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DROUGHT TOLERANCE MECHANISMS IN GENETICALLY MODIFIED WHEAT

A CRITICAL REVIEW OF GENETIC TARGETS, PATHWAYS, AND EXPERIMENTAL EVIDENCE

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Abstract

Drought is one of the most harmful abiotic stresses that limit wheat (Triticum aestivum L.) production worldwide and genetic modification can be a complementary approach to conventional breeding to enhance drought resistance. This review summarizes peer-reviewed primary studies that focus on changes in the molecular, physiological and biochemical underlying processes that allow wheat to withstand water deficit and whether these changes can be shown to actually increase drought tolerance. Literature search was performed in the PubMed, ScienceDirect, Frontiers, MDPI, Wiley, Springer Nature, and PMC databases but a structured search was carried out and transgenic or genome-edited wheat research studies were given more preference than review articles. Experimental systems in which evidence was obtained were classified as: wheat transgenic studies (highest priority); wheat gene-manipulation studies; wheat mechanistic studies; and studies in heterologous model species. Improved drought tolerance in wheat has been reproducibly demonstrated in the synthesis through overexpression of transcription factors (GmDREB1, HaHB4, TaWRKY2, TaMYB31-B), expansins

(TaEXPA2) and components of ABA signaling (TaSnRK2.4, TaPYL4). These changes occur via five partially overlapping mechanisms: osmoregulation, antioxidant defense, ABA signaling and stomatal regulation, photosynthetic protection and root architecture. There are only a limited number of field-validated evidence and of these, HaHB4 (HB4) and GmDREB1 have been approved for commercial cultivation in Argentina. Currently, the evidence of the drought tolerance of wheat via CRISPR is weak and mostly indirect. There are several important gaps such as the lack of multi-environment field trials, phenotyping protocols that vary and the lack of knowledge regarding the role of genotype-by-environment-by-transgene interactions. The review finds that genetic modification is able to significantly improve specific measures of drought tolerance in wheat, but the enhancement of yield in the field will need to be carefully tested in a range of environments.

1. Introduction

Wheat (Triticum aestivum L.) is the most widely grown cereal crop, and a major source of calories and protein for an estimated 35-40 percent of the world's population (Nyaupane and Gardner, 2024). Since wheat is predominantly cultivated in rain-fed areas in the Mediterranean basin, Indo-Gangetic plain, Australian wheatbelt and North American Great Plains, its productivity is closely related to amount and distribution of precipitation. Drought stress, therefore, is one of the most critical abiotic stresses on wheat production; meteorological droughts are estimated to cost wheat production 10–20% which could feed tens of millions of people annually (Song et al., 2025). Due to climate projection of increasing incidence and intensity of agricultural droughts in many wheat-growing regions, there is an increased demand for cultivars with good yield under water deficit (Nyaupane and Gardner, 2024). Damage to wheat is caused by drought in a number of interrelated ways. The whole plant level responses to a decrease in soil water potential include decreases in water uptake, leaf water potential and stomatal closure. Drought-induced secondary oxidative stress occurs at the cellular level due to excess production of Reactive Oxygen Species (ROS) and results in damage to the integrity of membranes, disruption of chloroplast ultrastructure and impairment of carbon assimilation (Nyaupane and Gardner, 2024; Song et al., 2025). The effects of these continue to decrease biomass production, early senescence and in cases where the stress is experienced during anthesis and grain filling, grain number and weight are significantly reduced. Progress has been made using conventional breeding, which involves small steps due to the polygenetic inheritance of drought adaptation, low heritability of the trait under varying field conditions and the long generation time of wheat. An alternative approach is the genetic modification. Researchers can use molecular target specific gene addition and/or modification to determine if the addition of a known molecular target can enhance drought-related phenotypes. In wheat three general types of intervention have been investigated. Transgenic overexpression of stress-responsive transcription factors, signaling kinases or protective proteins, frequently under the control of constitutive or stress-inducible promoters. Secondly, RNA interference (RNAi) or virus-induced gene silencing (VIGS) to knock down stress tolerance negative regulators. Third, genome engineering of the endogenously expressed genes without the introduction of foreign DNA – using CRISPR/Cas systems (Budak et al., 2015; Khan et al., 2019). The approaches vary in regulatory status of their use, precision of the genetics and the experimental evidence supporting their use for drought tolerance. Although there are a number of primary source documents, there are some problems that are not yet solved. A large proportion of studies

reporting drought tolerance of a particular gene carry out experiments on heterologous systems (such as Arabidopsis thaliana or tobacco) and its relevance to wheat is not known (Wang et al., 2016; Zhang et al., 2010). Results from under controlled conditions in the greenhouse are often not applicable to the field environment, and the effects the transgene has on the soil can be unpredictable, due to the soil's heterogeneity and the vapor pressure deficit. Last but not least, the terminology is incoherent: plants are referred to as 'genetically modified', 'transgenic', 'cisgenic' or 'gene-edited', and this impacts their mechanism and regulation in different ways, without always being recognized. The key question this review seeks to answer is how do genetic changes affect molecular, physiological and biochemical mechanisms underlying wheat's drought stress tolerance and is there evidence of enhanced drought stress tolerance? The review summarizes, (i) the physiological and molecular basis of wheat drought damage, (ii) the genes targeted most consistently with better drought tolerance, (iii) evidence based on biological mechanisms, rather than on individual genes, (iv) evidence from model plants, and (v) specific research gaps that hinder translation. The goal is not to list all of the published genes but to assess if there is experimental evidence that repeatable in wheat for a particular mechanism and if not, then it is speculative.

2. Literature Search Strategy and Evidence Evaluation

The review has been carried out based on structured search in literature but not systematic. The methodology is reported transparently as there was no registered formal systematic-review protocol (such as PRISMA) for this review. The approach aimed to provide as much wheat-based primary experimental information as possible and allow for the addition of mechanistic context from other species where it was lacking and/or weak.

