Genetic Structure and Mixed Linear Model-Based Association Analysis for Morphological Traits in a Collection of Tomato Landraces from Iran and Turkey

M. Henareh¹, B. Abdollahi Mandoulakani²*, A. Dursun³, and K. Haliloglu⁴

ABSTRACT

To extend the genetic base of Iranian tomato germplasm, 93 landraces were collected from the northwest of Iran and East Anatolian of Turkey, along with three commercial cultivars, and their genetic structure were studied using 39 SSR primers. Thirty-five polymorphic SSR loci generated a total of 118 alleles in the studied germplasm. Number of alleles per locus and effective number of alleles averaged 3.37 and 2.47, respectively. Expected heterozygosity of SSRs varied from 0.227 (TMS24) to 0.773 (LEta016), averaged 0.558. The mean number of alleles per genomic-SSRs (3.61) was more than that of EST-SSRs (2.66). Cluster analysis using Neighbour Joining (NJ) method placed 96 tomato genotypes in eight groups. Little congruence was found between NJ dendrogram and geographical distances. Genetic structure analysis of the germplasm using Bayesian method revealed two sub-populations and separated cherry tomatoes from the other landraces and commercial cultivars. Out of the 21 morphological characters, significant (P≤ 0.05) marker-trait associations were found for 18 characters. Each of SSR loci TC11, TC948, and Tom236-237 was associated with three characters. The genetic variability, structure, and markers associated with the studied traits in the current study can be used for planning tomato breeding programs and future studies.

Keywords: Association mapping, Bayesian clustering, Solanum lycopersicum, SSR.

INTRODUCTION

Tomato (Solanum lycopersicum L.), is one of the most economically important and widely cultivated plant in Solanaceae family (Kulus, 2018a). Because of high homozygosity, ease of controlled hybridization, small genome (900 Mbp), lack of gene duplication, and availability of a large number of mutants and genetic resources, tomato has been a good model system for plant genetic studies (The tomato genome consortium, 2012; Kulus, 2018b). Landrace populations are a significant part of genetic variation in crop species and usually characterized by a good stress tolerance and local adaptability (Corrado et al., 2014). Population bottlenecks and both natural and artificial selections occurred during domestication, and new cultivars production have reduced genetic variation in cultivated tomato germplasm (Foolad, 2007; Kulus, 2019). Also, lack of conservation of primary genotypes has caused an overall reduction in the genetic basis of tomato germplasms in the world in recent decades, making it difficult to

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identify polymorphisms between elite germplasm (Sim et al., 2009).

In the last three decades, most of the farmers in northwest of Iran and East Anatolian of Turkey cultivate tomato hybrids introduced from countries such as USA and Italy. Genetic variation of tomato has decreased in both regions during this time period because of the continuous replacement of many landraces by modern tomato cultivars. In recent years, the cultivation of tomato landraces has been significantly increased in Iran and programs have been started for genetic improvement of these genotypes, but the lack of information about their genetic diversity and structure has limited their utilization in breeding programs (Henareh et al., 2015). Globally, several molecular markers have been developed for precise assessment of genetic diversity in plant species, of which Simple Sequence Repeats (SSRs) are the most widely used, because of their polymorphism, reproducibility, and codominant nature (Abdollahi Mandoulakani et al., 2015; Amozaehe, et al., 2015; Emanuelli et al., 2013). The efficiency and usefulness of SSR markers for study of genetic variation in tomato has been demonstrated (He et al., 2003; Garcia-Martinez et al., 2006; Mazzucato et al., 2010; Todorovska et al., 2014).

Polygenic inheritance of the quality-related traits in plants makes their genetic description a very challenging task. The availability of genetic stocks and public databases, the appearance of Next Generation Sequencing (NGS)-based genotyping and the increased exploiting natural genetic variability make association mapping an ideal and reliable strategy to identify genes involved in quantitative variation of complex polygenic traits (Ruggieri et al., 2014; Tranchida-Lombardo et al., 2018). All morpho-physical and fruit quality-related association studies published in tomato to date have stated the usefulness and reliability of this method for dissecting quantitative traits (Mazzucato et al., 2008; Ranc et al., 2012; Shirasawa et al. 2013; Xu et al., 2013; Tranchida-Lombardo et al., 2018).

To extend the genetic base of Iranian tomato germplasm, 93 landraces were collected from northwest of Iran and East Anatolian of Turkey and an investigation was designed to describe the genetic variability of these tomato landraces using SSR markers for providing fundamental information to utilize these genetic resources in tomato breeding programs. Association between fruit quality and morphological traits and SSR markers were also investigated in this collection.

