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Mapping Quantitative Trait Loci for Salt Tolerance in Durum Wheat: Current Coping Strategy Adaptation to Climate Change

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Abstract

Durum wheat (Triticum turgidum L. var durum) is one of the most widely grown food grain crop in the world however, durum production and productivity is highly depending on many factors. Salinity is one of the major environmental factors limiting its growth. Improving salt tolerance in durum wheat is a big challenge in the world particularly in the consumer's durum countries. The present study was conducted with the objective of investigating the genetic architecture of salt tolerance in F3 lines and their parents grown under salt stress to identify QTLs related to salt tolerance in durum wheat. A total of 163 F3 plants were subjected to salt stress at seedling stage. Fifty- seven polymorphic markers were used for genotyping F2 plants and their parents. Using composite interval mapping, two major QTLs for % DL were detected on chromosome 4B and 5B with 25% and 43% of the phenotypic variation respectively.

Keywords: Durum Wheat; Salt Tolerance; QTL Analysis; Composite Interval Mapping

Abbreviations: QTL: Quantitative Trait Locus; PCR: Polymerase Chain Reaction; SSR: Simple Sequence Repeats; %DL: Proportion of Dead Leaves

Introduction

Durum wheat is one of the oldest cultivated plants in the world which is grown currently in Italy and Canada and previously in the middle, near East region and North Africa. These regions are considered as the centers of origin and diversification of durum wheat [1]. The adaptation of durum wheat largely overlaps that of bread wheat but is less widely grown. Additionally, durum wheat is better adapted to Mediterranean dry land than bread wheat. Therefore over 80 % of the total world durum wheat area is in the Mediterranean basin [2]. and this is why durum has been cultivated in the driest areas of the West Asia and North Africa region. These areas, where durum wheat is grown, are facing an increase of temperature due to the climate change. Due to this global climate change, it is predicted that abiotic stresses will increase soon and have substantial impacts on crop yields. Salinity is one of these abiotic stresses, which lead to soil degradation. In the globe, 19.5% of the irrigated land is affected by salt stress compared to 2.1 % of the dry land [3]. This problem is more acute in arid and semi-arid areas because of high evaporation rates in the soil. To cope with this risk, several issues should be addressed in breeding durum wheat varieties resistant to salt stress and climate change. Salt stress altered water status leads to initial growth reduction and limitation of plant productivity [4,5]. The immediate response to salt stress is reduction in the rate of leaf surface expansion inducing plant death [6]. Salt stress also affected fresh and dry weights of leaves and stems by resulting in decreasing productivity. The suppression of growth occurs in all plants; however, the response to salt stress varied widely among different plant species [7]. This variation in response to salt stress created a new challenge for breeders to better understand the machinery involved in salt tolerance. Numerous QTLs related to salinity tolerance have been identified and characterized in wheat. The gene Kna1 for sodium exclusion was detected on chromosome 4D in bread wheat [8]. Two Na^+ exclusion genes were determined in durum: Nax1 on chromosome 2AL [9]. and Nax2 on chromosome 5AL [10-12]. The present study was conducted with the objective

of mapping QTLs controlling salt tolerance in F2:3 populations of durum wheat derived from a cross between Razzek (salt sensitive variety) and Saragolla (salt tolerant variety).

Materials and Methods

Phenotypic data using F2 population

F2 populations, derived from a cross between a salt tolerant variety Saragolla from Italy and a salt sensitive variety Razzek from Tunisia, were used in this study. The genetic material involved 163 F3 families, each derived from bagged seeds of a single F2 plant. F3 lines (six plants in each family) were used to evaluate the salt tolerance.

Genomic DNA isolation

DNA isolation was performed using leaves of 25-day-old plants. Extraction of the DNA from the leaf tissues was based on the CTAB method as described by Murray and Thomson. Chloroform-isoamyl alcohol (24:1) extraction was used to eliminate proteins and plant debris. The precipitation of DNA was occurred by adding 2-propanol, after that the precipitate was rinsed with 70% and then 95.5% ethanol. The final precipitate was dissolved in 50µl 1/10 TE and stored at 4°c.

