Physio-Morphological Mechanisms for Adapting Crops to a Warming World and Breeding for Heat and Drought Tolerance

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Abstract

Climate change has heightened the frequency of drought and heat stress, presenting significant risks to global agriculture and food security. These abiotic stresses impair plant water relations, nutrient uptake, photosynthesis and reproductive development leading to yield instability across major crops. This review synthesizes recent advances in understanding morphological, physiological and molecular mechanisms underpinning tolerance to these stresses. Morphological traits such as leaf rolling, wax deposition, canopy adjustments, root architecture and hydraulic regulation contribute to maintaining water-use efficiency and thermal stability. Physiological mechanisms, including photosystem II protection, non-photochemical quenching, osmotic adjustment, antioxidant defense and Rubisco activase activity safeguard carbon assimilation under stress. At the molecular level, CRISPR/Cas-mediated editing of regulatory genes (e.g., ARGOS8, OsPYL9, TaDREB2) coupled with genomic selection and speed breeding has accelerated the development of stress-resilient varieties. Case studies in maize, rice, wheat and sorghum highlight progress in delivering climate-smart cultivars, including genome-edited rice (DRR Dhan 100, Pusa DST Rice 1) and advanced CIMMYT wheat lines with improved canopy temperature depression. Complementary innovations including digital agriculture, UAV-based high-throughput phenotyping, machine learning for stress prediction and microbiome-based biostimulants further strengthen resilience strategies. Despite these advances, research gaps remain in multi-stress field testing, exploitation of landraces & wild relatives and long-term socio-economic impact assessments. Future agricultural resilience will depend on integrating molecular breeding, digital decision-support tools and sustainable management practices. Such multidisciplinary approaches can secure global food systems by fostering crops capable of thriving under increasingly hot and water-limited environments.

Keywords: Climate change, Drought stress, Heat stress, Morpho-physiological traits, CRISPR/Cas genome editing, UAV-based monitoring, Food security

Significance | This review highlights integrated morphological, physiological, and molecular strategies to develop climate-smart crops resilient to drought and heat stress

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1. Introduction

Droughts create heavy negative effects on global agricultural systems. Global warming together with more severe droughts establishes conditions that pose severe challenges to agricultural systems operating effectively. Different plant physiological

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processes including photosynthesis, respiration, and water efficiency play essential roles in sustaining crop yields while such processes strongly react to elevated temperatures. The limited water supply caused by droughts adversely affects plant growth and yield potential since it reduces the necessary water amounts needed for both plant development and maximum production potential. The current climate alterations threaten our worldwide food supply systems. The continuation of sustainable crop production becomes nearly improbable unless farmers immediately put necessary adaptation measures into action (Change, 2007; Lobell et al., 2011). Climate specialists from the Intergovernmental Panel on Climate Change expect that the number of extreme droughts and their frequency will increase across agricultural areas due to global temperature elevation (Masson-Delmotte et al., 2021). Crop food security requires detailed knowledge of plant biological pathways and shape modification responses to rising temperatures alongside drought conditions. The acquisition of this knowledge will enhance agricultural outputs throughout the climatic warming process. Exploring crop responses to intense drought situations and elevated heat conditions became the focus for scientific researchers. The present breeding efforts aim to increase the productivity of crops while generating heat-resistant varieties that will function effectively with shifting conditions (Araus et al., 2002; Reynolds et al., 2018).

Crop yield experiences maximum impact from climate change effects. Rising climate change at an abrupt rate creates both heat strain and water shortage that limits important biological processes including photosynthesis as well as flowering and grain filling (Bita & Gerats, 2013). Crop yield loss affects growth and development by combining factors of drought stress with water intake and nutrient use as well as overall plant growth during developmental phases (Duque et al., 2013). The combination of these multiple stresses can result in greater adverse effects on agriculture productivity in regions where they tend to occur concurrently. There is also a need for new crop types that can sustain these environmental shifts, as traditional crops cannot endure harsher climatic conditions (Zandalinas et al., 2020).

Recent advances in precision biosciences provide powerful frameworks to dissect and manage complex plant responses to drought and heat stress. High-throughput genomics, transcriptomics, proteomics, and metabolomics now enable the identification of key regulators and metabolic signatures underlying tolerance mechanisms with unprecedented resolution (Satrio et al., 2024). Integration of omics data with phenotyping platforms such as UAV-based imaging, thermal sensors, and 3D canopy modeling has opened new avenues to precisely quantify morpho-physiological traits in dynamic field environments (Francesconi et al., 2021; Liang et al., 2025). These approaches overcome the limitations of conventional screening and allow the real-time detection of stress signatures, accelerating the discovery of resilience genes and traits for targeted improvement.

The convergence of computational biology, artificial intelligence, and molecular breeding has further transformed climate resilience research from descriptive to predictive science. Machine learning models can analyze complex multi-omics datasets and phenotyping records to predict plant performance under diverse climate scenarios (Wu et al., 2024), while CRISPR/Cas-based genome editing and genomic selection translate these predictions into rapid trait improvement (Li et al., 2023). Similarly, microbiome engineering, nanobiotechnology, and biostimulant applications represent precision interventions that fine-tune crop stress responses without compromising yield (Franzoni et al., 2022; Lau et al., 2022; Nawaz et al., 2023). Framing heat and drought tolerance within the lens of precision biosciences therefore not only enhances mechanistic understanding but also bridges fundamental discoveries with scalable solutions for sustainable agriculture under climate change.

