Heat Tolerance in Common Wheat

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Heat tolerance (HT) in plants is the capacity of plants to tolerate heat stress. It is a quantitative trait involving complex genetic, physiological, and biochemical controls and is affected by environmental factors. In response to heat stress, tolerant varieties generally activate an antioxidant defence system, express heat shock proteins (HSPs) and reduce senescence by staying green.

heat tolerance (HT) seedling stage recombinant inbreed lines (RILs)

1. Introduction

Heat has become a serious constraint for wheat production with global climate change ^[1]. Its damage may happen in arid, semiarid, tropical, and subtropical regions of the world ^[2]. Each 1 °C rise in temperature above the optimum can cause a 3–5% reduction in grain weight under both controlled environments ^[2] and field conditions ^[3]. Moreover, heat stress may affect not only harvest and yield but also grain quality ^[4]. Though reproductive stage is most sensitive for final yield and the most studied stage ^[5], heat damage may happen during different growth and developmental stages in the crop including seedling stage ^[6].

Heat tolerance (HT) in plants is a quantitative trait involving complex genetic, physiological, and biochemical controls and is affected by environmental factors. In response to heat stress, tolerant varieties generally activate an antioxidant defense system, express heat shock proteins (HSPs) and reduce senescence by staying green ^[Z]. Genotype evaluation at different stages is necessary to better understand the HT mechanism and to breed tolerant cultivars. Grain yield is significantly correlated with seedling traits such as root length and shoot length ^[B]. If the plant does not survive at a seedling stage, there will be no harvest. Seedlings have greater stress avoidance and resilience than reproductive organs ^[D], and seedling establishment often has large impact on crop yield ^[10]. Some genes that contribute to seedling HT may also contribute to later stage tolerance ^[11]. In response to heat stress, heat shock proteins play important roles at both seedling and reproductive stages ^[12]. Moreover, some reports indicated that some particular QTLs at seedling stage and reproductive stage were collocated on the same chromosomes ^[13], and some well-known heat-induced genes at reproductive stage were found significantly enhanced in acetylation levels in wheat seedlings ^[14]. Therefore, QTL identification and validation for seedling stage may help to understand the mechanism of heat tolerance at different stages.

Early-stage screening for seedlings began to attract the attention of scientists and breeders to study wheat tolerance under heat stress. However, in the limited number of such studies, the target traits were mainly focused on particular physiological indices such as chlorophyll content and chlorophyll fluorescence parameters ^[15] or on

traits of seedling shoot or leaf ^[6]. Root traits have seldom been studied for heat tolerance in wheat. Vigor and deep root systems are believed to contribute to water-deficit resistance ^[16]. Long root and shoot lengths at the seedling stage were reported to be highly correlated with high grain yield in lentil ^[17]. Initial root parameters and above-ground biomass were also reported to be positively correlated in wheat ^[16]. Genotypes with deep roots are able to extract water from lower soil by making use of water lost in the form of deep percolation ^[11].

Moreover, it was observed in the previous research on wheat cultivars that the seedling lengths reduced considerably under heat stress compared to the controls ^[18]. Meanwhile, the root length was found to be decreased the most with variation among varieties under heat stress compared to other root traits such as root surface area, root diameter, and root volume, etc., on an overall basis. Therefore, length-related traits were selected for measurement and comparison.

