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Cross-tolerance in crops under climate change: physiological and molecular perspectives

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Abstract

Climate change is intensifying the frequency, duration, and severity of environmental stresses affecting agricultural productivity, including drought, salinity, heat, flooding, and nutrient imbalance. These stresses frequently occur together or sequentially, creating complex challenges for crop growth, development, and yield stability. Cross-tolerance refers to the capacity of plants exposed to one stress or stress-conditioning treatment to develop enhanced tolerance to another stress through interconnected physiological, biochemical, and molecular mechanisms. This paper examines cross-tolerance in crops from physiological and molecular perspectives, focusing on water relations, photosynthesis, antioxidant defense, osmotic adjustment, hormonal signaling, transcriptional regulation, epigenetic modifications, and stress-responsive gene networks. It explores how abscisic acid, salicylic acid, jasmonic acid, reactive oxygen species, calcium signaling, heat-shock proteins, and compatible solutes contribute to adaptive responses under changing environmental conditions. The paper also discusses the importance of distinguishing genuine cross-tolerance from generalized stress responses, acclimation effects, and the physiological costs of stress priming. An experimental framework is developed to investigate cross-tolerance through controlled single-stress, sequential-stress, and combined-stress treatments, supported by measurements of growth, gas exchange, water status, oxidative damage, gene expression, and final yield. Artificial intelligence and machine learning for advanced data analytics are considered as complementary tools for integrating physiological, molecular, environmental, and genomic information to identify predictive biomarkers and improve crop selection. Because no original experimental dataset or completed laboratory measurements are supplied, the results section presents a proposed experimental design, analytical expectations, and criteria for evaluating cross-tolerance rather than fabricated numerical findings. The paper concludes that understanding cross-tolerance through integrated physiological, molecular, and computational approaches can support the development of climate-resilient crops, provided that laboratory findings are validated across developmental stages, field environments, and genetically diverse crop populations.

Keywords: cross-tolerance, climate change, crop resilience, drought stress, salinity stress, heat stress, physiological adaptation, molecular signaling, stress priming, artificial intelligence, machine learning, advanced data analytics

I. Introduction

Climate change is creating increasingly challenging conditions for agricultural production by altering temperature regimes, rainfall distribution, atmospheric humidity, soil moisture, and the frequency of extreme weather events. Crops may experience prolonged drought followed by heat waves, high temperatures combined with soil salinity, or waterlogging followed by renewed water limitation. These overlapping stresses affect germination, vegetative growth, flowering, pollination, grain filling, and final yield[1]. The severity of their effects depends on crop species, genotype, developmental stage, stress intensity, duration, and the availability of resources needed for recovery. Consequently, improving crop resilience requires an understanding of how plants respond not only to individual environmental stresses but also to interactions among multiple stresses.

Cross-tolerance is the capacity of a plant to acquire or express increased tolerance to one stress after exposure to another stress or conditioning stimulus. For example, a mild drought treatment may activate protective responses that improve a plant's subsequent performance during heat exposure. Similarly, controlled temperature conditioning can sometimes enhance the response to later osmotic or salinity stress. These outcomes are associated with overlapping stress-signaling pathways, antioxidant systems, compatible solutes, molecular chaperones, and changes in gene regulation. However, cross-tolerance is not universal: a response that benefits a plant under one combination of stress conditions may be ineffective or detrimental under another. The distinction between beneficial cross-tolerance, stress acclimation, and simple survival responses is therefore central to interpreting plant adaptation. Physiological and molecular mechanisms provide complementary perspectives for investigating this phenomenon. Physiological measurements reveal how plants maintain water status, photosynthetic activity, membrane integrity, nutrient balance, and reproductive performance during environmental stress. Molecular investigations identify the genes, regulatory networks, proteins, metabolites, and epigenetic processes associated with these responses. A plant that maintains high antioxidant activity, for instance, may experience less oxidative damage, but this association alone does not establish that antioxidant activity causes improved cross-tolerance. Molecular perturbation, controlled treatment comparisons, and measurements of final growth and yield are necessary to determine whether a particular mechanism contributes directly to adaptive performance.

The purpose of this paper is to examine cross-tolerance in crops under climate change through physiological and molecular perspectives, with particular emphasis on drought, heat, salinity, and their combinations. The study also considers artificial intelligence and machine learning for advanced data analytics as tools for integrating physiological measurements, molecular profiles, genomic variation, and environmental data. A controlled experimental framework is proposed to test whether prior exposure to one stress improves the response to a subsequent stress and whether this effect persists across crop genotypes and developmental stages. By connecting mechanistic biology with experimental validation and predictive analytics, the paper aims to establish a foundation for identifying cross-tolerance traits that can contribute to climate-resilient crop improvement.

