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Genetic Diversity and Population Structure of Tomato (*Solanum lycopersicum*) Germplasm Developed by Texas A&M Breeding Programs

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Abstract

Genetic variation developed in plant breeding programs is fundamental to creating new combinations that result in cultivars with enhanced characteristics. Over the years, tomato (*Solanum lycopersicum*) breeding programs associated with the Texas A&M University system have developed morphologically diverse lines of tomatoes selected for heat tolerance, fruit quality, and disease resistance to adapt them to Texas growing conditions. Here we explored the intraspecific genetic variations of 322 cultivated tomato genotypes, including 300 breeding lines developed by three Texas A&M breeding programs, as an initial step toward implementing molecular breeding approaches. Genotyping by sequencing using low coverage whole-genome sequencing (SkimGBS) identified 10,236 high-quality single-nucleotide polymorphisms (SNPs) that were used to assess genetic diversity, population structure, and phylogenetic relationship between genotypes and breeding programs. Model-based population structure analysis, phylogenetic tree construction, and principal component analysis indicated that the genotypes were grouped into two main clusters. Genetic distance analysis revealed greater genetic diversity among the products of the three breeding programs. The germplasm developed at Texas A&M programs at Weslaco, College Station, and by Dr. Paul Leeper exhibited genetic diversity ranges of 0.175 - 0.434, 0.099 - 0.392, and 0.183 - 0.347, respectively, suggesting that there is enough variation within and between the lines from the three programs to perform selection for cultivar development. The SNPs identified here could be used to develop molecular tools for selecting various traits of interest and to select parents for future tomato breeding.

Keywords

Genetic Diversity, Single-Nucleotide Polymorphism (SNP), *Solanum lycopersicum*, Tomato, Genotyping by Sequencing (GBS)

1. Introduction

Tomato (*Solanum lycopersicum* L.) is a major vegetable crop widely grown around the world [1] [2] [3]. In the USA, fresh and processed tomatoes accounted for more than $1.85 billion in US farm cash receipts in 2018 [4]. The two leading states for fresh-market tomato production are Florida and California, which together comprise almost two-thirds of the total US fresh tomato acreage. Historically, Texas grew as many acres of tomatoes as the leading producing states, with 13,315 ha planted in the 1960s. Because of the lack of adequate cultivars, pest/disease pressure, inefficient production practices, and competition from other production areas, however, Texas growers later migrated to other crops, largely abandoning fresh market tomatoes (harvesting only 304 ha. in 2017) [5]. To satisfy customer demand, Texas imports an estimated 2.4 billion pounds/year [6]. A recent study found that Texas consumers frequently request tomatoes with "vine ripe" flavor, aroma, and texture, and will pay a premium for locally produced selections [7]. This situation represents a great opportunity for local producers to re-claim their share of the Texas tomato market. For this to be possible, however, new cultivars and production practices need to be developed to support the industry.

The Texas A&M AgriLife Research tomato breeding programs at Weslaco and College Station have been breeding tomatoes for heat tolerance, fruit quality, and disease resistance adapted to Texas growing conditions for the past five and eighteen years, respectively. Recognizing that high temperatures significantly impact tomato flavor and appearance, our work has focused on introgressing heat tolerance and high-temperature fruit set genes. The two tomato breeding programs combined have developed more than 400 families, including heat-tolerant lines with disease resistance and diverse heirloom selections with multiple fruit colors and unique flavors. Much of this work targeted improvements in both flavor and content of beneficial phytochemicals [8]. This high-yielding, heat-tolerant base germplasm was developed over a period of 37 years at Weslaco by former Texas A&M breeder Dr. Paul Leeper and has been used extensively by the current Texas A&M breeding programs and others programs in tropical regions, including the cultivars Chico III, Chico, El Monte, Monte Grande, La Pinta, Chico Grande, and Saladette [9] [10] [11] [12]. To date, elite lines in our breeding programs have been selected using conventional phenotypic selection approaches, in which large populations are screened for several breeding cycles. Although this approach has produced high-quality, high-yield cultivars, it is time-consuming and requires substantial resources to develop each new cultivar.

An alternative approach to improve breeding efficiency involves the use of

modern molecular breeding techniques for population management, including methods to obtain desired genetic heterogeneity in the end-product cultivars. One of the first steps in implementing molecular breeding approaches is to estimate the genetic variation within the breeding lines. Genetic heritable variability is indispensable in plant breeding aimed at developing new cultivars that express desirable characteristics generation after generation [13]. Furthermore, the development of improved varieties is enhanced when parents are selected based on genetic heterogeneity [14], making genetic variation estimation necessary in breeding programs to allow the selection of parental lines either to increase breeding population variation or to develop hybrids for cultivar release [15].

Genetic variation between breeding lines can be effectively determined through the use of molecular markers. In tomato, genetic diversity has been extensively studied using a wide range of molecular data. Miller and Tanksley (1990) [16] used restriction-fragment-length polymorphism (RFLP) markers for genetic diversity analysis of self-incompatible and self-compatible tomato species. To unveil the genetic variations that underlie fruit sugar and organic acid production, Zhao *et al.* (2016) [17] conducted a genetic diversity analysis of 174 tomato accessions using simple sequence repeat (SSR) markers. To gain insight into the morphological traits of fruits, Sacco *et al.* (2015) [18] performed a genetic diversity analysis of 123 tomato genotypes using single-nucleotide polymorphisms (SNPs). Similarly, Lin *et al.* [19] and Aflitos *et al.* [20] performed an evolutionary study of tomato and its wild relatives involving SNPs.

The advent of next-generation sequencing technologies coupled with bioinformatics has led genetic diversity studies into a new era. Sequencing of tomato has resulted in the discovery of large numbers of SNPs distributed throughout the genome [20] [21] [22]. Furthermore, cultivated tomato genome has been fully sequenced [23] and the genotyping by sequencing (GBS) has emerged as a powerful tool for sequencing large populations. The availability of large numbers of SNPs distributed throughout the genome, a reference genome, and the GBS technique [23] [24] [25] has made large intraspecific studies possible. This is important as most prior studies focused on interspecific variations and only a few intraspecific studies have been performed [19] [20] [26] [27]. The SNPs postulated from such intraspecific studies offer better clues to the genetic control of agronomic traits and can be used to deduce phylogenetic relationships. Parent selection based on such genetic information can greatly enhance breeding efficiency and help to achieve breeding goals such as high quality (flavor, color, shape), long shelf life, disease resistance, and heat tolerance.

In the present study, we used three representative sets of tomato breeding lines from the current Texas A&M AgriLife Research breeding programs at Weslaco and College Station and from former Texas A&M breeder Dr. Paul Leeper to assess genotypic intraspecific variations within Texas A&M germplasm. Sequencing of these lines yielded 10,236 high-quality polymorphic SNPs. Genetic distance analysis revealed that the tomato breeding lines developed by the Texas

A&M breeding programs possess a high level of genetic diversity that, upon selection, can be used to develop high-yielding adapted cultivars for Texas production. Furthermore, intraspecific SNPs identified in the present study could be used to identify economically important traits in cultivated tomatoes. Finally, based on the results of phylogenetic and genetic distance analyses, hybridization strategies can be developed to increase diversity and optimize hybrid development within and between breeding programs.

2. Materials and Methods

2.1. Plant Material

A total of 322 tomato (*Solanum lycopersicum*) genotypes were evaluated in this study. Among them, 300 genotypes were developed by three independent tomato breeding programs in the Texas A&M University (TAMU) system. Out of them, 127 were developed by Dr. Kevin Crosby's breeding program at Texas A&M University, College Station, TX (designated TAM-CS); 125 by Dr. Carlos Avila's breeding program at the Texas A&M AgriLife Research and Extension Center at Weslaco, TX (designated TAM-W); and 48 by the breeding program of Dr. Paul Leeper, a former TAMU breeder at Weslaco, Texas (designated TAM-L) (**Table S1**). These genotypes were developed by hybridizations of Texas A&M germplasm with a diverse set of parents including accessions from the USDA National Germplasm System and other public breeding programs mentioned below and subsequent selfing up to the F_9 generation. Pedigree information for all the breeding lines developed in Leeper's program and some from Crosby's program have been lost (**Table S1**). Breeding lines developed from all the three breeding program harbor good phenotypic variations in tomato fruit shape, size, and color. Besides the genotypes from the Texas A&M University breeding programs, 16 genotypes from the USDA collection, 3 from the Asian Vegetable Research and Development Center (AVRDC), and 3 developed by University of Florida tomato breeding program (designated FLA) were also included in the present study (**Table S1**).

2.2. DNA Extraction

Leaves from twelve four-week-old seedlings of the respective genotypes were collected and combined into a single bulk sample. Tissue was lyophilized, homogenized, and stored at −20˚C until extraction. Genomic DNA was extracted from 50 mg of homogenized tissue using the CTAB method [28]. Qualitative and quantitative tests of the DNA were performed by electrophoresis and Qubit 2.0 fluorometry (Life Technologies, Carlsbad, CA), respectively. For each sample, 1.2 μg of DNA was sent to the Texas A&M Genomics and Bioinformatics services (College Station, TX) for sequencing.

2.3. GBS, SNP Discovery, and Population Structure

Genotyping of 322 tomato genotypes was performed using low-coverage whole-

genome sequencing (SkimGBS [29]) with a paired-end approach (150 bp × 150 bp) (Illumina HiSeq 4000) at the Texas A&M Genomics and Bioinformatics service (College Station, TX). Raw sequences from the 322 genotypes were filtered to remove low-quality reads and adapter sequences. High-quality sequence data were mapped to the tomato reference genome (*S. lycopersicum* v3.00) [23] using bowtie2 [30]. The aligned BAM files were sorted, quality filtered for mapping, and filtered for duplicate reads using SAMtools [31] and Picard (http://broadinstitute.github.io/picard/index.html). The GATK HaplotypeCaller (HC) [32] was used for SNP calling from the aligned data of the 322 tomato genotypes. These raw polymorphic SNPs were filtered to remove SNPs with a high percentage of missing genotypes and low minimum allele frequency (MAF). The resulting genotypes were imputed using Beagle (v4.00) [33]. The imputed genotypes were further filtered to keep only genotypes with probability ≥0.9. The polymorphic SNPs were subsequently filtered to remove the SNPs with >30% missing genotypes.

