

The Role of Quantitative Trait Loci Mapping in Advancing Drought and Heat Stress Tolerance in Cereals

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ABSTRACT

Climate change has intensified the frequency and severity of drought and heat stress, posing a major challenge to global cereal production. Quantitative trait loci (QTL) mapping has emerged as a powerful tool for dissecting the genetic architecture of complex traits associated with abiotic stress tolerance in crops such as rice, wheat, maize, barley, and sorghum. This review highlights the advances in QTL identification, validation, and utilization for improving stress tolerance in cereals. We summarize key QTLs associated with drought avoidance, osmotic adjustment, root architecture, flowering time regulation, and grain yield under stress. The integration of traditional QTL mapping with genome-wide association studies (GWAS), marker-assisted selection (MAS), and genomic selection has accelerated the translation of discoveries into breeding programs. Despite these advances, challenges remain in the stability of QTLs across environments, epistatic interactions, and the need for high-throughput phenotyping to match genomic data. Future perspectives emphasize the role of multi-omics integration, genome editing, and pan-genomic resources in refining QTL-based breeding for climate-resilient cereals. By bridging molecular genetics with applied breeding, QTL mapping continues to play a pivotal role in ensuring food security under changing climates.

Keywords: Quantitative trait loci, cereals, drought tolerance, heat stress, marker-assisted breeding, GWAS, genomic selection, crop improvement

1. Introduction

Cereal crops such as rice (*Oryza sativa*), wheat (*Triticum aestivum*), maize (*Zea mays*), barley (*Hordeum vulgare*), and sorghum (*Sorghum bicolor*) serve as the foundation of global food systems, collectively providing more than half of the daily caloric intake for the world's population. Their central role in food and nutritional security makes them particularly vulnerable to the challenges posed by climate change. Among the abiotic stresses affecting agriculture, drought and heat stress are the most widespread and damaging, often occurring simultaneously and compounding their negative effects [1]. These stresses disrupt critical physiological processes such as photosynthesis, pollination, and grain filling, ultimately leading to yield losses that threaten the stability of food production systems. Projections indicate that by 2050, crop yields in many regions could decline significantly due to increasing frequency and intensity of drought and heat waves, making the development of stress-tolerant cereal varieties a pressing scientific and agricultural priority.

Conventional breeding approaches have historically contributed to yield gains and stress adaptation in cereals, progress has often been slow when dealing with traits governed by complex genetic architectures. Drought and heat tolerance are classic examples of polygenic traits, meaning that they are controlled by multiple genes of small effect, influenced by environmental conditions, and often accompanied by strong genotype × environment interactions [2]. Traditional breeding strategies such as recurrent selection or phenotypic selection have limited efficiency when applied to these traits, largely because accurate phenotyping is challenging, and the heritability of stress tolerance traits tends to be low.

Thus, there is a strong need for modern genetic tools that can dissect the underlying genetic basis of stress responses and enable breeders to make precise and informed selections.

Quantitative trait loci (QTL) mapping has emerged as one of the most powerful tools in plant genetics for studying complex traits. QTLs are genomic regions associated with phenotypic variation, and their identification allows researchers to link observable traits to underlying genetic determinants. The concept of QTL mapping revolutionized crop genetics in the late 20th century, when the availability of molecular markers such as restriction fragment length polymorphisms (RFLPs), simple sequence repeats (SSRs), and later single nucleotide polymorphisms (SNPs), allowed precise mapping of chromosomal regions associated with traits of agronomic importance. Since then, QTL mapping has been widely applied to cereals, leading to the discovery of numerous QTLs conferring tolerance to drought and heat stress [3].

QTL mapping is that it allows breeders to identify and track genomic regions that may not have visible phenotypic expression under normal growing conditions but provide a yield advantage under stress. For example, in rice, major QTLs such as *qDTY12.1* and *qDTY3.1* have been reported to enhance yield under drought conditions, while in sorghum and maize, QTLs associated with the stay-green trait contribute to both drought and heat resilience [4]. These findings have paved the way for marker-assisted selection (MAS) and marker-assisted backcrossing (MABC), where beneficial QTLs are introgressed into elite varieties without compromising yield potential under favorable conditions.