The purpose of this review is to understand the physio-morphological systems employed by crops to adapt to a combination of heat and drought stress while looking at breeding methods to enhance crop resilience. It will be useful in understanding how a sustainable food supply can be attained in a drought and heat-stricken earth. Knowing these mechanisms and applying breeding methods will enable researchers to develop more drought and heat-resilient crop types. The study will address some physiological impacts such as stomatal response, protective antioxidant synthesizing systems, and some root and leaf structures as well as the morphology of the plant. Finally, the emphasis will be on both traditional and modern breeding methods and their roles in producing climate-resilient crops.

2. Impact of Heat and Drought Stress on Crops

2.1 Heat Stress

Growth and development of crops can be greatly affected by heat stress which emerges as a problem after a certain limit of temperature is exceeded. Primary functions such as respiration, photosynthesis, and even nutrient uptake can become restricted with an increase in temperature. At high temperatures, photosynthetic rates tend to drop which is as a result of low enzymatic activity and high levels of photorespiration which affects productivity and biomass accumulation negatively (Wani & Kumar, 2020). Additionally, heat stress can affect the process of pollination and flowering to reduce the grain harvest quality and set (Zinn et al., 2010). High temperatures during the flowering stage, for example, can induce sterility of spikelets in cereals which has a significant impact on yield.

Heat stress has also to be considered for its direct effects on plants as elevating temperatures tend to increase the thermosensitive

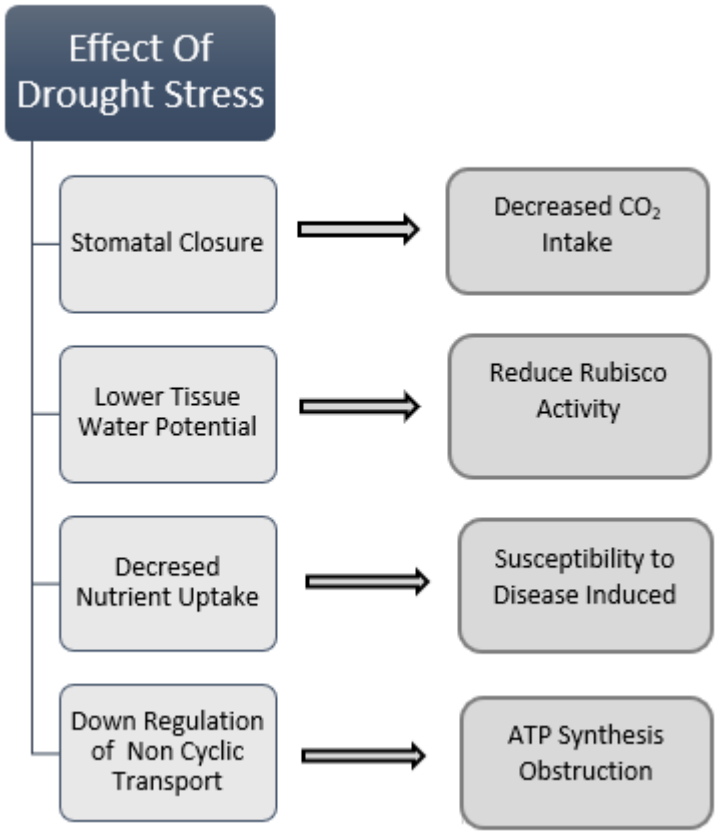

Figure 1. Effect of Drought Stress

period to induce faster development at the cost of vegetative growth and longevity. This impacts the food and economic value of the product due to excessive inadequate seed maturity and low yield (Hall, 2018). In addition, higher temperatures mean greater plant water stress that can escalate the impacts of already existing limited water supply (Shahzad et al., 2021).

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2.2 Drought Stress

The reduction of available water under drought stress affects plant water relations as well as nutrient absorption and growth performance and fundamental physiological functions. Drought decreases cell turgor making growth and expansion impossible (Pinheiro & Chaves, 2011). Plants respond to dry conditions through stomatal closure in order to preserve water. Plants that cut off carbon dioxide intake through stomata closure reduce both photosynthetic rates and carbon assimilation. Researchers (Aranda et al., 2012) explain that minimal biomass development and yield reduction occur because of this phenomenon.

The plant receives limited nutrient absorption and transportation when water availability is restricted. Plants require adequate water to transport potassium phosphorus and nitrogen thus severe water deficiency affects their availability therefore plant health becomes compromised (Blum, 2017).The cellular components face potential damage from oxidative stress that results from drought stress (Pérez-Llorca & Munné-Bosch, 2021).

