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REVIEW ARTICLE

Genetic and Genomic Insights into Drought and Heat Tolerance Co-adaptation in Wheat

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ABSTRACT

Wheat, one of the world main staple crops feeding a huge fraction of human being, faces an increasing threat of drought and heat stress that reduce its productivity. These abiotic stresses frequently occur together at key developmental stages and lead to significant yield losses due to decreased photosynthesis, increased senescence, limited grain filling and overall deterioration of grain quality. Overcoming these challenges necessitate an integrative knowledge of physiology, biochemistry, and molecular responses, underpinned by innovative breeding and genomics activities. This review integrates the available knowledge about the use of different genomic tools, such as high-throughput genotyping, genome-wide association studies, transcriptomics and whole-genome sequencing, to reveal genes and quantitative trait loci associated with stress tolerance. It also emphasizes both the epigenetic regulation and the integration of multi-omics as well as the cross-species trait mining for more profound understanding of complex stress adaptation mechanisms. In addition, breeding approaches including trait pyramiding, marker-assisted backcrossing, genomic prediction and pre-breeding with wild relatives should be assessed as desirable methods to stack adaptive traits into elite cultivars. Specifically, photosynthetic efficiency under combined stresses is indicated as a main target to increase resilience under integrated stressed conditions. This comprehensive framework leverages advances in genomics, systems biology and predictive breeding to provides a roadmap towards breeding wheat cultivars with the ability to stably perform under increasingly variable and extreme climates.

Key words: Triticum aestivum L, Drought stress, Heat stress, Combined stress, Photosynthesis, Genomics, QTL mapping, Transcription factors, HSPs, LEA proteins, Genomic selection, Multi-omics, Breeding strategies, Climate resilience.

INTRODUCTION

Wheat (Triticum aestivum L.) is still a staple food type in the worldwide food systems, in which more than one-third of the global population relay on wheat for their diet, and wheat has an important contribution in achieving food and nutrition security (Gupta et al., 2020; Reynolds et al., 2020). Yet wheat production stability is threatened by growing negative effects of drought and heat stress simultaneously, an impact intensified in changing climate regimes. Since these two abiotic stressors frequently occur together, particularly in arid and semi-arid regions, their synergic effects can lead to substantial reduction of photosynthetic efficiency, reproductive failure, and yield loss (Dubey et al., 2020). The simultaneous occurrence of heat and drought during vulnerable phenological stages like flowering (anthesis) and grain filling limits carbon fixation, changes hormonal signaling, and enhances oxidative stress damage to wheat plants (Fábián et al., 2011). The combination of these two increasingly serious stresses presents more risk than one alone, which needs a shift of attention in the research towards how wheat integrates physiological and molecular responses to combined stresses (Zhan et al., 2023). Thus, deciphering the underlying mechanisms of wheat tolerance to these combined abiotic stresses at the molecular level is needed for breeding climate-resilient cultivars that can maintain yield against future climate uncertainties.

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The coexistence of drought and heat in wheat leads to unique and greater physiological and molecular changes that are very different from and more severe than those driven by either stress alone, unlike individual stress responses. Since plants are stationary, they must always survey their surroundings for anything that might pose a threat to their very existence. This is the basis for the development of rapid cellular communication systems, enabling stress-sensing cells to quickly send out local distress signals to adjacent cells. A central aspect of this defense mechanism is the ability of the plant to sensitively sense physical and chemical alterations in the environment, mostly from the plasma membrane and energy-regulating organelles. Such sensory systems are associated with transient changes in ROS and cytosolic Ca^{2+} that activate multiple adaptive responses to alleviate environmental stresses. ROS not only serve as by-products of cellular metabolism but also act as important signaling molecules, communicating the metabolic and energetic status of plant cells. Instead of just being harmful, ROS are actually also regarded as key, central "pro-survival" signals in the biology of stress (Ravi et al., 2023). Different types of reactive oxygen species (ROS), such as singlet oxygen ($^1O_2$), superoxide anion ($\bullet O_2^-$), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($\bullet OH$), activate distinct molecular pathways with different functions in signal transduction and defense (Ravi et al., 2023).

An important mechanism of H_2O_2 signaling is the reversible oxidation of cysteine thiol groups in proteins. This redox modification changes protein function and activity, which serves as a key element of H_2O_2-mediated regulation of plant growth, development, and immunity (Kamran et al., 2025; Zafar et al., 2025). In recent years, some redox-sensitive receptor proteins have been identified in plants. Several of them appear to serve as crucial H_2O_2 sensors, including HPCA1 (Hydrogen Peroxide-induced Ca^{2+} increases 1) and QSOX1 (Quiescin Sulfhydryl Oxidase 1) (Devireddy et al., 2021; Dutta et al., 2024). An interesting feature of QSOX1 is its intricate structure, which harbors an oxidoreductase domain (similar to protein disulfide isomerases) with a 'CxxC' active site in a thioredoxin-like fold. Moreover, it harbors a domain similar to ERV/ALR, two CxxC motifs, a FAD-binding site, is essential for its enzymatic activity (Jing et al., 2024). These sensor proteins enable the perception of extracellular hydrogen peroxide and subsequently confer the redox signals necessary to activate downstream defense and developmental pathways. The concerted action requires a highly-regulated mechanism for transcriptional reprogramming that oversees the expression of numerous stress-responsive genes.

Recent research has shown that the fasting of co-tolerance in wheat plants involves the cumulative activation of a common set of cis-active/transcription factors such as DREB2, NAC, HSFs, and WRKY families that distinguish the relevant stress pathways (Kamran et al., 2025). Based on the degree of stress, timing as well as developmental stages, the transcriptional regulators often function in collaboration or opposition (H. Zhao et al., 2021). Additionally, some co-expression networks have identified specific gene modules that might be induced during particular conditions when multiple stresses are applied, but not during single-stress exposures (Haider et al., 2021). GWAS platforms that use high-throughput phenotyping are continuously increasing precision in mapping genetic loci, including quantitative trait loci (QTLs) and expression QTL (eQTL) associated with dual stress tolerance. Additionally, it has been found that epigenetic regulatory mechanisms such as DNA methylation and histone modifications can also have an effect on the activation and repression of various stress-specific genes during co-stress conditions (Shriti et al., 2024). This pejorative connotation is grounded in the data and highlights the need to understand the genetic and molecular basis of co-adaptive traits needed to inform breeding programs for multi-stress resilient wheat (Han et al., 2024; Singh et al., 2025).

The advances in molecular and genomic technologies in this 21st century have considerably improved the understanding of the genetic basis of tolerance for simultaneous drought and heat stress in wheat. High-throughput sequencing technologies, genome-wide association studies (GWAS), transcriptomic profiling, and integrative multi-omics approaches have emerged in recent years as powerful approaches for the isolation of stress-responsive genes, climate stress QTLs, key transcription factors, and even epigenetic regulators, revealing molecular components of complex adaptation to the stress (Abdulraheem et al., 2024; Bashir et al., 2025). In this regard, transcriptome analyses exhibit a specific group of transcription factors that are additionally activated under combined stress conditions, such as DREB, HSF, NAC, and WRKY family members, all of which are essential for modulatory gene expression in stress perception, signaling, and tolerance (Zulkiffal et al., 2021). On the other hand, proteomics and metabolomics have revealed a dynamic crosstalk among stress-responsive signaling pathways and stress-induced metabolic reprogramming, adding more dimensions of functional layers linking to stress co-tolerance (Zhan et al., 2023).

Genomic selection (GS) was introduced by Meuwissen and as both a theoretical and practical framework in plant breeding, has been extensively studied to assess its potential in expediting crop improvement programs. Marker-assisted selection (MAS) has been successfully used in the analysis of traits that are classified by a small number of major-effect genes often qualitative traits; MAS, however, is of limited use in the improvement of complex quantitative traits that are controlled by many genes each of small effect (Anilkumar et al., 2022; Bellundagi et al., 2022). To minimize this high bottleneck, GS provides a more holistic alternative by estimating genomic estimated breeding values (GEBVs) at the individual level using genome-wide molecular marker data. Using this approach, breeders can select candidates for advancement in the breeding pipeline by predicting performance instead of relying on classical phenotyping alone. Over the last two decades, this approach has found widespread utility in the animal breeding sector as it offers advantages such as increased selection accuracy, reduced breeding cycles, decreased requirement for expensive phenotypes and consequently fast-tracked genetic gain (Saini et al., 2022).

Development of an accurate and robust statistical model, portraying the underlying genetic architecture and maximizing the prediction accuracy of GS is a key factor for the success of GS in crop breeding, particularly under stress conditions. Once we are aware of the genetic changes due to combined drought and heat stress, we can incorporate that genetic knowledge directly into GS models to predict stress tolerance markers in rainfed ecologies (Lohithaswa et al., 2022). Therefore, genomic selection is becoming a feasible strategy for improving climate resilient crops, and even more recently as the Global Environmental Change proceeds rapidly. Combining different beneficial alleles that control different stress-resilience traits (trait pyramiding) into a single genotype has similarly been suggested to enhance tolerance to simultaneous environmental stresses (Seid & Andualem, 2021). These approaches, when employed in tandem, provide a sound framework for the breeding of climate-resilient wheat that maximizes yield while adapting to ever more extreme environmental conditions.

Physiological Basis of Drought and Heat Stress Interaction

Plant response to the combination of drought and heat stress is a response specific to this combination and is not an additive combination of the two stresses. During drought, in order to save water, stomata close, resulting in less carbon dioxide entry and decreased photosynthesis. Heat exposure however causes extra generation of ROS, lipid peroxidation and destruction of cell membranes. When both stresses occur concurrently especially during reproductive stages these impacts are magnified, leading to severe reductions in photosynthesis, grain filling, and yield (Bashir et al., 2025). Moreover, the interaction between drought and heat disrupts key physiological processes such as evapotranspiration, canopy temperature regulation, and enzymatic function. Heat stress impairs photosynthetic enzymes like Rubisco and Rubisco-activase and disrupts starch synthesis, while drought restricts water transport and triggers ABA-mediated stomatal closure (Degen et al., 2021). Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) is a central enzyme in the Calvin–Benson–Bassham cycle, and has long been recognized as a critical point of vulnerability under heat stress conditions (Krammer, 2025). Although Rubisco itself maintains catalytic activity at temperatures approaching 50 °C, its regulation becomes compromised due to the thermal sensitivity of Rubisco activase (Rca), a molecular chaperone that facilitates the activation of Rubisco by removing inhibitory sugar phosphates from its active site (Qu et al., 2023). As Rca loses efficiency under high temperatures, Rubisco becomes increasingly inactive, disrupting CO_2 assimilation and impairing photosynthesis (Aguiló-Nicolau et al., 2024; Qu et al., 2023).Together, these effects increase leaf temperature, reduce transpiration cooling, and accelerate metabolic imbalance. Plant antioxidant defense systems such as superoxide dismutase, catalase, and ascorbate peroxidase become crucial in countering oxidative damage under such dual stress. However, their capacity may be overwhelmed during prolonged combined stress, further compromising physiological stability (Lama et al., 2023).

