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Genetic Diversity and Genome-Wide Association Study for some agronomic traits in durum wheat (*Triticum turgidum* L.) Using whole genome DArTseq Markers

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Abstract

This research was conducted to study genetic diversity, population structure, linkage disequilibrium, and marker-trait relationship in durum wheat using DArTseq technology. Therefore, 94 durum wheat genotypes were evaluated in the form of augmented design with six repeated controls during the two cropping years, 2016–2017 and 2017–2018. Some Agronomic traits including the number of days to spike emergence, number of days to physiological maturity, plant height, thousand kernel weight, and grain yield were measured and recorded. The DNA samples were processed for DArTseq using the Genotyping by Sequencing (GBS) platform at Diversity Array Technology Pty, Ltd, Australia. The values of polymorphism information content (PIC) of SilicoDArT markers varied from 0.023 to 0.499 with an average of 0.38. The studied durum wheat genotypes were grouped into four separate groups based on the Bayesian model. LD analysis between A and B genomes showed that there is a high number of significant marker pairs (82052) in the B genome compared to the A genome (68885). In general, during two cropping years, 29 markers related to the studied traits were found, and out of these 29 related markers, 19 markers were identified in the first year and 10 markers were identified in the second year. The results revealed that the DArTseq markers are a very powerful tool for evaluating the genetic diversity and population structure of durum wheat genotypes and can be used in genotype screening as breeding parents and marker-assisted selection in breeding programs.

Introduction

Among cereal crops, wheat is one of the most grown crops that is essential for the human diet due to providing carbohydrates, proteins, zinc, calcium, fiber, and energy (Mehrabi et al. 2020). Durum wheat (*Triticum turgidum* L. Var. *Durum*) is a tetraploid species with an AABB genome that has been created from hybridization between two wild species *Aegilops speltoides* Tausch (B genome) and *Triticum urartu* Ghandilyan (A genome) (Giunta et al. 2019). This crop is well-adapted to various climatic conditions, and it's mainly cultivated in the Mediterranean region, North Africa, Northern plains, Southwestern USA, and Southern Europe. However, it has an important role in supplying food to local people in the Mediterranean region, which produces more than 50% of the world's durum wheat production (Mérida-García et al. 2020). Hence, detailed genetic information on important agronomic traits and grain yield of durum wheat is required as a basis in breeding programs (Mantovani et al. 2008).

Investigation of genetic diversity among plant populations is an important component of genetics and plant breeding programs. Indeed, the study of phenotypic and genotypic variation in plant genetic materials provides various insights for better utilizing undiscovered features that can be used to improve crop productivity and its adaptation to a wide range of environmental conditions (Mehrabi et al. 2020). Population genetic structure analysis and evaluation of the level of genetic diversity in durum wheat have a long history and so far numerous researches have been done using different markers from agro-morphological to molecular markers (Etminan et al. 2018). Characterization of genetic diversity using phenotypic markers is often not completely successful due to environmental influences on them, whereas molecular markers disclose genetic similarities in a better context without interference from environmental factors. Hence, molecular markers can provide complete information regarding genetic diversity and population structure in the targeted plant populations (Pour-Aboughadareh et al. 2017).

Several types of genetic markers, such as microsatellites, start codon targeted polymorphism (Scot), sequence-tagged sites (STS), CAAT-box derived polymorphism (CBDP), diverse array technology (DArT), and single-nucleotide polymorphisms (SNP) have been used for evaluating the genetic diversity and population structure analyses in durum wheat e.g. (Mantovani et al. 2008; Pozniak et al. 2012; Hu et al. 2015; Etminan et al. 2016, 2018; Baloch et al. 2017; Mehrabi et al. 2020; Mérida-García et al. 2020; Sansaloni et al. 2020). Of these, the SNP and DArT are identified as higher throughput molecular markers. These techniques are the most common polymorphism among plant materials (Deschamps and Campbell 2010). SNPs show the most frequent type of DNA polymorphism markers that therefore can provide a high density of genetic markers near a target locus (Batley and Edwards 2007). Hence, they are useful DNA-based markers to use in genetic studies. Besides, DArT is another high-throughput genotyping platform based on hybridizing DNA to microarrays (Li et al. 2002). The main advantage of this technique is that it does not require prior sequence information of test individuals. The provision of high-quality dominant markers with a cost- and time-competitive trade-off is another important advantage usage of the DArT technique in genetic studies (Li et al. 2002). In general, the accessibility of DArT and SNP genotyping techniques would facilitate the genetic analysis and the application of marker-assisted selection in breeding pragmas (Trebbi et al. 2011; Mehrabi et al. 2020).

One of the most efficient approaches currently used for the analysis of quantitative agronomic traits and quality features is association mapping or AM analysis (Flint-Garcia et al. 2003). This method is based on the conception that each quantitative trait that has entered a population will still be linked to the genetic background of the evolutionary ancestor (Gibson and Muse 2009). Hence, AM analysis can discover specific functional genetic alleles or loci associated with phenotypic variation in a trait to simplify the correlation between phenotypic and genome sequence polymorphisms (Ranieri 2015). In other words, this analysis is a powerful approach to discovering the relationship between phenotypic variations and genome polymorphisms in natural germplasm collections (Mehrabi et al. 2020). As a promising approach, several advantages such as much finer mapping resolution, providing broader genomic region coverage, and minimum confidence intervals of the detected loci have distinguished this approach compared to classical linkage analysis (Zhu et al. 2008). Albeit, many studies have represented the genetic diversity and AM analysis in durum wheat germplasm e.g. (Mantovani et al. 2008; Hu et al. 2015; Mwadzingeni et al. 2017; Fayaz et al. 2019; Mehrabi et al. 2020; Sansaloni et al. 2020), there are few studies on genetic diversity and AM analysis using SNP and DArT markers together in durum wheat e.g.(Baloch et al. 2017; Mérida-García et al. 2020). Hence, the main objectives of this study were (i) to the analysis of genetic diversity, genetic population structure, and linkage disequilibrium (LD) in a set of durum wheat genotypes, and (ii) to dissection associations between the several agronomic characters with the SNP and DArT markers.

Materials and Methods

Genetic materials

Ninety-six durum wheat genotypes including 92 breeding lines along with 4 local cultivars (as the check genotypes) were investigated. All plant genetic materials were provided by the Dryland Agricultural Research Institute (DARI), Kermanshah, Iran. Additional information about the pedigree of investigated genotypes is presented in Table S1.

Phenotypic assay

The field experiment was performed at the Sara-rood Dryland Agricultural Research Institute, Kermanshah, Iran (Latitude 34°20′N, Longitude 47°17′E, and Altitude 1351 m above sea level) during the 2017–2018 and 2018–2019 cropping seasons. The weather condition of the genotype evaluation site is shown in Fig. 1. In each cropping season, all genotypes were planted in an augmented design with 5 blocks and 4 repeated check genotypes. Sowing and crop management were done based on experts' advice. The plot size was six rows, 3 m in length, spaced 20 cm apart. Grain sowing was done manually. During plant growth and development, five agro-morphological traits were recorded based on the standard system of the National Gene Bank of Tunisia (NGBT). The measured traits were: (1) the number of days-to-heading, (2) the number of days-to-physiological maturities, (3) plant height, (4) thousand kernel weight, and (5) grain yield. After adjusting means for measured traits, Variance analysis on morphological data was done based on the Best Linear Unbiased Estimation model(BLUE) using the MIXED procedure of the SAS-STAT statistical package.

DNA Extraction

Ten grains from each genotype were sown in plastic pots under controlled conditions at the research greenhouse. The DNA of 94 durum wheat genotypes was extracted by the CTAB method with a few changes from fresh leaves(Doyle and Doyle 1990). To check the absence of breakage in the extracted DNA molecules, a standard 0.8% agarose gel was used. In this method, 5 microliters of the extracted DNA solution were stained and loaded with a dye, and gel electrophoresis was performed with a current of 75 volts for 30 minutes. To determine the quality of DNA, it is possible to compare the pattern and color intensity of the used lambda phage DNA with the position and intensity of the band obtained from the electrophoresed DNA. After determining the concentration of the extracted DNA by the spectrophotometric method in comparison with the control DNA, each of the extracted DNA tubes was diluted to a concentration of 50 ng/µl.

