International Journal of Agriculture, Environment and Biotechnology
Citation: *IJAEB*: **19**(03): 153-170, September 2026
DOI: 10.30954/0974-1712.03.2026.6

ASSOCIATION FOR AGRICULTURE ENVIRONMENT AND BIOTECHNOLOGY

REVIEW PAPER

Unraveling the Physiological and Molecular Mechanisms of Heightening Crop Resilience under Climatic Variability Coupled with Drought and Heat Stress

Miriam Githumbi[1*], Masina Sairam[2], Sumit Ray[2], Shaik Rishitha[2], Luciana Chappa[3], Victor Ngaiza[4], Emmanuely Nungula[5], Harun Gitari[1] and Sagar Maitra[2]

[1]Department of Agricultural Science and Technology, School of Agriculture and Environmental Sciences, Kenyatta University, P.O. Box 43844-00100, Nairobi, Kenya
[2]M.S. Swaminathan School of Agriculture, Centurion University of Technology and Management, Paralakhemundi, Odisha, India
[3]Department of Agricultural Sciences, College of Agriculture, Mwalimu Nyerere University of Agriculture and Technology, Butiama, Tanzania
[4]School of Life Sciences and Bio-engineering, Nelson Mandela Institution of Sciences and Technology, Arusha, Tanzania
[5]Department of Environment and Sustainable Development, Mzumbe University, Morogoro, Tanzania

*Corresponding author: miriamgithumbi@gmail.com (**ORCID ID:** 0009-0005-2870-483X)

Paper No. 1248 **Received:** 11-07-2026 **Revised:** 05-08-2026 **Accepted:** 27-08-2026

ABSTRACT

For the last two decades, most parts of the world have experienced frequent rising and severe co-occurrence of droughts and heat stress due to climate variability, posing a serious threat to global crop production and food security. Unlike an isolated stressful environment, which can easily be predicted by the results of a single stress experiment, the coexisting presence of high temperature and water deficit induces multifaceted molecular and physiological reactions that are difficult to forecast with certainty. In crops, essential physiological functions, such as water interactions, photosynthetic functionality, cell preservation, and membrane integrity, are highly interfered with by droughts coupled with heat stress, resulting in senescence and yield loss (Zaman *et al*. 2017). These malfunctions are most closely linked to severe stomatal limitations, photo-pharmacological inhibition of photosystem II (PSII), overaccumulation of reactive oxygen species (ROS), and oxidative destruction of a vast number of cells, leading to the imbalance of metabolism. Generally, plants adapt to concomitant drought and heat stress through interrelated signaling cascades of calcium ions (Ca^{2+}), heat shock factors (HSFs), mitogen-activated protein kinase (MAPK), and cascades of abscisic acid (ABA). The current multi-omics studies are giving strong supporting evidence that the combination of stresses triggers a different transcriptomic, proteomic, and metabolomic response that is qualitatively different than either the drought or heat stress. It is important to note that in experiments involving ABA-deficient mutants, the increased susceptibility to drought and heat is consistently observed, which shows that ABA is a key solution to integrating dehydration and thermal signals due to its interactions with both the ROS signaling and the HSF-controlled transcriptional networks. Parallel to this, molecular chaperones such as HSP70, HSP90, and small heat shock proteins (sHSPs) are differentially regulated to show specialized non-redundant participation in protein destabilization protection in the combined influence of high temperature and cellular dehydration. Recent developments in genome editing methods, especially the CRISPR/Cas-based methods, have now made it feasible to target specific genes that can respond to stress, including PP2C phosphatases in ABA signaling pathways and DREB2A transcription factor, potentially providing new opportunities to improve tolerance to dual stress with minimal yield penalties. In spite of these molecular discoveries, there is still a lack of success in translating these discoveries into field-adapted cultivars because of strong interactions between the genotype and the environment, phenotypic plasticity,

How to cite this article: Githumbi, M., Sairam, M., Ray, S., Rishitha, S., Chappa, L., Ngaiza, V., Nungula, E., Gitari, H. and Maitra, S. (2026). Unraveling the Physiological and Molecular Mechanisms of Heightening Crop Resilience under Climatic Variability Coupled with Drought and Heat Stress. *Int. J. Ag. Env. Biotech.*, **19**(03): 153-170.

Source of Support: None; **Conflict of Interest:** None

and the dynamics of agroecosystems. All these will require that integrative strategies be formulated, entailing the multi-omics analyses with the high-throughput phenotyping, predictive modeling, and translational breeding systems. This review is a review of the current research in the knowledge of physiological and molecular processes of crop resilience to combined drought and heat stress and the necessity to move beyond reductionist paradigms and adopt systems-based approaches that combine molecular biology and agronomy to enable sustainable crop production in the conditions of increasing climatic uncertainty.

HIGHLIGHTS

- Combined heat and drought create a unique and far more severe threat to crops than either stress factor applied in isolation.
- Closing leaf pores conserves critical water during dry periods, but it prevents transpirational cooling and causes crops to dangerously overheat.
- Exposure to simultaneous heat and water stress forces plants to activate a distinct genetic and cellular emergency response.
- Building climate-resilient crops requires using precision gene editing to target key master regulator genes rather than individual stress traits.
- Safeguarding future food production depends on combining resilient crop varieties with smart field practices such as precision irrigation and soil management.

Keywords: Climate change, Crop resilience, Molecular signaling networks, multi-omics integration, Abiotic stress interactions

Climate change is having a fundamental, transformative effect on agricultural systems all over the world as it is increasing the occurrence, intensity, and duration of extreme climatic events, with droughts and heat waves proving to be especially serious limitations on agricultural productivity and global food security (Lobell *et al.* 2011; Seleiman *et al.* 2021; Sagar *et al.* 2023; Prado *et al.* 2025; Maitra *et al.* 2026a). Compared to historical variability in climate, modern climate extremes are becoming more and more aligned in time and space, subjecting crops to complex stress environments, rather than individual stress factors (Sagar *et al.* 2024; Maitra *et al.* 2025; Nungula *et al.* 2025). The combination of drought and heat stress at the most important stages of development is one of the most harmful stress factors in modern cropping systems (Maitra *et al.* 2025). The existing body of empirical data on a wide range of crop species and in different production systems indicates that concomitant drought and heat stress exert disproportionately harmful effects on plant growth and development, yield formation, and product quality that are not accounted for by the effect of either stress factor individually (Bhardwaj *et al.* 2021; Rahimi *et al.* 2022; Li *et al.* 2025). When these compounds are subjected to stress, a decrease in moisture content in the soil is frequently accompanied by high canopy temperatures, which result in the disruption of the phenological development, a decrease in the length of reproductive stages, and a decrease in the ability to partition assimilates during grain filling and storage (Sato *et al.* 2024; Raza *et al.* 2025; Maitra *et al.* 2026b). These limitations directly undermine the performance of photosynthesis by enhancing stomatal limitation, photochemical inefficiency, and a metabolic imbalance, and at the same time increase oxidative stress by overwhelmingly generating reactive oxygen species (ROS) (Sagar *et al.* 2025).

Regardless of the increased understanding of the interactions of stress, most of the existing understanding of the physiology of plant stress has been based on single-stress experiments under controlled conditions (Cheptoek *et al.* 2021; Heydarzadeh *et al.* 2021; Rahimi *et al.* 2022). Although these studies have played a crucial role in the understanding of fundamental signaling pathways and molecular responses, they do not adequately reflect dynamic and heterogeneous landscapes of stress experienced in the field, where stress intensity, duration, and recovery vary with time (Zandalinas *et al.* 2017; Zhang *et al.* 2025). More and more comparative studies indicate that responses to combined drought and heat stress by plants are characterized by distinct physiological adaptations and molecular reprogramming that are qualitatively different from responses to each stress individually (Majeed *et al.* 2023; Seleiman *et al.* 2021; Pardo-Hernandez *et al.* 2024). With this kind

of result, it becomes apparent that the single-stress data cannot be used to predict the crop behavior in a real climate scenario. Both drought and heat stress at the same time at the molecular level bring about complex regulatory relationships between signaling pathways that may not necessarily be synergistic. One of the possible shortcomings that limit activation of cellular thermotolerance mechanisms is the antagonism of heat-responsive pathways by abscisic acid (ABA)-mediated drought responses that induce stomatal closure and avert water loss (ul Haq *et al.* 2019; Heydarzadeh *et al.* 2021; Waadt *et al.* 2022) (Fig. 1). This regulatory interference may lead to inefficient stress acclimation (which stresses the presence of physiological and molecular trade-offs) that restricts resilience in the presence of compound stresses (Githumbi *et al.* 2026). Such weaknesses are also compounded by the fact that traditional domestication of crops and contemporary breeding systems have traditionally focused on breeds that are yield-maximizing and tolerant to single stressors, as opposed to being resistant to interacting stressors (Heydarzadeh *et al.* 2021; Rahimi *et al.* 2022). This has led to the development of numerous current types of elite cultivars with lower adaptive capacity to the more changing and extreme climatic conditions predicted for future agroecosystems (Valliyodan and Nguyen, 2006; Prado *et al.* 2025). It is this inappropriateness of breeding that contradicts the new climate realities, highlighting the urgency of identifying molecular and physiological characteristics that confer robustness to combined stress exposure without undue reduction in yield, which is unacceptable. Recent technological improvements are facilitating a transition to reductionist models by enabling systems-level studies of crop stress resilience. A combination of drought and heat stress responses has been found to share some of the conserved and species-specific regulatory networks, exposing key signaling centers, transcriptional regulators, as well as metabolic routes, which have the adaptive potential (Zhang *et al.* 2025; Rahimi *et al.* 2022; Joshi *et al.* 2024; Duan *et al.* 2026). These molecular understandings are further supplemented by high-throughput technologies of phenotyping that record spatially and temporally resolved plant reactions in controlled and field settings (Seleiman *et al.* 2025).

