Salinity is one of the major limitations on plant growth and productivity throughout the world. Damage caused to plants by high salinity is observed as either loss of plant productivity or plant death. Water sources on earth contain 30 g of sodium chloride per liter so earth could be said to be a salty planet (Foolad 2007). Although soil salinity existed long before humans and agriculture, the problem is now increasing at a rate of 10% annually (Flowers 2004, Foolad 2007). With the increase of soil salinity over the years, it’s expected that by 2050, more than 50% of the land available for agriculture will be lost because of salinity (Hasanuzzaman et al. 2014). Salinity negatively affects crop productivity and quality. Thus, there is a growing need to produce crops that are salt-tolerant using a wide range of methods that have been extensively tested (Zhang et al. 2014). The tomato (Solanum lycopersicum L.), belonging to the Solanaceae family, is one of the most important vegetables being widely grown in both fields and under protected cultivation. In spite of its broad distribution, tomato production has been limited due to high salinity level of the soil or of the irrigation water (Zhai et al. 2015). Most tomato cultivars are sensitive to moderate levels of salinity (Singh et al. 2012). Indeed, all plant development stages, including seed germination, vegetative growth and reproduction, show salt stress sensitivity, that leads to poor harvests and reduced economic yield (Zhang et al. 2014). Tomato is considered as a vegetable model and has thus been subjected to molecular investigation resulting in abundant genomic information (http://solgenomics.net/). This includes the complete reference genome from which many molecular markers have been developed and used for the genetic analysis of accessions (Benor et al. 2008, Cao et al. 2015, Park et al. 2004, Zhou et al. 2015a, 2016). Over the past few years, DNA-based markers such as SSR (simple sequence repeats) markers have been developed as valuable tools for crop management and improvement. The high potential of SSR markers includes their high numbers in genomes, their high level of polymorphism, the codominance of alleles, and their arbitrary distribution throughout the genome (Kumar et al. 2015, Morgante et al. 2002). Development of SSR markers.
based on QTL or candidate genes related to an important agronomic trait is useful in marker-assisted breeding programs for the concerned trait. In line with this, SSR markers were combined with morphological traits to assess the genetic diversity of cultivated and wild tomatoes (Zhou et al. 2016). To our best knowledge, no study has been conducted to determine the molecular markers associated with salinity tolerance in Tunisian tomato varieties. Consequently, in the present study, we aimed at evaluating phenotypic behavior in a collection of 20 commercial tomato varieties submitted to salt stress and at analyzing genetic variation as well as population structure. We successfully exploited SSR data to perform marker salt trait associations. We built an integrative multi-layer network linking the most discriminating SSR loci and genotypes to phenotypes scored under salt stress. This integrative network provides genotype-phenotype associations that could be taken into account for tomato breeding programs to improve salt tolerance.

**Materials and Methods**

**Plant materials**

We used the most commonly cultivated tomato genotypes by Tunisian growers as plant material. They correspond to three TYLCV-tolerant lines (Ilanero, Romelia and San Miguel; Mejia et al. 2002, Vidavsky and Czosnek 1998) and 17 local genotypes corresponding to F1 hybrids (Hypeel HF1, Perfectpeel HF1, Mouna HF1) and to varieties (Heinz61, Pomodoro, Market Wonder, Frienz, Rio grande, Marmande Vr, Oxheart, USA gris, Chebli, Californie, Saint Peter, Heinz 1350, Sakata and Ventura). 10 Seeds of each were surface sterilized with a 0.5% NaCl solution then rinsed with water and incubated in Petri dishes on moist sterile filter paper at 27°C in darkness until the emergence of the radicle. Two days later, tomato seedlings were transferred to hydroponic tanks, each one containing 10 L of half-strength modified Hoagland solution (Epstein 1972). These hydroponic solutions were vigorously aerated and renewed every 2 days during the growing period. Plants were grown in an environmentally controlled chamber at 25°C/18°C, day/night with a 16-h light/8-h dark cycle at 40–50% relative humidity.

**Screening tomato varieties under salt**

Plants with four fully developed true leaves were individually transferred into plastic pots (30 cm of diameter) containing a mixture of peat and sand then irrigated with one-half Hoagland solution supplemented with 150 mM NaCl (15 dS/m, pH 7.5). Salt treatment was initiated with 50 mM of NaCl solution (6 dS/m), increased to 100 mM (12 dS/m) on day two and finally to 150 mM (15 dS/m) on day three. We used three biological replicates for each of the 20 varieties. Each replica consisted of a pool of 10 plants. A set of three plants for each genotype was growing in a non-saline conditions and watered with the nutrient solution. Three weeks later, salt-treated plants were evaluated for salt tolerance, based on their visual phenotypes comparing to watering control plants. Plants were rated for severity of salt susceptibility according to the salt scale established by Chookhampaeng et al. (2007).