Genotyping assay

For genetic evaluation in 94 wheat genotypes, the extracted DNA was prepared at a concentration of 50 ng/µl. From each genotype, at least 20 microliters of each sample were loaded into 96 DNA plates. The plates containing the samples were sent to the Diversity Arrays Technology Pty Ltd Center located at the Building 3, Level D, University of Canberra Bruce, ACT 2617, Australia (https://www.diversityarrays.com) for genotypic evaluation by Sililco DArT and SNP markers. DArT markers were first filtered in terms of unsuitable parameters such as minor allele frequency > 2%, repeatability > 90%, and unread rate > 90%. Finally, 7882 Silico DArT and 5455 SNP markers were yielded for further analysis. The obtained data are of two categories: Sililco DArT markers based on the presence and absence of a gene array sequence in each sample. Another category of SNP markers is based on the presence or absence of a mutation in a gene region. Sililco DArT markers are dominant markers and SNP markers are common markers(Alam et al. 2018).

Genetic analysis

The amount of polymorphism information content (PIC) for SilicoDArT markers was calculated by Power Marker $_{V.3.25}$ software(Powell et al. 1996). Analysis of population genetic structure (Population Structure) was read using STRUCTURE HARVESTER software. The number of sub-populations resulting from the population analysis by SilicoDArT markers data was determined by the number of K, and based on this, the genetic information between the sub-populations and their graphic plot were extracted from the population software(Evanno et al. 2005). The amount of linkage disequilibrium (LD) of molecular data (SilicoDArT and SNP) was calculated using TASSEL software and its graphical analysis was done in the R environment using the GAPIT package (Lipka et al., 2012). Finally, Association mapping was calculated separately by TASSEL and GAPIT software and compared to ensure their correctness. In both software, the FarmCPU method was calculated using PCA, KINSHIP MATRIX, and Q matrix data. Markers that had a significant level ($P < 0.001$) were considered correlated markers with each of the phenotypic data. Due to the high number of markers used, therefore, to determine markers with higher efficiency, Q-Q-Plot analysis was also performed simultaneously with FarmCPU and markers that had Log10 (P) greater than 3 were selected as markers with very high correlation. To identify the candidate genes, the physical location of each marker was searched in the IWGSC Refseq v1.0 genome, and if a gene is found 5–10 kb above the desired location, it will be considered correlated with the desired marker.

Results

Genetic diversity with pheno-morphological markers

The results of variance analysis using the BLUE & BLUP method and descriptive statistics are presented in Table 1, separately for the two years of the experiment (E1 and E2, respectively). According to the results of this analysis, it was found that the genotypic effect was significant for all traits in both years (except for seed yield in the first year). The estimated genotypic variance for each of the measured traits showed that in both crop years, the highest amount of variation was related to grain yield. In addition, the coefficient of variation for grain yield was estimated more than other traits. The highest and lowest heritability in the first year belonged to plant height and grain yield traits, which were 0.93 and 0.33, respectively. In the second year, grain yield was the lowest with 0.45, and thousand grain weight was the highest heritability with 0.91(Table 1). The GT charts shown separately in Fig. 2 for both experiment years. Based on the first year's data, 52.92% of the total genetic diversity among genotypes was justified by the first two components. By justifying the polygon diagram drawn in this bi-plot, genotypes No. 3, 4, 38, 77, 24, 43, and 86 are located at the polygon's vertices. Therefore, it can be said that genotype No. 43 had the highest value in terms of thousand kernel weight, and genotypes No. 3 and 4 had the highest value in terms of plant height. Also, the highest amount of grain yield belonged to genotype No. 86 (Fig. 2A). The bi-plot drawn based on the obtained data from the second year of the experiment showed that the first two components accounted for 33.22 and 26.53 % of the total variation related to studied traits among genotypes, respectively (Fig. 2B). Based on the

second year's data, genotypes No. 18, 14, 91, 44, 72, 41, 45, 47, and 65 were placed in the vertices of polygons. As shown in Fig.2B can be seen, genotype 72 was superior to other genotypes in terms of thousand kernel weight. On the other hand, the best genotypes in terms of plant height and the number of days to physiological maturity were genotypes No. 47 and 65. Genotype No. 41 was also identified as the latest genotype. In terms of grain yield, genotypes No. 9, 11, and 86 had better potential than other genotypes.

Molecular diversity by SilicoDArT markers

The SilicoDArT SNP markers with very high genome coverage were used to study genome diversity in a panel consisting of 92 durum wheat genotypes, which is a valuable and powerful tool for GWAS analysis in the future. Also, these germplasms will be valuable resources for extracting alleles and selecting genotypes that give resistance genes to various biotic and abiotic stresses through linkage mapping in the whole genome. Candidate SilicoDArT and SNP markers can be used to establish marker-trait association (MTA) concerning specific genes or large QTLs controlling valuable traits in durum wheat. The information (data) of these markers was estimated by polymorphism information content (PIC). Polymorphism information content (PIC) is used to provide information about the variation of a gene or segment of DNA in a population to indicate evolutionary pressure on an allele and mutations at a gene locus that may have occurred over some time. When the scoring of a marker is (0) and (1) with ratios of 50% to 50%, the maximum PIC value is calculated as 0.5. In this research, a large number (7882 and 8948) of high-quality SilicoDArT and SNP polymorphic markers were filtered out of 62269 and 54543 markers, respectively, and used for the analysis of genetic diversity and population structure in a set of 92 durum wheat genotypes. The average PIC values for all SilicoDArT markers were equal to 0.38, which indicates the high efficiency of these markers for measuring the genomic diversity of durum wheat (Table 2). In general, the distribution of PIC values among the markers was asymmetric and tended towards values higher than the average, so about 60% of the markers showed PIC above the average (Fig.S1). The average content of polymorphic information in SNP markers was equal to 0.25. The lowest value of PIC was observed in the chromosomal group (Chr2A) with a value of 0.235 and the highest value in the chromosomal group (Chr6A) and (Chr5B) was 0.261. The distribution of PIC values for SilicoDArT and SNP markers is shown in Fig. S1 and Fig.S2, respectively. The distribution of PIC values among markers was almost non-uniform, and more than 3000 SilicoDArT markers had PIC values close to 0.5. About 75% of SilicoDArT markers had PIC values greater than 0.3. In addition to the PIC values some other quality parameters, such as the call rate and the reproducibility of each marker within the panel of examined durum wheat genotypes, were also estimated. The average reproducibility in both SilicoDArT and SNP markers was more than 0.98. The call rate average in SilicoDArT and SNP markers were equal to 0.92 and 0.98, respectively (Table 2). Among 14 linkage groups, the distribution frequency of SNP markers was higher than SilicoDArT markers. The average distribution of SilicoDArT markers in each chromosome was equal to 563, and the same index in SNP markers was equal to 639 in each chromosome. The lowest number of identified SNP markers was observed in the linkage group (Chr4A) and (Chr6A) and the highest number of SNP markers was observed in the chromosomal group (Chr2B). Also, the Chr7B linkage group showed the highest markers with an average of 1.14 SilicoDArT markers per Mbp.

Kinship coefficients between pairs of genotypes

Based on the kinship coefficients matrix, the investigated genotypes were divided into 3 groups for gene data. Also, the results showed that about 60% of the kinship coefficients between pairs of genotypes were between zero (except zero) and 0.1 and about 39% of the values were between 0.1 (except 0.1) and 0.5. Only about one percent of the coefficients had values greater than 0.5. Therefore, the results of this analysis indicated that there is very little kinship in the studied genotypes (Fig.3).

Bayesian clustering

According to the results, K and Delta K statistics were extracted, and two-dimensional diagrams were drawn that clearly showed the curve at the maximum of K=4 (Fig.S3). Therefore, according to the obtained results, durum wheat genotypes were grouped into four separate subpopulations based on the Bayesian model (Fig. 4). The four subpopulations showed relatively high genetic diversity, which ranged from 0.02 in a subpopulation (POP4) to 0.34 in a subpopulation (POP3). Net Nucleotide Distance is a parameter to measure genetic diversity among populations that revealed the highest (0.270) and lowest (0.07) genetic distance between POP2 and POP4 subpopulations and POP1 and POP2 subpopulations (Table 3).

