



REVIEW

Cross-Tolerance in a Changing Climate: Physiological Responses to Combined Abiotic Stress

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ABSTRACT: Climate change is increasing the frequency and intensity of overlapping abiotic stresses, making cross-tolerance a critical component of plant resilience. While single stress responses have been extensively characterized, plants in natural and agricultural environments frequently encounter simultaneous or sequential stresses such as drought–heat, light–drought, and drought–salinity, which trigger nonadditive and often unpredictable physiological outcomes that vary with stress intensity, timing, and species. This review synthesizes current understanding of the mechanisms underlying cross-tolerance, emphasizing how contradictory signals, stress timing, and physiological integration shape plant responses under combined stress. We highlight how stomatal regulation, leaf energy balance, hydraulic function, and photosynthetic processes, including PSII stability and Rubisco activase activity, interact to determine stress vulnerability. At the biochemical level, osmotic adjustment, redox buffering, and hormone-mediated signaling networks reprogram metabolism so that the plant allocates resources to protection and damage repair rather than to just growth. We further discuss how stress memory, priming, and shared signaling pathways such as reactive oxygen species, abscisic acid, and mitogen-activated protein kinase cascades contribute to enhanced tolerance across stress types. Finally, we examine the implications of cross-tolerance for crop improvement, including breeding strategies, genomic selection, genome editing, and emerging technologies such as nanopriming and high-throughput phenotyping. Bridging the gap between controlled environment studies and field performance remains a major challenge, underscoring the need for multi-stress field trials and integrative breeding pipelines. Together, these insights provide a framework for developing climate-resilient crops capable of withstanding the complex stress environments of future agriculture.

KEYWORDS: Reactive oxygen species; stress memory; osmotic adjustment; physiological changes; redox homeostasis; multi-stress breeding

1 Introduction

Global climate change is intensifying the adverse effects of environmental stress on living organisms. Plants, as sessile organisms, are particularly vulnerable because they cannot escape unfavorable conditions; as a result, their growth, development, and productivity are consequently impaired. Among environmental challenges, abiotic stress represents one of the most significant constraints on plant growth and survival [1]. Abiotic stresses include non-living environmental factors such as drought, waterlogging, heat, cold, soil salinity, nutrient deficiencies, heavy metals or metalloids, ozone, and low or excessive light [2,3]. Although plants possess innate mechanisms that allow them to tolerate these stresses to some extent [4], most research has traditionally focused on single stress responses, such as drought [5] or salinity [6]. However, in natural environments, plants are far more likely to encounter multiple stresses simultaneously or sequentially,

including drought–heat, light–drought, or salinity–drought combinations [7,8]. The physiological and molecular responses to combined stress cannot be inferred from single stress studies alone [9]. Instead, they emerge from complex interactions that require experimental approaches capable of integrating multiple stresses to better reflect field conditions.

The concept of cross-tolerance provides a valuable framework for understanding how plants adapt to such multifaceted stress environments. Cross-tolerance refers to the phenomenon in which exposure to one stress (e.g., drought) enhances a plant's resilience to a different, often unrelated stress (e.g., salinity or heat) [10]. This enhanced tolerance arises from shared defense mechanisms, frequently mediated by common signaling molecules such as reactive oxygen species (ROS) and redox signals, which activate broad metabolic and genetic responses that promote systemic adaptation [11]. Understanding cross tolerance requires examining how plants integrate multiple signaling pathways during overlapping stress periods. This integration, known as crosstalk, can enhance or suppress stress responses depending on whether interactions are synergistic or antagonistic [12,13]. Crosstalk among ROS, calcium signaling, phytohormones, including abscisic acid (ABA), salicylic acid, and ethylene, and light-responsive pathways play a central role in shaping plant responses under combined stress conditions [14].

The significance of cross-tolerance extends beyond fundamental plant biology due to its implications for natural ecosystems, agriculture, and global food security. In natural ecosystems, cross-tolerance enables plants to survive in increasingly variable and extreme environments. In agricultural systems, climate change is causing abiotic stresses to occur more frequently and concurrently, posing major threats to crop production and food security [15,16]. These stress-induced yield losses impose substantial economic burdens worldwide, underscoring the urgency of understanding the physiological processes that enable plants to withstand combined stresses. While single stress studies have been instrumental in identifying core stress-response pathways, they often fail to capture the interconnected nature of stress signaling and metabolism that occurs under field conditions [17].

This review synthesizes current knowledge on plant physiology and cross-tolerance under combined abiotic stresses using a structured literature search method, with a focus on interactions such as drought–heat, drought–salinity, and light–drought. While both angiosperms and gymnosperms exhibit adaptive responses to abiotic stress, there are significant differences in their physiological responses. Gymnosperms are generally more drought-tolerant yet tend to be more sensitive to heat stress, whereas angiosperms are typically more heat-tolerant but exhibit species-dependent variability in drought tolerance. Given these contrasting features and the dominance of angiosperms in global agricultural systems, this review primarily emphasizes angiosperm row crops and the model plant *Arabidopsis thaliana*. It focuses on the key physiological and molecular mechanisms, including hormonal regulation, oxidative stress responses, photosynthetic adjustments, and signaling crosstalk, that underpin plant resilience under combined stress from peer-reviewed literature from 2000 to 2025. Earlier foundational studies are also included in this review where historically relevant. Finally, this review identifies critical knowledge gaps and highlights future research directions by comparing insights across diverse plant systems.

2 Cross-Tolerance Concept and Framework

Over evolutionary time, plants have adapted to continuously fluctuating environmental conditions. Current climate projections indicate that global surface temperatures are likely to exceed 1.5°C in the coming decades if greenhouse gas emissions remain unchanged [16]. As a result, the intensity and frequency of abiotic stresses are increasing. Although plants possess inherent adaptive capacities, these stresses disrupt water relations, cellular homeostasis, and carbon assimilation in plants [4], ultimately reducing

growth and productivity in both natural and managed ecosystems. In the field, plants rarely encounter a single stress in isolation; instead, they are frequently exposed to combined stresses, such as excessive light or heat occurring alongside drought or salinity-induced drought. Under such conditions, plants exhibit complex physiological responses that differ substantially from those triggered by individual stresses [7,8]. Understanding these physiological and molecular mechanisms is therefore essential for predicting plant performance under future climate scenarios and for developing sustainable cropping systems.