**MATERIALS AND METHODS**

**Plant Materials and Phenotypic Data**

Plant material (Table S1) consisted of 93 tomato landraces (79 from northwest of Iran and 14 from East Anatolian of Turkey) and commercial cultivars Rio Grande, Peto Early CH, and H-2274. The code of each genotype was defined according to the name of the collected geographical origin. The field trial was carried out at Kahriz Station of Agriculture and Natural Resources Research Centre of West Azerbaijan (Urmia, Iran) during 2012 and 2013. To assess the phenotypic diversity, 21 morphological traits (Table 1) were computed based on Union for the Protection Of new Varieties of plants (UPOV) descriptor. Morphological data were averaged for the two years and minimum, maximum, mean, genotypic variance and heritability of the traits were calculated.

**DNA Extraction and SSR Analysis**

Young leaves of each genotype were used to extract genomic DNA using CTAB method (Saghai-Marof et al., 1984). DNA quality and concentration were determined by spectrophotometer (NanoDrop 1000) and 0.8% agarose gel electrophoresis.

Thirty-nine SSR primer pairs (Table 2) (Areshchenkova and Ganal, 2002; He et al., 2003; Bredemeijer et al., 2002; Mazzucato et al., 2010; Garcia-Martinez et al., 2006; Mazzucato et al., 2008; Areshchenkova and Ganal, 1999; Areshchenkova, 2000), were used to assess genetic variability in the
Table 1. Phenotypic diversity among the tomato genotypes.*

<table>
<thead>
<tr>
<th>Trait</th>
<th>Min</th>
<th>Max</th>
<th>Mean</th>
<th>$\sigma^2_g$</th>
<th>h' (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cotyledon leaf length (cm)</td>
<td>3.1</td>
<td>5.2</td>
<td>4.1</td>
<td>0.42**</td>
<td>95.45</td>
</tr>
<tr>
<td>Cotyledon leaf width (mm)</td>
<td>4.6</td>
<td>7.2</td>
<td>6</td>
<td>0.76***</td>
<td>97.43</td>
</tr>
<tr>
<td>Leaf length (cm)</td>
<td>11.3</td>
<td>30.9</td>
<td>23.08</td>
<td>47.43**</td>
<td>99.08</td>
</tr>
<tr>
<td>Leaf width (cm)</td>
<td>6.3</td>
<td>22.1</td>
<td>13.63</td>
<td>21.73**</td>
<td>98.64</td>
</tr>
<tr>
<td>Days to flowering</td>
<td>72</td>
<td>86</td>
<td>79.86</td>
<td>16.65**</td>
<td>69.46</td>
</tr>
<tr>
<td>Flowers/Inflorescence</td>
<td>3.7</td>
<td>7.2</td>
<td>4.82</td>
<td>0.95**</td>
<td>91.34</td>
</tr>
<tr>
<td>Fruit set/Cluster (%)</td>
<td>51.5</td>
<td>95</td>
<td>72.64</td>
<td>165.4**</td>
<td>78.20</td>
</tr>
<tr>
<td>Fruits/Plant</td>
<td>8</td>
<td>143.7</td>
<td>30.35</td>
<td>1697.69**</td>
<td>98.38</td>
</tr>
<tr>
<td>Fruit weight (g)</td>
<td>8.8</td>
<td>232.4</td>
<td>117</td>
<td>7432.66**</td>
<td>99.48</td>
</tr>
<tr>
<td>Days to fruit maturity</td>
<td>113.3</td>
<td>143.8</td>
<td>129.9</td>
<td>56.65**</td>
<td>81.54</td>
</tr>
<tr>
<td>Fruit diameter (cm)</td>
<td>2.1</td>
<td>9</td>
<td>5.9</td>
<td>4.93**</td>
<td>97.82</td>
</tr>
<tr>
<td>Fruit length (cm)</td>
<td>2.5</td>
<td>7.5</td>
<td>5.5</td>
<td>3.49**</td>
<td>97.49</td>
</tr>
<tr>
<td>Days to 50% fruit maturity</td>
<td>136.5</td>
<td>172.8</td>
<td>155.7</td>
<td>99.8***</td>
<td>96.64</td>
</tr>
<tr>
<td>Pericarp thickness (mm)</td>
<td>2.7</td>
<td>8.8</td>
<td>6.05</td>
<td>3.86**</td>
<td>96.74</td>
</tr>
<tr>
<td>Carps/Fruit</td>
<td>2</td>
<td>12.4</td>
<td>4.91</td>
<td>8.18**</td>
<td>97.73</td>
</tr>
<tr>
<td>Seeds/Fruit</td>
<td>40.4</td>
<td>244.5</td>
<td>128.3</td>
<td>5270.41**</td>
<td>97.52</td>
</tr>
<tr>
<td>Fruit peduncle length (cm)</td>
<td>1.7</td>
<td>3.6</td>
<td>2.71</td>
<td>0.3**</td>
<td>88.23</td>
</tr>
<tr>
<td>Total soluble solids</td>
<td>3.4</td>
<td>6.8</td>
<td>5.03</td>
<td>0.77**</td>
<td>95.08</td>
</tr>
<tr>
<td>pH</td>
<td>4.07</td>
<td>4.5</td>
<td>4.28</td>
<td>0.02**</td>
<td>83.33</td>
</tr>
<tr>
<td>Acidity</td>
<td>0.34</td>
<td>1.17</td>
<td>0.652</td>
<td>0.07**</td>
<td>93.33</td>
</tr>
<tr>
<td>Yield/Plant (kg)</td>
<td>1.4</td>
<td>3.3</td>
<td>2.17</td>
<td>0.35**</td>
<td>87.5</td>
</tr>
</tbody>
</table>