Effect on Photosynthesis

Under simultaneous exposure to drought and elevated temperature, wheat suffers more than from either stress alone, with photosynthesis particularly compromised (Table 1). Drought-induced stomatal closure limits CO_2 uptake, while heat disrupts enzymatic activity including Rubisco and electron transport. These combined effects significantly reduce net photosynthesis (P_n), leaf relative water content (LRWC), and midday leaf water potential particularly during critical reproductive stages leading to severe grain filling impairment and yield losses (El Habti et al., 2020; Ru et al., 2023; Zafar et al., 2023). The structural integrity of the photosynthetic apparatus is also severely impacted. Combined stress accelerates chlorophyll degradation and destabilizes photosystem II (PSII), lowering Fv/Fm and reducing photochemical efficiency. Wheat genotypes vary in resilience modern cultivars often retain more chlorophyll, maintain higher stomatal conductance and leaf cooling capacity, and display better recovery post-stress (Alsamadany et al., 2023; Ru et al., 2023). Additional experiments under elevated CO_2 (800 ppm) further underline the complexity of interactions. While elevated CO_2 partially mitigates declines in photosynthetic rate and PSII efficiency under moderate heat and drought, recovery remains incomplete in many genotypes. Notably, heat-tolerant silos accumulate more simple sugars (glucose, fructose) under combined stress, suggesting that carbohydrate management influences stress tolerance (Chen et al., 2025).

Table 1: Effect of Heat and Drought Stress on Photosynthetic Pigments

Pigment	Control (mg g^{-1} FW)	Drought Stress	Heat Stress	Combined Stress	Reference
Chlorophyll a	1.85	1.42 (-23.2%)	1.36 (-26.5%)	1.12 (-39.5%)	(Kandel, 2021)
Chlorophyll b	0.78	0.59 (-24.4%)	0.55 (-29.5%)	0.43 (-44.9%)	(Wasaya et al., 2021)
Total carotenoids	0.42	0.35 (-16.7%)	0.31 (-26.2%)	0.28 (-33.3%)	(Hasanuzzaman et al., 2013)

The above given table shows the changes in chlorophyll a, chlorophyll b, and carotenoid contents in wheat leaves under drought, heat, and combined stress conditions (Table 1). Chlorophyll a content decreased by 23.2% under drought, 26.5% under heat, and 39.5% under combined stress, reflecting significant pigment degradation and reduced light capture capacity. Chlorophyll b showed a similar pattern, with losses of 24.4%, 29.5%, and 44.9% under drought, heat, and combined stress, respectively. Carotenoids, which play protective roles against photooxidative damage, decreased less severely but still declined by up to 33.3% under combined stress. The greater pigment loss under combined stress underscores the cumulative damage to photosynthetic apparatus, which limits energy capture and reduces the plant's ability to protect itself from excess light and oxidative stress.

Chlorophyll Degradation and PSII Damage

Light-harvesting chlorophyll a/b-binding (Lhc) proteins are integral constituents of the photosynthetic apparatus and play a key role in as a major antenna system in the thylakoid membrane, which collect and transfer light energy to Photosystem I (PSI) and II (PSII) (Levin & Schuster, 2023; Lokstein et al., 2021; Zafar et al., 2024). These antenna proteins can be divided into two groups; the chlorophyll a-binding core proteins are coded by plastid genes (PsaA, PsaB, PsbA b, PsbB, PsbC, and PsbD), which form the cores of PSI and PSII and the inner antenna proteins CP43/CP47; and the chlorophyll a/b binding peripheral antenna proteins coded by nuclear Lhc genes extend the range of light absorption through their association with chlorophyll b (Wang et al., 2023). The Lhc superfamily contains multiple nuclear-encoded protein families: Lhc (including Lhca and Lhcb subunits), Lil (light-harvesting-like), PsbS (Photosystem II subunit S) and FCII (ferrochelatase II) (Engelken et al., 2011). Among them, the members of Lhc subfamily are the most abundant membrane proteins of thylakoid in green plants and are vital for light harvesting, energy transfer, and stress recovery. Expression of Lhc genes is highly regulated by developmental and environmental cues, including light intensity, circadian rhythms, and abiotic stresses (e.g., drought and heat) (Patnaik et al., 2022; Roeber et al., 2021).

Functional analyses across species highlight the importance of specific Lhc members: in *Arabidopsis thaliana*, suppression of Lhcb1 results in pale leaves, reduced chlorophyll content, slower growth, and diminished capacity for photoprotective state transitions (Guardini, 2022). In apple (*Malus domestica*), overexpression of MdLhcb4.3 enhances drought tolerance and osmotic stress resistance by improving chlorophyll retention and photosynthetic performance under water deficit (S. Zhao et al., 2021). Similarly, in tomato, transgenic overexpression of LeLhcb2 alleviates ROS accumulation and photosynthetic damage under chilling stress, suggesting roles in broader abiotic stress resilience (D. Wang et al., 2024). Together, these findings underscore the dual functionality of Lhc proteins in energy harvesting and stress protection and identify them as promising targets for genetic improvement of photosynthetic efficiency and environmental tolerance in crops (Han et al., 2023; Levin & Schuster, 2023). Damage to thylakoid membranes worsens this pigment loss and impairs electron transport chain efficiency. As a result, the maximum quantum efficiency of Photosystem II (F_n/F_m) declines markedly, signaling impaired photochemical conversion in PSII reaction centers (Johnson, 2025; Sperdouli et al., 2023).

As stress intensifies, wheat leaves experience disruption of PSII super complexes and degradation of core proteins like the D1 protein, weakening parameters such as PSII and photochemical quenching (qP) (Fatma et al., 2021; Kalal et al., 2022). Initially, non-photochemical quenching (NPQ) increases as plants attempt to dissipate excess light energy. However, prolonged stress leads to NPQ decline due to collapse of the trans thylakoid proton gradient and damage to protective processes, thereby increasing photoinhibition susceptibility (Zuo, 2025). Heat stress further complicates this response by influencing PSII thermal tolerance thresholds. Short-term exposures to temperatures ≥36 °C can elevate this threshold, indicating some transient acclimation; nonetheless, longer durations exceed physiological limits, particularly in sensitive genotypes (Zuo, 2025). Variation in $T_{n(-C)}$ across genotypes signals the potential for breeding heat resilient PSII traits (Fatma et al., 2021) Genotypes displaying strong "stay-green" phenotypes often retain higher chlorophyll levels, maintain stable F_n/F_m ratios, and demonstrate better recovery following stress (Christopher et al., 2008). These genotypes typically have more efficient reactive oxygen species (ROS) scavenging and more robust PSII repair mechanisms, while sensitive genotypes suffer accelerated chlorophyll and protein degradation under comparable stress conditions (Zandi & Schnug, 2022).

Stomatal Closure and CO_2 Limitation

Under combined drought and heat stress, plants rapidly adjust their stomatal aperture as a primary defense to reduce water loss through transpiration (Dos Santos et al., 2022). The perception of water deficit triggers increased biosynthesis and signaling of abscisic acid (ABA), which accumulates in guard cells and activates specific ion channels, leading to the efflux of potassium and anions (H. Liu et al., 2022). This ionic movement causes a loss of guard cell turgor pressure, resulting in stomatal closure (Kashtoh & Baek, 2021). While this physiological adjustment minimizes transpirational water loss, it simultaneously limits the influx of carbon dioxide (CO_2) into the leaf intercellular spaces. Reduced CO_2 availability decreases the internal CO_2 concentration (C_i), thereby constraining Rubisco-mediated carboxylation and lowering net photosynthetic rates (Iñiguez et al., 2021; Ranawana et al., 2023). In wheat, drought-induced stomatal closure often overrides heat-driven stomatal opening, despite the latter's potential role in promoting evaporative cooling. This trade-off between water conservation and carbon assimilation is a central bottleneck under combined stress, with genotypic variation in stomatal density, conductance, and responsiveness offering valuable targets for breeding climate-resilient cultivars (Guo et al., 2024; Li et al., 2024). This is primarily mediated by the accumulation of abscisic acid (ABA) in guard cells, which triggers ion efflux, reducing turgor pressure and causing stomatal closure (Dutta et al., 2024). While this mechanism is essential for preventing excessive dehydration, it simultaneously restricts the diffusion of atmospheric CO_2 into the intercellular spaces of the leaf (Janová et al., 2024).

A reduction in CO_2 influx leads to a lower internal CO_2 concentration (Ci), which directly limits the substrate availability for the Calvin–Benson cycle (H. Zhao et al., 2021). This constraint impairs the carboxylation efficiency of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), the key enzyme responsible for CO_2 fixation. In C_3 plants like wheat, decreased Ci shifts the balance between carboxylation and oxygenation reactions catalyzed by Rubisco, increasing photorespiration at the expense of net carbon assimilation (Iñiguez et al., 2021; Jin et al., 2023). Under combined drought and heat stress, stomatal closure restricts CO_2 diffusion into the leaf, but the challenge does not stop there: mesophyll conductance (g_m) becomes an additional major constraint. Progressive water deficit in wheat reduces both stomatal conductance (g_s) and g_m, with the latter declining more severely under prolonged stress (Mu et al., 2022; Sommer et al., 2023). A strong positive correlation exists between g_s and g_m, but under combined stress, non-stomatal limitations dominate, driving down mesophyll CO_2 diffusion and hampering carbon assimilation (Sommer et al., 2023). Elevated temperatures further exacerbate biochemical limitations in the mesophyll. Heat stress induces inactivation of Rubisco activase (RCA), the critical enzyme that maintains Rubisco in its catalytically active state by facilitating the release of inhibitory sugar phosphates. RCA is thermo-labile, and its deactivation under heat leads to a rapid decline in Rubisco activation and carboxylation efficiency (Degen et al., 2021; Wijewardene et al., 2021). Studies in wheat demonstrate that long-term heat stress reduces Rubisco activation state and below-optimal RCA function, directly impairing photosynthetic performance (Ahmad et al., 2023).