Analysis of linkage disequilibrium (LD)

The linkage disequilibrium index was evaluated using 605212 pairs of DArTseq markers with specific map locations along 14 durum wheat chromosomes. Pairwise linkage disequilibrium values were estimated using the square of allelic frequency correlations (r^2) between markers. To identify differences in intra-chromosomal linkage disequilibrium, the average values of r^2 between pairs of markers are divided into five groups based on the genetic distance between them: markers with very high linkage (Distance less than 5 cM), Contiguous markers (with a distance of 5-10 cM), markers with medium continuity (with a distance of 10-12 cM), weakly connected markers (with a distance of 20-50 cM) and independent markers (with a distance of more than 50 cM). The evaluation of intra-chromosomal linkage disequilibrium showed that the linkage disequilibrium decreases with increasing genetic distance. Analysis of linkage disequilibrium was also investigated at the genome level. To show the extent of linkage disequilibrium at the level of the genome, the average reduction in disequilibrium was obtained by plotting intra-chromosomal r^2 values against the genetic distance between markers (Fig.5). The amount of LD within the chromosomes based on both SilicoDArT and SNP markers for both durum wheat genomes (A and B) is shown in Table 4. The amount of LD in both types of markers was very wide, in such a way that 605,212 pairs of significant markers were observed in the entire population. LD analysis between the A and B genomes revealed that there are a high number of significant marker pairs (82052) in the B genome compared to the A genome (68885). The average r2 values for the whole population were equal to 0.14, whereas about A and B genomes were equal to 0.12 and 0.11, respectively (Table 4). A graphic analysis of the distribution of LD markers is shown in Fig.5. In general, 15 kb of the genome was covered in LD. The highest amount of linkage disequilibrium was observed in chromosome 4B. Some of the markers are shown on this chromosome (Fig.6).

Genome-Wide Association Study

The correlation analysis was performed using markers with a frequency of more than ten percent, and the P-value statistic was considered with 1000 permutations. Also, the lowest P-value was used as the basis for selecting the correlated markers. The distribution of markers was studied based on the coefficient of determination of the marker in the regression model. The coefficient of determination (r^2) is the proportion of the phenotypic variance accounted for by the QTL for each locus. The association mapping of days-to-heading, day-to-physiological maturity, plant height, thousand kernel weight, and grain yield of durum wheat was performed using genotypic and phenotypic data. Association mapping analysis for each trait was done based on FarmCPU. To determine the significant markers associated with the studied traits (MATs), QQPlot analysis was also performed, and finally, the markers with -log 10(p) were selected. The Manhattan plots are shown based on all measured traits for two cropping years in Fig.7 and Fig.8, respectively. The full report of significant associations of markers related to all traits in both two years of the experiment is presented in Tables 5 and 6. The results of a genome-wide association study by the FarmCPU method in 2017 showed that 19 markers had a significant association with the studied traits (Table 5). The results of association mapping for studied traits in the first year of the experiment are summarized as follows:

- Two significant relationships were identified for the numbers of days to heading by 1703829 and 1087984 markers located on chromosomes 6B and 7A, respectively.
- The correlation of 3940462 markers on chromosome 4A with days to maturity was significant.
- Ten significant relationships were identified between plant height and DArT markers. These markers had chromosomal locations 3A, 3B, 4B, 5A, 5B, 6A, 6B, and 7B.
- Four significant associated markers with thousand-grain weight were identified (3570140, 992437, 3534094, and 3533907) on chromosomes 7A, 3A, 5B, and 3B, respectively.
- The effective trait of Grain yield had three significant relationships with 1108172, 4989009, and 1233550 markers located on chromosomal positions 3A, 2B, and 1B, respectively.

The results of genome-wide association analysis by the FarmCPU method in 2018 indicated that ten markers had a significant association with the studied traits (Table 6). The summary of the results was as follows:

- Association mapping for the numbers of days-to-heading revealed two significant markers (3935863 and 1211191) with the chromosomal locus 1A and 5B, respectively.
- Three markers (3064874, 1034732, and 1025860) with gene loci (794315843, 673038094, and 666991274) on chromosomes chr3B, chr4A, and chr4A respectively, had a significant relationship with the numbers of day to physiological maturity.
- The relationship of plant height was significant with the marker of 1057654 with gene locus 691163974 on chromosome chr7A. This is even though ten significant associations were identified for plant height in the previous year.
- The trait of a thousand-grain weight had a significant relationship with 3025786 and 981221 markers. These markers with gene loci 609888794 and 684637596 are located on chr6A and chr3B chromosomes, respectively.
- Two significant associations were identified between grain yield and DArT markers. The locus of these markers is located on chromosomes 6A and 7A, respectively.

In general, according to the results, the same marker (1057654) was identified for grain yield and plant height in the second experiment year. This marker with genetic locus 691163974 is located on chromosome 7A. By comparing the significant marker-trait relationships as well as the durum wheat consensus map, the position of the marker can be identified and checked by comparing them with physical maps. If the marker distance is more than +10 or -10 cM that position can be identified as a new QTL. Based on this, 29 quantitative positions were identified and confirmed in this study. Among the identified loci, 9 loci were not previously recorded in Durum's Consensus map (Table 7).

Discussion

Durum wheat (*Triticum turgidum* ssp. durum) in Iran and other major producer countries in the world, such as Canada, Mexico, the United States of America, Australia, Italy, Turkey, et cetera. is mainly grown under rain-fed conditions, so due to environmental stresses, especially drought stress, mostly has a low grain yield (Beres et al. 2020). The initial loss of durum wheat's genetic diversity during the domestication process is estimated at 84%. Therefore, as a consequence of this event, kinds of wheat (bread and durum) were domesticated, which has narrowed their genetic base and diversity, currently (Zeven 2000).One of the primary goals of any breeding program is to identify and select the desired genotypes in terms of various traits(Mohammadi et al. 2014). To achieve this goal, the traits used should be clearly defined in terms of quantity and quality, so that in combination with important economic traits, they can be used to maximize the Grain yield of the selected genotypes. In this regard, several statistical methods, including correlation analysis, multiple regression analysis, and path coefficient analysis, have been proposed and widely used by experts and breeders. In the meantime, one of the most important statistical methods introduced to achieve this goal is genotype-trait graphical analysis (GT), which is obtained through analysis into principal components(Yan 2001). In this method, the bi-plot used is obtained through the first two components extracted through the analysis of eigenvalues on the desired attribute data in several environments (year, place, or a combination of year and place). Although this method was introduced to analyze multi-environment experiments, it can be used for any type of data that has a two-way structure(Yan 2001). Generally, according to Yan and Rajcan (2002), the desired genotypes identified through this analysis can be used as parents in cross-breeding programs or directly to produce commercial cultivars. The best linear unbiased estimation (BLUE & BLUP) analysis revealed that the investigated durum wheat genotypes in this research have a high genetic diversity in grain yield and other agronomy traits (Table 1). Also, the different responses of each genotype in terms of measured traits to different environmental conditions (year) revealed the existence of the genotype × environment interaction effect. However, a more accurate evaluation of the selected genotypes to grain yield and other traits is necessary for their use in crossbreeding programs or to check their stability and adaptability to different regions. Graphical analysis of genotype-trait (GT)

indicated genotypes 24, 80, and 83 were superior to other genotypes in terms of studied traits (Fig. 2). Therefore, it's made possible to use them in breeding programs for the improvement of several characters simultaneously. Considering that the bi-plots showed all the available changes did not justify, these predictions may not accurately reflect the observed numbers. However, the predictions are highly close to reality, so it is possible to select genotypes with superior values compared to previously. Yan and Kang (2002) in soybean, Yan and Frégeau-Reid (2008) in oats, Dehghani et al. (2008) in winter rapeseed, and Rahmati et al. (2020) in cantaloupe have applied this method to evaluate, compare and select superior cultivars and indicated that this method in addition to showing the relationship between different traits graphically, can make the visual comparison between genotypes very possible.