* $\sigma^2_g$: Genotypic variance, h': Heritability. ** Significance at 0.01 level of probability.

The genotype of the individuals was scored at each locus according to the length of the amplified SSR bands. To characterize the capacity of each primer for polymorphism detection in the studied germplasm, Number of alleles (Na), Number of effective alleles (Ne), Shannon’s Information index (I) and mean of expected Heterozygosity (He) were calculated for each locus and the entire studied germplasm using the GenAIEx6.5 software (Peakall and Smouse, 2012).

Cluster analysis was performed using MEGA 4 (Tamura et al., 2007) by Neighbour Joining (NJ) method. To investigate the population structure, Bayesian model-based approach was used in the software STRUCTURE 2.3.4 (Pritchard et al., 2000) with the no-admixture model and correlated allele frequencies among populations. The number of subpopulations (k) with 10 independent runs were set from 1 to 20 and burn in period and MCMC iterations, both to 100,000. The mean of Fixation index ($F_{ST}$) values for the clusters obtained from STRUCTURE, were also estimated. STRUCTURE HARVESTER was used to determine the optimal number of k (Evanno et al., 2005; Earl and vonHoldt, 2012).
Table 2. Characteristics of the 35 SSR loci used in the current study.\(^a\)

<table>
<thead>
<tr>
<th>No.</th>
<th>SSR name</th>
<th>Ta</th>
<th>LG</th>
<th>Na(^*)</th>
<th>Na</th>
<th>Ne</th>
<th>I</th>
<th>He</th>
<th>Allele size (bp)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>EST268259 (E)</td>
<td>55</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>1.994</td>
<td>0.692</td>
<td>0.499</td>
<td>122-135</td>
</tr>
<tr>
<td>2</td>
<td>EST245053 (E)</td>
<td>58</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>1.958</td>
<td>0.682</td>
<td>0.489</td>
<td>221-226</td>
</tr>
<tr>
<td>3</td>
<td>TMS63 (G)</td>
<td>58</td>
<td>1</td>
<td>3</td>
<td>3</td>
<td>1.457</td>
<td>0.579</td>
<td>0.314</td>
<td>140-158</td>
</tr>
<tr>
<td>4</td>
<td>TMS24 (G)</td>
<td>54</td>
<td>2</td>
<td>-</td>
<td>3</td>
<td>1.293</td>
<td>0.450</td>
<td>0.227</td>
<td>362-385</td>
</tr>
<tr>
<td>5</td>
<td>TMS2 (G)</td>
<td>54</td>
<td>3</td>
<td>-</td>
<td>4</td>
<td>2.604</td>
<td>1.055</td>
<td>0.616</td>
<td>365-405</td>
</tr>
<tr>
<td>6</td>
<td>TMS8 (G)</td>
<td>55</td>
<td>3</td>
<td>-</td>
<td>2</td>
<td>1.929</td>
<td>0.675</td>
<td>0.482</td>
<td>460-496</td>
</tr>
<tr>
<td>7</td>
<td>TC11 (E)</td>
<td>58</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>1.843</td>
<td>0.650</td>
<td>0.457</td>
<td>95-105</td>
</tr>
<tr>
<td>8</td>
<td>EST259379 (E)</td>
<td>55</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>1.367</td>
<td>0.439</td>
<td>0.268</td>
<td>138-150</td>
</tr>
<tr>
<td>9</td>
<td>TMS22 (G)</td>
<td>56</td>
<td>4</td>
<td>4</td>
<td>3</td>
<td>1.709</td>
<td>0.737</td>
<td>0.415</td>
<td>155-168</td>
</tr>
<tr>
<td>10</td>
<td>TMS39 (G)</td>
<td>58</td>
<td>5</td>
<td>5</td>
<td>3</td>
<td>2.992</td>
<td>1.097</td>
<td>0.666</td>
<td>118-136</td>
</tr>
<tr>
<td>11</td>
<td>TMS37 (G)</td>
<td>55.5</td>
<td>5</td>
<td>6</td>
<td>4</td>
<td>3.141</td>
<td>1.196</td>
<td>0.682</td>
<td>186-201</td>
</tr>
<tr>
<td>12</td>
<td>EST253712 (E)</td>
<td>56</td>
<td>6</td>
<td>4</td>
<td>3</td>
<td>1.879</td>
<td>0.802</td>
<td>0.468</td>
<td>141-156</td>
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<tr>
<td>13</td>
<td>TC1843 (E)</td>
<td>58</td>
<td>7</td>
<td>3</td>
<td>4</td>
<td>2.745</td>
<td>1.037</td>
<td>0.579</td>
<td>528-593</td>
</tr>
<tr>
<td>14</td>