Recent studies have increasingly focused on dissecting the roles of negative regulator transcription factors and microRNAs that suppress stress-responsive pathways to engineer enhanced drought resilience. For example, CRISPR/Cas9-mediated editing of *OsWRKY12* in rice has relieved its repression of ABA signaling and secondary cell wall biosynthesis, substantially improving drought tolerance (Chavhan et al., 2025). Likewise, targeting *GmPRR3b* in soybean de-represses ABA-responsive transcription factor *GmABF3*, bolstering drought response. In maize, mutation of the *ZmGA20ox3* gene has been shown to reduce anthesis-silking interval (ASI) under water deficit, significantly mitigating yield penalties in field conditions. These insights underscore a precision strategy: by identifying and tampering with negative regulators (so-called “S-genes”), scientists can fine-tune stress signaling, preserve

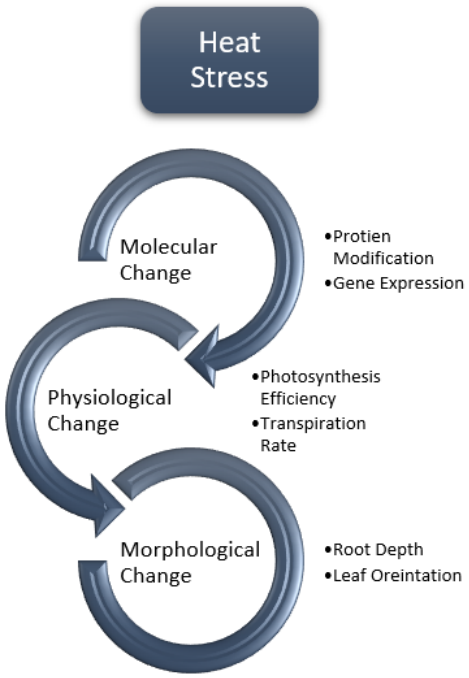

Figure 2. Adaptation of Heat Stress

growth and yield, and create tailored drought-tolerant cultivars (Khan et al., 2025).

Parallel to molecular approaches, recent agronomic and biotechnological innovations are proving effective in mitigating drought impacts. Notably, biochar soil amendments have consistently enhanced water retention, nutrient homeostasis and antioxidant enzyme activity across staples like maize, rice, and wheat, thereby improving photosynthetic capacity and drought resilience (Ma et al., 2024a). Additionally, editing ABA-receptor genes such as *OsPYL9* via CRISPR/Cas9 has been demonstrated to enhance both drought tolerance and yield in rice, by improving stress protein regulation and adjusting circadian rhythms (TopicsAgricultureResearchIndia, 2025).

2.3 Combined Stress Effects

Multiple factors of drought stress and heat exposure tend to stress crops to an extent beyond what each event would cause individually. Plants need to sustain tissue cooling while managing water loss which causes their metabolic functions to deteriorate substantially under hot temperature conditions with limited water supply (Fahad et al., 2017). Both stressors create worse transpirational water loss conditions and decrease carbon fixation capacity which leads to diminished growth and photosynthesis rates (Redden et al., 2014).

Plants divert their life forces to basic survival needs instead of development and growth processes therefore leading to earlier plant aging. The combined occurrence of drought and heat stress in wheat plants destroys grain filling capacity and speeds up leaf decay thus resulting in lower crop yields (Fábián et al., 2019). These conditions threaten both food safety and require urgent adoption measures because they exist across regions where agriculture occurs water resources are limited and temperatures are rising.

Recent metabolomic studies reveal that the plant response to combined heat and drought stress involves a substantial reprogramming of primary metabolism, including transient yet pronounced increases in soluble sugars (such as glucose, fructose, and raffinose), as well as key amino acids like proline, histidine, valine, and leucine—much more so than under single stresses (X. Xu et al., 2023). These compounds contribute both osmotic protection and antioxidant buffering under stress. Moreover, the balance of saturated versus unsaturated fatty acids shifts—saturated fatty acids increase, potentially reinforcing membrane rigidity, while unsaturated counterparts decline or remain stable, indicating a role in preserving membrane integrity under the dual stress of dehydration and heat (Dwivedi, 2023; Y. Xu & Fu, 2022). At the molecular signaling level, cross-talk in combined stresses is emerging: stress-specific transcription factors (e.g. *WRKY48* under heat plus light stress) exhibit unique roles not seen under single stresses (Zandalinas et al., 2024). In cool-season legumes, molecular regulators including *DREB2A*, reactive oxygen species signaling, calcium, and osmoprotectant-related genes coordinate to mediate tolerance against concurrent thermal and moisture deficits (Priya et al., 2025). Such findings illustrate that combined stress invokes distinct and complex metabolic and genetic responses that go beyond additive effects, demanding integrative study approaches.

3. Physio-Morphological Mechanisms for Heat and Drought Tolerance Morphological Adaptations

Leaf Morphology

Organic change in leaf structure protects crops from negative drought and heat stress outcomes. The sun exposure reduction achieved by leaf rolling helps avoid drought damage since this leaf movement minimizes water loss through transpiration (Gao et al., 2025). Of complements the leaf surfaces' waxy cuticle layer which blocks water loss while protecting the plant from heat stress shown in Figure 2. When functioning as a physical barrier the waxiness of the object reflects both heat and light which preserves water (Bi, 2016).

Beyond surface-level adaptations, plants frequently undertake deeper anatomical reconfiguration under drought and heat to sustain hydraulic efficiency. For instance, in cotton, drought stress reduces leaf hydraulic conductance (K_{leaf}) by decreasing xylem vessel diameter, vessel density, and aquaporin expression—but is counteracted by raised major vein length per area (VLA_{major}) and reduced overall leaf area, helping limit water loss while retaining photosynthetic capacity (X. Li et al., 2025). These modifications illustrate that, in addition to physical barriers like wax, plants balance hydraulic network design to mitigate the dual stresses of heat and dry conditions through more efficient water distribution.