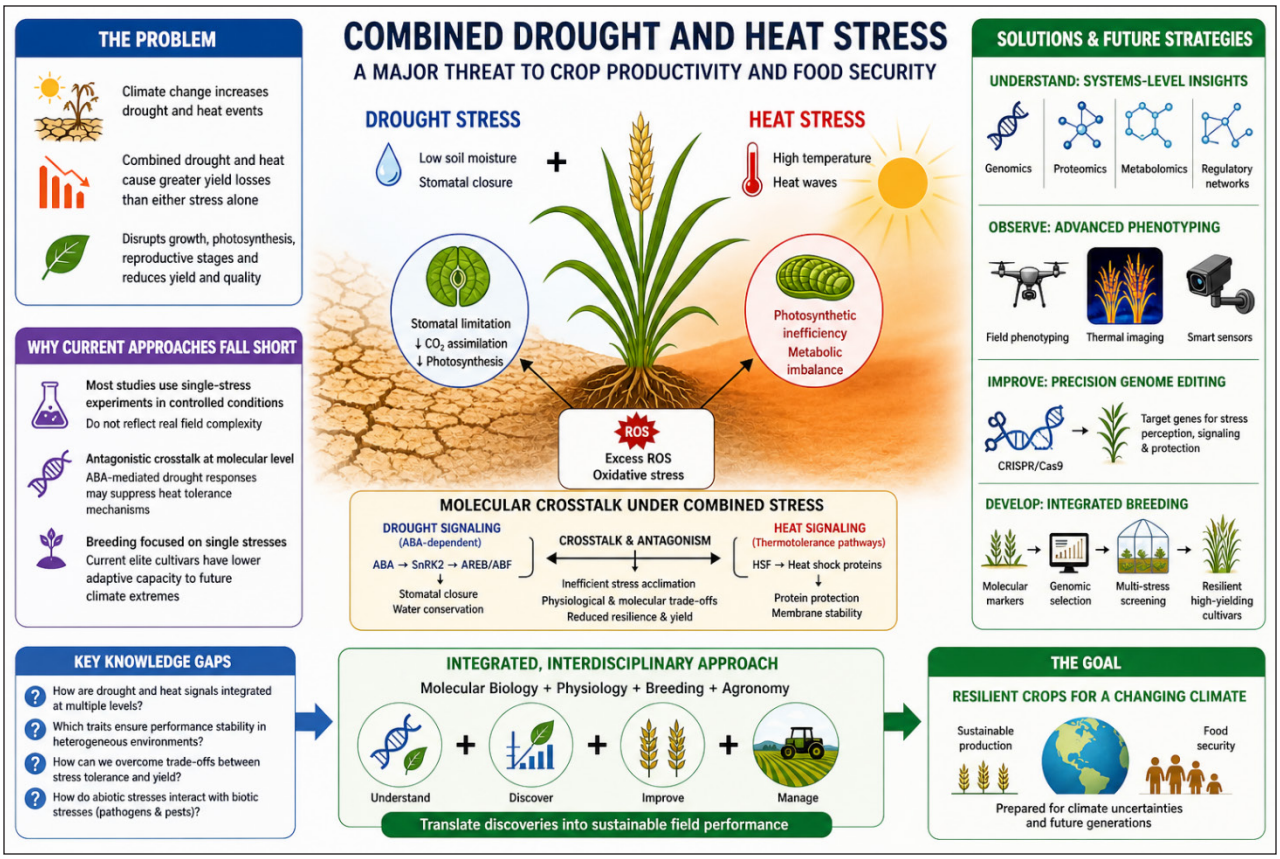


Fig. 1: Conceptual framework of crop responses to combined drought and heat stress and pathways to climate resilience

Simultaneously, the availability of precision genome editing technologies like CRISPR/Cas9 has provided the possibility to precisely target candidate genes that play a role in stress perception, signaling, and protection to provide unprecedented opportunities to increase combined stress tolerance in elite germplasm (Kumar *et al.* 2023; Joshi *et al.* 2023; Maitra *et al.* 2025).

However, there are still significant knowledge gaps on ways in which plants combine drought and heat signals at molecular and cellular scales, whole-plant scales, how the functional traits of performance stability in heterogeneous environments, and how evolution and physiological trade-offs may be avoided via accelerated breeding or genetic engineering (Prado *et al.* 2025; Sato *et al.* 2024). These issues are even exacerbated by increasing evidence that abiotic stress responses overlap with plant immune signaling, and plant vulnerability to pathogens and pests in climate stress conditions (Heydarzadeh *et al.* 2021; Rejeb *et al.* 2014; Maitra *et al.* 2025, 2026c). Much of these types of interactions shows the necessity of interdisciplinary research strategies that consider the concurrent and interacting influences of abiotic and biotic stresses in agroecological settings. We are now no longer free to choose whether to further develop our knowledge about the resilience of crops to high-temperature and concomitant drought conditions, as, in the face of steadily increasing global temperatures and increasingly unpredictable precipitation, such information is now necessary rather than desirable. Oncogenetic approaches, such as the incorporation of molecular biology, physiological, breeding, and agronomic management, will be instrumental towards converting the laboratory findings into sustainable field performance to protect the agricultural production and food security in future climate uncertainties.

Physiological Responses to Combined Drought and Heat Stress

The interactions between crop responses to the concomitant effects of drought and heat stress are highly integrated physiological network systems that act at a number of biological organization levels, including the entire-plant water balance and cellular and subcellular metabolic control. Unlike the case of individual stress scenarios, the relationship between water scarcity and high temperatures is producing non-additive and, in many instances, synergistic disturbances that are not consistently forecastable based on individual-stress response studies. All these stresses are known to limit some of the most crucial physiological functions, such as stomatal control, photosynthetic carbon consumption, membrane integrity, redox homeostasis, and hormonally mediated signaling, all of which have the overall effects of determining crop performance in real-world agricultural settings. Through this, productivity in the combined stressors is the covariance of several traits, and not the optimization of the physiological responses of individuals, which underlines the importance of integrative assessment frameworks (Table 1).

The plant water relations and stomatal behavior are among the first and the most badly influenced physiological processes in response to combined drought and heat stress (Nyawade *et al.* 2020). The drying of soil moisture and the stress on water resources in the atmosphere stimulate stomatal closure within a short time as one of the main mechanisms of excessive water loss, and it is the concentration of abscisic acid (ABA) in the guard cells that acts as the main coordinator of this mechanism (Waadt *et al.* 2022). Although this process is effective in inhibiting dehydration, it also curtails diffusion of the carbon dioxide into the leaf mesophyll, which results in a steep reduction in carbon assimilation in photosynthesis and evaporation cooling (Jamal *et al.* 2022). This loss of transpirational cooling increases the temperature of leaves and enhances thermal stress, which generates a physiological trade-off whereby water conservation becomes an unwanted increase in heat damage (Li *et al.* 2025). The latter contradiction is especially evident when the conditions of a high vapor pressure deficit (VPD) take place, as the transpiration within atmospheric pressure increases faster than the stomatal conductance would under usual conditions. Genotypic variation is decisive in regulating these effects, with the cultivars with higher hydraulic conductance, deeper or more recalcitrant root systems, and higher xylem embolism resistance able to maintain limited transpiration and partial stomatal performance in the extreme conditions of soil drying and remain photosynthetic (Sato *et al.* 2024). During chronic

Table 1: Combined drought and heat stress in crops. Integrated processes, mechanisms, and functional consequences

Physiological domain	Key mechanisms under combined stress	System-level implications	Breeding and management relevance	Key references
Whole-plant water relations	ABA-mediated stomatal closure; altered hydraulic conductance; embolism resistance; VPD amplification; stomatal density plasticity	Reduced water loss but elevated leaf temperature; non-linear trade-offs between cooling and dehydration avoidance	Selection for hydraulic resilience and partial stomatal functionality under stress	Waadt *et al.* 2022; Li *et al.* 2025; Sato *et al.* 2024; Prado *et al.* 2025
Photosynthetic performance	PSII photoinhibition; ROS overproduction; Rubisco repression and oxidation; increased photorespiration	Synergistic decline in carbon assimilation exceeding single-stress effects; yield penalties	Targeting enzyme thermostability and photoprotective capacity	Singh *et al.* 2024; Bhardwaj *et al.* 2021; Zandalinas *et al.* 2017
Chloroplast integrity	Thylakoid destabilization; impaired electron transport	Reduced photochemical efficiency and recovery capacity	Breeding for chloroplast structural resilience	Ul Haq *et al.* 2019
Membrane stability	Lipid peroxidation; fatty acid remodeling; electrolyte leakage	Loss of cellular compartmentalization and signaling efficiency	Enhancing membrane lipid composition and antioxidant systems	Zhang *et al.* 2025
Osmotic adjustment	Accumulation of proline, sugars, and glycine betaine	Cellular hydration, membrane, and protein stabilization	Selection for efficient osmoprotectant pathways	Pardo-Hernández *et al.* 2024
Hormonal cross-talk	ABA dominance; ethylene-induced senescence; reduced auxin and cytokinin signaling	Survival prioritized over growth and yield	Modulating hormonal balance to reduce yield penalties	Sato *et al.* 2024
Trait coordination	Integration of water use, photosynthesis, redox balance, and hormones	Determines field-level resilience under climate extremes	Systems-level breeding and phenotyping approaches	Kumar *et al.* 2023

exposure to compounded stress, the developmental acclimation could also occur, such as the changes in stomatal density and responsiveness, which makes the idea of phenotypic plasticity an important, yet context-specific, factor of stress response (Rezaei-Chiyaneh *et al.* 2023; Prado *et al.* 2025).

