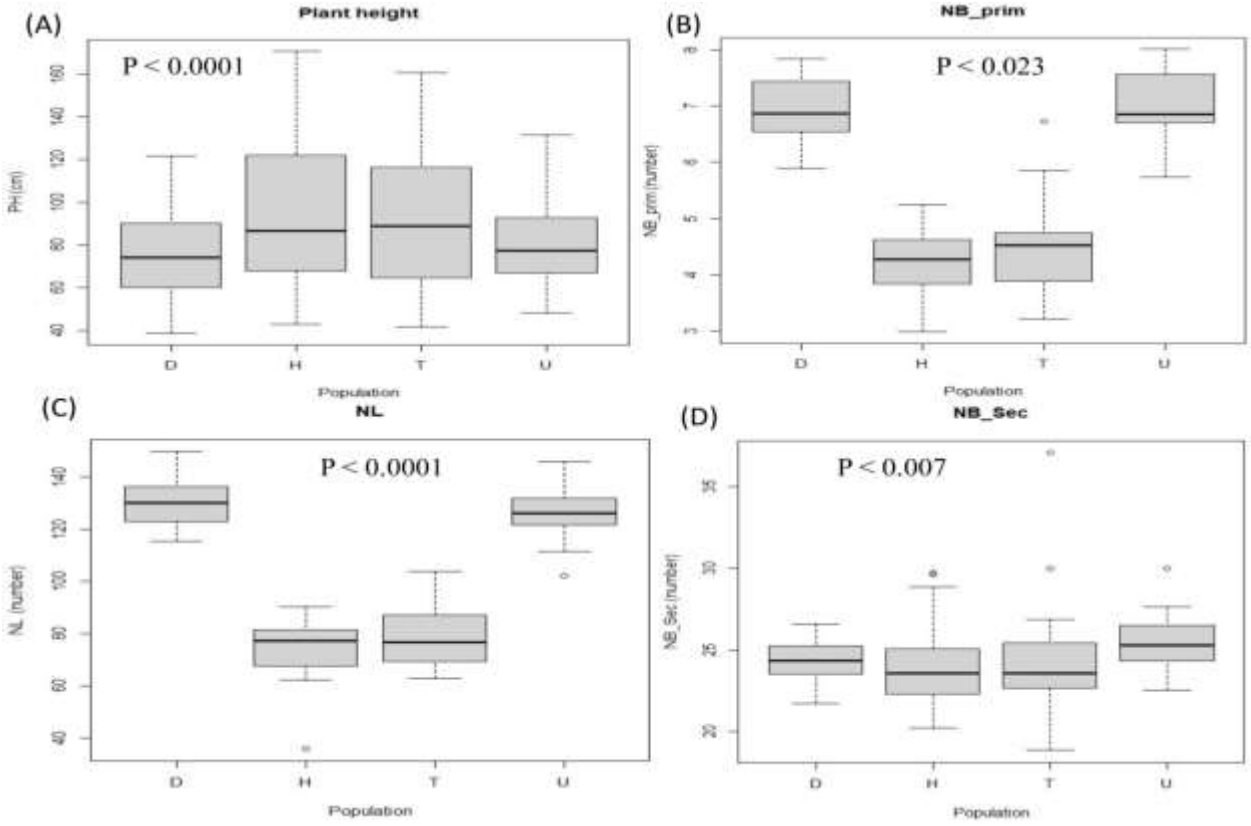
873
874 **Figure 12:** Phenotypic means for seventeen yield enhancing traits (A to Q) among the four F_3 clusters of
875 139 segregating lines of tomato using box plots. (A) Plant height (cm). (B) Number of primary branches.
876 (C) Number of leaves. (D) Number of secondary branches. (E) Number of nodes. (F) Days to first
877 anthesis. (G) Days to 50% anthesis. (H) Total number of flowers per plant. (I) Total number of fruits per
878 plant. (J) Days to 50% fruit set. (K) Days to first fruit emergence. (L) Days to first fruit ripening. (M)
879 Fruit weight per plant (g). (N) Days to 1st fruit spoilage. (O) Days to 100% fruit spoilage. (P) Number of
880 locules per fruit. (Q) Total fruit yield per hectare. Population D: 'pop_3_W/D1' (n = 34), Population H:
881 'pop_1_W/H1' (n = 35), Population T: 'pop_5_W/T1' (n = 33), and Population U: pop_7_W/U1' (n =
882 37).