The population structure and hybrid forms of tomato genotypes were inferred using the Bayesian model-based clustering program STRUCTURE (v2.3.4) [34] using polymorphic SNPs obtained from the GBS analysis. To determine the number of populations in a given genotype, the STRUCTURE was run with 5000 burn-in periods with 5000 Markov-chain Monte Carlo (MCMC) steps using an admixture model and correlated allele frequencies among populations. The program was run independently three times for each value K ranging from 1 to 10. To detect the true value of K (population), we used the uppermost level of structure calculated using the ΔK method as described in Evanno *et al.*, 2005 [35]. The tomato genotypes were assigned to each true population (Q) based on the value obtained for the proportion of population membership for a given K. The population structure of 322 tomato genotypes was visualized using a bar plot (sorted by Q) in the Python matplotlib package.

2.4. Phylogenetic and Principal Component Analysis

Phylogenetic analysis was performed using the unweighted pair-group method with arithmetic mean (UPGMA) algorithm implemented in TASSEL v5.2.52 [36]. The phylogenetic tree obtained from TASSEL was visualized using iTOL v4.3.3 and each population was annotated using customized annotation files [37]. The pairwise genetic distance matrix between each pair of genotypes was calculated using TASSEL v5.2.52 and visualized using the Python matplotlib package. The PCA was performed using the PCA function in TASSEL. The first three principal components were exported and visualized as a three-dimensional (3D) scatter plot using the Python matplotlib package.

3 Results

3.1. Generation of High-Quality Tomato GBS Data

We generated a total of ~598 million sequence reads (paired-end, 150 bp) using

low-coverage (average ~0.37×) whole-genome sequencing across 322 tomato genotypes. The raw sequence data were filtered to remove low-quality bases, adapter contamination, and uncalled bases to produce high-quality sequence data (~522 million reads). On an average, ~95% of high-quality reads mapped to the tomato reference genome for SNP discovery. In total, we obtained ~3.2 million SNPs from tomato SkimGBS data from the 322 genotypes, which we subsequently filtered to remove SNPs with >50% missing, rare alleles with MAF <5% across all 322 tomato genotypes, and SNPs with low genotype probability (<0.9) (Figure S1 and Figure S2). We used the remaining 10,236 high-quality SNPs for downstream analysis. SNPs were not distributed evenly across all chromosomes (Figure 1). Chromosome 12 and 1 had the highest numbers of identified SNPs with 1337 and 1208, respectively, whereas chromosomes 6 and 4 had the lowest number of identified SNPs with 173 and 255, respectively. In addition, 1279 SNPs were mapped to unanchored scaffolds (Chr00).

3.2. Genetic Distance between Tomato Genotypes

We calculated the pairwise genetic distance matrix for the 322 tomato genotypes in TASSEL v5.2.52. Genetic distance between tomato genotypes ranged from 0.092 to 0.443, with an average distance of 0.270 (Table 1 and Table S2). Among them, the combination of genotypes TAM-CS-138 and USDA-273 revealed the smallest genetic distance (0.092). Genotype TAM-CS-138 is an F_5 inbred heirloom type with large, pink fruit, developed by the Texas A&M College Station breeding program, and genotype USDA-273 is a cherry tomato that produces small red fruit, from the USDA germplasm bank (Table S1). Among all possible 100,142 combinations between the 322 genotypes, the largest genetic distance (0.443) was observed between genotypes TAM-CS-111 and TAM-W-322 (Table 1). Genotype TAM-CS-111 is an F_5 inbred that produces small, round red fruit, from

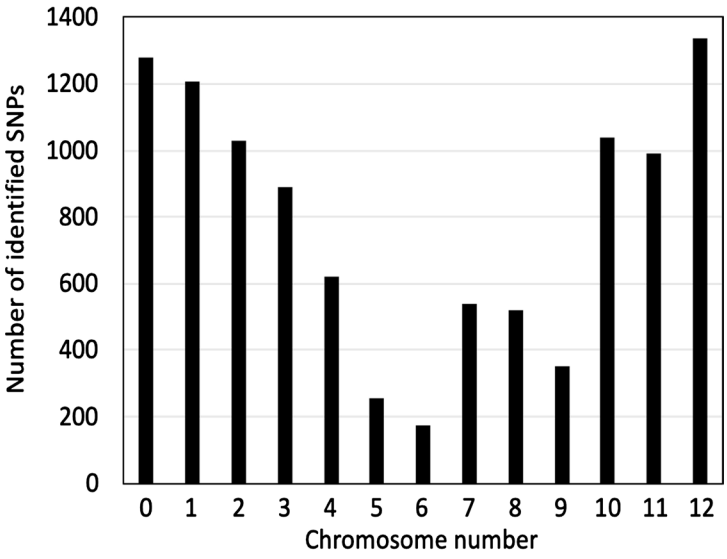

Figure 1. Distribution of 10,236 SNPs across tomato chromosomes. Unanchored scaffolds (Chr00) refers to SNPs not mapped to any chromosome.

Table 1. Genetic distances among tomato genotypes developed by different groups.

Genotype source	No. of genotypes	Minimum diversity		Maximum diversity		Mean Genetic distance
		Genotype combination	Genetic distance	Genotype combination	Genetic distance	
Overall	322	TAM-CS-138 and USDA-273	0.092	TAM-CS-111 and TAM-W-322	0.443	0.270
TAM-W	125	TAM-W-315 and TAM-W-316	0.175	TAM-W-322 and TAM-W-172	0.434	0.264
TAM-CS	127	TAM-CS-138 and TAM-CS-230	0.099	TAM-CS-111 and TAM-CS-165	0.392	0.282
TAM-L	48	TAM-L-13 and TAM-L-54	0.183	TAM-L-51 and TAM-L-16	0.347	0.255
USDA	16	USDA-238 and USDA-273	0.192	USDA-259 and USDA-320	0.292	0.234
AVRDC	3	AVRDC-119 and AVRDC-133	0.289	AVRDC-119 and AVRDC-126	0.309	0.296
FLA	3	FLA-154 and FLA-161	0.276	FLA-147 and FLA-154	0.315	0.298

Note: AVRDC = Asian Vegetable Research and Development Center; TAM-CS = Dr. Kevin Crosby's breeding program at Texas A&M at College Station; TAM-W = Dr. Carlos Avila's breeding program at Texas A&M AgriLife Research and Extension Center at Weslaco, TX; TAM-W = Dr. Paul Leeper's breeding program at Texas A&M AgriLife Research and Extension Center at Weslaco, TX; FLA = Florida Tomato Breeding Program; USDA = United States Department of Agriculture.

the Texas A&M College Station breeding program, while TAM-W-322 is an F_9 inbred that produces medium Roma-type pink fruit, developed by the Texas A&M AgriLife breeding program at Weslaco.

The genetic distances between the genotypes from the three Texas A&M University Breeding programs and control outgroups from the USDA, AVRDC, and Florida are presented in Table 1. Breeding lines developed by the Texas A&M College Station, Weslaco, and Leeper programs had overall intra-program genetic distance means of 0.282, 0.264, and 0.255, respectively (Table 1). The genetic diversity between germplasms from the different Texas A&M breeding programs indicates a high potential for introducing variability between programs. In regard to within-program variation, among lines from the Texas A&M AgriLife breeding program at Weslaco, the largest genetic distance (0.434) was between genotypes TAM-W-172 and TAM-W-322; among lines from the Texas A&M College Station breeding program, the largest genetic distance (0.392) was between TAM-CS-111 and TAM-CS-165; and for those from the Texas A&M Leeper program, the largest genetic distance (0.347) was between TAM-L-51 and TAM-L-16. The genotypes developed by the USDA were overall the least diverse group, with a mean genetic distance of 0.234 and a range of 0.192 - 0.292. Within that group, the genotype combination of USDA-259 and USDA-320 showed the largest genetic distance (Table 1). The sets of genotypes from the AVRDC and Florida breeding programs used in the present study showed mean genetic diversities of 0.296 and 0.298, respectively (Table 1).

