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Systematic review and critical evaluation of crop tolerance to combined drought and heat stress: from endogenous mechanisms to field reflection

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ABSTRACT

The concurrent occurrence of drought and heat stress intensified by anthropogenic climate change poses a synergistic and severe threat to global crop productivity and food security. This compound abiotic stress is particularly damaging in arid and semi-arid regions, where agricultural systems are already highly vulnerable. This systematic review aims to: (1) synthesize the integrated physiological, biochemical, and molecular responses of crop plants to combined drought-heat stress; (2) critically evaluate the proposed role of the interactive ABA-ROS signaling network; (3) assess inter- and intraspecific genetic diversity in tolerance strategies; and (4) review promising technological and management interventions, while acknowledging the major challenges in translating findings to real-world field conditions. Following the PRISMA 2020 guidelines, we conducted a comprehensive literature search across major databases for the period 2000-2025. From an initial pool of approximately 14,000 records, 102 peer-reviewed studies were ultimately cited. The selection process, summarized in the PRISMA flow diagram , identified 138 studies for initial qualitative synthesis. A final critical audit then refined the cited corpus to 102 studies. A final critical citation audit was then conducted to eliminate redundancy and ensure the direct relevance of each cited study. Our synthesis confirms that plant responses to combined stress are synergistic and hierarchical not merely additive. A consistent, well-supported finding across studies (particularly in model systems and controlled environments) is the central role of an interactive ABA-ROS signaling node as a key integrator of combined stress responses. Significant genetic diversity exists among and within species, and reproductive stages are critically vulnerable. Promising intervention strategies include genome editing, nanotechnology, and plant growth-promoting microorganisms (PGPMs). However, the efficacy of these approaches is often context-dependent and requires rigorous validation under complex field conditions. Ensuring yield stability under future climates will require a paradigm shift toward integrated approaches. Future research must prioritize field validation, address stage-specific vulnerabilities, and develop standardized phenotyping protocols to bridge the gap between controlled-environment studies and on-farm performance. This review concludes that although deep mechanistic insights are advancing primarily from controlled environments a critical translation gap remains in validating and deploying this knowledge across diverse, real-world agricultural systems.

Highlights

- The plant response to combined drought-heat stress is a synergistic and hierarchical program, with reproductive stages being critically vulnerable.
- The ABA-ROS signaling network is frequently proposed as a key integrator, supplemented by parallel pathways like ABA-independent regulation and somatic stress memory.
- Significant genetic diversity in tolerance strategies offers a valuable reservoir for breeding.

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- Advanced technologies and management tools show promise, but their efficacy is often context- and genotype-specific, requiring field validation.
- Future progress hinges on integrated research pipelines that connect mechanistic discovery with field performance and acknowledge the complexity of real-world environments.

1. Introduction

Global agriculture faces an unprecedented challenge from climate change, which is increasing the frequency, intensity, and simultaneous occurrence of extreme weather events (IPCC, 2022). Among these, the combination of drought and heat stress has emerged as a particularly severe threat to crop productivity and global food security (Lobell et al., 2014). The effects of individual stresses are well documented. However, their simultaneous occurrence creates a unique and often synergistic physiological environment, leading to disproportionate yield losses that exceed the sum of impacts from each stress applied alone (Mittler, 2006; Zandalinas et al., 2018). This interactive effect poses a critical risk to agricultural sustainability, especially in vulnerable arid and semi-arid regions including large parts of the Middle East and Iran where water scarcity and high temperatures already limit production (IPCC, 2022).

Plants facing combined drought and heat stress must simultaneously cope with water deficit and thermal damage. This triggers a complex, multi-layered response program. At the physiological level, rapid stomatal closure conserves water but also limits transpirational cooling, thereby raising leaf temperature and exacerbating heat damage. Consequently, a cascade of disruptions occurs: reduced leaf water content, impaired photosynthetic efficiency, and accelerated production of reactive oxygen species (ROS) (Zhou et al., 2019; Djanaguiraman et al., 2018). At the molecular level, these signals converge on key regulatory networks. The phytohormone abscisic acid (ABA) is a primary mediator of drought responses, whereas heat shock proteins (HSPs) and specific transcription factors such as Heat Shock Factors (HSFs) and Dehydration-Responsive Element Binding proteins (DREBs) are central to thermal acclimation. A large body of evidence, primarily from controlled studies, points to an interactive ABA-ROS signaling hub as a proposed central coordinator that integrates responses to this compound stress (Devireddy et al., 2021; Lawas et al., 2018). Recent studies have further revealed the importance of somatic stress memory and stage-specific vulnerability: prior exposure can prime plants for a more efficient response, and damage during flowering or seed filling is most detrimental to final yield (Akula et al., 2025; Sehgal et al., 2018; Liu, X. et al., 2024).

1.1. Gaps in translation from model to crop systems

Despite growing research, significant knowledge gaps and translational challenges persist. Foundational insights often come from model plants such as *Arabidopsis* (Rizhsky et al., 2002, Rizhsky et al., 2004). However, a critical gap remains: how do these pathways function and interact in diverse crop species under realistic, fluctuating field conditions? (Suzuki et al., 2014; Zandalinas et al., 2018). A synthesized yet critical understanding is urgently needed one that explains how signals are integrated across biological scales and how this knowledge can be reliably applied.

Furthermore, although substantial genetic variation in tolerance exists (El Habti et al., 2020; Fonseca et al., 2024), its practical exploitation in breeding programs faces considerable hurdles. At the same time, rapid technological advances offer new opportunities, but their path from proof-of-concept to field-scale impact is far from straightforward. High-throughput phenotyping, multiomics approaches, and CRISPR/Cas-based genome editing are powerful tools. Yet their success in conferring field resilience depends on overcoming complex trait genetics and genotype-by-environment interactions (Hickey et al., 2019; Bhat et al., 2021; Rivero et al., 2021). Moreover, novel management strategies such as root-canopy coordination irrigation (RC-CI) (Chen et al., 2025) and the application of specific microbial consortia (Khan et al., 2024) show promise but require validation across diverse agroecosystems.

To bridge this critical translation gap, emerging frameworks advocate for an integrated "pixels-to-proteins" approach. This paradigm uses multi-scale remote-sensing phenomics from satellite to proximal sensing combined with multi-omics analyses (transcriptomics, proteomics, metabolomics). It aims to establish high-throughput, non-destructive links between field-level stress phenotypes and their underlying molecular mechanisms. Such integrated pipelines are essential for decoding genotype × environment × management (G×E×M) interactions and for accelerating the development of climate-resilient crop varieties and management strategies (Liang et al., 2025).

1.2. Research question and objectives

This systematic review was guided by the following primary research question: What are the integrated physiological, biochemical, and molecular mechanisms underlying crop tolerance to combined drought and heat stress, and what evidence exists for their validation under field conditions?