883

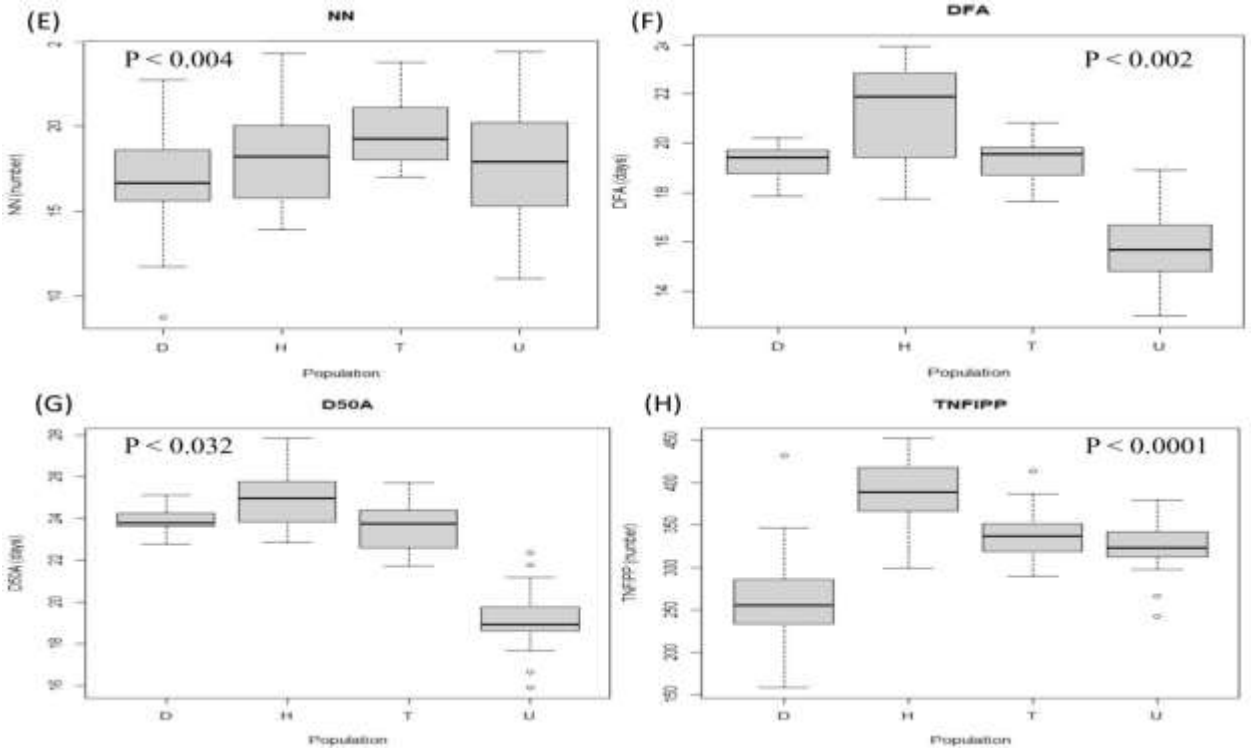


884

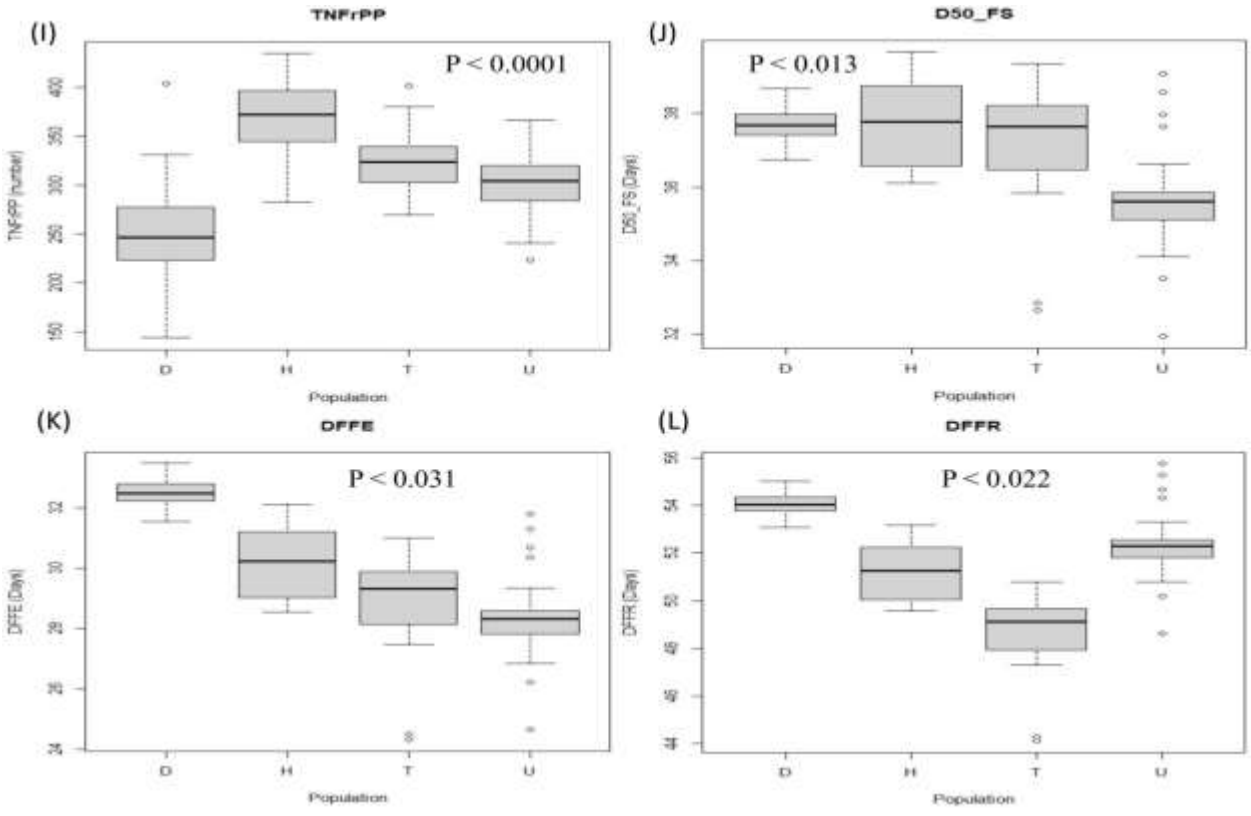
885 **Figure 13:** Factor map showing the clustering pattern of 137 BC_1F_2 lines of 4 biparental populations of
886 tomato based on the hierarchical clustering on principal components analysis (HCPC). Cluster D:
887 'pop_4_W/D2' (n = 34), Cluster H: 'pop_2_W/H2' (n = 34), Cluster T: 'pop_6_W/T2' (n = 33), and
888 Cluster U: 'pop_8_W/U2' (n = 36).


(A)
Plant height
P < 0.0001
PH (cm)
Population
D
H
T
U
(B)
NB_prim
P < 0.023
NB_prim (number)
(C)
NL
P < 0.0001
NL (number)
(D)
NB_Sec
P < 0.007
NB_Sec (number)