The average SNP and Silico-DArT PIC values (were 0.252 and 0.383, respectively) in the recent study were higher than the PIC value reported by Ren et al. (2013) using SNP markers in the global collection of 150 durum wheat genotypes (it was equal to 0.18888). Moragues et al.(2007) investigated the genetic diversity of 63 indigenous populations of durum wheat from Mediterranean countries using AFLP and SSR markers, the average PIC values for AFLP and SSR markers were 0.24 and 0.70, respectively. Sequence reading rate (Call Rate) is the percentage of valid scores among all possible scores for a marker, while reproducibility is measured as the percentage of scoring repeatability for repeated samples. Therefore, both of these parameters were estimated to determine the quality of each marker within the panel of durum wheat genotypes in this research (Table 2). Although the combination of restriction enzymes as well as the amount of diversity in the representative panel is different from other plant species; the proportion of technical replicate assay pairs for markers score and the success of reading the marker sequence across the samples were high and comparable with previous applications of SilicoDArTs in other plant species (Grzebelus et al. 2014; Ndjiondjop et al. 2017; O'Connor et al. 2019). The genomic coverage of SilicoDArT and SNP markers was generally homogenous for most of chromosomes. The highest number of SilicoDArT and SNP markers (853, 818) were observed in Chr7B and Chr2B linkage groups, respectively. Also, chromosome size covered by these markers were highly similar and its highest and lowest value were observed in the Chr3B **and** the Chr1A linkage groups, respectively (Table 2) which is similar to previous studies in durum wheat using high-performance GBS (Baloch et al. 2017).

Based on the Kinship matrix information, the studied genotypes were divided into 3 groups. Relative kinship among individuals in the population can lead to the identification of false associations between markers and traits and therefore it should be taken into consideration in relational mapping studies. The value of the matrix of kinship coefficients can vary from 3 to -3, as much as its average tends to be zero or less, it indicates a very high diversity in the population. Genotypes with high kinship coefficients are highly likely to have a common ancestry (Salgotra et al., 2015).

The results of population structure analysis based on the *Bayesian* model put the studied genotypes into four groups. Since some clusters showed a mixture of durum wheat genotypes, it can be concluded that most probably the same parental lines were used in the breeding programs of these genotypes. The existence of groups and subgroups in large populations can be reasons such as different geographical origins of genotypes, natural or human selection, genetic drift, etc. (Flint-Garcia et al., 2003).

Genome-wide Association study is the method that determines the QTL's location based on linkage disequilibrium (Gupta and Varshney 2005). Therefore, for association mapping, in addition to the composition of the population structure, the extent of linkage disequilibrium in the genome has fundamental importance (Al-Maskri et al. 2012). The results revealed that linkage disequilibrium varies from chromosome to chromosome. In our research, the highest amount of linkage disequilibrium was observed for markers with a distance of less than 5 cM on chromosome 4B, which indicates that linkage is one of the most effective forces that cause disequilibrium in the population. Previous studies have demonstrated that linkage disequilibrium varies along the chromosome and from chromosome to chromosome (Chao et al. 2010; Hao et al. 2011). The results also showed that increasing the distance between the markers does not completely remove the imbalance. This is due to the presence of other effective factors such as population structure, genetic drift, migration, selection, and mutation on linkage disequilibrium (Reich and Lander 2001). In the present study, the marker-trait association was investigated using the FarmCPU model. In general, 29 significant "marker-trait" associations were found during two cropping years, and out of these 29 related markers, 19 markers were identified in the first cropping year and 10 markers were identified in the second cropping year. Among the identified markers, there were 11 markers related to plant height. One of the most promising approaches to improving traits is the introduction of new alleles. As a first step, allele extraction approaches can be performed in different ways and with different sets of plant germplasm. Therefore, performing multiple trials in different environments and the phenotypic analysis of the studied germplasm can identify associated markers for a genetic description of complex traits. In addition, genetic relationships can be used to choose the desirable parents for breeding programs, if the genetic pedigree data is not available. The information produced here can be used to breeding programs tailored to regional and local needs. The presence of many SilicoDArT and SNP markers, the cost-effectiveness, and the high relatively polymorphism information content (PIC) have provided excellent aspects for widespread screening of the whole genome for genetic diversity, linkage disequilibrium studies, and genome-wide association analysis purposes.

Conclusion

Genetic diversity is the basis of each breeding program. Therefore, it is expected that the comprehensive knowledge about the genetic diversity of durum wheat from various eco-geographic regions will have a significant impact on the protection and use of desirable germplasms. This can help breeders in designing new approaches to achieve profitable diversity in breeding programs. The study of genetic diversity subordination from geographical and climatic diversity indicates the possible adaptation of plant germplasms with different habitats and environments. MTAs are the key elements to detecting genomic regions related to durum wheat morpho-phenologic traits. The current experiment found 29 highly significant MTAs under two consecutive cropping year. The markers detected would be useful genomic sources for cloning and fine mapping of underlying genes, and for conducting gene introgression and marker-based selection in durum wheat under rain fed condition. Further research attempts are needed for validating the markers detected in the current project using a larger durum wheat population.

Declarations

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Author's contribution:

A. Etminan conceived and the study, P. Ebrahimi and R. Mohammadi conducted the experiments, R. Talebi analyzed the data, E. Karami wrote the manuscript, all authors read and approved the final version.

Conflict of Interest:

The authors declare that they have no conflict of interest.

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This project did not have a financial supporter.

Data Availability Statement:

Data sharing is not applicable as no new data were generated or analyzed during this study

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Tables

Table 1. Analysis of variance for measured traits in investigated durum wheat genotypes based on BLUE models

Traits						
GY	TKW	PH	DM	DF	Statistics	Environments
0.33	0.91	0.93	0.90	0.90	Heritability	First Year(Env1)
26734.65	12.06	54.16	2.02	6.27	Genotypic Variance	
323321.56	6.83	24.10	1.27	4.23	Residual	
2275.8	31.3	62.8	171.3	109.2	MIN	
5375.8	54.7	112.7	183.7	132.2	MAX	
4071.91	44.55	80.20	175.65	124.32	Mean	
306.80	3.99	7.80	1.69	3.04	LSD	
13.72	5.92	6.12	0.64	1.66	Coefficients of Variation	
680.91	4.44	8.74	1.92	3.47	Standard Deviation	
0.64	0.0004	0.00001	0.00001	0.006	P-Value	
0.45	0.91	0.81	0.73	0.76	Heritability	Second Year(Env2)
30107	14.18	35	3.83	1.89	Genotypic Variance	
402432.41	8.34	50.05	8.59	3.54	Residual	
1441.5	29.2	67.5	161.8	118.7	MIN	
4802.0	61.7	122.5	181.5	131.9	MAX	
3472.40	39.04	89.65	167.89	125.03	Mean	
1090.54	4.38	8.73	3.14	2.14	LSD	
18.34	7.43	8.00	1.75	1.50	Coefficients of Variation	
759.34	5.31	9.87	4.24	2.68	Standard Deviation	
0.03	0.04	0.00002	0.0001	0.0002	P-Value	

Table 3. Genetic divergence among (Net Nucleotide Distance) and within (expected heterozygosity) population, the proportion of membership, and the mean value of Fst observed from the study of population structure of 92 durum wheat genotypes using SilicoDArT markers.

Population	Net Nucleotide Distance			Expected Heterozygosity	% 0f membership	Mean fixation index (Fst)
	POP2	POP3	POP4			
POP1	0.070	0.084	0.247	0.20	46	0.41
POP2		0.085	0.270	0.20	26	0.46
POP3			0.249	0.34	19.5	0.21
POP4				0.02	8.5	0.95

Table 4. Characteristics of linkage disequilibrium in durum wheat genome based on DArTseq markers

Genome	Total pairs	Significant pairs (P≤0.001)	% of Significant pairs	Mean r^2	Pairs in complete LD	Critical r^2 value
A-genome	269891	68885	24.7	0.13	1337	0.12
B-genome	335322	82052	24.4	0.12	1146	0.11
Whole-genome	605212	148937	24.6	0.13	2438	0.14

Table 2. SilicoDArT and SNP Markers Distribution on Durum Wheat Genome, Polymorphism Information Content (PIC), Call Rate, and Average of Reproducib