Building upon this framework, cross-tolerance can arise from shared cellular responses activated under different stress conditions, though the degree and specificity of this response vary substantially depending on plant species, stress intensity, developmental stage, and environmental context (Fig. 1) [18]. Because even a single stress activates numerous signaling pathways, the mechanistic basis of cross-tolerance remains complex and requires further investigation. One prevailing hypothesis proposes that cross-tolerance can arise from shared cellular responses induced by different stress exposures, particularly the enhanced production of signaling molecules such as ROS (e.g., H_2O_2) and methylglyoxal (MG), though the extent of these shared responses varies among species and stress combinations [19]. Under combined stress, H_2O_2 and MG function not merely as damaging byproducts but as key intermediates in redox and hormonal signaling pathways, influencing kinase activity, transcription factor function, and ultimately the expression of stress-responsive genes [8,20,21]. This integration provides a mechanistic foundation for cross-tolerance by allowing signals generated under one stress to enhance responses to future stresses whether occurring individually or in combination.

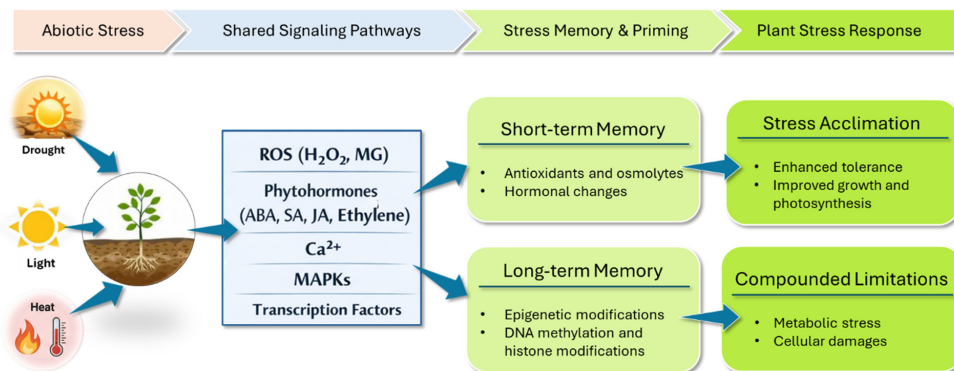


Figure 1: Mechanistic framework of cross-tolerance in plants.

Early cross-tolerance research often relied on priming treatments, in which plants were exposed to mild or moderate stress that was insufficient to cause permanent damage but capable of inducing physiological adjustments [22–24]. For example, brief drought priming reduces soil water availability enough to lower stomatal conductance and leaf water potential without causing irreversible wilting, and plants typically recover after rewatering [25]. Studies by [12,13] demonstrated that such priming-induced changes, such as enhanced antioxidant capacity and improved membrane stability, can persist beyond the initial stress period and increase tolerance to subsequent stress events. However, priming does not universally confer benefits; under novel stress combinations, previous exposure to stress can alter signaling responses [26,27]. This outcome depends critically on the nature, timing, and intensity of both the priming and the stress. With advances in physiological and molecular techniques, cross-tolerance research has progressed from descriptive observations to detailed mechanistic insights. Modern frameworks emphasize that shared signaling pathways, rather than stress-specific responses, are central to cross-tolerance. Key integrative components that appear broadly conserved across plant taxa include phytohormones, calcium ions (Ca^{2+}),

mitogen-activated protein kinases (MAPKs), and ROS, which coordinate transcriptional regulation and downstream physiological adjustments in both model species like *Arabidopsis* and major crops studied (wheat, rice, cotton, maize, and soybean) [12,13]. Through these interconnected networks, plants modulate their responses according to the type, severity, duration, and frequency of stress exposure.

Even though cross-tolerance studies have been widely reported, their results remain mostly context-dependent and sometimes contradictory. Some studies reported that prior exposure to abiotic stress enhanced tolerance to subsequent stress through antioxidant defense, hormonal regulation, and metabolic changes [12,13,25]. Other experiments showed that prior stress exposure caused significant constraints in metabolic and carbon allocation, especially under prolonged stress exposure [28,29]. These contradictory results indicate that cross-tolerance is not universal but emerges only when protective signaling and acclimation adjustments outweigh the total physiological damage. Therefore, it is important to consider these trade-offs while interpreting multi-stress experiments assessing cross-tolerance significance.

Due to abiotic stresses occurring as recurrent or overlapping episodes rather than isolated events, plants often do not fully recover before encountering subsequent stress [15,30,31]. Stress-induced signaling pathways may consequently remain partially active or altered, leading to long-lasting modifications in cellular signaling [31]. This phenomenon is known as stress memory, which is a key component of the cross-tolerance framework and refers to a plant's ability to "remember" prior stress exposure and respond more rapidly and effectively upon re-exposure [32,33]. Stress memory operates at multiple levels in plant species where it has been characterized. Short-term memory, demonstrated in *Arabidopsis*, rice, and wheat is driven by persistent changes in hormonal signaling, redox balance, and secondary metabolite accumulation following priming events [34–36]. These physiological adjustments can remain for days or weeks after stress removal, enabling faster and more efficient responses to subsequent stress. For instance, priming-induced accumulation of osmolytes or antioxidants can enhance tolerance to later heat or drought episodes [26]. Long-term or epigenetic stress memory arises when stable epigenetic marks, such as DNA methylation, histone modifications, and chromatin remodeling, are maintained and inherited across generations to allow an inherited stress response to become activated in the plant [27]. Increasing evidence suggests that such epigenetic modifications contribute to cross-tolerance by maintaining a transcriptionally primed state that enables rapid and robust responses to future abiotic stress.

Beyond differences in signal transduction mechanisms, the exposure memory, that is, the timing, sequence, and duration of stress events, represents a second major factor contributing to the complexity of plant responses under combined stresses. The duration and intensity of stress periods further determine whether timing leads to acclimation or compounded limitations. Short stress episodes often induce rapid acclimation, reflecting largely reversible processes that enhance tolerance during subsequent stress events. Particularly when recovery intervals allow physiological systems to reset. In contrast, prolonged or high-intensity stresses tend to produce compounded limitations, where multiple constraints interact to increase the risk of injury. For example, stomatal limitations on CO₂ uptake and carbon gain can become more severe under combined stress, amplifying the negative effects on plant performance [37,38]. This cause-effect perspective is valuable because it distinguishes early, reversible stress effects from later, more persistent limitations that contribute to long-term damage. Whether cross-tolerance leads to acclimatization or compounded adverse effects depends largely on the severity and length of stress exposure. Recurrent protective pathways are frequently triggered by mild or temporary stress, allowing for stress memory formation and acclimatization. On the other hand, persistent or severe stress can cause irreversible hydraulic or metabolic damage, overload repair mechanisms, and change ROS from signaling to harmful activities. Therefore, a limited physiological window is where cross-tolerance works best.