Accordingly, the primary objectives of this review are: (1) to provide a comprehensive synthesis of integrated crop responses to combined drought-heat stress, with special attention to stage-specific effects; (2) to critically analyze the role and interaction of core signaling components, weighing evidence from model systems against that from crops and field studies; (3) to examine the scope and implications of genetic diversity for breeding, while acknowledging practical constraints; (4) to review innovative technological and management strategies, explicitly addressing the challenges of translating them from controlled environments to the field; and (5) to identify prevailing knowledge gaps and outline priority research directions for developing climate-smart, sustainable agricultural systems. In conducting this

synthesis, we explicitly consider the methodological context of the evidence, distinguishing well-established field phenomena from mechanistic insights derived from controlled experiments, thereby offering a critically appraised perspective on translating knowledge into practice.

2. Materials and methods

This systematic review was conducted and reported in accordance with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) 2020 statement (Page et al., 2021) to ensure transparency, reproducibility, and rigor. The completed PRISMA flow diagram, detailing the study selection process, is presented in Figure 1.

2.1. Search strategy and information sources

We performed a comprehensive and systematic literature search across four major electronic databases and platforms: ScienceDirect (Elsevier), Google Scholar, Web of Science Core Collection (Clarivate Analytics), and Nature Portfolio. The search was restricted to peer-reviewed articles and reviews published in English between January 2000 and January 2025. To capture the full breadth of research on combined abiotic stresses, the Boolean search string was carefully adapted to the specific syntax and functionalities of each database. The core search terms included combinations of: ("combined heat and drought stress" OR "drought and heat stress" OR "multiple abiotic stress") AND ("physiological" OR "biochemical" OR "molecular" OR "genetic mechanisms" OR "mitigation strategies") AND ("crop" OR "plant"). No geographical restrictions were imposed.

2.2. Eligibility criteria

Studies were selected based on predefined PICOS (Population, Intervention, Comparison, Outcomes, Study design) criteria:

- Population: Cultivated crop plants.
- Intervention/Exposure: Simultaneous (concurrent) application of drought and heat stress.
- Comparison: Control plants (optimal conditions) and/or plants subjected to individual drought or heat stress.
- Outcomes: Data on physiological (e.g., photosynthesis, water relations), biochemical (e.g., antioxidant activity, osmolyte accumulation), molecular (e.g., gene expression, protein abundance), agronomic (e.g., yield, biomass), or management-related responses.
- Study Design: Original, peer-reviewed experimental research articles. Review articles, books, and non-English publications were excluded.

2.3. Study selection process

The selection process rigorously followed the PRISMA 2020 framework, as visualized in Figure 1. Initial searches across the four databases (Web of Science Core Collection, ScienceDirect, Google Scholar, and Nature Portfolio) yielded a combined total of approximately 14,000 records. After removing duplicates using a combination of automated tools (EndNote) and manual checking, 2,130 unique records remained for title and abstract screening. At this stage, 1,830 records were excluded, primarily because they focused on non-crop species, investigated individual stresses only, or were review articles.

The full text of the remaining 300 articles was then thoroughly assessed for eligibility. A further 162 articles were excluded after full-text evaluation for reasons including non-simultaneous application of stresses, irrelevant plant population, or insufficient primary data. Consequently, 138 studies were included in the initial qualitative synthesis. During the final stage of manuscript preparation, and to strengthen critical discussion points, 4 additional key studies meeting all eligibility criteria and published within the targeted timeframe were identified through citation tracking and incorporated, bringing the total pool of synthesized studies to 142.

To ensure maximum conciseness, direct relevance, and to eliminate thematic redundancy (where core concepts were more robustly covered by other included works), a final critical citation audit was performed. This audit excluded studies meeting one or more of the following criteria: (i) thematic redundancy – the core finding/concept was already comprehensively covered by another included study with stronger evidence (e.g., field validation or multi-genotype design); (ii) indirect relevance – the study focused on individual stresses rather than combined application, or on non-crop species; (iii) methodological limitations – studies with insufficient replication or unclear stress protocols. This transparent audit led to the exclusion of 43 studies from the final reference list.

During the final revision stage and in direct response to reviewer feedback, three additional high-quality systematic reviews and meta-analyses (Cohen et al., 2021; Li et al., 2025; Zhao et al., 2025) were incorporated to strengthen the critical appraisal of the ABA-ROS signaling model and stage-specific vulnerability. These were added to the existing corpus without removing any previously cited studies. Thus, the total number of cited studies increased from 99 to 102. Therefore, the final total number of studies cited in this systematic review is 102.

2.4. Data extraction and synthesis

Data from each included study were extracted into a standardized electronic form. Key extracted information included: crop species, genotype, growth environment (field, greenhouse, growth chamber), stress treatment details (intensity, duration, simultaneity), measured parameters (physiological, biochemical, molecular, yield), and key findings. Given the substantial heterogeneity in experimental designs, stress protocols, and measured outcomes across studies, a quantitative meta-analysis was not feasible. Instead, a qualitative narrative synthesis was employed, analyzing and presenting the extracted data thematically to identify consistent patterns, knowledge gaps, and overarching mechanisms.