3.3. Population Structure

We explored the population structure of tomato genotypes using a model-based clustering method implemented with STRUCTURE v2.3.4. The maximum value for ΔK was observed when $K = 2$ (Figure 2(a)), indicating the presence of two

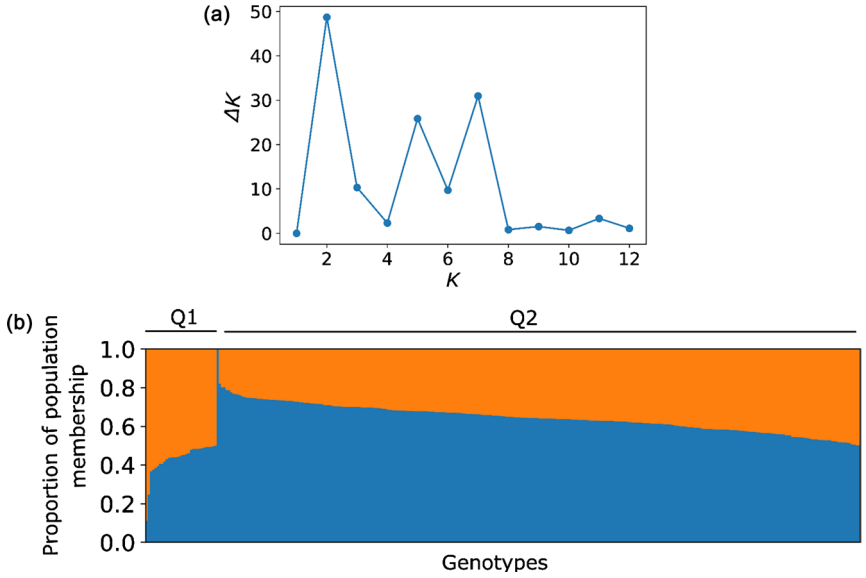

Figure 2. Identification of population structure using a model-based clustering method. (a) Calculated ΔK values for each number of expected populations (K); (b) The 322 tomato genotypes were assigned to two populations ($Q1$ and $Q2$) by model-based clustering. The distributions of genotypes in each population are represented in orange ($Q1$) and blue ($Q2$) based on their population membership.

main population clusters ($Q1$ and $Q2$) (Figure 2(b)). Out of the entire population evaluated in this study, 32 tomato genotypes (9.9%) were grouped into $Q1$, while the remaining 290 genotypes were placed into $Q2$ (90.1%) (Table 2). Of the two clusters, the genetic diversity assessment indicated that $Q1$ is more diverse, and it included the two genotypes with the largest genetic distance observed (genotypes TAM-W-322 and TAM-CS-111, Figure 3(a)). The range of genetic distances between genotypes assigned to cluster $Q1$ was 0.288 - 0.443, and the mean was 0.346 (Figure 3(a)). In cluster $Q2$, the range of genetic distances between genotypes was 0.092 - 0.334, with a mean of 0.268, and this cluster included the two genotypes with the smallest genetic distance (0.092), TAM-CS-138 and USDA-273 (Figure 3(b)).

The population structure analysis also revealed that genotypes from the breeding programs were distributed between the $Q1$ and $Q2$ clusters, while all evaluated genotypes from the USDA collection belonged to the $Q2$ cluster (Table 2 and Table S1). The majority of genotypes (62%) in the $Q1$ cluster were developed by the Texas A&M College Station breeding program, while germplasm developed by the Texas A&M AgriLife Weslaco and Leeper breeding programs accounted for 18.75% and 12.5%, respectively (Table 2). On the other hand, the Weslaco and College Station breeding programs contributed roughly equally (41% and 36.89%, respectively) to cluster $Q2$, with the Leeper program accounting for 12.5% (Table 2). The $Q2$ cluster included most of the genotypes from each of the three breeding programs, accounting for 95.2% of those from the Weslaco program, 84.26% of those from the College Station program, and 91.66% of those from the Leeper program.

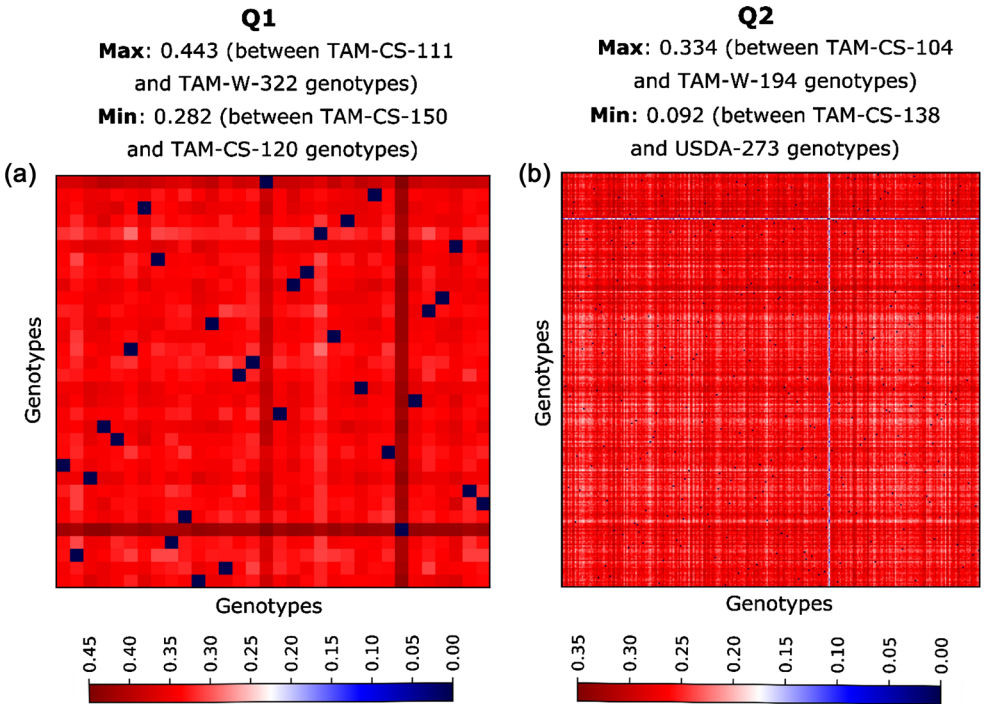

Figure 3. Distribution of genetic distance between genotypes in two populations. (a) Distribution of genetic distance in population *Q*1. The maximum genetic distance (0.443) occurred between TAM-CS-111 and TAM-W-322 and the minimum (0.282) between TAM-CS-150 and TAM-CS-120; (b) Distribution of genetic distance in population *Q*2. The maximum genetic distance (0.334) was between TAM-CS-104 and TAM-W-204 and the minimum (0.092) between TAM-CS-138 and USDA-273.

Table 2. Distribution of tomato genotypes from six different sources into two clusters. A model-based structure analysis performed on 322 genotypes divided them into two clusters *Q*1 and *Q*2.

Genotype source	No. genotypes	No. of genotypes in each cluster		Percentage of genotypes in each cluster	
		*Q*1	*Q*2	*Q*1	*Q*2
Overall	322	32	290	9.9	90.1
TAM-W	125	6	119	4.8	95.2
TAM-CS	127	20	107	15.74	84.26
TAM-L	48	4	44	8.34	91.66
USDA	16	0	16	0	100
AVRDC	3	1	2	33.34	66.64
Florida	3	1	2	33.34	66.64

Note: AVRDC = Asian Vegetable Research and Development Center; TAM-CS = Dr. Kevin Crosby's breeding program at Texas A&M at College Station; TAM-W = Dr. Carlos Avila's breeding program at Texas A&M AgriLife Research and Extension Center at Weslaco, TX; TAM-W = Dr. Paul Leeper's breeding program at Texas A&M AgriLife Research and Extension Center at Weslaco, TX; FLA = Florida Tomato Breeding Program; USDA = United States Department of Agriculture.

3.4. Phylogenetic Tree and Principal Component Analysis

Next, we constructed a phylogenetic tree based on the 10,236 SNPs and found

that it also divided the 322 tomato population into two groups and that these groups corresponded with the two population clusters *Q*1 and *Q*2 (Figure 4). Thus, the phylogenetic tree displayed consistency with the population structure revealed by the model-based clustering analysis with STRUCTURE v2.3.4 (Figure 2). Figure 4 shows that the genotypes producing the smallest genetic distance (USDA-273 and TAM-CS-138) had the shortest branches arising from the lowermost clade. Similarly, genotype TAM-W-322, which was one of the two genotypes producing the largest genetic distance with another, was placed on the

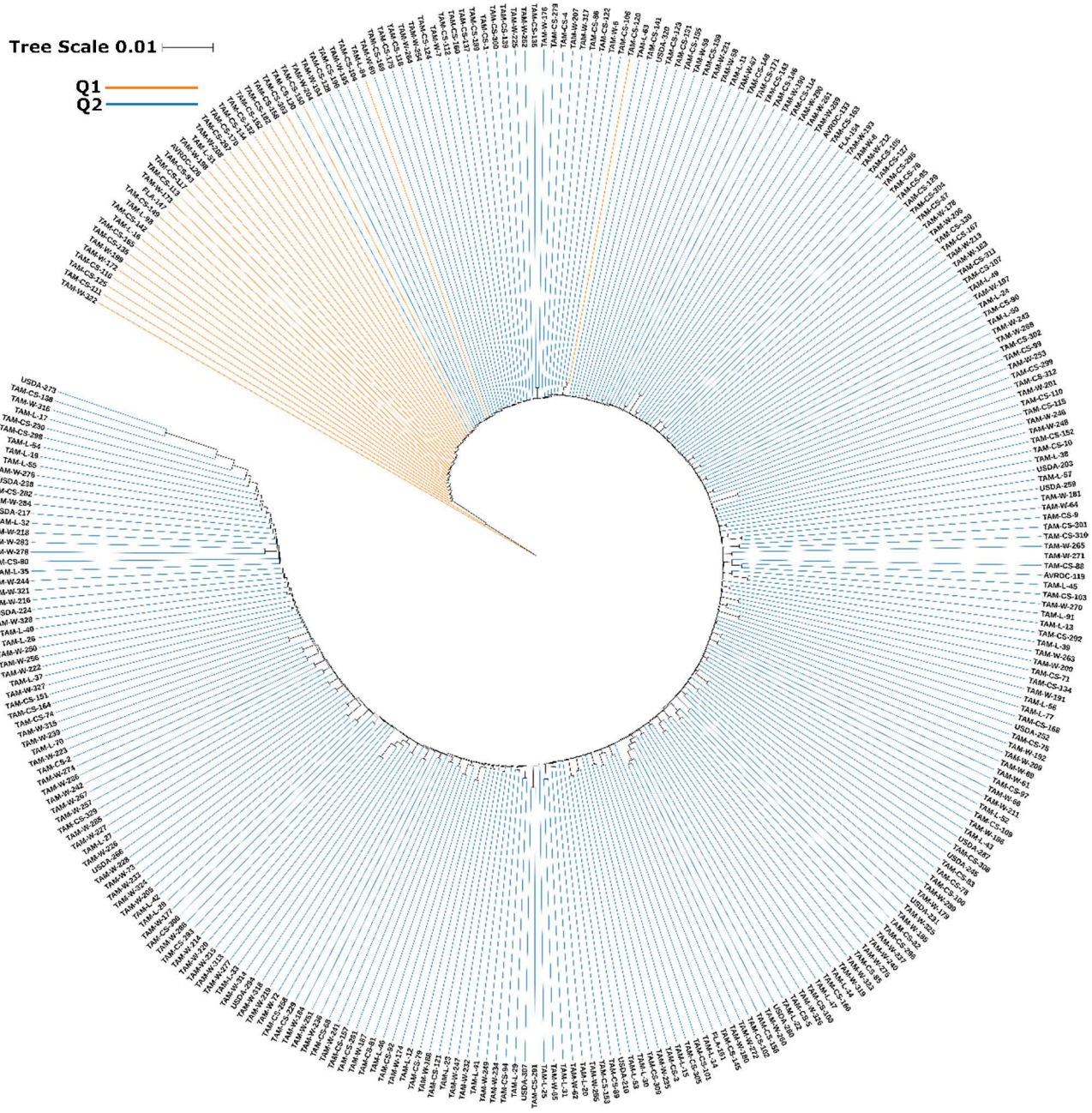

Figure 4. Phylogenetic analysis of 322 tomato genotypes built using the UPGMA hierarchical clustering method. The branches of the two predicted populations *Q*1 and *Q*2 are highlighted in orange and blue, respectively.