II. Climate change and the occurrence of multiple stresses

Drought is among the major environmental constraints affecting crop productivity because it reduces water availability for cell expansion, photosynthesis, nutrient transport, and reproductive development. Under water deficit, plants commonly reduce stomatal conductance to limit transpiration, but this response also restricts carbon dioxide uptake and can reduce photosynthetic carbon assimilation. Prolonged drought may disrupt membrane stability, accelerate leaf senescence, restrict root growth, and alter the distribution of assimilates between vegetative and reproductive organs[2]. The consequences depend on the timing of water shortage, soil characteristics, rooting depth, and the plant's ability to access available water. Mild drought may initiate acclimation, whereas severe or prolonged drought can exceed the capacity of protective systems and cause irreversible damage.

Heat stress affects plants through several interacting mechanisms, including protein destabilization, changes in membrane fluidity, increased respiratory demand, impaired photosynthesis, and reproductive injury. High temperatures can interfere with pollen development, pollen viability, fertilization, and seed formation, making reproductive-stage heat exposure particularly damaging in crops such as wheat, rice, maize, and legumes. Heat also increases atmospheric evaporative demand, which can intensify water loss when soil moisture is limited. Under combined drought and heat, stomatal closure restricts evaporative cooling while high temperature increases the need for heat dissipation. The resulting interaction can be more damaging than either stress alone, although the exact response depends on environmental intensity and crop characteristics. Salinity stress imposes both osmotic and ionic challenges. Initially, elevated salt concentrations in the root zone make water uptake more difficult, producing responses that resemble drought. With continued exposure, excessive accumulation of sodium and chloride may disturb cellular ion balance, interfere with potassium-dependent processes, damage photosynthetic machinery, and accelerate senescence. Some plants reduce salt entry or transport, compartmentalize ions in vacuoles, or maintain favorable potassium-to-sodium ratios in sensitive tissues[3]. These mechanisms may share components with drought responses, including osmotic adjustment, abscisic acid signaling, antioxidant regulation, and changes in membrane transport. Nevertheless, drought and salinity are not physiologically interchangeable because salinity introduces specific ionic effects that water deficit alone does not reproduce.

The agricultural significance of cross-tolerance arises from the fact that climate-related stresses frequently occur in sequences or combinations rather than as isolated events. A crop may experience early-season drought, subsequent heat exposure, and later rainfall that changes soil aeration or nutrient availability. Alternatively, irrigated crops may face rising soil salinity alongside higher temperatures and increased water demand. These conditions can alter the effectiveness of stress-priming strategies and the expression of inherited tolerance traits. Experiments that investigate only one stress at a time may therefore overlook important interactions among stress type, order, intensity, and duration. Research under climate change should incorporate realistic combinations of stresses and evaluate recovery, reproductive success, and final yield in addition to short-term physiological survival.

III. Physiological mechanisms underlying cross-tolerance

Water relations are a major component of cross-tolerance because drought, salinity, and heat can all influence the balance between water uptake and water loss. Plants regulate stomatal opening, root hydraulic conductance, leaf area, and root-to-shoot allocation to maintain hydration under changing environmental conditions. Osmotic adjustment through the accumulation of compatible solutes can help preserve cell turgor when external water potential declines. However, stomatal closure involves a trade-off: it conserves water but may reduce carbon assimilation and increase leaf temperature when evaporative cooling is limited. Effective cross-tolerance therefore depends on coordinating water conservation with photosynthetic function, root activity, and the capacity to dissipate heat.

Photosynthesis provides another important physiological basis for cross-tolerance. Environmental stress can affect chlorophyll content, photosystem II efficiency, electron transport, carbon fixation, and the activity of enzymes involved in the Calvin–Benson cycle. Heat can destabilize photosynthetic proteins, while drought-induced carbon dioxide limitation may increase the excitation pressure on photosynthetic electron transport[4]. These conditions can increase the production of reactive oxygen species and contribute to oxidative damage. Plants with more stable photosynthetic machinery, effective photoprotective responses, and appropriate energy dissipation may maintain a greater proportion of their photosynthetic activity during subsequent stress exposure. Chlorophyll fluorescence, gas-exchange measurements, and leaf-temperature observations can help distinguish genuine protection of photosynthetic function from changes caused by reduced leaf area or altered developmental timing.

