



Advances in the impact of abiotic stress on wheat spike development

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Abstract

Wheat is a staple crop of critical economic and food security importance, with its yield playing a decisive role in ensuring global food supplies. However, the increasing frequency of extreme climatic events poses a substantial challenge to achieving stable and high yields. The wheat spike, as the principal yield-determining organ, has become a central focus of research, and remarkable advances have been achieved in unraveling its developmental regulatory networks with the aid of genomic and biotechnological approaches. Nevertheless, beyond intrinsic genetic potential, environmental stresses remain critical constraints on wheat spike development and subsequent productivity. However, research progress in this field lags far behind that in other areas like root, seedling, and even grain development. Here, current advances on the direct and indirect effects of abiotic stresses such as temperature, drought, and salt on spike development, and QTL's and genes involved in stress responses during spike development, are summarized. Finally, we discussed emerging perspectives that may deepen our understanding of spike–environment interactions, and guide strategies to enhance spike resilience and optimize wheat yield under stress conditions.

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Introduction

Wheat (*Triticum aestivum* L.) is one of the most widely cultivated cereal crops and serves as a cornerstone for global food and nutritional security^[1]. As the global population continues to grow, wheat production must increase steadily to meet rising demands. However, achieving this goal is complicated by the challenges posed by climate change, which is driving an increased frequency of extreme weather events such as heat waves, drought, and salinity intrusion. These environmental stresses not only threaten the stability of global wheat production but also limit the potential for achieving yield gains^[1]. Therefore, understanding the mechanisms by which wheat adapts to abiotic stress has become an urgent priority in crop biology and breeding.

Crop yield is a complex trait determined by multiple interacting factors, among which spike architecture and development play a central role^[2]. The spike, as the direct yield-determining organ, defines the number of spikelets and fertility of florets, ultimately influencing grain number per spike (GNS), and grain size^[3]. Recent advances in wheat functional genomics have improved our understanding of spike development and its applications in breeding practices^[4]. However, in natural environments, the genetic potential of wheat yield is frequently constrained by abiotic stresses, which exert profound effects on both vegetative and reproductive growth^[5–7]. Among these, stress-induced alterations in spike development are of particular concern because they directly compromise reproductive success and harvestable yield.

Abiotic stress can impact spike development in diverse ways. For instance, drought stress during the reproductive phase often reduces spikelet number and grain setting^[8], while heat stress disrupts floret fertility, accelerates spike development at the expense of yield components, decreasing the GNS^[9]. Salinity stress, on the other hand, affects spike morphology and grain filling by

perturbing ion homeostasis and triggering oxidative stress^[7]. Similarly, cold stress during sensitive stages of spikelet and floret formation can also result in severe sterility^[10]. These stresses act not only as environmental challenges, but also as developmental signals that interfere with the regulatory networks controlling spike architecture. Consequently, understanding how abiotic stresses intersect with developmental pathways is crucial for designing strategies that safeguard yield under changing climatic conditions.

In this review, recent advances in understanding the impacts of abiotic stresses on wheat spike development, with an emphasis on the potential loci/genes, and molecular mechanisms that they are involved in, are summarized. Emerging research directions were also highlighted that may provide new strategies to enhance spike resilience and optimize yield under adverse environments. By bridging developmental biology with stress physiology, such insights are expected to contribute to the development of stress-resilient wheat varieties, ultimately ensuring stable productivity in the face of global climate challenges.

Spike development: a basis for yield and a target of abiotic stress

Grass crops such as rice, wheat, and maize exhibit a unique evolutionary trajectory in meristem development, which plays a critical role in the coordinated diversification of inflorescence architecture across this large plant family^[11–13]. Wheat produces a spike-like inflorescence, and in most cultivated wheat varieties, each rachis node of the spike bears a single sessile spikelet, which is different from that of rice and maize^[4,12,13]. The wheat spike development is composed of several programmed phases with distinct meristem morphology^[14]. During early spike development, the shoot apical meristem (SAM) is transferred into the inflorescence meristem (IM),

shortly after the floral transition from vegetative phase to reproductive phase, after which the spikelet meristems (SM's) are produced along both sides of the rachis at the double-ridge stage. The SM subsequently gives rise to floral meristems (FM's), ultimately forming an unbranched spikelet structure following the SAM-IM-SM-FM transition pathway (Fig. 1). The activity of the IM determines the number of spikelet meristems initiated; after a specific number of SM's are formed, the IM activity ceases and is terminated by a terminal spikelet. Thus, the number of spikelets per spike (SNS) is determined at the early spike development stage. The duration of IM activity is crucial; prolonging it increases the SNS. The IM phase can be further divided into the elongation stage, and the single-ridge, and double-ridge stages, while the SM stage includes the differentiation of glume primordia, and the FM stage corresponds to floret primordia formation^[13] (Fig. 1). By the end of these stages, the basic structure of the inflorescence is fully established. At late spike development, when all floret primordia are produced, the floral development and abortion processes are divided into seven stages, including the terminal spikelet stage, white anther stage, green anther stage, yellow anther stage, tipping stage, heading stage, and anthesis, in which floret fertility plays an important role in the determination of final grain number^[15]. Extending the duration from green anther stage to anthesis could enhance assimilate accumulation in the spike, and increase the fertility of the floret during the post-anthesis phase^[15].

The GNS that is determined by SNS and floret fertility, along with the grain weight and the number of spikes per plant, are the three key components determining crop yield. Among these, the GNS is directly influenced by the development of the spike, which is regulated by a complex genetic network interacting with external environmental conditions^[4]. Therefore, elucidating the key genes and molecular mechanisms that mediate the interaction between abiotic environmental factors and yield components is essential for

advancing crop genetic improvement. Abiotic stress refers to a range of environmental threats that plants encounter, including drought, high/low temperature, salinity, and waterlogging, among others. With ongoing global warming and the increasing frequency of extreme weather events, crop growth and development face severe challenges. In both winter and spring wheat, the transition of the IM's typically occur after spring regrowth, during the reviving stage, which is often vulnerable to late spring cold spells. The spike at the programmed developmental phases demands substantial resources such as water, nutrients, and light, making the yield highly susceptible to climatic conditions. Although the physiological and biochemical impacts of individual stress factors have been increasingly revealed, and their effects on various plant organs, especially roots and leaves, have been systematically summarized^[16,17], relatively little is known about how abiotic stress influences wheat spike development and the genetic bases underlying the stress response of wheat spike.

Effects of temperature stress on wheat spike development

Global climate change directly intensifies temperature rise, causing ecosystem fluctuations and imbalances while triggering extreme temperature events—both heatwaves and cold spells. Winter wheat, the world's dominant wheat species, is favored over spring wheat for its higher yield and superior grain quality. However, its extended growing cycle increases its exposure to frequent and severe temperature stress. Consequently, research on temperature stress represents a major focus in wheat breeding. Advances in wheat genome assembly, multi-omics technologies, and the accelerating pace of global climate change are driving rapid progress in this field.

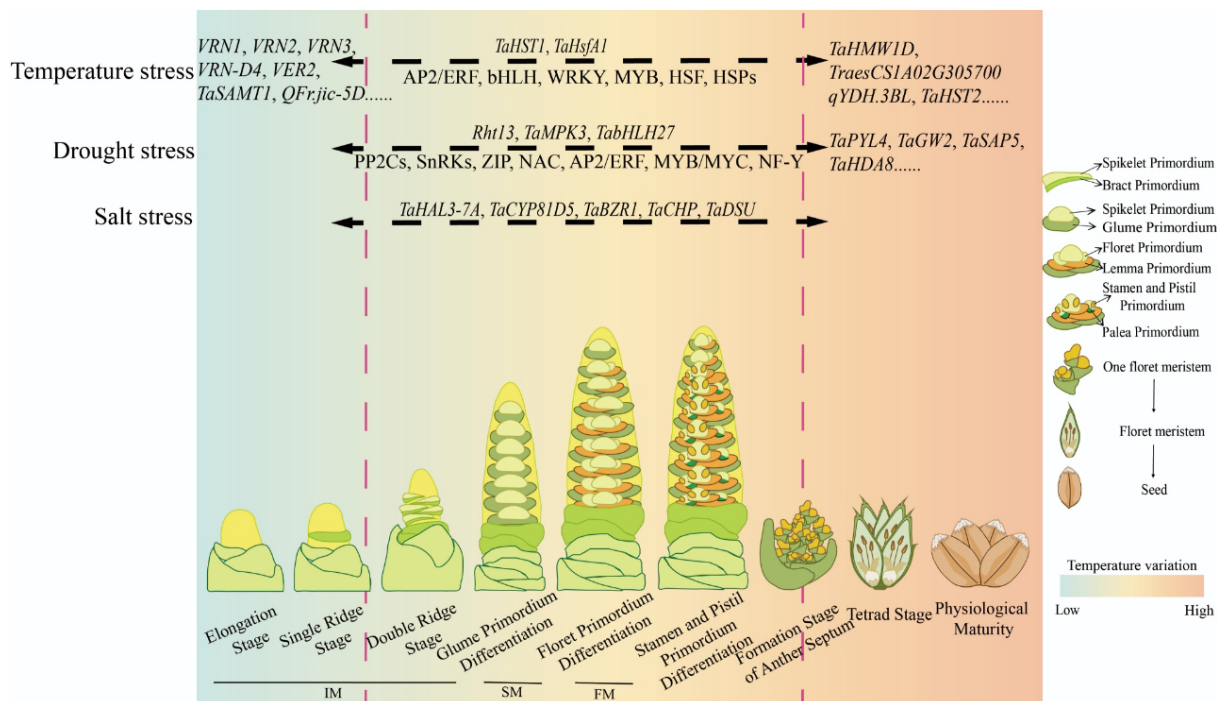


Fig. 1 Spike development and candidate genes involved in the stresses in wheat. Abbreviations: IM, inflorescence meristem; SM, spikelet meristem; FM, floral meristem; Bidirectional dashed arrows indicate functional genes or transcription factor families identified by omics analyses that may influence multiple or all stages of spike development.