extreme other side of the phylogenetic tree in the longest uppermost clade (Figure 4). The phylogenetic tree indicated that the genotypes TAM-W-322, TAM-CS-111, and TAM-L-16, from the Texas A&M Weslaco, College Station, and Leeper breeding programs, respectively, had the potential to yield greater genetic diversity when combined with other genotypes. We also performed PCA to check the number of population structure groups; Figure 5 presents the distribution of tomato genotypes in scatter plots of the first three principal components in a 3D space. This PCA also revealed that the tomato genotypes clustered into two groups, with some overlap indicative of the small genetic distances between some genotypes in *Q*1 and *Q*2.

4. Discussion

Genetic diversity studies have increased in recent years due to advances in high-throughput sequencing technologies and the availability of high-resolution SNPs. For example, 5.4 million SNPs were identified between wild and cultivated tomato genomes during the sequencing of the tomato reference genome from the cultivar Heinz 1706 [23]. Likewise, 11.6 million SNPs were found from the sequencing of 360 accessions that included both cultivated and wild tomato species [19] and 180,000 - 350,000 SNPs from the sequencing of four large-fruited cultivated tomato accessions [38]. In the present study, sequencing of 322 tomato genotypes from cultivated S. *lycopersicum* resulted in the discovery of 3.2 million SNPs. After filtering on the basis of quality parameters, 10,236 high-quality SNPs were obtained and used for genetic diversity analysis. Among them, the largest number of SNPs were observed in chromosome 12, followed by chromosome 1 and 10 (Figure 1). The existence of unanchored scaffolds (Chr00) and the large

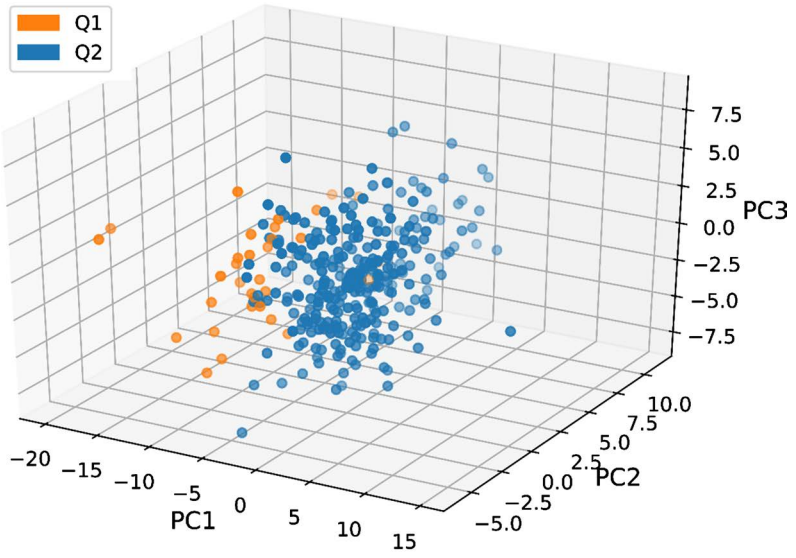

Figure 5. Principal component analysis (PCA) of 322 tomato genotypes. The first three principal components (PCs) are shown using a 3D scatter plot. The PCA clustered the 322 genotypes into two distinct clusters (populations) *Q*1 and *Q*2, represented by orange and blue dots, respectively. Most of the genotypes were assigned to the *Q*2 population.

number of SNPs mapped to it (1279 in total) indicate that numerous genomic regions have not yet properly placed in chromosomes [2]. It also highlights the importance of identifying new intraspecific SNPs in the tested tomato breeding lines.

Past efforts to develop diverse breeding populations in Texas A&M University breeding programs are reflected in the range of genetic diversity within and between the groups of tomato lines developed by the three Texas A&M programs as well as in comparison to the outgroup lines. High ranges were expected, since some of these lines were generated from diverse sets of parents, including some that the USDA, Florida, and AVRDC programs contributed to Texas A&M diversity (**Table 1** and **Table S1**). Among the breeding programs, the highest range and mean of genetic diversity were detected among the genotypes from the Texas A&M Weslaco (genetic distance range 0.175 - 0.434, mean 0.264) and College Station (range 0.099 - 0.392, mean 0.282) breeding programs (**Table 1**). These results can be explained by the possibility that a significant proportion of common parents shared has been shared between Texas A&M breeding programs and subsequent selections between programs. The largest genetic diversity was achieved from the combination of genotypes from the Weslaco and College Station programs (genetic distance of 0.443 between genotypes TAM-W-322 and TAM-CS-111), indicating that crossing germplasm from the two programs should generate more variation for cultivar development. However, in looking at the genetic diversity between the Weslaco and College Station breeding programs, we found that there was in general greater genetic diversity within than between programs, perhaps because the recently initiated program at Weslaco used College Station material for breeding population development. The broad range of genetic diversity of breeding lines within a breeding program was also reflected in the population structure analysis and the phylogenetic tree (**Figure 3** and **Figure 4**). Genotypes from all three Texas A&M breeding programs and also from AVRDC and Florida lines were observed in both the *Q*1 and *Q*2 clusters (**Figure 4**). Additionally, the grouping of genotypes into two clusters with some overlaps was further validated by the PCA.

Several inbred lines developed by the Texas A&M Weslaco and College Station breeding programs were developed from the hybridization of heirloom tomato parents with morphologically diverse fruit characteristics, including color, size, and shape, in an attempt to improve quality. Though distinct in nature, heirloom tomatoes possess comparatively low genetic diversity [2] [39] [40]. Thus, a genotype developed by hybridizing two heirloom tomato strains is expected to have low genetic diversity compared to genotypes evolved from contemporary lines since heirloom genotypes that are different only in shape and color may differ only by a handful of genes [41] [42] [43]. This may have contributed to the lower genetic diversity in some of the Texas A&M Weslaco and College Station breeding program lines in the *Q*2 cluster.

On the other hand, some of the breeding lines were developed by introgress-

ing one or more disease-resistance genes. Disease-resistance genes are primarily introgressed from wild relatives, which have been reported to carry 20 times higher genetic diversity than that of cultivated tomato [19] [20], and which thereby contributed to the high genetic diversity in Texas A&M breeding populations. Some examples of introgressed resistance genes in the Texas A&M AgriLife breeding population include the gene *Mi*-1, which confers resistance against root knot nematode caused by *Meloidogyne* spp. and was introgressed from *Solanum peruvianum* [44]; *Sw*-5, which confers resistance to the tomato spotted wilt virus (*TSWV*), introgressed from *S. peruvianum* [45] [46]; *Ty*-2 and *Ty*-3, which confer resistance to *tomato yellow leaf curl virus (TYLCV*), introgressed from *S. habrochaites* [47] [48] and *S. chilense* [49], respectively; and *I*-2 and *I*-3, conferring resistance to vascular wilt caused by *Fusarium oxysporum* race 2 (Fol2) and Fol1, Fol2, and Fol3, were introgressed from *S. pimpinellifolium* [50] and *S. pennellii* [51] [52], respectively. Thus, introgressions of disease-resistance genes during hybridization could have played an important role in producing the genetic diversity among breeding lines observed in the present study and thus in grouping the genotypes into two clusters.

The present study revealed that the tomato breeding lines developed by the Texas A&M breeding programs possess a high level of genetic diversity and thus should be capable, upon selection, of yielding a variety of cultivars adapted for Texas production. Furthermore, the broad genetic base of the breeding lines and the higher recombination generated through hybridization could be utilized to uncover QTLs for complex traits. As the SNPs identified here were intraspecific, they could be valuable for uncovering economically important traits within cultivated tomato. Finally, our work here suggests that through the use of a phylogenetic tree and genetic distances, it is possible to develop crossing strategies to increase diversity and encourage hybrid development within and between breeding programs.

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Conflicts of Interest

The authors declare that they have no competing interests.

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Supplementary

Table S1. The details of 322 tomato genotypes used in genetic diversity analysis. All the genotypes were from cultivated tomato *Solanum lycopersicum*.

