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Review Article

The Plant Defense Web: Decoding Convergent Mechanisms of Tolerance to Multiple Abiotic Stresses and Building Climate-Resilient Crops

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ABSTRACT

Plants are continuously exposed to an increasingly complex combination of environmental constraints rather than to individual stresses occurring in isolation. Drought, heat, salinity, flooding, chilling, high light, ultraviolet-B (UV-B) radiation, nutrient imbalance, heavy metals and atmospheric pollutants can occur simultaneously or sequentially, creating stress combinations that profoundly alter plant growth, metabolism and productivity. Conventional stress biology has predominantly examined individual stresses, but increasing evidence demonstrates that the response to combined stress cannot simply be predicted by adding the responses to individual stressors. Instead, plants employ an integrated defense network in which stress perception, calcium signalling, reactive oxygen species (ROS), reactive nitrogen species, phytohormones, protein phosphorylation, transcriptional regulation, metabolic reprogramming, antioxidant defense and epigenetic memory interact dynamically. This review proposes a conceptual framework termed the Plant Defense Web (PDW), in which multiple abiotic stresses converge on a limited number of regulatory hubs. Stress-induced perturbations in membrane integrity, cellular hydration, redox balance, temperature, photosynthetic electron transport and ion homeostasis generate early calcium and ROS signatures. These signals activate protein kinases, transcription factors and hormonal networks, which subsequently regulate stomatal behavior, osmotic adjustment, antioxidant metabolism, repair of damaged macromolecules, secondary metabolite biosynthesis and growth-defense trade-offs. Particular attention is given to the integration of abscisic acid, jasmonates, salicylic acid, ethylene, brassinosteroid, auxin, cytokinins, melatonin and Strigolactones. The review further examines flavonoids, phenolics, proline, soluble sugars, polyamines and antioxidant enzymes as components of the biochemical defense shield.

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UV-B perception through UVR8 and the relationship between light signalling and redox defense are discussed as important examples of stress-specific signalling converging with general defense mechanisms. Finally, the emerging importance of stress priming, epigenetic regulation, small RNAs, multi-omics, genome editing, nanotechnology and machine-learning-assisted phenotyping is discussed for developing crops capable of tolerating realistic combinations of environmental stresses. The proposed Plant Defense Web model shifts the conceptual focus from isolated stress tolerance genes toward network-level resilience, providing a framework for understanding and engineering crops capable of maintaining productivity under increasingly unpredictable climate conditions.

INTRODUCTION

Plants are sessile organisms and cannot escape unfavourable environmental conditions by changing their location. Consequently, survival depends on the ability to perceive environmental fluctuations rapidly and reorganize physiological, biochemical and molecular processes before cellular damage becomes irreversible. Drought, salinity, extreme temperature, flooding, ultraviolet radiation, high light, nutrient limitation and toxic metals are among the major abiotic constraints affecting plant growth and agricultural productivity. Historically, plant stress research has frequently treated these factors independently. Such an approach has generated substantial knowledge about drought-induced ABA signalling, salt-induced ion homeostasis, heat-shock responses, cold acclimation and UV-B signalling. However, natural and agricultural environments rarely reproduce these simplified experimental conditions. A crop experiencing summer drought may simultaneously experience high temperature and intense radiation, while coastal crops may encounter salinity together with heat and water deficit. Similarly, waterlogging can be accompanied by salinity, hypoxia and nutrient imbalance. This distinction is biologically important because combined stresses can produce molecular responses that are different from those generated by either stress alone. Studies of stress combinations have demonstrated that transcriptional, physiological and metabolic responses may be synergistic, antagonistic or additive depending on stress intensity, duration, order and developmental stage (Prasch and Sonnewald, 2015; Nadeem et al., 2023).