Moreover, leaf angle modulation and surface hairs (trichomes) are emerging as vital components of multifaceted resistance strategies. Recent ecological syntheses emphasize leaf angle's underrated role in regulating light interception, thermal load, and water-use efficiency, showing that dynamic adjustment of leaf orientation can reduce leaf temperature and improve carbon-water-energy trade-offs in high-radiation environments (Yavas et al., 2023). Parallelly, dense trichome layers—especially when combined with thick, reflective wax coatings—help scatter and reflect incoming solar radiation, reducing heat load and conserving moisture ("Ecophysiology," 2025).

3.1 Root Architecture

A plant requires adaptable root structures to endure drought stress. Under dry conditions of topsoil layers deep-rooted crops continue water absorption through access to deeper soil moisture reserves (Comas et al., 2013). The length and denser roots of crops under drought conditions enhance their soil resource acquisition ability by improving their capacity to extract water and essential nutrients from expansive soil areas (Lynch, 2013).

While leaf morphology provides the first defensive layer against drought and heat, shoot and root coordination is increasingly recognized as critical for whole-plant resilience. Recent work shows that plants exhibiting reduced aboveground growth—through smaller, thicker leaves with high wax deposition—often reallocate more assimilates toward root growth, enhancing soil water capture under stress (W. Li et al., 2023). This adaptive balance between transpiration demand and water acquisition capacity helps maintain hydraulic stability. In crops like wheat and maize, the integration of leaf rolling, stomatal regulation, and deeper rooting patterns has been linked to improved yield stability under combined heat and drought stress (KAUR, 2021). Thus, morpho-physiological adaptation is not confined to leaves alone but represents a systemic adjustment, where shoot moderation complements root exploration.

3.2 Reduced Leaf Area and Canopy Structure Adjustments

Low water consumption and heat stress prevention are possible through two adaptions involving reduced leaf area and modified canopy formation. The transpiration rate of smaller leaf areas becomes reduced during drought conditions as described by (Peguero-Pina et al., 2020). A structural alteration of plant canopies that causes leaves to grow vertically will both decrease light exposure and boost heat tolerance while improving water efficiency (Richards et al., 2002).

Recent advances in phenotyping and modeling highlight that canopy structural plasticity is a decisive trait for drought–heat resilience. Vertical leaf orientation (erectophile canopies) reduces self-shading while improving light penetration to lower leaves, thereby enhancing whole-canopy photosynthesis under water-limited conditions (Digrado et al., 2023a). Furthermore, modern wheat and sorghum breeding programs are actively selecting for genotypes with narrower leaves, higher leaf angle distribution, and optimized canopy temperature depression, which collectively delay premature senescence under stress (Digrado et al., 2023b; Liaqat et al., 2024). Integration of UAV-based imaging and thermal sensors has accelerated the identification of such canopy traits at field scale, demonstrating that reduced leaf area and erect canopies not only conserve water but also sustain photosynthetic efficiency and yield in increasingly hotter and drier climates (Bhardwaj et al., 2024a).

4. Physiological Mechanisms

4.1 Photosynthesis Efficiency

The survival of growing crops that produce harvests depends on maintaining constant photosynthetic activity under all stress conditions. Some plant species have built stress protection systems to keep photosynthetic rates constant thus ensuring plant development. Specific crops possess abundant enzymes of Rubisco activase for conducting photosynthesis under hot conditions. Plants face higher productivity because their effectiveness allows them to carry on carbon fixation processes when experiencing heat and drought stress (Farooq et al., 2018).

(Turc et al., 2024) findings emphasize that dynamic regulation of photosystem II (PSII) and non-photochemical quenching (NPQ) are central to sustaining photosynthetic efficiency under concurrent drought and heat stress. Crops with enhanced capacity to dissipate excess excitation energy through NPQ avoid photo-

oxidative damage and preserve electron transport. Advances in chlorophyll fluorescence imaging have also enabled the identification of genotypes that maintain higher PSII quantum yield (Fv/Fm) under stress, directly correlating with improved biomass and grain yield stability (Ali et al., 2023). Moreover, the integration of C_4 engineering and synthetic photorespiration bypass pathways into C_3 crops is emerging as a promising frontier, with recent trials by (G. Chen et al., 2024) demonstrating up to 17% increases in photosynthetic efficiency under water-deficit and high-temperature field conditions.

Stomatal Regulation

Proper manipulation of the stomatal aperture balances water conservation against photosynthetic CO_2 intake. When experiencing drought conditions plants have stomata regulation mechanisms that prevent water loss but these defense mechanisms simultaneously limit their ability to absorb carbon dioxide and so negatively affect photosynthesis (Romero Munar, 2019). Stressful conditions enable specific crop species to regulate their stomatal aperture for maintaining photosynthetic functions and water retention (Duque et al., 2013).

4.2 Heat Shock Proteins (HSPs)

Heat shock proteins serve as essential factors for cell protection and repair under conditions of elevated temperatures. Green plants create HSPs as a heat stress defense system to safeguard cellular parts and mend damaged proteins according to (Wani & Kumar, 2020). The cellular function known as molecular chaperoning enables HSPs to steady cell membranes and proteins and halt protein aggregation which allows cells to survive and restore themselves after heat exposure (Mtwisha et al., 2024).