The combined effects of limited CO_2 diffusion (via low g_s and g_m) and reduced enzymatic function (via RCA deactivation) lead to a significant decline in net photosynthetic rate (P_n). Research indicates that under simultaneous drought and heat conditions, the combined stress causes more severe limitations on photosynthesis than either stress alone, mainly due to compounded diffusional and biochemical constraints (Abdelhakim et al., 2022; X. Wang et al., 2024). This complex trade-off conserving water at the cost of carbon assimilation presents a central physiological bottleneck for wheat under future climate scenarios. Addressing this challenge requires breeding strategies that enhance g_m, stabilize RCA, and maintain Rubisco activation under elevated temperatures. Variation among wheat genotypes in mesophyll conductance and RCA thermostability offers promising targets for selection and improvement (Shao et al., 2021). In tolerant wheat genotypes, partial stomatal closure strategies or optimized stomatal density can help balance water loss prevention with sufficient CO_2 uptake, maintaining relatively higher carboxylation efficiency and sustaining photosynthetic performance under stress conditions.

Damage to Photosynthetic Apparatus

Heat stress can profoundly disrupt chloroplast structure, with the thylakoid membranes being among the most vulnerable components (Arachchige et al., 2024). These membranes house the pigment–protein complexes responsible for capturing light energy and driving the electron transport chain. Elevated temperatures increase membrane fluidity, which destabilizes the organization of photosystem complexes, particularly photosystem II (PSII) (Suresh, 2021; Zhang et al., 2025). This disorganization interferes with the efficient transfer of excitation energy from light-harvesting complexes to the PSII reaction center, reducing the plant's ability to convert light energy into chemical energy. The oxygen-evolving complex (OEC) of PSII, which is essential for splitting water molecules and supplying electrons to the transport chain, is especially sensitive to heat, leading to diminished water-splitting activity and impaired downstream electron flow (Luo et al., 2021; Sinha & Kumar, 2022). Beside the damage to PSII, heating exposure over an extended period may lead to the partial release of LHCII from the thylakoid membrane by which the capture of light was further impaired (Karlický et al., 2021). Loss of PSII D1-protein (essential for electron transport) leads to slow or no recovery of repair cycle to maintain photosynthetic capabilities. These structural declines in association with generation of reactive oxygen species by heat, cause the activity of other molecules within the thylakoid such as lipids, pigments, proteins to be damaged progressively that finally leads to a decrease in plant fitness during the heat(exposed) photosynthesis (Shanker et al., 2025; Su et al., 2024). High leaf temperatures enhance membrane fluidity, leading to disruption of pigment–protein complexes and release of light-harvesting complex (LHC) II from photosystem (PS) II. This results in the reduction of electron transfer (ET) efficiency, and hampering D1 protein repair which results in persistent PSII photoinhibition. The rate of thylakoid responses to change in temperature would seem to be at least partially due to the inactivation of PSII, more specifically, heat sensitive OEC that disrupts water splitting and electron transfer to plastoquinone (Bassi & Dall'Osto, 2021).

Drought further magnifies the interpret but imposes an even more direct constraint by limiting the water for photosynthetic electron transport. Water deficiency incompetes the electrons to be generated from the water-splitting reaction in PSII for the electron flow in the photosynthetic machinery (Kranz & Wächtler, 2021; Qiao et al., 2024). This bottleneck extends to photosystem I (PSI), where the reduced electron flow limits the conversion of $NADP^+$ to NADPH, a key molecule for the Calvin–Benson cycle. Over time, restricted electron movement in PSI can lead to photoinhibition, particularly when the electron transport chain becomes over-reduced due to an imbalance between light energy capture and its utilization in carbon fixation (Chen et al., 2022; Taghvimi et al., 2024). The situation is further worsened under combined drought and heat stress, as the excess absorbed light energy now unable to be fully processed drives the overproduction of reactive oxygen species (ROS) (Nawaz et al., 2021). These highly reactive molecules attack thylakoid membrane lipids, denature proteins, and degrade chlorophyll, resulting in structural and functional damage to both PSI and PSII. In wheat, such compounded stress can significantly lower the maximum quantum efficiency of PSII, measured as Fv/Fm, by more than 40% (Rai, 2023; Sachdev et al., 2021). This steep decline reflects severe photochemical impairment, meaning that a large portion of the photosystems are no longer capable of effectively converting light energy into usable chemical energy. The cumulative effect is a substantial reduction in photosynthetic performance, leading to lower biomass accumulation and yield under field conditions (Li et al., 2023).

The above given table summarizes the physiological impact of drought stress on wheat compared to well-watered control conditions, highlighting substantial reductions in parameters directly linked to plant water status, gas exchange, and photosynthetic performance. Leaf relative water content (LRWC) decreased from 92.5% in control plants to 68.3% under drought stress, indicating a 26.2% reduction. This decline reflects the limited water availability in plant tissues, which disrupts cell turgor and metabolic activities. Stomatal conductance dropped by 42.2%, from 320 mmol m^{-2} s^{-1} to 185 mmol m^{-2} s^{-1}, as plants responded to water deficit by closing stomata to reduce transpiration losses. However, this stomatal closure also restricted CO_2 entry into the leaves, directly impacting photosynthetic efficiency. The net photosynthetic rate fell by 39.1%, from 18.4 to 11.2 μmol CO_2 m^{-2} s^{-1}, demonstrating how reduced stomatal conductance and internal water deficit limit carbon assimilation. Chlorophyll content, measured in SPAD units, declined by 27.4%, suggesting pigment degradation or inhibited chlorophyll synthesis under drought stress. Since chlorophyll is essential for light harvesting during photosynthesis, this reduction further compounds the decrease in photosynthetic capacity. Overall, the table emphasizes how drought stress triggers a cascade of physiological limitations reduced water content, stomatal closure, pigment loss that collectively impair photosynthesis and growth in wheat (Table 2).

Rubisco Activity and Carbon Assimilation

Rubisco, short for ribulose-1,5-bisphosphate carboxylase/oxygenase, is the central enzyme responsible for fixing atmospheric CO_2 into organic molecules during the Calvin–Benson cycle (Iñiguez et al., 2021). Its activity largely determines the potential rate of carbon assimilation in C_3 plants such as wheat. However, Rubisco does not function optimally on its own it requires activation through a process called carbamylation, in which a CO_2 molecule binds to a specific lysine residue in the enzyme's active site (Bendou, 2025; Tommasi, 2021). This activation step is facilitated by Rubisco activase (RCA), a chaperone protein that removes inhibitory sugar phosphates from Rubisco's active sites, ensuring that the enzyme remains in a catalytically active form (Aguiló-Nicolau et al., 2024; Sareen et al., 2024). RCA is highly sensitive to temperature, and one of its known weaknesses is thermal instability. When leaf temperatures exceed approximately 35–38 °C, RCA undergoes conformational changes that reduce its ATPase activity and its ability to interact effectively with Rubisco (Amaral et al., 2024; Nagarajan et al., 2025). As a result, Rubisco molecules remain in an inactive or partially

Table 2: Impact of Drought Stress on Photosynthetic Apparatus

Parameter	Control (Well-watered)	Drought Stress	Change (%)	Reference
Leaf relative water content (%)	92.5	68.3	-26.2	(Heikal et al., 2023)
Stomatal conductance (mmol m^{-2} s^{-1})	320	185	-42.2	(Ali et al., 2025)
Net photosynthetic rate (μmol CO_2 m^{-2} s^{-1})	18.4	11.2	-39.1	(Bashir et al., 2021)
Chlorophyll content (SPAD units)	45.6	33.1	-27.4	(Wasaya et al., 2021)

inhibited state, which directly limits the maximum carboxylation rate (Vcmax). This temperature sensitivity becomes especially problematic during heat waves coinciding with key wheat growth stages such as anthesis and grain filling, when the demand for carbon assimilation is high (Latief Bashir et al.; Yanagi, 2024).

Drought stress compounds this problem by limiting ATP production in the chloroplast. Reduced photophosphorylation under water deficit conditions means there is less ATP available for RCA's function. Because RCA's activity is ATP-dependent, this energy shortage slows the removal of inhibitors from Rubisco and reduces the proportion of enzyme molecules in the active state (Farooq et al., 2024; Fathi et al., 2024; Karami et al., 2025). Consequently, even if CO_2 is available, the biochemical machinery required to fix it operates below capacity. Over prolonged drought, this effect is often accompanied by declines in Rubisco protein content itself, as resource allocation shifts toward stress-protective proteins rather than photosynthetic enzymes (Iñiguez et al., 2021).The combined effect of heat-induced RCA deactivation and drought-induced ATP limitation creates a strong biochemical bottleneck in photosynthesis. Carboxylation efficiency drops, and oxygenation activity by Rubisco becomes more prominent, increasing photorespiration (Salesse-Smith et al., 2025). This not only reduces net CO_2 assimilation but also consumes energy and releases previously fixed carbon, further decreasing the plant's energy-use efficiency. As a result, plants under combined heat and drought stress often exhibit steep declines in photosynthetic rates, even if stomatal conductance is only moderately reduced (Bernacchi et al., 2025; Slot et al., 2024; Vadez et al., 2024).

The above given (table 3) presents the impact of high temperature stress, defined as conditions exceeding 35°C, on key physiological and biochemical parameters of wheat compared to optimum growth temperatures. Photosystem II efficiency (Fv/Fm), an indicator of photochemical activity in the thylakoid membrane, declined by 15.9% under heat stress, showing damage to photosynthetic machinery and reduced light energy utilization. Rubisco activity dropped sharply by 38.2%, highlighting the enzyme's sensitivity to heat and its central role in limiting carbon fixation under thermal stress. Grain filling duration was reduced from 32 to 23 days (a 28.1% reduction), indicating accelerated development and shortened time for assimilate deposition in the grain. Protein content declined by 18.3%, suggesting disruptions in nitrogen assimilation and protein synthesis pathways. Together, these findings demonstrate that heat stress compromises both the photosynthetic capacity and grain quality of wheat through direct effects on enzyme activity, photosystems, and reproductive development.

Some wheat genotypes exhibit partial tolerance to these limitations, either through RCA variants that are more thermostable or by maintaining higher ATP production under stress conditions (Amaral et al., 2024; Long, 2025). Breeding programs and genetic engineering efforts are exploring ways to enhance RCA stability and improve Rubisco's catalytic properties, aiming to sustain carbon assimilation under the hotter, drier conditions projected for future growing seasons (Wijewardene et al., 2021). These strategies, combined with optimized water management, could help mitigate the severe productivity losses associated with impaired Rubisco function during combined drought and heat events (Ru et al., 2023). Combined drought–heat stress shifts the balance between carboxylation and oxygenation toward the latter, increasing photorespiration and decreasing net CO_2 fixation. Over time, stress-induced proteolysis can reduce Rubisco protein abundance, as reported in wheat flag leaves exposed to prolonged high temperature (Abdelhakim et al., 2022; Azarkina et al., 2025). Furthermore, in vivo measurements show that combined stress can reduce Rubisco's maximum carboxylation rate (Vcmax) by 30-50%, severely limiting photosynthetic capacity (Krammer, 2025).