**DNA extraction and Simple Sequence Repeat (SSR) assays**

Total DNA was extracted from 0.2 g of mature leaves according to the DNAeasy Plant Mini Kit (Qiagen). DNA quantification was performed with ND-1000 spectrophotometer (Nanodrop Technologies, USA). Twenty-five microsatellite markers were selected based on their previous use and their wide distribution through the tomato genome (https://solgenomics.net/search/markers, Villalta et al. 2007). Amplifications were carried out using PCR conditions described by Villalta et al. (2005).

**Allele scoring**

For each microsatellite marker, PCR-amplified bands were identified and scored by the Experion™ System (Automated Electrophoresis Station). Out of the 25 tested SSRs, 19 were highly informative and were selected for subsequent analysis. Data was used for genetic diversity, population structure and genotype-phenotype association network.

**Genetic diversity and analysis**

Based on the SSR profiles defined within the collection of tomato varieties, genetic diversity parameters such as the average number of alleles per locus (Na) and of genotypes (Nc), the major allele frequency (MAF), the observed (He) and the expected (Hs) heterozygosities were calculated using PowerMarker V3.23 software package (Liu 2002). Polymorphism information content (PIC) per each locus was calculated according to the equation described by Botstein et al. (1980). Principal coordinate analysis (PCA) was carried out to assess the partitioning of the genotypic variability at the population level. Population structure was estimated and the maximum likelihood and DK were used to calculate the number of subpopulations (K). Tomato genotypes were assigned to groups with a high threshold stringency of membership probability. All these analyses were performed using the R-PACKAGE version 3.0.1 (R-Development-Core-Team, Foundation for Statistical Computing, Vienna, Austria, 2013).

**Genotype discriminating network**

A network was generated by Cytoscape v3.0.2 (Cline et al. 2007) to set up associations between SSR alleles with tolerant, mildly tolerant and sensitive tomato genotypes. The algorithm MCODE28 from the Cytoscape Plug in Cluster Maker was then used to partition the network into layers where the most discriminating loci with corresponding alleles and phenotypes were linked. We removed modules that straddled loci shared by the different phenotypic groups in order to select only discriminating genotypes which contributed to population structure.
Results

Phenotyping for salinity tolerance

A collection of twenty tomato varieties was used for screening salinity tolerance. Differences among the phenotypes became appreciably visible and were progressively more pronounced three weeks post salt stress imposition. Taking into account 10 seedlings for each genotype, visual rating of salinity tolerance was meticulously recorded according to salt scale susceptibility (Chookhampaeng et al. 2007). This allowed varieties to be assorted in three groups corresponding to tolerant, moderately tolerant and sensitive genotypes. Salt-tolerant genotypes (Romelia, Llanero and San Miguel) were easily distinguishable since they displayed normal growth in spite of a few leaves being rolled and yellowed but not wilting. Mildly tolerant varieties (Heinz 1350 and Perfect peel HF1) showed a nearly normal growth with leaves slightly rolled, yellowed and sometimes wilting. The sensitive group (Mouna HF1, Heinz61, Market Wonder, Frientz, Rio grande, Marmande Vr, Oxheart, USA gris, Chebli, Hypeel HF1, Californie, Saint Peter, Ventura, Pomodoro and Sakata) showed typical symptoms of salt injury such as yellowing, leaf drying, rolling, tip whitening, reduction of the leaf area with the leaves always wilting (Fig. 1). The Pomodoro variety showed a behavior close to that of the moderately tolerant group with the younger leaves partly wilt (Fig. 2A). It can be considered as a mildly sensitive genotype. Within the highly sensitive Mouna HF1

Fig. 1. Behavior of tomato genotypes under salt stress conditions. A, tolerant, B mildly tolerant and C, sensitive genotypes.
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The average expected heterozygosity (He) was 0.475, from 0.4, revealing a wide genetic diversity. Over all SSR loci, 356, SSR 285, SSR 19 and CT 167), with an average value of 0.43.