3 Responses of Plants to Combined and Single Stresses

3.1 Contradictory Signals in Stomatal Regulation

Combined stress conditions are particularly challenging because plants must respond to regulatory signals that drive stomatal behavior in opposite directions. Under drought, plants need to conserve water by reducing stomatal aperture; a response largely mediated by abscisic acid (ABA). The magnitude and timing of this closure depend on the species, drought stress intensity, and atmospheric conditions [39,40]. In contrast, during heat stress, stomatal opening is often promoted to facilitate transpiration and initiate evaporative cooling. A further complication is that stomata also regulate the plant's hydraulic status, since transpiration drives water movement through the xylem. When abiotic stresses occur together, plants face a physiological conflict; they may not fully satisfy the demands of both stress responses simultaneously (i.e., conserving water via stomatal closure versus sustaining transpiration for evaporative cooling and CO₂ uptake). As a result, stomatal behavior may become constrained, which can lead to reduced transpiration, elevated leaf temperatures, and increased susceptibility to thermal and oxidative damage (Table 1) [39,40].

Plant stomatal responses may be mediated through shared signaling pathways. OST1 (protein/kinase OPEN STOMATA1), an ABA-activated kinase first characterized in *Arabidopsis thaliana*, phosphorylates key ion channel regulators in guard cells, promoting the efflux of osmotic solutes and drives stomatal closure [28,39,40]. Under combined drought and heat, this ABA-driven closure signal often tends to dominate over the cooling-associated opening response, creating a strong stomatal limitation that may restrict transpiration and evaporative cooling.

Stomatal regulation under combined stresses is also highly context and species dependent. Different tissues and developmental stages may not respond uniformly. Reproductive organs, for instance, may partially maintain stomatal opening to support short-term reproductive success (e.g., rice floral organs, *Oryza sativa*). Yet this may come at a cost: keeping stomata open under drought-heat conditions can intensify the carbon-water tradeoff, reduce photosynthetic efficiency, and increase photosynthetic limitations [29]. These tissue-specific adjustments illustrate how plants attempt to balance survival with reproductive function even when hydraulic and thermal constraints restrict optimal stomatal behavior.

This “push-pull” model of stomatal regulation further extends to stress combinations involving high irradiance. Under normal conditions, light, especially blue light, activates guard cell photoreceptors, stimulates H⁺-ATPase activity, hyperpolarizes the membrane, and increases K⁺ uptake, all of which promote stomatal opening and CO₂ entry for photosynthesis. However, during drought, the ABA/OST1-mediated closing signal (characterized in *Arabidopsis thaliana*) can override these light-induced opening cues. As a result, stomatal conductance may remain tightly restricted even under strong irradiance, reinforcing CO₂ limitation and increasing excitation pressure within the chloroplast. This strict stomatal control is a defining feature of drought combined with heat or high light, and it may contribute to the heightened risk of thermal and oxidative stress under these conditions. In some genotypes and stress regimes, partial stomatal opening may be maintained to support evaporative cooling, potentially reducing the heat load while exacerbating water loss [41].

3.2 Physiological Integration under Drought-Heat: Leaf Energy Balance, Water Status, and Hydraulic Risk

Under drought and heat stress, especially when accompanied by high irradiance, the challenge to leaf energy balance is constrained stomatal conductance due to hydraulic feedback (e.g., in crops such as wheat, *Triticum aestivum*, and cotton, *Gossypium hirsutum*). While controlled-environment studies allow single-stress and combined-stress effects to be isolated, field conditions often impose fluctuating

combinations of temperature, radiation load, and vapor pressure deficit (VPD), which dynamically alter transpirational demand and leaf cooling capacity. Fluctuating conditions of heat and drought-induced stomatal conductance can represent important constraints that not only initiate a response to the environment but also influence traits such as carbon dioxide uptake, water loss, and leaf temperature [42,43]. Stomatal limitation can affect plant growth and biomass, and plant adjustment to altered leaf energy balance can differ between short-term and long-term exposure. In some angiosperm species, high VPD increases atmospheric evaporative demand and can promote ABA-associated stomatal closure, which constrains hydraulic supply and reduces net photosynthesis. Under combined drought-heat-light conditions, the leaf energy balance shifts to limit evaporative cooling, which can amplify heat stress. As a result, leaf temperatures can increase by 5–10°C relative to heat stress alone [44] depending on the genotype, species, and environmental conditions (e.g., high radiation load and low wind speeds) [45]. When leaf temperatures exceed ambient air temperature, core metabolic processes and cellular function can decline, particularly net photosynthesis and membrane integrity [45].

The synergistic disruptions to leaf energy balance feed directly into plant water relations by accelerating dehydration by hydraulic failure. When heat stress coincides with drought, stomatal closure is non-linear, and drought stress signals not only reduce conductivity but also can drop leaf water potential, which further intensifies the plant's water supply and water use efficiency. While it is species specific to the sensitivity of speed of stomatal closure and water preservation, when the transpiration demand is increased, the xylem water potential gradient increases, increasing tension to pull more water for water use and leaf cooling/transpiration. The increase in xylem tension also increases the risk for cavitation (embolism) [45]. The consequence of xylem vessel cavitation is reduced hydraulic conductivity, lower leaf water potential, and lower relative water content [46–49].

This leaf balance of hydraulic responses is also shaped by the activity of aquaporins, membrane-bound water channel proteins that regulate hydraulic conductivity in roots and other tissues. Aquaporin function influences how rapidly plants can adjust to changes in water demand and maintain water status under combined drought-heat stress. Altered aquaporin activity can therefore accelerate or slow the decline in water potential and RWC during stress episodes, depending on aquaporin isoform, tissue type, and stress intensity/duration [50,51]. In species with high hydraulic efficiency, high heat and drought loads can cause plant death due to water hydraulic disconnection. Gymnosperm species (e.g., *Pinus radiata*) are often more drought resistant, with better hydraulic control, lower cavitation, and stronger stomatal control than their angiosperm counterparts [51].