Genotype source	Genotype ID	Cluster	Pedigree	Generation	Fruit type	*Fruit Size	Fruit color
TAM-CS	TAM-CS-1	*Q*2	Lost pedigree	F5	Round	S	Red
TAM-CS	TAM-CS-2	*Q*2	bl46 HD	F5	Cherry	XS	Orange
TAM-CS	TAM-CS-3	*Q*2	T105	F5	Roma	S	Red
TAM-CS	TAM-CS-4	*Q*2	BL30 med polated red	F5	Roma	S	Red
TAM-CS	TAM-CS-5	*Q*2	bl39 vroom small pink	F5	Roma	S	Red
TAM-W	TAM-W-6	*Q*2	Pink Ponderosa#3 × *I*-2	F6	Pear	S	Red
TAM-W	TAM-W-7	*Q*2	1500 × AVT1106 Plant 4	F6	Round	S	Red
TAM-W	TAM-W-8	*Q*2	275SBR × AVT1001 Plant B	F6	Roma	S	Red
TAM-CS	TAM-CS-9	*Q*2	Alamo T11 VR	F7	Roma	S	Red
TAM-CS	TAM-CS-10	*Q*2	Alamo T13	F7	Round	S	Red
TAM-L	TAM-L-11	*Q*2	35		Roma	S	Red
TAM-L	TAM-L-12	*Q*2	106		Round	S	Red
TAM-L	TAM-L-13	*Q*2	203				
TAM-L	TAM-L-14	*Q*2	221		Beefsteak	M	Red
TAM-L	TAM-L-15	*Q*2	249		Roma	S	Red
TAM-L	TAM-L-16	*Q*1	265				
TAM-L	TAM-L-17	*Q*2	489		Roma	S	Red
TAM-L	TAM-L-19	*Q*2	530		Roma	M	Red
TAM-L	TAM-L-20	*Q*2	701		Roma	S	Red
TAM-L	TAM-L-22	*Q*2	725		Roma	M	Red
TAM-L	TAM-L-23	*Q*2	761		Roma	M	Red
TAM-L	TAM-L-24	*Q*2	782		Round	S	Red
TAM-L	TAM-L-25	*Q*2	1116				
TAM-L	TAM-L-26	*Q*2	1125		Roma	S	Red
TAM-L	TAM-L-27	*Q*2	1131		Round	S	Red
TAM-L	TAM-L-28	*Q*2	1504		Roma	S	Red
TAM-L	TAM-L-29	*Q*2	1525		Roma	M	Red
TAM-L	TAM-L-30	*Q*2	1531				
TAM-L	TAM-L-31	*Q*2	1538		Roma	M	Red
TAM-L	TAM-L-32	*Q*2	1547		Roma	S	Red
TAM-L	TAM-L-33	*Q*2	1555		Beefsteak	L	Red
TAM-L	TAM-L-35	*Q*2	1576		Pear	S	Red
TAM-L	TAM-L-37	*Q*2	1587		Beefsteak	L	Red
TAM-L	TAM-L-38	*Q*2	1603		Beefsteak	M	Red

Continued

TAM-L	TAM-L-39	*Q*2	1615		Beefsteak	L	Red
TAM-L	TAM-L-40	*Q*2	1633		Pear	S	Red
TAM-L	TAM-L-41	*Q*2	1656		Beefsteak	M	Red
TAM-L	TAM-L-42	*Q*2	1666		Roma	L	Red
TAM-L	TAM-L-43	*Q*2	1672		Round	M	Red
TAM-L	TAM-L-44	*Q*2	1678		Beefsteak	L	Red
TAM-L	TAM-L-45	*Q*2	1689		Beefsteak	L	Red
TAM-L	TAM-L-46	*Q*2	1695				
TAM-L	TAM-L-47	*Q*2	1792				
TAM-L	TAM-L-49	*Q*2	1804		Round	S	Red
TAM-L	TAM-L-50	*Q*2	1813		Roma	M	Red
TAM-L	TAM-L-51	*Q*1	1838		Pear	M	Red
TAM-L	TAM-L-52	*Q*2	1869		Beefsteak	M	Red
TAM-L	TAM-L-53	*Q*2	1894		Roma	M	Red
TAM-L	TAM-L-54	*Q*2	1987		Roma	M	Red
TAM-L	TAM-L-55	*Q*2	2001		Roma	M	Red
TAM-L	TAM-L-56	*Q*2	2022		Roma	S	Red
TAM-L	TAM-L-57	*Q*2	W-9		Beefsteak	XL	Red
TAM-W	TAM-W-58	*Q*2	275SBR × DELICIOUS PI639212	F5	Round	S	Red
	TAM-W-59	*Q*2	Healani		Round	M	Red
TAM-W	TAM-W-60	*Q*2	W25 × CHEROKEE PURPLE P1639211	F5	Round	S	Pink
TAM-W	TAM-W-61	*Q*2	W25 × CHEROKEE PURPLE P1639211	F5	Round	L	Pink
TAM-W	TAM-W-62	*Q*2	W25 × DELICIOUS PI639212	F5	Beefsteak	L	Red
TAM-L	TAM-L-63	*Q*2	W-12		Beefsteak	L	Red
TAM-W	TAM-W-64	*Q*2	W25 × *I*-2	F5	Roma	S	Pink
TAM-W	TAM-W-65	*Q*2	W25 × *I*-2	F5	Beefsteak	L	Red
	TAM-W-66	*Q*2	Vit Kaspar		Cherry	XS	Red
TAM-W	TAM-W-67	*Q*2	W29 × YELLOW PEACH	F5	Round	S	Red
TAM-CS	TAM-CS-68	*Q*2	bl49	F5	Cherry	XS	Red
TAM-W	TAM-W-69	*Q*2	W9 × HILLBILLY POTATO LEAF PI 639219	F5	Round	S	Red
TAM-L	TAM-L-70	*Q*2	W-25		Round	M	Red
TAM-CS	TAM-CS-71	*Q*2	bl44	F5	Cherry	XS	Yellow
TAM-W	TAM-W-72	*Q*2	W25 × DELICIOUS PI639212	F5	Beefsteak	L	Red
TAM-W	TAM-W-73	*Q*2	W9 × HILLBILLY POTATO LEAF PI 639219	F5	Beefsteak	M	Red
TAM-CS	TAM-CS-74	*Q*2	RG1	F5	Beefsteak	XL	Pink

Continued

TAM-CS	TAM-CS-75	*Q*2	T106	F5	Beefsteak	L	Red
TAM-CS	TAM-CS-76	*Q*2	RG1	F5	Heirloom	XL	Pink
TAM-L	TAM-L-77	*Q*2	W-29		Roma	S	Red
TAM-CS	TAM-CS-78	*Q*2	bl49	F5	Heirloom	XL	Pink
TAM-CS	TAM-CS-79	*Q*2	Lost pedigree	F5	Beefsteak	XL	Pink
TAM-CS	TAM-CS-80	*Q*2	T65	F5	Round	S	Yellow
TAM-CS	TAM-CS-81	*Q*2	T22	F5	Beefsteak	L	Pink
TAM-CS	TAM-CS-82	*Q*2	RG2	F5	Beefsteak	XL	Pink
TAM-CS	TAM-CS-83	*Q*2	T74	F5	Beefsteak	L	Red
TAM-L	TAM-L-84	*Q*1	275 SBR		Round	S	Red
TAM-CS	TAM-CS-85	*Q*2	T74	F5	Beefsteak	XL	Red
TAM-CS	TAM-CS-86	*Q*2	Lost pedigree	F5	Beefsteak	L	Pink
TAM-CS	TAM-CS-87	*Q*2	T74	F5	Heirloom	XL	Pink
TAM-CS	TAM-CS-88	*Q*2	RG2	F5	Round	L	Tiger stripe
TAM-CS	TAM-CS-89	*Q*2	RG2	F5	Heirloom	XL	Tiger stripe
TAM-CS	TAM-CS-90	*Q*2	T36	F5	Beefsteak	XL	Red
TAM-L	TAM-L-91	*Q*2	276 SBR		Roma	S	Red
TAM-CS	TAM-CS-92	*Q*2	BL10	F5	Beefsteak	XL	Yellow
TAM-CS	TAM-CS-93	*Q*1	T37	F5	Beefsteak	XL	Pink
TAM-CS	TAM-CS-94	*Q*2	bl9	F5	Beefsteak	XL	Red
TAM-CS	TAM-CS-95	*Q*2	bl9	F5	Beefsteak	XL	Red
TAM-CS	TAM-CS-97	*Q*2	Lost pedigree	F5	Beefsteak	XL	Red
TAM-L	TAM-L-98	*Q*1	277 SBR		Beefsteak	L	Red
TAM-CS	TAM-CS-99	*Q*2	RG6	F5	Beefsteak	L	Red
TAM-CS	TAM-CS-100	*Q*2	BL 27 F'15	F5	Beefsteak	L	Red
TAM-CS	TAM-CS-101	*Q*2	BL 30 v small round yellow	F5	Cherry	S	Yellow
TAM-CS	TAM-CS-102	*Q*2	T67	F5	Beefsteak	L	Red
TAM-CS	TAM-CS-103	*Q*2	BL12	F5	Beefsteak	L	Red
TAM-CS	TAM-CS-104	*Q*2	BL27 @ red	F5	Round	L	Red
TAM-CS	TAM-CS-105	*Q*2	HT-1		Heirloom	XL	Pink
TAM-CS	TAM-CS-106	*Q*2	T37	F5	Beefsteak	XL	Pink
TAM-CS	TAM-CS-107	*Q*2	T39	F5	Beefsteak	XL	Pink
TAM-CS	TAM-CS-108	*Q*2	RG2	F5	Beefsteak	XL	Tiger stripe
TAM-CS	TAM-CS-109	*Q*2	Lost pedigree	F5	Beefsteak	L	Red
TAM-CS	TAM-CS-110	*Q*2	Lost pedigree	F5	Round	L	Red
TAM-CS	TAM-CS-111	*Q*1	T105	F5	Round	S	Red
TAM-CS	TAM-CS-112	*Q*2	TAM Hot Ty		Beefsteak	XL	Red