<td>TC948 (E)</td>
<td>58</td>
<td>8</td>
<td>2</td>
<td>3</td>
<td>1.812</td>
<td>0.793</td>
<td>0.448</td>
<td>143-184</td>
</tr>
<tr>
<td>15</td>
<td>EST248494 (E)</td>
<td>59</td>
<td>8</td>
<td>2</td>
<td>2</td>
<td>1.913</td>
<td>0.670</td>
<td>0.477</td>
<td>203-207</td>
</tr>
<tr>
<td>16</td>
<td>TMS29 (G)</td>
<td>55</td>
<td>8</td>
<td>3</td>
<td>3</td>
<td>2.174</td>
<td>0.844</td>
<td>0.540</td>
<td>340-372</td>
</tr>
<tr>
<td>17</td>
<td>Tom236-237 (G)</td>
<td>55</td>
<td>9</td>
<td>3</td>
<td>3</td>
<td>2.378</td>
<td>0.977</td>
<td>0.579</td>
<td>210-255</td>
</tr>
<tr>
<td>18</td>
<td>TMS43 (G)</td>
<td>54.5</td>
<td>9</td>
<td>2</td>
<td>2</td>
<td>1.732</td>
<td>0.614</td>
<td>0.423</td>
<td>332-346</td>
</tr>
<tr>
<td>19</td>
<td>TMS4 (G)</td>
<td>50</td>
<td>10</td>
<td>3</td>
<td>3</td>
<td>2.392</td>
<td>0.978</td>
<td>0.582</td>
<td>225-235</td>
</tr>
<tr>
<td>20</td>
<td>TC461 (E)</td>
<td>56</td>
<td>11</td>
<td>3</td>
<td>4</td>
<td>2.216</td>
<td>1.006</td>
<td>0.549</td>
<td>191-204</td>
</tr>
<tr>
<td>21</td>
<td>TMS42 (G)</td>
<td>54</td>
<td>11</td>
<td>5</td>
<td>3</td>
<td>2.179</td>
<td>0.917</td>
<td>0.541</td>
<td>282-298</td>
</tr>
<tr>
<td>22</td>
<td>TMS52 (G)</td>
<td>53</td>
<td>12</td>
<td>9</td>
<td>5</td>
<td>3.578</td>
<td>1.430</td>
<td>0.721</td>
<td>158-171</td>
</tr>
<tr>
<td>23</td>
<td>TMS9 (G)</td>
<td>53</td>
<td>12</td>
<td>5</td>
<td>5</td>
<td>3.347</td>
<td>1.388</td>
<td>0.701</td>
<td>330-358</td>
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<tr>
<td>24</td>
<td>TMS33 (G)</td>
<td>57.5</td>
<td>12</td>
<td>4</td>
<td>4</td>
<td>3.028</td>
<td>1.203</td>
<td>0.670</td>
<td>257-276</td>
</tr>
<tr>
<td>25</td>
<td>TMS48 (G)</td>
<td>54</td>
<td>12</td>
<td>3</td>
<td>3</td>
<td>2.289</td>
<td>0.904</td>
<td>0.563</td>
<td>178-200</td>
</tr>
<tr>
<td>26</td>
<td>TMS23 (G)</td>
<td>54</td>
<td>12</td>
<td>3</td>
<td>3</td>
<td>2.739</td>
<td>1.053</td>
<td>0.635</td>
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</tr>
<tr>
<td>27</td>
<td>TMS7 (G)</td>
<td>51</td>
<td>12</td>
<td>4</td>
<td>4</td>
<td>2.052</td>
<td>0.788</td>
<td>0.513</td>
<td>161-174</td>
</tr>
<tr>
<td>28</td>
<td>LEta024 (G)</td>
<td>55</td>
<td>-</td>
<td>4</td>
<td>4</td>
<td>2.983</td>
<td>1.213</td>
<td>0.665</td>
<td>170-188</td>
</tr>
<tr>
<td>29</td>
<td>LEta002 (G)</td>
<td>59</td>
<td>-</td>
<td>3</td>
<td>3</td>
<td>2.684</td>
<td>1.034</td>
<td>0.627</td>
<td>198-207</td>
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<tr>
<td>30</td>
<td>LEta003 (G)</td>
<td>61</td>
<td>-</td>
<td>4</td>
<td>4</td>
<td>3.762</td>
<td>1.353</td>
<td>0.734</td>
<td>142-164</td>
</tr>
<tr>
<td>31</td>
<td>LEta019 (G)</td>
<td>58</td>
<td>-</td>
<td>5</td>
<td>5</td>
<td>3.765</td>
<td>1.458</td>
<td>0.734</td>
<td>318-360</td>
</tr>
<tr>
<td>32</td>
<td>LEta020 (G)</td>
<td>58</td>
<td>-</td>
<td>4</td>
<td>4</td>
<td>2.459</td>
<td>1.045</td>
<td>0.593</td>
<td>198-208</td>
</tr>
<tr>
<td>33</td>
<td>LEta012 (G)</td>
<td>60</td>
<td>-</td>
<td>5</td>
<td>4</td>
<td>2.203</td>
<td>0.999</td>
<td>0.546</td>
<td>364-406</td>
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<td>34</td>
<td>LEta002 (G)</td>
<td>59.5</td>
<td>-</td>
<td>4</td>
<td>4</td>
<td>3.826</td>
<td>1.364</td>
<td>0.739</td>
<td>236-255</td>
</tr>
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<td>35</td>
<td>LEta016 (G)</td>
<td>60</td>
<td>-</td>
<td>6</td>
<td>6</td>
<td>4.405</td>
<td>1.579</td>
<td>0.773</td>
<td>208-230</td>
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</table>