A set of tomato genotypes, consisting of three salt clusters (tolerant, mildly tolerant and susceptible) was used. The 19 selected primers gave clear polymorphic patterns generating a total of 70 alleles with an average of 3.68 alleles per locus (Table 1). The PIC value denoting allelic diversity and frequency among genotypes ranged between 0.82 (SSR 356) and 0.22 (SSR 26, SSR 92, TG 35 and SSR 66) with an average value of 0.43. Allele size varied from 119 bp at the locus TG 69 to 788 bp at the locus CT 167. The observed heterozygosis (H o) ranged from 0.0 for a group of markers (SSR 9, SSR 344, SSR 22, TG 48, SSR 24, SSR 26, SSR 92, SSR 136, TG 35, SSR 66) to 1 (SSR 356, SSR 285, SSR 19 and CT 167), with an average value of 0.4, revealing a wide genetic diversity. Over all SSR loci, the average expected heterozygosity (H e) was 0.475, ranging from 0.84 (SSR 356) to 0.255 (SSR 66, SSR 26, TG 35 and SSR 92) (Table 1). For overall representation of diversity, principal coordinate analysis (PCA) involving test-bed tomato genotypes was performed on SSR data (Fig. 3). The first axis explained 48.1% of the total variation whereas the second one explained 18% of the total variation. Dispersion of tomato varieties revealed a particular panel overlapping two mainly distinct clusters without a single intermixing. The two clusters corresponded to salt tolerant and salt sensitive genotypes. PCA further showed a scattered distribution of the two moderately tolerant genotypes as well as the Pomodoro sensitive genotype, although they were particularly well differentiated from the rest. The Pomodoro variety, that showed symptoms relatively milder than the sensitive genotypes, was quite close to the moderately tolerant Heinz 1350 variety. Hence, this result based on SSR markers reinforces the clustering of tomato genotypes according to their behavior in salt stress.

Structure analysis

Based on 19 SSR markers, the population structure of the tomato genotypes was estimated using R-PACKAGE version 3.0.1. The optimum K value was determined and the highest peak was observed at delta K = 3. Maximum likelihood and DK were used to calculate the number of subpopulations (K), with varieties falling into three subgroups. Using a membership probability threshold of 0.817, the three-salt tolerant genotypes were assigned to group 1 (red), the two moderately tolerant genotypes to group 2 (green) and the sensitive genotypes, including Pomodoro variety, to group 3 (blue) (Fig. 4). It is worth to note that Pomodoro genotype is the only accession that showed two genetic backgrounds (blue and green). Overall, these results further indicated that the population structure assigned by the R software analysis is correlated to salt stress behavior of genotypes.

Discrimination genotype network

The Cytoscape v3.0.2 program was used to generate a phenotype-genotype association network based on saline scale classes and SSR data (Fig. 5). Out of 19 involved markers, 8 loci combinations, leading to 23 distinct genotypes were highly discriminative. Five loci combinations with corresponding alleles permitted to unambiguously

Table 1. Genetic diversity parameters calculated for the 19 tested microsatellite loci

| Locus | Nr | Sr | MAF | Na | He  | Ho  | PIC |
|-------|----|----|-----|----|-----|-----|-----|
| SSR 356 | 7  | 279–973 | 0.30 | 9  | 0.84 | 1   | 0.82 |
| SSR 285 | 5  | 257–675 | 0.48 | 7  | 0.76 | 1   | 0.56 |
| TG 69   | 5  | 119–640 | 0.35 | 5  | 0.6287 | 0.95 | 0.68 |
| SSR 30  | 4  | 206–213 | 0.55 | 5  | 0.665 | 0.9 | 0.56 |
| SSR 63  | 4  | 228–307 | 0.35 | 4  | 0.725 | 0.7 | 0.72 |
| SSR 9   | 4  | 234–244 | 0.43 | 4  | 0.345 | 0   | 0.61 |
| SSR 344 | 4  | 348–721 | 0.80 | 4  | 0.615 | 0   | 0.33 |
| SSR 43  | 4  | 312–491 | 0.83 | 4  | 0.3063 | 0.05 | 0.29 |
| SSR 22  | 3  | 150–210 | 0.55 | 3  | 0.335 | 0   | 0.37 |
| TG 48   | 3  | 350–361 | 0.80 | 3  | 0.265 | 0   | 0.30 |
| SSR 19  | 2  | 178–213 | 0.33 | 4  | 0.7275 | 1   | 0.68 |
| SSR 24  | 2  | 247–512 | 0.80 | 2  | 0.32  | 0   | 0.27 |
| SSR 26  | 2  | 502–522 | 0.85 | 2  | 0.255 | 0   | 0.22 |
| SSR 92  | 2  | 155–163 | 0.85 | 2  | 0.255 | 0   | 0.22 |
| SSR 136 | 2  | 175–200 | 0.80 | 2  | 0.32  | 0   | 0.27 |
| TG35    | 2  | 286–296 | 0.85 | 2  | 0.255 | 0   | 0.22 |
| CT 167  | 2  | 150–788 | 0.40 | 4  | 0.66  | 1   | 0.60 |
| SSR 66  | 2  | 181–186 | 0.85 | 2  | 0.255 | 0   | 0.22 |