Wheat spike development is a highly temperature-sensitive process that largely determines final grain number and yield. As global climate change intensifies, wheat is increasingly exposed to fluctuating temperatures, including low and freezing temperatures in winter and early spring, heat waves around anthesis, and persistent warm nights during the grain-filling period. Each of these temperature regimes imposes distinct physiological and molecular constraints on spike development, disrupting reproductive organ formation and carbon allocation and corresponding spike development.

Low-temperature and frost stress: disturbance of spikelet initiation and floret development

Global warming, coupled with the breeding emphasis on high-yield and superior grain, has led to the neglect of cold tolerance in winter wheat selection, resulting in cultivars with reduced frost resistance. Extreme low temperatures frequently occur in major wheat-growing regions such as Australia, China, Europe, and the United States. When canopy temperatures fall below 0 °C, late spring frosts severely damage vegetative and reproductive tissues, particularly during the highly temperature-sensitive stages of spike and floret differentiation, ultimately leading to significant yield reduction^[10]. At the booting or early floret differentiation stages, low temperature and frost stress highly inhibits spikelet initiation and delays floret maturation. Morphologically, these stresses reduce GNS and thousand-grain weight (TGW). Physiologically, cold exposure alters sucrose metabolism by enhancing sucrose phosphate synthase activity, but suppressing sucrose synthase and invertase, leading to sucrose accumulation in young spikes. Concurrently, low temperatures elevate abscisic acid (ABA) levels while reducing auxin (IAA) and gibberellin (GA) contents, collectively repressing spike elongation^[18]. And at the molecular level, transcriptome analyses of young spikes in response to late spring coldness revealed extensive reprogramming of carbohydrate metabolism, hormone signaling, and circadian rhythm pathways. Transcription factors such as AP2/ERF, bHLH, WRKY, MYB, and HSF families were regulated under cold stress, coordinating cold-responsive gene expression^[19]. Moreover, temperature-sensitive genic male sterile lines exhibited DNA hypermethylation^[20] and microRNA (miR167, tasiRNA-ARF)-mediated regulation of auxin signaling, linking epigenetic control to male sterility under cold stress^[21]. In addition, transcriptomic profiling of durum wheat under 5 °C at the reproductive stage identified nearly 900 differentially expressed genes involved in photosynthetic activity, lipid and carbohydrate synthesis, and amino acid and seed protein accumulation, alongside 28 transcription factors and 31 long noncoding RNA's, suggesting that lncRNA-miRNA-TF networks contribute to moderate cold tolerance^[22]. These findings collectively suggest that cold stress interferes with carbon partitioning and hormonal homeostasis, leading to delayed or aborted floret development and consequent yield loss.

Current genetic and molecular research on low-temperature response mechanisms in wheat remains relatively limited. Freezing temperatures restrict the geographical distribution of wheat and cause major yield losses. To date, freezing resistance-associated loci in wheat, including *Fr1* and *Fr2*, both containing several tandemly duplicated *C-REPEAT BINDING FACTOR* (*CBF*) genes that regulate cold-responsive pathways^[23]. Vernalization, required for flowering in winter wheat, involves genes such as *VRN1* (*VERNALIZATION1*), *VRN2*,

VRN3/TaFT1 (*FLOWERING LOCUS T1*), *VRN-D4*, and *VER2* (*VERNALIZATION-RELATED 2*)^[24], which are critical for the SAM-IM transition to start flowering. Winter wheat exhibits significantly stronger cold hardiness than spring wheat. *Vrn-A1* not only determines the spring/winter growth habit but also contributes to freezing tolerance. Notably, distinct haplotypes within the *Vrn-A1–Fr-A1* region on chromosome 5AL-where *Fr-A1* lies ~2 cM from *Vrn-A1*-underlie natural variation in freezing tolerance and have been strategically exploited in breeding programs^[25]. Freezing tolerance typically declines with the onset of reproductive growth, linking cold response to the developmental phase^[26]. Studies using *maintained vegetative phase* (*mvp*) diploid wheat mutants, which lack functional *VRN-1* revealed that plants without *VRN-1* (*mvp/mvp*) retain high freezing tolerance, whereas those with functional *VRN-1* (*Mvp/-*) flower normally but display reduced freezing tolerance and lower expression of *CBF* and *COR* genes. Additional evidence from *VRN-1* promoter mutants and expression analyses indicate that *VRN-1* initiates a regulatory cascade suppressing cold acclimation under long day conditions, although other photoperiod-regulated genes are also involved. The results demonstrate that allelic variation in *VRN-1* alone is sufficient to confer differences in freezing tolerance, suggesting that QTL for freezing tolerance previously mapped to this chromosomal region represents a pleiotropic effect of *VRN-1*, not the effect of a separate, closely linked *Fr-1*^[26]. Another QTL, *QFr.jic-5D*, was mapped near *Vrn-D1* on chromosome 5D^[27]. Breeding efforts have introduced the recessive *vrn-D1* allele from the cold-tolerant cultivar Shijiazhuang 8 into Shimai 12, producing the winter cultivar Lunxuan 103, which exhibits enhanced frost tolerance and reduced winterkill compared to spring types. However, how *VRNs* genes regulate meristems' activity under low-temperature stress at early spike development waits for further investigation.

Wheat possesses 37 *CBF* genes, five *INDUCER of CBF EXPRESSION* (*ICE*) genes, and eleven *COLD REGULATED* (*COR*) genes. Phylogenetic analysis has revealed that *ICE1* and *COR* genes exhibit closer evolutionary relationships within monocots compared with *CBF* genes. Functional studies demonstrate that overexpression of *TaCBF14* or *TaCBF15* in barley promotes the upregulation of downstream *HvCOR14b*, thereby increasing barley's cold tolerance^[28]. In wheat, both ABA-dependent *COR* genes and ABA-independent *COR* genes are significantly upregulated under cold stress^[29]. Additionally, plant hormones also regulate cold signaling. SnRK2's are core kinases in ABA signaling, and are induced by low temperatures. For example, *PKABA1*, encoding an ABA-responsive SnRK2 protein kinase, is induced by drought, low temperature, and osmotic stress, while *TaSnRK2.3* and *TaSnRK2.4*^[30] are cold-induced. Epigenetic regulation also contributes to wheat cold response. Salicylic acid (SA), a key defense hormone, can be converted into methyl salicylate (MeSA) through the catalytic activity of SAMT enzymes^[31]. MeSA has been shown to enhance cold tolerance in multiple species, including *Arabidopsis*, tomato, wheat, and several fruit trees^[27,32]. In *Arabidopsis*, this enzyme is S-ADENOSYL-L-METHIONINE-DEPENDENT METHYLTRANSFERASE1 (*SAMT1*), which uses SA as the substrate and forms MeSA^[33]. In wheat, the orthologous gene *TaSMT1* was identified by transcriptome analysis. Overexpression of *TaSMT1* increased MeSA accumulation, reduced SA levels, and markedly improved freezing tolerance, whereas knockout lines were freezing-sensitive. Importantly, yield-related traits such as spike length, spikelet number, and TGW were unaffected under field conditions, suggesting that *TaSMT1* is a promising target for breeding cold-tolerant wheat varieties^[34]. However, the direct evidence about the functions and underlying mechanisms of these genes in regulating spike development under low-temperature stress is still missing.

Furthermore, cold tolerance in wheat is highly complex. Beyond conserved mechanisms shared with *Arabidopsis*, whether wheat-specific regulatory pathways exist remains to be elucidated.

High-temperature stress: damage to reproductive organs and floral fertility

Global warming threatens wheat production by reducing both yield and grain quality, largely due to heat stress^[9]. Heat stress during reproductive stages, particularly during meiosis and pollen development, causes severe fertility loss. Elevated temperature reduces pollen viability, disturbs anther morphology, ultimately decreasing spike fertility and grain weight^[35]. At the whole-plant level, heat stress shortens the grain-filling period and promotes premature aging of photosynthetic tissues, thereby limiting carbohydrate supply to developing spikes. Physiologically, this leads to reduced floret fertility and decreased SNS and TGW. Recent physiological and genetic analyses have demonstrated that spike fertility and spike harvest index, two critical determinants of yield formation, are highly sensitive to high-temperature stress. Under heat exposure, disrupted carbon assimilation and restricted assimilate partitioning toward developing spikes weaken sink strength and reproductive success. A genome-wide association study (GWAS) identified 109 marker-trait associations under heat stress, including loci related to spike fertility and spike harvest index on chromosomes 1B, 3B, 4A, 6B, and 7D, with candidate genes encoding heat-responsive proteins such as β -glucanase, α/β -hydrolase, protein kinase, and HSP's, suggesting a coordinated molecular response to maintain carbon flux and spike fertility^[36]. GWAS and QTL mapping identified key loci on chromosomes 2A, 4B, and 6B associated with post-anthesis heat tolerance and stay-green traits^[37]. Notably, chromosome 5D was shown to confer protection during meiosis, as its absence resulted in enhanced susceptibility to heat-induced sterility^[38]. Furthermore, *TaHMMW1D*, a high-molecular-weight glutenin gene, produces multiple transcript variants under heat stress, especially in distal spike grains, suggesting structural plasticity of seed storage proteins as a compensatory mechanism^[39]. Collectively, these results indicate that high temperature disrupts both male and female gametophyte development and carbon assimilation, leading to reduced GNS and filling rate.