Different families of HSPs, such as HSP70, HSP90, HSP60, and small HSPs (sHSPs), work in coordination to protect vital metabolic functions during stress (Chen et al., 2006). For instance, sHSPs accumulate rapidly in leaves and reproductive tissues, safeguarding photosystem II, Rubisco activase and enzymes of energy metabolism (Ray & Dalal, 2025) while larger HSPs participate in protein refolding and signaling cascades that regulate stress tolerance (Kumar et al., 2024). In addition to their protective role, HSPs also influence hormonal balance and antioxidant activity, thereby linking cellular defense with broader stress response pathways (Lubkowska et al., 2023). These multifaceted functions make HSPs key targets in breeding programs aimed at enhancing plant thermotolerance under climate change scenarios.

4.3 Osmotic Adjustment

Plants use osmotic adjustment to build solutes like proline and glycine betaine and carbohydrates so they can preserve cellular turgor under water scarcity. Through osmotic adjustment cell water retention becomes possible which actively maintains both cell structure and functionality (Sanders & Arndt, 2012). The process of osmotic adjustment protects important proteins and enzymes that assist photosynthesis and metabolism during stress periods while it also enhances cell expansion and growth (Zivcak et al., 2016).

Beyond simple solute accumulation osmotic adjustment represents a coordinated strategy involving compatible solutes, ion transporters and vacuolar compartmentalization (Joshi et al., 2022). Organic osmolytes such as proline, sugars and polyols not only help retain water but also act as antioxidants (Sachdev et al., 2023) stabilizing membranes and scavenging reactive oxygen species during stress (Anjum et al., 2023). Similarly, inorganic ions like potassium and calcium are redistributed to balance osmotic pressure and regulate stomatal function. Together, these mechanisms allow plants to sustain cell division, maintain metabolic activity and delay senescence under prolonged heat and drought conditions.

4.4 Antioxidant Defense Systems

Plants develop oxidative stress when heat stress combined with drought conditions elevates reactive oxygen species (ROS) levels. Plants counteract these unwanted reactions using antioxidant defense mechanisms that combine enzymatic activities to both deactivate ROS and protect cellular structures with peroxidase, catalase, and superoxide dismutase (Hasanuzzaman et al., 2012). The antioxidant defense mechanisms help people tolerate heat and drought because they enable both metabolic system maintenance and structural cell protection during stressful conditions (Sewelam et al., 2016).

In addition to enzymatic antioxidants plants rely on non enzymatic compounds such as ascorbate, glutathione, carotenoids and flavonoids (Mishra et al., 2023) which provide rapid detoxification of ROS and stabilize cellular membranes (Rudenko et al., 2023). This dual system of enzymatic and non enzymatic antioxidants maintains redox homeostasis preserves chloroplast and mitochondrial function additionally protects nucleic acids and proteins from oxidative damage. Enhanced antioxidant activity also contributes to delayed leaf senescence and improved reproductive success under combined stresses which are making it a critical mechanism for sustaining yield in hot and water limited environments (Carillo, 2025).

5. Strategies for breeding plants to acquire resistance to heat and drought conditions

5.1 Conventional Breeding Approaches

Selection for Drought- and Heat-Tolerant Varieties

Conventional heat and drought tolerance breeding starts with selecting those plants that display natural resistance within severe conditions. This strategy for improving tolerance has successfully utilized characteristics such as blooming time and canopy temperature and yield stability per (Jha et al., 2014). Breeders enhance crop performance under adverse conditions through

generations of selection which leads them to choose heat-tolerant and drought-tolerant cultivars (Simova-Stoilova et al., 2016).

Phenotyping and Screening of Traits Like Root Depth and Transpiration Efficiency

Traditional breeding needs accurate measurement of crop characteristics which boost tolerance against heat and drought conditions. Plants that demonstrate efficient transpiration together with appropriate root characteristics can effectively use water reserves at lower soil depths (Comas et al., 2013). The exploration of genotypes with enhanced water-use efficiency and heat tolerance potential occurs through breeding program screening according to (Bakala et al., 2024).

Molecular and Genomic Breeding

Breeders can accomplish targeted genomic regions by utilizing molecular breeding that features genetic markers connected to heat and drought tolerance. QTL mapping has discovered genome areas that drive osmotic adjustment together with stomatal control and root architectural attributes (Tuberosa et al., 2019). The creation of advanced-tolerance cultivars becomes faster because breeders select the identified QTLs.

Genome-wide association Studies (GWAS) for Identifying Resilience Genes

The identification of genes associated with complex stress tolerance features is best accomplished through GWAS. This genetic approach finds marker associations linked to tolerance characteristics through whole-genome comparison of numerous crop plants which identifies resistance genes (Huang & Han, 2014). Enhanced identification of stress tolerance genes and regulatory mechanisms linked to stress tolerance arises from GWAS discoveries which breeding strategies can focus on for practical applications (Afzal et al., 2023).