At the whole-plant level, these interacting constraints help explain the non-linear nature of combined drought-heat responses. Yield-related traits in angiosperms, such as reproductive retention, organ structure, and grain filling duration, often decline more rapidly under elevated VPD associated with combined stresses than would be predicted from single stress responses [47], particularly under severe stress and during sensitive developmental windows. This contradictory response to heat and drought is evident when examining case studies for crops. For example, in wheat, when both heat and drought are imposed during reproductive growth, it can affect pollen functionality and grain development, resulting in a shorter grain filling period and affecting yield components [52]. In cotton, when both elevated temperature and drought are imposed, it can lead to a reduction in carbohydrate and energy metabolism in the anthers, affecting pollen fertility due to heat stress and, consequently, reproductive success and yield components [53]. In maize, when both drought and heat are imposed, it can result in a greater reduction in kernel set than when either stress is imposed individually, indicating reproductive sensitivity to both stresses, although

the magnitude of these impacts can vary across genotypes and environments in all angiosperms [54]. Key physiological parameters associated with these crop-specific outcomes are summarized in Table 1.

Persistent reductions in stomatal conductance restrict carbon assimilation and intensify imbalances in leaf energy exchange. As evaporative cooling declines, more absorbed radiation must be dissipated as heat, reinforcing the rise in leaf temperature and further constraining photosynthetic capacity. Under combined drought-heat conditions, this feedback loop, reduced conductance, impaired cooling, elevated leaf temperature, and declined biochemical function to affect growth and yield. In angiosperms, this accelerates the loss of metabolic performance and reproductive success. Although the extent of this impact may depend on stress severity, duration, and species-specific thresholds [47,55].

3.3 Light As a Co-Stressor: PSII Vulnerability, Rubisco Activase Bottlenecks, and Photoinhibition

When high light occurs together with drought and/or elevated temperature, photosynthesis becomes limited not only by plant water status and thermal sensitivity but also by excess excitation pressure within the chloroplast. Drought-induced stomatal closure restricts CO₂ uptake [56], yet light-harvesting reactions continue even when carbon assimilation is constrained. As a result, absorbed light can exceed the capacity for carbon fixation and downstream electron use, leading to photoinhibition and photooxidative stress [57,58]. Light intensities that would normally support assimilation under well-watered conditions can become inhibitory during drought and combined stress (drought-heat, drought-light, drought-heat-light), leading to sharp reductions in CO₂ assimilation, PSII operating efficiency, and electron transport rate when stresses occur concurrently, particularly under severe stress and prolonged exposure [59,60].

Under high irradiance, leaf photosynthetic machinery rapidly reaches light saturation, beyond which additional absorbed photons cannot be used for carbon fixation. Once photochemical capacity is exceeded, the excess excitation energy must be dissipated to prevent photodamage. Plants regulate this imbalance through non-photochemical quenching (NPQ), thermal dissipation in the xanthophyll cycle, and adjustments in leaf optical properties, all of which convert surplus absorbed light into heat. When drought or heat simultaneously restricts stomatal conductance and reduces evaporative cooling, this thermal dissipation becomes a larger fraction of the leaf energy budget, elevating leaf temperature and increasing the risk of photoinhibition and oxidative stress. Thus, under combined drought-heat-light stress, the interaction between light saturation and limited cooling capacity intensifies leaf thermal load and constrains photosynthetic performance [41].

High light intensity rapidly saturates photochemistry and increases excitation pressure on the photosystems, elevating the risk of reaction-center damage and triggering photoprotective mechanisms such as non-photochemical quenching (NPQ) [59]. NPQ is activated by a shift in the pH gradient across the thylakoid membrane and is mediated by the xanthophyll cycle and the PsbS protein, thereby reducing excitation pressure and constraining ROS formation [61,62]. Under drought-heat, photosynthesis declines not because of a limiting energy supply, but because stomatal closure restricts CO₂ availability and heat stress destabilizes metabolic and enzymatic processes, reducing the capacity to use absorbed light [63,64]. As excess photons continue to drive the electron transport chain, excitation pressure rises, and NPQ becomes essential for dissipating surplus energy as heat; however, under severe or prolonged stress, photoprotection may be insufficient to prevent over-excitation and photoinhibition [59,60]. Additional protective strategies include cyclic electron transport, enhanced antioxidant capacity [65,66], and pigment-based mechanisms such as anthocyanin accumulation [67].

At the photosystem level, this imbalance increases the vulnerability of photosystem II (PSII), where excess absorbed light enhances charge recombination and alternative electron transfer pathways within

PSII, thereby promoting the formation of ROS, including singlet oxygen generated near the reaction center. These oxidative reactions damage PSII proteins and cofactors, particularly the D1 protein, which must be continuously degraded and resynthesized to maintain electron transport [68]. Although photosystem I (PSI) can be impaired under specific conditions, photoinhibition is typically initiated and most strongly expressed at PSII [69]. Elevated temperatures further exacerbate PSII susceptibility by increasing membrane fluidity and disrupting lipid-protein interactions required to stabilize PSII super complexes, the oxygen-evolving complex, and associated repair machinery [70,71]. Therefore, maintenance of photosystem function under combined stress depends strongly on the capacity of photoprotective energy dissipation and redox homeostasis.

A second major bottleneck arises from the heat sensitivity of Rubisco activase (RCA) (e.g., in *Arabidopsis thaliana* and wheat, *Triticum aestivum*). RCA is required to maintain Rubisco in its catalytically active form, yet its activity declines sharply under heat stress. When RCA becomes impaired (no longer active in its carbamylated state), Rubisco remains partially or fully inactive even if ATP and NADPH continue to be produced by the light reactions [72]. Under drought, restricted CO₂ diffusion further increases the probability that Rubisco will engage in oxygenation rather than carboxylation, initiating photorespiration. This oxygenase activity consumes additional ATP and reduces the power to make sugars, thereby increasing the chloroplast reductive pressure and increasing the mismatch between light capture and carbon assimilation [61,73]. As a result, excess excitation energy accumulates in the photosynthetic electron transport chain, elevating the risk of photodamage unless protective mechanisms intervene [61,73].