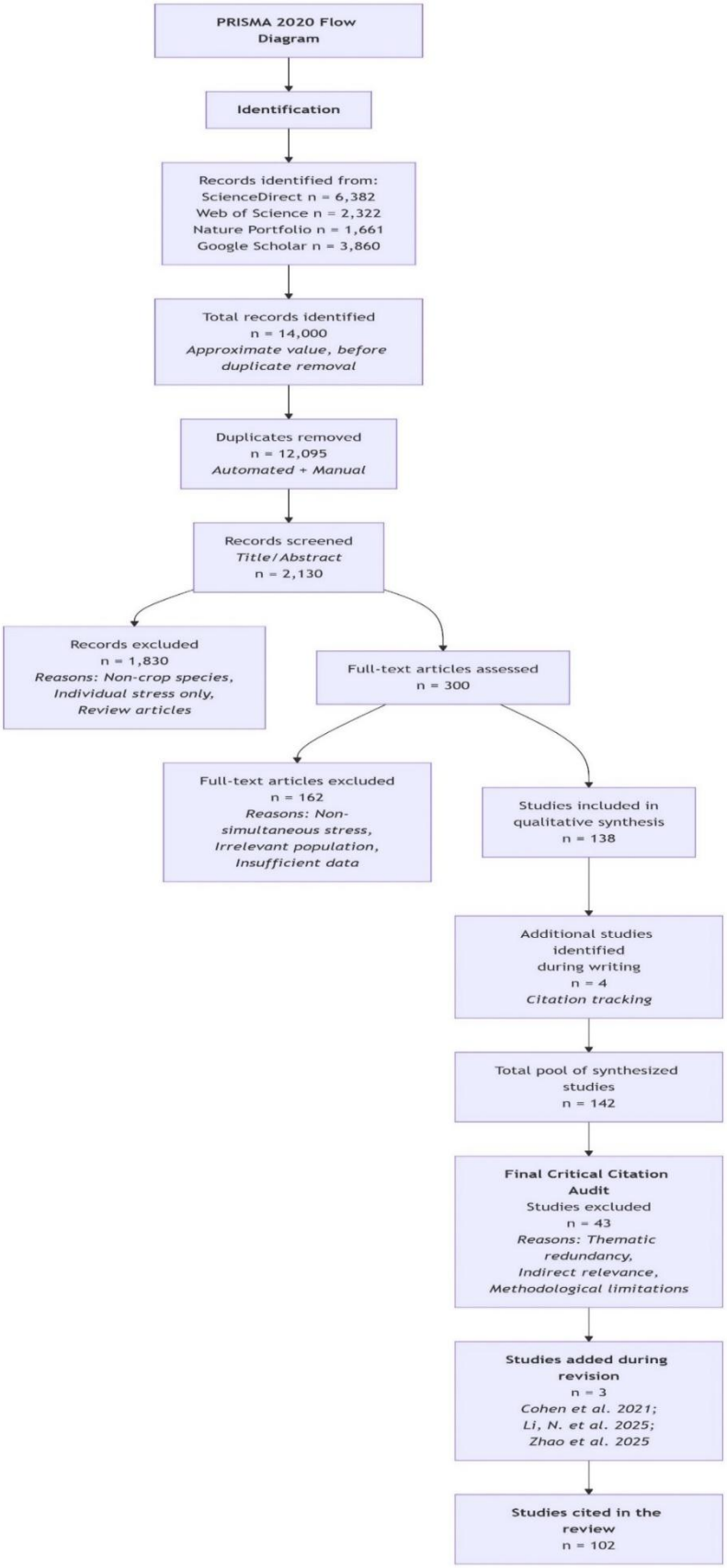


Figure 1. PRISMA 2020 flow diagram detailing the study selection process for the systematic review (Page et al., 2021). During the final manuscript preparation, four additional eligible studies were identified and incorporated into the synthesis pool. A final critical citation audit was then conducted to ensure direct relevance and eliminate thematic redundancy, resulting in the 102 studies cited in this review.

2.5. Quality assessment and risk of bias

Given the descriptive and mechanistic nature of the included studies (physiological, biochemical, molecular), a formal quantitative risk-of-bias tool (e.g., for clinical trials) was not applicable. Instead, a tiered qualitative weighting approach was employed, adapted from established frameworks for evidence synthesis in plant sciences. Each study was assessed based on three methodological criteria:

1. Environmental realism: Field or semi-field studies were given greater interpretive weight than controlled environment (growth chamber/greenhouse) studies.
2. Multi-parameter validation: Studies reporting integrated data across physiological, biochemical, and yield parameters were prioritized over those reporting a single parameter.
3. Genetic diversity: Studies including multiple genotypes were considered more robust for drawing generalizable conclusions.

This approach is explicitly described, and the applied weighting is noted in the footnotes of all results tables.

2.6. Approach to evidence synthesis and consideration of study quality

In conducting the narrative synthesis, we explicitly considered the methodological context and inherent limitations of the included studies to weight the evidence appropriately, as detailed in Section 2.5. Findings from highly controlled environments using model plants or specific genotypes (e.g., *Arabidopsis* or single crop cultivars) were interpreted as revealing fundamental mechanisms that require further validation in diverse genetic backgrounds and under complex field conditions. Greater interpretive weight was given to studies that: (a) applied combined stresses simultaneously under field or semi-field (e.g., rainout shelter) conditions; (b) reported robust, multi-parameter physiological data alongside agronomic yield or yield component measurements; and (c) included multiple genotypes to capture genetic diversity in stress response. This tiered, critical approach allows for a synthesis that distinguishes between well-established phenomena supported by field-relevant data and promising mechanistic insights derived from controlled experiments.

3. Results

The systematic screening and qualitative synthesis process identified 138 studies for in-depth analysis. Following a final critical audit to refine the corpus and ensure each citation provided direct, non-redundant value to the narrative synthesis (see Section 2.3), 102 studies are cited in this review. The findings are organized into six thematic areas.

3.1. Integrated physiological and biochemical responses: a synergistic vicious cycle

Our analysis consistently revealed that combined drought and heat stress induces a synergistic negative impact on plant physiology, which is greater than the additive effects of each stress alone. By 'hierarchical,' we refer to the cascading nature of stress response: primary sensing events (e.g., osmotic and thermal perception) trigger secondary signaling cascades (e.g., ABA-ROS), which in turn activate tertiary transcriptional and metabolic reprogramming, ultimately leading to quaternary physiological and agronomic outcomes. This directional flow of information from perception to response constitutes the hierarchy.

Key responses include a concurrent decline in relative leaf water content (RWC) and stomatal conductance (gs), triggering a severe reduction (30-60%) in net photosynthetic rate (Pn) (Abdelhakim et al., 2021a; Silva et al., 2010). A follow-up study by the same research group further demonstrated that this synergistic stress interaction and its negative physiological effects persist even under elevated atmospheric CO_2 conditions, a key factor in future climates (Abdelhakim et al., 2021b). In soybean, combined stress limited yield primarily by reducing nodes per branch (Liu, Y. et al., 2025). In cotton, heat was more detrimental to photosynthesis, while drought more severely impacted water relations and yield components, underscoring stress-specific effects (Bista et al., 2024). Similarly, in maize, post-flowering heat and drought stress significantly impaired kernel setting and accelerated leaf senescence, leading to substantial yield and quality losses (Bheemanahalli et al., 2022). This synergy is not limited to annual crops; perennial species like *Eucalyptus globulus* also activate unique protective physiological responses only under combined stress, not under each stress individually (Correia et al., 2018).

At the biochemical level, systematic overproduction of ROS leads to increased lipid peroxidation (Gill and Tuteja, 2010). In response, plants activate a coordinated antioxidant defense, with enzymes like SOD, CAT, and APX increasing by 40-70% under combined stress (Zhou et al., 2019). Tolerance in edamame was linked to both enhanced antioxidant capacity and structural cell wall modifications (Hlahla et al., 2025). This biochemical defense is complemented by the accumulation of compatible solutes. For instance, metabolic studies in peanut demonstrate a critical role for dynamic proline metabolism in sustaining drought tolerance, a mechanism likely vital under combined stress scenarios (Furlan et al., 2017).