Linkage Groups	No. DArT Markers	No. SNP Markers	Chr Size(kbp) Silico DArT	Chr Size (kbp) SNP	DArT Call Rate (mean)	SNP Call (mean)Rate	DArT One Ratio (mean)	SNP One Ratio(mean)	SNP (mean)PIC	DArT PIC (mean)	AV. of Reprod
Chr1A	**300**	582	**589293.8**	**591612.294**	0.926811	0.983	0.53253	0.423	0.257	0.392783	0.984
Chr2A	574	695	779665.3	780499.087	0.928376	0.982	0.531615	0.396	0.235	0.378022	0.981
Chr3A	454	685	750610.4	750170.104	0.926852	0.983	0.528354	0.411	0.251	0.371944	0.981
Chr4A	489	**445**	742808.8	743151.257	0.929105	0.984	0.507459	0.434	0.253	0.382376	0.982
Chr5A	436	726	708977.0	708511.745	0.928146	0.982	0.520776	0.421	0.259	0.375594	0.981
Chr6A	456	**445**	616320.1	617227.837	0.928312	0.982	0.510363	0.468	0.261	0.392759	0.981
Chr7A	789	750	735262.1	736431.403	0.929175	0.981	0.510735	0.383	0.241	0.384203	0.981
Ch1B	681	591	688589.5	688256.279	0.92758	0.981	0.533268	0.427	0.244	0.385003	0.98
Chr2B	759	**818**	800769.3	800987.529	0.927394	0.98	0.531767	0.41	0.243	0.393895	0.982
Chr3B	582	772	**829200.1**	**829329.004**	0.922085	0.983	0.564573	0.391	0.241	0.369268	0.984
Chr4B	333	456	671754.7	671277.981	0.924849	0.984	0.538444	0.42	0.259	0.37495	0.98
Chr5B	586	757	708929.4	712833.876	0.923233	0.983	0.566275	0.43	0.261	0.382289	0.982
Chr6B	590	638	720840.0	720898.912	0.926843	0.982	0.534025	0.41	0.241	0.382743	0.981
Chr7B	**853**	588	749946.8	750031.822	0.92991	0.982	0.515027	0.449	0.282	0.392338	0.978
Sum	**7882**	**8948**	-	-	-	-	-	-	-	-	-
Mean	**563**	**639**	720926.2	721515.7	0.927048	**0.98229**	0.530372	0.4195	**0.252**	0.382726	0.9813
Group A	**499.72**	**618**	703276.78	703943.4	0.928111	**0.982**	0.520261	0.419	**0.251**	0.382525	0.981
Group B	**626.3**	**660**	738575.7	739087.9	0.925985	**0.982**	0.540483	0.419	**0.253**	0.382927	0.981

Table 5 Associated markers with studied traits in 94 durum wheat genotypes using linkage analysis in the 2017 cropping year.

Traits	Marker	Linkage Group	Locus	value*P*-	Maf	Consensus map(cM)
Days to Flowering	1703829	Chr6B	4863112	0.000075	0.309783	3.34
	1087984	Chr7A	42448091	0.000083	0.141304	3.34
Days to Maturity	3940462	Chr4A	606757033	0.000087	0.943478	54.26
Plant Height	1228105	Chr5A	4994308	0.000000	0.288043	5.94
	3946051	Chr3A	697061451	0.000000	0.13587	-
	4004958	Chr5B	648289673	0.000001	0.130435	-
	4405812	Chr5A	109937709	0.000002	0.369565	-
	1068144	Chr6A	613084911	0.000013	0.70652	98.22
	1093423	Chr6B	33427529	0.000026	0.375	13.14
	2275869	Chr3B	19232431	0.000034	0.483696	17.44
	5410721	Chr7B	625701808	0.000041	0.065217	81.31
	1671913	Chr3A	497297304	0.000043	0.233696	-
	1090315	Chr4B	629706516	0.000067	0.413043	-
Thousand-grain weight	3570140	Chr7A	71591095	0.000031	0.211957	149.67
	992437	Chr3A	541246518	0.000041	0.391304	68.59
	3534094	Chr5B	27137735	0.000044	0.255435	161.82
	3533907	Chr3B	739839965	0.000056	0.461957	-
Grain Yield	1108172	Chr3A	652905402	0.000071	0.059783	65.11
	4989009	Chr2B	106775933	0.000021	0.179348	-
	1233550	Chr1B	558575664	0.000033	0.190217	-

Table 6 Correlated markers with studied traits in 94 durum wheat genotypes using linkage analysis in the 2018 cropping year.

Traits	Marker	Linkage Group	Locus	value*P*-	Maf	Consensus map(cM)
Days to Heading	3935863	Chr1A	30133162	0.000032	0.086957	35.82
	1211191	Chr5B	700372980	0.000037	0.065217	137.12
Days to Maturity	3064874	Chr3B	794315843	0.000006	0.097826	133.21
	1034732	Chr4A	673038094	0.0000028	0.25	96.08
	1025860	Chr4A	666991274	0.000078	0.304348	96.16
Plant Height	1057654	Chr7A	691163974	0.000051	0.097826	129.67
Thousand Grain Weight	3025786	Chr6A	609888794	0.000044	0.070652	98.83
	981221	Chr3B	684637594	0.000090	0.0157609	81.17
Grain Yield	1057654	Chr7A	691163974	0.000016	0.097826	129.67
	7918245	Chr6A	611855760	0.000040	0.141304	-

Table 7 Comparison of gene locations identified by Consensus map of durum wheat			
Traits	Marker	Linkage Group	cM
Days to Heading	1703829	Chr6B	3.34
	1087984	Chr7A	3.34
	3935863	Chr1A	35.82
	1211191	Chr5B	137.12
Days to Maturity	3940462	Chr4A	54.26
	3064874	Chr3B	133.21
	1034732	Chr4A	96.08
	1025860	Chr4A	96.16
Plant Height	1228105	Chr5A	5.94
	3946051	Chr3A	-
	4004958	Chr5B	-
	4405812	Chr5A	-
	1068144	Chr6A	98.22
	1093423	Chr6B	13.14
	2275869	Chr3B	17.44
	5410721	Chr7B	81.31
	1671913	Chr3A	-
	1090315	Chr4B	-
	1057654	Chr7A	129.67
Thousand-grain weight	3570140	Chr7A	149.67
	992437	Chr3A	68.59
	3534094	Chr5B	161.82
	3533907	Chr3B	-
	3025786	Chr6A	98.83
	981221	Chr3B	81.17
Grain Yield	1108172	Chr3A	65.11
	4989009	Chr2B	-
	1233550	Chr1B	-
	1057654	Chr7A	129.67
	7918245	Chr6A	-