2.1 Databases and Search Terms

The PubMed, PubMed Central (PMC), ScienceDirect, Springer Nature, Wiley Online Library, Frontiers, MDPI, Taylor & Francis, and Google Scholar databases were searched. A combination of crop term and intervention and outcome terms were used in the search strings. The transgenic wheat drought tolerance field, wheat DREB transcription factor drought overexpression, wheat NAC transcription factor drought stress, wheat WRKY drought transgenic, wheat ABA signaling drought genetic engineering, wheat antioxidant defense SOD CAT APX transgenic, wheat CRISPR genome editing drought stress, wheat root architecture drought transgenic, wheat proline P5CS overexpression drought, and wheat HaHB4 HB4 drought were included as representative combinations. As genes were identified during screening, additional searches were conducted to find genes and gene families (TaEXPA2,

TaSnRK2, TaAREB3, TaMYB31, etc.). Backward citation tracking was conducted by referring to a list of key prime studies and recent reviews and forward citation tracking was done for influential studies.

2.2 Inclusion and Exclusion Criteria

Only primary research articles reporting a specific genetic manipulation (transgenic overexpression, RNAi, VIGS or genome editing), and at least one drought-related phenotype at the molecular, biochemical, physiological or whole plant level, were included. Review articles were used to map the scene and find primary studies, but were not utilized as the primary evidence of specific claims unless the original primary study could not be found. Only expression profiling studies in which salinity, heat or cold tolerance was not studied alone and without a drought treatment were excluded. There was no restriction of publication dates, although studies were prioritised according to the post genome era of wheat studies (published after 2010) where these were the most relevant and foundationally important studies of a gene or mechanism were retained.

2.3 Evidence Classification

All retained studies were rated on one of four evidence tiers, which was used to differentiate the level of strength and the importance of the conclusions to wheat drought tolerance. Genetically modified wheat plants under drought stress with measurable phenotypic, physiological, biochemical or molecular response were included in Level 1 studies. The Level 2 studies were those that used wheat genetic manipulation (overexpression, silencing or editing) to relate to stress-related phenotypes without drought treatment or with a limited number of phenotypes characterized. The wheat research at level 3 focused on molecular or physiological studies on drought mechanisms not involving genetic modification. In Level 4 studies wheat genes were tested in heterologous systems (Arabidopsis, tobacco, rice or cereals) and/or used to give mechanistic context. All non-wheat evidence is clearly identified as such in the review and it is never presented as wheat evidence.

2.4 Synthesis Approach

Findings were consolidated based on biological mechanism, not on a gene-by-gene basis. The review follows the same pattern of reasoning for each mechanism: (1) propose the mechanism (claim); (2) list the experimental studies supporting the proposed mechanism (evidence); (3) identify the genetic intervention (biological change); (4) assess the drought phenotype (outcomes); and (5) summarize any limitations of the evidence (limitations). This structure was selected because it more truly represents the mechanism of drought tolerance as it exists in

planta (as an integrated network of overlapping mechanisms) than would a gene-by-gene listing.

3. Drought Stress in Wheat

To know how to make wheat more drought resistant, it is important to have a clear understanding of the impact of drought on wheat. Drought stress in wheat is a gradual process and the type of physiological and molecular processes most affected depends on the severity, duration and timing of the water stress. The effects act at several different scales and are highly interactive with development stages.

3.1 Physiological Effects

The first physiologic change in response to soil drying is a decrease in leaf water potential (LWP), followed by a decrease in stomatal conductance. The stomatal closure will decrease transpirational water loss but also limit the diffusion of CO2 into the leaf and thus the intercellular CO2 concentration, which in turn will decrease the net photosynthetic rate (NP) (Song et al., 2025; Nyaupane and Gardner, 2024). The activity of Calvin cycle enzymes decreases, the chlorophyll content reduces and photochemical efficiency decreases as the stress increases. Cell expansion is one of the most drought sensitive processes in plants and is inhibited early, prior to the detection of any effect on photosynthesis, which limits leaf area and root elongation. Pollen viability and seed set can be especially susceptible to drought during anthesis and moderate levels of stress at this time may result in an excessive yield loss. Apart from the water deficit effect on metabolism, the mass flow and diffusion of ions to the root surface are also decreased during drought, aggravating the impacts of water deficiency (Nyaupane and Gardner, 2024).

3.2 Biochemical Effects and Oxidative Stress

Drought stress results in an increase of the concentration of reactive oxygen species, a major biochemical effect. The level of CO2 fixation in chloroplast is reduced, while the surplus of excitation energy produces superoxide, hydrogen peroxide and hydroxyl radicals (Dudziak et al., 2019; Rashid et al., 2021). These ROS degrade unsaturated fatty acids present in membrane lipids into malondialdehyde (MDA) which is used as a marker of oxidative damage to membranes. ROS also are harmful to components of the photosynthetic apparatus, proteins and nucleic acids. Drought also causes a build up of compatible solutes, such as proline, soluble sugars, glycine betaine and sugar alcohols, which reduce apoplastic water potential and keep water potential lower than the cell, so preventing macromolecules from denaturing. The antioxidant defense system consists of enzymatic (superoxide dismutase (SOD), catalase

(CAT), ascorbate peroxidase (APX), glutathione reductase and peroxidase (POD)) and non-enzymatic components (ascorbate, glutathione, tocopherols and carotenoids) (Rashid et al., 2021). This system, especially the simultaneous induction of SOD, CAT and APX is highly associated with drought tolerance in wheat cultivars.

3.3 Molecular and Signaling Responses

There are two pathways in which drought stress is sensed at the cell level, the ABA-dependent and the ABA-independent. Under water deficit, water deprivation will activate ABA biosynthesis in root and leaves, leading to water transport to guard cells, binding to PYR/PYL/RCAR receptors, which results in the release of SnRK2 kinases from PP2C-mediated regulation. The SnRK2 kinases activate other transcription factors, including the AREB/ABF bZIP factors, as well as other ion channels like SLAC1, leading to stomatal closure (Wang et al., 2016; Zhang et al., 2024). The DRE/CRT binding by DREB transcription factor in the promoter of stress responsive genes is part of the ABA-independent pathway. Both pathways lead to a common set of downstream functional genes, such as LEA proteins, dehydrins, biosynthesis enzymes of osmolytes and antioxidant enzymes. Other transcription factor families such as WRKY, NAC, MYB and ERF are involved in the combination of drought signals and development and other stresses. The molecular reaction is therefore a reorganization of the transcriptome preparing the plant to maintain metabolism in water-limiting conditions, when it works.

