



In-silico Mining and Characterization of Drought Tolerance Genes in Wheat (*Triticum aestivum* L.) using a Digital Candidate Gene Approach

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ABSTRACT

The study was conducted in 2019 at the Department of Genetics and Plant Breeding, Chaudhary Charan Singh University, Meerut, Uttar Pradesh, India. The research aimed to identify drought-responsive candidate genes in wheat (*Triticum aestivum* L.) through a comparative genomics approach using previously characterized drought-related genes from barley and rice. A total of 21 reported genes from these reference crops were examined to identify their putative wheat orthologues based on sequence homology and genome annotation using publicly available wheat genomic resources. RNA-seq datasets retrieved from the WheatExp database were analysed to assess tissue-specific expression patterns of the identified wheat orthologues under drought conditions. Functional domain analysis was further performed to predict the biological roles of the encoded proteins in drought tolerance mechanisms. Six wheat orthologues were identified, encoding proteins such as alcohol dehydrogenase, chaperonin, dehydrin, and serine/threonine protein kinase. These genes exhibited distinct and reproducible expression profiles across tissues including leaves, roots, grains, spikes, and stems under drought stress. Functional annotation revealed their involvement in osmotic adjustment, protein stabilization, cellular protection, and signal transduction during water-deficit conditions. The identified drought-responsive wheat genes represent potential targets for downstream functional validation and molecular breeding. The findings provide gene-level insights into drought-related mechanisms in wheat and offer a genomic resource for developing improved genotypes suited to water-limited environments.

KEYWORDS: Drought, candidate genes, gene expression, bioinformatics, genomics, tolerance

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1. INTRODUCTION

Wheat (*Triticum aestivum* L.) is one of the most important staple crops globally, providing a major share of daily caloric intake for millions of people. However, its productivity is increasingly threatened by drought stress, which has become more widespread and severe across major wheat-producing regions (Nyaupane et al., 2024). Drought negatively impacts plant growth, physiological functions, and grain yield, especially during sensitive developmental stages such as flowering and grain filling (Bohra et al., 2024). As climate change continues to intensify water scarcity in both rainfed and irrigated agroecosystems, enhancing the drought resilience of wheat has become a critical priority for ensuring long-term food security (Gokkus et al., 2024). Understanding drought tolerance in wheat is particularly challenging because it is a complex and polygenic trait governed by multiple interconnected pathways. These pathways regulate osmotic adjustment, stomatal behavior, antioxidant defense systems, signal transduction networks, and cellular homeostasis (El Gataa et al., 2025). The polygenic nature of drought tolerance, combined with strong genotype×environment interactions, often limits the effectiveness of conventional breeding approaches (Lim et al., 2019). Furthermore, precise phenotyping of drought-related traits under field conditions remains difficult and inconsistent. Consequently, the identification of key candidate genes associated with drought response provides a more targeted, reliable, and efficient avenue for genetic improvement (Lim et al., 2019). To overcome these challenges, comparative genomics has emerged as a promising strategy for identifying drought-responsive genes using resources from closely related cereals such as barley (*Hordeum vulgare* L.) and rice (*Oryza sativa* L.) (Baldoni et al., 2021; Baghyalakshmi et al., 2024). Barley, recognized for its natural drought hardiness, has provided valuable insights into genes involved in hormone signalling, antioxidant mechanisms, Osmoprotection, and stress-regulated transcription factors (Xiong et al., 2023). Similarly, extensive research in rice has uncovered drought-induced genes encoding kinases, dehydrins, transporters, chaperonins, and other stress-adaptive proteins (Hassan et al., 2023). The evolutionary conservation of these genes and pathways across cereals creates an opportunity to identify orthologous genes in wheat that may perform functionally similar roles (Chachar et al., 2024). Thus, comparative genomics serves as a powerful framework that allows drought-responsive genes validated in barley and rice to be efficiently explored as promising candidates for wheat improvement. Building on this, recent advances in genomic technologies have dramatically accelerated the discovery and characterization of drought tolerance genes in wheat. High-quality genome assemblies, transcriptome profiling