The overlapping occurrence of drought and heat stress is also especially perilous to photosynthesis, and photosystem II (PSII) is one of the primary locations of damage. High temperatures and dehydration of the cell cause the unstable oxygen-evolving complex of PSII, which increases photoinhibition and excessive generation of reactive oxygen species (ROS) (Singh *et al.* 2024). These are further enhanced by low CO_2 availability due to stomata closure that elevates the excitation pressure on the photosynthetic electron transport chain, besides redirecting carbon metabolism towards photorespiration. Both transcriptional repression and oxidative alterations of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) at the biochemical level inhibit carbon fixation ability, and photosynthetic recovery is limited even with the removal of stress (Bhardwaj *et al.* 2021). The ultrastructural analyses also reveal that mixed drought and heat interfere with the organization of chloroplast membranes, destabilize the thylakoid structure, and reduce the efficiency of electron transport, which causes long-term declines in photochemical functioning (ul Haq *et al.* 2019). Notably, experimental studies invariably indicate that stress-related inhibition of photosynthesis is synergistic but not additive and that damage is greater than the accumulated damage if a particular stress treatment, be it drought or heat, is applied (Zandalinas *et al.* 2017). The thermal stability of photosynthetic enzymes, antioxidant capacity, and repair mechanisms have a high degree of genotypic variation that should be emphasized because the genes are the targets of breeding programs to increase photosynthetic ability under extreme climatic conditions (Joshi *et al.* 2024).

The other important factor in determining the survival of plants when subjected to combined drought and heat stress is the stability of the cellular membrane. The two stressors enhance oxidative stress, which enhances the lipid peroxidation of polyunsaturated fatty acids in plasma and organelle membranes, resulting in decreased membrane fluidity, leakage of electrolytes, and disruption of electrochemical gradients needed in nutrient transport and signal transmission (Maheswari *et al.* 2025; Zhang *et al.* 2025). These effects are further enhanced by heat stress, which increases the speed of the lipid phase transitions, and dehydration, which increases the concentration of solutes and oxidative damage. Plants also respond to destabilization of membranes by changing the lipid content and especially by altering the proportion of saturated fatty acids to unsaturated fatty acids, which improves thermostability and tolerance to dehydration. Simultaneously, osmotic adjustment is also achieved through the accumulation of compatible solutes that include proline, glycine betaine, and soluble sugars, which reduce the water potential of a cell and preserve turgor (Pardo-Hernandez *et al.* 2024). These compounds have direct interaction with membrane phospholipids, membrane proteins, stabilize macromolecular structures, and are ROS scavengers, in addition to their osmotic role, preserving enzymatic activity and cellular integrity during cell exposure and recovery to stress.

These physiological responses find a multitude of outlets in hormonal cross-talk, where abscisic acid is a key product of drought-heat stress response (Fig. 2). High levels of ABA facilitate stomatal closure and stimulate osmolyte accumulation and antioxidant defense transcriptional programs and molecular chaperones synthesis (Waadt *et al.* 2022). But the ABA-mediated responses are dynamically correlated with other phytohormones, which control growth, development, and senescence. The interaction of drought and heat stress may promote ethylene biosynthesis and signaling, accelerate the senescence and abscission of leaves, and decrease the photosynthetically active canopy, limiting yield potential (Maitra and Ray, 2019; Mwadalu *et al.* 2022). Alterations in the auxin transport and

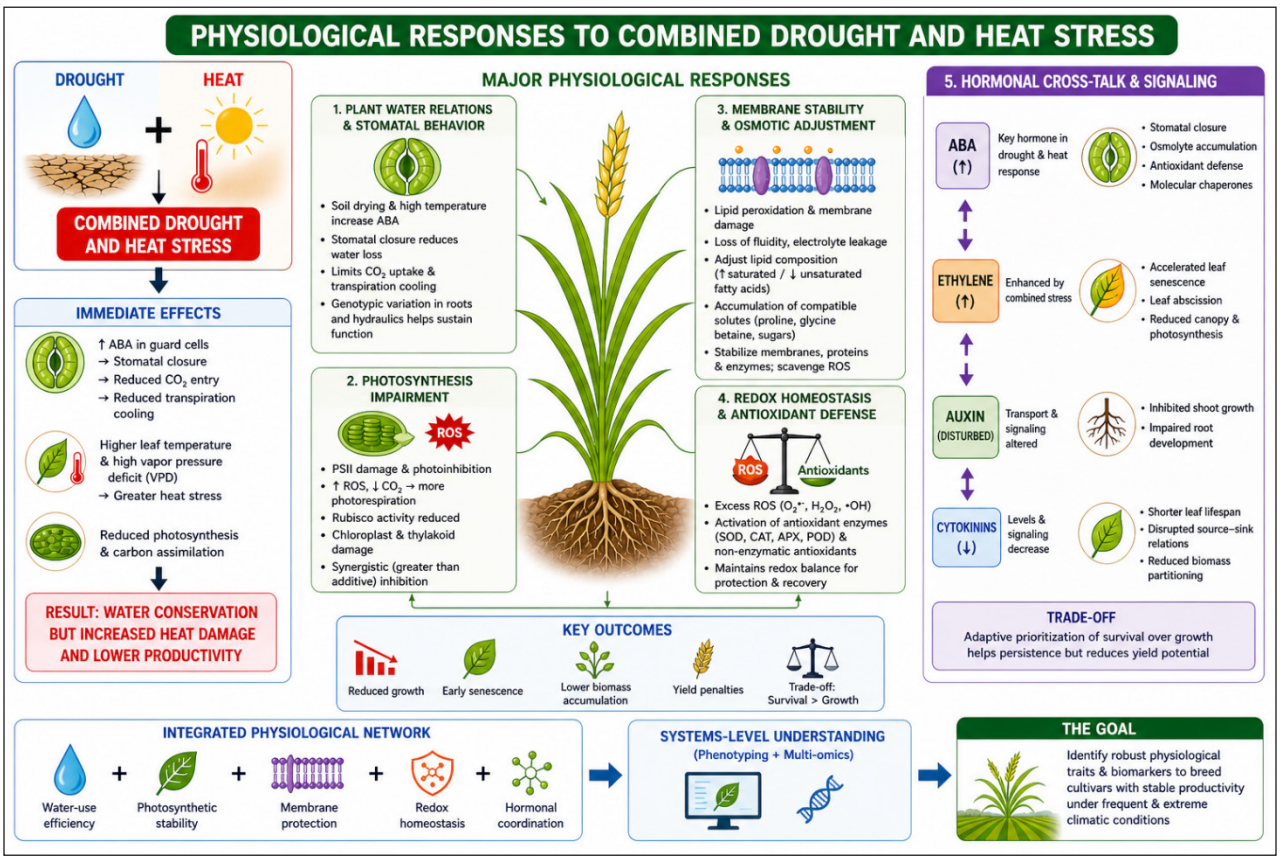


Fig. 2: Physiological mechanisms underlying crop responses to combined drought and heat stress

signaling in the absence of interferon disrupt shoot growth and root development, as well as alleviate cytokinins decrease the leaf life and undermine relationships between sources and sinks needed to accumulate and partition biomass (Sato *et al.* 2024). Such trade-offs, which are determined by hormones, are evidence of an adaptive prioritization of survival over growth, a strategy that is useful to increase persistence in the face of stress, but is a significant burden to agricultural systems that require yield stability.

All these physiological responses indicate that the effects of coexisting drought and heat stress are due to strongly interacting mechanisms of water-use efficiency, photosynthetic stability, membrane protection, redox homeostasis, and hormonal coordination, which cannot be sensibly understood alone. It is now possible to solve these complex interactions on a systems level due to the increasing access to high-throughput phenotyping platforms and multi-omics datasets and to potential robust physiological biomarkers and trait combinations linked to resilience (Kumar *et al.* 2023; Mohapatra *et al.* 2023; Seleiman *et al.* 2025). The future research should thus emphasize integrative methods that will bridge the gap between genetic variation and coordinated physiological characteristics at various scales so that crop cultivars that can sustain productivity under more and more frequent and extreme weather patterns can be developed.

Interactions of Molecular Signaling Networks in Combinations with Stresses

Crop resiliency to drought and heat stress simultaneously is controlled by multilayered and highly coordinated molecular signaling networks linking perception of stress, signal amplification, and adaptive regulation of genes. In contrast to the situations related to a single stressor, simultaneous water shortage and high temperature create incompatible physiological needs, which cause non-additive molecular interactions that require specific regulatory architectures with the ability to prioritize and compensate multiple signals (Fig. 3). These networks cut across several compartments of cells and include dynamic crosstalk of calcium signaling, phytohormonic pathways, redox regulation, molecular chaperone systems, and large-scale

