

Review and Progress

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Identification of Drought-Responsive QTLs in *Triticeae* under Field Conditions

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✉ Corresponding email: shiying.yu@cuixi.orgTriticeae Genomics and Genetics, 2025, Vol.16, No.3 doi: [10.5376/tgg.2025.16.0012](https://doi.org/10.5376/tgg.2025.16.0012)

Received: 29 Mar., 2025

Accepted: 11 May, 2025

Published: 27 May, 2025

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Preferred citation for this article:

Yu S.Y., 2025, Identification of drought-responsive QTLs in *Triticeae* under field conditions, Triticeae Genomics and Genetics, 16(3): 110-119 (doi: [10.5376/tgg.2025.16.0012](https://doi.org/10.5376/tgg.2025.16.0012))

Abstract Drought stress represents a significant constraint on *Triticeae* crop productivity, particularly affecting wheat, barley, and rye in semi-arid regions. In this review, we systematically examine field-validated quantitative trait loci (QTLs) that are associated with drought-responsive traits in *Triticeae*, emphasizing their relevance to breeding programs. We begin by addressing the agricultural impact of drought stress and the limitations of controlled-environment studies compared to field-based evaluations. We then explore the methodologies used for QTL mapping under field conditions, including phenotyping strategies, statistical models, and the challenges posed by environmental heterogeneity. The review identifies key drought-responsive QTLs linked to traits such as root architecture, water-use efficiency, stay-green, canopy temperature, and grain yield components. A detailed case study on wheat highlights successful QTL discovery, validation across genetic backgrounds, and integration into elite lines via marker-assisted selection. Furthermore, we discuss how genomic resources such as high-density SNP arrays, GWAS, and transcriptomic tools are enhancing the precision of QTL identification. Looking ahead, we outline the promise of genomic selection, gene editing, and participatory breeding in accelerating the development of drought-resilient *Triticeae* cultivars. This study underscores the importance of multidisciplinary approaches and real-world validation in translating QTL research into sustainable agricultural outcomes under climate variability.

Keywords Drought tolerance; *Triticeae*; QTL mapping; Field phenotyping; Marker-assisted selection

1 Introduction

Wheat and barley are among the world's most important food crops, but their sensitivity to drought has always been a challenge. In recent years, the frequency and intensity of droughts have been on the rise, especially against the backdrop of climate change, which has had a considerable impact on yield and quality and posed a threat to food security (Nevo and Chen, 2010). Although there are many countermeasures, enhancing the drought resistance capacity of wheat plants from the root is still a key step for sustainable agricultural development (Shakir et al., 2025).

In this regard, quantitative trait loci (QTLs) offer an entry point. In simple terms, these loci represent genomic regions associated with complex traits, such as drought resistance. Such traits are influenced by the combined effect of multiple genes and are also easily affected by the environment. Through QTL mapping and meta-QTL analysis, researchers were able to further identify those key regions related to important agronomic and physiological traits in arid environments-such as yield, root structure, photosynthetic efficiency, etc. (Kumar et al., 2020). However, for the discoveries in the laboratory to be ultimately implemented, it still depends on those robust QTLs that have been verified under field conditions (Salarpour et al., 2020), in order to truly serve breeding.

Therefore, this study does not focus on all drought-resistant QTLs, but rather on those key QTLs that have been tested in the field and remain stable under different genetic backgrounds and environmental conditions. We will also integrate the information of relevant candidate genes to explore their application potential in actual breeding. Ultimately, this review aims to narrow the gap between basic genetic research and the development of drought-resistant varieties, especially in drought-prone areas.

2 Drought Stress in *Triticeae*: Agricultural Relevance and Impact

2.1 Physiological consequences of drought on *Triticeae* (wheat, barley, rye)

What happens when plants lack water? In wheat crops, the most obvious manifestation is the closure of stomata and the reduction of water content, which directly affects the efficiency of photosynthesis. Like wheat, when drought occurs, its stomatal conductance and leaf water content will decrease significantly, while substances related to stress response such as malondialdehyde and proline will increase (Qiao et al., 2024). Not only that, but their leaves and roots also grow more slowly. However, not all genotypes respond in the same way. Some drought-tolerant types, such as wild species or local varieties, tend to grow deeper or wider roots, which can absorb more water (Ullah et al., 2017). Of course, these "smart" response mechanisms are not always capable of withstanding prolonged drought. For instance, when stomata close, although it can reduce water loss, it also limits photosynthesis and affects the final yield (Hussein et al., 2022). Different varieties and different genetic backgrounds also have varying "tolerance" to drought.