Consistent with this integrated view, combined drought-heat stress induces pronounced diffusive-biochemical interactions, where restricted CO₂ supply and temperature-dependent biochemical inhibition jointly reduce photosynthetic capacity and contribute to yield losses across species [74,75], although the magnitude of these interactions may vary with genotype, stress intensity, and exposure duration. As photosystem efficiency declines and repair processes become increasingly constrained under combined drought-heat stress, the capacity to convert absorbed light into fixed carbon is reduced, resulting in sustained declines in net photosynthesis despite high irradiance.

Within the chloroplast, combined drought, heat, and high irradiance disrupt the balance among carbon assimilation, water availability, and repair capacity, leading to enhanced formation of ROS within stressed thylakoid membranes [76]. As CO₂ availability declines and electron sinks become constrained, excess excitation energy is increasingly diverted toward ROS production. At moderate levels, these ROS function as signaling molecules, including through chloroplast-to-nucleus (retrograde) pathways that activate drought-responsive gene expression [77]. Under some conditions, such light-dependent signaling promotes acclimation and enhances tolerance to subsequent drought stress, although under severe or prolonged stress, ROS accumulation may instead contribute to oxidative damage and trade-offs [78,79].

As water limitation intensifies and carbon assimilation declines sharply, this regulatory balance collapses. Photochemical excess can no longer be effectively dissipated; ROS production overwhelms antioxidant capacity, and PSII repair processes become increasingly constrained. Under these conditions, high light transitions from a potential acclimatory signal to a dominant driver of photoinhibition and oxidative photodegradation, particularly when recovery windows are short. These interactions generate strongly non-additive damage patterns under combined drought-heat-light stress [60,80]. The non-additive nature of PSII efficiency declines across species under these combined conditions is reflected in Table 1.

Table 1: Comparison of key physiological responses to combined abiotic stresses in major crop species.

Species	Stress	Stomatal Conductance	PSII Efficiency/ Photosynthetic Capacity	Osmolyte Response	ROS	Ref.
Wheat (<i>Triticum aestivum</i>)	Drought + Heat	Reduced: non-linear decline under combined stress; xylem cavitation risk elevated under severe stress	Reduced: RCA thermostability limits Rubisco activation under heat; shorter grain filling period and impaired pollen functionality under reproductive stage stress	Proline + sucrose ↑; sucrose accumulation dominates under prolonged combined stress	↑; NPQ partially buffers excitation pressure under moderate stress	[52,81]
Maize (<i>Zea mays</i>)	Drought + Heat	Reduced; non-linear response, greater restriction under combined stress; genotype dependent magnitude	Reduced; greater kernel set reduction under combined stress; genotype and environment dependent	Sucrose ↑; osmolyte pattern varies across genotypes and environments	↑	[54,73]
Cotton (<i>Gossypium hirsutum</i>)	Heat + Drought	Reduced; stomatal limitation compounded by heat-driven transpiration demand	Reduced: RCA inactivation contributes to CO ₂ fixation limitation; pollen fertility impaired through anther carbohydrate and energy disruption released	Carbohydrate destruction	↑	[58,70]
<i>Arabidopsis thaliana</i>	Drought + Heat	Strongly reduced	Reduced (non-additive)	Sucrose + maltose ↑; non-additive accumulation pattern; osmolyte response differs from single stress	↑	[25,82]
Okra (<i>Abelmoschus esculentus</i>)	Drought + Heat	Photosynthetic efficiency and water retention partially maintained	Evidence of effective photoprotective capacity under moderate combined stress	Osmolytes ↑: contributes to tolerance under moderate stress	Buffered, effective antioxidant and photoprotective capacity under moderate stress	[83]
Sorghum (<i>Sorghum bicolor</i>)	Drought + Light	Reduced	Synergistic photoinhibition under combined stress		↑ Strong photoinhibition consistent with increased photoprotective capacity	[59]

4 Metabolic and Hormonal Recovery Modules: Osmotic Adjustment, Redox Control, and Growth Reprogramming

Under combined abiotic stresses, water loss and reduced water potential impose osmotic stress that threatens turgor, membrane stability, and cellular function. A core recovery module is osmotic adjustment, in which compatible solutes accumulate to maintain cytosolic osmotic potential relative to the external environment and to support continued cellular function under dehydration. When photosynthetic capacity becomes restricted by stomatal closure, leaf heating, and chloroplast excitation pressure, plants often shift their metabolism from growth toward protection, conservation, and repair. The osmolyte and ROS responses associated with this shift, as documented in Table 1, reflect highly variable but consistently non-additive metabolic responses under combined stress [81,82,84–87]. Under drought-heat stress, this shift is reflected in substantial changes in carbon metabolism, particularly in carbohydrate and amino acid pools. These changes arise from reduced carbon assimilation combined with an increased need for plants to conserve resources [88–90]. A characteristic of this metabolic reprogramming is the remodeling of compatible solutes (osmolytes). Soluble sugars (e.g., sucrose and trehalose), polyols (e.g., mannitol), amino acids (e.g., proline), and quaternary ammonium compounds (e.g., glycine betaine) can accumulate to support turgor maintenance and mitigate oxidative stress, although the pattern of accumulation is highly osmolyte specific rather than a uniform increase across all solutes (including studies in rice, *Oryza sativa*, and winter wheat, *Triticum aestivum*), and it may vary with species, genotype, plant type, and stress intensity/duration [81,84,85].

Sugars and other compatible solutes are key players in stress protection and energy balance under drought-heat stress. Under combined drought-heat stress, sugars often accumulate due to both reduced utilization from growth suppression and mobilization of carbohydrate reserves in response to declining photosynthetic rates. Metabolomic studies (e.g., rice floral organs, *Oryza sativa*, and *Arabidopsis thaliana*) often show that sucrose and other sugars, such as maltose, increase in a non-additive manner under these conditions, reflecting distinct metabolic signatures that are often specific to the drought-heat interaction [25,82,86,87]. While proline is commonly emphasized as a primary osmoprotectant under drought, supporting osmotic adjustment, membrane stabilization, and oxidative stress mitigation [91], combined drought-heat stress can shift protective emphasis toward sucrose-centered mechanisms. This shift may be driven by starch-to-sucrose conversion and broader sugar rebalancing, linking carbohydrate metabolism directly to osmotic regulation and maintenance of cellular homeostasis under conditions of constrained carbon assimilation [91]. In parallel, polyols (e.g., mannitol), trehalose, and glycine betaine can contribute to osmotic buffering and macromolecular stabilization, supporting continued function when carbon fixation is constrained [81,84,85].