Biotechnological Advances

The genetic modification enables direct insertion of genes containing abiotic stress resistance enhancement. Research has shown that plant drought tolerance improves when scientists successfully integrate genes responsible for osmoprotectant production including proline, glycine betaine, and trehalose (Masood et al., 2016). The introduction of antioxidant-producing genes allows plants to manage oxidative stress during heat and drought conditions (Bhalani et al., 2019).

Gene Editing (e.g., CRISPR/Cas9 for Targeted Trait Enhancement)

The traits of tolerance can be enhanced through precise genetic modifications performed by CRISPR/Cas9 and other gene editing techniques. Different from traditional genetic alterations CRISPR/Cas9 enables targeting of native genes that express features involving stress-responsive proteins root development and stomatal regulation according to (Zhang et al., 2019). Genetic manipulation of the genes that control stomatal closure enables crop plants to conserve water more efficiently and better survive heat along with drought conditions (Lawson & Blatt, 2014).

Role of Polygenic Traits: Managing Multi-Trait Breeding for Complex Stress Resistance

Complex adaptations to heat and drought conditions involve multiple genes thereby making them polygenic characteristics. Tolerance manifests from multiple genes instead of one resulting gene so breeding this feature demands management of multiple traits in tandem (Ashraf, 2010). Many stress tolerance characteristics such as root structure and osmotic adjustment along with photosynthetic efficiency can be specified through genomic selection together with marker-assisted selection (Varshney et al., 2018). Crop breeding programs should implement polygenic features as a sustainable solution for developing heat-tolerant plants in a warming climate to raise crop resilience in all environmental conditions.

6. Integrative Approaches for Resilient Crop Development

6.1 Combining Physio-Morphological Traits with Genomic Tools

Genomic tools enable better comprehension of heat and drought tolerance in crops when used in conjunction with physio-morphological evaluations. According to (Ye & Fan, 2021), the method brings together modern genomic approaches such as genomic selection and marker-assisted breeding with basic phenotypic assessment of traits like root depth, leaf area, and transpiration efficiency measurement.

Connecting particular phenotypic traits to genetic markers helps breeders identify important qualities that enhance their breeding program effectiveness (Varshney et al., 2018). Under drought conditions scientists can identify drought-resistant genotypes that have excellent water consumption efficiency and deep rooting capabilities through the analysis of genomic and phenotypic root data (Comas et al., 2013).

6.2 Systems Biology and Modeling

Systems biology procedures help scientists estimate future crop performance in changing climates through digital simulations of these reactions to environmental stressors (Cobb et al., 2013). A system of interconnected plant-environment relations becomes visible through research models that unite information derived from molecular and physiological and ecological analysis levels. (Hajihashemi et al., 2018) state that these models enable scientists to evaluate genotype-level responses to stressors while uncovering which physiological responses provide stress tolerance. Systems biology helps researchers establish the best combinations of traits to improve resilience when breeding under forecasted climatic conditions (Marsh et al., 2021).

6.3 Climate-Smart Agriculture Practices

The methods that boost climate resilience and simultaneously boost sustainability alongside food security make up the framework of

climate-smart agriculture (CSA). The Climate-Smart Agriculture program supports crop rotation and intercropping together with conservation tillage through adaptive management techniques because these practices maintain healthy soil and increase water content (Lipper et al., 2017). Crop variety resilience for farming systems can be boosted through the integration of conventional and genomic breeding innovations into these management systems according to (Rodrigues et al., 2021). When performing crop planning during unpredictable weather conditions farm owners can plant either drought-resistant cultivar along with conventional crops which provides protection against failure (Anser et al.). CSA employs local insight and team-based methodology to let farmers participate in product selection and method choice processes which create optimal solutions for their particular agricultural conditions (Gardezi et al., 2022).

6.4 Integration of Digital Agriculture and AI-Based Decision Support

The adoption of digital agriculture tools—such as remote sensing, UAVs, IoT-based soil moisture sensors, and AI-driven crop models—has transformed drought and heat stress monitoring. Machine learning algorithms now predict stress onset, optimize irrigation scheduling, and support genotype selection for resilience under variable climates. These technologies enable site-specific management, minimizing water use while maximizing yield stability, and are increasingly integrated into breeding pipelines for rapid phenotyping and trait prediction (Al-Najadi et al., 2025; Parra-López et al., 2025).

6.5 Harnessing Microbiome and Biostimulant Innovations

Beneficial soil microbes, including arbuscular mycorrhizal fungi and plant growth–promoting rhizobacteria (PGPR), play vital roles in enhancing crop tolerance to heat and drought through improved nutrient acquisition, root hydraulic conductance, and activation of antioxidant pathways (Chukwudi et al., 2025). Alongside microbial inoculants, biostimulants such as seaweed extracts, protein hydrolysates, and nanopriming agents are being deployed as eco-friendly strategies to strengthen stress tolerance (Rai et al., 2021). These approaches represent scalable, low-input solutions that complement genetic improvement and adaptive management practices for climate-smart farming.

7. Case Studies and Examples

7.1 Precision Breeding for Drought Tolerance

Maize (Zea mays)

The worldwide cultivation of maize now receives extensive breeding efforts to enhance its tolerance against heat and drought conditions. At present the implementation of drought-tolerant maize varieties created through traditional breeding and marker-assisted selection has delivered marked enhancements to drought tolerance under such conditions. The Drought-Tolerant Maize for Africa (DTMA) initiative brought forward cultivars capable of producing 30% more yield in drought-prone areas (Lobell & Lee, 2024). The cultivars demonstrate wide-climate adaptability due to their improved root depth and more efficient water management and management requirements.