2.2 Economic and food security implications in drought-prone regions

When it comes to the impact of drought, the decline in output is just the tip of the iceberg. The situation is even more serious in those arid or semi-arid regions that are already short of water (Begna et al., 2021). According to some studies, drought can reduce wheat production by more than half, while those droughts that are not particularly extreme but last for a long time are more likely to cause cumulative losses (Figure 1) (Wan et al., 2022). These losses are not just a matter of figures in the granary. They directly affect the wallets of farmers and even the food and clothing problems of the population who rely on these staple grains for survival (Fadiji et al., 2022). Moreover, climate change has made droughts increasingly difficult to predict, making it impossible to prevent them. To address these issues, technical means can be used to find solutions, but there are also many places to spend money-especially when adaptive measures need to be invested, the cost pressure rises significantly.

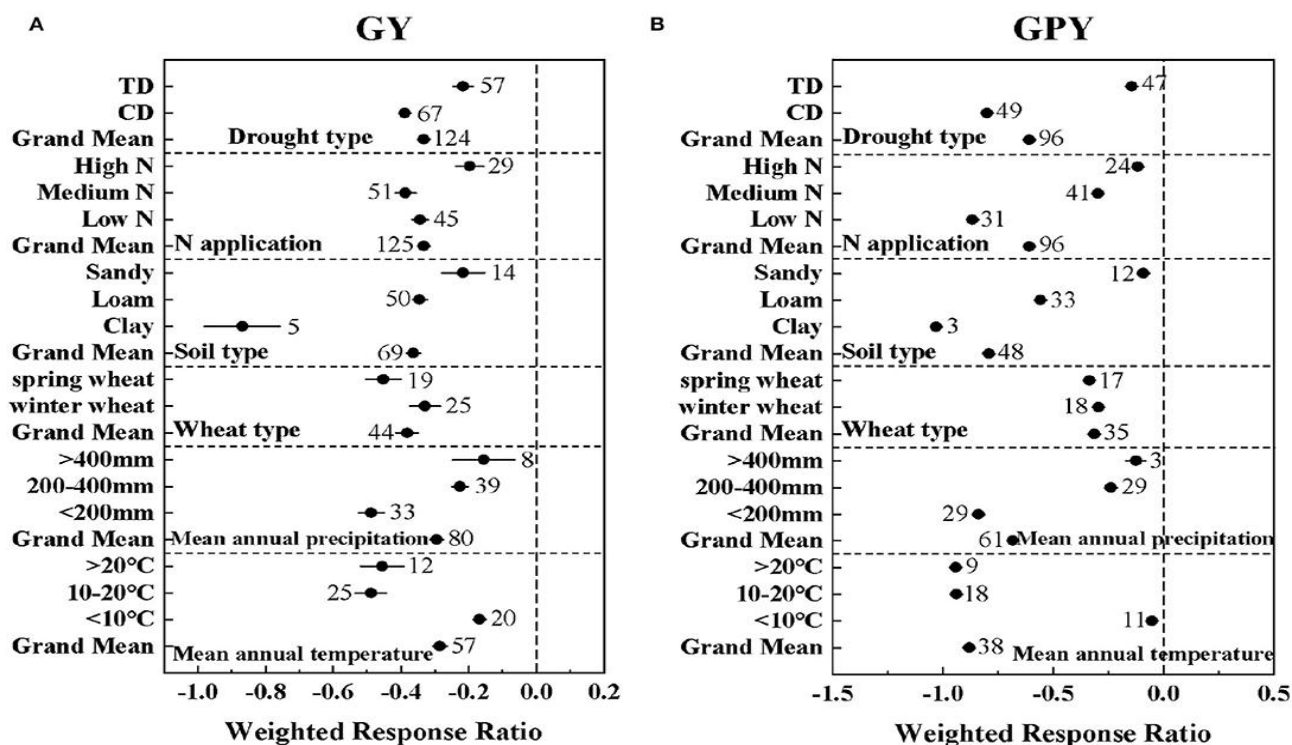


Figure 1 The effect of drought type (TD: Terminal drought stress; CD: Continuous drought stress), N application level [Low N (0-100 kg/ha); Medium N (100-200 kg/ha); High N (>200 kg/ha)], soil type, wheat type, mean annual precipitation, and mean annual temperature on the lnRRs of (A) GY: grain yield and (B) GPY: grain protein yield. The sample size of each variable is noted beside each bar. The effect of drought is significant if the $\pm 95\%$ confidence intervals of effect size do not overlap zero (Adopted from Wan et al., 2022)

2.3 Limitations of controlled-environment studies vs. field-based evaluations

No matter how realistic the drought simulation in the laboratory is, it can never imitate the "temper" in the fields. Studies under controlled conditions have indeed provided us with a considerable understanding of the drought response mechanism. However, once it comes to real fields, variables such as wind, rain, soil structure, and even insects and microorganisms complicate matters (Sallam et al., 2019). So, relying solely on laboratory data is not enough. To truly determine whether a variety is drought-tolerant or not, it is still necessary to observe its performance in the field. The performance of QTL and specific traits is more convincing in real-world contexts (Pantha et al., 2024). Of course, field experiments are not easy either. They are not only time-consuming and labor-intensive, but also easily disturbed by weather or other uncontrollable factors. So, at present, it seems that combining controlled research with field assessment might be a comprehensive and practical approach.

3 Principles of QTL Mapping under Field Conditions

3.1 Approaches to phenotyping drought-related traits in natural environments