<table>
<thead>
<tr>
<th>Mean</th>
<th>Total</th>
</tr>
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<tbody>
<tr>
<td>3.37</td>
<td>118</td>
</tr>
</tbody>
</table>

\(^a\) E: EST-SSR, G: Genomic-SSR, Ta: Annealing temperature, LG: Linkage Group, Na\(^*\): Number of alleles detected in previous studies, Na: Number of alleles, Ne: Effective Number of alleles, I: Shannon’s Information index, He: Mean of expected Heterozygocity.

Association Mapping Analysis

Pair-wise \( r^2 \) between 35 SSR loci and their \( P \)-values (using 1000 permutations) were estimated using TASSEL 3 (Bradbury et al., 2007). This parameter was calculated for each Linkage Group (LG) and for genomic- and EST-SSRs as well. To identify marker-trait associations, Mixed Linear Model (MLM), which incorporates both Q- and kinship (K)-matrices as covariates in the analysis, was used. K-matrix, the matrix of pairwise relationship of genotypes, was estimated based on SSR data using the software TASSEL 3. The Q-matrix was obtained at \( K = 2 \) using STRUCTURE 2.3.4. A threshold for significant associations was adopted at a False Discovery Rate (FDR) of 0.01 using Bonferroni’s correction (Sidák, 1967).
RESULTS

Morphological Analysis

Analysis of variance revealed significant differences ($P \leq 0.01$) and a large range of variation among genotypes for all the characters studied. For example, percentage of fruit set per cluster ranged from 51.5 to 95, number of fruits per plant from 8 to 143.7, fruit weight from 8.8 to 232.4 g, Total Soluble Solids (TSSs) from 3.4 to 6.8 and yield per plant from 1.4 to 3.3 kg. The heritability varied from 68.5% for days to flowering to 99.48% for fruit weight (Table 1).

Genetic Diversity

Out of the 39 SSR loci used for germplasm genotyping, 35 loci (89.74%) generated 118 alleles (Table 2). Loci TC1107 and EST258529 amplified monomorphic banding pattern and loci TMS35 and TMS60 failed to yield PCR fragments. The number of alleles per locus ranged from 2 (EST268259, EST245053, TMS8, TC11, EST259379, EST248494 and TMS43) to 6 (LEta016), averaged 3.37. Size of the allele fragments varied from 95 (TC11) to 593 bp (TC1843). The minimum and maximum of Ne, I, and He were observed for loci TMS24 and LEta016, respectively. These parameters in the studied landraces averaged 2.47, 0.963, and 0.558, respectively.

Cluster Analysis

Cluster analysis using NJ method placed 96 genotypes in eight groups (Figure 1). Out of the 16 landraces located in the first group, eight were from two adjacent regions of Piranshahr and Sardasht. Three commercial cultivars were placed in the second group in the vicinity of each other. Most of the landraces originating from Urmia were located in cluster IV. Cherry tomato landraces constituted 45.5 and 85.7% of the landraces in groups V and VII, respectively. Landraces collected from Iğdır (Turkey) distributed in different clusters.

Population Structure

Inferring the appropriate number of clusters using STRUCTURE HARVESTER.
showed the highest peak at $k=2$ (Figure S1), suggesting two genetically distinct groups in the analyzed tomato germplasm (Figure 2). $F_{ST}$ values of the groups were 0.13 and 0.20, respectively.