Figures

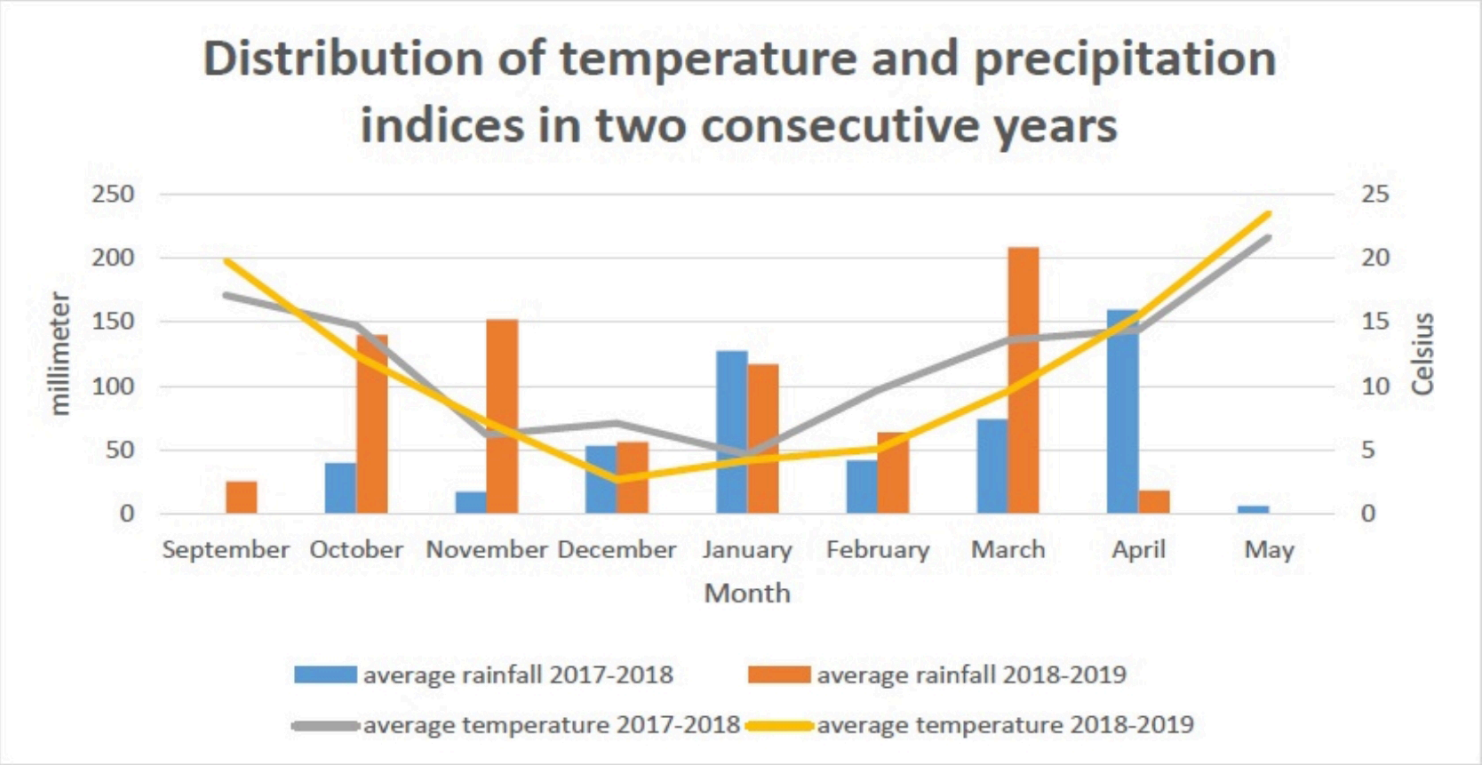


Figure 1

Distribution of temperature and precipitation indices in two consecutive years

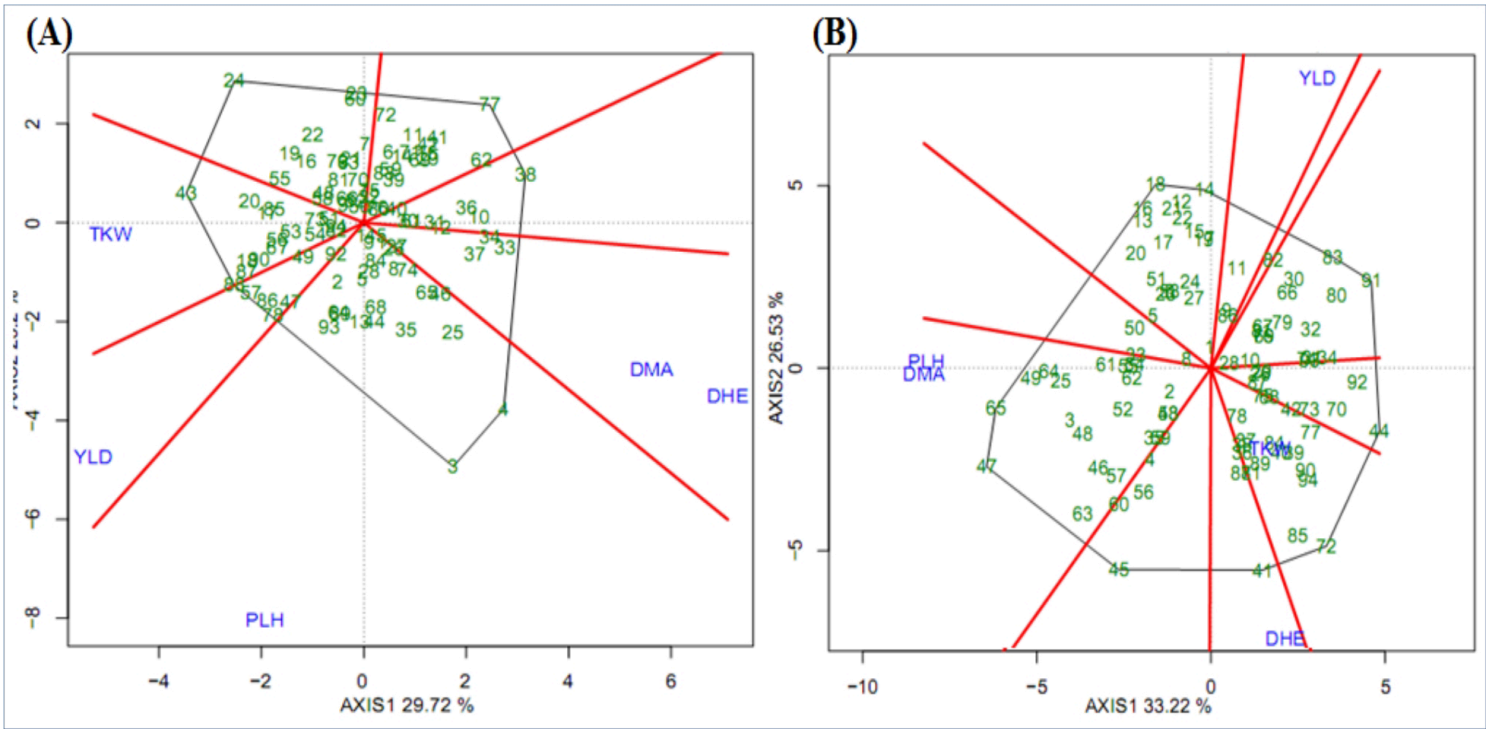


Figure 2

Polygon bi-plot drawn based on the first two components for the measured traits in the first (A) and second (B) years of the experiment. DHE, DMA, PLH, TKW, and YLD represent the number of days until the emergence of the spike, the number of days to the physiological maturity, the plant height, the thousand kernel weight, and the grain yield, respectively.

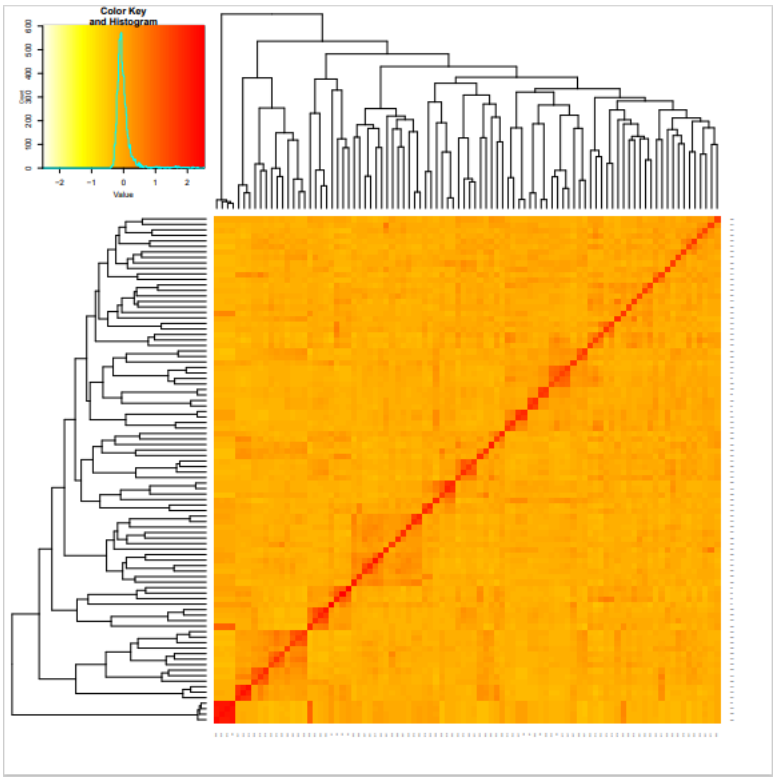


Figure 3

Grouping of genotypes based on relative kinship coefficients between pairs of genotypes