3.4 Root Responses and Water Acquisition

The root system architecture is an important factor in drought avoidance, especially when water is available at depth. Usually, under drought stress, assimilate partitioning moves towards root growth, which results in higher root-to-shoot ratio; it can also affect the root growth angle, lateral root density, and formation of root cortical aerenchyma (Maqbool et al., 2022). By virtue of deeper rooting systems, the water in subsoil would be utilized during the terminal drought, which has been well characterized in rice using the DEEPER ROOTING 1 (DRO1) locus. Wheat cultivars in history have shown some variation in root architecture which has been linked to drought adaptation, however genetic and molecular basis of root growth angle and depth in wheat is less well understood than in rice (Maqbool et al., 2022). The relative gap is important because root traits are one of the most promising, but challenging to be phenotyped, targets for drought tolerance.

4. Genetic Basis of Drought Tolerance in Wheat

Drought tolerance is known to be a polygenetic, quantitative trait and the genetic basis for drought tolerance in wheat is a reflection of the convergence of multiple functional genes. This section presents a summary of the main gene families and pathways investigated as possible targets for genetic modification, highlighting those genes that have been shown to have functional effects in wheat and others for which there is more evidence in model species.

4.1 Transcription Factors

The most common class of drought-tolerant genes targeted in drought-tolerant engineering is transcription factors (TFs) which are able to control a whole chain of downstream stress-responsive genes. Members of the DREB family, which belongs to the AP2/ERF family, are well studied and recognise DRE/CRT elements in promoters of ABA-independent stress genes. TaDREB genes and heterologous DREBs like GmDREB1 of soybean etc are over-expressed with reproducible drought-tolerance phenotypes in wheat (Zhou et al., 2020; Khan et al., 2019). The AREB/ABF subgroup of bZIP TFs functions downstream of ABA signaling and promote the expression of genes controlled by ABRE, with wheat AREB3 being characterized mostly in the heterologous context of Arabidopsis (Wang et al., 2016). There are extra layers of regulation, namely, inactivation of TaWRKY2 and MYB in wheat leads to improved and reduced drought tolerance, respectively (Gao et al., 2018; Wei et al., 2018), and TaMYB31 silencing results in a decrease in the activity of antioxidant enzymes, suggesting that the endogenous TFs are both positive and negative regulators of drought tolerance.

4.2 Signaling Components: ABA, Kinases, and Phosphatases

The ABA receptor–PP2C–SnRK2 module is a key pathway for signal transduction downstream of drought perception. The wheat orthologs of this module, TaPYL receptors, TaPP2C phosphatases and TaSnRK2 kinases have been functionally characterised. TaSnRK2.4 interacts with other members of its module to mediate drought adaptation in Triticum aestivum (Zhang et al., 2024); overexpression of TaSnRK2.8 has been shown to confer drought, salt and cold tolerance, although that was not shown for T. aestivum (Zhang et al., 2010). Wheat evidence that altering drought physiology via ABA perception is possible is provided by the direct wheat evidence that under-drought conditions, ABA receptor TaPYL4 overexpressing wheat had reduced transpiration and improved water-use efficiency (Mei et al., 2022; see TaPYL5 work for a similar mechanism) The results suggest that in addition to TFs downstream of ABA signaling, downstream components of ABA signaling play a role in efficacy as well.

4.3 Osmolyte Biosynthesis and Protective Proteins

Classical targets are genes for enzymes involved in biosynthetic pathways of osmolytes. In wheat, Proline accumulation is dependent on P5CS (Δ1-pyrroline-5-carboxylate synthase), with the expression of TaP5CS1 coordinately controlled by TaERF87 and TaAKS1, and TaAKS1 overexpression resulted in an increase in drought tolerance through proline accumulation (Sun et al., 2022). The synthesis of glycine betaine has been reported to enhance drought tolerance of wheat by enhancing photosynthesis due to the introduction of the codA gene from bacteria (reviewed in Khan et al., 2019). Late embryogenesis abundant (LEA) proteins and dehydrins protect against protein aggregation and membrane damage during dehydration while the overexpression of wheat DHN-5 increased tolerance to salt and osmotic stress, with the primary functional evidence provided using Arabidopsis (Brini et al., 2007). Small heat shock proteins like TaHSP23.9 function as chaperones, but are functional characterisations mainly known from heterologous systems (Frontiers, 2020). The protective-protein category is thus both mechanistically well understood and has only a few wheat-specific functional data.

4.4 Antioxidant Enzymes and ROS Scavenging

The idea of direct overexpression of antioxidant enzymes seems an obvious way to minimize oxidative damage under drought is intuitively appealing. In wheat, the coordinated induction of SOD, CAT, APX and POD have been studied under water deficit, and cultivar comparisons invariably indicates that wheat cultivars with water stress tolerance exhibited higher activity levels of antioxidant enzymes and less MDA content (Rashid et al., 2021). Single-gene overexpression of antioxidants in wheat has had more varied results, however, with ROS also being signaling molecules, the complete knock down may have an adverse impact on the signaling. This trade-off is further discussed in Section 6.2.

4.5 Root Architecture Genes

The genetic control of root traits is complex and very few specific genes have been shown to be clearly associated with a positive effect on wheat drought tolerance when modifying root traits. In rice, the DRO1 pathway has been demonstrated to change the root growth angle and root depth, and sequences related to DRO1 in wheat yield deeper root architectures (Uga et al., 2013; DRO1 patent US10513708B2). Expansins loosen cell walls and thus affect root growth, and overexpression of wheat TaEXPA2 results in drought tolerant wheat plants with phenotypes that are consistent with increased root and leaf cell expansion (Yang et al., 2020).

While above-ground genetic modification is fairly well developed, the development of root-targeted genetic modifications in wheat is less advanced.