3.2. Hormonal reconfiguration and central signaling hub

The phytohormone ABA is a key regulator, with concentrations increasing 2-4-fold under combined stress (Dobra et al., 2010). However, the response is unique; for example, Persian walnut showed concurrent increases in both ABA and salicylic acid (SA) (Habibi et al., 2025). Beyond individual hormone levels, a critical layer of regulation exists at the signaling level. Core components of the ABA signaling network itself have been identified as central players in abiotic stress responses (Cutler et al., 2010; Vishwakarma et al., 2017). Furthermore, the homeostasis of other hormones like cytokinins can be strategically modulated to improve tolerance, as demonstrated by the down-regulation of the cytokinin receptor gene *SlHK2* , enhancing combined stress tolerance in tomato (Mushtaq et al., 2022).

A pivotal concept emerging from numerous studies is the interactive ABA-ROS signaling network as a proposed central hub for signal integration (Devireddy et al., 2021; Mittler and Blumwald, 2015). In this model, ABA and ROS function in a positive feedback loop to amplify defense signals. This intricate crosstalk is foundational, as ROS are not merely damaging agents but key signaling molecules interacting with hormone pathways during combined and multiple abiotic stresses (Choudhury et al., 2017). Importantly, this model is complemented by evidence for ABA-independent pathways, such as the FL7-PP2C module (Li et al., 2025), and differential hormonal contributions across genotypes (Karamzadeh et al., 2025), suggesting a modular and context-dependent regulatory network rather than a single universal hub.

3.3. Molecular and genetic insights from omics approaches

Omics studies confirm that the molecular response to combined stress is distinct. There is strong induction of genes encoding heat shock proteins (HSPs) and antioxidant system components (Lawas et al., 2018; Grigorova et al., 2011). Integrated analyses in perennial ryegrass identified LpmiR397 as a positive regulator (Xu et al., 2025). QTL mapping and GWAS have identified genomic regions for tolerance traits in maize and wheat (Elmyhun et al., 2024; Shi et al., 2024). The concepts of somatic stress memory (where a prior stress primes a more efficient response) and transgenerational memory are emerging as important layers of regulation (Akula et al., 2025; Elkelish et al., 2025).

3.4. Genetic diversity in tolerance strategies: from avoidance to tolerance

Substantial genetic diversity exists in coping strategies. Wheat often employs tolerance strategies (maintaining physiology) (El Habti et al., 2020), while rice frequently uses avoidance (e.g., phenological escape) (Ishimaru et al., 2022). In maize, priming drought at a vegetative stage relieved yield loss from subsequent combined stress at flowering (Liu, X. et al., 2024). This intra- and inter-specific diversity is a valuable, yet underexploited, resource for breeding.

3.5. Stage-specific vulnerability and critical growth phase responses

The reproductive phase (flowering and seed filling) is consistently the most sensitive window. In lentil, combined stress during seed development severely compromised seed quality (Sehgal et al., 2018). In rice, combined stress at flowering caused significant yield loss (Lawas et al., 2018). The acute vulnerability of the reproductive phase is decisively confirmed by field-omics studies. For instance, a detailed metabolomic analysis of rice under field-imposed combined drought and heat stress during flowering revealed severe, genotype-specific disruptions in central metabolic pathways. This work provides direct mechanistic validation under real-world conditions, linking the physiological collapse during this critical window to a definitive metabolic catastrophe (Lawas et al., 2019).

This sensitivity is critically important for food security, as it directly threatens grain development. In wheat, combined stress during grain filling disrupts starch deposition and storage protein synthesis, compromising both yield and nutritional quality (Zahra et al., 2021).

Similarly, in chickpea, terminal heat and combined stress severely impact seed development, leading to reduced grain size and altered nutritional composition (Awasthi et al., 2017; Benali et al., 2023). A more recent study specifically focused on combined drought-heat stress further details its synergistic negative impact on chickpea seed development, yield, and nutritional quality (Awasthi et al., 2024). A systematic review underscores that concurrent heat and drought stress can profoundly modulate floral development, affecting fertility and ultimately seed set across species (Kumari et al., 2024).

This stage-specificity dictates that phenotyping and management interventions must be timed to protect these vulnerable periods.

3.6. Novel management and biotechnological strategies for resilience

Promising avenues include:

1. Genome Editing and Molecular Tools: Enables precise modification of tolerance genes (Bhat et al., 2021). This includes leveraging the CRISPR-Cas9 system as a transformative technology for enhancing abiotic stress tolerance (Mohamed et al., 2024), and employing novel molecular tools to unlock crop resilience (Mushtaq, W. et al., 2025). Challenges for Field Translation: Success depends on validating edits in relevant genetic backgrounds and complex field environments, overcoming potential epistatic interactions and fitness trade-offs (Rivero et al., 2021).
2. Nanotechnology: Nanoparticles (e.g., SiO_2, ZnO) can improve resilience via enhanced uptake and antioxidant effects (El-Saadony et al., 2022). This approach is part of a broader strategy where nanoparticles play a documented role in enhancing tolerance to multiple stresses (El-Saadony et al., 2022).
3. Biostimulants and PGPMs: PGPR, AMF, and novel probiotics (e.g., *Lactobacillus*) alleviate stress via multiple mechanisms (Khan et al., 2024; Abdelaal et al., 2021). In addition to microbial biostimulants, systematic reviews highlight the potential of specific protective metabolites, such as gamma-aminobutyric acid (GABA) and trehalose (Choudhary et al., 2025). The broader category of biostimulants, including non-microbial formulations, demonstrates significant power in enhancing plant resilience to abiotic stress (Lau et al., 2025). A specific mechanism involves the modulation of plant hormone homeostasis by plant growth-promoting rhizobacteria (Tsukanova et al., 2017). Furthermore, the use of inactivated endophytes, such as strain LSE01, has shown efficacy in ameliorating combined high-temperature and

drought stress in crops like tomato (Wan et al., 2023). Critical Consideration: Efficacy is highly strain- and context-specific, and results from pot trials may not translate directly to the field (Duc et al., 2023; Sharma and Joshi, 2025).

4. Seed Priming and Somatic Stress Memory: Low-cost strategies to "pre-program" defense responses (Janah et al., 2025; Liu, X. et al., 2024). This can involve hormonal or osmotic priming to induce a state of enhanced preparedness (Janah et al., 2025).
5. Innovative Irrigation (e.g., RC-CI): A systems-based approach to optimize water use under stress (Chen et al., 2025).
6. Digital Agriculture and Databases: HTP phenotyping and resources like the SCIP Database accelerate gene discovery and selection (Priya et al., 2023; Shi et al., 2024). Beyond traditional phenotyping, hyperspectral remote sensing is revolutionizing stress diagnostics (Zhong et al., 2024). Machine learning applied to novel data streams, such as bioelectrical signals from plants, offers another frontier for real-time decoding of crop health under stress (Wen and Ma, 2025).
7. Integrated Systems Approaches: Ultimately, the most robust solutions may arise from integrated systems approaches. These include field-omics-modeling pipelines that combine high-throughput phenotyping (HTP), multi-omics analyses, and predictive modeling to unravel complex G×E×M interactions (Jiang et al., 2025; Shi et al., 2024). Such approaches are essential for tailoring agroecological solutions to specific regional challenges, such as combined abiotic stresses in Mediterranean citrus orchards (Balfagón and Gómez-Cadenas, 2024).