Recent studies further emphasize that heat may act as a dominant component of several stress combinations and reshape transcriptional and metabolic responses to drought, salinity and high light. The emerging view is that diverse stresses converge on common signalling components, including calcium ions (Ca^{2+}), reactive oxygen species (ROS), reactive nitrogen species, mitogen-activated protein kinases (MAPKs), calcium-dependent protein kinases (CDPKs), phytohormones and stress-responsive transcription factors. These signalling components form a highly interconnected network rather than independent linear pathways. (Mittler, 2006; Prasch & Sonnewald, 2015; Nadeem et al., 2023).

The present review develops an integrated framework called the Plant Defense Web (PDW). The model proposes that plant resilience is generated through coordinated interactions between five major layers:

1. Stress perception
2. Signal integration
3. Molecular decision-making
4. Cellular protection
5. Acclimation, memory and recovery

This framework provides a mechanistic basis for developing climate-resilient crops capable of responding to multiple stress combinations. The major stress types and their characteristic defense responses are summarized in Table 1, while the integrated signaling and protection layers are brought together in the Plant Defense Web model (Figure 1; Table 2).

From Single-Stress Responses to Multiple-Stress Biology

Individual stresses impose characteristic primary disturbances. Drought primarily reduces cellular water availability and hydraulic conductivity. Salinity generates both osmotic stress and ion toxicity. Heat disrupts protein folding, membrane stability and photosynthetic machinery. Cold restricts membrane fluidity and enzymatic activity. Flooding produces oxygen deficiency and metabolic reprogramming. UV-B can induce DNA damage, oxidative stress and photosynthetic impairment. (Mittler, 2006; Choudhury et al., 2017; Nadeem et al., 2023).



Although these primary effects differ, they eventually converge on several common cellular consequences:

Water imbalance → ionic imbalance → redox imbalance → metabolic disturbance → growth inhibition

This convergence explains why some defense mechanisms provide cross-protection. For example, accumulation of proline can contribute to osmotic adjustment, ROS regulation, protein stabilization and membrane protection. Similarly, antioxidant enzymes can protect cells against oxidative stress generated by drought, salinity, heat, heavy metals and excessive radiation. (Baxter et al., 2014; Mittler, 2017; Kaur & Garg, 2022).

However, cross-tolerance should not be interpreted as universal. A defense response beneficial under one stress can become detrimental under another. For example, excessive stomatal closure conserves water during drought but can reduce CO₂ assimilation and increase excitation pressure when temperature and radiation are high. (Prasch & Sonnewald, 2015; Nadeem et al., 2023).

Thus, the plant must continuously solve a physiological optimization problem:

survival protection ↔ carbon gain ↔ growth ↔ reproduction

This explains why multiple-stress responses are highly dependent on stress intensity, duration, sequence, tissue and developmental stage.

The First Layer of Defense: Stress Perception

Membrane and cellular sensing

The plasma membrane represents one of the earliest sites affected by environmental disturbance. Changes in membrane fluidity, osmotic pressure, mechanical properties, ion concentration and lipid composition can activate stress signalling. Temperature fluctuations alter membrane physical properties, whereas salinity modifies ionic gradients and water potential. Drought affects membrane tension and cellular hydration. Mechanical and osmotic changes can activate mechanosensitive channels and Ca²⁺ influx. Thus, the membrane can be viewed not merely as a barrier but as an environmental sensor.

Calcium as an information carrier

Ca²⁺ is one of the most conserved secondary messengers in plant stress signalling.

Different stress conditions generate characteristic calcium signatures that vary in:

- amplitude,
- frequency,
- duration,
- cellular location, and
- timing.

These calcium signatures are decoded by proteins such as:

- calmodulins,
- calmodulin-like proteins,
- calcium-dependent protein kinases,
- CBL-CIPK complexes, and
- calcium-responsive transcriptional regulators.

Consequently, Ca²⁺ signalling provides an important communication bridge between environmental perception and gene regulation.

ROS as both signal and damage molecule

Reactive oxygen species include: (Baxter et al., 2014; Mittler, 2017; Choudhury et al., 2017).

- superoxide radicals,
- hydrogen peroxide,
- hydroxyl radicals, and
- singlet oxygen.