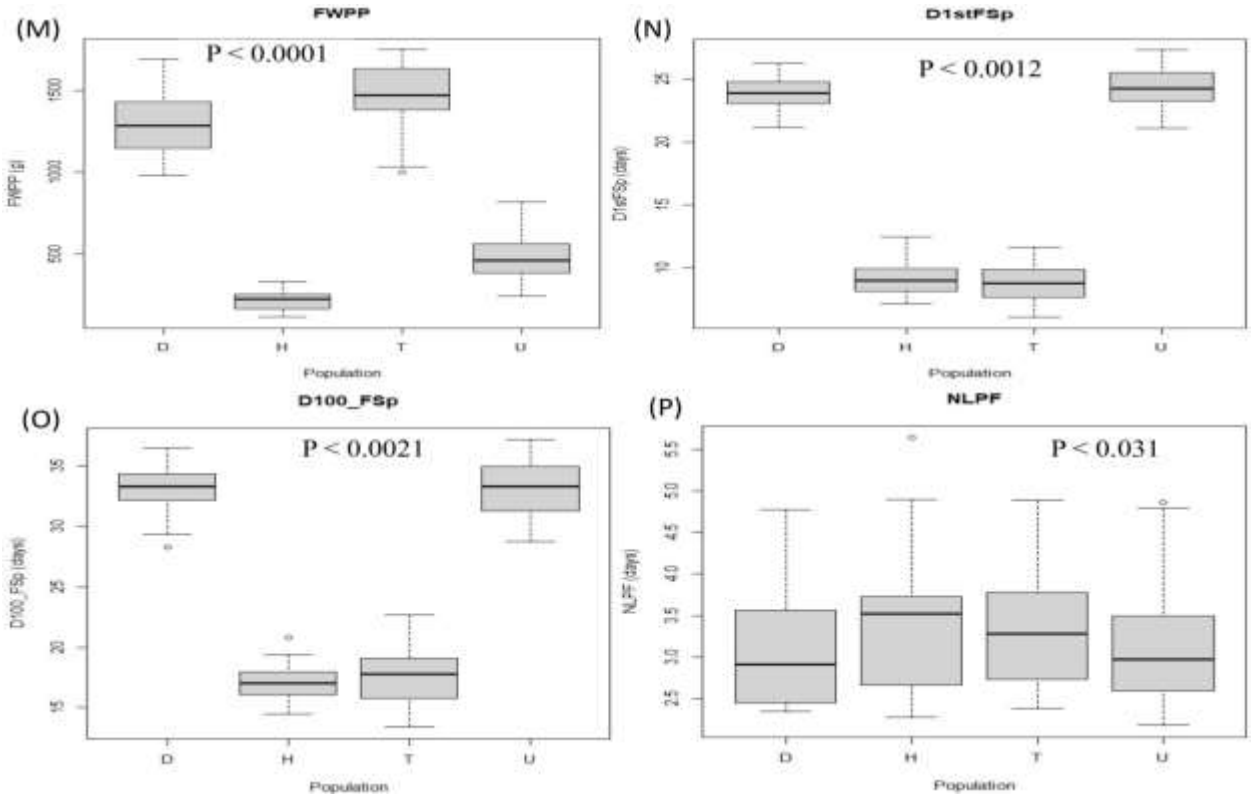
889


(E)
NN
P < 0.004
NN (number)
(F)
DFA
P < 0.002
DFA (days)
(G)
D50A
P < 0.032
D50A (days)
(H)
TNFIPP
P < 0.0001
TNFIPP (number)

890


(I)
TNFrPP
P < 0.0001
TNFrPP (number)
Population
D
H
T
U
(J)
D50_FS
P < 0.013
D50_FS (Days)
(K)
DFFE
P < 0.031
DFFE (Days)
(L)
DFFR
P < 0.022
DFFR (Days)

891


(M)
FWPP
P < 0.0001
FWPP (g)
(N)
D1stFSp
P < 0.0012
D1stFSp (days)
(O)
D100_FSp
P < 0.0021
D100_FSp (days)
(P)
NLPF
P < 0.031
NLPF (days)

892

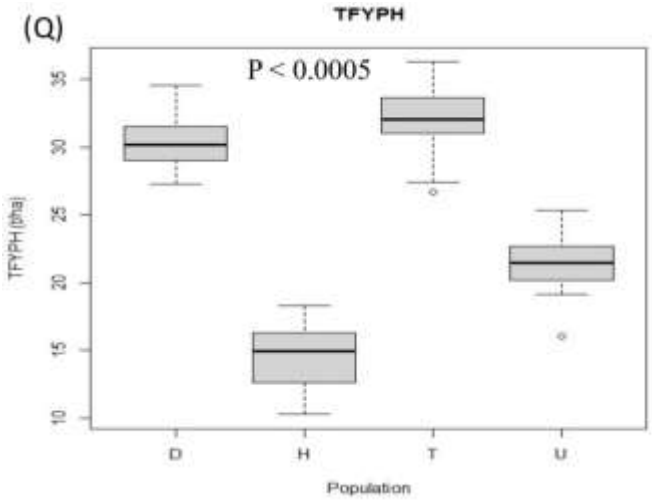


Figure 14: Phenotypic means for seventeen yield enhancing traits (A to Q) among the four BC_1F_2 clusters of 137 segregating lines of tomato using box plots. (A) Plant height (cm). (B) Number of primary branches. (C) Number of leaves. (D) Number of secondary branches. (E) Number of nodes. (F) Days to first anthesis. (G) Days to 50% anthesis. (H) Total number of flowers per plant. (I) Total number of fruits per plant. (J) Days to 50% fruit set. (K) Days to first fruit emergence. (L) Days to first fruit ripening. (M) Fruit weight per plant (g). (N) Days to 1st fruit spoilage. (O) Days to 100% fruit spoilage. (P) Number of locules per fruit. (Q) Total fruit yield per hectare. Population D: 'pop_4_W/D2' (n = 34), Population H: 'pop_2_W/H2' (n = 34), Population T: 'pop_6_W/T2' (n = 33), and Population U: 'pop_8_W/U2' (n = 36)

Supplementary Files

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