through RNA-seq, and genome-wide association studies have improved the resolution and accuracy with which drought-responsive loci can be detected (Wang et al., 2023; Qiu et al., 2025; Kamali and Singh, 2023). Several key genes encoding proteins such as alcohol dehydrogenase, dehydrins, serine/threonine protein kinases, and molecular chaperones have already been implicated in protecting wheat plants from dehydration, stabilizing proteins and membranes, and mediating stress-responsive signalling networks (Sun et al., 2021; Trono and Pecchioni, 2022; Dubrovna et al., 2025). This study aims to identify drought-responsive candidate genes in wheat using a comparative genomics approach informed by drought-related genes reported in barley and rice. Twenty-one previously characterized genes were screened, and putative wheat orthologues were identified through sequence homology and genome annotation analyses. Conserved protein domains, gene structures, and drought-induced expression patterns were assessed using publicly available RNA-seq datasets. The primary objective was to characterize these wheat orthologues and evaluate their structural and expression features under drought stress to determine their potential roles in wheat drought tolerance.

2. MATERIALS AND METHODS

2.1. Candidate gene identification

The study was carried out in 2019 in the Bioinformatics Laboratory, Department of Genetics and Plant Breeding, Chaudhary Charan Singh University, Meerut, Uttar Pradesh (250 001), India. A comprehensive literature survey was conducted to compile genes experimentally validated as drought-responsive in barley (*Hordeum vulgare* L.) and rice (*Oryza sativa* L.). Gene names, nucleotide and protein sequences, and functional annotations were systematically extracted from published articles, genomic databases, and authoritative reviews. Based on the survey of barley and rice, a total of 21 candidate genes showing drought tolerance were shortlisted. Details of these candidate genes, including gene ID, location, function, and trait association, are summarized in Supplementary Table 1. To enhance the accuracy and efficiency of candidate gene identification, an integrated digital candidate gene approach (DigiCGA) was employed. This modern method leverages bioinformatics tools and publicly accessible genomic and transcriptomic databases to systematically mine for drought-associated genes. Using DigiCGA, the shortlisted genes served as queries for homology-based searches against the *Triticum aestivum* reference genome, facilitating the precise identification of potential wheat orthologues for subsequent functional analysis. The application software and online tools related to DigiCGA that facilitated gene mining, annotation, and functional prediction in this study are summarized in Supplementary Table 2. These tools were selected based on

Supplementary Table 1: List of candidate genes derived from the literature survey							
Sl. No.	Crop name	Gene Id	Gene name	Gene location	Function of a gene	Trait affected by a gene	References
1.	Barley	X12733	Adh2	5	Kinase: protein kinase ABC1	Leaf	42-Lee et al., 2011
2.	Barley	AJ234407	-	1		Root	42-Lee et al., 2011
3.	Barley	AJ507091	RgaS-226	3	-	Grains	42-Lee et al., 2011
4.	Barley	X97771	-	4	-	Leaf	42-Lee et al., 2011
5.	Barley	AY268139	-	7	-	Grains	42-Lee et al., 2011
6.	Barley	X66376	LOC548245	6	J a s m o n a t e - induced protein	Leaf	42-Lee et al., 2011
7.	Barley	AJ507213	-	2		Leaf	42-Lee et al., 2011
8.	Barley	M36650	LOC548217	1		Root, Grains	42-Lee et al., 2011
9.	Barley	AY268139	-	2		Leaf	42-Lee et al., 2011
10.	Barley	AF043094	Dhn9	2		Stem	42-Lee et al., 2011
11.	Barley	X66376	-	4		-	42-Lee et al., 2011
12.	Barley	X15287	Dhn4	5		Leaf & root	42-Lee et al., 2011
13.	Barley	AJ291295	-	6		-	42-Lee et al., 2011
14.	Barley	AF043094	-	4		leaf	42-Lee et al., 2011
15.	Barley	AY164911	-	5		-	42-Lee et al., 2011
16.	Rice	LOC4333435	SAPK10-like	3		Broad expression in mature seeds	Lu, et al., 2009
17.	Rice	LOC4339480	Lea 3	5		Restricted expression toward mature seeds	Lu, et al., 2009
18.	Rice	3974662	Newentry	-		Ubiquitous expression in leaves after flowering	Lu, et al., 2009
19.	Rice	LOC4345807	TRAB1	8		bZIP transcription factor TRAB1-like	30-Wang et al., 2005
20.	Rice	LOC4325867	P0557A01.8	1		Ubiquitous expression in leaves after flowering	30-Wang et al., 2005
21.	Rice	LOC4326435	P0010B10.12	1		-	30-Wang et al., 2005

their relevance, user-friendliness, and prior validation in biological research, enabling an integrated computational framework for candidate gene identification and analysis