Unlike daytime heat stress, elevated nighttime temperature (HNT) mainly increases respiration and shortens developmental duration^[40,41]. Continuous warm nights during anthesis and grain filling accelerate senescence and increase the number of sterile spikelets, reduce effective tiller number and GNS, with yield reductions of 20%–25% under HNT conditions^[40]. Physiologically, increased respiratory carbon loss and reduced assimilate partitioning between source and sink tissues disturb energy balance, leading to poor spike fertility and degraded end-use quality^[41]. Gene-based haplotype analysis identified a haplotype Hap1 of *TraesCS1A02G305700* exhibited higher biomass and spike number under HNT^[42]. Across different thermal stresses, temperature-mediated changes in sucrose metabolism, hormone signaling, transcriptional regulation, and epigenetic modification form an interconnected network governing spike development. QTL's and haplotypes associated with thermal tolerance (e.g., on 2A, 5D, and 6B) provide valuable molecular targets for marker-assisted breeding. Integrating multi-omics approaches, including transcriptomics, metabolomics, and epigenomics will deepen our understanding of spike developmental plasticity under temperature fluctuations. Ultimately, dissecting these regulatory cascades will facilitate the

breeding of climate-resilient wheat cultivars capable of maintaining spike fertility and yield stability under temperature stress.

During the grain filling stage, heat stress impairs carbon assimilation and starch biosynthesis, leading to reduced yield and quality. Multiple wheat heat stress tolerance (HST) loci have been identified, including *qYDH.3BL* and *TaHST1*^[43,44]. The *qYDH.3BL* QTL is associated with increased yield performance under hot and dry environments. Its delimited genomic region (~ 690 kb) contains 12 putative genes with a sequence variant in the promoter region of the gene *Seven in absentia (TaSINA)*. Near-isogenic lines carrying the positive allele at *qYDH.3BL* under-expressed *TaSINA*, and had increased vigor and water use efficiency in development, as well as increased biomass, grain number and grain weight following heat stress^[43]. *TaHST1* is essential for HST at both the seedling and adult stages, with gene losses in its region, compromising tolerance, and resulting in significantly lower values of GNS, grain weight per spike, TGW, grain length, and grain width under either thermo-stressed or control conditions^[44]. In addition, *TaHST2* enhances the conversion of soluble sugars into starch during heat-stressed grain filling, thereby enabling faster grain filling and higher yield potential^[45].

High temperatures disrupt key developmental and physiological processes, and even modest increases above the optimum can cause significant yield losses. To mitigate these effects, wheat activates various protective mechanisms such as ROS scavenging and the induction of heat shock proteins, and several heat-tolerance genes have been identified, including *TaGCN5* and *TaOPR3*^[46]. Heat shock transcription factors (HSF's) are key regulators of heat-induced transcriptional reprogramming. Upon exposure to heat stress, HSF's recognize conserved heat shock elements (HSE's) in promoters of heat-inducible HSP genes. In wheat, multiple HSF genes, including *TaHsfA2d*, *TaHsfA6f*, *TaHsfC2a*, and *sHsp26*^[44,47], function in heat signaling and stress response pathways. Among these, *HsfA* genes primarily exert a positive regulatory function in abiotic stress response, in which *TaABF5b*, a critical regulatory factor of the ABA signaling pathway, has been identified as a modulator of the expression of *TaHsfA2h*. *TaHsfA2h* interacts with *TaHsfC2a*, co-regulating key heat-responsive genes such as *TaNCED2B*, *TaPOD4*, and *TaHSP26*, thereby forming a positive regulatory module (ABF5b-HsfA2h/HsfC2a-NCED2b/POD4/HSP26) that enhances wheat heat tolerance. *TaHsfA1* is essential for heat tolerance at both the seedling and grain-filling stages. Knockout mutants show severely reduced seedling survival under high temperature, and produce shrunken grains with lower TGW, highlighting its critical regulatory role throughout wheat development under heat stress^[47].

During heat acclimation, cereals adjust their metabolism to high temperatures and protect critical cell structures against the effects of high temperatures, and enzymes play a crucial role in this stress defense process. For example, TaSG-D1, a Ser/Thr kinase, negatively regulates brassinosteroid (BR) signaling, and its variant TaSG-D1^{E286K} improves heat tolerance via enhanced phosphorylation of TaPIF4, though at a cost to grain yield^[48]. Similarly, the TaSERL2-TaBZR2 module regulates heat tolerance by modulating TaBZR2 stability. Overexpression of *TaBZR2* enhances thermotolerance, whereas TaSERL2 promotes degradation of TaBZR2 under stress conditions, demonstrating a negative regulatory mechanism independent of BR signaling^[49].

Drought stress

Rising global temperatures are anticipated to aggravate crop losses, and agricultural water supplies must be increased by an

estimated 17% by 2025 to compensate for global population growth. Drought poses a significant challenge to wheat production globally, leading to substantial yield losses and affecting various agronomic and physiological traits^[50]. Plants have strategies to prevent water loss, balancing optimal water allocation to vital organs, maintaining cellular water content, to persevere through periods of drought. Conceptually different from drought tolerance which means the survival of plants under drought stress, water-use efficiency (WUE) refers to the ability of a plant to produce biomass or yield using minimal amounts of water, which measures how efficiently a plant utilizes water to carry out photosynthesis and produce the desired outputs.

Quantitative trait locus (QTL) and GWAS have provided valuable insights into how drought stress reshapes the genetic regulation of wheat spike architecture and reproductive success. In multiple water-deficit field trials, spike-related traits showed high plasticity under drought. A large-scale GWAS across diverse genotypes identified 8 GNS and spikelet fertility loci linked specifically to a drought tolerance coefficient (DTC), which was mapped to chromosomes 1B, 2A, 5B, 6B, and 7D, reflecting how water stress reduces floral fertility gradients from base to tip^[51]. Chromosome-specific mapping also revealed novel loci controlling spike fertility and structure. Notably, a 5B:20cM locus (TduRuM_contig25432_1377) showed a stable association with the number of fertile spikes across both favorable and semiarid environments^[52]. Likewise, the GA-responsive dwarfing allele *Rht13* improved peduncle length, spike length, grain number per spike, and grain weight under drought stress, suggesting that certain semi-dwarf alleles can redistribute assimilates toward the spike rather than merely reducing plant height^[53]. In parallel, a high-density linkage map was constructed using genotyping-by-sequencing (GBS) enabled the identification of 85 QTL's across 19 chromosomes for grain yield and spike-related traits under irrigated and water-deficit conditions, explaining 6%–19% of phenotypic variance. Among these, 20 novel loci were located mainly on 1A, 1B, 1D, 2B, 3A, 3B, 6A, 6B, and 7A, and 35 QTL's were functionally linked to drought-responsive genes involved in osmotic regulation and redox balance^[54].

Meanwhile, simulating drought stress during the breeding process has been proposed as a useful strategy for screening drought-tolerant lines under otherwise favorable conditions. A GWAS revealed 263 significant marker-trait associations (MTA's), including 246 loci associated with days to anthesis, spike length, SNS, GNS, and TGW^[55]. A subsequent multi-environment GWAS further detected 57 stable markers, among which nine were pleiotropic, governing flowering time and spike yield components^[56]. These loci provide targets for marker-assisted selection (MAS) to stabilize spike performance under combined heat-drought stress^[56]. Collectively, these findings, based on QTL analysis and GWAS, highlight the complex genetic architecture underlying wheat spike development under drought. The integration of chromosome-specific loci (e.g., 5B:20cM, 1B, 2A, 6B, 7D), regulatory alleles such as *Rht13*, and multi-environment stable markers provides a foundation for dissecting both the structural and physiological bases of spike resilience. By linking spike fertility gradients, assimilate allocation, and flowering-related traits, these studies bridge phenotypic plasticity with genomic control, offering actionable targets for MAS-based breeding of drought-resilient, yield-stable wheat cultivars.

While QTL and GWAS studies have identified key loci controlling spike fertility under drought, multi-omics analyses have now illuminated the underlying molecular and cellular mechanisms by which these loci act to maintain spike development, fertility, and assimilate flow during water deficit. High-resolution RNA-seq analyses under

field conditions demonstrate that drought at the early reproductive stages triggers a pronounced reprogramming of gene expression in spike tissues, far more severe than stress at anthesis. Across 115,656 expressed genes, 309 differentially expressed genes (DEG's) were identified, primarily involved in floral organ initiation, photosynthesis, redox regulation, and hormone signaling^[57].