3.7. Integrated frameworks for translational research

In line with the emerging "pixels-to-proteins" paradigm introduced in the introduction (Liang et al., 2025), our synthesis of the literature reveals that while mechanistic insights from controlled environments are abundant, few studies have systematically linked multi-scale remote-sensing phenomics with molecular data under field conditions. This gap is explicitly addressed in our proposed strategic framework (Table 6), which positions integrated "field-omics" pipelines as a primary research imperative for decoding G×E×M interactions and accelerating the development of climate-resilient crop varieties.

Table 1. Physiological and ecophysiological responses to combined drought–heat stress
This table presents a thematic synthesis. The strength and direct applicability of evidence vary across cited studies (see Section 2.5).

Study focus / key finding	Species/crop	Key findings	Reference
Synergistic photosynthetic decline	Wheat, Rice (Meta-analysis)	Reduction in gs and RWC under combined stress significantly greater than additive effects.	Abdelhakim et al. (2021a)
Tolerance via transpiration and carbohydrate allocation	Wheat	Tolerant genotypes maintain transpiration and accumulate soluble carbohydrates in grain.	El Habti et al. (2020)
Yield limitation via architecture	Soybean	Combined stress primarily reduces yield by limiting nodes per branch.	Liu, Y. et al. (2025)
Photosynthetic and oxidative damage	Tomato	Pn and PSII efficiency (Fv/Fm) decreased far more under combined vs. individual stress.	Zhou et al. (2019)
Negative interaction on growth/yield	Lentil	Combined stress caused greater biomass and survival reduction than individual stresses.	Sehgal et al. (2017)
Tolerance linked to water retention	Okra	Sustained photosynthetic efficiency and superior water retention are key for tolerance.	Asante et al. (2024)
Integrated phenotyping and genetics	Maize (Mediterranean)	HTP combined with GWAS dissects physiological underpinnings of resilience.	Shi et al. (2024)
Pre-anthesis morpho-physiology	Sorghum (Tropical)	Reductions in leaf area and chlorophyll pre-anthesis are critical for final yield.	Ndlovu et al. (2024)
Stomatal density trade-off	Wheat	Gas exchange responses vary with stomatal density, key for water/heat trade-off.	Pflüger et al. (2024)
Differential stress impacts	Cotton	Heat is more damaging to photosynthesis; drought is more impactful on water relations and yield.	Bista et al. (2024)
Photosynthetic inhibition and protection	Jatropha	Combined stress caused severe photosynthetic inhibition, activating unique protective mechanisms.	Silva et al. (2010)
Priming-induced resilience	Maize	Priming drought at six-leaf stage relieved yield loss from combined stress at flowering.	Liu, X. et al. (2024)
Yield and quality loss in maize	Maize	Post-flowering combined stress impairs kernel set, accelerates senescence, and reduces yield and quality.	Bheemanahalli et al. (2022)
Unique protective response in perennials	*Eucalyptus globulus* (Perennial)	Activates specific protective physiological responses only under combined stress, not individual stresses.	Correia et al. (2018)

Table 2. Biochemical, hormonal, and oxidative signaling responses under combined stress
This table presents a thematic synthesis. The strength and direct applicability of evidence vary across cited studies (see Section 2.5).

Study focus / key finding	Species/crop	Key findings (integrated signaling network)	Reference
Unique hormonal crosstalk	Tobacco	Drastic ABA increase and cytokinin decline occurred only under combined stress.	Dobra et al. (2010)
Coordinated signaling framework	Review (Systematic)	Proposed framework involving ROS, ABA, SA, JA, and ethylene.	Devireddy et al. (2021)
Concurrent SA and ABA increase	Persian Walnut	Combined stress intensified antioxidant responses and gene expression.	Habibi et al. (2025)
Supra-additive antioxidant activation	Barley	ROS levels and SOD, CAT, APX activities increased exponentially under combined stress.	Zhanassova et al. (2021)
Enhanced antioxidant and cell wall remodeling	Edamame (Soybean)	Tolerance linked to boosted antioxidant capacity and cell wall modifications (lignin, suberin).	Hlahla et al. (2025)
Tissue-specific proteomic response	Sorghum	Roots favored osmolyte-related proteins; leaves prioritized photosystem protection.	Ali et al. (2024)
Phenolic and hormonal contributions	Barley (Wild/Cultivated)	Different contributions from phenolics and hormones in antioxidant defense between genotypes.	Karamzadeh et al. (2025)
Multi-functional proline role	Citrus (Triple stress)	Metabolic reconfiguration with proline-mediated responses enhanced tolerance.	Balfagón et al. (2025)
Protective role of brassinosteroids	Maize (Waxy)	Exogenous BRs improved starch structure/quality under post-silking combined stress.	Li, et al. (2025)
Transcription factor engineering	Potato (Transgenic)	Overexpression of StERF94 enhanced tolerance to individual and combined heat/drought.	Charfeddine et al. (2023)
Core ABA signaling components	Review (Model Systems)	Describes the core ABA perception and signaling network central to abiotic stress responses.	Cutler et al. (2010)
ABA signaling and stress tolerance	Review (Plants)	Reviews ABA biosynthesis, signaling, and its pivotal role in abiotic stress tolerance.	Vishwakarma et al. (2017)
ROS as signaling molecules in stress combination	Review (Plants)	Highlights the essential signaling role of ROS in mediating responses to combined abiotic stresses.	Choudhury et al. (2017)
Core ABA signaling network and ROS signaling	Review (Model systems / Plants)	Foundational reviews describing the core ABA perception and signaling machinery (Cutler et al., 2010; Vishwakarma et al., 2017), and the essential signaling role of ROS in abiotic stress combination (Choudhury et al., 2017).	Cutler et al. (2010); Vishwakarma et al. (2017); Choudhury et al. (2017)

Table 3. Molecular and genetic responses to combined drought–heat stress
This table presents a thematic synthesis. The strength and direct applicability of evidence vary across cited studies (see Section 2.5).