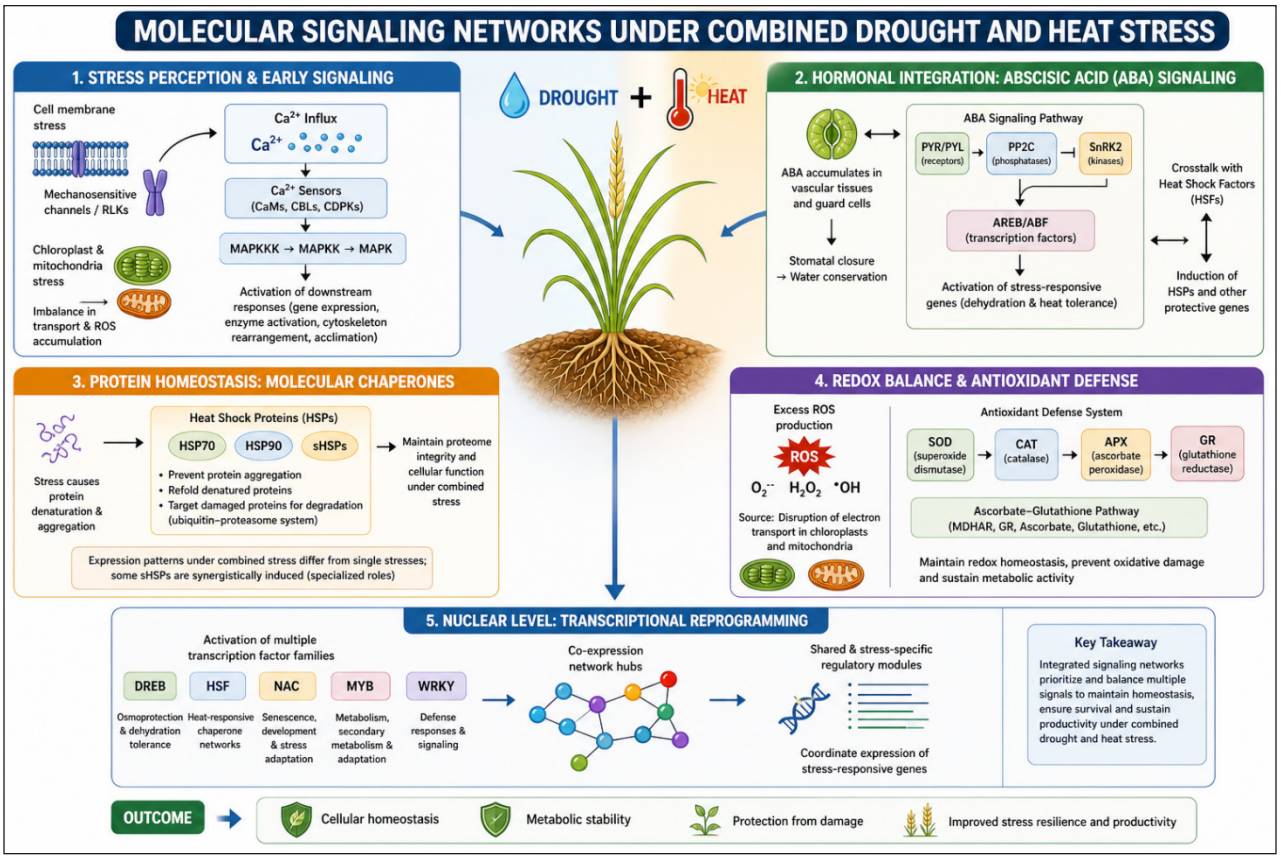


Fig. 3: Integrated molecular signaling networks regulating crop responses to combined drought and heat stress

transcriptional reprogramming. Instead of being linear pathways, these components act as signaling hubs, which are connected, and together they establish cellular homeostasis, metabolic stability, and survival in harsh environmental conditions.

The perception of stress starts at the important cellular interfaces, especially the plasma membrane and organelles that generate energy, like chloroplasts and mitochondria. The alterations in membrane tension and osmotic potential due to dehydration are detected by mechanosensitive ion channels and receptor-like kinases (RLKs), and the chloroplasts are considered the central stress sensors because of the detection of imbalance in photosynthetic electron transport and reactive oxygen species (ROS) accumulation (Zhang *et al.* 2025). These perception events are quickly followed by short-term bursts of transient cytosolic calcium (Ca^{2+}) influxes, which give rise to stress-related temporal and spatial Ca^{2+} signatures. This information on stress duration and intensity is coded in such signatures and interpreted by calcium-binding proteins such as calmodulins (CaMs), calcium-binding-like proteins (CBLs), and calcium-dependent protein kinases (CDPKs). These receptors trigger downstream signaling cascades, including MAPKKs, MAPKKs, and MAPKs, which enhance signals of stress and the regulation of different cellular events, including transcriptional regulation, enzyme activation, cytoskeleton activity, and acclimation responses when combined with drought and heat stress (Rejeb *et al.* 2014).

Protein homeostasis is also one of the most susceptible cellular functions in combined thermal and dehydration stress conditions, and molecular chaperone systems gain critical significance in preserving the integrity of the proteome. Heat shock proteins (HSPs), especially HSP70, HSP90, and small heat shock proteins (sHSPs), inhibit irreversible aggregation of proteins, refolding of stress-denatured polypeptides, and degradation of damaged proteins via the ubiquitin–proteasome system. Interestingly, transcriptomic and proteomic studies indicate that the induction pattern of these chaperones in combined stress conditions is significantly different from the cases in which these stresses are applied separately, i.e., drought stress and heat stress, and this implies that there are disparate regulatory programs that exist. Some sHSPs are only synergistically expressed when acting in a dual stress environment, suggesting they have a specialized role in complex stress tolerance and not generic heat protection (Zandalinas *et al.* 2017). Additional evolutionary evidence is provided by comparative genomic and phylogenetic analysis, which reveals that HSP gene families are highly conserved in the major crops (wheat, rice, and maize) and play a central role in abiotic stress resistance, and have the potential to improve crops (ul Haq *et al.* 2019; Maitra *et al.* 2025).

Abscisic acid (ABA) plays the role of a central integrator of the molecular signaling network that makes drought and heat responses. ABA biosynthesis and transport are caused by drought, which causes it to increase in the vascular tissues and guard cells, where it stimulates stomata closure to minimize the loss of water. In addition to its classical effect on dehydration avoidance, ABA also regulates the heat stress responses by interacting, functionally, with heat shock factor (HSF) networks, and, therefore, with HSPs and other protective genes expression (Pardo-Hernandez *et al.* 2024). Signaling Canonical ABA PYR/PYL receptors, clade A PP2C phosphatases, and SnRK2 kinases result in the activation of AREB/ABF transcription factors, which bind ABA-binding elements in promoters of stress-response genes. The abacus's role in integrating ABA-driven responses to both dehydration and heat is also justified by the fact that ABA mutants lack tolerance to dehydration and thermotolerance, which is also a major feature of convergent signaling of stress (Pardo-Hernandez *et al.* 2024).

Reactive oxygen species are a focal point of stress perception, signal transmission, and damage to cells during combined drought and heat stress. The over-accumulation of ROS, such as superoxide (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals (•OH), happens as a result of the disruption of electron transport chains in chloroplasts and mitochondria. Although oxidative damage to lipids, proteins, and nucleic acids is caused by uncontrolled ROS accumulation, these radicals are primary messengers that regulate the expression of stress-responsive genes and mediate systemic signaling (Rejeb *et al.* 2014). To ensure redox homeostasis, plants have a complex system of antioxidant defense that is encompassed by enzymatic and non-enzymatic mechanisms. Superoxide dismutase (SOD) is the enzyme that converts O_2 in the

deficiency to H_2O_2, which is then relieved by catalase (CAT) and other enzymes of the ascorbate-glutathione pathway, such as ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), and glutathione reductase (GR). Such synchronized antioxidant responses restrain oxidative damage and maintain metabolic activity with extended exposure to stress (ul Haq *et al.* 2019)(Fig. 3).

At the nuclear level, the process of adaptation to combined drought and heat stress is gained by extensive transcriptional reprogramming, including the stress-specific and shared regulatory modules. Several groups of transcription factors, such as DREB, HSF, NAC, MYB, and WRKY, have been found to have varying expression profiles in response to stress (Pardo-Hernandez et al, 2024). DREB transcription factors mainly control the genes concerned with osmoprotection and dehydration tolerance, and HSFs initiate heat-responsive chaperone networks. NAC and WRKY factors have been shown to typically mediate between senescence, programmed cell death, and defense-related pathways in response to cumulative stress signals. Co-expression network studies have found preserved hub genes, which are concurrently controlled during drought and heat and a mixture of both, showing regulatory nodes that form the basis of generalized stress reactions and are new potential genetic manipulation targets (Joshi *et al.* 2024; Nori *et al.* 2025). The results of these studies indicate the weaknesses of the single-gene-based approach and the need to adopt systems-level approaches, which consider the integrated regulation of gene networks in the generation of crops that can survive more frequent and severe weather extremes.

Omics-based Insights into Combined Drought and Heat Stress

Climate change has radically changed our knowledge of how crops react to the co-occurring presence of drought and heat stress, as omics technologies have been rapidly developed (Maitra *et al.* 2022; Ranjan *et al.* 2025; Sakha *et al.* 2026; Mishara *et al.* 2026). As opposed to individual-stress experiments, which tend to simplify the reaction of plants to various conditions, omics-related studies allow querying the system of plant stress biology in natural conditions of multi-stressor interactions in realistic settings. This methodology can be used with both transcriptomic, proteomic, and metabolomic datasets to reveal non-additive interactions, regulatory cascades, and stress-specific trade-offs that cannot be determined with individual responses to stress (Zandalinas *et al.* 2017; Pardo-Hernandez *et al.* 2024). These integrative studies are necessary in finding conserved and species-specific response patterns, revealing post-transcriptional and post-translational controls, and predictive models of stress adaptation that, in turn, are directly applicable in breeding climate-tolerant crops.

Transcriptomic profiling has offered important information on dynamic re-programming of the gene expression in concurrent drought and heat stress, with a consistent pattern of demonstrating that dual stress produces transcriptional landscapes that are qualitatively different from those of single stress. RNA sequencing research on high-throughput statuses reveals that, whereas some typical agents of stress response, e.g., those encoding dehydrins, late embryogenesis abundant (LEA) proteins, genes involved in the synthesis of osmoprotectants are generally up-regulated under individual and combined stresses, a large fraction of the genes are uniquely responsive to the co-stress situation (Bhardwaj *et al.* 2021; Seleiman *et al.* 2025). Among them, the stronger or stress-specific activation of key families of transcription factors, such as DREB and NAC, by combined drought and heat stress is of particular importance, indicating that the regulators are convergence points of taking dehydration and thermal signals into account (Li *et al.* 2025). Comparative transcriptomic studies of key crops, including rice, wheat, and maize, also show that there is conservation of regulatory modules linked to reactive oxygen species detoxification, hormone signaling, and protein folding, which further shows evolutionary convergence in central strategies of stress-response (Prado *et al.* 2025). Meanwhile, strong crop-specific variations have also been reported, particularly in the use of abscisic acid-dependent transcriptional programmes, with reference to differences in domestication events, ecology, and selection, as have been found in comparisons between cereals, tomato, and legumes (Mohapatra *et al.* 2023; Pardo-Hernández *et al.* 2024).