Under drought conditions, plants close their stomata, which reduces the intake of CO₂, in which ABA mediates stomatal closure and stress-gene upregulation^[58]. The ABA signaling pathway has been identified as a central regulator of abiotic stress response in plants, triggering major changes in gene expression and adaptive physiological responses. Currently, extensive research has been conducted on ABA-mediated drought responses in model plants such as *Arabidopsis thaliana*^[59], rice^[60], and maize^[58,61]. Notably, significant advances have also been made in wheat, especially at the seedling stage^[62]. In grass crops, grain number depends on the number of fertile florets at flowering^[63,64], and exposure to stress during the young microspore (YM) stage causes a pronounced reduction. At this developmental stage, an adequate assimilate supply to the anthers is critical, with the sub-apical internodes (the two internodes below the spike, TIS), and the flag leaf serving as key organs for assimilate transport^[65,66]. Transcriptomic studies have shown that ABA signaling genes, including *PP2C's*, *SnRK's*, and ZIP family members are down-regulated in the spike and TIS under water stress at the YM stage. Concurrently, ABA levels increase and correlate positively with cell wall invertase (CWIN), and sucrose:sucrose 1-fructosyl-transferase (1-SST) activities in TIS, suggesting that stress-induced changes in ABA signaling modulate sucrose conversion and allocation, ultimately affecting grain number^[8]. PYL proteins, which are abscisic acid (ABA) receptors, play crucial roles in drought stress responses. Overexpression of *TaPYL1-1B* or *TaPYL4* increases wheat ABA sensitivity to improve drought tolerance and increase grain size and weight, tuning water-use efficiency and drought tolerance in wheat^[67]. Moreover, TaMPK3 was identified as a candidate interacting protein of TaPYL4. Functional analyses revealed that *TaMPK3* overexpression reduces drought tolerance and ABA sensitivity, leading to lower survival rates and decreases in spikelet number, tiller number, panicle length, and grain yield. Conversely, *TaMPK3*-RNAi lines showed enhanced growth and productivity compared with WT^[68]. Meanwhile, several core ABA signaling components such as *TaPYL9*, *TaSnRK2.10*^[69], and *TaABF2*^[70] in wheat, have been shown to contribute significantly to drought tolerance, while their functions on spike development remains unclear.

The ubiquitin/26S proteasome (UPS) pathway degrades misfolded or unnecessary proteins through ubiquitination and plays a central role in maintaining cellular homeostasis and regulating diverse processes such as hormone signaling, stress response, and plant development^[71–73]. Among E3 ligases, RING finger proteins are particularly important. In rice, *Grain Width* and *Weight 2* (GW2), a C5HC2-type E3 ligase regulates grain size by ubiquitinating the cell proliferation regulator *WIDE GRAIN 1* (WG1)^[74]. Its wheat homolog *TaGW2* has been widely studied, with allelic variations linked to drought tolerance. Functional studies reveal that *TaGW2* modulates both yield and stress responses. Mechanistically, *TaGW2* ubiquitinates and degrades *TaARR12*, a negative regulator of drought responses, which suppresses bZIP transcription factors. Notably, CRISPR-mediated knockout of *TaGW2*, combined with *TaARR12* knockdown resulted in plants with both improved drought tolerance and higher yields, highlighting the TaGW2-TaARR12 module as a promising breeding target for wheat genetic improvement^[75]. In addition to RING-type ligases, stress-associated proteins (SAP's),

containing A20/AN1 zinc finger domains, also function as ubiquitin ligases regulating stress adaptation^[76]. For instance, *TaSAP5* overexpression in wheat increased drought tolerance by maintaining tiller and spike numbers under stress, leading to higher grain weight and grain number without yield penalties under normal conditions, consistent with findings in *Arabidopsis* and rice^[76]. Beyond ubiquitination, other post-translational modifications such as acetylation play equally critical roles in drought stress adaptation^[77]. Histone deacetylases (HDAC's), recently termed lysine deacetylases (KDAC's), regulate not only chromatin remodeling but also the stability, activity, and localization of non-histone proteins. In rice and *Arabidopsis*, HDAC's modulate stress responses and development through selective deacetylation of key regulators. However, their functional roles in wheat remain less understood. Recent work identified *TaHDA8* as a crucial regulator of root elongation under drought conditions. Under drought stress, *TaHDA8* knockout lines showed higher yield per plant, mainly due to increased GNS. Under stress, reduced *TaHDA8* levels restore acetylation-dependent DNA-binding activity of *TaAREB3*, which subsequently activates *TaKOR1* expression to promote root meristem cell proliferation. Moreover, natural variations in the *TaKOR1* promoter affecting *TaAREB3* binding have been selected in wheat breeding, underscoring the adaptive significance of the *TaHDA8-TaAREB3-TaKOR1* module^[78]. Nevertheless, the direct functions and mechanisms of these genes or modules in regulation spike development under drought stress are waiting for further investigation.

Different from drought tolerance, WUE of crops prioritizes the balance between maximizing yield and minimizing water consumption^[79]. Recently, research on WUE of crops has received increasing attention due to its critical roles in crop production improvement^[50]. However, although numbers of QTL's and transcription factors (TF's) in key TF families such as NAC, AP2/ERF, MYB/MYC, bZIP, NF-Y, WRKY, and regulators in various morphological or physiological processes targeting drought adaptation or tolerance have been characterized in wheat^[50,80], relatively few key genes were identified to enhance WUE. QTL's for stomatal opening are spotted on chromosome 7A, where *TaER2* resides. Further studies revealed that *TaER* genes can help develop mechanisms to mitigate drought stress in wheat crops^[81]. Varieties with enhanced ABA signaling pathways could also improve water-use efficiency. For example, overexpression of *TaPYL1-1B* genes, an ABA-sensitive gene, consequently increases WUE and photosynthesis. The atypical bHLH TF *TabHLH27* directly coordinates both root growth and spike development, thereby affecting WUE and yield-related traits, including spikelet and grain number. The favorable Hap-II allele enhances drought tolerance, increases root system size and improves spikelet number and WUE, and has been positively selected in modern breeding programs^[82]. Recently, integrative omics analysis identified 73 QTL's for WUE-traits, in which 85 high-confidence candidate genes, including *TaMYB7-A1* were underscored. Overexpression of *TaMYB7-A1* enhances photosynthesis, WUE, root development, and grain yield under drought conditions^[80].

In summary, these studies revealed that wheat responds to drought stress by coordinating spike development through multi-layered regulatory mechanisms, including hormone signaling, ubiquitin/proteasome pathways, metabolic regulation, and transcription factor mediated gene regulatory networks. Understanding and integrating these key molecular modules provides promising strategies for improving drought resilience, while maintaining or enhancing grain yield during breeding^[50].

Salt stress

Soil salinization affects over 800 million ha worldwide, posing a major threat to crop yield and ecological security. Salt stress induces ionic, osmotic, and oxidative stresses, to which wheat is particularly sensitive, especially during the spring growth period, when surface soil salinity is elevated^[83]. High salinity is commonly due to high concentrations of Na⁺ and Cl⁻ in the soil solution, resulting in hyper-osmotic and hyper-ionic conditions, which impede plant absorption of water and nutrients from the soil^[84]. Wheat employs multiple mechanisms to cope with the detrimental effects of salinity, in which numbers of key factors were identified in response to salt stress such as *TabZIP15*, *TaASR1-D*, *TaERF3*, *TaHAG1*, and *GCN5*^[78,85,86]. Na⁺ exclusion via the key transporter HKT1;5 is central to salt tolerance. Its upstream regulator, *TaSPL6-D*, represses *HKT1;5*; natural variation or knockout of *TaSPL6-D* enhances Na⁺ exclusion, preserves spike development and improves yield under saline conditions^[83]. A group of K⁺-preferring HKT transporters, *TaHKT8*, *TaHKT9*, and *TaHKT10* were identified which negatively regulate the wheat shoot K⁺ accumulation and salt tolerance. A GWAS combined with candidate gene association analysis further revealed that *TaHKT9-B* substantially underlies the natural variation of wheat shoot K⁺ accumulation under saline soil conditions. The *tae-miR390/TaTAS3/TaARF4* pathway was identified to regulate the salt-induced root development and salt tolerance in wheat, indicative of the trade-off between development and salt tolerance^[87].

Crop productivity can be improved by effectively regulating various photosynthesis-related traits, including photosynthetic pigments and photosynthetic efficiency, as well as yield-related traits. Halotolerance 3 (HAL3) is known for its conserved roles in enhancing salt tolerance, cell-cycle control, and cell wall integrity. In wheat, *TaHAL3-7A* plays a key role in regulating photosynthetic pigments and yield-related traits. It is highly expressed in shoots and grains, and overexpression in wheat and rice increases chlorophyll and carotenoid levels, grain number per spike, and yield per plant. Mechanistically, *TaHAL3-7A* enhances photosynthesis by upregulating light-harvesting chlorophyll a/b-binding (LHC) genes, and interacts with *TaUFD1-3A* to coordinate pigment accumulation and grain yield. Combining favorable haplotypes of *TaHAL3-7A* and *TaUFD1-3A* further boosts chlorophyll content, TGW, and yield, highlighting its potential as a target for molecular breeding to improve wheat productivity^[88]. In addition, *TaCYP81D5*, a member of the cytochrome P450 monooxygenase (CYP) gene family, enhances wheat salinity tolerance by promoting ROS scavenging. Its expression is induced by salt stress and chromatin modifications, and constitutive overexpression improves both the seedling and reproductive-stage tolerance. Overexpressing lines (*TaOE1/TaOE2*) produce larger seeds and higher yields under moderate salinity, with *Zat12* acting as a crucial component of this ROS-mediated pathway. These findings highlight *TaCYP81D5* as a promising target for the development of salt-tolerant, high-yield wheat varieties^[89].