Redox regulation is closely related to osmotic adjustments during recovery. Simultaneous abiotic stresses can increase ROS production as carbon assimilation and electron sink activities become limited; ROS can act as signals at moderate levels but can also lead to oxidative damage if excessively produced. Thus, plants have developed redox buffering and antioxidant systems to detoxify excitation pressure-generated ROS and to support repair and metabolic recovery under stress [83,92].

These metabolic adjustments are coordinated through a suite of hormonal and systemic signaling pathways that integrate local stress cues with whole plant recovery needs. Abscisic acid (ABA) remains a central regulator of drought responses, controlling stomatal closure, growth inhibition, and stress-responsive gene expression. Other defense-related hormones, such as jasmonates, can contribute to protective reprogramming under combined stress conditions [40]. At the organismal level, stress coordination involves ABA, hydraulic signals, ROS, and electrically mediated signals, and mobile peptides such as CLE25 (reported

in *Arabidopsis thaliana*) and CEP family members. These signaling networks can regulate source-sink dynamics and direct carbon and nitrogen resources toward survival rather than growth, although the relative contribution of each pathway may differ across species, tissues, and stress intensities [93–95].

Thus, the interaction between osmolyte remodeling, redox buffering, and hormone-regulated gene expression creates a unique and complex, and sometimes non-linear response to balance growth and stress tolerance. Through these mechanisms, plant growth must be balanced with stress tolerance to maintain cellular hydration, membrane stability, control ROS generated by excitation imbalances, and shift metabolically to maintain cell function and yield [83,92]. These recovery mechanisms allow the plant to maintain a “memory” of stress for faster and more adaptive ability to have transcriptional reprogramming to future environmental stress.

5 Cross-Tolerance in Crop Improvement

5.1 Implications of Cross-Tolerance for Breeding Multi-Stress Resilient Crops

Crop improvement programs have achieved notable success in developing varieties tolerant to individual abiotic stresses such as drought, heat, or salinity [7,8]. However, progress has been constrained by the time-consuming nature of breeding, the complexity and polygenic basis of stress tolerance traits, strong genotype-by-environment interactions, and the difficulty of selecting for multiple stress responses while maintaining biomass and yield [96–100]. Increasing evidence shows that tolerance to single stresses does not reliably predict performance under combined stresses [101,102].

These insights have motivated a shift toward breeding strategies that explicitly target cross-tolerance, with the goal of developing crop varieties resilient to multiple abiotic stresses through overlapping adaptive mechanisms. Cross-tolerance relies on understanding how exposure to one stress can enhance tolerance to another via shared physiological and molecular pathways, including ROS and redox signaling, osmotic regulation, and hormonal crosstalk [18,103,104]. Breeding programs educated by this perspective should prioritize integrative traits that confer resilience across stress combinations. Such traits include efficient stomatal regulation that balances carbon gain with water conservation; robust root system architecture to enhance water and nutrient capture under heterogeneous soil conditions; maintenance or enhancement of photosynthetic capacity under fluctuating stress; strengthened antioxidant and redox-buffering systems; and phenological plasticity that enables developmental adjustment to the timing and severity of stress events. The effectiveness of these traits, however, depends strongly on the stress timing, intensity, and plant developmental stage, highlighting the importance of evaluating candidate varieties under multi-stress conditions that reflect real-world diverse environmental conditions. This need is increasingly urgent due to documented inconsistencies in field performance of varieties selected under single-stress conditions only. Key integrative traits identified for cross-tolerance breeding, along with their mechanistic basis, stress combination, taxonomic scope, and known limitations, are summarized in Table 2.

Table 2: Integrative traits for cross-tolerance breeding.

Integrative Trait	Category	Mechanistic Bases	Stress Combinations	Taxonomic Scope	Key Limitations	Ref.
(A) Stomatal & Hydraulic Regulation						
Stomatal Conductance Optimization	Stomatal	ABA/OST1-mediated guard cell regulation balancing CO ₂ uptake against water conservation; blue light H ⁺ -ATPase signaling	Drought + Heat Light + Drought All combinations	Wheat, maize, <i>Arabidopsis</i> , Eucalyptus	Tissue and stage-specific reproductive organs may maintain opening at cost of carbon water tradeoff.	[23,40,41,45]
Root hydraulic conductivity & aquaporin regulation	Hydraulic	Aquaporin-mediated water channel activity in roots adjusts hydraulic conductance under combined drought-heat; modulates rate of water potential decline.	Drought + Heat Drought + Salt	<i>Pinus radiata</i> , <i>Arabidopsis</i>	Mostly studied in model systems; field-level evidence in crops limited; isoform-specific responses vary considerably by species	[50,51]
Xylem cavitation resistance	Hydraulic	Resistance to air-seeding in xylem conduits under tension prevents hydraulic failure under combined drought-heat; linked to vessel anatomy and pit membrane properties.	Drought + Heat	Woody species	Difficult to phenotype at scale; trade-off between hydraulic safety and efficiency; understudied in cereals and annual crops	[46–49]
(B) Photosynthetic Capacity & Photoprotection						
PSII stability & D1 repair capacity	Photosynthetic	Maintenance of PSII supercomplex integrity and oxygen-evolving complex under elevated temperature; rapid D1 protein turnover sustains electron transport	Light + Drought Drought + Heat	<i>Arabidopsis</i> , Sorghum, Pearl millet,	Heat sensitivity of PSII varies substantially across genotypes; repair machinery becomes increasingly impaired under sustained combined stress	[68–71]

Table 2: Cont.