Mean: 3.32 – 0.63 – 3.78 – 0.475 – 0.4 – 0.43

N_a, Number of alleles per locus, N_G, number of genotypes per locus, S_R, Size range of alleles. MAF, Major Allele Frequency, H_e, observed Heterozygosity, H_o, observed Heterozygosity, PIC, Polymorphism Information Content, P value (0.02403) < 0.05.

Fig. 2. Diversity in the salt stress sensitivity of two sensitive genotypes belonging to scale class 3. A, Pomodoro, the mildly sensitive genotype, displayed wilting of older leaves. B, Mouna HF1, the highly sensitive genotype, showed premature senescence and death (Fig. 2B).

Genetic diversity

Out of the 25 SSR markers used to characterize the genetic diversity of tomato genotypes, 6 were monomorphic and were excluded from analysis. 19 markers were subsequently selected for their reproducibility and allele richness. 2 sets of tomato genotypes, consisting of three salt clusters (tolerant, mildly tolerant and susceptible) was used.

The Cytoscape v3.0.2 program was used to generate a particular panel overlapping two mainly distinct clusters without a single intermixing. The two clusters corresponded to salt tolerant and salt sensitive genotypes. PCA further showed a scattered distribution of the two moderately tolerant genotypes as well as the Pomodoro sensitive genotype, although they were particularly well differentiated from the rest. The Pomodoro variety, salinity suppressed growth of the leaves leading to the complete cessation of growth in the whole plant, premature senescence and death (Fig. 2B).

Fig. 4. Discrimination genotype network based on saline backgrounds (blue and green). Overall, these results further indicated that the population structure assigned by the R software analysis is correlated to salt stress behavior of genotypes.

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separate out tolerant cultivars from the rest. These combinations corresponded to SSR 22 (210/210) and TG 69 (344/640), SSR 22 (210/210) and TG 69 (124/124), SSR 26 (502/502) and TG 35 (286/286), SSR 92 (155/155) and CT 167 (300/788), SSR 63 (242/242) and SSR 344 (348/348).

The Pomodoro salt-sensitive variety shares SSR combinations corresponding to SSR 26 (522/522) and TG 35 (296/296), SSR 92 (163/163) and CT 167 (150/700) as well as SSR 344 (681/681), and TG 69 (124/529) loci with the mildly tolerant Heinz 1350 variety and thus, both seem to have a common genetic background. This could explain why these two varieties were close to each other in the PCA analysis. Linking genotypes to salt-stress behavior may provide strategies for targeting valuable markers to introgress in commercial varieties to improve tomato salt tolerance.

**Discussion**

**Evaluation of tomato genotypes under salt stress**

Despite the agricultural importance of tomato in Tunisia,
little is known about the adverse effect of salt stress on currently cultivated genotypes. Indeed, knowledge about contrasting lines is crucial to avoid close genetic relationship between parental cultivars for efficient selection in segregating populations. This can be achieved through phenotypic assortment of genotypes for salt response. Therefore, a collection of 20 tomato varieties, the most cultivated by Tunisian growers because of their valuable agronomic traits was used. Screening for salt tolerance was carried through hydroponic assays in a controlled environment. This method is the most easy, simple and economical for efficient genotype screening for such abiotic stress (Singh et al. 2016). With regard to the increasing degrees of leaf wilting which appeared first in the older leaves, tomato genotypes were classified into salinity-tolerant scale classes from 1 to 4 (Choookhampaeng et al. 2007). With regard to the increasing degrees of leaf wilting which appeared first in the older leaves, tomato genotypes were classified into salinity-tolerant scale classes from 1 to 4 (Choookhampaeng et al. 2007). In our work, tomato genotypes responded differently to salinity stress and were consequently assigned into three groups according to their visual appearance. The first one, tolerant, included three slightly affected genotypes with normal growth. The second, moderately tolerant, comprised two genotypes that showed old leaves rolling, yellowing and sometimes wilting. The third, sensitive, comprised the remaining varieties that suffered from severe wilting of both younger and older leaves. Within the last group, Pomodoro genotype displayed wilting of older leaves while Mouna HF1 variety was the most sensitive, showing premature senescence and death. Considering differences in sensitivity towards salt stress, we have previously assigned 60% of local tomato genotypes into sensitive classes according to Dasgan’s scale (Gharsallah et al. 2016).