5. Drought Tolerance Mechanisms in Genetically Modified Wheat

Here, the experimental evidence is presented in order of biological mechanisms, not by genes. The review considers the proposed mode of action, the wheat genetic interventions that have been evaluated, the biological consequences of the interventions and the level of evidence for a true drought-tolerance phenotype in wheat for each mechanism.

5.1 Water Relations and Osmotic Adjustment

Osmotic adjustment is the active accumulation of compatible solutes which reduces the osmotic potential of the cell allowing water uptake and maintenance of turgor under increasingly negative water potential. Only a few solutes, including proline, soluble sugars, glycine betaine and polyols are major components. The mechanistic argument is simple: greater ability to synthesize osmolytes should enable transgenic plants to continue to grow, photosynthesize and metabolize at lower leaf water potentials than non-transgenic plants. The most obvious wheat evidence has to do with proline metabolism. Sun et al. (2022) showed that TaERF87 regulates TaP5CS1 in wheat; that TaERF87 and TaAKS1 both regulate TaP5CS1, in concert; and that TaAKS1 is a gene associated with drought tolerance, which they showed to be increased in wheat by TaAKS1 overexpression with increased proline accumulation (Level 1 criteria: GM wheat, drought treatment, measurable phenotype). There are reports of glycine betaine engineering using the codA gene to enhance tolerance and photosynthesis in wheat (Khan et al., 2019), but the main wheat transformation studies for this are very old and would benefit from replication in accordance with current phenotyping standards. The wheat DHN-5 was over-expressed to increase osmotic adjustment and the most important functional evidence was done in Arabidopsis (Brini et al., 2007), which corresponds to Level 4 in wheat. Osmolyte-based strategies have limitations: side-by-side effects of the diversion of carbon and nitrogen to make compatible solutes could negatively impact growth under non-stress conditions – which would need to be taken into account in field trials.

5.2 Antioxidant Defense and ROS Homeostasis

In wheat there is a considerable amount of correlative evidence that supports the antioxidant mechanism. Consistently, tolerant cultivar have higher level of SOD, CAT and APX activity and lower MDA under drought condition in cultivar comparison (Rashid et al., 2021; Dudziak et al., 2019). Overexpression of AtWRKY30 in wheat led to the activation of antioxidant machinery and osmolyte biosynthesis, and increased the tolerance to combined heat and

drought stress in wheat, providing direct evidence that a TF regulating the antioxidant network is able to improve tolerance in wheat (El-Esawi et al., 2019). In contrast, wheat endogenous TFs TaWRKY31 silencing resulted in a decrease in drought tolerance along with a decrease in endogenous TFs TaSOD, TaPOD and TaCAT, indicating that endogenous TFs are essential for normal antioxidant induction in wheat (Ge et al., 2024). All these interventions have biological effects that can be measured as a reduction in oxidative damage of the membrane and a improvement in the preservation of the chlorophyll and photosynthetic apparatus. In greenhouse pot tests the drought phenotype is always positive. A major drawback is the inconsistent results of single gene modification of antioxidant enzymes reported in different studies which may be attributable to the involvement of ROS in signaling leading to acclimation responses. The negative effects of over-scavenging ROS can dampen positive signaling, and can paradoxically decrease tolerance, which has not been thoroughly quantified in wheat field conditions and is a key uncertainty.

5.3 ABA and Stress Signaling

ABA is the main hormone involved in drought response and genetic modification of ABA signalling components have yielded some of the most impressive wheat evidence in this review. The mechanism is the canonical ABA receptor–PP2C–SnRK2 module; ABA induces the release of SnRK2 kinases from inhibition by PP2C, and then the SnRK2s are able to phosphorylate downstream TFs (AREB/ABFs) and ion channels, leading to stomatal closure and induction of stress genes. TaSnRK2.4 has been identified as a functional mediator of drought adaptation in wheat, and has been shown to be an interacting partner of a wheat drought adaptation signaling module (Zhang et al., 2024). In wheat, the overexpression of the ABA receptor TaPYL4 did indeed enhance ABA sensitivity, reduced water use (transpiration), and boosted water-use efficiency under water deficit, all of which can be directly observed (as reported in the TaPYL5/TaPP2C53/TaSnRK2.1 study and referred to supporting literature; Mei et al., 2022). The downstream transcription factor TaAREB3 activates ABRE driven genes including RD29A, RD29B, COR15A and COR47, and enhances drought tolerance, but has not been tested in wheat, so is a strong candidate with only Level 4 evidence for wheat drought tolerance (Wang et al., 2016). One drawback is the occurrence of stress-inducible, but not constitutive, promoters, which allows growth in non-stressed conditions but at the expense of growth and production when stressed.

5.4 Photosynthetic Protection

Photosynthesis is not only a key drought stress response, but also a key factor determining post drought yield recovery. In general, genetic modification for maintaining chlorophyll content, photochemical efficiency and stomatal conductance in water deficit will maintain the biomass and yield. A drought tolerance event in wheat (HB4) from sunflower was developed and characterized as a sunflower HD-Zip transcription factor that will improve drought tolerance in wheat in field trials in Argentina and is associated with maintenance of photosynthetic performance under water deficit (González et al. 2019; Ribichich et al. 2020). It is believed that the mechanism involves modulation of ethylene signaling (HaHB4 co-suppresses ethylene related genes, thus postponing the onset of senescence and the duration of active photosynthetic activity in response to drought stress). In wheat, the overexpression of AtWRKY30 led to an enhancement in gas exchange traits and a better photosynthetic stability under combined heat and drought stress (El-Esawi et al., 2019). The engineering of glycine betaine has also been reported to be beneficial in protecting photosynthesis under drought (Khan et al., 2019). In greenhouse studies there is high level of evidence for photosynthetic protection as the mechanism, but in the field, VPD and canopy temperature is related to photosynthetic protection in complex ways in relation to stomatal traits.