Study focus / key finding	Species/crop	Key findings (transcriptional and post-transcriptional regulation)	Reference
Central regulatory hubs	Cereals (Review)	TFs like HSF, DREB, NAC, and MYB function as central hubs.	Lawas et al. (2018)
Candidate gene identification	Maize	QTLs and candidate genes (e.g., HSPs, membrane proteins) validated.	Mandyal et al. (2025)
HSP accumulation	Wheat	HSP18, HSP70, HSP90 accumulation exceeded levels under individual heat stress.	Grigorova et al. (2011)
HSP/Chaperone network	Review	The HSP/chaperone network acts as an integrative hub.	Jacob et al. (2017)
Transgenerational memory	Wheat	Parental exposure induced epigenetic memory, enhancing offspring tolerance via ABA genes.	Elkelish et al. (2025)
Integrated omics view	Mulberry	Transcriptomics and proteomics provided a systems-level view of metabolic impact.	Song, F. et al. (2024)
Holistic mechanism coordination	Sugarcane	Tolerance involves intricate coordination of physiological, biochemical, and molecular mechanisms.	Dhansu et al. (2024)
Regulatory module for recovery	Wheat	TaSnRK2.10-TaNLP7 module mediates post-drought recovery.	Mu et al. (2025)
HSP60 gene family	Tea Plant	CsHSP60 family members linked to heat/drought responses.	Zheng et al. (2025)
miRNA-mediated regulation	Perennial Ryegrass	LpmiR397 and caffeic acid metabolism play positive regulatory roles.	Xu et al. (2025)
ABA-independent pathway	Model/Crops	FL7 is an ancient ABA-independent inhibitor of PP2C-As.	Li, et al. (2025)
Somatic stress memory	Wheat	Prior stress primes a more efficient response to subsequent stress; differs in old/modern genotypes.	Akula et al. (2025)
'Omics' for tolerance development	Review (Food crops)	'Omics' approaches are key for identifying mechanisms and targets for combined stress tolerance.	Bhardwaj et al. (2022)
Alternative splicing trigger	Tea Plant	Drought, heat, and combined stress extensively triggered alternative splicing.	Ding et al. (2020)

Table 4. Novel strategies for enhancing resilience to combined drought–heat stress
This table presents a thematic synthesis. The strength and direct applicability of evidence vary across cited studies (see Section 2.5).

Strategy	Application details / target	Primary mechanism of action	Key outcomes and relevance	Reference(s)
Genome editing and molecular tools	CRISPR-Cas9 systems; Novel molecular toolkits.	Precise editing of key regulatory genes; RNAi/miRNA approaches; Engineering stress-responsive pathways.	Transformative potential for trait development. Challenges: Field validation, epistasis, regulatory hurdles.	Bhat et al. (2021); Mohamed et al. (2024); Mushtaq, W. et al. (2025); Balasubramaniam et al. (2025); Song, B. et al. (2025); Rivero et al. (2021)
Nanotechnology	SiO_2, ZnO, TiO_2 nanoparticles; Nanocarbon.	Smart delivery; Enhanced uptake; Catalytic antioxidant effects; Membrane protection.	Documented role in enhancing multi-stress tolerance in controlled studies. Requires ecotoxicology and field studies.	El-Saadony et al. (2022)
Biostimulants and PGPMs	PGPR, AMF, *Lactobacillus* spp.; Inactivated endophytes (e.g., LSE01); Non-microbial biostimulants; Protective metabolites (e.g., GABA, trehalose).	Hormonal modulation (e.g., ABA, ethylene); Induced Systemic Resistance (ISR); Improved nutrient/water uptake; Priming of defense responses; Osmotic adjustment.	Alleviates oxidative/hormonal imbalance. Critical: Efficacy is highly strain-/product- and context-specific; field validation essential. Potential for holistic soil-plant health management.	Abdelaal et al. (2021); Sharma and Joshi (2025); Duc et al. (2023); Khan et al. (2024); Tsukanova et al. (2017); Wan et al. (2023); Lau et al. (2025); Choudhary et al. (2025)
Seed priming and somatic stress memory	Hormonal, osmotic, or nano-priming; Controlled priming drought.	Induction of stress memory; Early antioxidant/HSP activation; Metabolic preconditioning.	Low-cost enhancement of early-stage and subsequent stress resilience. Demonstrated in crops like maize and wheat.	Janah et al. (2025); Liu, X. et al. (2024); Akula et al. (2025)
Genetic screening and selection	Germplasm screening; EMS mutants; Field phenotyping.	Identification of resistance alleles; Yield stability trait selection.	Identification of elite genotypes with stable yield under stress. Moderate-high heritability supports breeding.	Fonseca et al. (2024); Elmyhun et al. (2024)
Growth-defence carbon allocation	Chickpea (Combined stress).	Physiological and biochemical analysis.	In tolerant genotypes, carbon allocation to growth and defense is complementary; competitive in sensitive genotypes. Novel insight for breeding.	Chimphango et al. (2025)
Innovative irrigation: RC-CI	Grapevine (Deficit irrigation strategy).	Optimizes water distribution in time/space to match canopy demand and root activity.	Synergistically elevated yield, quality, and water productivity under stress in field trials. Systems-based approach.	Chen et al. (2025)
Databases and digital agriculture	SCIP Database; Bioelectrical signals + ML.	Centralized data for combined stresses; Real-time analysis of plant electrical signals.	Facilitates meta-analysis and systems biology. Decodes crop health/productivity in real-time for precision monitoring.	Priya et al. (2023); Wen and Ma (2025)
Hyperspectral diagnostics	Metabolite-derived spectral modeling; Field imaging.	Non-invasive detection of stress-specific spectral signatures linked to physiological/metabolic shifts (e.g., ABA, chlorophyll).	Enables real-time differentiation between heat and drought stress in field conditions. Critical for precision management.	Zhong et al. (2024)
Integrated systems approaches	Field-omics-modeling; Tailored agroecological solutions (e.g., for Mediterranean citrus).	Combines HTP, multi-omics, and modeling to predict G×E×M interactions; Holistic farm management.	Essential for bridging the mechanism-field gap. Enables design of context-specific, climate-smart agricultural systems.	Jiang et al. (2025); Balfagón and Gómez-Cadenas (2024); Shi et al. (2024)

Table 5. Key Studies on stage-specific vulnerability and yield/quality impacts of combined drought–heat stress
This table synthesizes studies highlighting the reproductive phase as a critical window and detailing the consequences for yield components and seed quality.