Following setting the number of clusters to two, inferred ancestry estimates of genotypes (Q-matrix) was obtained for the subpopulation using STRUCTURE output (Table S2). Model-based clustering put cherry tomatoes in group I and separated them from the remaining landraces. Of the eight tomato landraces from Sardasht, seven were cherry tomatoes (group I). A lot of landraces originating from the divers geographical locations along with commercial cultivars were placed in cluster II.

### LD Decay and Association Mapping Analysis

The LD extent ($r^2$) in the studied germplasm (Figure 3) ranged from 0.001 (LG 5) to 0.057 (LG 12), averaging 0.018. LD extent for genomic-SSRs (0.019) was slightly more than that of EST-SSRs (0.011).

Out of the 21 studied traits, associated markers were found for 18 traits (Table 3). Seven markers (29.16%), out of the 24 associated markers, were EST-SSRs. No linked SSR markers were detected for cotyledon leaf width, days to flowering, and fruit weight. Only one associated marker was identified for each trait of leaf length and width, carpel numbers in fruit, seed numbers in fruit, TSS, and yield. The most number of the associated markers (five markers) were found for pericarp thickness, three markers on LG 12 (year 2012) and two markers on LGs 4 and 8 (year 2013). All three markers associated with cotyledon leaf length in both years were common. The identified associated markers for all traits (except for pericarp thickness) were on different LGs. Two out of the three markers associated with each trait fruit set/cluster and fruit length were the same in both years. Marker LEta016 was associated with number of days to 50% fruit maturity in both years and explained 15.3 and 14.7% of the variation of this trait in 2012 and 2013, respectively. Marker LEta020 showed significant association with TSS only in 2012 and illustrated 12.1% of its variation. Markers EST259379, TMS29, LEta020 and EST253712 were associated with pH and markers TMS63 and TMS7 were associated with acidity. Marker TMS23 on LG 12 revealed significant association with yield and explained 9.5% of the yield total variation. Marker TC11 was associated with cotyledon leaf length, days to fruit maturity, and days to 50% fruit maturity. Associated markers Tom236-237 were common for fruit set/cluster, days to fruit maturity, and fruit peduncle length. Marker TMS7 was also associated with fruits/plant, fruit length and...

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**Figure 2.** A Bayesian model-based clustering of the analyzed landraces demonstrated the occurrence of two clusters within the tomato germplasm based on 35 SSR loci. Bar colours and lengths represent inferred clusters and Q, respectively, identified by STRUCTURE for $K=2$. 1072
Figure 3. Linkage Disequilibrium (LD) values ($r^2$) throughout the tomato genome. Markers were ordered on the x and y axes. Marker numbers corresponded to Table 2. Each cell of the heat map represents a single marker pair. The $r^2$ values for each marker pair are on the top half of the heat map and are represented from 0.0 (white) increasing equal increments of 0.1 to 1.0 (red). The $P$-values of each $r^2$ estimate are on the bottom half of the heat map and are represented from non-significant ($P > 0.05$; white) to highly significant ($P < 0.0001$; red).

Table 3. List of the markers linked to various traits and their $R^2$ and associated $P$-values. $^a$

<table>
<thead>
<tr>
<th>Marker</th>
<th>LG</th>
<th>2012 $R^2$</th>
<th>$P$-value</th>
<th>2013 $R^2$</th>
<th>$P$-value</th>
<th>Days to 50% fruit maturity</th>
<th>2012 $R^2$</th>
<th>$P$-value</th>
<th>2013 $R^2$</th>
<th>$P$-value</th>
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<td>Cotyledon leaf length</td>
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<td>0.038</td>
<td>0.062</td>
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<td>0.040</td>
<td>0.147</td>
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<td>0.021</td>
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<td>-</td>
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<td>0.044</td>
<td>0.089</td>
<td>0.026</td>
<td>Leaf length</td>
<td>0.089</td>
<td>0.014</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Leaf width</td>
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<td>-</td>
<td>-</td>
<td>0.046</td>
<td>0.033</td>
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<td>0.023</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
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<td>0.099</td>
<td>0.010</td>
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<td>Flowers/Inflorescence</td>
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<td>-</td>
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<td>0.092</td>
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<td>TMS23</td>
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<td>Fruit diameter</td>
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<tr>
<td>Fruit length</td>
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<td>0.009</td>
<td>0.068</td>
<td>0.041</td>
<td>TMS37</td>
<td>0.119</td>
<td>0.009</td>
<td>0.068</td>
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$^a$LG: Linkage group.
acidity. Markers TMS37, TMS48, TMS43, TMS39, TMS23, EST259379 and LEta020 were found to be associated each with two traits.