2.2. Supplementary information

2.2.1. Sequence retrieval and orthologue identification

Nucleotide and protein sequences of the shortlisted candidate genes were retrieved from NCBI GenBank and Ensembl Plants. These sequences were used as queries for tBLASTx searches against the *Triticum aestivum* reference genome (IWGSC RefSeq v2.1). High-confidence orthologs were identified using thresholds of >80% sequence identity and E-value $\leq 1e-5$, and their genomic coordinates were recorded.

2.2.2. Gene structure and functional annotation

Exon-intron organization of the wheat orthologs was analysed using the Ensembl Plants genome browser and BioMart. Protein-coding sequences were translated to confirm open reading frame conservation. Functional domains and motifs relevant to drought response were identified using InterProScan and Pfam databases.

2.2.3. Expression profiling

RNA-seq data across developmental stages and drought stress conditions were retrieved from the WheatExp database. TPM (Transcripts Per Million) values were extracted for candidate genes in leaves, roots, stems, grains, and spikes. Tissue-specific and stress-responsive expression

Supplementary Table 2: Summary of application software and online tools related to digital candidate gene approach.			
Sl. No.	Name	Literature source	Website
1.	GeneSeeker	van Driel, et al., Nucleic Acids Res. 2005;33: W758-61	http://www.cmbi.ru.nl/GeneSeeker/
2.	GFSST	Zhang, et al., BMC Bioinformatics. 2006; 7: 135	http://gfsst.nci.nih.gov
3.	Endeavour	Aerts et al. Nat Biotechnol. 2006; 24:537-44	http://www.esat.kuleuven.be/endeavour
4.	POCUS	Turner et al. Genome Biol. 2003; 4: R75.	http://www.hgu.mrc.ac.uk/Users/Colin.Semple/
5.	G2D	Perez-Iratxeta, et al. Nucleic Acids Res. 2007;35: W212-6.	http://www.ogic.ca/projects/g2d_2/
6.	Suspects	Adie et al. Bioinformatics. 2006; 22: 773-4.	http://www.genetics.med.ed.ac.uk/suspects/
7.	TOM	Rossi et al. Nucleic Acids Res. 2006; 34: W285-92.	http://www-micrel.deis.unibo.it/~tom/
8.	BioMercator	Arcade et al. Bioinformatics. 2004; 20: 2324-26	http://moulon.inra.fr/~bioinfo/BioMercator
9.	FunMap	Ma et al. Bioinformatics. 2004; 20: 1808-11.	
10.	GFINDER	Masseroli et al. Nucleic Acids Res. 2005;33: W717-23	http://www.bioinformatics.polimi.it/GFINDER/
11.	Prospector	Adie et al. BMC Bioinformatics. 2005; 6:55.	http://www.genetics.med.ed.ac.uk/prospectr/
12.	eVOC	Tiffin et al. Nucleic Acids Res. 2005; 33:1544-52	
13.	QTL Mixer	Serrano-Fernández et al. Bioinformatics. 2005; 21:1737-8	http://qtl.pzr.uni-rostock.de/qtlmix.php
14.	DGP	Lopez-Bigas N, Ouzounis CA. Nucleic Acids Res. 2004; 32:3108-14	
15.	CoGenT++	Goldovsky et al. Bioinformatics. 2005; 21:3806-10	http://cgg.ebi.ac.uk/cogentpp.html
16.	KNN classifier	Xu, et al. Bioinformatics. 2006; 22:2800-05	available on request: jianzxu@hotmail.com
17.	SNPs3D	Yue et al. BMC Bioinformatics. 2006; 7:166	http://www.SNPs3D.org
18.	PhD-SNP	Capriotti et al. Bioinformatics. 2006; 22:2729-34	http://gpcr.biocomp.unibo.it/cgi/predictors/PhD-SNP/PhD-SNP.cgi

patterns were visualized using bar graphs generated in R (version 4.3.1).