BR's are vital plant steroid hormones involved in numerous aspects of plant life, including growth, development, and responses to various stresses. BR signal core transcription factor *BRASSINAZOLE-RESISTANT1 (TaBZR1)* is significantly upregulated by salt treatment. Overexpression of *Tabzr1-1D* (a gain-of-function *TaBZR1* allele) enhances wheat salt tolerance, accompanied by reduced plant height and spike length, but slightly increased grain length. Mechanistically, *TaBZR1* directly activates *TaNCED3* to promote ABA biosynthesis and associates with *TaGPX2/3* to enhance ROS scavenging. Thus, *TaBZR1* confers salt tolerance by coordinately regulating

ABA production and ROS detoxification, providing a promising strategy for wheat improvement^[90].

Transcriptional regulation is crucial under salt stress, controlling stress-responsive genes to maintain ion balance, antioxidant activity, and growth. For instance, *TaCHP*, encoding a Cys-, His-, and Pro-rich zinc finger protein, confers enhanced tolerance to saline—alkaline stress in wheat. Overexpression lines displayed stronger germination, photosynthesis, and ROS scavenging, and more importantly, showed increased spike number, grain number per ear, and thousand-grain weight, leading to stable yield gains of ~4% to 14% across multi-year, multi-location field trials without growth penalties under normal conditions. Natural variation analysis further revealed a favorable haplotype (Hap1) associated with stronger stress-induced expression, highlighting *TaCHP* as a valuable genetic resource for breeding salt-tolerant and high-yielding wheat^[91]. While transcription factors play key roles in mediating salt-stress responses, post-translational modifications also provide crucial regulation. Reversible conjugation (sumoylation and desumoylation) of Small Ubiquitin-Like Modifiers (SUMO) is a crucial kind of protein modification. The wheat SUMO protease gene *TaDSU* confers salt tolerance through desumoylation. *TaDSU* overexpression enhances salt tolerance in wheat by interacting with the transcription factor *MYC2*, reducing its sumoylation, and thereby boosting its transcriptional activity, which in turn reinforces *TaDSU* expression. This regulatory loop leads to lower Na⁺, higher K⁺, and improved K⁺:Na⁺ balance under salt stress. Beyond stress adaptation, *TaDSU* also promotes yield-related traits: overexpression lines produce more spikes per plant and larger TGW, resulting in 9.8%–25.0% yield increases in saline soils and 6.8%–9.2% in saline-alkaline fields, without penalties under normal conditions. Moreover, its ectopic expression in *Arabidopsis* also improves salt tolerance, highlighting its broad role in stress adaptation and agronomic improvement^[92]. While more and more key regulators were identified in response to salt stress, and even balance the developmental processes and stress tolerances^[83,93], few of them were characterized by showing distinct functions and mechanisms in wheat spike development, which is waiting for further investigation.

Future prospects

Recent studies have highlighted the pivotal role of multiple regulations in mediating the crosstalk between stress responses and developmental processes, such as transcriptional control, post-transcriptional modulation, epigenetic regulation, and hormone signaling^[6,75,94–96]. Despite the growing body of research, significant knowledge gaps remain. While most studies have focused on stress responses in vegetative tissues at the wheat seedling stage^[1,5], research about reproductive development was generally more vulnerable and remain underexplored. Under field conditions, compound heat—drought episodes frequently occur during wheat spike development and early grain filling. Available evidence, largely from field observations and physiological assessments, suggested that such compound events were associated with impaired floral development and fertility, including reduced pollen viability, increased pollen sterility, and decreased stigma receptivity, ultimately shortening effective grain-filling duration and reducing yield^[97]. Notably, direct and stage-resolved evidence connecting salt-induced ionic accumulation, or salt signaling perturbations to wheat inflorescence meristem activity, spikelet initiation, or floral meristem determinacy/floral organ patterning, remains scarce (Table 1). Moreover, much of the current understanding derives

from model species such as *Arabidopsis*, rice, soybean, and maize^[1,5,6,31], highlighting the requirement for wheat-specific studies that account for its unique polyploid genome and developmental complexity. Addressing these gaps will require integrative approaches that combine genomics, transcriptomics, and functional validation, as well as field-based evaluations under realistic stress conditions.

Although the programmed spike development is critical for GNS, the most important component for the crop yield and QTL related spike morphology traits were mapped^[98], limited key genes were identified to regulate spike development^[99], particularly under stress conditions. Before heading, the entire wheat spike development is concealed within the leaf sheath, which hinders the real-time observation of spike development and subsequent gene cloning. Previously, several transcriptome profile analyses and multi-omics analysis using meristem tissues uncovered the cascaded gene expression at early spike development, in which genes in different TF families were involved and interact with phytohormones^[100]. Subsequently, distinct gene families such as MADS and TCP TFs, as well as particular genes like *WFZP*, *DUO*, *VRT2*, *TaSPL17*, and *TaARF12* were characterized in spike development^[101–103]. At the same time, several studies focused on the floral fertility were carried out and QTL's for floral fertility were spotted on different chromosomes^[24–26]. Particularly, a number of key genes involved in floral death were identified in cereal crops, including wheat^[19]. These genes and loci provide a genetic resource for functional analysis on spike development under stress conditions in future. Recently, new techniques such as Single Cell-RNA Sequencing (scRNA-seq), and Spatial Transcriptomics (ST-seq), combined with other techniques like single-molecule fluorescence *in situ* hybridization (smFISH), and co-expression network analysis, were utilized to unveil the programmed developmental processes and identify distinct groups of genes in particular tissues in different wheat organs like roots, grains, and spikes^[104,105]. Therefore, using these technologies to screen genes that specifically respond to stresses in different cell types will be a promising strategy to discover molecular mechanisms of spike development under different stress conditions, similar to the study in wheat leaf and root^[106].

In general, both spatio-temporal expression patterns, and expression levels of genes are determined by the interaction between cis-acting elements and trans-acting factors^[107]. The promoters of stress response genes generally contain typical stress response elements. ABA-independent cold- and drought-responsive genes often contain dehydration-responsive elements (DRE) in their promoters, which are recognized and bound by CBF (DREB1), and DREB2 transcription factors, members of the AP2/ERF family, which activate target gene expression^[108,109]. Therefore, finding and testing novel stress-inducible promoters for optimization of expression levels of transgenes is one of the critical methodologies to improve plant developmental phenotypes and yields^[106]. On the other hand, gene editing using clustered, regularly interspaced, short palindromic repeats (CRISPR)/CRISPR-associated protein 9 (Cas9) technique, targeting specific elements in the gene promoter region will precisely identify the function of the gene under stress conditions and will be beneficial to crop breeding^[110]. Moreover, taking advantage of CRISPR- Cas9 techniques to generate a promoter random deletion mutation library, followed by spike development defects screening under stress conditions will identify particular genes and cis-elements that respond to stresses and regulate wheat spike development^[111,112].

Table 1. Genes associated with abiotic stress and spike development in wheat.

Stress type	QTL/gene	Function
Temperature		
Low temperature	<i>VRN-1</i>	Enabling the SAM-to-IM transition to initiate flowering while reducing freezing tolerance ^[26] .
	<i>QFr.jic-5D</i> <i>TaSAMT1</i>	Enhancing frost tolerance and reducing winterkill compared with spring-type alleles ^[27] . Increasing MeSA accumulation, reducing SA levels, and markedly improving freezing tolerance ^[34] .
High temperature	<i>TraesCS1A02G305700</i>	Conferring higher biomass and spike number under high nighttime temperature ^[42] .
	<i>qYDH.3BL</i>	Increasing biomass, grain number, and grain weight following heat stress ^[43] .
	<i>TaHST1</i>	Increasing GNS, grain weight per spike, TGW, grain length and grain width under either thermo-stressed or control conditions ^[44] .
	<i>TaHST2</i>	Enhancing the conversion of soluble sugars into starch during heat-stressed grain filling ^[45] .
	<i>TaHsfA1</i>	Knockout mutants reducing seedling survival under high temperature and producing shrunken grains with lower TGW ^[47] .
Drought	<i>TaSG-D1</i>	Improving heat tolerance though at a cost to grain yield ^[54] .
	<i>TduRuM_contig25432_1377</i>	Maintaining stable association with fertile spike number across favorable and semiarid environments ^[52] .
	<i>Rht13</i>	Increasing peduncle length, spike length, grain number per spike, and grain weight under drought stress ^[56] .
	<i>TaPYL1-1B</i> , <i>TaPYL4</i>	Enhancing ABA sensitivity to improve drought tolerance and increase grain size and weight ^[67] .
	<i>TaMPK3</i>	Reducing drought tolerance and ABA sensitivity, thereby lowering survival rates and decreasing in spikelet number, tiller number, panicle length, and grain yield ^[68] .
	<i>TaGW2</i>	Improving drought tolerance and higher yields through increasing grain width and weight yields ^[75] .
	<i>TaSAP5</i>	Increasing drought tolerance by maintaining tiller and spike numbers under stress, leading to higher grain weight and grain number without yield penalties under normal conditions ^[76] .
	<i>TaHDA8</i>	Knockout lines showing higher yield per plant, mainly due to increased GNS under drought stress ^[78] .
	<i>TabHLH27</i>	Coordinating root growth and spike development to affect WUE and yield-related traits, including spikelet and grain number ^[81] .
	Salt	<i>TaMYB7-A1</i>
<i>TaSPL6-D</i>		Knockout of <i>TaSPL6-D</i> enhances Na ⁺ exclusion, preserves spike development, and improves yield under saline conditions ^[83] .
<i>TaHAL3-7A</i>		Improving salt stress tolerance while further boosts chlorophyll content, TGW, and overall yield ^[88] .
<i>TaCYP81D5</i>		Promoting ROS scavenging to enhance salinity tolerance and producing larger seeds and higher yields under moderate salinity ^[151] .
<i>TaBZR1</i>		Enhancing salt tolerance while reducing plant height and spike length but slightly increasing grain length ^[89] .
<i>TaCHP</i>		Enhancing tolerance to saline-alkaline stress strengthening germination, improving photosynthesis, increasing ROS scavenging, and increasing spike number, grain number per spike, and TGW ^[91] .
	<i>TaDSU</i>	Enhancing salt tolerance and increasing spike number per plant and thousand-grain weight in overexpression lines ^[92] .