Antioxidant defense is central to regulating oxidative stress across multiple environmental challenges. Reactive oxygen species, including superoxide and hydrogen peroxide, are produced during normal metabolism and can function as signaling molecules when maintained within controlled ranges. Excessive accumulation, however, can damage lipids, proteins, nucleic acids, and cellular membranes. Enzymatic defenses such as superoxide dismutase, catalase, ascorbate peroxidase, and components of the ascorbate–glutathione cycle contribute to controlling reactive oxygen species, while nonenzymatic antioxidants provide additional protection. Cross-tolerance may arise when an initial stress activates antioxidant capacity that remains available during a later challenge. Yet greater antioxidant activity is not automatically evidence of greater tolerance, because enzyme activity may increase in response to severe damage as well as successful acclimation. Osmotic adjustment and cellular protection also involve the accumulation of compatible solutes, including proline, glycine betaine, soluble sugars, and certain sugar alcohols. These compounds can contribute to osmotic balance, stabilize proteins and membranes, and influence cellular redox status. Heat-shock proteins and other molecular chaperones help preserve protein structure, prevent inappropriate aggregation, and support the repair or removal of damaged proteins. Changes in membrane lipid composition can help maintain membrane function under temperature and water stress, while improved root architecture may increase access to water and nutrients. The most effective physiological response is therefore usually a coordinated combination of water regulation, photosynthetic protection, redox control, and cellular maintenance rather than a single trait operating independently.

IV. Molecular signaling and gene regulation in cross-tolerance

Plant stress perception initiates signaling processes that translate environmental changes into cellular responses. Changes in membrane properties, cellular calcium concentrations, reactive oxygen species, and protein phosphorylation can activate downstream signaling networks. Calcium-dependent protein kinases, calcium sensors, and mitogen-activated protein kinase cascades participate in transmitting information about stress intensity and duration. These signaling systems can influence transcription factors, metabolic enzymes, ion transporters, and cellular protective mechanisms. Because several environmental stresses activate overlapping signaling components, a response initiated by one stress can sometimes alter the plant's readiness to respond to another. However, the same signaling component may produce different outcomes depending on its timing, cellular location, and interactions with other regulatory pathways.

Phytohormones coordinate growth and stress responses through interconnected regulatory networks[5]. Abscisic acid commonly contributes to stomatal regulation, osmotic adjustment, and the activation of stress-responsive genes, particularly under water limitation. Salicylic acid, jasmonates, ethylene, auxins, cytokinins, gibberellins, and brassinosteroids also influence plant development and responses to environmental challenges. Their effects are context-dependent, and interactions among hormonal pathways can either reinforce or oppose particular responses. For example, a hormonal state that conserves water during drought may not be optimal for maintaining growth or reproductive development during prolonged heat exposure. Cross-tolerance therefore depends on the regulation of hormonal networks as a whole rather than on maximizing the concentration of one hormone.

Transcription factors help convert signaling events into changes in gene expression. Members of the DREB/CBF, NAC, WRKY, bZIP, MYB, and heat-shock factor families have been associated with different aspects of abiotic stress responses. Some regulate genes involved in osmotic adjustment, antioxidant defense, ion homeostasis, protein protection, and cellular repair. Heat-shock factors can activate genes encoding heat-shock proteins, while selected bZIP transcription factors participate in abscisic acid-responsive signaling. The effects of these regulators depend on the crop species, genetic background, developmental stage, and environmental conditions. A gene associated with tolerance in one genotype may have a weaker or different effect in another because the wider regulatory network and downstream targets differ.

Epigenetic regulation and stress memory provide a potential mechanism through which prior exposure influences later responses. DNA methylation, histone modifications, chromatin remodeling, and regulatory small RNAs can alter gene activity without necessarily changing the underlying DNA sequence. In some cases, the effects of priming persist after the initial stress has ended, enabling a plant to respond more rapidly or differently when stress recurs. Such changes may influence transcriptional readiness, antioxidant regulation, protein maintenance, and hormonal responses. However, stress memory is not always permanent, beneficial, or transmitted to subsequent generations. Its duration and adaptive value depend on the conditioning treatment, plant genotype, developmental context, and the costs of maintaining a primed physiological state.

V. Cross-tolerance among drought, heat, salinity, and flooding

Drought-induced cross-tolerance to heat is an important area of crop stress research because water limitation and high temperature frequently coincide. A mild drought episode may induce abscisic acid signaling, osmotic adjustment, antioxidant responses, and changes in protective gene expression that influence the response to a later heat event. Some of these changes may help maintain membrane integrity and reduce oxidative damage during heat exposure. Nevertheless, drought can also reduce leaf cooling through stomatal closure and restrict the resources required for cellular repair. Whether drought conditioning improves heat tolerance therefore depends on the severity of the initial water deficit, the interval before heat exposure, and the plant's ability to recover between treatments.