The functional layer Proteomic studies provide important supplementary information to transcriptomic data by revealing significant

Table 2: Multi-omics understanding of crop behavior to combined drought and heat stress during climatic change.

Omics layer	Key responses under combined drought and heat stress	Functional significance for crop resilience	References
Transcriptomics	Non-additive, stress-specific gene expression profiles unique to combined stress	Reveals integrated regulatory networks not predictable from single stresses	Zandalinas *et al.* 2017; Pardo-Hernández *et al.* 2024
	Upregulation of dehydrins, LEA proteins, and osmoprotectant biosynthesis genes	Enhances dehydration tolerance and membrane stability	Bhardwaj *et al.* 2021
	Stress-specific induction of DREB and NAC transcription factors	Coordinates the convergence of drought and heat signaling	Li *et al.* 2025
	Conserved ROS detoxification and protein-folding modules across cereals	Indicates evolutionary convergence of core stress responses	Prado *et al.* 2025
Proteomics	Accumulation of HSP70, HSP90, and sHSPs	Maintains proteostasis under protein-denaturing conditions	ul Haq *et al.* 2019
	Upregulation of ubiquitin–proteasome components	Removes irreversibly damaged proteins	Kumar *et al.* 2023
	Dynamic phosphorylation of MAPKs and SnRK2s	Fine-tunes stress signaling and stomatal regulation	Zhang *et al.* 2025
Metabolomics	Accumulation of compatible solutes and polyamines	Supports osmotic balance and ROS detoxification	Bhardwaj *et al.* 2021
	Enhanced flavonoid and phenolic biosynthesis	Improves antioxidant capacity and photoprotection	Joshi *et al.* 2024
	Shift toward glycolysis, TCA cycle, and alternative respiration	Meets defense energy demands at the cost of growth	Sato *et al.* 2024; Singh *et al.* 2024
Integrated multi-omics	Reconstruction of gene–protein–metabolite networks	Identifies hub regulators and resilience-associated traits	Joshi *et al.* 2024; Prado *et al.* 2025
	Predictive G×E modeling incorporating climate variables	Guides precision breeding for future climates	Li *et al.* 2025

uncoupling between mRNA levels and protein levels during combined stress conditions, which places great emphasis on translational regulation, protein stability, and selective degradation. Drought and heat stress rapidly increase the levels of molecular chaperones (HSP70, HSP90, and small heat shock proteins) in plants, which stabilize partially unfolded polypeptides before refolding and protecting against aggregation to support cellular proteostasis (ul Haq *et al.* 2019). Simultaneously, the elements of the ubiquitin system are enhanced to intensify the activity of the proteasome system to eliminate the irreversibly damaged proteins, which is an expensive but necessary activity in a situation when dehydration and high temperature destabilize the protein structure together (Kumar *et al.* 2023). Phosphoproteomic experiments also show that the signal of stress in mixed conditions is highly regulated by post-translational phosphorylation, especially by ABA signaling SnRK2 and mitogen-activated protein kinases. The changes optimize the stomatal regulation, ion transport, and transcriptional activity, which are not evident when exposed to single-stress treatment (Zhang *et al.* 2025**;** Duan *et al.* 2026). Chronic stress combined exposure also causes selective translation of stress-responsive proteins via upstream open reading frame mechanisms, and also by internal ribosome entry site, so that plants can be able to choose to synthesize defense-related proteins at the cost of minimum overall energy usage.

Metabolomic profiling is a snapshot of the biochemical consequences of these regulatory activities, which indicate massive metabolic reprogramming, to enhance survival instead of growth in a collective drought and heat stress environment. The osmotic adjustment of plants is facilitated by the high amounts of compatible solutes, such as proline, glycine betaine, soluble

sugars, including trehalose and sucrose, and polyamines, which jointly aid in maintaining membrane stability and cleaning up of reactive oxygen species (Bhardwaj *et al.* 2021). Secondary metabolites (especially flavonoids and phenolic compounds) also become significantly higher, facilitating antioxidant ability and protection against the high irradiance commonly connected with heat waves (Joshi *et al.* 2024). At the same time, the metabolism of central carbon is diverted to glycolysis and the tricarboxylic acid cycle as opposed to anabolic synthesis of starch and cellulose to sustain the increased energy requirements of the stress defense mechanism. Such a metabolic change is characterized by major trade-offs, particularly in situations with a limited photoinhibition capacity of photosynthetic capacity by stomata, light-induced damage to photosystems, and temperature (Sato *et al.* 2024). The metabolic fluxes also suggest that alternative respiratory routes and the accumulation of the products of fermentation, especially ethanol and lactate, are being increased, especially during the recovery periods of the night, which also reflects the local hypoxic conditions and redox imbalance even in the tissues of the air (Singh *et al.* 2024).

A combination of transcriptomic, proteomic, and metabolomic data sets is a significant breakthrough in combined stress biology and allows for the reconstruction of multiscale regulatory networks that connect genes, proteins, metabolites, and phenotypic features. Different network-based methods, such as weighted gene co-expression network analysis and machine learning algorithms, have been successful in identifying hub genes and master regulators, such as specific heat shock factors, MAPKs, and ABA-responsive transcription factors that coordinate molecular response to key physiological characteristics such as water-use efficiency, membrane thermostability, and yield stability during field conditions (Joshi *et al.* 2024; Prado *et al.* 2025). Notably, predictive modeling of crop performance in future climate conditions can also be done using multi-omics data by including environmental factors, such as vapor pressure deficit, soil moisture dynamics, and diurnal temperature changes that can be predicted by genotype-by-environment models, which are limited to a single-gene framework (Li *et al.* 2025). Taken together, these results indicate that overlapping drought and heat stress are not merely ineffective in activating overlapping stress pathways, but rather, they result in a qualitatively different physiological and molecular state. The superposition of omics-based discoveries onto known signaling pathways identifies the main areas of convergent activities, such as ROS, ABA, MAPK cascades, and nuclear transcriptional regulation, which are projected strategic approaches to crop enhancement (Rejeb *et al.* 2014; Oyebamiji *et al.* 2024). Biomarker identification can therefore be accelerated through the integrative breeding regimes that can be pragmatic to augment crop resistance under varied and difficult climatic conditions.

Implications for Breeding and Agronomy

With climate change, a shift of reductionist breeding methods into combined and systems-based approaches due to the intensity of comorbid drought and heat stress, hence transmuting the objectives of crop improvement. Where crops experience competing and varying stresses at varying developmental stages, the classical approaches based on a consideration of individual traits or tolerance to individual stress are increasingly failing to capture the field environment (Fig. 4). The development of resilience in such circumstances is not only a matter of intentional coordination of genetic strength and agronomic adaptability but also an expansion of the net effect of stabilizing the yield, physiological functionality, and resource-use efficiency to climatic uncertainty. This theoretical system highlights the notion of resilience as an emergent characteristic of genotype-management-environment interactions instead of a genetic characteristic, with the need to develop breeding strategies that are clearly structured to meet the demands of heterogeneous and unpredictable production systems.

The progress in genomics helped to substantially enhance the ability to unravel the genetic architecture of tolerance to integrated drought and heat stress and locate quantitative trait loci and candidate genes that determine complex adaptive traits (Prado *et al.* 2025). Co-localization of loci regulating canopy depression of temperature, membrane thermostability, delayed senescence, and yield retention has continually been observed to be physiologically interdependent in dual stress scenarios by high-resolution mapping, multi-

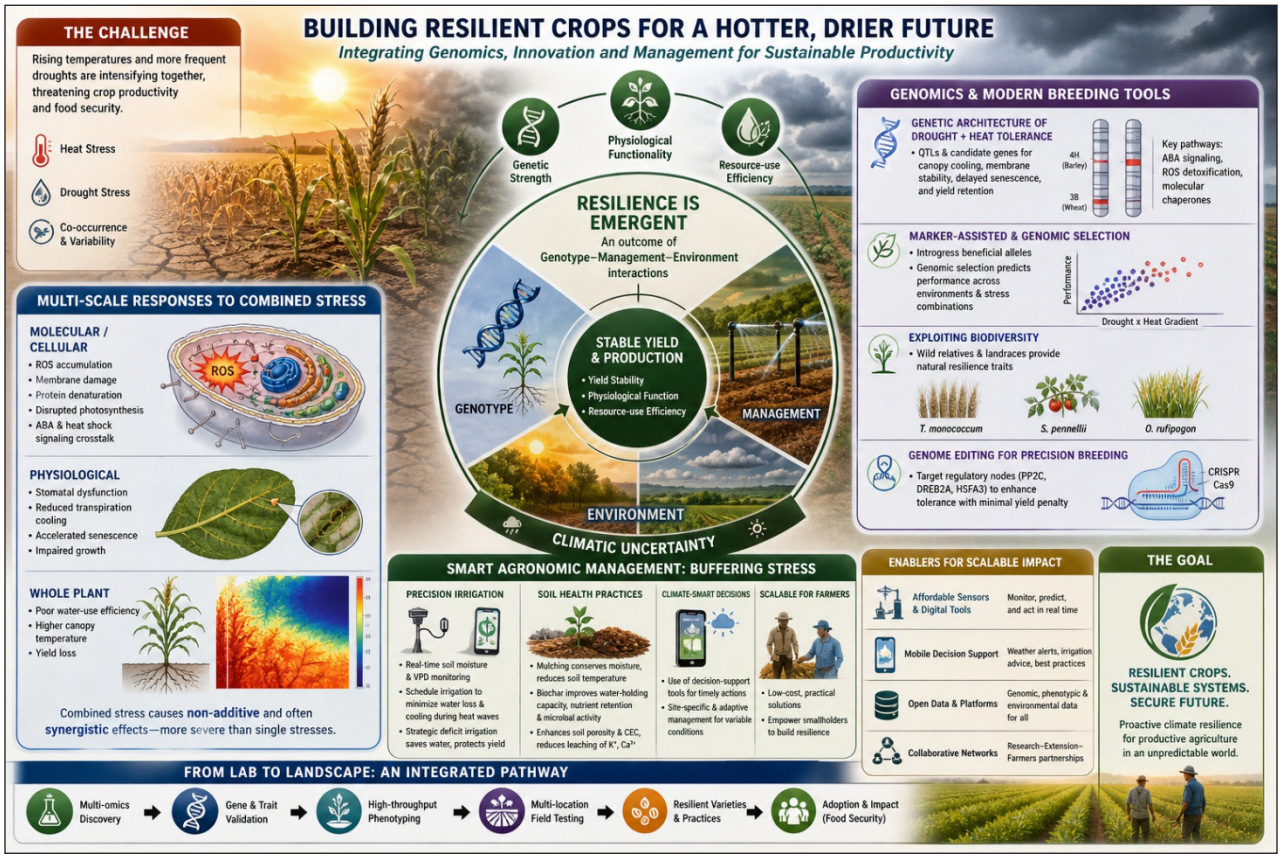


Fig. 4: Building Climate-Resilient Crops Through Integrated Science and Smart Farming