5.5 Root Architecture and Water Acquisition

In most cases, root traits have their greatest impact on drought tolerance by how they acquire water rather than by means of cellular drought tolerance mechanisms, and they are most important during progressive drought and/or terminal drought where subsoil water is present. Overexpression of TaEXPA2 in wheat results in drought-tolerant wheat phenotypes similar to increased cell wall loosening and root and leaf growth (Yang et al., 2020; Chen et al., 2016). In rice, the DRO1 pathway is well characterized with root growth angle and water uptake being affected as a result of the introduction of DRO1 related sequences into wheat (Triticum) rooting phenotypes were created (Uga et al., 2013; DRO1 patent US10513708B2). The main proof for the yield advantage of DRO1 was in rice, however, similar field level yield data for wheat is scarce. Phenotyping is the main drawback of root-targeted approaches: root architecture is hard and time-consuming to assess in field soil and many potential root phenes have not been tested at the required scale to ensure yield benefit under realistic drought.

5.6 Stress-Responsive Transcriptional Regulation

The most consistent category of genetic modification in wheat for drought tolerance, in that multiple independent studies have reported positive phenotypes, is for transcription factor overexpression. In a multi-year, multi-site field experiment, GmDREB1 (soybean DREB1)

was found to be able to generate drought-tolerant phenotypes in two wheat varieties (Zhou et al., 2020). The drought tolerant phenotype from HaHB4 (sunflower HD-Zip) has been shown in wheat under field-grown conditions (under different environments) (González et al., 2019) and is the basis for the HB4 wheat event that is commercially approved in Argentina (Sheridan, 2021). Overexpressed TaWRKY1 in wheat led to the improvement of drought tolerance and better grain yield under harsh conditions (Gao et al., 2018). Overexpression of TaMYB31 in wheat resulted in an enhanced drought tolerance in wheat (Wei et al., 2018). A novel drought-tolerant gene TaPUB57, which is an E3 ubiquitin ligase, was found to impart drought tolerance in wheat (Yu et al., 2025). Overexpression of GmTDN1 in wheat resulted in increased drought and low nitrogen tolerances and good performance in field trials (Zhou et al., 2022). TF overexpression acts to up-regulate its downstream stress genes, which are typically a recapitulation of the natural stress transcriptome, and the downstream phenotypes are typically beneficial in greenhouse settings. The main drawback is that overexpression of stress TFs may lead to yield penalties under non-stress conditions as shown in some stress TF overexpressing cereals. An approach to reduce this trade-off is to regulate stress-inducible promoters, such as the TaWRKY2 promoter identified by Gao et al. (2018) which is drought-, salt- and ABA-responsive; however, few field studies have investigated whether inducible expression allows for an avoidance of yield penalty without compromising yield benefit.

5.7 Summary of Mechanistic Evidence

For the five mechanisms, the best wheat specific evidence is for transcription factor overexpression (DREB, WRKY, MYB, HD-Zip) and manipulation of ABA signaling components (TaSnRK2, TaPYL4). Mechanistically well understood and supported by correlative cultivar data, osmotic adjustment and antioxidant defence are two processes for which a single-gene manipulation has generated a more variable transgenic phenotype. Mechanistically, there is interest in modifying roots, but there are phenotyping limitations. Photosynthetic protection is not a single gene target, but is a consequence of multiple interventions upstream. The experimental evidence on genetically modified wheat is summarised in Table 3 (section 7).

6. Summary Tables

The evidence considered in Sections 3–5 has been summarised in the following tables. The wheat-specific experimental evidence is separated from evidence collected in other systems (heterologous evidence) in each table. When there is enough evidence to make a determination

about a cell, that cell is filled in, but if there is not enough evidence, then that cell is marked instead of being filled in with unconfirmed information.

Table 1. Major drought-response mechanisms in wheat and their primary molecular components.

Mechanism	Key molecular components	Functional effect	Evidence base in wheat
Osmotic adjustment	Proline (P5CS); glycine betaine (codA); soluble sugars; LEA/dehydrin proteins	Lowers cellular osmotic potential; maintains turgor and hydration	Level 1 (TaAKS1/TaP5CS1); Level 4 (DHN-5 in Arabidopsis)
Antioxidant defense	SOD; CAT; APX; POD; glutathione; ascorbate	Scavenges ROS; reduces membrane lipid peroxidation (MDA)	Level 1 (AtWRKY30 in wheat); Level 1 (TaWRKY31 silencing)
ABA and stress signaling	PYR/PYL receptors; PP2C phosphatases; SnRK2 kinases; AREB/ABF bZIP TFs	Stomatal closure; induction of stress-responsive genes	Level 1 (TaSnRK2.4, TaPYL4 in wheat); Level 4 (TaAREB3 in Arabidopsis)
Photosynthetic protection	Chlorophyll maintenance; stomatal conductance; ethylene regulation (HaHB4)	Sustains carbon assimilation and photochemical efficiency	Level 1 (HaHB4 field wheat; AtWRKY30 in wheat)
Root architecture and water acquisition	Expansins (TaEXPA2); DRO1-related genes; root growth angle	Deeper rooting; improved access to subsoil water	Level 1 (TaEXPA2 in wheat); Level 4 (DRO1 in rice; patent data in wheat)
Transcriptional reprogramming	DREB, NAC, WRKY, MYB, HD-Zip TFs; stress-inducible promoters	Coordinate induction of downstream stress gene networks	Level 1 (GmDREB1, TaWRKY2, TaMYB31-B, HaHB4 in wheat)

Note: Evidence levels are defined in Section 2.3. Level 1 = transgenic wheat under drought with measurable phenotype; Level 4 = evidence from heterologous systems.

Table 2. Representative genetic targets investigated for drought tolerance in wheat and related systems.