QTL mapping has evolved significantly. Traditional biparental QTL mapping, while useful, has limitations in terms of resolution and genetic diversity.

Genome-wide association studies (GWAS) have complemented this by enabling the exploration of natural variation in diverse germplasm collections, identifying novel loci with higher precision. Furthermore, the integration of QTL mapping with genomic selection (GS) approaches has expanded the predictive power of breeding programs, allowing the simultaneous capture of large- and small-effect alleles across the genome. High-throughput genotyping platforms and next-generation sequencing have accelerated the pace of QTL discovery, while advanced phenotyping tools such as drones, imaging technologies, and sensor-based platforms are improving the accuracy of trait measurement under field conditions, significant challenges remain in fully harnessing QTLs for breeding drought- and heat-resilient cereals. Many identified QTLs explain only a small proportion of phenotypic variation, and their effects often vary across environments, limiting their direct application in breeding programs. Additionally, interactions among QTLs (epistasis) and pleiotropic effects complicate the translation of genetic discoveries into practical outcomes [5]. To overcome these hurdles, researchers are increasingly integrating multi-omics approaches, including transcriptomics, metabolomics, and proteomics, to better understand the molecular networks underlying stress responses. Genome editing technologies such as CRISPR-Cas are also being deployed to validate candidate genes within QTL regions and engineer specific allelic variants that confer stress resilience. QTL mapping stands as a cornerstone of modern plant breeding, bridging the gap between molecular genetics and applied crop improvement. The identification and deployment of QTLs for drought and heat tolerance not only hold promise for stabilizing yields under adverse conditions but also contribute to the broader goal of sustainable agriculture in a changing climate. This review provides a comprehensive overview of the role of QTL mapping in advancing drought and heat stress tolerance in cereals. It examines the progress achieved in mapping key QTLs, their integration into breeding programs, the limitations that remain, and the future perspectives for leveraging QTL knowledge in the genomic era. By doing so, it aims to highlight both the scientific advances and practical implications of QTL research in ensuring global food security.

2. QTL Mapping for Drought Tolerance in Cereals

Drought tolerance in cereals is a multifaceted trait governed by a wide range of morphological, physiological, and biochemical adaptations. Because these adaptations are controlled by many small-effect genes distributed across the genome, quantitative trait loci (QTL) mapping has become a vital tool in identifying genomic regions that underpin stress-resilient traits. Through careful linkage and association mapping studies, researchers have been able to dissect the genetic basis of drought responses and apply this knowledge to cereal improvement programs [6]. One of the most critical traits linked to drought resilience is root system architecture. Deep and extensive root systems allow plants to access water stored in deeper soil layers, thereby sustaining physiological functions during prolonged water scarcity. QTL mapping studies have revealed several loci controlling root-related traits across cereals. In rice, QTLs such as *qDTY1.1* and *qDTY3.1* have been consistently associated with improved yield under drought, largely due to enhanced root depth and distribution. In maize, QTLs located on chromosome 1 regulate root angle and density, traits that determine the plant's ability to capture soil moisture.

Such QTLs are particularly valuable because root phenotyping is challenging under field conditions, yet genetic markers allow indirect selection for improved root traits, physiological mechanisms such as water-use efficiency (WUE) and osmotic adjustment play central roles in drought adaptation. QTLs associated with traits like leaf rolling, relative water content, and stomatal conductance have been identified in wheat and sorghum, indicating conserved genetic pathways across cereals [7]. These physiological adaptations minimize water loss, maintain cell turgor, and support photosynthesis under stress. For example, QTLs controlling osmotic adjustment help plants accumulate compatible solutes, which buffer metabolic processes against dehydration. Marker-assisted selection (MAS) targeting these QTLs enables breeders to combine multiple physiological traits that collectively enhance drought resilience.