The genetic mechanism of seedling tolerance to heat stress remains largely unknown so far, and the reported study of HT in wheat was mainly focused on reproductive and grain-filling stages [19]. To date, QTL mapping for wheat response to heat has identified several OTL for yield and key morpho-physiological characteristics, for example, Yang et al. ^[20] found QTL on the short arms of chromosomes 1B and 5A linked to grain-filling duration. Mason et al. [21][22] reported several QTL for heat susceptibility indices and yield traits on chromosomes 1A, 1B, 2A, 2B, 3B, 5A, and 6D. Paliwal et al. ^[23] reported OTL on chromosome 2B, 7B, and 7D for thousand grain weight, grain fill duration, and canopy temperature depression, respectively. Vijayalakshmi et al. ^[24] reported QTL on chromosomes 2A, 3A, 4A, 6A, 6B, and 7A with significant effects on grain yield, grain weight, grain filling, stay green, and senescence-associated traits under post-anthesis high temperature stress in wheat. All these studies focused on the reproductive stage, and there has rarely been reports for HT at seedling stage. Crop improvement demands an extensive search for genetic variability and comprehensive understanding of genetic mechanism, so traits conferring HT must be explored thoroughly to maximize germplasm exploitation ^[25]. The identification of QTL or genes related to HT during wheat seedling stage may help dissect the molecular mechanism of HT in wheat through a comparative study of the plant response to heat at seedling and reproductive stages. International Triticeae Mapping Initiative (ITMI) mapping population derived from synthetic hexaploid wheat 'W7984' and bread wheat cultivar 'Opata' is available at the GrainGenes database, and it is a useful resource to identify QTL ^[26]. This population facilitated the development of the first RFLP [27] and SSR [28] linkage maps in wheat. It has been used for QTL identification of different abiotic stresses such as drought and waterlogging, etc., in wheat [29][30][31].

2. Chromosome 4D Quantitative Trait Locus Hotspot Conferring Heat Tolerance in Common Wheat

Phenotypic variation in the population was high for all the traits investigated in this research, which was fundamental for the successful identification of QTL conferring HT at the seedling stage. Mapping information of the ITMI population is available at GrainGenes database, and it has been successfully used for some QTL identification of different abiotic stresses in wheat ^{[29][30][31]}. Alsamadany investigated the diversity of heat tolerance performance of 499 genotypes with different origins at seedling stage under heat stress ^[32]. In his study, Opata 85 was identified as heat-tolerant at seedling stage, while synthetic W7984 was identified as heat-susceptible at

seedling stage. Because of the high variation between the two parents of the ITMI population, researchers consider it a good material for identification and validation of QTL associated with heat stress.

Early stage phenotypic screening has been conducted on traits including plant fresh weight, dry weight, carbon isotope discrimination, canopy temperature, and spectral reflectance indices, etc., for the selection of tolerant genotypes ^[33]. Researcher have previously investigated the relationship between heat tolerance at the seedling stage and reproductive stage and found significant correlations in response to heat stress between the two stages ^[18]. As the plant materials in this research were young and small, the variations in some traits such as plant fresh weight and dry weight were relatively low in general. In the previous research, it was found that there were variations in the seedling lengths, especially root lengths, among different wheat genotypes under heat stress condition ^[18], so researcher chose seedling length and corresponding DI for phenotypic screening in this research. DI is the ratio of the decrease in length under heat stress treatment to the length in the non-stress condition ^[32], it was extensively used in HT research and breeding. In this research, a QTL hotspot was identified by both direct length under heat stress, and DIs derived from length related traits. Thus, seedling length, especially root length under heat stress, could be used as a selection criterion apart from DIs to evaluate HT performance at seedling stage.

Six QTL conferring seedling heat tolerance with high LOD and R² were identified on chromosome 4D with the same flanking SSR markers (Xmwg634 and Xbarc225). Researcher searched the genes within this QTL hotspot, and in total, 572 genes with their function annotations (IWGSC Annotation v 2.1) were found; three genes, namely, "TraesCS4D01G009600LC.1", "TraesCS4D01G018700LC.1", and "TraesCS4D01G046000LC.1", were described as related to heat stress and are worth further focusing on. "TraesCS4D01G009600LC.1" is related to DNAJ heat shock N-terminal domain-containing protein, "TraesCS4D01G018700LC.1" is related to heat stress transcription factor A-9, and "TraesCS4D01G046000LC.1" is related to Class I heat shock protein [34]. The genomic region of 4D was also reported as a rich hub for genes controlling yield and yield-related agronomic traits in previous studies ^[35] ^[36][37][38]</sup>. Some QTL were already identified on chromosome 4D as related to spike dry weight ^[33], grain yield ^[39], as well as plant height [37]. Cabral et al. [37] reported a significant QTL for the grain shape traits located on chromosomes 4D, accounting for up to 53.3% of the total phenotypic variation; in addition, similar to the situation in this entry, several QTL associated with various traits were also found to locate at the same locus: For example, the most significant QTL for plant height, 1000 grain weight, and test weight were also detected on chromosome 4D at the same locus, suggesting that the hot spots on chromosome 4D may harbor some key genes related to yield in common wheat. It is notable that some major OTL clusters (\geq 15 individual OTL) were previously identified in MOTL regions on 4D, appearing to align with markers for dwarf gene Rht-D1 [40]. It suggests that the chromosome 4D region may play key roles in determining agronomic traits, which could affect all developmental stages including seedling and adult stages.