In the field research of the wheat tribe, to figure out which traits are related to drought resistance, the first step is actually to measure clearly whether they are growing well or not. Traits such as yield, plant height, panicle emergence time and root length usually need to be measured repeatedly. They should be examined in different years and different plots. Only in this way is it possible to catch those variations that "evade drought manifestations" (Xu et al., 2023). Especially for some more sensitive physiological indicators, such as leaf water content, chlorophyll level, canopy temperature, and whether the leaves are curled, these indicators must be measured at key developmental stages. To minimize the interference brought by the field environment as much as possible, the experimental design is generally made into repetitive plots and a unified observation standard is adopted. Nowadays, high-throughput phenotypic platforms-such as SPAD meters for measuring chlorophyll or soil column methods for observing roots-are increasingly being used to enhance the efficiency and accuracy of detection. These methods are not complicated, but in complex field environments, they can help us more clearly "see" those subtle genetic differences.

3.2 Statistical models and experimental designs for QTL detection in the field

In the field research of the wheat tribe, to figure out which traits are related to drought resistance, the first step is actually to measure clearly whether they are growing well or not. Traits such as yield, plant height, panicle emergence time and root length usually need to be measured repeatedly. They should be examined in different years and different plots. Only in this way is it possible to catch those variations that "evade drought manifestations" (Xu et al., 2023). Especially for some more sensitive physiological indicators, such as leaf water content, chlorophyll level, canopy temperature, and whether the leaves are curled, these indicators must be measured at key developmental stages. To minimize the interference brought by the field environment as much as possible, the experimental design is generally made into repetitive plots and a unified observation standard is adopted. Nowadays, high-throughput phenotypic platforms-such as SPAD meters for measuring chlorophyll or soil column methods for observing roots-are increasingly being used to enhance the efficiency and accuracy of detection. These methods are not complicated, but in complex field environments, they can help us more clearly "see" those subtle genetic differences.

3.3 Challenges in environmental heterogeneity and genotype-by-environment interactions

Ultimately, there are too many variables in the field environment, which is precisely the most headache-inducing aspect for QTL positioning. Even if you design it thoroughly, as long as there are differences in weather, soil and management methods, the originally "visible" genetic effects may be obscured (Milner et al., 2016). Moreover, the interaction between G and E is also quite common. Some QTLS are quite obvious in one place but become "silent" in a different environment (Su et al., 2018). To deal with these interferences, researchers usually choose a strategy of multi-point repetition, large sample size, and long-term tracking, and combine it with more robust statistical models to strip the "noise" out of the signal as much as possible. Although there are many challenges, to screen out truly drought-tolerant QTLS with breeding value, it still depends on solid field testing.