Gene / target	Class	Modification	Primary host system	Evidence level
GmDREB1 (soybean)	AP2/ERF TF	Overexpression (Ubi promoter)	Wheat (field, multi-site)	Level 1
HaHB4 (sunflower)	HD-Zip TF	Overexpression	Wheat (field); commercialized as HB4	Level 1
TaWRKY2 (wheat)	WRKY TF	Overexpression	Wheat	Level 1
TaMYB31-B (wheat)	MYB TF	Overexpression	Wheat	Level 1
TaWRKY31 (wheat)	WRKY TF	BSMV:γ silencing	Wheat	Level 1 (loss-of-function)
AtWRKY30 (Arabidopsis)	WRKY TF	Overexpression	Wheat (heat + drought)	Level 1
TaSnRK2.4 (wheat)	SnRK2 kinase	Functional module / overexpression	Wheat	Level 1
TaSnRK2.8 (wheat)	SnRK2 kinase	Overexpression	Arabidopsis	Level 4
TaPYL4 / TaPYL5 (wheat)	ABA receptor	Overexpression / knockdown	Wheat	Level 1
TaAREB3 (wheat)	AREB/bZIP TF	Overexpression	Arabidopsis	Level 4
TaP5CS1 / TaAKS1 (wheat)	Osmolyte biosynthesis	Overexpression	Wheat	Level 1

codA (bacterial)	Glycine betaine synthesis	Overexpression	Wheat (reported)	Level 1–2
DHN-5 (wheat)	Dehydrin	Overexpression	Arabidopsis	Level 4
TaEXPA2 (wheat)	Expansin	Overexpression	Wheat (Yang 2020); tobacco (Chen 2016)	Level 1 (wheat)
GmTDN1 (soybean)	Nodulin-like	Overexpression	Wheat (greenhouse + field)	Level 1
TaPUB57 (wheat)	E3 ubiquitin ligase	Overexpression	Wheat	Level 1
TaHSP23.9 (wheat)	Small HSP	Overexpression	Arabidopsis	Level 4
DRO1 (rice, homologs)	Root growth angle	Introgression / overexpression	Rice (primary); wheat (patent data)	Level 4 for wheat

Note: 'Level 1 (loss-of-function)' denotes a silencing study in wheat that demonstrates the gene's requirement for tolerance. Where a gene was tested in both wheat and a heterologous system, the highest applicable wheat evidence level is reported.

Table 3. Experimental evidence from genetically modified wheat with drought-related phenotypes.

Gene / intervention	Wheat material	Drought treatment	Key phenotypic / physiological result	Scale	Reference
GmDREB1 overexpression	Two wheat varieties	Multi-year, multi-site field drought	Drought-tolerant phenotype across environments	Field	Zhou et al., 2020
HaHB4 overexpression (HB4)	Wheat	Field, multiple	Drought-tolerant phenotype;	Field (commercialized)	González et al., 2019

		environments (Argentina)	yield increase under stress		
TaWRKY2 overexpression	Wheat	Greenhouse / pot drought	Enhanced drought tolerance; increased grain yield	Greenhouse	Gao et al., 2018
TaMYB31-B overexpression	Wheat	Drought treatment	Increased drought tolerance	Greenhouse	Wei et al., 2018
TaEXPA2 overexpression	Wheat	Drought treatment	Drought-tolerant phenotype; improved cell expansion	Greenhouse	Yang et al., 2020
GmTDN1 overexpression	Wheat	Drought + low-N; greenhouse and field	Improved drought and low-N tolerance; field yield benefit	Greenhouse + field	Zhou et al., 2022
TaSnRK2.4 functional module	Wheat	Drought-related assays	Mediates drought adaptation	Greenhouse / lab	Zhang et al., 2024
TaPYL4 overexpression	Wheat	Water deficit	Lowered transpiration; improved water-use efficiency	Greenhouse	Cited in Mei et al., 2022
AtWRKY30 overexpression	Wheat	Combined heat + drought	Enhanced tolerance; antioxidant	Greenhouse	El-Esawi et al., 2019

			and osmolyte induction		
TaWRKY31 silencing (BSMV:γ)	Wheat	Drought treatment	Reduced antioxidant enzyme activity; reduced tolerance	Greenhouse	Ge et al., 2024
TaAKS1 overexpression	Wheat	Drought treatment	Increased proline accumulation; improved tolerance	Greenhouse	Sun et al., 2022
TaPUB57 overexpression	Wheat	Drought-related	Drought tolerance; ubiquitin-mediated regulation	Greenhouse / lab	Yu et al., 2025

Note: Only studies reporting drought-related phenotypes in genetically modified wheat are included. Studies in which a wheat gene was characterized only in Arabidopsis or tobacco are listed in Table 2 but not here.

Table 4. Comparison of genetic strategies for drought tolerance in wheat and their limitations.

Strategy	Mechanistic basis	Demonstrated benefit in wheat	Principal limitations	Maturity
Transgenic TF overexpression	Coordinate induction of stress gene networks (DREB, WRKY, MYB, HD-Zip)	Field-validated for GmDREB1 and HaHB4; greenhouse-validated for several others	Constitutive expression may reduce yield under non-stress; regulatory barriers for transgenics	Mature (some commercial)

ABA signaling component manipulation	Modified stomatal regulation and stress-gene induction (SnRK2, PYL)	Direct wheat evidence for TaSnRK2.4 and TaPYL4	Growth–defense trade-off; few field data	Intermediate
Osmolyte engineering	Proline / glycine betaine accumulation maintains turgor	TaAKS1/TaP5CS1 and codA reported in wheat	Metabolic cost; variable transgenic phenotypes	Intermediate
Antioxidant enzyme manipulation	ROS scavenging reduces oxidative damage	Correlative cultivar evidence strong; transgenic phenotypes variable	ROS also serve as signals; over-scavenging trade-off not quantified in field	Intermediate
Root architecture modification	Deeper rooting improves water acquisition	TaEXPA2 in wheat; DRO1-related data limited	Difficult phenotyping; few field yield data in wheat	Emerging
RNAi / VIGS	Suppression of negative regulators	TaWRKY31 silencing demonstrates gene requirement	Generally used for proof-of-function, not as a trait delivery route	Mature (as a tool)
CRISPR/Cas genome editing	Targeted modification of endogenous genes	Limited direct drought evidence in wheat; TaGW2 editing linked to drought-related traits	Mostly proof-of-concept; few drought phenotypes; regulatory uncertainty in some jurisdictions	Emerging

Cisgenic / precision breeding	Introduction of alleles from sexually compatible species	Not sufficiently established for wheat drought tolerance	Limited demonstrated cases; depends on available allelic variation	Emerging

Note: 'Maturity' reflects the readiness of the strategy for translation, not its scientific validity. A strategy rated 'Emerging' indicates that primary evidence in wheat is currently limited.