Key Genes and QTLs Involved in Co-tolerance

Wheat's ability to cope with simultaneous drought and heat stress relies heavily on a network of genes that regulate protective proteins, signaling pathways, and adaptive metabolic responses. These genetic factors include stress-responsive proteins, like heat shock proteins (HSPs) and late embryogenesis abundant (LEA) proteins, and regulatory transcription factors, which orchestrate the expression of tolerance mechanisms (Mao et al., 2022; Trono & Pecchioni, 2022). Moreover, genome-wide associations, QTL mapping, and meta-QTL analysis, have all facilitated the identification of genomic regions consistently linked with dual stress tolerance (S. Kumar et al., 2023). An understanding of the molecular components and their genomic locations is an essential prerequisite for being able to breed wheat varieties that maintain yield stability under future climatic scenarios.

Table 3: Impact of Heat Stress on Enzymatic Activity

Trait	Optimum Temperature (°C)	Heat Stress (>35°C)	Change (%)	Reference
Photosystem II efficiency (Fv/Fm)	0.82	0.69	-15.9	(Bashir et al., 2021)
Rubisco activity (μmol CO_2 m^{-2} s^{-1})	15.2	9.4	-38.2	(Tyagi & Pandey, 2022)
Grain filling duration (days)	32	23	-28.1	(Mokhtari et al., 2024)
Protein content (%)	12.6	10.3	-18.3	(Panigrahi et al., 2022)

Heat Shock Proteins

Heat shock proteins (HSPs) are one of the most critical defense systems to modulate the impact of heat and the associated oxidative stress in plants. They are evolutionarily conserved proteinaceous chaperones which are important actors of the maintenance of the proteostasis, that is of the stability of the cellular proteome both at the basal level and under stress conditions (Poznyak et al., 2023). They act mainly in nonreversible prevention of protein denaturation, in the correct folding of newly synthetized polypeptides, and in the repair or degradation of damaged proteins. S-CP interaction is particularly important during heat stress, a condition for which unfolded proteins are in a non-native and aggregated form. In wheat, the HSP network is rapidly upregulated when leaves are exposed to high temperatures, within minutes to hour, to protect crucial metabolic and structural proteins from loss of activity (Jaworek et al., 2022).

Different HSP families such as HSP100, HSP90, HSP70, and small HSPs (sHSPs) work in concert to provide multi-level protection. The HSP100 family consists of large, ATP-dependent chaperones that specialize in rescuing severely aggregated proteins. They are unique among HSPs because they can actively disaggregate protein clumps, threading unfolded polypeptides through their central channel for refolding or degradation. This activity is particularly valuable when stress-induced protein aggregates form during extreme heat events. In plants like wheat, HSP100 proteins often work together with HSP70 and co-chaperones to re-solubilize aggregates that would otherwise be irreversible, thereby restoring enzymatic activity and preventing toxic buildup of misfolded proteins. HSP100 members are localized in both the cytoplasm and organelles, including chloroplasts, where they protect photosynthetic enzymes and membrane proteins from aggregation under high temperature and dehydration conditions (Gallas, 2025; R. Kumar et al., 2023). HSP90 proteins are abundant and highly conserved chaperones that not only stabilize unfolded proteins but also play an integral role in regulating key components of signal transduction pathways. They are often involved in the late stages of protein folding and are critical for the maturation of a range of client proteins, including kinases, hormone receptors, and transcription factors. In stress responses, HSP90 helps maintain the structural integrity of proteins involved in ABA signaling, ROS detoxification, and heat shock transcriptional regulation. In wheat, HSP90 has been implicated in sustaining the function of signal proteins that orchestrate downstream activation of protective genes during drought and heat episodes. Without functional HSP90, these stress response pathways can collapse, leading to poor adaptation under prolonged stress conditions (Kozeko, 2021; Peng et al., 2024).

HSP70 proteins form the core of the plant's protein quality control system during and after stress events. They bind to nascent polypeptide chains emerging from ribosomes to prevent premature folding or aggregation, and they assist in refolding proteins that have been partially denatured by heat or oxidative stress. This binding and release cycle is ATP-dependent and is often assisted by co-chaperones such as HSP40 and nucleotide exchange factors. In wheat, chloroplast-localized HSP70 is particularly important because it safeguards photosynthetic enzymes, including Rubisco, which is highly vulnerable to heat denaturation. Under combined drought and heat stress, the ATP-dependent activity of HSP70 may be limited by reduced ATP supply, but its role becomes more critical as oxidative damage from ROS increases the pool of misfolded proteins (Berka et al., 2022; Chen et al., 2023). Small heat shock proteins, typically ranging from 15 to 42 kDa, act as the first line of defense against protein aggregation. They form oligomeric complexes that bind to partially unfolded proteins, keeping them in a refolding-competent state until ATP-dependent chaperones like HSP70 or HSP100 can complete the repair. sHSPs are unique because their activity is ATP-independent, allowing them to function even when cellular energy levels are low as is common under drought stress. In wheat, several sHSP isoforms are targeted to chloroplasts, mitochondria, and the cytosol, where they protect membrane-associated proteins and maintain the stability of photosystem II reaction centers. This is particularly relevant under combined drought and heat conditions, where dehydration and high temperature jointly threaten protein stability (Lal et al., 2022; Wen et al., 2023).

In wheat, the expression of heat shock proteins (HSPs) is orchestrated by a specialized group of regulatory proteins known as heat shock transcription factors (HSFs) (Kumar et al., 2024). These transcription factors are molecular thermometers, registering when proteins are not folded properly when temperatures become too high. When such stress is detected, HSFs are activated typically by trimerization and relocation to the nucleus and they bind to structural DNA sites of HSP genes called heat shock elements (HSEs) that are implicated in the promoters of HSP genes (Fujimoto et al., 2023). This binding then triggers a fast induction of transcriptional response that results in the accumulation of several HSPs that allows to recover cellular protein homeostasis (Roncarati et al., 2025). The combined action of drought stress with high temperature commonly elicits a stronger and sustained induction of HSP genes in wheat (Yadav et al., 2022). The higher expression of these proteins may be related to plant response to the dehydration-mediated inactivation of proteins as well as to the heat–induced denaturation. Cross-talk under double stress conditions is also induced between HSF-controlled heat response and ABA-mediated drought response, for additional HSP fine-tuning. This coordination is critically important since it provides for an abundance of molecular chaperones that are thus available to protect essential enzymes and structural proteins and thereby maintain cellular function under environmentally compounded stress (Chaffai et al., 2024; Chowdhary & Songachan, 2025).

Some HSPs in wheat are strategically localized to energy-producing organelles such as chloroplasts and mitochondria, where metabolic activity is highly sensitive to stress damage (Christian et al., 2023). In chloroplasts, certain small HSPs (sHSPs) have been shown to protect photosystem II (PSII) reaction centers, maintain the integrity of the electron transport chain, and safeguard the structure and activity of Rubisco (Singh et al., 2022). This targeted protection enables continued CO_2 fixation during stress episodes, which is critical for sustaining energy supply and biomass production. Similarly, mitochondrial-localized HSPs help maintain respiratory efficiency, preventing declines in ATP production that would otherwise impair recovery from stress (Song et al., 2021).

Late Embryogenesis Abundant Proteins

Late Embryogenesis Abundant (LEA) proteins are a class of highly hydrophilic, stress-associated proteins that play an essential role in protecting plant cells under water-deficient conditions. Originally discovered in the seeds of cotton during the late stages of embryogenesis, LEA proteins were found to accumulate as seeds begin to desiccate. This observation led to their classification as key contributors to desiccation tolerance (Gechev et al., 2013; Subramanian et al., 2024; Yang et al., 2021). However, it is now well established that LEA proteins are also expressed in vegetative tissues in response to abiotic stresses such as drought, heat, cold, and salinity. In wheat, LEA proteins are significantly upregulated during prolonged drought or heat episodes, where they help preserve the functional integrity of proteins and membranes(Bhardwaj et al., 2013; Kosová et al., 2014). Structurally, LEA proteins are unique. Most are intrinsically disordered under hydrated conditions, which means they lack a stable three-dimensional shape (Rani & Biswas, 2015; Shraddha et al., 2024). However, during dehydration or heat stress, they undergo conformational changes that enable them to interact with a wide range of cellular targets. This structural flexibility enables LEA proteins to execute various protective functions, such as protecting enzymes, retaining membrane fluidity and inhibiting the aggregation of unfolded proteins (Londoño Vélez et al., 2022). These functions are especially important under joint drought and heat stress where the cellular desiccation is confounded by thermal instability of macromolecules (Bakery et al., 2024). LEA proteins also participate in the maintenance of photosynthetic capacity in the chloroplast. They protect the thylakoid membranes from heat-induced lipid peroxidation and prevent damage to photosystem proteins under conditions of oxidative stress (Sarma et al., 2023). In mitochondria, LEA proteins help maintain respiratory enzyme function by stabilizing inner membrane integrity, which is often compromised during water deficit. Additionally, in the cytoplasm and nucleus, LEA proteins act as molecular shields, forming hydration layers around proteins and nucleic acids to prevent irreversible damage (Abdul Aziz et al., 2021; Hernández-Sánchez et al., 2022). This multi-compartment localization highlights the versatility of LEA proteins in safeguarding essential cellular processes.