4 Key Drought-Responsive Traits and Associated QTLs in *Triticeae*

4.1 QTLs linked to root architecture and water-use efficiency

When it comes to drought resistance, the "ability" of the root system is often the most crucial. Just like the roots can grow deeper and expand outward, this is particularly useful for the wheat tribe in "finding water" during drought. In fact, many years ago, some studies had already locked the QTLs that control such root traits on chromosomes 2B, 4A, 5A and 7B (Peleg et al., 2009). Interestingly, these loci are often crowded together with QTLs of yield or other drought resistance traits, which may indicate that the mechanisms behind their "management" are similar. On the other hand, some QTLs regarding leaf water use efficiency (LWUE) have also been identified, and they are often related to yield. Although some traits are not easy to observe directly, these indirect indicators are actually very valuable for reference when breeding drought-resistant varieties.

4.2 QTLs associated with stay-green, leaf rolling, and canopy temperature

When drought strikes, whether the leaves will turn yellow early, whether they will curl, and whether the temperature on the leaf surface will soar-these seemingly small details actually all reveal the "stress response" of crops. Like the "greenness retention" that delays leaf aging, one of its indicators is the chlorophyll content, and the corresponding QTL appears on chromosomes 1A and 6B. As for leaf curling, the currently known related QTLs are concentrated in 3B and 4A (Khaled et al., 2022). And the canopy temperature-which can reflect the transpiration status and water utilization of plants-its significant QTL is mainly also on chromosome 3B. These physiological traits do not exist in isolation; the QTLs corresponding to them are often associated with yield. This also indicates that genotypes that can maintain normal photosynthetic function under drought conditions are worthy of close attention.

4.3 Yield-related QTLs under drought conditions (grain number, biomass, harvest index)

Many people regard yield as the ultimate goal, but in fact, in a drought situation, this "outcome" is determined by many factors together, such as the number of grains per panicle, biomass accumulation, and even the harvest index. Interestingly, multiple studies have found that the QTLs of these traits are not isolated. Chromosomal regions like 1B, 1D and 7D can often stably "appear on camera" in different environments. Some QTLs on 7D-b, which are related not only to the 1000-grain weight but also to the heading period and yield, have also been verified in the field experiments under high temperature and drought. There are still many such yield QTLs that are "superimposed" on QTLs with physiological or morphological traits. This overlap suggests that drought adaptation does not rely on a single trait but on a set of closely collaborating genetic mechanisms.

5 Case Study

5.1 Field studies in semi-arid regions identifying consistent QTLs for drought tolerance

There are many field trials in semi-arid areas, but the ones that can truly screen out stable QTLs from them still rely on long-term, cross-regional multi-point studies. For instance, in some experiments using double haploid and recombinant inbred line populations, under both irrigation and rain-fed conditions, hundreds of QTLs related to key agronomic traits or physiological indicators have been identified. However, not every QTL can perform consistently in various environments. Those major QTLs on chromosomes 5A, 7A, and 1B can be regarded as "stable" only when they repeat in multiple situations (Tahmasebi et al., 2017). Of course, there are also studies that distinguish specific QTLs under different water pressures through environmental clustering or meta-analysis (Acuna-Galindo et al., 2015; Touzy et al., 2019). These results not only enrich our understanding of the genetic basis of drought tolerance, but also point out several potential areas that may be applicable to multiple ecological regions.

5.2 Validation of QTLs across genetic backgrounds and multi-year trials

Ultimately, whether a QTL is trustworthy or not depends on whether it can still hold its own in different varieties and years. Some studies have demonstrated that QTLs at sites such as 5A and 7A perform quite stably both under irrigation conditions and in water-scarce environments (Figure 2) (Gahlaut et al., 2017; Xu et al., 2017). More importantly, they can also be repeatedly detected in different genetic backgrounds, which is no accident. Later, there were studies that conducted Meta-QTL analyses, integrating dozens of results and ultimately summarizing

some QTLs with high consistency and significant influence. Incidentally, several reliable candidate genes were also identified (Shakir et al., 2025). These verified QTLs provide clear "targets" for subsequent breeding practices.