Following these advances, recent integration of genomic selection, doubled haploids, and speed breeding has accelerated the development of elite maize hybrids with superior resilience to heat–drought combinations. For instance, CIMMYT's Stress Tolerant Maize for Africa (STMA) program released multiple hybrids in 2023–2024 that consistently outperformed commercial checks by 15–20% under both managed drought trials and farmer-field conditions (Allendorf et al., 2023). Moreover, CRISPR/Cas9-edited maize lines targeting ARGOS8, a negative regulator of ethylene responses, displayed significantly improved yields (up to 5 bushels per acre) under water-limited environments without yield penalties under optimal conditions (Sami et al., 2021). In parallel, high-throughput UAV-based phenotyping has enabled breeders to identify genotypes with favorable canopy temperature depression and early vigor traits that enhance maize productivity in hot, arid landscapes (Bhardwaj et al., 2024b).

Rice (Oryza sativa)

Breeding of rice as an important crop involved developing versions that exhibit tolerance to heat and drought conditions. Through its work the International Rice Research Institute (IRRI) developed multiple rice lines with tolerance against different environmental conditions. Traditional breeding resulted in the production of Swarna Sub1 through its drought-tolerant breeding work. The ability of this variety to survive underwater submergence enables it to yield better crops in flood-prone regions due to rapid post-flooding recovery (Hori et al., 2021). Breeders enhance crop tolerance through their ability to discover heat-tolerant rice variations with genetic links to enhanced yields in hot conditions (Hori et al., 2021).

In recent years, rice improvement programs have advanced beyond traditional breeding by leveraging genomic selection, CRISPR/Cas editing, and speed breeding to accelerate the development of climate-resilient varieties. For example, the DRR Dhan 100 (Kamala) and Pusa DST Rice 1 varieties, released in 2025 by the Indian Council of Agricultural Research, represent the world's first genome-edited rice lines officially deployed for farmers; they mature faster, consume significantly less water, and exhibit enhanced drought and salinity tolerance while maintaining high yield stability (Bureau, 2025). At the molecular level, manipulation of OsPYL/RCAR ABA receptor genes has improved drought and heat tolerance without reducing grain yield, underscoring the potential of precision editing in safeguarding photosynthesis and reproductive success under stress (Ma et al., 2024b). Additionally, high-throughput phenotyping platforms integrating drone-based

imaging and thermal sensors have enabled IRRI and partner institutes to identify elite rice genotypes with cooler canopies, deeper rooting systems, and efficient transpiration use, traits strongly linked to resilience in combined heat–drought field environments (R. Chen et al., 2024) . Together, these advances demonstrate how integrating molecular breeding, genome editing, and digital phenotyping is rapidly transforming rice into a climate-smart crop adaptable to intensifying abiotic stresses.

Wheat (Triticum aestivum)

Wheat stands as one of the significant crops which undergoes harm from drought and heat stress conditions. The International Maize and Wheat Improvement Centre known as CIMMYT has placed wheat cultivar breeding for drought and heat tolerance at the center of its mission. The main goal behind "Heat-Tolerant Wheat" (HTW) development focused on choosing delayed maturation and a higher harvest index that maintains yield stability in stressful conditions (Reynolds et al., 2018). The "Drought Tolerant Wheat" breed released by CIMMYT in Mexico shows how breeding technology enhances crop survival in dry areas (Tarekegne et al., 2024).

Recent breakthroughs in wheat breeding have combined genomic prediction, speed breeding, and high-throughput phenotyping to accelerate climate-resilient cultivar development. CIMMYT's Heat and Drought Wheat Improvement Consortium (HeDWIC) has released multiple lines that show up to 20% yield advantage under combined stress conditions, with traits including cooler canopy temperature, efficient transpiration, and improved spike fertility (Correia et al., 2022; Reynolds et al., 2021). Cutting-edge molecular research has also identified allelic variants of DREB1 and HSP70 genes that enhance drought and heat tolerance by protecting photosystem stability and improving osmotic adjustment (Kokkanti et al., 2022; Q. Li et al., 2024). Meanwhile, CRISPR/Cas9 editing of *TaERF3* and *TaDREB2* regulators has successfully improved both water-use efficiency and grain yield under heat–drought environments, demonstrating the potential of genome editing in wheat (Hafeez et al., 2024; Osama, 2025). Complementing these genetic advances, UAV-based canopy temperature imaging and spectral indices are now widely applied in international wheat nurseries, expediting the identification of high-performing stress-resilient lines at a global scale.

8. Challenges and Future Directions

The research requires expanded field testing combined with studies exploring various forms of germplasm. Research needs additional extensive field testing of heat and drought-tolerant crop types across different natural environments due to substantial advancements in their development. Multiple studies focus on controlled environments that lack proper representation of actual field performance of their tested crop types. New investigations need to explore both landraces and wild related species germplasm due to their ability to carry unique genes for stress tolerance (Lazaridi et al., 2024). The underused genetic resources will create adapted modern crop varieties.