Screening of SSR markers

The parental lines were subjected to genotypic screening using 244 SSR markers; and the primers exhibiting polymorphism (57) were used to amplify the DNA of each plant of F2 population issued from the cross between selected parents. The other primer sets were discarded because no band, or no polymorphic nature. Markers used in this study were chosen from previous studies: barc [13], cfa [14], cfd [15], gdm [16], gwm [17] and wmc [18].

PCR conditions and electrophoresis

Polymerase chain reaction (PCR) was carried out using 25 ng of template DNA. PCR amplification was performed on a thermal cycler (Biometra Uno II, Göttingen, Germany) in Plant Genetics and breeding Science (PGBS) laboratory of Japan. The PCR profile was maintained as initial denaturation at 94 °C for 2 min, and then the reaction was subjected to 40 cycles of 94 °C for 30 seconds, Annealing temperature for 1,3 min, and 72 °C for 30 seconds, with a final elongation step of 7 min at 72 °C. The annealing temperature changed depending on the marker. The amplification products were separated on 8% acrylamide gel with ethidium bromide in TBE buffer (10×). Finally, the gel was photographed using Kodak Digital Science EDAS 290 ver.3.6 with Kodak ID Image analysis software ver.3.5. Different bands for the same SSR primer were grouped according to their respective size by comparison with a 100 bp ladder DNA size marker.

Construction of genetic linkage maps and mapping of QTLs controlling salt tolerance

Genotypic data of 32 SSR markers were used for QTL analysis. This data set was used for mapping the quantitative trait loci correlated with salt-tolerance of F2:3 population. Map distances between primers were measured in cM using the [19]. Function of the mapping program. In order to determine both the linkage groups and the order of markers a Logarithmic Odds (LOD) score of 2.5 was used. The initial linkage map was constructed based on segregation at 32 microsatellite markers loci using Mapdisto software [20]. QTL cartographer [21]. used to identify QTLs affecting salt tolerance on the basis of composite interval mapping (Zeng 1994) analysis. The percentage of total phenotypic variation explained by each QTL, and the additive effects were estimated by this software. Test performed at 2-cM interval, and cofactors were selected by forward/backward stepwise regression (Model 6) with QTL Cartographer v 2.5 [21]. Significance threshold for Composite Interval Mapping (CIM) were determined at likelihood ratio (LR) 11.5 (LOD = 2.5). The phenotypic variation explained by a QTL (r2) conditioned by the CIM cofactors included in the model was calculated at the most likely QTL position. The additive effect of an allelic substitution at each QTL was also obtained. The LOD peak of each significant QTL was considered as the QTL location on the linkage map.

Results

Choice of parental lines for QTL analysis

Two parental lines were chosen among 119 genotypes, showing the highest variation of the proportion of dead leaves and belonging to different clusters [22]. These are Saragolla from Italy and Razzek from Tunisia. These parental lines, showing a higher phenotypic and genotypic variation, will be used with their progenies lines to detect QTLs controlling the %DL under salt stress.

Phenotypic data analysis of F3 population

The proportion of dead leaves (%DL) varied widely among the parental accessions and F3 plants grown under salt stress in pots. The tolerant parent (Saragolla) from Italy showed 0% of %DL, whereas the susceptible parent Razzek from Tunisia showed around 80% of %DL under salt stress. The frequency distribution for the proportion of dead leaves in the F3 plants ranged from 0 to 80% and was almost within the variation of their parents (Figure 1). The analysis indicated considerable differences between the parental cultivars and their F3 lines with regards to the variation in response to salt stress. Analyses of variance showed a significant variation (Table 1) within F3 plants due to the presence of segregation effect. The coefficient of heritability of %DL is greater than 0.5 (Table 1). This result showed that most of the variance for this trait is genetic, especially because of the higher diversity of genotypes regarding the same trait. This may reduce the environmental effect and thus Vg will be greater than Ve and giving a high value of heritability.