Study focus / key finding	Species/crop	Key findings on stage-specific impact	Reference
Grain development disruption	Wheat	Combined stress during grain filling impairs starch and protein accumulation, reducing yield and nutritional quality.	Zahra et al. (2021)
Seed development and nutritional quality	Chickpea	Terminal heat and combined stress during seed filling reduce grain size and alter nutritional composition.	Awasthi et al. (2017); Benali et al. (2023)
Modulation of floral development	Review (Multiple Crops)	Systematic review on how concurrent stresses affect floral development, fertility, and seed set.	Kumari et al. (2024)
Independent and combined effects at anthesis	Wheat	Dissects the independent and interactive effects of heat and drought around anthesis on yield components.	Mahrookashani et al. (2017)
Physiological basis of terminal stress resilience	Wheat (Genotypes)	Evaluates physiological traits associated with resilience to terminal drought, heat, and their combination.	Sareen et al. (2023)

Table 6. A strategic framework for future research: translating knowledge to action under combined drought–heat stress
This table presents an interpretative framework by the authors, aligning mechanisms derived from the synthesis with potential intervention points and future research priorities.

Domain of current knowledge (based on present synthesis)	Key translational limitation or identified gap	Proposed research strategy	Examples of foundational studies (from reviewed corpus)
Molecular/physiological mechanisms under controlled conditions (abundant evidence)	Gap in validation under complex field conditions and across wide genetic diversity.	Integrated "Field-Omics" Studies: Combining non-destructive field phenotyping with multi-omics analyses on the same plants under real-world stress scenarios.	Lawas et al. (2019) – Field metabolomics in rice; Karamzadeh et al. (2025) – Hormonal responses in barley under field conditions.
Substantial genetic diversity in tolerance (e.g., El Habti et al., 2020; Fonseca et al., 2024)	Challenge in converting diversity into superior cultivars with stable performance in variable target environments.	Reproductive-Stage Phenotyping and Genomic Selection: Focusing on traits related to fertility and grain filling under combined stress, developing molecular markers for these specific traits.	Shi et al. (2024) – HTP and GWAS in Mediterranean maize; Kumari et al. (2024) – Systematic review on reproductive stage vulnerability.
Promising efficacy of novel management strategies (e.g., Chen et al., 2025; Khan et al., 2024)	High context-dependency of outcomes (soil, climate, cultivar, background management).	Multi-Location, Long-Term Systems Trials: Evaluating strategies (e.g., RC-CI, microbial inoculation) within realistic crop rotations, monitoring sustainability indicators.	Chen et al. (2025) – RC-CI testing in grapevine; Duc et al. (2023) – Testing mycorrhizal efficacy across contexts.
Concept of stress memory and priming (e.g., Akula et al., 2025; Liu, X. et al., 2024)	Lack of standardized, cost-effective, and reliable protocols for large-scale use.	Development of Applied Protocols: Research on uniform, stable, and low-cost chemical, physical, or biological methods for seed or seedling priming.	Janah et al. (2025) – Review of seed priming strategies.
Dominant ABA-ROS hub model (from controlled studies)	Need to define its interactive boundaries and plasticity within the broader stress-response network in field-grown crops.	Network Biology Approaches in Field Settings: Employing systems biology tools to model ABA-ROS interactions with other pathways (e.g., HSPs, alternative hormones) across genotypes and environments.	Devireddy et al. (2021) – Signaling integration review; Jacob et al. (2017) – HSP network as an integrator; Cohen et al. (2021) – Meta-analysis; Li et al. (2025) – Differential responses review; Zhao et al. (2025) – Emerging mechanisms of abiotic stress responses.

4. Discussion

4.1. Deconstructing the vicious cycle: from synergistic damage to integrated defense

The evidence supports a "vicious cycle" where drought-induced stomatal closure suppresses cooling, thereby elevating leaf temperature and intensifying stress (Zandalinas et al., 2018). This synergistic interaction, leading to greater-than-additive detrimental effects, was documented in early foundational studies on perennial grasses (Jiang and Huang, 2000) and has since been extensively validated across a wide range of crops. This explains the supra-additive reductions in photosynthesis observed under combined stress (Zhou et al., 2019).

The plant's counter-response is a multi-layered defense involving antioxidant upregulation, metabolic reconfiguration (Balfagón et al., 2025), and structural adaptations (Hlahla et al., 2025). This cycle and the resultant physiological dysfunction have been systematically documented to impact growth, physiology, and yield across a wide range of crops (Kamatchi et al., 2024).

4.2. The ABA-ROS hub and beyond: a critical appraisal of signal integration

The ABA-ROS signaling network is a dominant and well-supported paradigm in the literature for understanding integrated stress responses under controlled experimental conditions (Devireddy et al., 2021; Mittler and Blumwald, 2015). Its role in plausibly synchronizing stomatal closure with transcriptional reprogramming is compelling. However, it is crucial to evaluate this model within the full spectrum of available evidence.

While the involvement of ABA and ROS components is robustly documented, the interpretation of their control as centralized and hierarchical is more nuanced. Emerging evidence highlights significant modulation and alternative wiring within this network. For instance, genotype-specific hormonal blends (Karamzadeh et al., 2025) and ABA-independent pathways (Li et al., 2025) demonstrate the system's plasticity. Furthermore, studies comparing single and combined stresses reveal both shared and unique signaling modules (Pandey et al., 2015; Zhang and Sonnewald, 2017), and the heat-shock protein/chaperone network itself can act as a critical, parallel integrative hub (Jacob et al., 2017).

This nuanced view is supported by recent systematic reviews and meta-analyses. A meta-analysis of over 120 studies confirmed that the reproductive stage is critically vulnerable under combined stress, with effects often being supra-additive, indirectly supporting the central role of ABA-ROS while also revealing strong genotype- and species-specificity (Cohen et al., 2021). Furthermore, a systematic review on differential plant responses explicitly documented that the ABA-ROS signaling network interacts and competes with other hormonal pathways (e.g., ethylene, jasmonic acid, brassinosteroids) under combined stress, demonstrating that the network is plastic and context-dependent rather than a solitary universal hub (Li et al., 2025). A systematic review on floral development under concurrent stress further confirmed that complex signaling networks involving ABA, ROS, and ethylene regulate fertility and seed set (Kumari et al., 2024). Similarly, a comprehensive review on emerging mechanisms of abiotic stress responses highlights that ABA-centered hormonal crosstalk operates within a broader network that includes ROS waves, epigenetic priming, and stress-specific modules under combined drought–heat conditions, further supporting the view that the ABA-ROS hub is not a solitary universal regulator but part of a flexible, integrated system (Zhao et al., 2025).

Therefore, the preponderance of evidence supports viewing the ABA-ROS interplay not as a solitary universal hub, but as a core module within a broader, flexible, and context-dependent regulatory system.

4.3. Stage-specific vulnerability: a non-negotiable focus for application

The extreme sensitivity of reproductive stages is a critical finding. It implies that tolerance mechanisms active in vegetative tissues may not suffice during flowering and grain filling. This makes reproductive-stage phenotyping non-negotiable for breeding and necessitates stage-specific management interventions.