Continued

TAM-CS	TAM-CS-113	*Q*1	t38	F5	Beefsteak	L	Red
TAM-CS	TAM-CS-114	*Q*2	bl50	F5	Cherry	S	Red
TAM-CS	TAM-CS-115	*Q*2	T104	F5	Round	M	Red
TAM-CS	TAM-CS-116	*Q*1	T94	F5	Beefsteak	L	Red
TAM-CS	TAM-CS-117	*Q*1	T69	F5	Beefsteak	M	Red
TAM-CS	TAM-CS-118	*Q*2	RG2	F5	Beefsteak	L	Pink
AVRDC	AVRDC-119	*Q*2	AVT1001		Beefsteak	M	Red
TAM-CS	TAM-CS-120	*Q*1	RG2	F5	Round	M	Pink
TAM-CS	TAM-CS-121	*Q*2	BL17	F5	Beefsteak	L	Red
TAM-CS	TAM-CS-122	*Q*2	BL9	F5	Roma	S	Red
TAM-CS	TAM-CS-123	*Q*2	T40	F5	Beefsteak	L	Pink
TAM-CS	TAM-CS-124	*Q*2	TSW3P4	F5	Beefsteak	L	Pink
TAM-CS	TAM-CS-125	*Q*1	T73	F5	Beefsteak	L	Red
AVRDC	AVRDC-126	*Q*1	AVT1106		Roma	S	Red
TAM-CS	TAM-CS-127	*Q*2	BL15	F5	Beefsteak	L	Pink
TAM-CS	TAM-CS-128	*Q*2	RG2	F5	Heirloom	XL	Pink
TAM-CS	TAM-CS-129	*Q*2	Diablo bc vr	F5	Round	S	Red
TAM-CS	TAM-CS-130	*Q*2	Lost pedigree	F5	Round	L	Red
TAM-CS	TAM-CS-131	*Q*2	T20	F5	Round	L	Red
TAM-CS	TAM-CS-132	*Q*1	T101	F5	Round	M	Red
AVRDC	AVRDC-133	*Q*2	AVT1110		Round	M	Red
TAM-CS	TAM-CS-134	*Q*2	BL15	F5	Beefsteak	XL	Red
TAM-CS	TAM-CS-135	*Q*1	bl41 vroom bulk small red	F5	Cherry	XS	Yellow
TAM-CS	TAM-CS-136	*Q*2	BL15	F5	Roma	S	Red
TAM-CS	TAM-CS-137	*Q*2	T44	F5	Beefsteak	XL	Red
TAM-CS	TAM-CS-138	*Q*2	T102	F5	Heirloom	XL	Pink
TAM-CS	TAM-CS-139	*Q*2	T19	F5	Beefsteak	L	Red
TAM-CS	TAM-CS-141	*Q*2	T53	F5	Beefsteak	L	Pink
TAM-CS	TAM-CS-142	*Q*1	bl46 @ small red	F5	Beefsteak	L	Red
TAM-CS	TAM-CS-143	*Q*2	T107	F5	Beefsteak	L	Red
TAM-CS	TAM-CS-144	*Q*1	T99	F5	Cherry	S	Yellow
TAM-CS	TAM-CS-145	*Q*2	BL30	F5	Beefsteak	M	Red
TAM-CS	TAM-CS-146	*Q*2	t58 @ red cherry	F5	Cherry	S	Red
FLA	FLA-147	*Q*1	Fla8624		Beefsteak	L	Red
TAM-CS	TAM-CS-148	*Q*2	T97	F5	Cherry	S	Yellow
TAM-CS	TAM-CS-149	*Q*1	T55	F5	Heirloom	XL	Pink
TAM-CS	TAM-CS-150	*Q*1	T61	F5	Campari	S	Red

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TAM-CS	TAM-CS-151	*Q*2	RG1P4F2	F5	Beefsteak	M	Pink
TAM-CS	TAM-CS-152	*Q*2	BL30 vr lg red	F5	Beefsteak	L	Red
TAM-CS	TAM-CS-153	*Q*2	BL16	F5	Beefsteak	XL	Yellow
FLA	FLA-154	*Q*2	Fla417-8		Round	M	Red
TAM-CS	TAM-CS-155	*Q*2	T82	F5	Beefsteak	XL	Red
TAM-CS	TAM-CS-156	*Q*2	T79	F5	Italian	M	Red
TAM-CS	TAM-CS-157	*Q*2	T27	F5	Beefsteak	XL	Red
TAM-CS	TAM-CS-158	*Q*1	T33	F5			
TAM-CS	TAM-CS-159	*Q*2	T39	F5	Beefsteak	L	Red
TAM-CS	TAM-CS-160	*Q*2	T89	F5	Campari	S	Pink
FLA	FLA-161	*Q*2	154712-1		Beefsteak	L	Red
TAM-CS	TAM-CS-162	*Q*1	BL12	F5	Heirloom	L	Tiger stripe
TAM-CS	TAM-CS-163	*Q*2	BL18	F5	Cherry	S	Yellow
TAM-CS	TAM-CS-164	*Q*2	b38 red round pink flesh	F5	Beefsteak	XL	Pink
TAM-CS	TAM-CS-165	*Q*1	t59 @ red cherry	F5	Beefsteak	M	Orange
TAM-CS	TAM-CS-166	*Q*2	T23	F5	Round	M	Red
TAM-CS	TAM-CS-167	*Q*2	T35	F5	Beefsteak	L	Red
TAM-CS	TAM-CS-168	*Q*2	*Mi*-1		Beefsteak	XL	Red
TAM-CS	TAM-CS-169	*Q*2	T57	F5	Beefsteak	M	Pink
TAM-CS	TAM-CS-170	*Q*1	T62	F5	Heirloom	XL	Pink
TAM-CS	TAM-CS-171	*Q*2	RG6WESF2P2	F5	Beefsteak	M	Red
TAM-W	TAM-W-172	*Q*1	PI 633505 Yellow Peach × *I*-3 *Ty*-3	F6	Campari	S	Yellow
TAM-W	TAM-W-173	*Q*1	PI 633505 Yellow Peach × *I*-3 *Ty*-3	F6	Campari	S	Pink
TAM-W	TAM-W-174	*Q*2	PI 633505 Yellow Peach × *I*-3 *Ty*-3	F6	Round	M	Red
TAM-CS	TAM-CS-175	*Q*2	*I*-3 *Ty*-2		Beefsteak	XL	Red
TAM-W	TAM-W-176	*Q*2	PI 633505 Yellow Peach × *I*-3 *Ty*-3	F6	Round	M	Yellow
TAM-W	TAM-W-177	*Q*2	PI 639208 Black from Tula × LA4440 Plant A	F6	Round	M	Red
TAM-W	TAM-W-178	*Q*2	PI 639209 Brandywine#1 × *I*-2 *Ty*-2	F6	Beefsteak	M	Red
TAM-W	TAM-W-179	*Q*2	PI 639213 Juane Flamme × *I*-2 *Ty*-2	F6	Heirloom	M	Yellow
TAM-W	TAM-W-180	*Q*2	PI 639213 Juane Flamme × *I*-2 *Ty*-2	F6	Beefsteak	S	Red
TAM-W	TAM-W-181	*Q*2	PI 639213 Juane Flamme × *I*-3 *Ty*-3	F6	Round	M	Yellow
TAM-CS	TAM-CS-182	*Q*1	*I*-2-*Ty*-2		Round	S	Red
TAM-W	TAM-W-183	*Q*2	PI 639213 Juane Flamme × *I*-3 *Ty*-3	F6	Beefsteak	L	Orange
TAM-W	TAM-W-184	*Q*2	PI 639215 Principe Borguese × *I*-2 *Ty*-2	F6	Round	XS	Red
TAM-W	TAM-W-185	*Q*2	PI 639215 Principe Borguese × *I*-3 *Ty*-3	F6	Cherry	S	Red
TAM-W	TAM-W-186	*Q*2	PI 639215 Principe Borguese × *I*-3 *Ty*-3	F6	Cherry	XS	Red
TAM-W	TAM-W-187	*Q*2	PI 639217 Striped Cavern × *I*-2 *Ty*-2	F6	Heirloom	S	Tiger stripe