Linkage mapping and identification of QTLs controlling %DL under salt stress

Of the 244 markers screened using the parental cultivars Saragolla and Razzek, a total of 57 SSR primers generated polymorphic bands and showed a clear and polymorphic banding

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pattern between the parental cultivars. The polymorphic SSR markers were used for the construction of linkage maps and the mapping of the QTLs controlling salt tolerance in durum wheat. The final map constructed contained 32 SSR markers. Using composite interval mapping analysis, two QTLS controlling the proportion of dead leaves were identified in the F2:3 plants grown under salt stress conditions (Table 2): qDL4 on chromosome 4 and qDL5 on chromosome 5. The first QTL detected on chromosome 4B explained 25% of phenotypic variation; however, the second one on chromosome 5B explained 43% of phenotypic variation. QDL4 and qDL5 were mapped with an additive effect of 1.74 and -2.88 respectively.

Table 1: Analysis of variance of %DL within F3 plants.

Source of Variation	SS	DF	MS	F	P Value	Fcrit	VG*	VE*	VP*	Heritability
Between Groups	14593,24	5	2918,64	3,82	0,0019	2,22	1078,18	762,27	1840,45	0,59
Within Groups	750078,14	984	762,27	-	-	-	-	-	-	-
Total	764671,39	989	-	-	-	-	-	-	-	-

*VP (total phenotypic variance) = VG (genetic variance) + VE (environmental variance)

Table 2: QTLs for the proportion of dead leaves identified under salt stress.

QTLs	Chr	Interval	LOD	Additive Effect	Phenotypic Variation
qDL4	4	Gwm6 Wmc251	13.34	1.75	25
qDL5	5	Barc128 Gwm159	23.75	-2.85	43

Discussion

QTL analysis and phenotypic variation in F3 population

Most QTL mapping studies in cereals have been limited to seedling-stage tolerance because phenotyping for salt tolerance at reproductive stage is very tedious and time consuming. Few studies on salt tolerance have been conducted in durum wheat. There have been only few reports on QTL analysis of durum wheat salt tolerance at either the seedling or maturity growth stage. Salt tolerance has often been found to be associated with lower accumulation of sodium (Na) in the shoot. Using this trait and other related parameters of salt tolerance, major and minor QTLs have been mapped in various crop species [23,24]. As Na accumulation is highly dependent on transpiration rate, salinity tolerance may depend on crop growth stage. Many genes were associated with salt tolerance in different crops such as those members of the HKT (for high-affinity K^+ transporter) family of K+ and Na+ transporters [25,26] which are implicated to control natural variation in salinity tolerance at a number of loci in rice, wheat, and Arabidopsis. Two loci, Nax1 and Nax2, controlling shoot Na accumulation were identified by QTL mapping in durum wheat [27,10]. TmHKT7-A2 is the candidate for Nax1 on chromosome arm 2AL [28]. TmHKT1;5-A (HKT8) is the candidate for Nax2 on chromosome arm 5AL, and the corresponding homolog in the D genome (TaHKT1;5-D) is the candidate for the Kna1gene on chromosome arm 4DL, which is responsible for the superior salt tolerance of bread wheat compared with durum wheat [11]. Plant HKT transporters reduce shoot Na accumulation by facilitating the unloading of Na from the xylem [28,29]. Nax1 promotes Na retention in the leaf sheath relative to the leaf blade, whereas Nax2 and Kna1 do not affect this relative accumulation, suggesting that the former promotes xylem unloading of Na in the leaf sheath as well as in the roots [11]. Many researchers studied the relationship between salt tolerance, Na+ concentration and many others agronomic parameters [30,31]. In this study, the variation of the proportion of dead leaves within durum wheat varieties Saragolla and Razzek and their F3 plants grown under salt stress (Figure 1) might be related with their ability to prevent salt toxicity in the leaves. Additionally, the cause of the injury is probably due to the accumulation of salts (Na^+ and Cl^-) which overcomes the toxic concentrations. Thus, the old leaves die (usually old, expanded leaves) and the young leaves, no more supported by the export of photosynthates, undergo a reduction of growth and new leaves production [32]. In our study, most of F3 plants showed an increase in the proportion of dead leaves. This result is in accordance with other researchers [27]. who recorded that among susceptible genotypes, where salt is not effectively excluded from the transpiration stream, salt may accumulate to toxic levels in the leaves, resulting in the death of old leaves and injury to new leave that may become succulent in order to dilute the salts. Thus, only tolerant plants could cope with salinity stress and prevent salt from reaching toxic levels in the transpiring leaves by producing photo synthetically active leaves.