Heat-induced cross-tolerance to drought may develop when moderate temperature conditioning activates heat-shock proteins, antioxidant defenses, and cellular repair pathways that remain effective during later water limitation[6]. These responses can protect proteins and membranes and may improve the stability of cellular metabolism. However, temperature conditioning that is too intense or prolonged can consume energy, impair photosynthesis, and damage reproductive tissues. Consequently, a conditioning treatment should be evaluated not only by survival during subsequent drought but also by its effects on biomass accumulation, flowering, seed production, and recovery. A treatment that protects seedlings but reduces grain yield under field conditions would have limited agricultural value.

Drought and salinity share an osmotic component, creating opportunities for cross-tolerance through compatible-solute accumulation, water regulation, and selected hormonal signaling pathways. Prior drought exposure may alter root growth, osmotic adjustment, and transporter activity in ways that influence the response to saline conditions. Likewise, mild salinity conditioning may change osmotic regulation and antioxidant activity before a subsequent water deficit. However, successful adaptation to drought does not necessarily provide protection against sodium toxicity, chloride accumulation, or nutrient imbalance. Salinity-related cross-tolerance must therefore be assessed using ion concentrations, tissue-specific ion distribution, potassium-to-sodium balance, and growth measurements alongside conventional indicators of water status.

Flooding and waterlogging present a more complex challenge because their primary effects differ from those of drought and salinity. Water-saturated soil limits oxygen diffusion to roots, potentially reducing aerobic respiration and ATP availability while altering nutrient uptake and root metabolism. Some plants develop aerenchyma, adventitious roots, or metabolic adjustments that improve survival under oxygen deficiency. These changes may influence later drought or salinity responses, but they do not necessarily confer beneficial cross-tolerance. Flooding followed by drought can impose contrasting demands on root function, water transport, and energy metabolism. Consequently, the direction of cross-tolerance must be determined experimentally for each stress sequence rather than inferred from the presence of shared stress-response pathways.

VI. Experimental methodology for evaluating cross-tolerance

A controlled experiment can be designed using wheat, rice, maize, or another agriculturally important crop with known variation in abiotic stress responses. The study should include several genetically distinct cultivars, ideally representing contrasting levels of drought or heat tolerance. Plants should be grown under standardized conditions until a defined developmental stage, with consistent soil composition, nutrient supply, light exposure, and irrigation management. The choice of crop and growth stage should reflect the intended agricultural application because cross-tolerance in seedlings may not predict responses during flowering or grain filling. Independent biological replicates and randomized treatment allocation are necessary to distinguish treatment effects from natural variation among plants.

The experimental design should include an unstressed control, a conditioning-stress-only group, a target-stress-only group, and a sequential-stress group receiving the conditioning stress followed by the target stress. For example, a mild drought treatment could be followed by a controlled heat challenge after a defined recovery interval. Additional treatment groups should reverse the order of the stresses or apply both stresses simultaneously. A separate recovery period should be included to determine whether treatment effects persist after the stress is removed. Treatment intensity should be calibrated using preliminary experiments to avoid confusing cross-tolerance with differences in the severity of the initial injury. Soil moisture, temperature, relative humidity, and, where possible, vapor-pressure deficit should be monitored throughout the experiment.

Physiological measurements should include plant height, leaf area, biomass, relative water content, stomatal conductance, net photosynthetic rate, transpiration, chlorophyll content, and chlorophyll fluorescence. Oxidative stress can be evaluated through measurements such as hydrogen peroxide accumulation, lipid peroxidation, and antioxidant enzyme activity. Proline and soluble sugar concentrations can provide information about osmotic adjustment, while tissue sodium and potassium concentrations are particularly important in salinity experiments. Reproductive-stage studies should measure flowering time, pollen viability where relevant, grain number, seed weight, and final yield. Measurements should be collected before conditioning, after conditioning, during the target stress, and after recovery to distinguish pre-existing differences from treatment-induced responses.

Molecular analyses should be performed on appropriately selected tissues collected at standardized times relative to stress exposure[7]. Quantitative PCR can measure the expression of candidate stress-responsive genes, while transcriptomics can identify broader changes in gene-expression networks. Proteomics and metabolomics can provide complementary information about changes in proteins, metabolites, and biochemical pathways. When resources permit, epigenomic measurements may help identify persistent regulatory changes associated with stress memory. Molecular findings should be linked to physiological outcomes using prespecified statistical models, with multiple-testing correction for large-scale molecular data. The experiment should be repeated across independent batches or environments, and promising findings should subsequently be tested in field trials under realistic climate conditions.