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TAM-W	TAM-W-188	*Q*2	PI 639217 Striped Cavern × *I*-2 *Ty*-2	F6	Beefsteak	S	Red
TAM-CS	TAM-CS-189	*Q*2	I2		Beefsteak	M	Red
TAM-W	TAM-W-190	*Q*2	PI 639217 Striped Cavern × *I*-2 *Ty*-2 Plant A	F6	Heirloom	M	Tiger stripe
TAM-W	TAM-W-191	*Q*2	PI 647526 Brandywine#1 × *I*-2 *Ty*-2	F6	Beefsteak	XL	Red
TAM-W	TAM-W-192	*Q*2	PI 647526 Brandywine#1 × *I*-2 *Ty*-2	F6	Heirloom	XL	Pink
TAM-W	TAM-W-193	*Q*2	PI 647526 Brandywine#1 × *I*-2 *Ty*-2	F6	Heirloom	XL	Red
TAM-W	TAM-W-194	*Q*2	PI 639215 Principe Borguese × *I*-2 *Ty*-2	F6	Heirloom	M	Red
TAM-W	TAM-W-195	*Q*2	PI639209 Brandywine#1 × AVT1001 Plant A	F6	Beefsteak	M	Pink
TAM-CS	TAM-CS-196	*Q*2	I3		Beefsteak	L	Red
TAM-W	TAM-W-197	*Q*2	PI639209 Brandywine#1 × AVT1001 Plant B	F6	Round	M	Red
TAM-W	TAM-W-198	*Q*1	PI639209 Brandywine#1 × AVT1001 Plant B	F6	Round	M	Red
TAM-W	TAM-W-199	*Q*1	PI639209 Brandywine#1 × AVT1001 Plant C	F6	Round	M	Red
TAM-W	TAM-W-200	*Q*2	Supersteak#1 × *I*-2 *Ty*-2	F6	Beefsteak	L	Red
TAM-W	TAM-W-201	*Q*2	Supersteak#1 × *I*-2 *Ty*-2	F6	Beefsteak	L	Red
USDA	USDA-203	*Q*2	440		Round	XS	Black
TAM-W	TAM-W-204	*Q*2	W-25#1 × *Mi*-1	F6	Beefsteak	XL	Red
TAM-W	TAM-W-205	*Q*2	W-25#2 × *I*-3 *Ty*-3	F6	Round	S	Red
TAM-W	TAM-W-206	*Q*2	W-25#4 × *Mi*-1	F6			
TAM-W	TAM-W-207	*Q*2	W-25#4 × *Mi*-1	F6	Beefsteak	L	Red
TAM-W	TAM-W-208	*Q*1	W-29#3 × LA3473 Plant A	F6	Round	S	Red
TAM-W	TAM-W-209	*Q*2	PI 639208 Black from Tula × LA4440 Plant A	F7	Round	S	Red
USDA	USDA-210	*Q*2	Prospero		Beefsteak	M	Red
TAM-W	TAM-W-211	*Q*2	W-9#1 × *I*-3 *Ty*-3	F6	Beefsteak	M	Red
TAM-W	TAM-W-212	*Q*2	W-9#1 × LA3473	F6	Beefsteak	XL	Red
TAM-W	TAM-W-213	*Q*2	W-9#2 × *Mi*-1	F6	Beefsteak	XL	Red
TAM-W	TAM-W-214	*Q*2	W-9#2 × *Mi*-1	F6	Beefsteak	XL	Red
TAM-W	TAM-W-215	*Q*2	W9#1 × FLA417-8	F6	Beefsteak	L	Red
TAM-W	TAM-W-216	*Q*2	PI 639211 Cherokee Purple × *I*-2 *Ty*-2	F6	Beefsteak	M	Red
USDA	USDA-217	*Q*2	Ailsa Craig		Round	S	Red
TAM-W	TAM-W-218	*Q*2	PI 639211 Cherokee Purple × *I*-2 *Ty*-2	F6	Beefsteak	L	Red
TAM-W	TAM-W-219	*Q*2	PI 639213 Juane Flamme × *I*-3 *Ty*-3	F6	Beefsteak	L	Orange
TAM-W	TAM-W-220	*Q*2	PI 639217 Striped Cavern × *I*-2 *Ty*-2	F6	Heirloom	M	Tiger stripe
TAM-W	TAM-W-221	*Q*2	PI 639217 Striped Cavern × *I*-2 *Ty*-2	F6	Bell pepper	M	Tiger stripe
TAM-W	TAM-W-222	*Q*2	Supersteak#2 × *I*-2 *Ty*-2	F6	Round	L	Red

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TAM-W	TAM-W-223	*Q*2	W-25#2 × *I*-3 *Ty*-3	F6	Beefsteak	M	Red
USDA	USDA-224	*Q*2	Moneymaker		Round	S	Red
TAM-W	TAM-W-225	*Q*2	W-25#2 × *Mi*-1	F6	Beefsteak	L	Red
TAM-W	TAM-W-226	*Q*2	W-25#3 × *Mi*-1	F6	Beefsteak	L	Red
TAM-W	TAM-W-227	*Q*2	W-25#3 × *Mi*-1	F6	Beefsteak	XL	Red
TAM-W	TAM-W-228	*Q*2	PI 639217 Striped Cavern × FLA417-8 Plant A	F6	Heirloom	XL	Red
TAM-CS	TAM-CS-229	*Q*2	AVT1110 × Redline	F6	Cherry	S	Pink
TAM-CS	TAM-CS-230	*Q*2	AVT1001 × Black Tula	F6	Beefsteak	L	Red
USDA	USDA-231	*Q*2	Tres Cantos		Round	M	Red
TAM-W	TAM-W-232	*Q*2	106 × AVT1110 Plant B	F7			
TAM-W	TAM-W-233	*Q*2	106 × AVT1110 Plant C	F7	Round	L	Red
TAM-W	TAM-W-234	*Q*2	1212 × AVT1001 Plant A	F7	Pear	L	Red
TAM-W	TAM-W-235	*Q*2	1212 × AVT1001 Plant A	F7	Beefsteak	L	Red
TAM-W	TAM-W-236	*Q*2	1212 × AVT1001 Plant B	F7	Round	S	Red
TAM-W	TAM-W-237	*Q*2	1212 × AVT1001 Plant B	F7	Beefsteak	S	Red
USDA	USDA-238	*Q*2	Chico Grande		Roma	M	Red
TAM-W	TAM-W-239	*Q*2	1500 × AVT1110	F7	Round	M	Red
TAM-W	TAM-W-240	*Q*2	1680 × AVT1106	F7	Round	M	Red
TAM-W	TAM-W-241	*Q*2	1790 × AVT1001 Plant A	F7	Round	M	Red
TAM-W	TAM-W-242	*Q*2	1790 × AVT1001 Plant B	F7	Beefsteak	M	Red
TAM-W	TAM-W-243	*Q*2	1790 × AVT1001 Plant B	F7	Round	S	Red
TAM-W	TAM-W-244	*Q*2	1790 × AVT1106 Plant A	F7	Roma	M	Red
USDA	USDA-245	*Q*2	Heinz 1350		Beefsteak	M	Red
TAM-W	TAM-W-246	*Q*2	1803 × AVT1001 Plant A	F7	Round	M	Red
TAM-W	TAM-W-247	*Q*2	1803 × AVT1001 Plant B	F7	Round	S	Red
TAM-W	TAM-W-248	*Q*2	1820 × AVT1110 Plant 2	F7	Pear	S	Red
TAM-W	TAM-W-249	*Q*2	1820 × AVT1001 Plant A	F7	Beefsteak	XL	Red
TAM-W	TAM-W-250	*Q*2	1999 × AVT1001 Plant B	F7	Beefsteak	M	Red
TAM-W	TAM-W-251	*Q*2	1999 × AVT1001 Plant B	F7	Round	M	Red
USDA	USDA-252	*Q*2	Heinz 1370		Round	M	Red
TAM-W	TAM-W-253	*Q*2	1999 × FLA417-8 Plant A	F7	Beefsteak	L	Red
TAM-W	TAM-W-254	*Q*2	2015 × AVT1001 Plant A	F7	Beefsteak	L	Red
TAM-W	TAM-W-255	*Q*2	203 × AVT1001 Plant A	F7	Beefsteak	L	Red
TAM-W	TAM-W-256	*Q*2	W12 × AVT1106 Plant A	F7	Roma	S	Red
TAM-W	TAM-W-257	*Q*2	277SBR × AVT1001 Plant A	F7	Round	M	Red
TAM-CS	TAM-CS-258	*Q*2	T5 × NC946 (*Ty*-2, *Sw*-5, *I*-3)	F7	Cherry	S	Pink
USDA	USDA-259	*Q*2	NC 50-7		Beefsteak	L	Red

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TAM-W	TAM-W-260	*Q*2	330 × AVT1106 Plant A	F7	Roma	S	Red
TAM-W	TAM-W-261	*Q*2	330 × AVT1106 Plant A	F7	Round	L	Red
TAM-W	TAM-W-262	*Q*2	330 × FLA417-8 Plant A	F7	Round	M	Red
TAM-W	TAM-W-263	*Q*2	W12 × AVT1001 Plant A	F7	Beefsteak	XL	Red
TAM-W	TAM-W-264	*Q*2	W12 × AVT1001 Plant A	F7	Round	M	Red
TAM-W	TAM-W-265	*Q*2	W12 × AVT1001 Plant B	F7	Beefsteak	XL	Red
USDA	USDA-266	*Q*2	Peto 460		Roma	L	Red
TAM-W	TAM-W-267	*Q*2	W12 × FLA417-8 Plant 1	F7			
TAM-W	TAM-W-268	*Q*2	W4 × AVT1106 Plant 1	F7			
TAM-W	TAM-W-269	*Q*2	W4 × AVT1106 Plant 2	F7	Round	M	Red
TAM-W	TAM-W-270	*Q*2	W4 × AVT1106 Plant 2	F7	Round	M	Red
TAM-W	TAM-W-271	*Q*2	106 × AVT1001 Plant A	F7	Beefsteak	M	Red
TAM-W	TAM-W-272	*Q*2	106 × AVT1106 Plant A	F6	Round	M	Red
USDA	USDA-273	*Q*2	Baxter's Early Bush Cherry		Cherry	XS	Red
TAM-W	TAM-W-274	*Q*2	2015 × AVT1001 Plant B	F7	Heart	S	Red
TAM-W	TAM-W-275	*Q*2	203 × AVT1001 Plant A	F7	Beefsteak	S	Red
TAM-W	TAM-W-276	*Q*2	275SBR × AVT1001 Plant A	F7	Round	S	Red
TAM-W	TAM-W-277	*Q*2	275SBR × AVT1106 Plant A	F7	Round	S	Red
TAM-W	TAM-W-278	*Q*2	277SBR × AVT1001 Plant A	F7	Beefsteak	XL	Red
TAM-CS	TAM-CS-279	*Q*2	T5 × NC946 (Ty-2, Sw-5, I-3)	F7	Roma	S	Red
USDA	USDA-280	*Q*2	NC 8288		Beefsteak	XL	Red
TAM-CS	TAM-CS-281	*Q*2	T5 × NC946 (*Ty*-2, *Sw*-5, *I*-3)	F7	Round	S	Red
TAM-CS	TAM-CS-282	*Q*2	T5 × NC946 (*Ty*-2, *Sw*-5, *I*-3)	F7	Roma	M	Red
TAM-W	TAM-W-283	*Q*2	CLN2498XFLA619y	F9	Roma	M	Red
TAM-W	TAM-W-284	*Q*2	130710 × T55	F8	Beefsteak	XL	Red
TAM-W	TAM-W-285	*Q*2	130710 × T55	F8	Beefsteak	XL	Red
TAM-W	TAM-W-286	*Q*2	130710 × T55	F8	Round	L	Red
USDA	USDA-287	*Q*2	Yellow Peach		Cherry	S	Yellow
TAM-W	TAM-W-288	*Q*2	130710 × T55	F8	Beefsteak	L	Red
TAM-W	TAM-W-289	*Q*2	T11-5-1 × T55	F8	Beefsteak	M	Red
TAM-W	TAM-W-290	*Q*2	PI 639208 Black from Tula × LA4440 Plant C	F8			
TAM-CS	TAM-CS-291	*Q*2	T215 VR × Manyell	F8	Beefsteak	XL	Yellow
TAM-CS	TAM-CS-292	*Q*2	Gold Nugget × T5	F8	Beefsteak	XL	Red
TAM-CS	TAM-CS-293	*Q*2	Black Seaman × T215	F8	Beefsteak	XL	Pink
USDA	USDA-294	*Q*2	Rosa		Heirloom	XL	Pink
TAM-CS	TAM-CS-295	*Q*2	AVT1110 × Redline	F8	Heirloom	L	Pink
TAM-CS	TAM-CS-296	*Q*2	Alamo T13	F8	Heirloom	XL	Pink