Identification of QTLs controlling the proportion of dead leaves under salt stress

During the linkage map construction, a large distance was observed between the adjacent markers compared to the previous studies maps. This result may be due to the few numbers

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of markers used in this study and the high distortion between them. This Segregation distortion could be observed in all types of populations, and it is frequently reported in various crops including wheat [30]. In our study, two QTLs for the proportion of dead leaves were detected under salt stress. These are qDL4 on chromosome 4B and qDL5 on chromosome 5B. These QTLs explained 25 and 43% of phenotypic variation respectively. The qDL4 was mapped in the region delimited by gwm6 and gwm251 (0.24 cM) (Figure 2) on chromosome 4B. A QTL for the proportion of dead leaves was mapped to the neighboring region of the marker gwm 251 on chromosome 4B by Turki et al. (2015) using association mapping analysis. Similary, [33] find that the region xgwm6-xgwm538 on chromosome 4B was a major locus for total dry weight under salt stress. Additionaly, a QTL controlling seedling shoot biomass and tiller number was located in a similar region, both near the marker xgwm6 [30]. This region could be considered in future studies to improve salinity tolerance in durum wheat, and the marker xgwm6 could be also useful in MAS breeding. The qDL5 was mapped in the region delimited by barc128 and gwm159 with long distance (0-55 cM) (Figure 5). QTLs for the number of leaves and the root length were reported by [22]. in a region adjacent to qDL5. Similary, [34] mapped a QTL for shoot fresh weight using 254 recombinant inbred lines (RILs) at seedling stages. The long distance found between flanking markers in qDL5 gave inaccuracy about its location between these two markers. For this reason, further analyses were conducted in order to better understand the relationship between this QTL and flanking markers. For this regard, association between alleles at franking marker loci and variation in phenotypic values were evaluated among durum varieties used in this study. The phenotypic data (%DL) was recorded among all genotypes exhibited the same allele of each parent. Regarding qDL4, the genotypes at SSR loci co-segregated with salinity tolerance, these results were confirmed by the significant (α=0.05) variation between tolerant and susceptible varieties on the basis of %DL (Table 3,4). Indeed, tolerant varieties presenting the same allele as "Saragolla" (tolerant parent) had mostly a lower proportion of dead leaves however, susceptible varieties exhibited the same allele as "Razzek" (susceptible parent) had mostly a higher %DL (Figure 3,4). The marker gwm159 was mapped with the genetic distance of 55 cM but the linkage between gwm159 and qDL5 was not confirmed because there was no difference in %DL between tolerant and susceptible varieties at gwm159 locus (Table 5). These results were also confirmed by the frequency distribution of tolerant and susceptible varieties (Figure 5). Further experiments are still needed to confirm the location of qDL5 using backcross or by increasing more markers in this region.

Table 3: Analysis of variance of %DL of varieties with same alleles as tolerant and susceptible parents at gwm6 locus.