As tomato genotypes adapted differently to salt stress and the most of them were assigned to sensitive clusters, salinity is expected to be a major constraint limiting tomato yields in Tunisia.

**Genetic diversity**

The genetic architecture of cultivars can be estimated by assessing the structure of the population using molecular marker (Horst and Wenzel 2007, Varshney et al. 2007). In our work, SSR markers were able to assess the level of genetic diversity that exists among commercial cultivars and to perform an association between markers to salinity tolerance. Out of 25 SSR genomic markers, 19 were polymorphic and allowed a total of 70 alleles to be detected across

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**Fig. 5.** Genotype-phenotype association network. Larger purple nodes represent SSR loci while smaller black nodes represent alleles. Branches, color-coded by phenotypes, are associating screened varieties to corresponding genotypes and phenotypes as well (red, green and blue).
screened genotypes with an average of 3.68 alleles per locus. The PIC value ranged between 0.82 and 0.22 with a mean value of 0.43. These results are consistent with a previous study involving 15 morphic genomic SSRs in 50 tomato genotypes. It was reported that 64 alleles were detected with a mean of 4 alleles per primer and a mean PIC value of 0.49 ranging from 0.8 to 0.08 (Zhou et al. 2015b). Using 33 SSR markers to screen 63 tomato varieties, Kwon et al. (2009) reported a higher PIC value (0.628) ranging from 0.210 to 0.880. According to Xie et al. (2010), high, medium and low locus polymorphism is defined as PIC > 0.5; 0.5 > PIC > 0.25 and PIC < 0.25, respectively. Consequently, the mean PIC determined in our study indicates medium locus polymorphism. Indeed, we involved cultivated varieties, which are always characterized by low genetic diversity. The domestication and intensive selection of valuable agronomic traits with a particular focus on yield has led to a narrow genetic base in tomato cultivars.

PCA analysis showed two contrasting clusters corresponding to tolerant and sensitive genotypes. It is worth noticing that no genotype from a particular cluster (salinity tolerant or susceptible) was intermixed with another cluster. However, PCA also showed a scattered distribution of the moderately tolerant genotypes as well as the mildly sensitive one.

For a successful association between molecular data and agronomic traits, an understanding of the population structure seems to be essential. Based on the criterion of maximum membership probability with a stringent threshold of 81.17%, tomato genotypes were significantly assigned into three distinguishable groups. These three main clusters corresponded to three different salt tolerance scale classes. The first consisted of the three tolerant genotypes, the second of the two mildly tolerant genotypes and the third of the remaining sensitive. Pomodoro variety, a mildly sensitive genotype, was equated with the susceptible group. Such clustering was probably due to the lower genetic distance of the gene types among genotypes. The structure result agreed with the clustering of PCA analysis in that the different behavior adaptation to salt stress contributes to structuring populations.

Genotype-phenotype associations

Tomato phenotypic and genotypic assortment proposed in the present study had distinguished tolerant, moderately tolerant and sensitive genotypes. By combining SSR data with phenotypic evaluation under salt stress, we developed an integrative genotype-phenotype association network. Indeed, we focused on the most discriminating loci and genotypes while shared loci were not taken into account. Selective genotyping of the salt-tolerant and salt sensitive commercial tomato varieties was performed using SSR markers related either to Na+ and K+ concentrations in aerial parts of the plant (SSR 63/92/26/344; CT 167; TG 35) or to the leaf dry weight and area (SSR 22 and TG 69, respectively). Whether each of these markers is linked to QTLs is not explored in our study. Integrating data within a network representation is a key feature of the present analysis that facilitated the association of phenotypes and SSR-generated genotypes. The network presented here could be used to unravel the contribution of these loci on structuring tomato populations. Each pathway can identify which genotypes are involved in salt-stress tolerance and have to be targeted to overcome this stress. Such a network is used in exploring human diseases to link cofactors, proteins and biological processes (Scott-Boyer et al. 2015). Our findings may allow breeders to select contrasting lines for introgressing SSR effective markers in high-yield cultivars. The information gained from such a network also provides insights into valuable SSR markers closely related to salt tolerance. Further analyses are required to define the role of these markers in this trait.

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