3. RESULTS AND DISCUSSION

3.1. Candidate genes identified from barley and rice

Based on an extensive literature survey, 21 candidate genes associated with drought tolerance in barley and rice were shortlisted, which belong to diverse functional categories, including protein kinases, dehydrins, jasmonate-induced proteins, transporters, and transcription factors, that are central to the regulation of physiological and molecular drought responses (Paudel et al., 2024). For example, protein kinases are known to regulate stress signalling cascades, while dehydrins play a protective role in membrane stabilization during water deficit. Jasmonate-induced proteins function

as regulators of stress-induced secondary metabolism, and several transcription factors, such as DREB and NAC families, which directly regulate downstream drought-responsive genes. Their selection was based on well-documented roles in drought adaptation across tissues and developmental stages, positioning them as valuable targets for cross-species comparative analysis and wheat breeding. Notably, comparative approaches allow the transfer of knowledge from well-studied species like rice and barley to less characterized crops like wheat, which possesses a more complex polyploid genome and presents greater challenges in direct gene /orthologue characterization.

3.2. Homology-based identification of wheat orthologues

Comparative sequence analysis with respect to 21 barley-

rice candidate/query genes against the wheat genome revealed that five barley-derived candidate genes and one rice-derived candidate gene showed significant similarity to putative wheat orthologues. These wheat orthologues displayed exceptionally high conservation, with E-values of zero and % identities ranging from 80% to 100%, averaging around 90%. Such strong sequence conservation underscores the evolutionary stability of these genes within the *Poaceae* family and highlights their fundamental role in drought response. For example, stress-associated kinases and dehydrin proteins have been reported to be highly conserved across cereals (Ding et al., 2022). Such a high degree of conservation validates the utility of barley and rice genomic data as references for identifying functionally relevant genes in wheat (Geng et al., 2023) and even in other cereals. Moreover, identifying conserved orthologues provides a practical entry point for functional characterization of the wheat genome. However, redundancy and gene dosage effects arising from polyploidy often complicate gene discovery in wheat.

3.3. Tissue-specific expression analysis of identified wheat candidate genes

Expression profiling using RNA-seq data revealed distinct spatiotemporal patterns of wheat candidate gene expression across grain, leaf, root, spike, and stem tissues at various developmental stages (Figure 1). These patterns illustrate the tissue- and stage-specific regulation of drought tolerance mechanisms. For example, *TraesCS5A02G193900*, an alcohol dehydrogenase gene, showed elevated expression in drought-stressed leaves, consistent with its role in maintaining redox balance and protecting photosynthetic tissues under oxidative stress. Similarly, *TraesCS2D02G049500*, encoding a chloroplast-localized chaperonin, was strongly expressed in photosynthetic tissues, particularly during vegetative growth, indicating its importance in maintaining protein stability under water deficit. Interestingly, *TraesCS7B02G234400*, encoding glyceraldehyde-3-

phosphate dehydrogenase, exhibited strong expression in developing grains, suggesting its involvement in sustaining energy metabolism and carbohydrate allocation during reproductive stages. Such roles are critical for ensuring grain filling and yield stability under drought conditions (Rupngam and Messiga, 2024). In addition, several candidate genes showed clear upregulation in roots. For instance, *TraesCS1D02G296500* (phosphatidylethanolamine-binding protein) and *TraesCS5A02G424800* (dehydrin) displayed moderate-to-high root expression (Figure 1a, 1d), suggesting their roles in enhancing water uptake capacity, membrane stabilization, and root system plasticity under water deficit. These root-specific expression patterns align with previous studies demonstrating that root-expressed dehydrins and lipid-binding proteins contribute to drought avoidance and improved water-use efficiency (Kulkarni et al., 2017). Together, these results demonstrate that wheat drought tolerance involves the coordinated expression of multiple gene families across diverse tissues, ensuring both vegetative survival and reproductive success under stress.