LEA proteins are also thought to contribute to osmotic adjustment. Some LEA family members can bind water molecules directly, helping maintain intracellular hydration even when external water availability is low (Li et al., 2021). This buffering capacity reduces the risk of cellular collapse and helps maintain turgor pressure, particularly in leaf and root tissues. In wheat, the expression of LEA genes has been positively correlated with survival and growth maintenance under both drought and combined drought–heat stress environments, making them valuable candidates for stress-resilient breeding. From a genetic regulation standpoint, LEA protein expression is typically controlled by ABA-dependent signaling pathways (Mohanty & Hembram, 2025). During water stress, abscisic acid (ABA) levels increase, activating stress-responsive transcription factors such as DREB, ABF, and NAC, which in turn upregulate LEA gene transcription. Some LEA promoters contain specific cis-regulatory elements like ABREs (ABA-responsive elements), enabling fine-tuned expression based on the severity and duration of stress. This tightly regulated induction ensures that LEA proteins are synthesized only when needed, conserving energy during non-stress conditions (Hibshman & Goldstein, 2021; Pantelić et al., 2022). Advances in molecular breeding and genetic engineering have demonstrated that overexpression of LEA genes can significantly enhance abiotic stress tolerance. Transgenic wheat and other crops engineered to express specific LEA proteins show improved growth, membrane stability, and yield under drought and high-temperature stress (Lata & Shivhare, 2021; Zakariya et al., 2022). As a result, LEA proteins are increasingly recognized as promising targets for genetic improvement programs aimed at developing climate-resilient wheat cultivars. Their multifunctional nature, organelle-specific activity, and inducibility by stress hormones make them indispensable components of the plant stress response toolkit.

Transcription Factors

Transcription factors (TFs) are master regulators that play a central role in modulating wheat's response to environmental stresses, particularly heat and drought. These proteins function by binding to specific cis-regulatory elements in the promoter regions of target genes, enabling the plant to rapidly adjust its physiological and metabolic responses. Under heat and drought stress, transcription factors help activate genes that control stomatal conductance, Osmo protectant accumulation, antioxidant defense, and the stabilization of cellular structures all of which are critical for stress survival and recovery (Hrmova & Hussain, 2021; Khoso et al., 2022). In wheat, heat and drought often occur simultaneously during key developmental stages such as flowering \and grain filling, leading to compounded physiological stress. Transcription factors such as DREB (Dehydration-Responsive Element-Binding) proteins are pivotal in drought signaling. These TFs activate the expression of genes involved in osmotic adjustment, including those coding for proline, sugars, and late embryogenesis abundant (LEA) proteins. Some DREB members, like DREB2A, also play roles in heat stress by activating genes that function independently of the abscisic acid (ABA) pathway (Ain-Ali et al., 2021; Yang et al., 2025). This dual functionality makes DREB TFs highly valuable for engineering or breeding wheat varieties with enhanced resilience to multiple stresses. NAC transcription factors are also a key class of developmental and stress-regulated genes. Some NAC genes can regulate root growth and senescence which may contribute to water saving and nutrient transportation in the plant during drought. Others are involved in the expression of stress inducible protective proteins and of antioxidant enzymes. The capability of NAC TFs to respond to hormonal and environmental signals suggests NAC TFs can contribute to a well-defined system for stress adaptation in wheat (Mao et al., 2022; N. Wang et al., 2024).

In this table, we focus on the plant response to drought and heat stresses which is regulated by the key transcription factor families (Table 4). Members of the DREB family, especially DREB1 and DREB2A, regulate a series of LEA protein-related genes related to Osmo protectant biosynthesis and ROS scavenge. DREB1 is upregulated by drought, whereas DREB2A is induced by heat as well as by drought. This NAC family, which involves NAM and ATAF members, modulates processes like senescence, root development, and antioxidant defense, is induced in response to both stresses, and one of the most important traits related with tolerance is the "stay-green". Heat shock factors (HSF) family including HSFA2 and HSFB is a key regulator of HSPs and chaperones and is a central player of heat stress response, but it also crosstalk's with drought signaling. The WRKY family members WRKY40 and WRKY53 are associated with ABA signaling and biotic stress-related gene expression and modulation of oxidative stress, playing a role for plants under stress to bring about a balance between defense and growth. Finally, the bZIP family members ABF3 and ABF4 also regulate the ABA-responsive genes that are important for stomatal closure, which is critical for drought adaptation, with their activity being modified by heat shock. In general, these TFs form a synergistic regulation network to contribute to plant adaptation to multiple abiotic stresses.

Heat shock factors (HSFs) have a specific function in the heat stress response by regulating the expression of heat shock protein (HSP) genes. These HSPs are involved in the stabilization and refolding of unfolded and misfolded proteins, especially in the chloroplast and cytosol. HSFs can also be implicated in response to drought by cross-regulating genes common to both heat and water-deficit stress pathways (Fujimoto et al., 2023). Likewise, the WRKYs, which were initially considered to function in plant defense, have been more recently appreciated to also be involved in abiotic stress tolerance. They modulate the expression of genes that participate in ROS detoxification and stress hormones signaling, and thus mitigate oxidative stress under both heat and drought (Ge et al., 2024). In summary, wheat transcription factors exhibit a certain interaction pattern. They are one component of a vast interconnected program that ties together many signaling pathways. This network orchestrates the expression of protective genes to cope with extreme environmental conditions, contributing to the maintenance of cellular homeostasis, photosynthetic capability, and reduced yield loss in wheat. The regulatory power and diversity of function of the transcription factor in molecular breeding and genetic engineering aimed at enhancing climate tolerance in wheat are attractive.

QTL Mapping for Combined Heat and Drought Stress

Drought and heat stress are among the main abiotic constraints limiting cereal production

Table 4: Major transcription factor families in wheat regulating drought and heat stress responses, their representative members, downstream target genes, and associated stress-responsive functions.

Transcription Factor Family	Key Members	Target Genes	Response to Stress	Reference
DREB	DREB1, DREB2A	LEA proteins, osmoprotectant biosynthesis, ROS detoxification	Strong induction by drought; DREB2A also responsive to heat	(Yu et al., 2022)
NAC	NAM, ATAF1/2	Senescence, root development, antioxidant defense	Activated by both drought and heat; regulates "stay-green"	(Xiong et al., 2025)
HSF	HSFA2, HSFB	Heat Shock Proteins (HSPs), chaperones	Master regulators of heat response; crosstalk with drought pathways	(D. Wang et al., 2024)
WRKY	WRKY40, WRKY53	ABA signaling, PR genes, oxidative stress mitigation	Induced by both stresses; role in balancing defense and growth	(Cheng et al., 2021)
bZIP	ABF3, ABF4	ABA-responsive genes, stomatal closure	Central to ABA-mediated drought response; modulated by heat	(Sato et al., 2024)

worldwide and impact wheat (Triticum aestivum) production, particularly during reproductive growth stages like flowering and grain filling. Such stresses combined produce what is known as an overlapping effect, the effect of which is worse than the sum of the individual stresses. The events of wheat in response to this complex network of stresses are highly complex and including a physiological, biochemical and molecular (Farhad et al., 2023; Manjunath et al., 2024). This complexity stems, in part, from the polygenic control of ST, where many small-effect genes modulate traits such as the ability to regulate canopy temperature, to maintain chlorophyll and to produce sufficient grain number. Especially, it is possible to increase resistance of plants to such processes through conventional breeding, but little is known about genetic basis of these complex traits. QTL (Quantitative Trait Loci) mapping and analysis is a strategic genetic tool to dissect the genetic control of complex traits, and to identify genomic regions which control traits response to stress. These QTLs could be used for QTL specific breeding for biotic stresses and further to employ MAS to improve resistance in relevant cultivars of wheat (Mapari & Mehandi, 2024). Under field conditions, it is common that drought and heat coexist, especially in arid and semi-arid areas, so it is necessary to investigate their interactive effects rather than separately. Wheat plants display specific physiological and metabolic changes in response to the combined stress, reflected in inhibition of photosynthetic activity, modification of hormone signaling, and oxidative damage. Therefore, QTLs detected under concomitant drought and heat stress are more biologically relevant and potentially more applicable in breeding program of practical utility than the QTLs detected under individual stress conditions (Oukaddour et al., 2023; Raj & Nadarajah, 2022). Several QTLs related with traits such as CTD, stay-green duration, Fv/Fm, TKW, and spikelet fertility, under dual stress, have been also reported through research. These QTLs are distributed throughout different chromosomes among 1B, 2A, 3B, 4A, 5A, and 7D and many are co-localizes with genes that are coding for stress-related proteins, transcription factors, and osmoprotection, detoxification enzymes (Soriano et al., 2021).

The (table 5) represents major meta-QTLs (MQTLs) on drought and heat stress tolerance in wheat and their target genes. MQTL-2A. 1, on chromosome 2A (4.2–6.8 cM) related to canopy temperature depression and spike fertility. Target genes on this carrier include TaDREB3, a drought-responsive transcription factor and HSP90, a heat shock protein which sustains cellular proteins during stress. MQTL-3B. 2 (32.1–35.5 cM) on 3B is associated with stay-green and chlorophyll content (SPAD), as well as photosystem II efficiency (Fv/Fm). Target genes in this regard are PsbA, encoding the D1 protein of photosystem II repair, and Lhcb1, one of the subunits of the light-harvesting chlorophyll-binding complex. MQTL-5A. 1 on chromosome 5A (18.7–21.3 cM) which is associated with grain yield and thousand kernel weight (TKW) and has candidate genes including SnRK2, an ABA signaling kinase and a LEA1, a Late embryogenesis abundant protein which protects cells during insult18. MQTL-7D. 1 on 7D (11.5–14.0 cM) governs WUE and root biomass. Its candidate genes are NAC7, a stress-induced transcription factor, and PIP2;1, an aquaporin involved in water transport. Finally, MQTL-1B. 1 on chromosome 1B (55.0–58.2 cM) are concomitantly linked to heat susceptibility index and Rubisco activity. The target genes are Rca (Rubisco activase) that is responsible for maintaining Rubisco active during stress and sHSP (small heat shock protein), a protein stabilizer of enzymes and membranes. Collectively, these MQTLs offer potential QTL targets for marker-assisted breeding for enhanced wheat tolerance to a combination of drought and heat stresses.