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TAM-CS	TAM-CS-297	*Q*1	T215 VR × Manyell	F8	Beefsteak	XL	Red
TAM-CS	TAM-CS-298	*Q*2	Gold Nugget × Sungold	F8	Round	M	Orange
TAM-CS	TAM-CS-299	*Q*2	Estrella × AVT1109	F8	Italian	L	Red
TAM-CS	TAM-CS-300	*Q*2	Gold Nugget × T5	F8	Round	M	Red
TAM-CS	TAM-CS-301	*Q*2	Black icicle × T5	F8	Pear	L	Red
TAM-CS	TAM-CS-302	*Q*2	AVT1110 × Redline	F8	Beefsteak	M	Red
TAM-CS	TAM-CS-303	*Q*1	T135 × Black Tula	F8	Beefsteak	L	Red
TAM-CS	TAM-CS-304	*Q*2	AVT1110 × BL60	F8	Beefsteak	L	Red
TAM-CS	TAM-CS-305	*Q*2	AVT1104 × J & D 7	F8	Cherry	S	Yellow
TAM-CS	TAM-CS-306	*Q*2	AVT 1001 × Black Cherry	F8	Cherry	S	Pink
USDA	USDA-307	*Q*2	Flora-dade		Beefsteak	XL	Red
TAM-CS	TAM-CS-308	*Q*2	AVT 1001 × Black Cherry	F8	Cherry	S	Pink
TAM-CS	TAM-CS-309	*Q*2	Gypsy × T135 VR	F8	Beefsteak	L	Pink
TAM-CS	TAM-CS-310	*Q*2	AVT1104 × J & D 7	F8	Beefsteak	L	Yellow
TAM-CS	TAM-CS-311	*Q*2	AVT1104 × J & D 7	F8	Round	M	Orange
TAM-CS	TAM-CS-312	*Q*2	P278 × AVT 1106	F8	Roma	S	Red
TAM-W	TAM-W-313	*Q*2	AVT1108 × BL100	F9	Round	L	Pink
TAM-W	TAM-W-314	*Q*2	CLN2498XFLA619y	F9	Roma	M	Pink
TAM-W	TAM-W-315	*Q*2	CLN2498XFLA619y	F9	Pear	L	Pink
TAM-W	TAM-W-316	*Q*2	CLN2498XFLA619y	F9	Roma	L	Pink
TAM-W	TAM-W-317	*Q*2	CLN2498XFLA619y	F9	Round	M	Red
TAM-W	TAM-W-318	*Q*2	CLN2498XFLA619y Plant B	F9	Round	S	Red
TAM-W	TAM-W-319	*Q*2	Zapotec × Avt1104	F9	Roma	S	Red
USDA	USDA-320	*Q*2	Pomodoro Superselezione di Marmande		Heirloom	L	Red
TAM-W	TAM-W-321	*Q*2	T75= (WT 501 × Merced) × (T2-25 × CLN2498) F6	F9	Heirloom	M	Pink
TAM-W	TAM-W-322	*Q*1	Zapotec × Avt1104 Plant A	F9	Roma	M	Pink
TAM-W	TAM-W-323	*Q*2	Zapotec × Avt1104 Plant B	F9			
TAM-W	TAM-W-324	*Q*2	CLN2498XFLA619y	F9	Round	M	Red
TAM-W	TAM-W-325	*Q*2	FLA417-8 × FM9	F10	Beefsteak	M	Red
TAM-W	TAM-W-326	*Q*2	FLA417-8 × FM9	F10	Round	L	Red
TAM-W	TAM-W-327	*Q*2	FLA417-8 × FM9	F10	Round	M	Red
TAM-W	TAM-W-328	*Q*2	FLA417-8 × FM9	F10	Round	M	Red
TAM-CS	TAM-CS-329	*Q*2	AVT1104 × J & D 7	F8	Round	M	Orange
TAM-CS	TAM-CS-330	*Q*2	(Merced F6 × (Black Krim × FLA 417-8)	F11	Beefsteak	L	Pink

AVRDC = Asian Vegetable Research and Development Center; TAM-CS = Dr. Kevin Crosby's breeding program at Texas A&M at College Station; TAM-W = Dr. Carlos Avila's breeding program at Texas A&M AgriLife Research and Extension Center at Weslaco, TX; TAM-W = Dr. Paul Leeper's breeding program at Texas A&M AgriLife Research and Extension Center at Weslaco, TX; FLA = Florida tomato breeding program; USDA = United States Department of Agriculture; *Fruit size: XS = extra small, S = small, M = medium, L = large, XL = extra large.

Table S2. Distance Matrix of 322 Genotypes Based on Identified SNPs Markers

https://agrilife.org/avilalab/

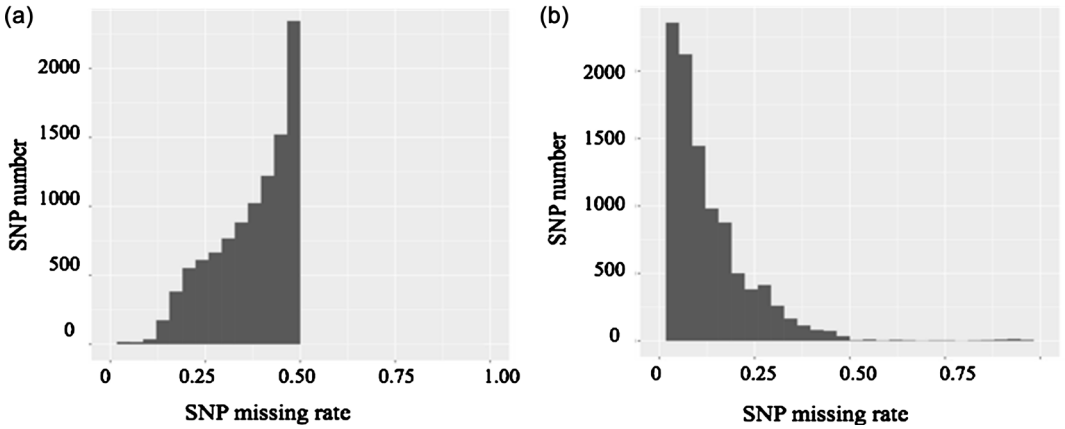

Figure S1. Distribution of the SNP missing rate (a) before imputation and (b) after imputation. SNPs with >50% missing, rare alleles with minor allele frequency (MAF) < 5% across all 322 tomato genotypes, and SNPs with low genotype probability (<0.9) were imputed.

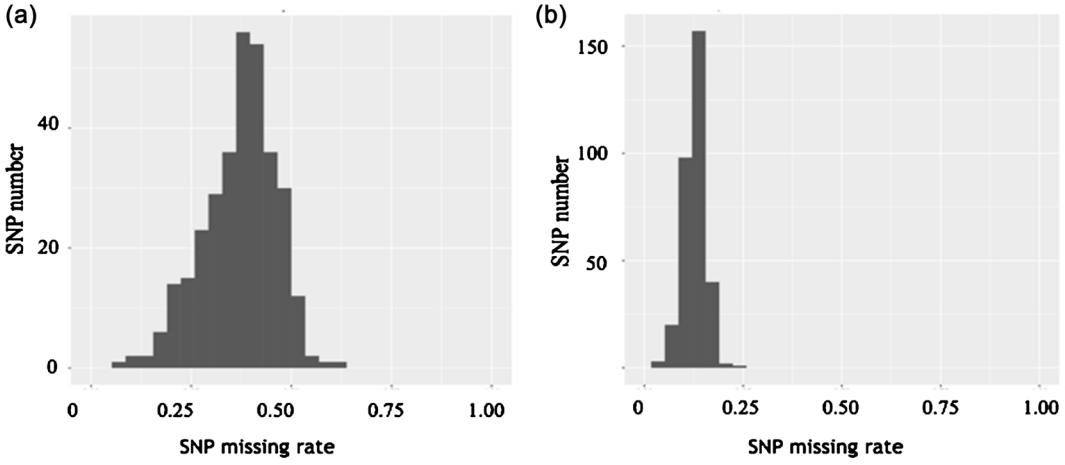

Figure S2. Average missing rate of SNPs across 322 tomato genotypes (a) before imputation and (b) after imputation. SNPs wit > 50% missing, rare alleles with minor allele frequency (MAF) < 5% across all 322 tomato genotypes, and SNPs with low genotype probability (<0.9) were imputed.

Abbreviations

AVRDC = Asian Vegetable Research and Development Center

GBS = Genotyping by Sequencing

HC = Haplotype Caller

MAF = Minor Allele Frequency

PCA = Principal Component Analysis

SNP = Single-Nucleotide Polymorphism

TAMU = Texas A&M University