SUMMARY						
Groups	**Number of varieties**	**Sum**	**Average**	**Variance**		
Tolerant varieties	18	604	33.55556	318.3791		
Susceptible varieties	8	423	52.875	184.4107		
ANOVA						
Source of variation	**SS**	**df**	**MS**	**F**	**P-value**	**F crit**
Between varieties	2067.181	1	2067.181	7.401159	0.011931	4.259677
Within varieties	6703.319	24	279.305			
Total	8770.5	25				

Table 4: Analysis of variance of %DL of varieties with same alleles as tolerant and susceptible parents at gwm251 locus.

SUMMARY						
Groups	**Number of varieties**	**Sum**	**Average**	**Variance**		
Tolerant varieties	24	771	32.12	294.8		
Susceptible varieties	28	1357	48.46	330.55		
ANOVA						
Source of Variation	**SS**	**df**	**MS**	**F**	**P-value**	**F crit**
Between varieties	3450.103	1	3450.103	10.983	0.001715	4.034
Within varieties	15705.59	50	314.111			
Total	19155.69	51				

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Table 5: Analysis of variance of %DL of varieties with same alleles as tolerant and susceptible parents at gwm159 locus.

SUMMARY						
Groups	**Number of varieties**	**Sum**	**Average**	**Variance**		
Susceptible varieties	14	550	39.28571	300.2198		
Tolerant varieties	17	614	36.11765	350.4853		
ANOVA						
Source of Variation	**SS**	**df**	**MS**	**F**	**P-value**	**F crit**
Between varieties	77.05557	1	77.05557	0.23496	0.631512	4.182964
Within varieties	9510.622	29	327.9525			
Total	9587.677	30				

QTLs for leaf mortality were mapped in several chromosomes, while no QTL for this parameter was detected on chromosome 4B. In this study qDL4 and qDL5 were detected with small additive effect. This finding was in according with [30]. who detected 6 QTLs for leaf symptoms under salt stress with small additive effect: 4 QTLs with negative additive effect and 2 QTLs with positive effect? The smaller additive effects reflect the dominance of some genes which can appear at different salinity levels and might be beneficial in a breeding program aiming at increased salinity tolerance. The higher non additive component suggested that the pattern of inheritance was complex [35]. as was reported in sorghum at higher salinity levels [36]. Inheritance mechanism of salinity tolerance appeared to be complex, whereas in pearl millet the additive genetic components were less than the additive components in controlling degree of salt tolerance [37]. In this study, qDL4 was mapped in chromosome 4B with positive additive effect, this is meaning that Saragolla decrease the proportion of dead leaves on chromosome 4B, while Razzak decrease %DL on chromosome 5B. Furthermore, [38]. reported in his study on bread wheat 5 QTLs for leaf injury index which explain 35% of phenotypic variation. These QTLs were as follows: 1 QTL on chromosome 3A, 1 QTL on chromosome 5B, 2 QTLs in chromosome 6B and finally 1 QTL on chromosome 6D. Zhou et al, 2012 identified a single QTL for leaf injury under saline conditions. The QTL in the syntenic region as the previously reported Nax1 locus in wheat which explained 40% of shoot Na+ exclusion [9]. This finding suggests that gene(s) for shoot Na+ exclusion which associate with salt tolerance are present in this QTL region. Nax1 (HvHKT1;4) removes Na^+ from the xylem in the root, older leaves and leaf sheath and therefore reduces leaf blade/ leaf sheath ratio [39]. In other crops such as rice, barley and sorghum, leaf death rate was considered as a selective parameter for salt tolerance. In our previous study, we detected a correlation between this parameter and yield related parameters [40-45]. Similary, the survival of plant is highly depending on leaf death rate. If production of new leaf is more than older leaves then plant has enough leaves for flowers and seeds production. Conversely, if death rate of older leaves is greater than the leaves produced plant might not stay alive. Thus, this parameter was important for the evaluation of durum wheat under salt stress.

Conclusion

Despite the few numbers of markers used in this study we succeeded to identify new QTLs for the proportion of dead leaves with major effects. However, the assessment of salt tolerance using F3 population under field conditions is still needed to confirm the stability of these QTLs.

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