environment trials (Bhardwaj *et al.* 2021). The finding of major-effect loci on the 4H chromosome of barley and the 3B chromosome of wheat in dissimilar environments indicates the possibility of conserved regulatory centres that regulate the integration of stress in cereal (Sato *et al.* 2024). Genes related to the signaling of abscisic acid, detoxification of reactive oxygen species, and molecular chaperone activity are often enriched in these genomic regions and make them functional in supporting cellular homeostasis in the presence of cooperating conditions of dehydration and thermal stress (Waadt *et al.* 2022). Convergence like this suggests that an individual should breed to be highly stress-tolerant when selection is on regulatory nodes that regulate many physiological pathways, but not individual downstream responses.

The adoption of marker-assisted selection into breeding pipelines has enhanced the introgression of desirable alleles that regulate stress resilience as well as the limitation of penalties under optimal environments, hence maintaining the yield potential of high-input systems (Kumar *et al.* 2023). In more recent studies, genomic selection methods involving the combined use of genome-wide marker data and multi-environment phenotypic data are more efficient in predicting the stability of performance in diverse and varying circumstances of drought and heat (Joshi *et al.* 2024). Genomic selection, in contrast to traditional selection plans, which assess tolerance to single stresses in isolation, represents cumulative and interactive effects of stress, which is more in line with agroecological reality in breeding decisions. The significance of this paradigm shift is particularly high based on the fact that the co-occurrence of stress and not intensity is becoming a determining factor in the farming fields.

There has been a more complementary trend in increasing multi-stress tolerance in contemporary cultivars by increasing the genetic base of contemporary cultivars with purposeful exploitation of wild relatives or traditional landraces. The above-mentioned species, such as *Triticum monococcus*, *Solanum pennellii*, and *Oryza rufipogon*, are those that have had their naturally resilient adaptation properties, i.e., deeper and more plastic root systems, altered stomatal controls, and stress-tolerant metabolic networks, lost during domestication

(Prado *et al.* 2025; Sato *et al.* 2024). These genetic materials can be used to access useful alleles to enhance stress responsiveness without necessarily impairing productivity, especially when used together with modern genomic technology, where introgression and pyramiding of adaptive characters can be done with precision. Recent changes to the translational capabilities of stress biology involving the introduction of CRISPR/Cas9-mediated genome editing have allowed the targeted manipulation of the main regulatory elements found in multi-omics analyses (Kumar *et al.* 2023; Maitra *et al.* 2025). Stress protection has been demonstrated to be improved by conditional modulation of negative regulators of ABA signaling pathways, e.g., individual PP2C phosphatases or the controlled expression of master transcription factors, e.g., DREB2A and HSFA3, to reduce pleiotropic growth penalties (Singh *et al.* 2024). These narrow-band interventions enable crops to dynamically regulate the balance between defense and development to counter one of the main limitations of previous transgenic techniques, where the conferred tolerance was usually at the cost of the yield. These precision breeding plans would be an important move towards creating crops that would maintain their productivity on stress gradients as opposed to surviving extreme events.

Agronomic management is still needed despite these genetic advances in buffering crops to combined drought and heat stress, especially in areas where farmers do not have access to improved cultivars. Real-time monitoring of the soil moisture, measuring atmospheric vapor pressure deficit, will allow scheduling irrigation to minimize transpirational water loss and evaporative cooling during heat waves through the use of atmospheric vapor pressure deficit (Li *et al.* 2025). Deficit irrigation, particularly when done in a strategic manner, particularly when not during very sensitive reproductive stages, has been effective in saving water without incurring a disproportionate decrease in yield (Bhardwaj *et al.* 2021). In addition, complementary soil management techniques, such as mulching and the use of biochar, also increase the resiliency of the system through their ability to increase the water-holding capacity of soil, its nutrient retention, and microbial activity (Maitra and Zaman, 2017; Pramanick *et al.* 2023; Oyebamiji *et al.* 2024). Amendments with biochar specifically enhance soil porosity and cation exchange capacity, which subsequently decreases the amount of essential ions such as potassium and calcium lost to leaching during the drought150C period and maintains nutrient supply throughout the long-term stress (Oyebamiji *et al.* 2024).

The growing prominence of the combined state of drought and heat stress is forcing a radical reassessment of stress resilience as a multiscale process that results in an interaction between molecular, physiological, and environmental processes. In contrast to the single-stress conditions, combined stress triggers both non-additive and, in many cases, synergistic perturbations that cannot be forecasted with any high level of reliability by a single study of stress (Li *et al.* 2025). They involve fastened leaf senescence, radical decreases in photosynthetic activities by photoinhibition and deactivation of Rubisco, and widespread destruction of membranes by lipid peroxidation (Sato *et al.* 2024; Singh *et al.* 2024). At the entire plant scale, maladaptive stomatal control undermines both the transpirational cooling and water-use efficiency and increases thermal and hydraulic stress. Both crosstalk and coordination of these signals cause quick activation of drought and heat shock responses and limit the optimization of drought and heat tolerance at the same time (Waadt *et al.* 2022; Pardo-Hernandez *et al.* 2024; Vennela *et al.* 2026). The restricted ability of most contemporary cultivars to integrate such responses tells about the breeding interests of the past that were inclined towards tolerance to single stress factors, and the present-day germplasm is ill-equipped to combat interacting extremes in climate (Prado *et al.* 2025). Recent developments with multi-omics technologies have enabled the resolution of these complex responses to stress significantly better, and at which they can be assembled.

Comparative genomics, transcriptomics, proteomics, and metabolomics layers investigations are going to present preserved regulatory modules, namely, DREB-NAC-HSF transcriptional networks and ABA-dependent signaling cascades that trigger a coordinated reaction both on a molecular scale and an entire-plant scale (Bhardwaj *et al.* 2021; Joshi *et al.* 2024). These findings are complemented by high-throughput phenotyping platforms that also offer the possibility to measure the resilience-associated

characteristics, such as canopy temperature depression, membrane thermostability, and delayed senescence in conditions of controlled and field settings (Kumar *et al.* 2023). Simultaneously, the rise in functional genomics has made testing the role of candidate genes much faster, enabling the manipulation of stress integrators, including PP2C phosphatases and heat shock proteins, to be directed as an intervention to promote tolerance without further decrease in yield in usable settings (Joshi *et al.* 2023; Kumar *et al.* 2023; Maitra *et al.* 2025; Muui *et al.* 2026). However, the conversion of such molecular advantages into uniformly field-level advantages has remained stunning because of the robust genotype-environment interaction, which alters trait expression in a variety of agroecological conditions.

The closing of the gap between laboratory findings and practice in the field can be achieved through an organized investment in stress-controlled experimental systems and multi-location testing systems that are realistic in terms of capturing climatic variability (Rahimi *et al.* 2023; Zhang *et al.* 2025). The controlled-environment facilities allow the accurate dissection of the stress onset, acclimation, and recovery periods, and decentralized field phenotyping provides validation of the conditions of relevance to the farmers (Joshi *et al.* 2023). Nonetheless, the problem of scalability and affordability still restricts large-scale implementation, especially when it comes to smallholder farmers who are proportionately exposed to the effects of climate extremes. In order to address these constraints, developing open technologies so that more people have access to climate-resilient solutions, including low-cost environmental sensors, mobile decision-support solutions, and open-source genomic and phenotypic databases (Joshi *et al.* 2023). Finally, molecular breeding coupled with adaptive agronomic management and scalable delivery systems offers a resilient channel to transforming agriculture to a less reactive approach to crisis management and a more proactive climate management approach to protect crop productivity and food security in an increasingly unpredictable climate.

CONCLUSION

Finally, resistance of crops to the more pronounced and frequent integration of drought and heat stress is a key border in climate change agricultural science. Both physiological and molecular and omics-based studies indicate that combined stress leads to interactions that are complex, non-additive interactions that are not predictable by single stress responses. On the physiological level, integrated stress interferes with water relations, photosynthetic performance, membrane stability, and hormonal integration, which leads to trade-offs between survival and growth that are strongly genotype-dependent. These multi-scale physiological reactions provide the significance of taking systems-level approaches in the assessment of stress tolerance and not basing it on individual characteristics. On a molecular level, drought and heat stress have been shown to focus on densely interacting signaling webs that comprise ABA, ROS, calcium, and heat shock factors, which control transcriptional programs, protein homeostasis, and metabolic changes. Current studies using omics-based methods have demonstrated that combined stress responses are qualitatively different from those of individual stresses, and that there exists a set of common regulatory modules and crop-specific responses. These findings highlight the application of integrative approaches combining high-resolution molecular profiling and functional phenotyping to discover the main regulatory centers and biomarkers of action to be taken to achieve resilience.