A critical gap exists in multi-stress evaluations, since most breeding pipelines still assess tolerance to drought and heat separately, even though these stresses often co-occur in the field. Recent reviews emphasize the urgent need for integrated multi-stress phenotyping platforms to capture realistic crop responses under fluctuating environments (Jain & Strahl, 2023). Furthermore, the genetic diversity bottleneck created by modern breeding remains a major limitation; many elite cultivars are derived from narrow genetic pools, making them vulnerable to climate extremes. Unlocking resilience traits from underutilized crops (e.g., millets, teff, quinoa) and wild relatives through pre-breeding and genomic introgression could provide untapped alleles for heat- and drought-resilient agriculture (Arinarayanasamy et al., 2025; Jha et al., 2024; Pathirana & Carimi, 2022).

The adaptation of breeding programs represents one approach to handle unpredictable weather patterns. The unpredictable climate patterns of our present age create considerable hurdles during breeding attempts to develop resilient plants. The change in temperature and rainfall patterns produces different stress conditions alongside heat and drought for crops which impacts their performance. Directing breeding efforts requires that programs integrate climate forecasting models to predict feature performances across potential scenarios so they can select tolerant crop variations (Begna, 2022). The strategy of conceiving flexible traits that adapt to environmental change stands as a vital method of climate-resilient breeding (Cvejić et al., 2022).

The effort to develop heat and drought-resistant cultivars encounters major difficulties because smallholder farmers in developing nations need cultivars that are both accessible and acquirable. Multiple farmers from these regions lack sufficient resources to accept farming improvements that require special inputs and specific management requirements. The successful breeding strategies need to select agricultural features compatible with low-input farming methods which also possess abiotic stress resistance (Baramati et al.). Participatory breeding approaches succeed in boosting variety adoption by adequately designing crops to conform with farmers' distinct constraints and restrictions (Begna, 2022).

Breeding programs should enhance resilience and follow worldwide sustainability goals that consist of climatic resilience, environmental sustainability, and food security. Sustainable breeding demands agricultural varieties that maintain biodiversity together with healthy soils because these elements support enduring agroecosystem resilience (Lipper et al., 2017). The integration of sustainability factors with productivity goals along with resilient

strategies will help provide growing food demand across the world through sustainable resource management.

9. Conclusion

This review discusses how physio-morphological adaptations enable crops to survive against planetary warming pressures and particularly help plants endure heat and drought conditions. These adaptations include modifications of root structures together with better photosynthetic functions altered stomatal response mechanisms and improved cellular protection against harsh environmental stress. Breeding plans focused on these characteristics must exist to manufacture crops that thrive in dry and hot climates. Heat and drought-resistant cultivars can be developed more efficiently through traditional breeding combined with current gene editing and molecular marker and genomic selection methods. Emerging irregular weather trends call for an integration of plant adaptive farming strategies with these physiological adaptations to boost harvest results. Developing climate-resilient crops should be the main priority since temperatures keep increasing worldwide. The future stability of food security depends intensively on these crops since many regions consistently affected by heat waves and droughts stress. The crucial element in this process is to develop extended strategic plans that link innovation to adaptive techniques along with a solid understanding of environmental transformation.

The accelerating impacts of climate change underscore the urgency of developing crops that can withstand the simultaneous pressures of drought and heat stress. This review highlights the significant progress achieved through conventional breeding, molecular approaches, and advanced genomic tools, yet also reveals persistent gaps in field validation, multi-stress evaluations, and the utilization of untapped genetic diversity. Crops such as maize, rice, wheat, and sorghum illustrate how integrative breeding and biotechnology pipelines have already delivered climate-resilient cultivars, but their large-scale deployment remains uneven across regions.

Looking forward, future research must prioritize holistic, systems-level strategies. Integrating genome editing (CRISPR/Cas), speed breeding, and genomic prediction with high-throughput phenotyping and remote sensing will accelerate the identification of resilient genotypes. Moreover, AI-driven decision support systems and digital agriculture tools will enable precise monitoring of stress onset, optimize irrigation management, and guide genotype selection under diverse agroecological conditions. Expanding the use of landraces, crop wild relatives, and underutilized species offers untapped reservoirs of alleles conferring resilience to combined stresses.

Equally important, the incorporation of plant–microbiome interactions, biostimulants, and nanopriming strategies into breeding and crop management provides eco-friendly avenues to enhance tolerance without yield penalties. Scaling these innovations will require collaborative efforts that link molecular research, agronomic practices, and policy frameworks to ensure equitable access for smallholder farmers in stress-prone regions.

Ultimately, the future of climate-smart agriculture depends on multi-disciplinary collaboration that bridges genetics, physiology, ecology, and digital technologies. By combining advanced biotechnological interventions with sustainable agronomic practices, agriculture can transition toward resilient, resource-efficient systems capable of securing global food supplies under rising temperatures and declining water availability.

Author contributions

Asad Ullah, Hammad, Muhammad Anas, Farrukh and Sameer reviewed literature and drafted the manuscript. Mujahid and Bazgha designed figures. Muhammad Haider, Minahil and Mauwiz managed references. Maria Javed contributed in formatting the manuscript. Muhammad Sajad supervised and guided the whole work.

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Competing financial interests

The authors have no conflict of interest.

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