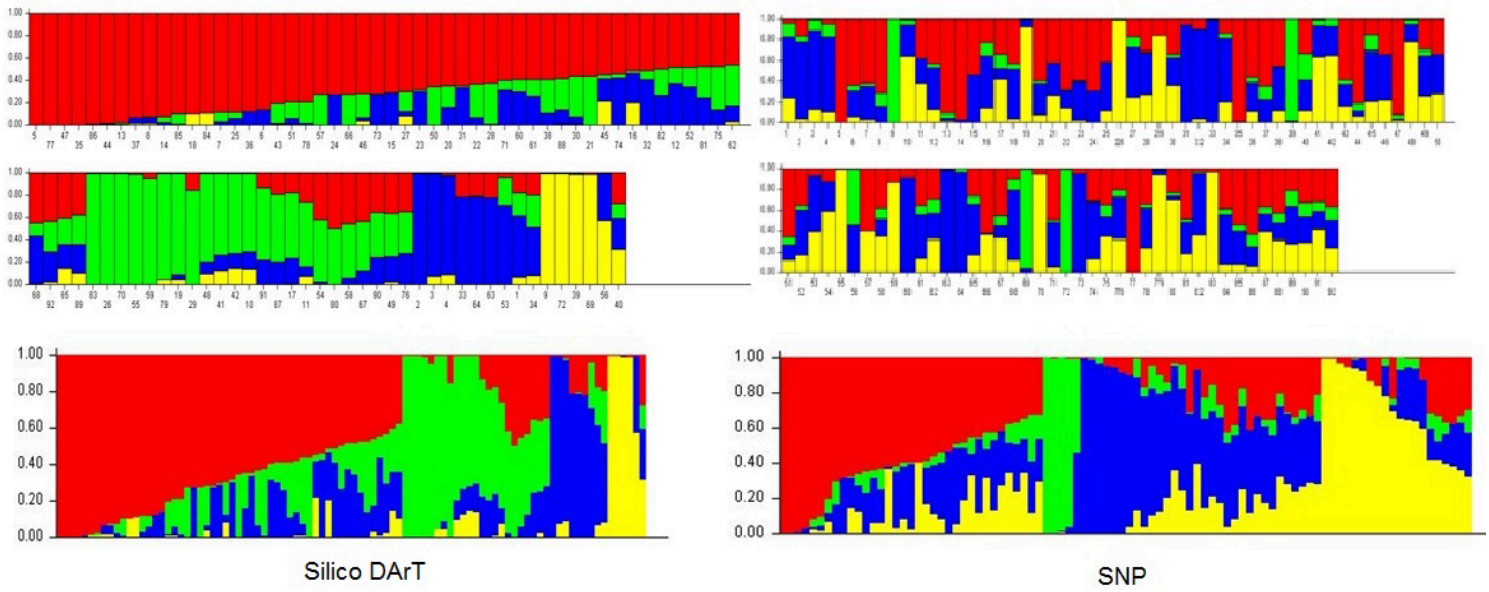


Figure 4

Distribution of the 92 durum wheat genotypes using SilicoDArT and SNP markers in subpopulations according to the structure analysis (k = 4). The individuals were represented in vertical bars, each color associated with a different group.