To translate this knowledge into action solutions, there must be a synergy between the technologies used in breeding and management of agronomics, which is adaptive. More than ever before, genomic selection, marker-assisted breeding, and precision genome editing provide new opportunities to control fundamental stress regulatory networks, and complementary agronomic approaches, such as optimal irrigation, soil supplementation, and stress control at the field level, protect crops against environmental extremes. Notably, these trials of multiple locations and phenotyping networks that can be scaled are necessary to measure genotype × environment effects so that the molecular and physiological benefits can be converted into stability of yield under non-homogeneous field conditions. On the whole, the need to establish robust crop resilience to changes in climate requires a comprehensive strategy, which will combine

molecular knowledge, physiological explanations, and agronomic technologies. The areas of future research that the researchers ought to focus on are: the dissolution of scale-dependent trait coordination, identification of general and crop-specific stress integrators, and the evolution of practical approaches to apply laboratory results into field-appearing solutions. Hence, generation of crop systems that can not only provide food security but also productivity under more intricate and interacting climatic stressors can be achieved by closing the divide between agronomic practice and molecular processes.

FUTURE DIRECTIONS

In order to handle the issues of integrated drought and heat stress, a stringent shift to integrative, system-based research paradigms that are not only explicit in their effort to bridge the existing gulf between molecular discovery and agronomic application is needed. Among the immediate issues are increased multi-stress field-based experiments that are realistic to simulate climate variability, including that of different vapor pressure deficits, dynamic soil moisture regimes, and diurnal temperature fluctuations. The coordinated multi-location testing networks and inclusion of G x E interactions are required to capture G x E interactions and dynamic testing networks, which will allow the derived markers of resilience using omics to be applicable in settings beyond the controlled settings. Another relevant area of development in crop resiliency enhancement is the model of predictive systems. Multi-omics data may be useful to combine with environmental variables to identify hub genes and regulatory networks that ensure the stability of the yield in the environment of joint stress using such methods as machine learning and weighted gene co-expression network analysis (WGCNA). Such models can anticipate the performance of crops under future climatic conditions and guide the breeding strategies to make the most suitable combinations of traits rather than basing the plans on the whim of a single gene marker. Genetic selection in agreement with adaptive environmental responsiveness has a major boost to the efficiency and power of climate-tolerant breeding schemes, which such instruments can provide.

It is also important to strengthen the translational structures that interact with the agronomic decision-making and molecular biology. The promotion of real-time and data-driven crop management, particularly in resource-constrained settings, could be achieved with the help of genomic tools that are publicly available at low cost, cost-effective sensor devices, and mobile decision support systems. Access to such inventions for the smallholder farmers who are the worst affected by loss of yields to climate change would be important as a means of having fair adaptation. But in the long run, it will turn out that interdisciplinary collaboration between plant scientists, breeders, agronomists, climatologists, and social scientists will be required to develop scientific research of scalable, socially inclusive solutions to secure global food, feed, and industrial crop security in the face of increasing climate change.

GENERATIVE AI DECLARATION

The author(s) confirm that there was no use of artificial intelligence (AI)-assisted technology for assisting in the writing or editing of the manuscript. The figures were originally drawn by authors and Gemini used only for final fine tuning for clarity. The authors developed and verified all scientific content, data analysis, interpretation of results, and conclusions. The authors take full responsibility for the accuracy, integrity, and originality of the work presented, and no AI tool was listed as an author.

REFERENCES

Bhardwaj, A., Devi, P., Chaudhary, S., Rani, A., Jha, U.C., Kumar, S., Bindumadhava, H., Prasad, P.V.V., Sharma, K.D., Siddique, K.H.M. and Nayyar, H. 2021. Omics approaches in developing combined drought and heat tolerance in food crops. *Plant Cell Reports*, **41**(3): 699–739.

Cheptoek, R.P., Gitari, H.I., Mochoge, B., Kisaka, O.M., Otieno, E., Maitra, S., Nasar, J. and Seleiman, M.F. 2021. Maize productivity, economic returns and phosphorus use efficiency as influenced by lime, Minjingu Rock Phosphate and NPK inorganic fertilizer. *International Journal of Bioresource Science*, **8**(1): 47–60.

Duan, S., Chen, H., Chen, S., Li, X., Zhou, Z., Parsons, D. and Du, T. 2026. 3D reconstruction analysis of maize-soybean intercropping competition under water stress. *Plant Phenomics*, 100165. https://doi.org/10.1016/j.plaphe.2026.100165

Githumbi, M., Sairam, M., Ray, S., Chappa, M., Ngaiza, V., Nungula, E., Gitari, H. and Maitra, S. 2026. Multi-omics approaches for deciphering salinity stress tolerance in food and industrial crops. *International Journal of Agriculture and Environmental Biotechnology*, **19**(3).

Heydarzadeh, S., Hosseinpour, A., Maitra, S. and Rahimi, A. 2021. Improving quantitative and qualitative properties of cotton through the use of organic and chemical fertilizers under water deficit stress conditions. *International Journal of Bioresource Science,* **8**(2): 69–80.

Jamal, N., Wang, G.Y., Ahmad, S., Muhammad, I., Zeeshan, M. and Hasan, M.E. 2022. Nitrogen fertilization coupled with iron foliar application improves the photosynthetic characteristics, photosynthetic nitrogen use efficiency, and the related enzymes of maize crops under different planting patterns. *Frontiers in Plant Science,* **13**: 988055.

Joshi, A., Yang, S.Y., Song, H. G., Min, J. and Lee, J.H. 2023. Genetic databases and gene editing tools for enhancing crop resistance against abiotic stress. *Biology,* **12**(11): 1400.

Joshi, S., Patil, S., Shaikh, A., Jamla, M. and Kumar, V. 2024. Modern omics toolbox for producing combined and multifactorial abiotic stress-tolerant plants. *Plant Stress,* **11**: 100301.

Kumar, M., Prusty, M.R., Pandey, M.K., Singh, P.K., Bohra, A., Guo, B. and Varshney, R.K. 2023. Application of CRISPR/Cas9-mediated gene editing for abiotic stress management in crop plants. *Frontiers in Plant Science,* **14**.

Li, N., Geng, Z., Huang, X., Huang, S., Song, L., Chen, R., Chen, Z., Du, L. and Xu, C. 2025. A review of differential plant responses to drought, heat, and combined drought + heat stress. *Current Issues in Molecular Biology,* **47**(12): 975.

Lobell, D.B., Schlenker, W. and Costa-Roberts, J. 2011. Climate trends and global crop production since 1980. *Science*, **333**(6042): 616–620.

Maheswari, N., Maitra, S., Sairam, M., Ray, S., Sagar, L., Santosh, D.T. and Gaikwad, D.J. 2025. Impact of real-time nitrogen management on the performance of maize-cowpea intercropping system. *Crop Research*, **60**(3/4): 139–154.

Maitra, S. and Ray, D.P. 2019. Enrichment of biodiversity, influence in microbial population dynamics of soil and nutrient utilization in cereal-legume intercropping systems: A review. *International Journal of Bioresource Science,* **6**(1): 11–19.

Maitra, S. and Zaman, A. 2017. Brown manuring, an effective technique for yield sustainability and weed management of cereal crops: A review. *International Journal of Bioresource Science,* **4**(1): 1–5.

Maitra, S., Praharaj, S., Hossain, A., Pramanick, B., Shankar, T. and Palai, J.B. 2022. Small millets: The next-generation smart crops in the modern era of climate change. In:*Omics of Climate Resilient Small Millets.* Pudake, R. N., Solanke, A. U., Sevanthi, A. M. and Rajendrakumar, P. (Eds.), Springer, Singapore, pp. 1–25. https://doi.org/10.1007/978-981-19-3907-5_1

Maitra, S., Ray, S., Pradhan, P., Pattanayak, S., Nanda, S.P., Battaglia, M.L., Sagar, L., Sairam, M., Gitari, H.I., Maity, B. and Santosh, D.T. 2026c. Repercussions of salinity on field crops and achieving Sustainable Development Goals. In: *Salinity Stress and Remediation in Agro-Ecosystems.* Moulick, D., Sarkar, S., Brahmachari, K. (Eds.), Springer Nature Switzerland, Cham, pp. 367–414.

Maitra, S., Ray, S., Sagar, L., Sairam, M., Pramanick, B. and Chappa, L.R. 2025. Cropping system approach in climate-resilient food crop production. In: *Climate-Smart Agricultural Technologies: Approaches for Field Crops Production Systems*. Pramanick, B., Singh, S.V., Maitra, S., Celletti, S. and Hossain, A. (Eds.), Springer Nature Singapore, Singapore, pp. 327–356. https://doi.org/10.1007/978-981-96-7699-6_15

Maitra, S., Ray, S., Sairam, M., Sagar, L., Rishitha, S., Gaikwad, D.J., Santosh, D.T., Ravindranath, N., Jena, C., Nanda, S.P. and Pattanayak, S., 2026a. Cropping system approach to horticultural crop production for agricultural sustainability: A climate-smart production strategy. In: *Remunerative horticulture: Strategies for profitable growth*. Das, A., Sharangi, A.B. (Eds), Springer Nature Singapore, Singapore, pp. 671–702. https://doi.org/10.1007/978-981-92-1007-7_22

Maitra, S., Santosh, D.T., Jena, J., Behera, S.D., Ray, S., Sairam, M., Palai, J.B., Gaikwad, D. J., Rishitha, S., Gitari, H.I. and Atapattu, A.J. 2026b. Understanding plant responses to abiotic stress through systems biology. In: *Systems Biology in Crop Improvement.* Academic Press, pp. 59–100. https://doi.org/10.1016/B978-0-443-36457-0.00011-0

Majeed, Y., Fiaz, S., Teng, W., Rasheed, A., Zhu, X., Seleiman, M.F. and Diatt, A. A. 2023. Evaluation of twenty genotypes of wheat (*Triticum aestivum* L.) grown under heat stress during germination stage. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*, **51**(2): 13207.