Integrative Trait	Category	Mechanistic Bases	Stress Combinations	Taxonomic Scope	Key Limitations	Ref.
(B) Photosynthetic Capacity & Photoprotection						
Non-photochemical quenching (NPQ) capacity	Photosynthetic	Xanthophyll cycle-mediated dissipation of excess absorbed light energy as heat via PsbS protein and pH gradient across thylakoid membrane; prevents excitation pressure accumulation.	Light + Drought Drought + Heat	<i>Arabidopsis</i> , <i>Quercus</i> ; C3 species primarily; C4 responses differ	NPQ regulation differs substantially between C3 and C4 species; findings from model plants may not directly translate to C4 crops with distinct chloroplast architecture.	[61,73–75,105]
Rubisco activase (RCA) thermostability	Photosynthetic	RCA maintains Rubisco in active form; thermostable RCA isoforms or engineered variants sustain carbon fixation under heat stress even when ATP and NADPH supply from light reactions is adequate	Drought + Heat	Cotton, <i>Arabidopsis</i> ; wheat at engineering stage	The degree of RCA impairment varies across isoforms and species; field validation of engineered RCA variants limited across diverse environments.	[59]
(C) Osmotic Adjustment & Redox Buffering						
Compatible solute accumulation (osmolytes)	Osmotic	Accumulation of sucrose, proline, and other osmolytes lowers osmotic potential to maintain turgor; also stabilizes membranes and scavenges ROS; pattern shifts from proline- to sucrose-dominated under drought-heat combination	Drought + Heat Drought + Salt	Wheat, maize, rice, <i>Arabidopsis</i> ; C4 crops may show different rebalancing patterns	Osmolyte identity and magnitude vary considerably across species and stress combinations; constitutive accumulation can impose metabolic cost under non-stress conditions	[82,84–87,90]
Antioxidant & redox-buffering capacity	Redox	Enhanced enzymatic (SOD, CAT, APX, GR) and non-enzymatic (ascorbate, glutathione, tocopherols) antioxidant systems scavenge ROS generated by excitation imbalance; prevents oxidative damage to proteins, lipids, and DNA	Light + Drought Drought + Heat	<i>Arabidopsis</i> , cereals, legumes, okra	Protective under moderate combined stress; overwhelmed under severe or prolonged combined stress; constitutive overexpression may reduce yield under non-stress conditions	[13,19,76,83,92]

Table 2: Cont.

Integrative Trait	Category	Mechanistic Bases	Stress Combinations	Taxonomic Scope	Key Limitations	Ref.
(D) Hormonal & Signaling Integration						
ABA-mediated stress signaling	Signaling	BA coordinates stomatal closure, growth inhibition, osmolyte biosynthesis, and stress-responsive gene expression; integrates hydraulic and chemical signals from root to shoot via mobile peptides (CLE25, CEP family)	Drought + Heat Drought + Salt	most studied in <i>Arabidopsis</i> and wheat; pathway conserved across angiosperms	ABA–SA antagonism under simultaneous biotic stress may compromise pathogen defense; concentration-dependent effects complicate genetic engineering approaches	[39,40,93–95]
ROS/MAPK signaling hubs	Signaling	H ₂ O ₂ and methylglyoxal function as signaling intermediates activating MAPKs and transcription factors; cross-stress signal integration through shared kinase cascades enables priming and cross-tolerance	All combinations	<i>Arabidopsis</i> ; increasingly documented in crop specie	Dual role of ROS as signal versus damaging agent is concentration- and context-dependent; threshold levels differ across species and developmental stages	[12,13,19–21]
Jasmonate & salicylate crosstalk	Signaling	Jasmonates contribute to protective metabolic reprogramming under combined stress; SA-mediated defense priming can enhance systemic resistance; interaction with ABA determines stress versus defense resource allocation	Drought + Heat All combinations	<i>Arabidopsis</i> , tomato; limited crop characterization	ABA–SA antagonism is well-documented; simultaneous abiotic and biotic stress can produce conflicting hormonal signals with unpredictable physiological outcomes	[17,40,106]

Field validation of cross-tolerance breeding has shown some important inconsistencies. Wheat germplasm selected for enhanced drought tolerance in a controlled environment often maintains this ability under combined drought-heat stress in the field due to maintained photosynthetic ability [107], while in some other cases, drought-tolerant selected lines show no cross-tolerance benefits or even increased vulnerability when heat co-occurs [38,107]. This possibly is due to trade-offs between water capture and canopy cooling capacity. These different field validation outcomes emphasize that tolerance mechanisms effective for single stresses do not reliably transfer to stress combinations [101,102], and that selection under realistic field conditions, rather than assuming transferability from single-stress screening or from controlled environment breeding selection, is essential for developing robust cross-tolerance varieties.

Genomic selection (GS) and high-throughput phenotyping have emerged as powerful tools for improving breeding efficiency for complex traits such as combined stress tolerance [108,109]. Unlike conventional marker-assisted selection (MAS), which relies on identifying large-effect QTLs, GS captures the combined effects of many small-effect loci across the genome. In maize breeding programs, GS has increased genetic gains for drought tolerance by 50–100% [110,111]. However, prediction of yield and crop performance accurately declines under stress combinations, prompting the development of GS models trained on combined stress datasets that incorporate environmental covariates and genotype-by-environment interactions [40,107]. This substantial decline in predictive accuracy is partly because field environments introduce variability in stress intensity, soil variability, and microclimate effects that controlled environment cannot replicate. Also, mechanisms that confer tolerance under controlled environment combined stress, such as enhanced antioxidant capacity or proline accumulation, may confer negligible yield benefit under field conditions due to the metabolic cost of the constitutive activation of stress response pathways, the context-dependency of stress combinations and plant's developmental stage [112,113]. An underutilized reservoir of genetic diversity for breeding cross-tolerance involves gene banks, landraces, and wild relatives that could diversify crop genotypes for enhanced tolerance to multiple co-occurring stresses and lead to the addition of alleles that may have been lost during domestication. For example, wild tomato species from saline and arid regions have contributed drought-salt tolerance genes to our cultivated tomato [114–116].

5.2 Genetic Engineering Approaches to Enhance Cross-Tolerance to Major Crop Species

Genetic engineering has emerged as a powerful strategy for improving cross-tolerance in crop plants by targeting key regulatory sequences that integrate multiple stress response pathways [117]. Early transgenic efforts often focus on manipulating single genes, such as those involved in osmoprotectant biosynthesis or antioxidant defense. However, these approaches frequently produce limited or inconsistent outcomes in field testing. While some tolerance was observed under controlled conditions, these single gene modifications rarely translated into robust field performance or tolerance across diverse stress combinations [99,118].

More recent strategies emphasize the manipulation of signaling networks, ion homeostasis, and transcriptional and posttranslational regulators that coordinate responses to multiple stresses simultaneously. Although validated primarily in model systems like *Arabidopsis* and tobacco, as well as major crops such as rice, wheat, cotton and tomato [76,99,105,119,120], though the broader applicability of specific genes across plant families requires further validation. These approaches aim to modify upstream regulatory hubs rather than isolated downstream effectors, thereby enhancing the plant's ability to integrate drought, heat, salinity, and light stress signals.