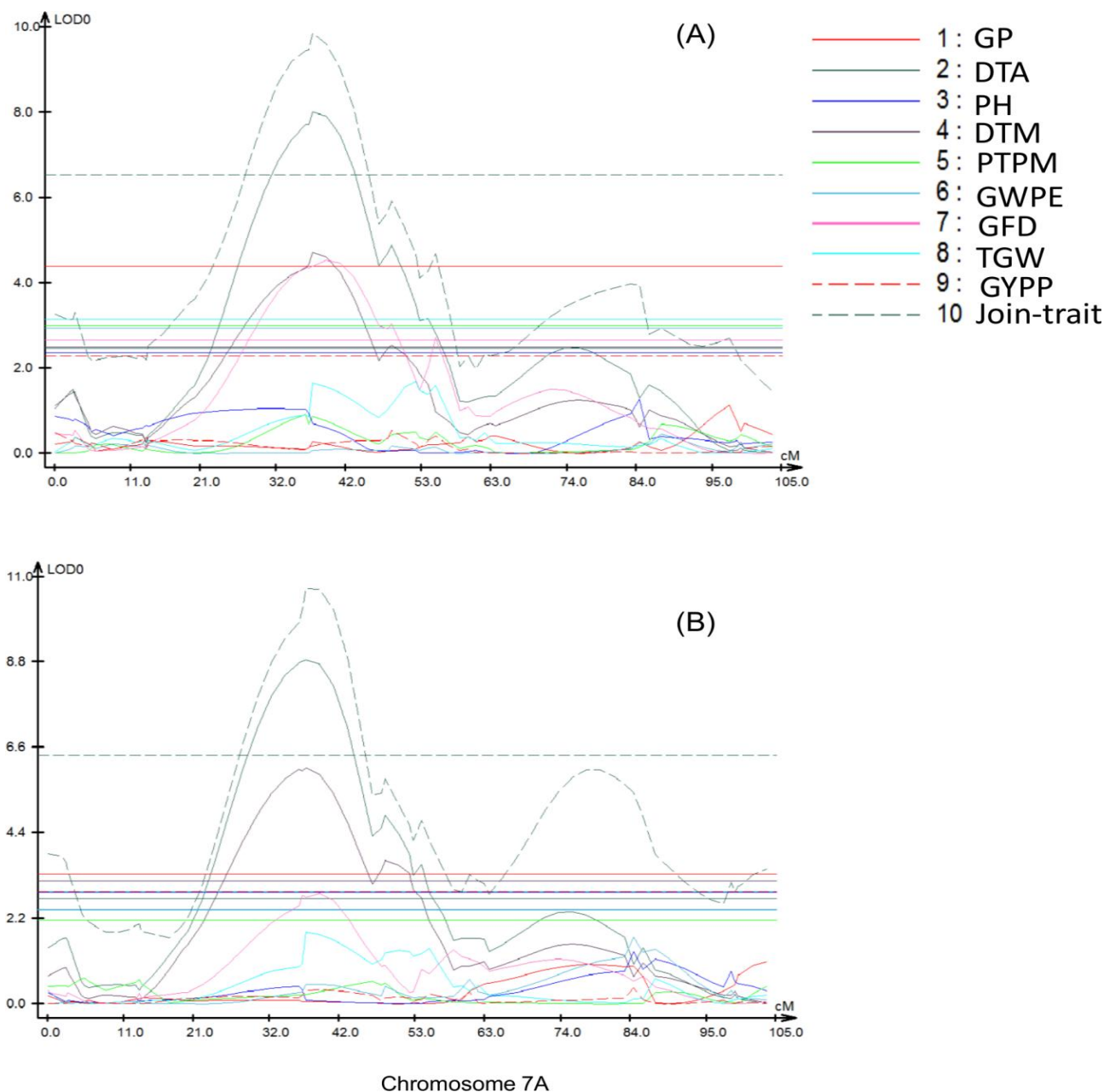


Figure 2 QTL cartographer plots showing a multi-trait QTL detected on chromosome 7A by multi-trait composite interval mapping (MCIM) using data pooled over IR and RF environments. (A) IR environment; (B) RF environment. GP, germination percentage; DTA, days to anthesis; DTM, days to maturity; GFD, grain filling duration; PH, plant height; PTPM, productive tillers/m²; GWPE, grain weight/ear; TGW, 1000 grain weight; GYPP, grain yield per plot (Adopted from Gahlaut et al., 2017)