Mohapatra, P.P., Seleiman, M.F., Mandal, R., Pramanik, K., Maity, T.K., Tarafdar, J. and Khan, N. 2023. Efficiency of RAPD and SSR markers in assessing genetic diversity in summer onion (*Allium cepa* L.) genotypes. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca,* **51**(3): 13369.

Muui, C.W., Muasya, R.M., Lelei, D.K. and Maitra, S. 2026. Soil properties and rainfall variability as determinants of yields for sorghum landraces. *International Journal of Experimental Research and Review,* **51**: 1–22.

Mwakidoshi, E.R. 2026. Organic and Inorganic Soil Amendments' Effects on Potato (*Solanum tuberosum* L.) Productivity, Nutrient Use Efficiency and Exchangeable Acidity in Nakuru County, Kenya. PhD thesis. Kenyatta University, Nairobi, Kenya. https://doi.org/10.13140/RG.2.2.30353.80482

Nori, M., Masina, S., Sagar, M., Sumit, R., Hemasree, K.R., Romnan, K.M., Gaikwad, D.J. and Kalasare, R.K. 2025. Influence of precision nitrogen management in Rabi maize and cowpea intercropping system under varied planting proportions in South Odisha. *Plant Science Today,* **12**(3).

Nungula, E.Z., Chappa, L.R., Ngaiza, V.V., Msangi, G.S., Dlamini, J.C., Saeed, A., Mwadalu, R., Raza, M.A., Soratto, R.P., Rezaei-Chiyaneh, E., Nasar, J. and Gitari, H.I. 2025. Climate change and carbon emission trading. In:*Carbon Trading in Agroforestry under Changing Climate.* Raj, A., Jhariya, M.K. and Meena, R.S. (Eds.), Springer, Cham, pp. 23–57. https://doi.org/10.1007/978-3-031-97151-8_2

Nyawade, N., Karanja, N.N., Gachene, C.K., Schulte-Geldermann, E., Sharma, K. and Parker, M.L. 2020.

Enhancing climate resilience of rain-fed potato through legume intercropping and silicon application. *Frontiers in Sustainable Food Systems,* **4**: 566345.

Oyebamiji, Y.O., Adigun, B.A., Shamsudin, N.A.A., Ikmal, A.M., Salisu, M.A., Malike, F.A. and Lateef, A.A. 2024. Recent advancements in mitigating abiotic stresses in crops. *Horticulturae,* **10**(2): 156.

Pardo-Hernández, M., García-Pérez, P., Lucini, L. and Rivero, R.M. 2024. Multi-omics exploration of the involvement of ABA in identifying unique molecular markers for single and combined stresses in tomato plants. *Journal of Experimental Botany,* **76**(21): 6389–6409.

Prado, K., Holland, B.L., McSpadden Gardener, B., Lundquist, P.K., Santiago, J.P., VanBuren, R. and Rhee, S.Y. 2025. Building climate-resilient crops: Genetic, environmental, and technological strategies for heat and drought stress tolerance. *Journal of Experimental Botany,* **76**(16): 4395–4413.

Pramanick, B., Bera, A., Saha, P., Barman, A., Paramanick, B., Maitra, S. and Hossain, A. 2023. Soil microflora and their interaction with plants under changing climatic scenarios. In: *Microbial Symbionts and Plant Health: Trends and Applications for Changing Climate.* Springer Nature Singapore, Singapore, pp. 19–40. https://doi.org/10.1007/978-981-99-0030-5_2

Rahimi, A., Lyons, G., Heydarzadeh, S., Tuncturk, M. and Tuncturk, R. 2023. Effects of vermicompost, compost and animal manure on vegetative growth, physiological and antioxidant activity characteristics of *Thymus vulgaris* L. under water stress. *Yuzuncu Yil University Journal of Agricultural Sciences*, **32**(1): 40–53.

Rahimi, A., Mohammadi, M.M., Moghadam, S.S. and Heydarzadeh, S. 2022. Effects of stress modifier biostimulants on vegetative growth, nutrients and antioxidants contents of garden thyme (*Thymus vulgaris* L.) under water stress. *Journal of Plant Growth Regulation,* **41**: 2059–2072.

Ranjan, S., Padhan, S.R., Kumar, S., Sow, S., Roy, D.K., Sahoo, R. and Sadhu, S. 2025. Impact of climate change and abiotic stresses on food crop production. In: *Climate-Smart Agricultural Technologies: Sustainability Sciences in Asia and Africa.* Pramanick, B., Singh, S. V., Maitra, S., Celletti, S. and Hossain, A. (Eds.), Springer, Singapore, pp. 71–88. https://doi.org/10.1007/978-981-96-7699-6_4

Raza, M.A., Din, A.M.U., Yasin, H.S., Gull, H., Shah, G.A. and Zhongming, M. 2025. Maize/legume intercropping increases nutrient uptake, crop yields, land productivity, and economic profits in resource-intensive arid-irrigated areas. *Journal of Soil Science and Plant Nutrition,* **25**: 8316–8332.

Rejeb, I., Pastor, V. and Mauch-Mani, B. 2014. Plant responses to simultaneous biotic and abiotic stress: Molecular mechanisms. *Plants*, **3**(4): 458–475.

Rezaei-Chiyaneh, E., Mahdavikia, H., Alipour, H., Dolatabadian, A., Battaglia, M.L., Maitra, S. and Harrison, M.T. 2023. Biostimulants alleviate water deficit stress and enhance essential oil productivity: A case study with savory. *Scientific Reports,* **13**(1): 720.

Maitra, S., Sahoo, U., Sairam, M., Rezaei-Chiyaneh, E., Battaglia, M.L. and Hossain, A. 2023. Cultivating sustainability: A comprehensive review on intercropping in a changing climate. *Research on Crops,* **24**(4): 702–715.

Maitra, S., Sairam, M., Ray, S., Santosh, D.T., Gaikwad, D.J., Mukesh, G. and Maheswari, N. 2024. Applauding soil quality improvement through legume-based intercropping system: A review. *International Journal of Bioresource Science*, **11**(1): 59–69.

Maitra, S., Santosh, D.T., Jena, J., Behera, S.D. and Hossain, A. 2025. Understanding plant responses to abiotic stress through systems biology. In: *Systems Biology in Crop Improvement: Emerging Tools and Technologies*. Aftab, T. (Ed.), Elsevier, Chapter 3, pp. 59–100. https://doi.org/10.1016/B978-0-443-36457-0.00011-0

Sakha, M., Maitra, S., Mutua, L., Wambua, J.M. and Gweyi-Onyango, J. 2026. Soil properties as key drivers of greenhouse gas emissions and climate change. *International Journal of Experimental Research and Review,* **51**: 74–89.

Sato, H., Mizoi, J., Shinozaki, K. and Yamaguchi-Shinozaki, K. 2024. Complex plant responses to drought and heat stress under climate change. *The Plant Journal*, **117**(6): 1873–1892.

Seleiman, M.F., Ahmad, A., Alotaibi, M., Al-Saif, A.M., Ranjan, S. and Sow, S. 2025. High-throughput metabolomics for studying plant stress physiology under a changing climate. In: *High Throughput Plant Metabolomics*. Chen, J. (Ed.), CAB International, Wallingford, UK, pp. 114–131. https://doi.org/10.1079/9781800626911.0006

Seleiman, M.F., Aslam, M.T., Alhammad, B.A., Hassan, M.U., Maqbool, R., Chattha, M.U. and Battaglia, M.L. 2021. Salinity stress in wheat: Effects, mechanisms and management strategies. *Phyton-International Journal of Experimental Botany*, **91**(4): 667–694.

Singh, S., Praveen, A., Dudha, N. and Bhadrecha, P. 2024. Integrating physiological and multi-omics methods to elucidate heat stress tolerance for sustainable rice production. *Physiology and Molecular Biology of Plants*, **30**(7): 1185–1208.

ul Haq, S., Khan, A., Ali, M., Khattak, A.M., Gai, W.X., Zhang, H.X., Wei, A.M. and Gong, Z.H. 2019. Heat shock proteins: Dynamic biomolecules to counter plant biotic and abiotic stresses. *International Journal of Molecular Sciences,* **20**(21): 5321.

Valliyodan, B. and Nguyen, H.T. 2006. Understanding regulatory networks and engineering for enhanced drought tolerance in plants. *Current Opinion in Plant Biology,* **9**(2): 189–195.

Vennela, M., Varma, D.D., Sadhu, S., Padhan, S.R. and Roy, D.K. 2026. Accelerating role of artificial intelligence and robotics in crop improvement. In: *Climate-Resilient Agriculture for Sustainable Crop Production.* Kumar, S., Ranjan, S., Sow, S., Padhan, S. R. and Roy, D. K. (Eds.), CRC Press, Taylor & Francis Group, pp. 187–208. https://doi.org/10.1201/9781998511150-7

Waadt, R., Seller, C.A., Hsu, P.K., Takahashi, Y., Munemasa, S. and Schroeder, J.I. 2022. Plant hormone regulation of abiotic stress responses. *Nature Reviews Molecular Cell Biology,* **23**(10): 680–694.

Zaman, A., Zaman, P. and Maitra, S. 2017. Water resource development and management for agricultural sustainability. *Journal of Applied and Advanced Research,* **2**(2): 73–77.

Zandalinas, S.I., Mittler, R., Balfagón, D., Arbona, V. and Gómez-Cadenas, A. 2017. Plant adaptations to the combination of drought and high temperatures. *Physiologia Plantarum,* **162**(1): 2–12.

Zhang, H., Lang, Z., Zhu, J.K. and Wang, P. 2025. Tackling abiotic stress in plants: Recent insights and trends. *Stress Biology,* **5**(1).