Perhaps the most significant outcome of drought-related QTL mapping is its contribution to stabilizing grain yield under stress. Grain yield is the ultimate trait of interest for breeders and farmers, but it is highly sensitive to drought during reproductive and grain-filling stages. Large-effect QTLs such as *qDTY12.1* in rice have shown consistent contributions to yield across multiple environments and genetic backgrounds. Such stability makes them prime candidates for marker-assisted backcrossing (MABC), where beneficial QTLs are introgressed into elite but drought-sensitive cultivars. This approach has already produced rice varieties that maintain higher yields under drought without sacrificing performance under normal conditions, highlighting the practical utility of QTL mapping in breeding programs, QTL mapping has significantly advanced our understanding of the genetic architecture underlying drought tolerance in cereals [8]. The identifying loci associated with root traits, physiological adjustments, and yield stability, researchers have provided a genetic toolkit for breeders to develop resilient cultivars. However, the translation of QTL discoveries into field-ready varieties requires careful validation across diverse environments, as drought is inherently variable in intensity, duration, and timing.

3. QTL Mapping for Heat Stress Tolerance

Heat stress is a major abiotic constraint on cereal productivity, particularly during the reproductive and grain-filling stages. High temperatures during flowering disrupt pollen viability and fertilization, while stress during grain filling accelerates senescence, reduces kernel weight, and lowers overall yield. Because heat tolerance is a complex quantitative trait, QTL mapping has been instrumental in identifying the underlying genomic regions that contribute to plant resilience.

One of the most studied traits associated with heat tolerance is the stay-green phenotype, which is characterized by delayed leaf senescence and prolonged photosynthetic activity under stress conditions. In both sorghum and maize, several stay-green QTLs have been identified that allow plants to maintain chlorophyll content and sustain carbon assimilation during episodes of heat and drought stress. These QTLs not only contribute to yield stability under adverse environments but also represent robust targets for breeding programs, as the stay-green trait is relatively easy to phenotype and correlates strongly with grain yield [9]. Another critical target for QTL mapping is grain filling and spike fertility, which are highly sensitive to elevated temperatures. In wheat, QTLs located on chromosomes 3B and 6D have been shown to regulate both grain number and kernel weight under heat stress.

These loci influence processes such as pollen fertility, ovary development, and assimilate partitioning, ultimately determining yield potential in hot climates. Incorporating these QTLs into breeding pipelines through marker-assisted selection could significantly enhance the resilience of wheat cultivars to terminal heat stress, a frequent occurrence in regions with late-season temperature spikes.

Flowering time regulation is another mechanism through which cereals adapt to heat stress. Heat tolerance is often associated with altered phenology, as plants that flower earlier can avoid the most damaging temperature extremes. QTLs for early flowering have been reported in barley and wheat, with several loci showing pleiotropic effects on yield under stress conditions. By fine-tuning flowering time through genetic selection, breeders can align crop development with more favorable thermal windows, reducing yield losses due to heat waves. QTL mapping has provided critical insights into the genetic basis of heat tolerance in cereals [10], traits such as stay-green, grain filling, and flowering time regulation, breeders now have genomic tools to develop cultivars that maintain productivity under rising global temperatures. The integration of these QTLs into molecular breeding programs represents a promising strategy for sustaining cereal yields in heat-stressed environments.

4. Integration with Marker-Assisted Selection and GWAS

Traditional QTL mapping has provided valuable insights into stress tolerance, but the genomic intervals identified are often large and contain multiple candidate genes. For breeding applications, fine mapping is essential to narrow these regions to specific functional alleles. Marker-assisted selection (MAS) has been particularly effective in utilizing major drought-related QTLs. For instance, qDTY2.2 and qDTY3.1 have been introgressed into high-yielding rice cultivars, significantly improving yield under water-limited conditions without compromising performance in irrigated environments. These successes highlight the utility of QTLs with consistent effects across multiple environments and genetic backgrounds, genome-wide association studies (GWAS) have revolutionized QTL discovery by leveraging natural genetic variation in diverse germplasm panels. GWAS provides higher resolution than biparental mapping and can uncover novel alleles associated with stress adaptation. For example, in maize, GWAS has identified several loci linked to the anthesis-silking interval, a critical trait influencing drought tolerance [11]. The integration of GWAS and MAS enables breeders to harness both well-established QTLs and novel alleles for improving stress resilience in cereals.