DISCUSSION

Generally, genetic diversity in plants detectable by molecular markers depends on the reproduction mode, the domestication history, and the size of the analyzed samples. First studies with molecular markers have clearly indicated low level of genetic diversity in the cultivated tomato germplasm in contrast to other self-pollinating species (Williams and Clair, 1993). High numbers of alleles per polymorphic SSR locus (8.5) were reported for several wild tomato accessions (Alvarez et al., 2001) while cultivated tomato germplasm generated values close to 2.5 (He et al., 2003; Tam et al., 2005). Early studies also indicated that traditional cultivars from South America maintained more genetic diversity than modern tomato cultivars (Williams and Clair, 1993).

The number of alleles per locus in our study averaged 3.37. The Ne, I, and He in the landraces averaged 2.47, 0.963, and 0.558, respectively. In a genetic diversity study of 30 tomato genotypes using 25 SSR loci, Dhaliwal et al. (2011) reported a value of 2.86 for average number of alleles per locus. In assessment of genetic diversity in 61 accessions of Italian cultivated tomato using 29 SSRs, He was recorded 0.44 (Mazzucato et al., 2008). The high number of alleles per locus and He detected in our study may be due to the wide geographical regions of the collection sites and high numbers of the studied landraces. The less number of alleles per locus, found for EST-SSRs compared to genomic SSRs, might be attributed to the the intensive protection of sequences and low frequency of mutation in coding regions of the genome (Ellis and Burke, 2007; Zeng et al., 2010). In diversity assessment of 36 Gossypium species using 20 genomic- and 27 EST-SSRs, the average number of alleles per locus was 2.33 and 3.6, respectively (Tabbasam et al., 2014).

Grouping obtained with NJ cluster analysis was not in concordance with geographical distances of the landraces and did not give a reasonable category. This might be due to the gene flow among regions, even in two countries (Iran and Turkey). Despite having genotypes with different fruit shape, genetic structure analysis divided the studied germplasm into two genetically distinct groups. F_\text{ST} (a measure of population differentiation due to genetic structure) value of the groups was 0.13 and 0.20, respectively. F_\text{ST} values of 0 and 1 show non-differentiation and perfect differentiation between an original population and its sub-populations, respectively. The F_\text{ST} range from 0 to 0.05 indicates small genetic differentiation, the ranges from 0.05 to 0.15, 0.15 to 0.25, and above 0.25 exhibits moderate, large, and very large genetic differentiation, respectively (Cho et al., 2008). Nevertheless, in our study, genetic variation in sub-populations 1 and 2 were moderate and large, respectively.

Population structure analysis separated cherry tomatoes from the remaining genotypes. In study of 48 Spanish tomato genotypes using 19 SSRs and 7 AFLPs (Garcia-Martinez et al., 2006) and 35 Brazilian cultivars and landraces using 20 RAPDs (Carelli et al., 2006), similar results were also obtained. Cherry tomatoes have small fruits, characterized by small leaves and flowers, a lot of flowers and fruits per plant, a lot of seed per fruit and high vegetative growth. These characters can be found in S. pimpinellifolium. The investigations have demonstrated that the genome of S. lycopersicum var. cerasiforme is a mixture of S. lycopersicum and S. pimpinellifolium genomes due to the frequent hybridizations between these species (Nesbitt and Tanksley, 2002; Ranc et al., 2008). These reasons may explain why cherry tomatoes constituted a separate cluster.

SSR markers used in our study were applied to identify marker-trait associations. In the recent years, association mapping has been widely used to identify candidate genes affecting complex quantitative traits (Hall et
al., 2010). Unbiased estimation of LD and population structure in the used collection are the prerequisites of the association mapping studies (Fusari et al., 2008). LD over genetic distance is high in tomato and decayed at 6-8 cM within 102 tomato varieties, 6-14 cM within 39 processing varieties, and 3-16 cM within 24 fresh market varieties (Robbins et al., 2011). The low level of LD (0.018) was observed in the whole collection in the current study, although more SSR markers with enough genome coverage are needed to have a thorough estimation of the r².

The results of association mapping studies were influenced by a number of factors including type and size of mapping population, traits examined, number of environments and years used for phenotyping, and type and genome coverage of molecular markers (Ruggieri et al., 2014). As previously reported for tomato (Ranc et al., 2012), the size of our tomato collection was enough for association mapping studies. The population used in our study represented a huge amount of diversity for most of the traits targeted. To identify associated markers with low level of interactions with environment, phenotyping was performed in two years, although more phenotyping data over several years and environments are needed for identification of reliable associated markers for further breeding programs.