Author contributions

The authors confirm contributions to the paper as follows: study conception and design: Cui Y, Liu X, and Zhang H; data collection: Ding Y, Li C, Mao R, He M, Zhang H; draft manuscript preparation: Ding Y, Li C, Cui Y, Liu X; language editing: García-Caparrós P. All authors reviewed the results and approved the final version of the manuscript.

Data availability

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

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Conflict of interest

The authors declare that they have no conflict of interest.

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References

- [1] Mao H, Jiang C, Tang C, Nie X, Du L, et al. 2023. Wheat adaptation to environmental stresses under climate change: molecular basis and genetic improvement. *Molecular Plant* 16:1564–1589
- [2] Li Y, Li L, Zhao M, Guo L, Guo X, et al. 2021. Wheat *FRIZZY PANICLE* activates *VERNALIZATION1-A* and *HOMEBOX4-A* to regulate spike development in wheat. *Plant Biotechnology Journal* 19:1141–1154
- [3] Finnegan EJ, Ford B, Wallace X, Pettolino F, Griffin PT, et al. 2018. Zebularine treatment is associated with deletion of *FT-B1* leading to an increase in spikelet number in bread wheat. *Plant, Cell & Environment* 41:1346–1360
- [4] Luo X, Yang Y, Lin X, Xiao J. 2023. Deciphering spike architecture formation towards yield improvement in wheat. *Journal of Genetics and Genomics* 50:835–845
- [5] Kerblar SM, Wigge PA. 2023. Temperature sensing in plants. *Annual Review of Plant Biology* 74:341–366
- [6] Kidokoro S, Shinozaki K, Yamaguchi-Shinozaki K. 2022. Transcriptional regulatory network of plant cold-stress responses. *Trends in Plant Science* 27:922–935
- [7] Melino V, Tester M. 2023. Salt-tolerant crops: time to deliver. *Annual Review of Plant Biology* 74:671–696
- [8] Zhang Z, Huang J, Gao Y, Liu Y, Li J, et al. 2020. Suppressed ABA signal transduction in the spike promotes sucrose use in the stem and

- reduces grain number in wheat under water stress. *Journal of Experimental Botany* 71:7241–7256
- [9] Asseng S, Ewert F, Martre P, Rötter RP, Lobell DB, et al. 2015. Rising temperatures reduce global wheat production. *Nature Climate Change* 5:143–147
- [10] Frederiks TM, Christopher JT, Sutherland MW, Borrell AK. 2015. Post-head-emergence frost in wheat and barley: defining the problem, assessing the damage, and identifying resistance. *Journal of Experimental Botany* 66:3487–3498
- [11] Yuan Z, Persson S, Zhang D. 2020. Molecular and genetic pathways for optimizing spikelet development and grain yield. *ABIOTECH* 1:276–292
- [12] Zhang D, Yuan Z. 2014. Molecular control of grass inflorescence development. *Annual Review of Plant Biology* 65:553–578
- [13] Huang Y, Schnurbusch T. 2024. The birth and death of floral organs in cereal crops. *Annual Review of Plant Biology* 75:427–458
- [14] Bonnett OT. 1936. The development of the wheat spike. *Journal of Agricultural Research* 53:445–451
- [15] Guo Z, Chen D, Röder MS, Ganai MW, Schnurbusch T. 2018. Genetic dissection of pre-anthesis sub-phase durations during the reproductive spike development of wheat. *The Plant Journal* 95(5):909–918
- [16] Li JY, Yang C, Xu J, Lu HP, Liu JX. 2023. The hot science in rice research: how rice plants cope with heat stress. *Plant, Cell & Environment* 46:1087–1103
- [17] Yang Z, Cao Y, Shi Y, Qin F, Jiang C, et al. 2023. Genetic and molecular exploration of maize environmental stress resilience: toward sustainable agriculture. *Molecular Plant* 16:1496–1517
- [18] Zhang W, Wang J, Huang Z, Mi L, Xu K, et al. 2019. Effects of low temperature at booting stage on sucrose metabolism and endogenous hormone contents in winter wheat spikelet. *Frontiers in Plant Science* 10:498
- [19] Jiang G, Hassan MA, Muhammad N, Arshad M, Chen X, et al. 2022. Comparative physiology and transcriptome analysis of young spikes in response to late spring coldness in wheat (*Triticum aestivum* L.). *Frontiers in Plant Science* 13:811884
- [20] Liu YJ, Li D, Gong J, Wang YB, Chen ZB, et al. 2021. Comparative transcriptome and DNA methylation analysis in temperature-sensitive genic male sterile wheat B5366. *BMC Genomics* 22:911
- [21] Tang Z, Zhang L, Xu C, Yuan S, Zhang F, et al. 2012. Uncovering small RNA-mediated responses to cold stress in a wheat thermosensitive genic male-sterile line by deep sequencing. *Plant Physiology* 159:721–738
- [22] Díaz ML, Soresi DS, Basualdo J, Cuppari SJ, Carrera A. 2019. Transcriptomic response of durum wheat to cold stress at reproductive stage. *Molecular Biology Reports* 46:2427–2445
- [23] Kobayashi F. 2005. Regulation by *Vrn-1/Fr-1* chromosomal intervals of CBF-mediated *Cor/Lea* gene expression and freezing tolerance in common wheat. *Journal of Experimental Botany* 56:887–895
- [24] Dixon LE, Karsai I, Kiss T, Adamski NM, Liu Z, et al. 2019. *VERNALIZATION 1* controls developmental responses of winter wheat under high ambient temperatures. *Development* 146(3):dev172684
- [25] Serrano L, Vazquez BN, Tischfield J. 2013. Chromatin structure, pluripotency and differentiation. *Experimental Biology and Medicine (Maywood)* 238:259–270
- [26] Dhillon T, Pearce SP, Stockinger EJ, Distelfeld A, Li C, et al. 2010. Regulation of freezing tolerance and flowering in temperate cereals: the *VRN-1* connection. *Plant Physiology* 153:1846–1858
- [27] Snape JW, Sarma R, Quarrie SA, Fish L, Galiba G, et al. 2001. Mapping genes for flowering time and frost tolerance in cereals using precise genetic stocks. *Euphytica* 120:309–315
- [28] Soltész A, Smedley M, Vashegyi I, Galiba G, Harwood W, et al. 2013. Transgenic barley lines prove the involvement of TaCBF14 and TaCBF15 in the cold acclimation process and in frost tolerance. *Journal of Experimental Botany* 64:1849–1862
- [29] Sun X, Hu C, Tan Q, Liu J, Liu H. 2009. Effects of molybdenum on expression of cold-responsive genes in abscisic acid (ABA)-dependent and ABA-independent pathways in winter wheat under low-temperature stress. *Annals of Botany* 104:345–356
- [30] Tian S, Mao X, Zhang H, Chen S, Zhai C, et al. 2013. Cloning and characterization of *TaSnRK2.3*, a novel SnRK2 gene in common wheat. *Journal of Experimental Botany* 64:2063–2080
- [31] Peng Y, Yang J, Li X, Zhang Y. 2021. Salicylic acid: biosynthesis and signaling. *Annual Review of Plant Biology* 72:761–791
- [32] Sibozza XI, Bertling I, Odindo AO. 2014. Salicylic acid and methyl jasmonate improve chilling tolerance in cold-stored lemon fruit (*Citrus limon*). *Journal of Plant Physiology* 171:1722–1731
- [33] Chen F, D'Auria JC, Tholl D, Ross JR, Gershenzon J, et al. 2003. An *Arabidopsis thaliana* gene for methylsalicylate biosynthesis, identified by a biochemical genomics approach, has a role in defense. *The Plant Journal* 36:577–588
- [34] Chu W, Chang S, Lin J, Zhang C, Li J, et al. 2024. Methyltransferase TaSAMT1 mediates wheat freezing tolerance by integrating brassinosteroid and salicylic acid signaling. *The Plant Cell* 36:2607–2628
- [35] Patidar A, Yadav MC, Kumari J, Tiwari S, Chawla G, et al. 2023. Identification of climate-smart bread wheat germplasm lines with enhanced adaptation to global warming. *Plants* 12(15):2851
- [36] Pradhan S, Ali Babar M, Robbins K, Bai G, Mason RE, et al. 2019. Understanding the genetic basis of spike fertility to improve grain number, harvest index, and grain yield in wheat under high temperature stress environments. *Frontiers in Plant Science* 10:1481
- [37] Touzy G, Lafarge S, Redondo E, Lievin V, Decoopman X, et al. 2022. Identification of QTLs affecting post-anthesis heat stress responses in European bread wheat. *Theoretical and Applied Genetics* 135:947–964
- [38] Draeger T, Moore G. 2017. Short periods of high temperature during meiosis prevent normal meiotic progression and reduce grain number in hexaploid wheat (*Triticum aestivum* L.). *Theoretical and Applied Genetics* 130:1785–1800
- [39] Ko CS, Kim JB, Hong MJ, Seo YW. 2021. Wheat (*Triticum aestivum* L.) *TaHMW1D* transcript variants are highly expressed in response to heat stress and in grains located in distal part of the spike. *Plants* 10(4):687
- [40] Li D, Xiao Y, Guo L, Shan B, Liu X, et al. 2024. Effect of high nighttime temperatures on growth, yield, and quality of two wheat cultivars during the whole growth period. *Plants* 13(21):3071
- [41] García GA, Dreccer MF, Miralles DJ, Serrano RA. 2015. High night temperatures during grain number determination reduce wheat and barley grain yield: a field study. *Global Change Biology* 21:4153–4164
- [42] Kumar Saini D, Hein NT, Somayanda I, Bheemanahalli R, Ostmeier T, et al. 2025. Genetic mapping and haplotype analysis identify novel candidate genes for high night temperature tolerance in winter wheat. *The Plant Genome* 18:e70075
- [43] Thomelin P, Bonneau J, Brien C, Suchecki R, Baumann U, et al. 2021. The wheat *Seven in absentia* gene is associated with increases in biomass and yield in hot climates. *Journal of Experimental Botany* 72:3774–3791
- [44] Zhai H, Jiang C, Zhao Y, Yang S, Li Y, et al. 2021. Wheat heat tolerance is impaired by heightened deletions in the distal end of 4AL chromosomal arm. *Plant Biotechnology Journal* 19:1038–1051
- [45] Zhang R, Liu G, Xu H, Lou H, Zhai S, et al. 2022. *Heat Stress Tolerance 2* confers basal heat stress tolerance in allohexaploid wheat (*Triticum aestivum* L.). *Journal of Experimental Botany* 73:6600–6614
- [46] Tian X, Qin Z, Zhao Y, Wen J, Lan T, et al. 2022. Stress granule-associated TaMBF1c confers thermotolerance through regulating specific mRNA translation in wheat (*Triticum aestivum*). *New Phytologist* 233:1719–1731
- [47] Suneja Y, Gupta AK, Chhuneja P, Bains NS. 2019. Molecular evolution and structural variations in nuclear encoded chloroplast localized heat shock protein 26 (sHSP26) from genetically diverse wheat species. *Computational Biology and Chemistry* 83:107144
- [48] Cao J, Qin Z, Cui G, Chen Z, Cheng X, et al. 2024. Natural variation of STKc_GSK3 kinase TaSG-D1 contributes to heat stress tolerance in Indian dwarf wheat. *Nature Communications* 15:2097
- [49] Hao XY, Yu TF, Peng CJ, Fu YH, Fang YH, et al. 2025. Somatic embryogenetic receptor kinase TaSERL2 regulates heat stress tolerance in wheat by influencing TaBZR2 protein stability and transcriptional activity. *Plant Biotechnology Journal* 23:2537–2553