5. Emerging Tools Enhancing QTL-Based Breeding

The increasing complexity of stress tolerance traits has driven the adoption of advanced tools that complement QTL mapping.

- **Genomic Selection (GS):** Unlike MAS, which relies on a few major QTLs, GS uses genome-wide marker data to predict the breeding value of individuals, thereby capturing both small- and large-effect loci. This approach has accelerated breeding cycles in crops like wheat and maize by enabling early selection of superior lines.
- **Multi-omics Integration:** Combining transcriptomics, metabolomics, and proteomics with QTL mapping allows for the functional dissection of stress responses. For instance, metabolite-QTL (mQTL) studies have revealed drought-related pathways involving osmolyte accumulation and

antioxidant metabolism, providing molecular markers closely tied to physiological responses.

- **Genome Editing:** CRISPR-Cas technologies now allow for the direct validation of candidate genes underlying QTLs. Editing stress-responsive alleles provides a precise method to enhance tolerance traits while minimizing linkage drag.
- **Pan-genomics:** By examining structural variation across multiple genotypes, pan-genome studies expand the understanding of genetic diversity underlying stress adaptation. This approach uncovers rare alleles and presence-absence variations that conventional QTL mapping might overlook.

6. Challenges in QTL Mapping for Stress Tolerance

The significant advancements, QTL-based breeding for stress tolerance faces persistent challenges. One major limitation is environmental instability, as many QTLs are highly context-dependent and lose statistical significance under variable field conditions. This complicates their direct use in breeding programs that target wide adaptation. A second challenge is the small effect size of most QTLs. While a few large-effect loci have been identified, the majority explain only a small fraction of phenotypic variation, making it difficult to achieve meaningful genetic gains. Further complexity arises from epistasis and pleiotropy, where interactions among QTLs or between QTLs and other traits obscure their functional contributions [7]. Such interactions limit the predictability of QTL performance across different genetic backgrounds, phenotyping bottlenecks remain a critical barrier. High-throughput, precise, and cost-effective phenotyping under realistic field conditions is still lacking, limiting the ability to map QTLs accurately. While remote sensing, drones, and imaging technologies offer promising solutions, their integration into large-scale breeding pipelines is still in its early stages.

7. Conclusion

Quantitative Trait Loci (QTL) mapping has provided invaluable insights into the genetic basis of drought and heat stress tolerance in cereals, enabling the identification of key genomic regions linked to adaptive traits. Notable examples include qDTY12.1 in rice, which consistently enhances yield under drought, and stay-green QTLs in sorghum that maintain photosynthetic activity under heat stress. These discoveries highlight the potential of QTLs as foundational tools for developing stress-resilient cereal varieties. The integration of QTL mapping with complementary approaches has further strengthened its impact. Genome-wide association studies (GWAS) allow for high-resolution mapping of alleles from diverse germplasm, while genomic selection (GS) accelerates breeding cycles by predicting performance from genome-wide markers. Emerging tools such as CRISPR-based genome editing and pan-genomics add precision to the identification and deployment of stress-responsive genes, offering unprecedented opportunities for targeted crop improvement, significant challenges remain. Many QTLs exhibit environment-specific effects, limiting their stability across locations and seasons, most identified loci explain only a fraction of phenotypic variation, and complex interactions such as epistasis and pleiotropy complicate breeding applications. Phenotyping constraints, particularly under field conditions, continue to restrict the accuracy and scalability of QTL mapping, addressing these challenges will require the integration of molecular genetics with advanced breeding technologies, high-throughput

phenotyping, and systems biology, QTL mapping can remain a cornerstone of climate-smart breeding strategies, ensuring cereal crop productivity and global food security in the era of climate change.

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