In order to map these QTLs more accurately, geneticists often utilize genetically diverse populations, e.g., recombinant inbred lines (RILs), doubled haploid (DH) lines, and multi-parent advanced generation inter-cross (MAGIC) populations (Sinha et al., 2022). Such populations are tested in controlled conditions as well as stress-hit field environments for ensuring uniform and identifiable phenotypic data. Next, high-density systems for genotyping (e.g., SNP arrays and genotyping-by-sequencing: GBS) are utilized for the estimation of molecular polymorphism. Statistical

Table 5: Meta-QTLs identified in wheat associated with drought and heat stress tolerance, their chromosomal positions, associated physiological and agronomic traits, and candidate genes linked to stress adaptation mechanisms (Ismail & Nadarajah, 2024)

Meta-QTL	Chromosome	Confidence Interval (cM)	Associated Traits	Target Genes / Function
MQTL-2A.1	2A	4.2 – 6.8	Canopy temperature, spike fertility	*TaDREB3* (drought-responsive TF), *HSP90* (heat shock protein)
MQTL-3B.2	3B	32.1 – 35.5	Stay-green, chlorophyll content (SPAD), Fv/Fm	*PsbA* (D1 protein in PSII), *Lhcb1* (light-harvesting complex)
MQTL-5A.1	5A	18.7 – 21.3	Grain yield, thousand kernel weight (TKW)	*SnRK2* (ABA signaling kinase), *LEA1* (stress-protective protein)
MQTL-7D.1	7D	11.5 – 14.0	Water use efficiency, root biomass	*NAC7* (stress-responsive TF), *PIP2;1* (aquaporin for water transport)
MQTL-1B.1	1B	55.0 – 58.2	Heat susceptibility index, Rubisco activity	*Rca* (Rubisco activase), *sHSP* (small heat shock protein)

methodologies such as composite interval mapping, multiple interval mapping, or genome-wide association studies (GWAS) are used to detect loci that are linked to those stress-adaptive traits. The success of QTL mapping studies for this trait depends on several parameters and the magnitude and uniformity of QTL effect over different environments and growing seasons is critical for successful QTL detection (S. Kumar et al., 2023; Mallikarjuna et al., 2022). Advances in phenotyping technology have significantly enhanced the precision of QTL detection. Current phenotyping instrumentation utilizes methods such as infrared thermal imaging to measure canopy temperature, hyperspectral cameras to measure pigment content, and chlorophyll fluorescence sensors to measure photosynthetic performance. These tools make it possible to collect high-resolution large-scale data and thus improve the accuracy of QTL determination (Acuña-Galindo et al., 2015; Langridge & Reynolds, 2021). Further, small QTLs with consistent expression across a wide range of environments that could not be detected using conventional methodologies can now be found and used in breeding. The minor QTLs may act in an additive manner in that their combined performance is likely to add up and collectively make better plants capable of tolerating the stress condition (Ren et al., 2021). In sum, mapping QTLs under dual d/severe drought and heat is essential to achieving a more complete understanding of the genetic basis of d and h adaptation in wheat. Discovered QTLs for stress-response may allow breeders to make genetic selections and to combine favorable alleles by MAS or genomic selection strategies (Kamara et al., 2021; Manjunath et al., 2024). This method not only enhances genetic gain but accelerates the breeding cycle of climate-resilient wheat ideotypes. With the further increase in the frequency of combined stress events with the risk of climate change, the QTL mapping is more and more necessary to sustain wheat productivity and global food security (Yadav et al., 2022).

Genomic Tools and Resources

Wheat, one of the most important staple crops cultivated globally, is particularly sensitive to climate change, in particular to water and heat stress. These stresses are particularly detrimental at reproductive and grain filling stages of growth and can result in severe yield reductions. The decrease in soil moisture during drought greatly decreases water uptake by root systems of plants at cellular and tissue levels, reducing directly cellular turgor pressure and hence cell expansion and elongation. This results in an impaired vegetative growth and lower leaf area, and thus a reduction of the plants photosynthetic capacity (Alsamadany et al., 2023). Moreover, drought stress induced the stomatal closure to increase water use efficiency, thus, reducing CO2 uptake and photosynthesis as well. Consequently, energy is depleted and oxidative stress develops as a result of build-up of reactive oxygen species (ROS) in the plants (Chowdhary & Songachan, 2025). Prolonged drought can also accelerate leaf senescence, shorten the grain filling period, and lead to incomplete seed development, drastically reducing both yield and grain quality (Fábián et al., 2011). Heat stress, on the other hand, interferes with numerous physiological and biochemical processes in wheat. Elevated temperatures disrupt the stability and functionality of cellular proteins and enzymes, particularly those involved in photosynthesis and respiration (Chaffai et al., 2024). Key enzymes like Rubisco become less efficient, and the photosynthetic apparatus is damaged, especially the photosystem II complex (Sperdouli et al., 2023). Heat also increases membrane fluidity, resulting in leakage of cellular contents and loss of ion balance. Additionally, reproductive processes such as pollen viability, fertilization, and embryo development are highly sensitive to temperature extremes. Heat stress during anthesis and grain filling accelerates senescence, shortens the grain development phase, and causes shriveled or chalky grains, thereby diminishing grain weight, protein content, and overall market value (Soriano et al., 2021).

One of the foundational genomic tools used against abiotic stresses is high-throughput genotyping, which includes SNP arrays and genotyping-by-sequencing (GBS) (De Ronne et al., 2023). These technologies permit screening at thousands of genomic loci at the same time and for allelic diversity that is associated with drought-or heat-tolerance. Through the use of Genome-Wide Association Studies (GWAS), the genetic markers can be correlated to phenotypic traits such as canopy temperature depression, root architecture, relative water content, chlorophyll stability and membrane thermostability (Abou-Elwafa & Shehzad, 2021). As a result of these studies QTLs for traits including stay-green, early vigor, deep rooting, and delayed senescence that contribute to stress resilience have been identified in wheat (Acuña-Galindo et al., 2015). At the same time, Whole Genome Sequencing (WGS) and the existence of the annotated wheat reference genome have greatly increased the resolution at which stress-responsive genes can be studied. WGS enables discovery of new gene variants, structural rearrangements and promoter polymorphisms regulating gene expression during drought and heat stress (Khan et al., 2024). Furthermore, comparative genomics based on wild wheat relatives, such as Triticum dicoccoides, Aegilops tauschii, and Triticum urartu, offers access to alleles not present in current wheat varieties. These wild relatives usually have an intrinsic tolerance to environmental extremes and their genome sequences facilitate researchers to detect novel stress-resistance genes which can be transferred into elite germplasm through pre-breeding programmes (Tekin et al., 2022).

Great progress in analyzing the molecular stress response has been achieved using transcriptomics, especially RNA-sequencing (RNA-seq). Genome-wide analysis shows that thousands of genes are dynamically expressed in response to drought and heat. Enabling the detection of genes for hormonal signaling (e.g., abscisic acid, ethylene) and osmoprotectant biosynthesis, antioxidant defence, heat shock proteins, as well as aquaporins and transcription factors, such as DREB, HSF, NAC and WRKY (Wen et al., 2023; Yang et al., 2025). These studies not only help identify candidate genes for further functional validation but also reveal co-expression networks clusters of genes that are coordinately regulated during stress. This information is crucial for selecting multiple target genes that work synergistically to improve tolerance. Genomic Selection (GS) is a second revolutionary approach that is ideally adapted to increasing quantitative complex traits such as drought and heat tolerance. Unlike traditional marker-assisted selection, GS uses genome-wide markers to predict the performance of individuals based on their genetic makeup(Abou-Elwafa & Shehzad, 2021). It enables breeders to select superior genotypes even before phenotypic data is available, saving time and cost. GS models are trained using historical genotype and phenotype data, and then applied to predict the genomic estimated breeding values (GEBVs) of new breeding lines. GS has shown success in improving traits such as grain yield under water-limited conditions, biomass production, grain-filling duration, and kernel weight under heat stress (Langridge & Reynolds, 2021). Additionally, MAS continues to be efficient for the introgression of known major-effect genes for tolerance of stress. For example, makers/scanners which are associated with genes such as Dreb1, HSP17, Rht haplotypes are employed for selection of drought and heat tolerant traits among breeding populations (Singh et al., 2022). MAS is especially valuable for pyramiding multiple desirable alleles as well as in backcross programs for introgression of traits from donor lines. Using phenotypic selection and/or GS, MAS adds to the accuracy and increases the rate of selection response, particularly in the early generations (Serikbay et al., 2024; Sunilkumar et al., 2023). The (table 6) gives brief overview of the genomic tools for Improvement against Drought and Heat Stress in wheat plant.

Gene Regulations and Epigenetics

Gene regulation forms a core part of such wheat response and adaptation to drought and heat. Wheat plants come under stress from poor environmental conditions they induce a series of genetic programmes which allow them to survive and reduce damage. These molecules are regulated at the transcriptional, post-transcriptional, and translational levels. Transcription factors such as DREB (Dehydration-Responsive Element-Binding), NAC (NAM, ATAF1 /2, and CUC2), WRKY, bZIP and MYB families are key regulators of the stress-inducible genes (Ge et al., 2024; Mao et al., 2022). These transcription factors bind to the promoter of related target genes and induce downstream osmotic adjustment, stomatal regulation, antioxidant and cellular protective pathways. Fine control of these genes means turning on stress responses only when necessary and adjusting them to level of the stress and its duration. Under drought circumstances, certain genes are over expressed to regulate water homeostasis and protect cell structures. For example, genes for producing osmoprotectants like proline, glycine betaine, and sugars are switched on to help cells hold on to water and keep their proteins in order. Similarly, expression of heat shock proteins (HSPs) is induced by heat stress, and serves as molecular chaperones to prevent protein denaturation and aggregation. Transcription factors like HSFs (Heat Shock Factors) directly regulate the expression of HSP genes in response to rising temperatures (Fujimoto et al., 2023; Singh et al., 2022). Many of these regulatory genes are considered master regulators because they control multiple downstream genes in large stress-responsive networks. Functional studies have demonstrated that overexpression or silencing of key transcription factors can significantly alter wheat's tolerance to drought and heat, making them powerful targets for genetic improvement.

In addition to conventional gene regulation, epigenetic mechanisms provide an additional layer of control over gene expression in response to environmental stress. Epigenetics refers to heritable changes in gene function that do not involve changes in

Table 6: Overview of Genomic Tools for Improving Drought and Heat Tolerance in Wheat

Tool / Approach	Primary Function	Application in Wheat Stress Breeding	Key Outcome
GWAS	Identify marker–trait associations	Discover alleles for CTD, root depth, senescence	Catalog of candidate genes and markers for MAS
RNA-Seq	Profile transcriptome-wide gene expression	Identify stress-responsive genes (HSPs, TF, antioxidants)	Co-expression networks; novel gene discovery
Whole Genome Sequencing (WGS)	Discover all variants in a genome	Characterize structural variation in wild relatives & landraces	Source of novel alleles for pre-breeding
Genomic Selection (GS)	Predict breeding value using genome-wide markers	Select for complex yield-under-stress traits	Accelerated breeding cycles; higher genetic gain
CRISPR/Cas9	Targeted gene editing	Validate gene function (e.g., Rca, HSF); create novel alleles	Development of non-GMO edited lines with enhanced resilience

the DNA sequence. These include DNA methylation, histone modifications, and small non-coding RNAs such as microRNAs and siRNAs (Abdulraheem et al., 2024; Vaschetto, 2024). During drought or heat stress, specific epigenetic marks are added or removed from chromatin, altering the accessibility of genes to transcriptional machinery. For example, stress-responsive genes may be demethylated or associated with active histone marks (like H3K4me3) to facilitate their rapid activation under stress. Conversely, genes that are not needed may be repressed through increased methylation or histone deacetylation (Y. Liu et al., 2022). DNA methylation plays a particularly important role in stress memory, where wheat plants exposed to stress "remember" the experience and respond more effectively upon future exposures. This effect, referred to as stress priming, is believed to be mediated by enduring epigenetic adaptations that outlast the withdrawal of the stress. Studies In ad wheat, drought or heat stress have been reported to cause genome-wide alterations in DNA methylation patterns that may be inherited into the next generation (Vaschetto, 2024). This transgenerational epigenetic inheritance has significant implications for plant breeding, as it provides new avenues to create wheat varieties with increased resilience without genetically altering the plant.