7. Comparative Evidence Across Genetic Targets

A major problem of comparing the genetic targets from different studies is the significant study-to-study variability in experimental design. Wheat genotype, drought severity and timing, growth medium, transformation method, promoter and the measurements of the phenotype reported vary among studies. There are very few studies that have a standardized phenotyping method and even fewer that report the results of more than one environment. Allowing for these reservations, there are several patterns of comparison.

7.1 Transcription Factors versus Enzyme Overexpression

Based on the results from the over-expression of transcription factors, a more consistent positive wheat phenotype has been achieved than in the case of single-enzyme over-expression. Five genes, GmDREB1, HaHB4, TaWRKY2, TaMYB31-B and AtWRKY30, all over-expressed in wheat improved drought tolerance when expressed in wheat, with two of these (GmDREB1 and HaHB4) being field-tested (González et al., 2019; Zhou et al., 2020). By contrast, the effects of single-gene overexpression of antioxidant enzymes have been more variable, perhaps because there are a number of tightly coupled antioxidant pathways and because ROS also play signaling roles that are important to maintaining cellular function. This is a general rule that TF regulation of an entire gene network is more effective than TF regulation of a single downstream enzyme.

7.2 Heterologous versus Wheat-endogenous Genes

The wheat-endogenous genes TaWRKY2, TaMYB31-B, TaEXPA2, TaSnRK2.4, TaPYL4, TaPUB57 and TaAKS1 have led to beneficial wheat phenotypes, as has the heterologous genes GmDREB1, HaHB4, GmTDN1, AtWRKY30 and codA. The advantage of using heterologous TFs is that they are 'naive' to the wheat regulatory network and may not be down-regulated by endogenous feedback mechanisms that could reduce its activity and underlie the ability of GmDREB1 and HaHB4 to perform well. The advantages of using wheat endogenous genes are the regulatory compatibility, especially if they are used by the cisgenic or genome editing

strategies. Therefore, preference should not be given to either one of the two sources unless the regulation and breeding pathway is considered.

7.3 Greenhouse versus Field Performance

Translating greenhouse performance to field performance is the most impactful uncertainty for this field. Only three of these studies; two on HaHB4 (González et al., 2019; Ribichich et al., 2020) and one on GmDREB1 (Zhou et al., 2020) and GmTDN1 (Zhou et al., 2022) have reported field-level phenotypes, with only HaHB4 commercialized (Sheridan, 2021). The vast majority of other wheat transgenic research uses greenhouse pot experiments with controlled soil water content, root volume and other environmental factors. The results from the greenhouse are informative in terms of mechanism but not a good indicator of yield as field drought is not uniform in time and space, interacts with vapour pressure deficit and canopy temperature, and is accompanied by other stresses (heat stress, nutrient deficiency, disease). The case of wheat with drought-tolerance phenotypes which were observed under controlled conditions and brought benefit to wheat in some Argentinean environments, but which have been questioned for consistency and independence of the supporting data (Friends of the Earth, 2024) is also relevant for this field validation. Independent multi-environment field trials still have the highest priority unmet need.

7.4 Stress-inducible versus Constitutive Promoters

The promoter driving the expression of the transgenes is a key factor in the stress benefit/non-stress yield penalty trade-off. Promoters like ubiquitin or 35S are used to ensure continuous expression, and can be known to negatively affect growth and yield under non-stress conditions, so over-expression of DREB can do the same. The use of stress-inducible promoters, like the drought-, salt-, heat, and ABA-responsive TaWRKY2 promoter characterized by Gao et al. (2018), should help to avoid this cost, by limiting the expression of transgenes to stress conditions. For wheat, direct comparison of constitutive and inducible expression of the same transgenic gene in the field under stress and non-stress conditions has been little studied, and is a clear, tractable research need.

8. Emerging Approaches

8.1 CRISPR/Cas Genome Editing in Wheat

CRISPRs/Cas systems will allow the targeted changes of the endogenous wheat genes without the insertion of foreign DNA, an important scientific and regulatory point. Several targets have been multiplex CRISPR/Cas9 edited in wheat, and editing of TaGW2, the focus of many studies on wheat grain weight, has been associated with drought-related traits (Plantae, 2024).

But there is so far little direct evidence that the modification of a specific wheat gene by CRISPR, results in a drought-tolerant phenotype. Most wheat published CRISPR studies have focused on domestication related traits, disease resistance, or grain traits, not specifically drought tolerance. The use of CRISPR for creating drought-tolerant wheat is therefore classified as an emerging technology with great promise but with little published primary research to back it up: statements that genome editing is already providing drought-tolerant wheat are not supported by the primary literature.

8.2 Promoter Engineering and Gene Stacking

Planning of transgenic expression via promoter engineering, that is the design of synthetic or modified promoters that have defined stress responsiveness, provides a way of combining the benefits of transgenic expression with the benefits of stress-inducible timing. When gene stacking (simultaneous introduction of multiple transgenes, each acting on different mechanisms) is combined with stress-inducible promoters, it may be possible to achieve higher levels of tolerance than any single-gene approach can. There are many examples in the primary literature of well-characterised stacked drought-tolerant events from other cereals, but not many examples from wheat. A major hurdle is the difficulty of regulatory assessment of multiple transgenes and their level of expression, which needs to be carefully balanced to mitigate metabolic burden.

8.3 Cisgenic and Precision Breeding Approaches

In some jurisdictions, the introduction of genes from a sexually compatible wheat or wild relatives (cisgenics) may have fewer regulatory hurdles than introducing genes from a different wheat species (transgenics). The introduction of drought resistance alleles from wild relatives like Aegilops tauschii or wild emmer (Triticum dicoccoides) through introgression (AMBC) is per se not a genetic modification but, if these alleles are transferred into the crop by transformation of the nucleus, it is cisgenic. The events already demonstrated in wheat as cisgenics that can withstand drought are not yet well established in the primary literature to make strong claims and they are largely prospective.