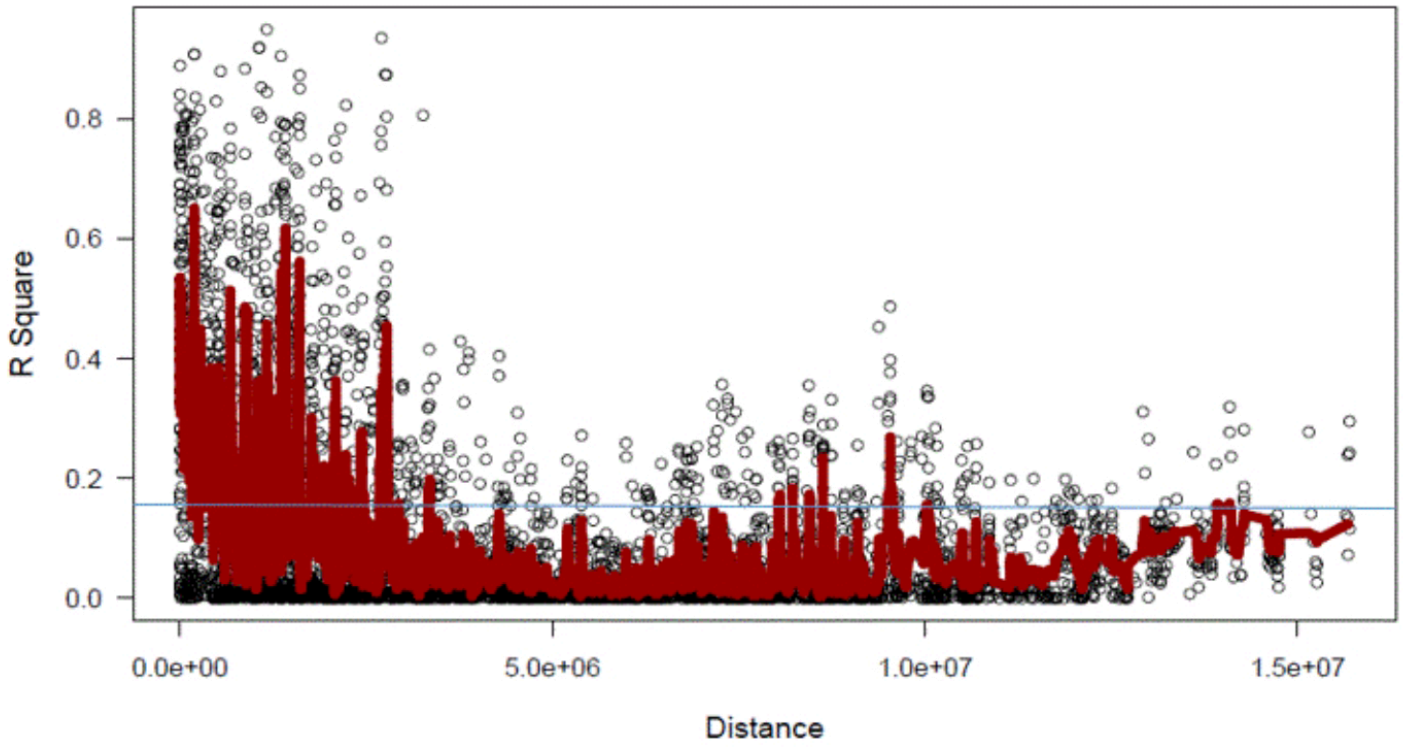


Figure 5

Reduction of linkage disequilibrium at the genome level

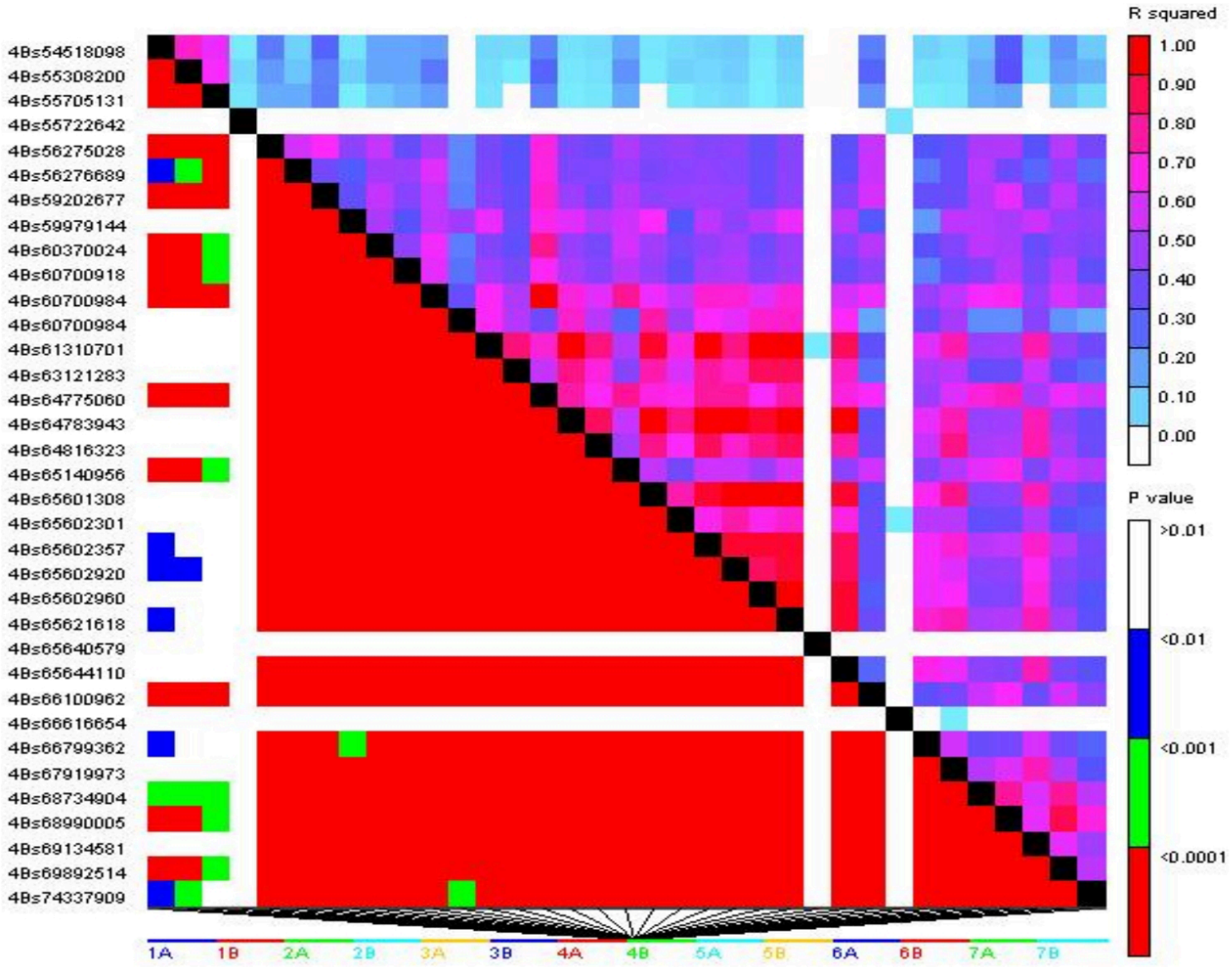


Figure 6

Distribution of some DArTseq markers on chromosome 4B

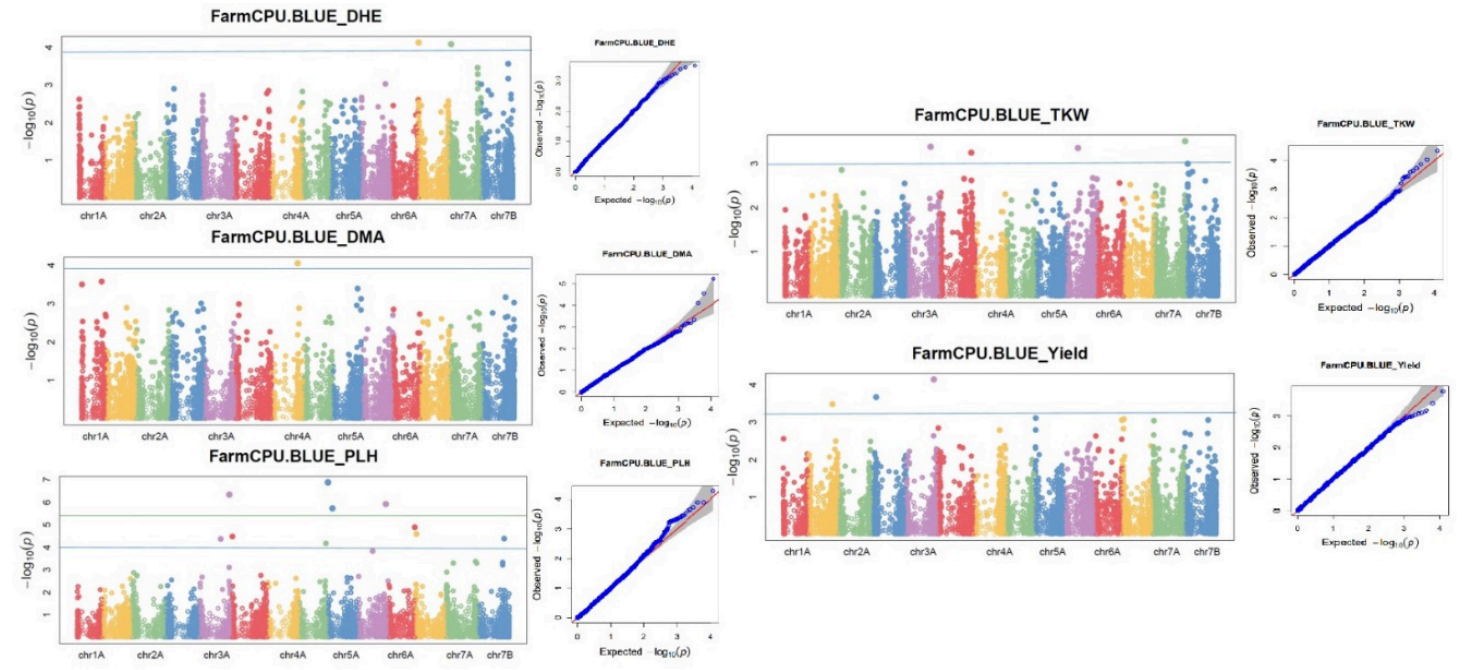


Figure 7

Manhattan plot resulting from linkage location along the length of durum wheat chromosomes in the crop year 2017 for the traits of day to flowering (DHE), day to maturity (DMA), plant height (PLH), thousand-grain weight (TKW) and grain yield

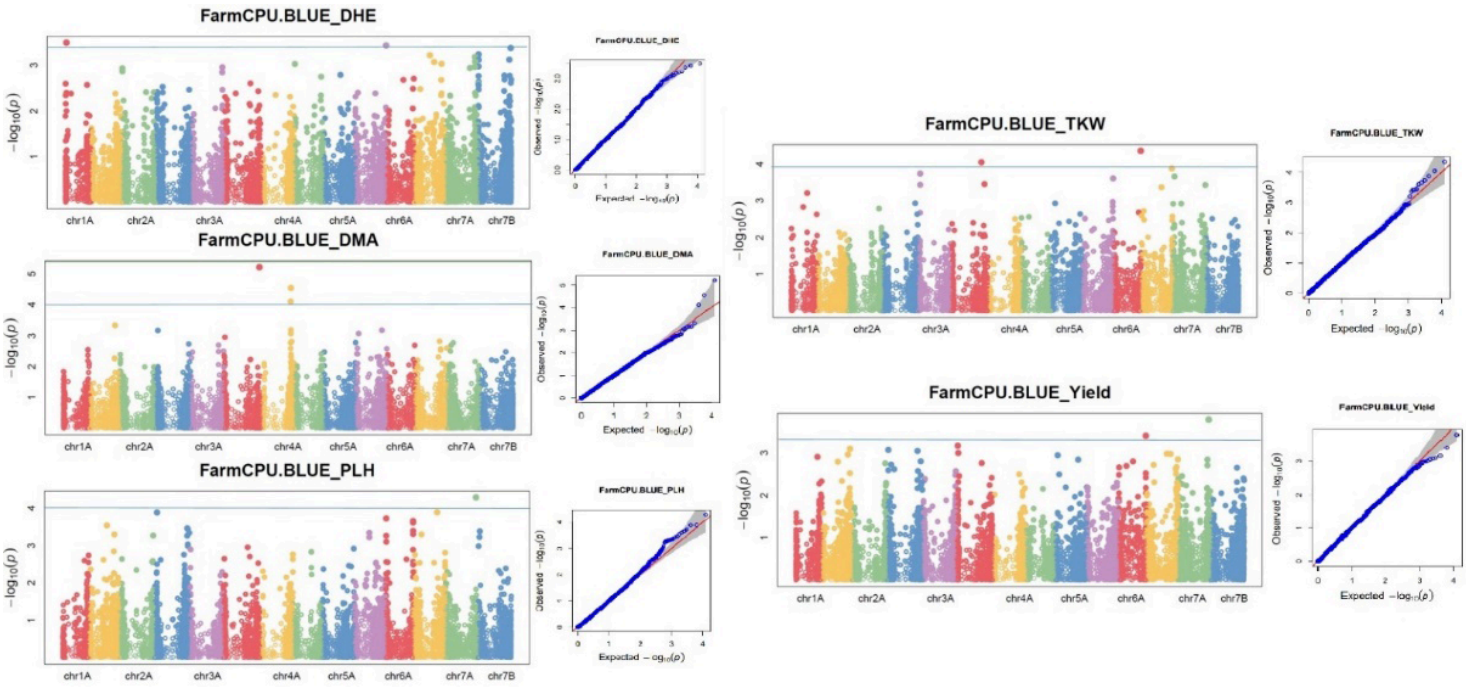


Figure 8

Manhattan plot resulting from linkage location along the length of durum wheat chromosomes in the 2018 crop year for the traits of day to flowering (DHE), day to maturity (DMA), plant height (PLH), thousand-grain weight (TKW) and grain yield

Supplementary Files

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