The QTL hotspots, as genomic regions rich in QTL, are important since they may harbor key genes for the quantitative traits ^[41]. The introgression of such a QTL-hotspot region was reported to enhance drought tolerance and grain yield in chickpea cultivars ^[42].

A group of genes within an organism that were inherited together from a single parent is called a "haplotype", and haplotype-based breeding has been regarded recently as a promising breeding approach ^[43]. In this research, the six major QTL in the QTL hotspot associated with different HT traits were all contributed by the tolerant parent Opata. QTL hotspot with a series of individual QTL clustered together may be the genetic region rich of favorable haplotypes. For example, a QTL hotspot on chromosome 2 in sweet cherry was used for positive selection of favorable haplotypes ^[44].

All the major QTL in this entry and previously reported QTL on the same chromosomes identified under heat stress (HS) or heat and drought combined stress (HS + DS) were compared ^{[20][24][39][45][46][47][48]}, no overlapping was found. The closest distance was about 11.6 Mbp between QRIhti.uwa.3D in this research and MQTL3D.1 identified by Liu et al. ^[48]. Researcher further compared the QTL hotspot in this research with previously identified yield-related genomic region on chromosome 4D ^{[37][39][46][48][49][50][51][52][53][54][55], it was found that some particular regions were within the identified locus in this entry. These particular genomic regions include MTAs (marker trait association) associated with grain number ^[56], QTL associated with spike number and thousand-grain weight, and a gene (Rht2) associated with plant height ^[48], suggesting that the identified QTL hotspot in this research may be related to yield-component traits of common wheat.}

Normally, the validation of the identified QTL is carried out by validating the flanking markers of QTL in other cross populations ^[30]. In this entry, researcher used a different approach for QTL validation, which is validating the flanking SSR marker by other kind of marker (i.e., SNP marker), if the two kinds of markers could agree with each other for both the genotypic and phenotypic data, then the QTL was considered to be validated. Therefore, in this entry, six QTL on chromosome 4D were identified and validated by genotyping-phenotyping association analysis using SNP assays.

A series of QTL related to wheat yield under abiotic stress were identified or validated by the same ITMI Synthetic/Opata population. For example, Onyemaobi et al. ^[30] identified and validated a major chromosome region for high grain number per spike under meiotic stage water stress. Two major QTL were detected on chromosome 5A when plants were exposed to water stress during meiosis, and one QTL was detected on chromosome 2A under normal watering condition. In another study, a high-density linkage map was constructed for seedling morphology under drought stress in common wheat by using synthetic/Opata population ^[29]. The map consisted of 2639 genotyping-by-sequencing markers and covered 5047 cm with an average marker density of 2 markers/cm. Moreover, 16 identified QTL explained 4 to 59% of the phenotypic variance. An interesting phenomenon is that most of the positive alleles identified in the previous studies were mostly contributed by parent Synthetic W7984, whereas for the current heat tolerance study, the positive alleles were mostly contributed by parent Opata, suggesting that different parents may contribute to resistance against different abiotic stresses, which emphasized the importance of germplasm diversity in practical breeding.

Much is unclear about the genetic mechanism of heat tolerance in wheat so far; therefore, it is important to further study HT at different developmental stages. A comparative study of the QTL between early stage and adult stage

may provide a better understanding of the genetic mechanism of HT in wheat. The major QTL, especially the QTL hotspot, should be further studied for fine mapping and functional research for breeding of heat-tolerance.

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