3.4. Functional annotation and domain characterization

Functional annotations derived from InterProScan and Pfam analyses revealed that each candidate gene harboured conserved domains relevant to drought stress tolerance (Table 1). For instance, *TraesCS5A02G193900* contained NAD(P)-binding domains typical of alcohol dehydrogenase enzymes, which are essential for maintaining cellular redox homeostasis during oxidative stress caused by drought. *TraesCS2D02G049500* encoded a chloroplast-localized chaperonin, vital for refolding denatured proteins under heat and dehydration stress, thereby maintaining photosynthetic efficiency. *TraesCS7B02G234400* encoded glyceraldehyde-3-phosphate dehydrogenase, a key glycolytic enzyme with additional signalling roles in stress adaptation. Furthermore, *TraesCS5A02G424800* was classified as a dehydrin, a group of late embryogenesis abundant (LEA) proteins that accumulate under

Table 1: Functional annotation and domain characterization of candidate genes associated with drought stress tolerance in wheat

Sl. No.	Gene ID	Genomic location	E-value	Identity (%)	Tissue specific expression	Annotation Function
1.	TraesCS5A02G193900	5AL	0	92	Leaf	Alcohol dehydrogenase, zinc-type, conserved site
2.	TraesCS2D02G049500	2DS	0	91.5	Leaf	Chaperonin Cpn60/TCP-1 family
3.	TraesCS7B02G234400	7BL	0	96	Root and stem	Glyceraldehyde 3-phosphate dehydrogenase, NAD(P) binding domain
4.	TraesCS5A02G424800	5AL	0	93.5	Grain	Dehydrin, conserved site
5.	TraesCS1D02G296500	1D	0	100	Grain	Phosphatidylethanolamine-binding protein
6.	TraesCS4A02G235600	4A	0.0017	100	Grain	Serine/threonine-protein kinase, active site