5.3 Integration of QTLs into elite wheat varieties via marker-assisted selection (MAS)

Verification alone is not enough; only QTLs that can truly be implemented make sense. Nowadays, many breeding projects have begun to integrate these QTLs into superior wheat varieties through marker-assisted selection (MAS) or marker-assisted cycle selection (MARS). Generally speaking, those main effect QTLs with strong explanatory power and outstanding effects will be given priority for integration (Kirigwi et al., 2007). With the increasing maturity of high-density typing techniques and genomic selection methods, the efficiency of this process has also significantly improved (Kumar et al., 2020). In fact, some projects have incorporated

drought-resistant markers into the breeding process, making them one of the regular selection indicators. According to the current progress, the unified use of those QTLS and corresponding markers that have been repeatedly verified is very likely to make drought-resistant breeding both faster and more accurate.

6 Molecular Tools and Genomic Resources Enhancing QTL Discovery

6.1 Use of high-density SNP arrays and genotyping-by-sequencing (GBS)

In the past, QTL positioning relied on low-density tagging, which was time-consuming, costly and not very efficient. But now the situation has changed. High-density SNP arrays and GBS enable researchers to genotype large populations more quickly and at a lower cost, and with much higher resolution. These methods can provide dense markers across the entire genome, which helps to more accurately lock onto QTLS, especially those rare or harmful variations that are easily missed by traditional methods (Borevitz and Chory, 2004). Of course, typing alone is not enough. After combining genome-wide variation data with SNP markers, the detection ability will be stronger, especially in complex field environments (Macleod et al., 2016). In addition, tools such as QTLseqr and FastQTL have also saved a lot of trouble in data processing and are convenient and efficient for batch analysis (Ongen et al., 2015; Mansfeld and Grumet, 2017).

6.2 Genome-wide association studies (GWAS) complementing QTL mapping

When many people mention QTL, they only think of location maps, but in fact, GWAS has long been a main tool. Its approach is different-instead of relying on population construction, it uses existing natural variation resources to find loci related to traits (Zhang et al., 2022). The strength of GWAS lies in "casting a net" on a whole-genome scale. When used in combination with QTL data and annotation information, the effect will be better (Huang et al., 2022). Nowadays, there are also many online tools assisting this type of analysis, such as ezQTL and QTLbase2. They not only make the results more intuitive but also superimpose and compare the results of GWAS and QTL, making it convenient to identify those loci with true biological significance.

6.3 Integration of transcriptomics and gene annotation in QTL fine-mapping

To understand the mechanism behind QTL, merely relying on position is far from enough. At this point, transcriptome data, gene expression and various annotation information all need to be brought in for analysis together. Data like eQTL (expression QTL), in combination with transcriptional information and variant annotations, can significantly improve localization accuracy and also help infer functional mechanisms (Wen, 2016). Especially for those variations that are not very obvious in location but have important functions, it is even more necessary to rely on these integrations. Some new methods have emerged, such as BayesRC or EPISPOT. These models incorporate biological background knowledge, omics data, and regulatory characteristics into the analysis, which are very helpful for identifying specific variations (Ruffieux et al., 2020). Furthermore, databases such as QTLbase2 and QTLtools have been able to support the exploration of QTL under various biological conditions and molecular levels, and the integration of resources is becoming increasingly in place (Delaneau et al., 2016).