Gene stacking has shown promise. By combining multiple stress-responsive functions, such as improved water use efficiency, enhanced redox buffering capacity, and increased protein stability, stacked transgenes often confer broader and more durable cross-tolerance than single gene modifications [105,119,120]. However,

activating multiple stress response pathways simultaneously can impose growth and yield penalties, reflecting the metabolic costs of constitutive defense activation. This highlights the importance of inducible, tissue-specific, or stress-responsive promoters that restrict transgene expression to conditions where it is beneficial [121].

5.3 Genome Editing As a Precision Strategy for Cross-Tolerance

Genome editing technologies, particularly CRISPR/Cas-based systems, have transformed plant biotechnology by enabling precise modification of endogenous genes without introducing foreign DNA. This capability addresses concerns associated with conventional transgenics and can facilitate regulatory approval [122,123]. CRISPR-based editing has shown strong potential for enhancing cross-tolerance by targeting stress-responsive regulatory genes that coordinate multiple defense pathways. Such targeted approaches are well-suited for cross-tolerance engineering, where fine-tuning response thresholds are essential for balancing growth with stress defense. For example, Han et al. [124] demonstrated in strawberry (a perennial crop) that editing the *FvICE1* gene revealed its role as a positive regulator of both cold and drought tolerance, illustrating how a single regulatory gene can integrate responses to distinct stresses through convergent signaling networks. While *ICE1* orthologs function in cold response across diverse angiosperms, whether their dual role in cold-drought cross-tolerance extends to cereals and other major crop families requires systematic comparative research.

The multiplexing capability of CRISPR systems allows simultaneous editing of multiple genes, which further enhances their value for engineering complex cross-tolerance traits [125]. By modifying several components of stress response networks at once, multiplex editing can facilitate coordinated responses to multifactorial stress environments. However, successful agricultural application depends on careful targeted selection, informed by an understanding of regulatory hierarchies to minimize growth tolerance tradeoffs. In addition, extensive field validation trials under co-occurring abiotic stresses and integration with breeding programs are essential to ensure performance stability across diverse environments [118].

5.4 Stress Priming and Emerging Technologies

Beyond CRISPR-based genome editing, several emerging biotechnologies are being developed to enhance cross-tolerance in plants. Nanopriming, which involves using nanoparticles to improve seed viability and stress memory, represents a promising approach for enhancing stress tolerance without genetic modification [126,127]. Nanoparticles such as carbon nanotubes and metal oxide particles have been shown to induce stress-responsive gene expression, improve germination, and strengthen stress memory during subsequent exposure to stressors [84]. According to [128], seed priming with nanoparticles can activate multiple defense pathways, increase yield and viability, improve early growth, and enhance overall plant resilience to abiotic stress [129,130].

Despite these promising results, nanopriming remains in its early stages. Field validation is limited, and concerns persist regarding environmental safety, nanoparticle persistence, and the precise mechanisms underlying their effects. Additional emerging tools, such as RNA interference (RNAi), offer further opportunities to modulate stress response pathways by selectively silencing key regulatory genes. Together, these technologies expand the toolbox for enhancing cross-tolerance, though their practical deployment in breeding programs will require careful evaluation of safety, efficacy, and scalability.

5.5 Challenges and Limitations

A major challenge in engineering stress-tolerant crops is the tradeoff between growth or yield under optimal conditions versus enhanced outcomes under multi-stress conditions. Activation of stress response pathways often diverts energy and resources away from growth and reproduction towards defense mechanisms [112,131]. For example, overexpression of *DREB* transcription factors can enhance cold and drought tolerance but frequently results in severe growth retardation [113,132]. These tradeoffs reflect antagonistic interactions between growth-promoting and stress-responsive signaling pathways, such as those involving DELLA proteins and brassinosteroid signaling [133,134].

Several strategies can help minimize these tradeoffs. Stress-inducible promoters (e.g., *rd29A*) restrict transgene expression to stress conditions, reducing metabolic costs under favorable environments [135]. Fine-tuning rather than maximizing stress responses is also critical, as natural allelic variation often operates through subtle regulatory adjustments rather than strong overexpression [26,136]. Field trials remain essential for validating cross-tolerance mechanisms, but they are time-consuming and resource intensive. Addressing these challenges will require high-throughput field phenotyping technologies, improved predictive modeling, and stronger partnerships between researchers and breeding programs to ensure that mechanistic discoveries translate into practical crop improvement.

6 Future Prospects and Research

Understanding cross-tolerance requires the integration of data across multiple biological systems, from genome to phenotype. Recent advances in high-throughput omics technologies now enable simultaneous profiling of genomes, transcriptomes, proteomes, metabolomes, and epigenomes under combined stress, generating unprecedented datasets for systems-level analysis [137,138]. Multiomics approaches reveal regulatory networks and identify core genes and key metabolic intermediates and precursors that coordinate responses across diverse stress types. The incorporation of machine learning into these datasets has further improved the ability to predict stress tolerance phenotypes from molecular profiles with high accuracy [139,140]. A recent study by [141], which integrated five omics layers in potato, demonstrated that combined stresses trigger responses distinct from the sum of individual stresses, with unique transcription factors, metabolic pathways, and signaling networks activated only under stress combinations.

To date, most cross-tolerance research has focused on abiotic-abiotic stress combinations. However, plants in agricultural systems frequently encounter abiotic and biotic stresses simultaneously, producing highly nonadditive and often unpredictable outcomes [8,142]. For example, drought often increases susceptibility to biotrophic pathogens through antagonistic ABA-SA signaling, while potentially enhancing resistance to necrotrophs [17,143]. Elevated temperatures can increase insect herbivory and alter the production of secondary defensive metabolites in species-specific ways [106]. Future research must expand beyond simplified stress combinations to incorporate multifactorial stress environments that more accurately reflect agricultural reality [144].

Emerging technologies offer powerful tools for advancing this research frontier. CRISPR-based genome editing provides precision for engineering stress tolerance traits [123], while artificial intelligence and machine learning enable more accurate prediction of gene targets and stress response networks [139,140]. High-throughput phenotyping platforms will be essential for evaluating plant performance under realistic, dynamic stress conditions. Despite these advances, the persistent gap between controlled environment results and field performance remains a major limitation. Addressing this challenge will require multi-stress field trials, improved modeling of stress interactions, breeding programs explicitly designed around realistic

stress combinations, and stronger integration of fundamental research with applied breeding pipelines to translate mechanistic insights into climate-resilient crops.

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