VII. Experimental results and statistical analysis

The proposed experiment is intended to determine whether prior exposure to one environmental stress improves crop performance during a subsequent, different stress. Since no original experimental dataset, laboratory measurements, or completed statistical analyses have been supplied, numerical results cannot be reported as observed findings. The results described in this section therefore specify the comparisons, statistical tests, and evidence required to establish cross-tolerance without inventing measurements or claiming that the proposed experiment has already been performed.

The primary analysis should compare the performance of the sequential-stress group with that of the target-stress-only group. For example, plants receiving mild drought conditioning followed by heat exposure should be compared with plants receiving the same heat treatment without prior drought conditioning. Measurements should include physiological function during heat stress, the degree of cellular damage, recovery after treatment, and final reproductive performance. A positive cross-tolerance effect would be supported if conditioned plants demonstrate a reproducible improvement in prespecified outcomes relative to plants experiencing the target stress alone, while accounting for differences in initial plant size and any costs caused by the conditioning treatment. Improved survival alone would not establish agronomically meaningful cross-tolerance if the treatment substantially reduces final yield.

Statistical analysis should use models appropriate to the experimental design, including treatment, cultivar, stress sequence, and relevant interactions. Analysis of variance may be suitable for balanced experiments with assumptions that are adequately satisfied, while mixed-effects models can account for random effects associated with experimental blocks, batches, or repeated measurements. Repeated physiological observations should be analyzed using methods that account for correlations among measurements from the same plant or experimental unit. Effect sizes and confidence intervals should accompany significance tests to indicate the magnitude and uncertainty of treatment differences. Where numerous physiological or molecular outcomes are tested, false-discovery-rate control should be applied to reduce the likelihood of identifying spurious associations.

The molecular analysis should examine whether improved physiological performance is associated with consistent changes in stress-responsive genes, antioxidant systems, compatible solutes, hormone-related pathways, or protein-protection mechanisms. Correlation and multivariate analysis can identify relationships between molecular measurements and cross-tolerance outcomes, but they cannot independently establish causal mechanisms. Stronger evidence would require targeted perturbation of candidate genes or pathways, followed by testing under the same stress sequence. Independent validation in additional cultivars and growing conditions would help establish whether the identified mechanism is broadly useful or restricted to a particular genetic background. The most convincing evidence would connect a molecular change to a physiological benefit, improved recovery, and an agronomically relevant outcome.

The final results should include treatment-wise means and variability, the number of independent biological replicates, effect sizes, confidence intervals, statistical significance where appropriate, and the complete model specifications. Graphical outputs could include time-series plots of photosynthesis and water status, comparisons of oxidative damage, gene-expression profiles, and yield responses across stress treatments[8]. A useful summary table would report the response of each cultivar under individual and sequential stresses, making it possible to identify genotype-dependent differences. Until the experiment is executed, however, the direction and magnitude of these effects remain unknown. This distinction is essential for ensuring that a proposed research framework is not misrepresented as a completed experimental study.

VIII. Conclusion

Cross-tolerance represents a valuable biological mechanism for improving crop resilience under climate change because it enables certain protective responses activated by one environmental stress to influence the response to another. This paper has examined the physiological and molecular foundations of cross-tolerance, including water regulation, photosynthetic stability, antioxidant defense, osmotic adjustment, hormonal interactions, transcriptional regulation, epigenetic modifications, and stress memory. It has also outlined an experimental framework for investigating cross-tolerance through controlled stress conditioning, sequential and combined stress treatments, physiological measurements, molecular profiling, and statistical validation. Artificial intelligence and machine learning for advanced data analytics provide additional opportunities to integrate complex datasets, identify predictive biomarkers, classify stress-response patterns, and prioritize promising crop genotypes for breeding. However, cross-tolerance is not universal, and its effectiveness depends on the stress type, intensity, sequence, duration, genetic background, and developmental stage of the crop. Because no original experimental measurements were provided, the proposed experimental results require validation through actual laboratory and field investigations before quantitative conclusions can be established. Future research should prioritize multi-stress experiments, causal validation of molecular mechanisms, independent testing across environments, and assessment of final yield and reproductive performance rather than relying exclusively on short-term stress indicators. Integrating plant physiology, molecular biology, genomics, precision phenotyping, and machine learning can help identify the mechanisms and genetic resources most useful for climate-resilient agriculture. Ultimately, a comprehensive understanding of cross-tolerance can contribute to developing crop varieties that maintain productivity under increasingly variable environmental conditions, provided that proposed tolerance mechanisms are experimentally validated and translated into reliable agricultural performance.

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