ROS are traditionally associated with oxidative damage. However, moderate and spatially controlled ROS production also functions as an essential signalling mechanism.

Stress-induced ROS can activate:

- antioxidant genes,
- MAPK cascades,
- transcription factors,
- hormonal pathways,
- cell-wall responses, and



- acclimation mechanisms.

The biological challenge is therefore not simply to eliminate ROS but to maintain ROS homeostasis. A resilient plant does not have the lowest ROS level; it has the greatest capacity to control ROS production, signalling and detoxification.

The ROS–Ca²⁺–MAPK Signalling Hub

One of the central features of the Plant Defense Web is the interaction among Ca²⁺, ROS and protein kinase signalling. Environmental stress can activate ROS-producing enzymes, particularly respiratory burst oxidase homologues (RBOHs). ROS can influence calcium channels, while Ca²⁺ can regulate ROS production through calcium-dependent protein kinases. (Baxter et al., 2014; Choudhury et al., 2017).

This creates a positive feedback system:

Stress → Ca²⁺ influx → kinase activation → RBOH activation → ROS production → further Ca²⁺ signalling

If uncontrolled, this feedback may cause oxidative damage. If properly regulated, it becomes an information-processing system. MAPK cascades provide another major signalling layer. Stress-responsive MAPKs can phosphorylate transcription factors and other proteins involved in metabolism, defense and growth.

Therefore:

Ca²⁺ + ROS + MAPK = central signalling intersection

This intersection represents a promising target for engineering multiple-stress tolerance.

Phytohormonal Crosstalk: The Decision-Making Network

Plant hormones do not operate as isolated pathways. Instead, they form a dynamic regulatory network that determines whether the plant should prioritize growth, defense, reproduction or survival. (Zhu, 2016; Li et al., 2019; Müller, 2021; Gan et al., 2025; Mehrabi et al., 2026).

Abscisic acid

ABA is a major regulator of drought and osmotic stress responses.

The canonical ABA signalling pathway involves:

ABA → PYR/PYL/RCAR → PP2C inhibition → SnRK2 activation → ABF/AREB transcription factors → stress-responsive genes

This pathway regulates:

- stomatal closure,
- osmotic adjustment,
- aquaporin regulation,
- stress-responsive genes,
- antioxidant defense,
- root architecture, and
- growth restraint.

ABA therefore represents one of the major hubs connecting water availability with whole-plant stress adaptation.

Jasmonates

Jasmonates contribute to both biotic and abiotic stress responses. They participate in ROS detoxification, antioxidant activation, Osmo protectant accumulation and regulation of growth. (Li et al., 2019; Müller & Munné-Bosch, 2021).

JA can interact with ABA, ethylene, salicylic acid and other hormonal pathways, creating context-dependent responses.

Salicylic acid

Although traditionally associated with pathogen defense, SA also participates in oxidative signalling, photosynthetic regulation and abiotic stress acclimation.

SA-mediated regulation of antioxidant systems can contribute to redox homeostasis under environmental stress.

Ethylene

Ethylene becomes particularly important under flooding, mechanical stress, heat and combined environmental stress.

Ethylene interacts with ABA and other hormones to regulate the balance between stress survival and continued growth.



Brassinosteroid

Brassinosteroid influence:

- antioxidant activity,
- photosynthesis,
- membrane stability,
- growth,
- ROS signalling, and
- stress-responsive gene expression.

They therefore provide an important connection between growth regulation and stress protection.

Melatonin

Melatonin has emerged as an important plant signalling molecule associated with:

- ROS scavenging,
- antioxidant enzyme activation,
- chloroplast protection,
- mitochondrial protection,
- hormonal crosstalk,
- stress-responsive gene expression, and
- recovery from oxidative damage.

Its ability to influence several stress pathways makes melatonin particularly interesting for multiple-stress tolerance.

Hormonal balance rather than hormonal dominance

The most important principle is that plant stress adaptation is not controlled by one “master hormone.”