Since previous investigations demonstrated the high efficiency of the MLM method in detecting false associations in tomato populations (Ranc et al., 2012), this model was used in our study and identified 24 associated markers for 18 traits. Markers Leta016 (R² = 15.3%) and TMS37 (R² = 14.7%) (associated with days to 50% fruit maturity and cotyledon leaf length, respectively) would be interesting for marker-assisted selection because of the high R² values and stability in both years. Markers TMS7 and TMS39 were highly associated (P = 0.009) with fruit length and carpels/fruit, respectively. The highly significant associated markers showing a great effect on targeted traits might be appropriate candidates for future marker-assisted selection programs, although such markers should be validated in different mapping populations or germplasms. Three markers associated with cotyledon leaf length and two out of the three markers associated with fruit set/cluster and fruit length were similar in both years. Marker Leta020 with a R² value of 12.1% had significant association with TSS only in 2012. Markers EST259379, TMS29, Leta020 and EST253712 were associated with pH and markers TMS63 and TMS7 were associated with acidity. In contrast to our investigation, Mazzucato et al. (2008) reported that EST253712 was associated with fruit weight, locule number and inflorescence type. They also indicated association between TMS63 and fruit shape. This probably suggests the pleiotropy effects of these SSR loci. Marker TC11 showed to be significantly associated with cotyledon leaf length, days to fruit maturity and days to 50% fruit maturity. Significant association was also detected between marker TC948 and leaf width, fruit diameter and pericarp thickness. Positive significant correlation has been already reported among these traits (Henareh et al., 2016). Associated marker Tom236-237 was common for fruit set/cluster, days to fruit maturity, and fruit peduncle length. In another investigation, this marker was significantly associated with green shoulder (Mazzucato et al., 2008). Several other markers such as TMS7, TMS37, TMS48, TMS43, TMS39, TMS23, EST259379 and Leta020 were found to be associated each with more than one trait. The pleiotropic effects of the same genes or genetic linkage could be the reasons of such co-localized associations, as previously shown for QTLs (Lecomte et al., 2004).

In conclusion, phenotypic evaluation on the 21 studied traits revealed a broad phenotypic variability within the tomato collection investigated. Population structure analysis clearly differentiated cherry tomato landraces from the remaining ones, but grouping of tomato landraces was not in congruence with their geographical information. This study revealed that tomato landraces grown in these regions have maintained enough genetic diversity that would be valuable for utilization in tomato breeding programmes. These
Table S1. Description of the tomato landraces used in the current study.

<table>
<thead>
<tr>
<th>Code</th>
<th>Fruit size</th>
<th>Fruit shape</th>
<th>Origin</th>
<th>Longitude (°)</th>
<th>Latitude (°)</th>
</tr>
</thead>
<tbody>
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<td>L</td>
<td>Obl</td>
<td>I-U</td>
<td>45 14</td>
<td>37 32</td>
</tr>
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<td>I-U</td>
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<td>37 30</td>
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<td>37 30</td>
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<td>I-U</td>
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<td>37 26</td>
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<tr>
<td>IRU5</td>
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<td>Ci</td>
<td>I-U</td>
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<td>37 30</td>
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Table S2. The estimated cluster membership coefficients of tomato landraces obtained with STRUCTURE software at K=2.

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Figure S1. Estimation of the optimum number of sub-populations for tomato genotypes according to the Evanno’s method. The graph shows DeltaK for each K value.

landraces are well adapted to the growing environments of the collection sites and stresses, therefore, we suggest to replace some modern cultivars by elite landraces. The association mapping approach used allowed detection of 24 SSRs associated with 18 traits. The use of the markers highly associated with a given trait in both years could be a valuable starting point for marker-aided selection. The findings suggest that use of SSR markers and a highly valid statistical model (MLM) are appropriate for identification of the associations with the traits targeted. In addition, identified SSRs could be exploited as markers aiming the specific-interest traits for assisted selection in tomato breeding programs. A further validation and confirmation of the markers in a different set of accessions or mapping populations would be in any case necessary.

ACKNOWLEDGEMENTS

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REFERENCE


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زمینه تحقیق
گوجه فرنگی را در هشت گروه قرار داد. همگرایی کمی بین گروه‌هایی حاصل تجزیه خوشه‌ای، Bayesian جغرافیائی ارقام وجود داشت. تجزیه ساختار زنیکی با استفاده از روش مورفولوژیکی مورد مطالعه را به دو گروه تقسیم کرد. ارقام گوجه فرنگی های ریز (چری) را از سایر ارقام محلی و تجاری متمایز کرد. متوسط شاخص تثبیت (FST) برای دو گروه 13/0 و 2/0 بود. از 21 صفت (SSR) ارتباط معنی‌داری (P≤0/05) نشان دادند. نشانگرهای Tom236، TC948، TC11، TC948 و 237-236 حاصل از مطالعه تنوع و ساختار زنیکی و نشانگرهای پیوسته محاسبه‌شده در این تحقیق، در طراحی برنامه‌های اصلاحی گوجه فرنگی و در مطالعات آینده مورد استفاده قرار گیرد.