7 Future Directions in Drought-Resilient *Triticeae* Breeding

7.1 Potential of genomic selection (GS) and machine learning in predicting drought performance

Traditional breeding methods are not ineffective, but when it comes to the complex trait of drought resistance, their efficiency often causes concern. Nowadays, genomic selection (GS) is being adopted by an increasing number of breeding projects. One of its advantages is that it can make predictions based on the markers of the entire genome, without having to wait for field trials to know the results. This is indeed quite effective in saving time and accelerating the breeding process. Moreover, once the GS model combines high-throughput phenotypic and environmental data, the accuracy of prediction is usually higher than that of traditional methods (Mwadzingeni et al., 2016). Of course, GS alone is not enough. In recent years, the integration of machine learning has further advanced this type of prediction. It can integrate data from omics, environment, and even planting management, simulate the interaction between genotypes and the environment, and help breeders more accurately select materials suitable for arid regions (Cooper and Messina, 2022). Some projects have already started to test the waters with these tools on wheat and barley, and the prospects seem quite promising (Caccialupi et al., 2023).

7.2 CRISPR and gene editing to validate candidate genes from QTL regions

A suspected key gene has been found in the QTL interval. What should be done next? In the past, verification might have relied on repeated hybridization and backcrossing, but now, gene editing tools like CRISPR have made the verification process more direct and faster. By precisely modifying a certain allele, it is possible to verify whether it is useful or not. If ideal traits are exhibited, such mutations can be introduced into existing superior germplasms without worrying about introducing other "burdens" (Singh et al., 2025). For those small QTLS with insignificant effects or when multiple drought-tolerant genes are to be superimposed simultaneously, gene editing is clearly an efficient solution (Rosero et al., 2020). However, the prerequisite is to have a clear target gene first, which still requires the support of QTL mapping and functional annotation.

7.3 Importance of participatory breeding and testing under farmer-managed fields

Not all breeding achievements can be smoothly "implemented". Sometimes, some varieties perform well at experimental stations but fail to adapt to the local conditions in farmers' fields. Therefore, more and more breeding projects are beginning to attach importance to the participation of farmers. Participatory breeding is not a new concept. It emphasizes the opinions of farmers during the seed selection and testing stages, making the final selected strains more in line with local needs (Khadka et al., 2020). Especially in areas where management methods vary greatly and there are significant differences in soil and water resources, allowing new varieties to be trial-planted in real farmers' plots can more accurately reflect drought resistance performance. In addition, this approach can also protect the diversity of local germplasm and promote the development of varieties adapted to specific ecological zones, which is of great practical significance for ensuring food security.

8 Concluding Remarks

Although the research on QTLS has been ongoing for many years, it is those QTLS that have been verified in field environments that have truly given us a clearer understanding of how the *Triticeae* family ADAPTS to drought. Especially in wheat and barley, many meta-analyses and cross-environmental field experiments have identified a considerable number of stable QTLS and meta-Qtls (MQTLS), which can all be linked to key traits such as yield, plant height, canopy temperature, and root structure under different conditions. It is worth noting that many QTLS are also overlapping and concentrated in several regions related to drought response. Most of the candidate genes in these regions are involved in stress signaling, water regulation or antioxidant mechanisms, and thus have become very practical objects for molecular marker selection in the breeding process.

But then again, there are quite a few problems. Many QTLS are only effective in specific environments or genotypes, and there are actually not many that can be stably expressed under different conditions. This specificity, coupled with the fact that drought resistance is not controlled by a single gene, leads to frequent interactions between QTLS and the environment. However, there are still not many examples that can be truly applied in breeding practice. Not to mention that some candidate genes still lack precise localization and functional verification, which has also slowed down the promotion pace of drought-resistant varieties.

To solve these difficult problems, it is probably necessary to adopt multiple methods simultaneously. Only by integrating genomics, high-throughput phenotyping, bioinformatics analysis, and breeding models with the actual participation of farmers can the task of "finding QTLS" be made more effective. Nowadays, many studies have begun to combine QTL localization with GWAS, transcriptome data and statistical modeling to enhance the accuracy of screening. From the laboratory to the field, from data to practice, this process cannot do without the collaboration among geneticists, breeding experts, physiological researchers, and even farmers. Only in this way can drought-resistant breeding truly run fast and bear fruit, and hold the bottom line of food security in the face of climate change.

Acknowledgments

I am grateful to Mr. Ma for critically reading the manuscript and providing valuable feedback that improved the clarity of the text.

Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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