Small RNAs like microRNAs (miRNAs) also participate in controlling gene expression in response to drought and heat stress in wheat. They function by degradation of target mRNAs or by blocking their translation, and thus fine tune the level of stress proteins. A number of miRNAs have also been reported in wheat that is responsible for genes related to root development, hormone signaling and antioxidative responses to the stress condition (Mishra et al., 2023). For instance, miR398 targets superoxide dismutase genes, a critical enzyme responsible for ROS detoxification, whereas miR159 and miR164 control the activity of transcription factors that are involved in ABA signaling and stress response70–72. Identification of the roles of these small RNAs could provide breeders and molecular biologists with new regulatory elements to improve crops (Li et al., 2022). Gene regulation and epigenetics are important for wheat's perception, response and recovery from drought and heat stress. Such mechanisms function together in a concerted manner to rapidly and efficiently activate protective genes, and at the same time save energy by inhibiting unneeded pathways. Advancements in genomic technologies, such as RNA sequencing, methylome, and chromatin immunoprecipitation, have significantly expanded our knowledge of these complex machineries (Abdulraheem et al., 2024; Haider et al., 2021). The (table 7) describes the key Epigenetic changes in Wheat plants due to heat and drought stress.

Integration of Multi-Omics Approaches

The combination of multi-omics technologies has emerged as a most powerful strategy in deciphering complex biological responses in crops like wheat, particularly under abiotic stresses viz., drought and heat. Conventional genomics contributes to the understanding of DNA sequence and genetic variation, which can effectively control the environmental challenges of plants, but cannot account for the manner in which plants dynamically respond to environmental challenges (Roychowdhury et al., 2023). Multi-omics solutions that integrate different levels of biological information genomics, transcriptomics, proteomics, metabolomics and phenomics provide an overall perspective on how plants sense, respond to and adapt to stress. This knowledge aids in pinpointing the most crucial points and molecular markers, the knowledge which can be useful in establishing new climate-resilient wheat cultivars (Ijaz et al., 2024). Proteomics, the analysis of proteins and their post-translational modifications on a global scale, is instrumental for detection of changes occurring at the protein level as a consequence of stress. Proteins are the working molecules that transmit the genetic information and convey the cell reactivity to the environmental stresses. Wheat plants change their protein expression patterns to trigger stress-responsive signaling under drought or heat stress (Xiong et al., 2024). For instance, proteins that participate in antioxidant defenses, osmotic adjustment, heat shock response, and signaling are frequently upregulated under stress conditions. Comparing proteomes of wheat genotypes tolerant and susceptible to stress can facilitate the discovery of the candidate proteins as a biomarker for stress tolerance. Such proteins could perhaps be used as markers for functional validation or selection programs (Halder et al., 2022; Kaya & Corpas, 2025).

Table 7: Epigenetic Changes in Response to Heat and Drought stress in Wheat (Rao et al., 2024; Rodriguez et al., 2023)

Epigenetic Mechanism	Change Under Stress	Target Genes	Functional Outcome
DNA Methylation	Hypomethylation (promoters)	HSP18, LEA3, APX	Activation of stress-responsive genes
DNA Methylation	Hypermethylation (transposons)	Genomic repetitive regions	Genome stability; suppression of transposable elements
Histone H3 Acetylation (H3K9ac)	Increase	DREB2A, HSFA2	Enhanced transcription and stress memory
Histone H3 Trimethylation (H3K27me3)	Decrease	Flowering repressors (e.g., VRN2)	Accelerated flowering to escape stress
miRNA Regulation	Differential expression (e.g., miR398 ↓)	CSD1 (Cu/Zn-SOD), MYB TFs	Post-transcriptional control of ROS scavenging and development

Metabolomics, a third key omics discipline, specializes on small molecules, the metabolites, which are generated as end-points of the cellular activity. These particular metabolites represent the physiological condition of the plant and they are modified under stress. Wheat accumulates several compatible solutes, including proline, sugars, polyamines, and organic acids, in response to drought and heat stresses to maintain cellular homeostasis. Metabolomics profiling provides potential stress specific metabolic signatures and pathways that are important for acclimatization (Danzi et al., 2023; Yadav et al., 2022). The combination of metabolomics with transcriptomic and proteomic approaches provides insights into gene expression and enzyme activities that drive metabolite accumulation, providing a broader picture of the stress response. One benefit of multi-omics integration is the capacity to explore conserved stress-related mechanisms between species. Researchers can mine traits and genes from model plants or wild relatives and introduce these into wheat through cross-species genomic comparisons. For example, stress-resistant characteristics discovered in rice, maize, Arabidopsis, or barley can be assessed in wheat using ortholog analysis and functional genomics. Besides that, the wild relatives of wheat (e.g., Aegilops tauschii and Triticum dicoccoides) harbor useful alleles for drought and heat tolerance which can be discovered through comparative omics studies. This knowledge can be used in pre-breeding and trait introgression platforms aiming the broadening the genetic base of wheat cultivation (Tekin et al., 2022). The application of multi-omics assays is a game changer in the way we study and enhance wheat under stress. The integration of genomics, transcriptomics, proteomics, metabolomics and systems biology is also useful for unravelling the stress tolerance mechanisms (Ashraf et al., 2022). This information not only helps the understanding of basic plant science but also dish out accurate and efficient breeding program. With the impending global climate change impacting on food security, the use of multi-omics approaches will be the cornerstone for the innovative wheat varieties of the next generation in terms of resilience, productivity and sustainability.

Breeding Strategies for Dual Tolerance

Breeding strategies for dual tolerance in wheat involve a combination of trait pyramiding, marker-assisted backcrossing, genomic prediction, and pre-breeding. Each approach contributes uniquely to the development of varieties capable of withstanding both drought and heat stresses (Arachchige et al., 2024).

The (table 9) pins out the effects of drought, heat and their concurrent stresses on wheat physiology and yield. Net photosynthesis was 25.0 μmol CO_2 m^{-2} s^{-1} in control and reduced by 38% in drought, 33% in heat, and 59% in combined, indicating strong suppression of carbon assimilation. Stomatal conductance was reduced from 450 mmol H_2O m^{-2} s^{-1} under control conditions to 180 under drought (−60%), 350 under heat (−22%) and 120 under the combination of stresses (−73%), with a stronger impact of water deficit than heat. The grain filling duration of control plants, 35 days, reduced to 30 (−14%), 28 (−20%) and 22 (−37%) days under drought, heat, and combined stresses, respectively, indicating the stress-induced advancement in crop maturity. These results showed that there were reduced thousand grain weights from the 45 g under control to 38 g under drought (−16%), 36 g under heat (−20%) and 28 g under combined stress (−38%) suggesting the disruption of grain development. Final grain yield was reduced from 6.0 t ha^{-1} in control treatment to 4.3 t ha^{-1} in drought treatment (−28%), 4.1 t ha^{-1} in heat treatment (−32%) and 3.2 t ha^{-1} in combined stress (−47%). Other yield data in separate studies also substantiate the same losses: 28.1% for drought, 30.6% for heat, and 43.3% for combined stress. This, collectively, indicates that combined drought and heat stress are the most significant with additive and synergistic effects on physiological process and yield.

Molecular breeding together with conventional breeding strategies improves selection power, reduces breeding time and raises genetic gain. With an increasing variability of climate, these approaches will be integral in maintaining food security by providing high-yielding and well-adapted wheat varieties that are stable across a range of future environmental variables. Trait pyramiding Sophisticated targeted breeding efforts aim at combining a number of genes or QTLs responsible for desirable traits in a single genotype. In wheat, this approach is especially relevant for dealing with multiple environmental stresses such as drought and heat, which usually coincide at critical growth stages (flowering and grain filling) (Lamba et al., 2023; Saleem et al., 2024). Each one of these stresses can be

Table 8: Comparative effects of drought, heat, and combined stress on key physiological and yield-related traits in wheat.

Parameter	Control	Drought	Heat	Combined Stress	Reduction (%)	Reference (Example)
Net Photosynthesis (μmol CO_2 m^{-2} s^{-1})	25.0	15.5	16.8	10.2	−38% (D), −33% (H), −59% (C)	(Abdelhakim et al., 2022)
Stomatal Conductance (mmol H_2O m^{-2} s^{-1})	450	180	350	120	−60% (D), −22% (H), −73% (C)	(Pflüger et al., 2024)
Grain Filling Duration (days)	35	30	28	22	−14% (D), −20% (H), −37% (C)	(Ullah et al., 2022)
Thousand Kernel Weight (g)	45	38	36	28	−16% (D), −20% (H), −38% (C)	(Abdelhakim et al., 2021)
Final Grain Yield (t ha^{-1})	6.0	4.3	4.1	3.2	−28% (D), −32% (H), −47% (C)	(Lama et al., 2023)
Grain Yield (t ha^{-1})	5.20	3.74	3.61	2.95	−28.1% (D), −30.6% (H), −43.3% (C)	(Abdelhakim et al., 2021; Naseer et al., 2022)

governed by other genes and combined effect of which can lead to severe yield and grain quality reduction. In pyramiding, the breeders target various genes that control the adaptive characters like deep-root system, improved osmotic adjustment, regulation of stomata, developed photosynthetic rate, and stable grain filling under stress (Saleem et al., 2024). When we stack these genes into a single elite line, varieties of wheat are more likely to perform dependably across various challenging environments. Trait pyramiding is largely dependent on the molecular markers of the QTLs of interest (Acuña-Galindo et al., 2015; Manjunath et al., 2024). These markers also act as genetic tags that allow breeders to follow the presence of stress tolerance alleles in breeding populations and no longer have to rely just on phenotype selection, which can be labor intensive and affected by environmental variability. Marker assisted backcrossing (MABC) and Marker assisted recurrent selection (MARS) are two popular methods for pyramiding. Thus, breeders also have the option of stacking several tolerance traits across successive generations while retaining the high-yielding background of elite cultivars (Halder et al., 2022; Sunilkumar et al., 2023). The strategy is not only 'speed breeding', but also guarantees precise transfer of favorable alleles. In the context of climate change and rise in temperature and water scarcity, trait pyramiding represents strategic importance in the development of high yielding and stable multi-trait stress tolerance wheat cultivars, thus, in a long-term perception, addressing the food security in stress-prone environments.