- [50] Hafeez A, Ali S, Javed MA, Iqbal R, Khan MN, et al. 2024. Breeding for water-use efficiency in wheat: progress, challenges and prospects. *Molecular Biology Reports* 51:429
- [51] Zheng X, Qiao L, Liu Y, Wei N, Zhao J, et al. 2022. Genome-wide association study of grain number in common wheat from Shanxi under different water regimes. *Frontiers in Plant Science* 12:806295
- [52] Bennani S, Birouk A, Jlibene M, Sanchez-Garcia M, Nsarellah N, et al. 2022. Drought-tolerance QTLs associated with grain yield and related traits in spring bread wheat. *Plants* 11(7):986
- [53] Khalid MA, Ali Z, Tahir MHN, Ghaffar A, Ahmad J. 2023. Genetic effects of GA-responsive dwarfing gene *Rht13* on plant height, peduncle length, internodal length and grain yield of wheat under drought stress. *Genes* 14(3):699
- [54] Abdollahi Sisi N, Stein N, Himmelbach A, Mohammadi SA. 2022. High-density linkage mapping of agronomic trait QTLs in wheat under water deficit condition using genotyping by sequencing (GBS). *Plants* 11(19):2533
- [55] Tarawneh RA, Szira F, Monostori I, Behrens A, Alqudah AM, et al. 2019. Genetic analysis of drought response of wheat following either chemical desiccation or the use of a rain-out shelter. *Journal of Applied Genetics* 60:137–146
- [56] Devate NB, Krishna H, Parmeshwarappa SKV, Manjunath KK, Chauhan D, et al. 2022. Genome-wide association mapping for component traits of drought and heat tolerance in wheat. *Frontiers in Plant Science* 13:943033
- [57] Ma J, Li R, Wang H, Li D, Wang X, et al. 2017. Transcriptomics analyses reveal wheat responses to drought stress during reproductive stages under field conditions. *Frontiers in Plant Science* 8:592
- [58] Kuromori T, Seo M, Shinozaki K. 2018. ABA transport and plant water stress responses. *Trends in Plant Science* 23:513–522
- [59] Zhang J, Shao W, Xu Y, Tian FA, Chen J, et al. 2025. Unveiling the regulatory role of GRP7 in ABA signal-mediated mRNA translation efficiency regulation. *Nature Communications* 16:3947
- [60] Wang X, Lin G, Wang H, Zhang Z, Wang Y, et al. 2025. Rice B2 and B3 subgroup RAF kinases play central roles in both ABA and osmotic stress signaling. *Cell Reports* 44:115894
- [61] Feng Z, Li H, Sun Z, Cheng J, Hua D, et al. 2025. ZmGCT1/2 negatively regulate drought tolerance in maize by inhibiting ZmSLAC1 to maintain guard cell turgor. *Proceedings of the National Academy of Sciences of the United States of America* 122:e2423037122
- [62] Zhang T, Zhang Y, Ding Y, Yang Y, Zhao D, et al. 2025. Research on the regulation mechanism of drought tolerance in wheat. *Plant Cell Reports* 44(4):77
- [63] Borràs-Gelonch G, Rebetzke GJ, Richards RA, Romagosa I. 2012. Genetic control of duration of pre-anthesis phases in wheat (*Triticum aestivum* L.) and relationships to leaf appearance, tillering, and dry matter accumulation. *Journal of Experimental Botany* 63:69–89
- [64] Ferrante A, Savin R, Slafer GA. 2013. Is floret primordia death triggered by floret development in durum wheat? *Journal of Experimental Botany* 64:2859–2869
- [65] Carmo-Silva E, Andralojc PJ, Scales JC, Driever SM, Mead A, et al. 2017. Phenotyping of field-grown wheat in the UK highlights contribution of light response of photosynthesis and flag leaf longevity to grain yield. *Journal of Experimental Botany* 68:3473–3486
- [66] González FG, Miralles DJ, Slafer GA. 2011. Wheat floret survival as related to pre-anthesis spike growth. *Journal of Experimental Botany* 62:4889–4901
- [67] Mega R, Abe F, Kim JS, Tsuboi Y, Tanaka K, et al. 2019. Tuning water-use efficiency and drought tolerance in wheat using abscisic acid receptors. *Nature Plants* 5:153–159
- [68] Liu Y, Yu TF, Li YT, Zheng L, Lu ZW, et al. 2022. Mitogen-activated protein kinase TaMPK3 suppresses ABA response by destabilising TaPYL4 receptor in wheat. *New Phytologist* 236:114–131
- [69] Zhang Y, Wang J, Li Y, Zhang Z, Yang L, et al. 2023. Wheat TaSnRK2.10 phosphorylates TaERD15 and TaENO1 and confers drought tolerance when overexpressed in rice. *Plant Physiology* 191:1344–1364
- [70] Du L, Yu M, Wang Q, Ma Z, Li S, et al. 2024. The ABF transcription factor TaABF2 interacts with TaSnRK2s to ameliorate drought tolerance in wheat. *Journal of Genetics and Genomics* 51:1521–1524
- [71] Santner A, Estelle M. 2010. The ubiquitin-proteasome system regulates plant hormone signaling. *The Plant Journal* 61:1029–1040
- [72] Ding S, Zhang B, Qin F. 2015. *Arabidopsis* RZFP34/CHYR1, a ubiquitin E3 ligase, regulates stomatal movement and drought tolerance via SnRK2.6-mediated phosphorylation. *The Plant Cell* 27:3228–3244
- [73] Liu Q, Ning Y, Zhang Y, Yu N, Zhao C, et al. 2017. OsCUL3a negatively regulates cell death and immunity by degrading OsNPR1 in rice. *The Plant Cell* 29:345–359
- [74] Yang W, Wu K, Wang B, Liu H, Guo S, et al. 2021. The RING E3 ligase CLG1 targets GS3 for degradation via the endosome pathway to determine grain size in rice. *Molecular Plant* 14:1699–1713
- [75] Li S, Zhang Y, Liu Y, Zhang P, Wang X, et al. 2024. The E3 ligase TaGW2 mediates transcription factor TaARR12 degradation to promote drought resistance in wheat. *The Plant Cell* 36:605–625
- [76] Zhang N, Yin Y, Liu X, Tong S, Xing J, et al. 2017. The E3 ligase TaSAP5 alters drought stress responses by promoting the degradation of DRIP proteins. *Plant Physiology* 175:1878–1892
- [77] Wu X, Gong F, Cao D, Hu X, Wang W. 2016. Advances in crop proteomics: PTMs of proteins under abiotic stress. *Proteomics* 16:847–865
- [78] Liu Z, Yang Q, Liu X, Li J, Zhang L, et al. 2025. Suppression of TaHDA8-mediated lysine deacetylation of TaAREB3 acts as a drought-adaptive mechanism in wheat root development. *Molecular Plant* 18:1222–1240
- [79] Tardieu F. 2022. Different avenues for progress apply to drought tolerance, water use efficiency and yield in dry areas. *Current Opinion in Biotechnology* 73:128–134
- [80] Zhou Y, Wang D, Wang H, Qiao Y, Zhao P, et al. 2025. Integrative omics of the genetic basis for wheat WUE and drought resilience reveal the function of TaMYB7-A1. *Nature Communications* 16:8622
- [81] Zheng J, Yang Z, Madgwick PJ, Carmo-Silva E, Parry MAJ, et al. 2015. TaER expression is associated with transpiration efficiency traits and yield in bread wheat. *PLoS One* 10:e0128415
- [82] Wang D, Zhang X, Cao Y, Batool A, Xu Y, et al. 2024. TabHLH27 orchestrates root growth and drought tolerance to enhance water use efficiency in wheat. *Journal of Integrative Plant Biology* 66:1295–1312
- [83] Wang M, Cheng J, Wu J, Chen J, Liu D, et al. 2024. Variation in *TaSPL6-D* confers salinity tolerance in bread wheat by activating *TaHKT1;5-D* while preserving yield-related traits. *Nature Genetics* 56:1257–1269
- [84] Liang X, Li J, Yang Y, Jiang C, Guo Y. 2024. Designing salt stress-resilient crops: current progress and future challenges. *Journal of Integrative Plant Biology* 66:303–329
- [85] Bi C, Yu Y, Dong C, Yang Y, Zhai Y, et al. 2021. The bZIP transcription factor TabZIP15 improves salt stress tolerance in wheat. *Plant Biotechnology Journal* 19:209–211
- [86] Qiu D, Hu W, Zhou Y, Xiao J, Hu R, et al. 2021. TaASR1-D confers abiotic stress resistance by affecting ROS accumulation and ABA signalling in transgenic wheat. *Plant Biotechnology Journal* 19:1588–1601
- [87] Du L, Ding L, Huang X, Tang D, Chen B, et al. 2024. Natural variation in a K⁺-preferring HKT transporter contributes to wheat shoot K⁺ accumulation and salt tolerance. *Plant, Cell & Environment* 47:540–556
- [88] Xu H, Dong J, Meng X, Jiang H, Ding G, et al. 2025. *TaHAL3-7A* increases grain yield by enhancing photosynthetic pigment content in wheat (*Triticum aestivum* L.). *The Plant Journal* 122:e70274
- [89] Wang M, Yuan J, Qin L, Shi W, Xia G, et al. 2020. *TaCYP81D5*, one member in a wheat cytochrome P450 gene cluster, confers salinity tolerance via reactive oxygen species scavenging. *Plant Biotechnology Journal* 18:791–804
- [90] Yang R, Yang Z, Xing M, Jing Y, Zhang Y, et al. 2023. TaBZR1 enhances wheat salt tolerance via promoting ABA biosynthesis and ROS scavenging. *Journal of Genetics and Genomics* 50:861–871