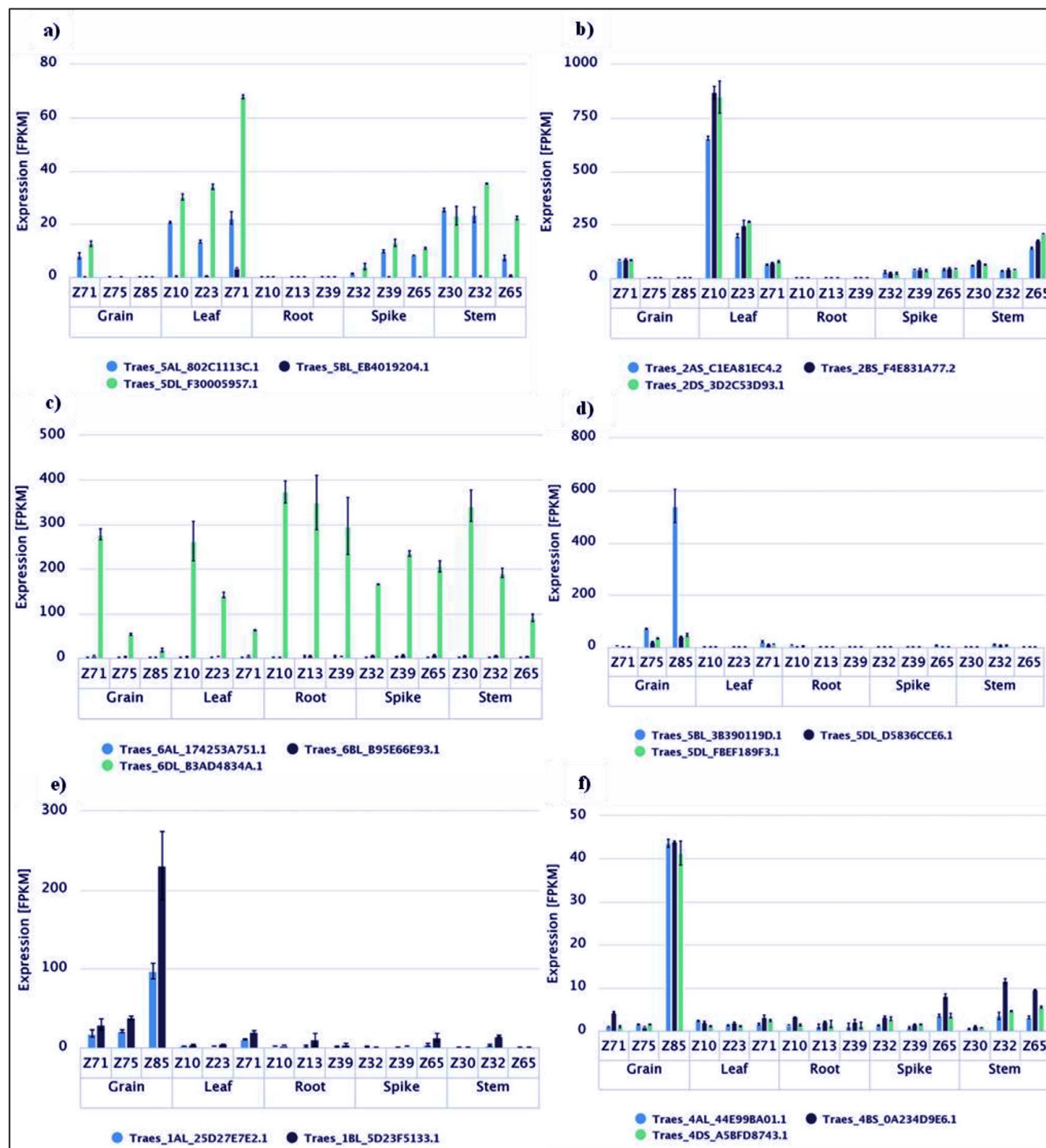


Figure 1: Tissue-specific expression profiles of selected wheat candidate genes related to drought tolerance. Expression levels (FPKM fragments per kilobase of transcript per million) are shown for grain, leaf, root, spike, and stem across multiple developmental stages (Z71, Z75, Z85, Z10, Z23, Z30, Z32, Z36, Z39, Z65, Z210, Z213, Z230, Z232, Z239, Z265). Panels (a–f) compare isoforms or homologues within each gene family. Data illustrate distinct spatiotemporal patterns, with certain candidate genes highly expressed in leaves and grains, while others show root- or spike-specific expression

dehydration and protect cellular membranes and proteins from destabilization. *TraesCS1D02G296500* encoded a phosphatidylethanolamine-binding protein, implicated

in membrane remodelling and reproductive growth under stress conditions. Finally, *TraesCS4A02G235600* was identified as a serine/threonine kinase, a central regulator

of phosphorylation signalling cascades activated during drought responses (Zhang et al., 2023). Together, these annotations highlight the multifaceted nature of drought tolerance mechanisms in wheat, ranging from protein protection and metabolic regulation to signal transduction

3.5. Predicted subcellular localization of candidate genes

Subcellular localization predictions further supported the functional relevance of the identified candidate genes. Alcohol dehydrogenase and glyceraldehyde-3-phosphate dehydrogenase were predominantly localized to the cytoplasm and plastids, consistent with their roles in energy metabolism and redox regulation. Chaperonins were predicted to localize in chloroplasts, aligning with their function in protecting photosynthetic machinery. Dehydrins and phosphatidylethanolamine-binding proteins were associated with cellular membranes, providing structural stability under dehydration (Andersson et al., 2020). The serine/threonine kinase showed dual localization in the cytoplasm and nucleus, reflecting its role in transmitting stress signals and regulating downstream gene expression. This compartmentalization suggests that drought tolerance in wheat is achieved through an integrated cellular network, where metabolic adjustment, structural stabilization, and signalling are coordinated across multiple organelles. Such spatial coordination of gene functions has also been reported in barley and rice (Lv et al., 2020), highlighting evolutionary conservation of drought tolerance strategies.

4. IMPLICATIONS FOR WHEAT BREEDING

The conserved expression profiles, functional domains, and subcellular localization of the identified candidate genes in this study collectively demonstrate their central roles in wheat drought stress response. Their identification provides molecular markers for breeding programs and potential targets for transgenic or genome editing approaches aimed at enhancing drought resilience. Integrating these candidate genes with existing QTL data and genome-wide association studies could accelerate marker-assisted selection. Moreover, functional validation of these genes under field conditions will be critical for developing drought-resilient wheat cultivars that can withstand future climate challenges (Bashir and Husaini, 2025).

5. CONCLUSION

Six drought-responsive wheat orthologues were identified from 21 previously reported genes in barley and rice. Five corresponded to barley genes and one to a rice gene. These wheat genes are involved in regulating drought tolerance. Functional annotation revealed that they encode proteins associated with alcohol dehydrogenase activity, NAD(P)-binding domains, serine/threonine protein kinase domains, ATP-binding sites, chaperonin and AAA+

ATPase functions, as well as NB-ARC, leucine-rich repeat, and Rx-N-terminal domains, highlighting their roles in stress-response mechanisms.

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