4.4. Harnessing diversity and technology: bridging the proof-of-concept to field gap

The genetic diversity in tolerance strategies provides a tangible toolkit for breeders. Modern tools like CRISPR and omics facilitate the understanding and utilization of this diversity (Mandyal et al., 2025). However, a major translational challenge lies ahead. It must be explicitly recognized that the promising efficacy of genome editing, nanotechnology, and specific PGPM strains is predominantly reported from controlled or proof-of-concept studies (e.g., Bhat et al., 2021; El-Saadony et al., 2022; Wan et al., 2023). Their real-world impact in heterogeneous fields will be contingent on complex G×E×M interactions, economic viability, and socio-ecological acceptance. This translation challenge is a central theme in developing climate-resilient crops, requiring a concerted focus on improving tolerance to stress combinations (Rivero et al., 2021). Strategies like somatic stress memory induction and RC-CI may offer more readily scalable near-term solutions.

4.5. Synthesis: towards an integrated and critically-informed framework

We propose a framework where combined stress triggers a Vicious Cycle, mitigated by the plant's innate Defense Network (with the ABA-ROS node as a key, but not sole, component). This network's output is shaped by Genetic Blueprint and is most critically tested during Stage-Specific Vulnerabilities. Targeted Interventions (genetic, biological, agronomic) aim to strengthen this system, but their design must be informed by a critical understanding of evidence levels and translation challenges.

Future research and translation efforts must be guided by integrated, scale-bridging frameworks. The proposed "pixels-to-proteins" paradigm (Liang et al., 2025)

exemplifies this need, advocating for the convergence of remote-sensing phenomics, multi-omics profiling, and advanced data analytics. This approach is vital to move beyond correlative observations and establish causal, predictive links between canopy-level stress phenotypes detected from air/space and the molecular networks activated within the plant. Embedding such frameworks into breeding and agronomy pipelines is the next frontier for developing predictive, climate-smart agriculture.

4.6. Limitations of the review and critical knowledge gaps

This review has limitations that reflect gaps in the field. First it focused on simultaneous stress application, whereas stresses in nature can be sequential or intermittent (Suzuki et al., 2014). Recent perspectives emphasize that plant responses to such multifactorial stress combinations under climate change are immensely complex and require new experimental frameworks (Zandalinas and Mittler, 2022). Second, there is an inherent bias in the literature towards physiological and molecular studies under controlled conditions over long-term agronomic assessments in the field. Third, while we included field studies, many proposed mechanisms are inferred from controlled environments, highlighting a critical validation gap.

Future research must prioritize field-omics, long-term multi-location trials, and the development of frameworks to manage stress combinations that are temporally dynamic. The scientific community is increasingly calling for integrated 'omics' perspectives to unravel these complex interactions (Vandenbroucke and Metzlaff, 2023), and comprehensive reviews continue to outline the complex plant responses to drought and heat stress under the overarching reality of climate change (Sato et al., 2024).

5. Conclusion

5.1. Key evidence-based takeaways

This systematic review of 138 studies (with 102 cited) elucidates the complex nature of plant responses to combined drought and heat stress. The evidence robustly supports several key conclusions:

(1) The physiological impact is synergistic and often supra-additive, initiating a "vicious cycle" centered on photosynthetic collapse and oxidative damage; (2) Reproductive stages, particularly flowering and seed filling, are points of critical vulnerability, disproportionately affecting final yield; (3) Significant genetic diversity exists in tolerance strategies, ranging from physiological tolerance (e.g., wheat) to phenological avoidance (e.g., rice), providing a vital resource for breeding; (4) The ABA-ROS signaling network is a major and well-characterized component of the stress integration machinery, as evidenced by numerous controlled studies However, field-relevant evidence simultaneously underscores that it operates within a broader, more flexible regulatory system inclusive of parallel pathways and significant genetic variation in its deployment.

5.2. Informed pathways for research and application

Translating this mechanistic understanding and the identified knowledge gaps into climate-resilient agriculture requires a paradigm shift from singular solutions to integrated, scale-aware, and validation-centric approaches. Future efforts must be strategically aligned along the following reinforced pathways:

- Breeding for Real-World Resilience: Breeding programs must prioritize reproductive-stage phenotyping under combined stress conditions, leveraging the vast genetic diversity in tolerance strategies (e.g., avoidance vs. tolerance) and modern tools like genomic selection. The incorporation of traits related to somatic stress memory, optimal growth-defense carbon allocation, and transgenerational memory shows particular promise for creating stable yields.
- Validation-Centric Biotechnology and Biostimulants: While genome editing (e.g., CRISPR-Cas), nanotechnology, and novel biostimulants (including PGPMs, protective metabolites, and inactivated endophytes) offer precision and novel modes of action, their development pipelines must incorporate early and iterative field validation. Success depends on overcoming strain-/product- and context-specificity, epistasis, G×E interactions, and ensuring socio-ecological acceptance.
- Systems-Based Agronomic and Digital Management: Ready-to-deploy strategies such as seed priming, somatic stress memory induction, and innovative irrigation like Root-Canopy Coordination Irrigation (RC-CI) enhance near-term resilience. These must be coupled with digital agriculture tools, including hyperspectral remote sensing for stress diagnosis and machine learning for predictive management, to optimize decisions in real-time.
- Bridging the Gap via Integrated Frameworks: The primary research imperative is to adopt integrated "field-omics-modeling" pipelines. As exemplified by the "pixels-to-proteins" paradigm, the convergence of multi-scale remote-sensing phenomics, multi-omics profiling, and advanced data analytics is non-negotiable for decoding G×E×M interactions. This approach is essential to move beyond correlation, establish causal, predictive links between field phenotypes and molecular mechanisms, and ultimately design tailored, climate-smart agricultural systems capable of withstanding multifactorial stress combinations.

This review synthesizes that while our mechanistic knowledge is substantial, its ultimate value lies in its rigorous translation into sustainable agricultural systems. The evidence robustly supports the ABA-ROS signaling node as a core module, but one that operates within a broader, flexible, and context-dependent regulatory network.

5.3. Implications for integrated research and policy

Moving forward requires a conscious shift. We must move from siloed solutions toward co-designed, scale

-aware approaches.Breeding programs need to integrate reproductive-stage phenotyping under combined stress with farmer participatory selection. This ensures that new varieties are not only resilient but also relevant to local conditions. Technology development pipelines should embed socio-economic and environmental impact assessments from the outset. Early evaluation of these factors increases the likelihood of real-world adoption.Ultimately, policy and investment must support long-term, system-level research platforms. Such platforms can validate resilience strategies across the diverse landscapes that define global agriculture.

In conclusion, securing crop productivity under a changing climate demands more than singular solutions. It requires the conscious integration of resilient genetics, validated biotechnologies, and adaptive management practices. Above all, this integration must occur within a framework that continuously acknowledges and addresses the complexity of real-world field environments.

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