- [91] Xiao G, Wang M, Li X, Jiang Z, Zhang H, et al. 2024. *TaCHP* encoding C1-domain protein stably enhances wheat yield in saline-alkaline fields. *Journal of Integrative Plant Biology* 66:169–171
- [92] Xiao G, Jiang Z, Xing T, Chen Y, Zhang H, et al. 2025. Small ubiquitin-like modifier protease gene *TaDSU* enhances salt tolerance of wheat. *New Phytologist* 245:2540–2552
- [93] Cui M, Li Y, Li J, Yin F, Chen X, et al. 2023. Ca²⁺-dependent TaCCD1 cooperates with TaSAUR215 to enhance plasma membrane H⁺-ATPase activity and alkali stress tolerance by inhibiting PP2C-mediated dephosphorylation of TaHA2 in wheat. *Molecular Plant* 16:571–587
- [94] Danquah A, de Zelicourt A, Colcombet J, Hirt H. 2014. The role of ABA and MAPK signaling pathways in plant abiotic stress responses. *Biotechnology Advances* 32:40–52
- [95] Kumar V, Thakur JK, Prasad M. 2021. Histone acetylation dynamics regulating plant development and stress responses. *Cellular and Molecular Life Sciences* 78:4467–4486
- [96] Park J, Lim CJ, Shen M, Park HJ, Cha JY, et al. 2018. Epigenetic switch from repressive to permissive chromatin in response to cold stress. *Proceedings of the National Academy of Sciences of the United States of America* 115:E5400–E5409
- [97] Liu X, Zhao Y, Zhang J, Tang G, Zhu W, et al. 2025. Wheat source-sink metabolic network dynamics during grain filling under drought-heat combined stress. *Journal of Agricultural and Food Chemistry* 73:7003–7018
- [98] Shen K, Ye B, Yu X, Shen P, Yu R, et al. 2025. Dissection of genomic drivers of spike morphology changes in wheat by high-throughput phenotyping. *Cell Reports* 44:116120
- [99] Wang C, Yang X, Li G. 2021. Molecular insights into inflorescence meristem specification for yield potential in cereal crops. *International Journal of Molecular Sciences* 22:3508
- [100] Feng N, Song G, Guan J, Chen K, Jia M, et al. 2017. Transcriptome profiling of wheat inflorescence development from spikelet initiation to floral patterning identified stage-specific regulatory genes. *Plant Physiology* 174:1779–1794
- [101] Kong X, Wang F, Wang Z, Gao X, Geng S, et al. 2023. Grain yield improvement by genome editing of *TaARF12* that decoupled peduncle and rachis development trajectories via differential regulation of gibberellin signalling in wheat. *Plant Biotechnology Journal* 21:1990–2001
- [102] Backhaus AE, Lister A, Tomkins M, Adamski NM, Simmonds J, et al. 2022. High expression of the MADS-box gene *VRT2* increases the number of rudimentary basal spikelets in wheat. *Plant Physiology* 189:1536–1552
- [103] Liu Y, Chen J, Yin C, Wang Z, Wu H, et al. 2023. A high-resolution genotype – phenotype map identifies the TaSPL17 controlling grain number and size in wheat. *Genome Biology* 24:196
- [104] Xu X, Lin H, Zhang J, Burguener G, Paraiso F, et al. 2025. Spatial and single-cell expression analyses reveal complex expression domains in early wheat spike development. *Genome Biology* 26:352
- [105] Millstead T, Kainer D, Sullivan R, Sun X, Li KL, et al. 2025. Spatial transcriptomics of developing wheat seed reveals concentric gene expression zones and subgenome biased expression of key genes. *Plant Biotechnology Journal* 23:5934–5949
- [106] Zhu M, Hsu CW, Peralta Ogorek LL, Taylor IW, La Cavera S, et al. 2025. Single-cell transcriptomics reveal how root tissues adapt to soil stress. *Nature* 642:721–729
- [107] Cui Y, Cao Q, Li Y, He M, Liu X. 2023. Advances in cis-element- and natural variation-mediated transcriptional regulation and applications in gene editing of major crops. *Journal of Experimental Botany* 74:5441–5457
- [108] Yamaguchi-Shinozaki K, Shinozaki K. 2006. Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. *Annual Review of Plant Biology* 57:781–803
- [109] Liu Q, Kasuga M, Sakuma Y, Abe H, Miura S, et al. 1998. Two transcription factors, DREB1 and DREB2, with an EREBP/AP2 DNA binding domain separate two cellular signal transduction pathways in drought- and low-temperature-responsive gene expression, respectively, in *Arabidopsis*. *The Plant Cell* 10:1391–1406
- [110] Rodríguez-Leal D, Lemmon ZH, Man J, Bartlett ME, Lippman ZB. 2017. Engineering quantitative trait variation for crop improvement by genome editing. *Cell* 171:470–480.e8
- [111] Hendelman A, Zebell S, Rodríguez-Leal D, Dukler N, Robitaille G, et al. 2021. Conserved pleiotropy of an ancient plant homeobox gene uncovered by cis-regulatory dissection. *Cell* 184:1724–1739.e16
- [112] Song X, Meng X, Guo H, Cheng Q, Jing Y, et al. 2022. Targeting a gene regulatory element enhances rice grain yield by decoupling panicle number and size. *Nature Biotechnology* 40:1403–1411



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