8.4 Base Editing and Prime Editing

Base editing and prime editing are methods for changing a single nucleotide without double-strand breakages and have been shown to work in a few plant species. In wheat, these technologies are technically possible and in the context of drought tolerance, the technologies are still in the early stage of development; no wheat base-editing studies to the authors' knowledge have been published with drought phenotypes validated in the field. The scientific

value lies in having the option of introducing specific regulatory and/or coding changes to alter the expression of endogenous genes without completely knocking it out; this is not yet a reality, but is a future possibility.

9. Research Gaps and Future Directions

Literature reviewed here lends support to several conclusions about what is still missing, and these are not 'more research' calls but those that are the most justifiable next steps in the field.

9.1 Multi-Environment Field Validation

The most important deficiency is the lack of multiple field trials of transgenic wheat in different environments and different years under drought stress. There have been only a few transgenic events that have been field-tested (HaHB4 and GmDREB1) and independent replications in other genetic backgrounds and environments are needed. Specifically, the trials should cover at least three target mega-environments with varying drought timing (terminal, intermittent and early-season), must be conducted with the near-isogenic line as the relevant control and yield data should include physiological phenotypes. Entitled claims of drought tolerance are tentative without such trials.

9.2 Genotype-by-Environment-by-Transgene Interactions

Only a few studies have detailed whether or not a particular wheat background is comparable to the others in regard to the phenotypes produced by a given transgene. Elite cultivars have varying stress responses, so a transgene that works well in one cultivar might not work well in another. Replication of the same transgene in at least 3 different genetic backgrounds, at least 2 different drought regimes, would help determine the stability of transgenic drought tolerance and identify modifiers of this transgenic response in different backgrounds. Technically possible, but needs synchronized investments.

9.3 Phenotyping Standardization

A lack of a common phenotyping protocol makes it difficult to compare results across studies. The intensity of drought depends on the fraction of transpirable soil water, leaf water potential, relative water content or visual drought score and the moment of drought stress application varies. A minimum phenotyping protocol agreed by the community (e.g. stomatal conductance, leaf water potential, chlorophyll fluorescence (Fv/Fm), MDA, proline, antioxidant enzyme activity at specific development stages) would significantly increase comparability of studies.

9.4 CRISPR for Drought Tolerance in Wheat

Although promising, there are no field-tested drought tolerant wheat lines available using CRISPR. Specific testable hypotheses must be formulated, e.g., editing of negative regulators

of ABA signaling (specific TaPP2C isoforms) or of promoter elements of endogenous stress TFs (to make them more inducible). A clear phenotyping plan should accompany each one of such targets, and ideally, should be accompanied by field testing.

9.5 Translation of Heterologous Evidence to Wheat

A few wheat genes with good mechanistic supports have been characterized solely in heterologous systems, such as TaAREB3, TaSnRK2.8, DHN-5, TaHSP23.9. These genes should be validated for function in transgenic wheat under drought conditions prior to their use as breeding targets. Until validated, these are genes that should be considered as candidate targets and not as confirmed targets.

9.6 Root Phenotyping and Field-scale Root Measurement

The difficulty of measuring root architecture in field soil limits modifications to the genetic makeup of the roots. Field root phenotyping has been facilitated by non-invasive techniques like ground-penetrating radar, mini-rhizotrons and shovelomics, although standardized protocols and the integration with transgenic evaluation have not been developed. This would open up the possibility to use the genes responsible for the wheat root-architecture as a tractable target for drought resistance.

9.7 Trade-offs under Non-Stress Conditions

Some transgenes have a yield penalty in non-stress environments, which has been well documented in principle, but poorly quantified in wheat field trials. Even a small reduction in yield under good conditions of a transgenic drought-tolerant variety may be too great a price to pay. Future studies should include reports of yield under stress and non-stress conditions and should explicitly test stress-inducible promoters to reduce this trade-off.

10. Conclusion

This review assessed the techniques used to induce genetic modifications and the molecular, physiological and biochemical pathways that allow wheat to withstand drought, as well as the quality of the available evidence that drought resistance is improved. The main conclusion is that genetic modification of wheat plants can be used to significantly boost specific drought-tolerance mechanisms and the most compelling evidence lies with the overexpression of transcription factors and manipulation of ABA signaling components. Significant reproducible drought-tolerant wheat phenotypes can be obtained through transgenic overexpression of GmDREB1, HaHB4, TaWRKY2, TaMYB31-B and AtWRKY30; and field validation has been done for GmDREB1 and HaHB4, with HaHB4 given commercial approval to grow in

Argentina. A second well-supported axis of plant water use regulation relates to manipulation of ABA signaling pathways by TaSnRK2.4 and TaPYL4 in wheat.

These modifications have partly overlapping mechanisms of action: the downstream stress gene networks are coordinate induced by the overexpression of transcription factors, the stomatal conductance and stress-gene induction is regulated by ABA signaling, the osmotic adjustment keeps the cell hydrated, the antioxidant defense limits oxidative stress, and the root architecture modifications improve water acquisition. None of these mechanisms alone are enough and combinations of upstream regulatory and downstream functional genes may be most likely to produce high tolerance.

The evidence also is limited and specific. Transgenic wheat experiments are almost exclusively conducted on a pot basis in a greenhouse and there are few reports of field trials. Currently there is a limited amount of direct evidence for drought tolerance in wheat via CRISPR. There are several genes that are quite mechanistically convincing, but have not been characterized in other systems and need to be validated in wheat. Processes of phenotyping are not standardized; genotype by environment interaction is not well understood; and interactions in non-stress situations are rarely measured. These are the key limitations for achieving genetic modification to a stable field-level drought-resistant crop—and they're not caused by the lack of candidate genes.

The central research question is thus answered but subject to qualification: genetic modification can indeed help to increase the tolerance of a specific drought-tolerance mechanism in wheat and a few transgenic events have led to field level tolerance. The generality, stability and yield effect of these changes in the different environment in which wheat is cultivated, however, are not sufficiently tested. This will take co-ordinated investment in multi-environment field trials, standardisation of phenotyping and validation of new genome-editing technologies as tools for drought-tolerance from proof-of-concept to drought-tolerant wheat.

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