Marker-assisted backcrossing (MABC) is a strategy that is being used to transfer one or more desired genes or QTLs from a donor parent into the background of an elite well-adapted cultivar. In wheat breeding programmes, MABC has been especially beneficial by introgressing stress tolerance alleles (e.g., for drought, heat, and salinity) from exotic, wild, or landrace gene pools, into modern high yielding, but stress susceptible (Bellundagi et al., 2022; Sunilkumar et al., 2023). One of the main advantages of MABC is that it is a very accurate system: the molecular markers associated to the targeted traits enable the breeder to identify the plants that contain the desired gene as soon as at young growth stages, therefore, avoiding having to wait for visible characteristic expression and the eventual influence of environmental variation. In every backcross generation, markers are employed not only to identify the presence of the target allele (foreground selection), but also to determine the level of recovery of the recurrent parent genome (background selection). Such a two-stage selection regime results in the selected lines being highly similar to the elite parent with respect to the ornamental characteristics (grain quality, plant architecture, and yield potential) but exhibiting the extra stress tolerance derived from the donor parent (Song et al., 2023). Introduction of unwanted donor traits can at the same time be more successful than if only conventional backcrossing is used, which may otherwise take several generations to perform as efficiently, due to the reduction in linkage drag by MABC. This approach becomes even more effective in resources limited countries like Bangladesh, developing new climate resilient wheat cultivars with fewer major genes or QTLs to be introgressed into the genetic background of locally adaptable cultivars of wheat than traditional breeding strategy to meet the challenges of for diverse agro-ecological condition (Bellundagi et al., 2022)

Genomic prediction is a powerful genetic tool that makes use of genome-wide molecular marker information to predict the genetic potential, or breeding value, of individual plants for complex traits. In wheat breeding, this approach is especially useful to increase dual resistance to heat and drought as two major abiotic stresses that often co-occur and are generally polygenic. Those characters are highly affected by gene–environment interactions, making traditional selection less efficient and slower(Abou-Elwafa & Shehzad, 2021). The concept of genomic prediction is based on fitting statistical models that connect high-density genotypic data to measured phenotypic performance. After being trained, such models have the ability to predict how well a new genotype is likely to perform in certain conditions, all without the initial field observation. This is particularly useful in the case of breeding for joint stress tolerance because the approach permits breeders to anticipate performance under drought, heat or their combination before carrying out expensive and time-consuming multi-environment experiments. The breeding period is diluted, driving down the cost (Kamara et al., 2021). The accuracy of genome prediction relies on the quality and effective size of both the phenotypic and genotypic data. Models are typically trained using multi-environment trial data from a genetically diverse set of genotypes to capture diverse genetic variation and response to environment (Cooper et al., 2022). Models that include environmental covariates, such as temperature, soil moisture, and radiation, can increase prediction power as they have more predictive for environmental sensitive traits. Moreover, coupling with crop growth simulation models improves the ability to predict performance of genotypes in the future climate. Genomic prediction facilitates early and accurate determination of best breeding lines, enabling more informed decisions for breeders with respect to parent selection, cross combinations, and resource investment(Tadano & Ota, 2025). Finally, this rapid screening enhances the rate of formation of climate-ready wheat genotypes, which preserve both yield and quality amidst fluctuating and harsh environments.

Pre-breeding is a key step towards disentangling the genetic diversity of wild relatives and landraces and introducing novel alleles into elite wheat breeding germplasm. The wild relatives, Aegilops tauschii, Triticum dicoccoides, and several Thinopyrum species

Table 9: Breeding Strategies for Dual Tolerance in Wheat Plant

Breeding Strategy	Methodology	Key Advantages for Dual Tolerance
Trait Pyramiding	Using MAS to combine multiple genes/QTLs for different stress-adaptive traits into a single elite genotype.	Stacks complementary traits (e.g., deep roots + heat-stable enzymes + osmotic adjustment) to create cultivars resilient to concurrent stresses.
Marker-Assisted Backcrossing (MABC)	Backcrossing a donor parent (with a target trait) to an elite cultivar, using markers for foreground (trait) and background (recurrent genome) selection.	Precisely introgresses valuable alleles from wild relatives or landraces into high-yielding backgrounds while minimizing "linkage drag" of unwanted genes.
Genomic Prediction	Using statistical models trained on genotype–phenotype data to predict the performance of new breeding lines.	Overcomes the complexity of polygenic traits; enables selection for performance under combined stress scenarios before costly multi-environment trials.
Pre-Breeding	Crossing elite lines with wild relatives (e.g., *Aegilops tauschii*) to introduce novel genetic diversity into breeding programs.	Accesses "lost" adaptive traits from wild germplasm that evolved under extreme conditions, broadening the genetic base of cultivated wheat.

are natural drought and heat tolerant as they have developed in an adverse environment (Tekin et al., 2022). These adaptive attributes are frequently eliminated in current cultivars by genetic bottlenecks occurring during domestication and breeding. The pre-breeding process usually includes crossing wild relatives with elite lines, followed by the selection and stabilization of the desirable traits by recurrent backcrossing or marker-assisted selection. Although wild germplasm provides opportunities to introgressive favorable genes, it also poses risks such as linkage drag, poor agronomic performance, and incompatibility barriers (Pour-Aboughadareh et al., 2021). New techniques, such as chromosome engineering, genotyping-by-sequencing, and genome editing, support breeders in bypassing these limitations, by accurately discovering, tracking, and moving favorable alleles. Further, combination of pre-breeding with high-tech genomic platforms helps in identification of candidate genes and molecular markers associated with dual stress tolerance. Diversity through this integrated approach contributes to widen genetic basis of cultivated wheat and accelerate their development for climate-smart-varieties (Langridge & Reynolds, 2021). The following table gives insights into different breeding strategies for Dual tolerance in Wheat plant.

Conclusion

Drought and heat stress are two major limitations of wheat productivity in the age of climate change, and the combined effect of the two stresses is usually more serious than the individual one. These stresses interfere with basic physiological functions and photosynthesis is the major focus. In drought, where water supply is limited, leaf water potential decreases, stomata close, limiting the uptake of CO2 and chlorophyll content is reduced; these factors all contribute to directly reduce photosynthesis. Heat damage damages photosynthetic enzyme activities, thylakoid membrane integrity, accelerates leaf senescence, and causes early decline in photosynthetic capacity. And when the two stresses coincide; damage to the photosynthetic system could be additive leading to limited product of assimilates, grain filling impairment, and reduced final yield. These physiological responses emphasize the necessity of producing wheat varieties capable of holding a high photosynthetic effectiveness in such stress conditions.

Developments in genomic tools, providing unparalleled opportunities to tackle these challenges. High-throughput genotyping, genome-wide association studies, whole-genome sequencing, and comparative genomics now facilitate fine mapping of quantitative trait loci (QTLs) and positional cloning of candidate genes associated with drought and heat tolerance. Transcriptomic and co-expression network studies have offered knowledge about the regulation of photosynthesis genes, stress signaling pathways and the rewiring of metabolic networks in unfavorable situations. These molecular resources allow breeders to target specific adaptive traits such as improved stomatal conductance, enhanced antioxidant defense, and heat-stable photosynthetic enzymes that sustain carbon assimilation even in stress environments. Epigenetic mechanisms have emerged as a crucial layer of regulation in stress adaptation, including photosynthetic resilience. DNA methylation, histone modifications, and small RNAs play roles in activating or repressing genes involved in photosynthetic capacity, chloroplast protection, and photoprotective responses. Some of these epigenetic changes persist as stress memory, allowing plants to respond more effectively to repeated stress episodes. Harnessing this adaptive memory through breeding and molecular interventions offers an additional pathway for enhancing tolerance in wheat.

The integration of multi-omics approaches has further strengthened the capacity to dissect complex stress responses. Proteomics and metabolomics reveal how stress impacts protein abundance, enzyme activity, and metabolite accumulation in pathways directly linked to photosynthesis, such as carbon fixation and photorespiration. Systems biology and network modeling integrate these datasets to identify central regulators that coordinate multiple adaptive mechanisms, including chlorophyll biosynthesis, energy balance, and osmotic adjustment. Cross-species genomic studies provide valuable alleles from wild relatives and model crops, which often possess photosynthetic traits adapted to extreme environments. Breeding strategies for dual tolerance, including trait pyramiding, marker-assisted backcrossing, genomic prediction, and pre-breeding, have proven effective in combining photosynthetic resilience with other adaptive traits. Trait pyramiding allows stacking of genes for heat-stable RuBisCO activase, drought-induced osmolyte accumulation, and efficient stomatal regulation. Marker-assisted backcrossing accelerates the transfer of these traits from donor germplasm into elite backgrounds while maintaining yield potential and grain quality. Genomic prediction models, trained on multi-environment data, can forecast photosynthetic performance under combined stresses, guiding early selection of superior genotypes. Pre-breeding with wild relatives introduces novel photosynthetic traits, such as more efficient light capture or enhanced thermal stability of photosystems, into cultivated wheat.

The rapid advancement of computational tools adds a predictive and decision-making advantage to wheat improvement. Machine learning, environmental modeling, and crop simulation platforms integrate genetic, physiological, and climatic data to forecast how candidate lines will perform under projected drought and heat scenarios. Such tools can simulate the maintenance of photosynthetic efficiency under varying stress intensities, helping breeders prioritize crosses and selection strategies. In summary, the combined effects of drought and heat stress on photosynthesis underscore the importance of developing wheat cultivars that can sustain carbon assimilation and energy production under adverse conditions. Achieving this goal requires the seamless integration of genomics, epigenetics, multi-omics, and advanced breeding strategies into a unified framework. The ability to identify, stack, and stabilize traits for photosynthetic resilience will be central to ensuring yield stability in the face of increasing climatic variability. Long-term success will depend on continued investment in germplasm diversification, high-resolution phenotyping, molecular breeding infrastructure, and breeder training. By bridging fundamental research with practical breeding applications, it is possible to deliver climate-resilient wheat cultivars capable of securing food production in a warming, water-limited world.

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