Instead:

ABA + JA + SA + ET + BR + auxin + CK + melatonin + SLs

form a regulatory network whose output depends on stress combination and developmental context.

Antioxidant Defense: The Biochemical Shield

Multiple abiotic stresses commonly increase oxidative pressure. Plants therefore possess enzymatic and non-enzymatic antioxidant systems. (Baxter et al., 2014; Mittler, 2017; Nawaz et al., 2024).

Enzymatic antioxidants

Major enzymes include:

- superoxide dismutase (SOD),
- catalase (CAT),
- ascorbate peroxidase (APX),
- glutathione reductase (GR),
- glutathione peroxidase (GPX),
- peroxiredoxins, and
- glutathione-S-transferases.

SOD converts superoxide into hydrogen peroxide, while CAT and APX contribute to hydrogen peroxide detoxification.

The ascorbate–glutathione cycle is particularly important for maintaining chloroplast and cellular redox balance.

Non-enzymatic antioxidants

Important metabolites include:

- ascorbate,
- glutathione,
- tocopherols,
- carotenoids,
- phenolics,
- flavonoids,
- anthocyanins, and
- melatonin.

These molecules also have signalling functions.

Thus, antioxidant metabolism should not be viewed simply as a “clean-up system.” It is part of the information-processing machinery of the stressed cell.

Osmotic Adjustment and Compatible Solutes

Water deficit, salinity and temperature stress disturb cellular water relations. Plants compensate by accumulating compatible solutes.

Important Osmo protectants include:

- proline,
- glycine betaine,



- trehalose,
- raffinose-family oligosaccharides,
- soluble sugars,
- polyols, and
- polyamines.

These compounds contribute to:

1. osmotic adjustment,
2. protein stabilization,
3. membrane protection,
4. ROS regulation,
5. enzyme stabilization,
6. cellular hydration, and
7. signalling.

Proline is particularly interesting because its role extends beyond osmotic adjustment to antioxidant defense, redox regulation and cellular signalling. (Kaur & Garg, 2022).

The accumulation of osmolytes therefore represents a multifunctional biochemical adaptation.

Photosynthesis as a Major Stress Target

Photosynthesis is one of the earliest physiological processes affected by combined abiotic stress. (Choudhury et al., 2017; Mittler, 2006).

Drought can reduce stomatal conductance and CO₂ availability. Heat can destabilize photosystem II and Rubisco activase. Salinity can induce ionic and oxidative stress. UV-B can damage photosynthetic components and increase ROS production.

Consequently, multiple stress conditions may produce: **stomatal limitation → electron transport imbalance → ROS accumulation → PSII damage → reduced carbon assimilation**

However, tolerant genotypes frequently maintain:

- higher chlorophyll content,
- better PSII efficiency,
- greater antioxidant capacity,
- improved photoprotection,
- stable electron transport, and

- faster recovery.

Parameters such as:

- Fv/Fm,
- ΦPSII,
- ETR,
- NPQ,
- qP,
- OJIP parameters, and
- performance index

can therefore provide valuable indicators of stress tolerance.

UV-B as a Special Case of Stress Perception

UV-B represents an interesting example because it can act as both an environmental signal and a damaging stress. (Rizzini et al., 2011; Shi & Liu, 2021).

Plants perceive UV-B primarily through the UVR8 photoreceptor.

The simplified pathway is:

UV-B → UVR8 activation → COP1 interaction → HY5 activation → protective gene expression

UVR8 signalling promotes flavonoid and phenylpropanoid biosynthesis, which can provide UV-screening protection. (Rizzini et al., 2011; Shi & Liu, 2021).

At excessive intensity, however, UV-B can promote DNA damage, ROS accumulation and photosynthetic impairment.

This demonstrates an important concept:

The same environmental factor can function as information at one intensity and stress at another intensity.

This principle is highly relevant to multiple-stress biology because high temperature, light intensity, drought and UV-B frequently interact in field environments.



Phenylpropanoid Metabolism: The Chemical Armor

Phenylpropanoid metabolism represents a major biochemical defense pathway. (Nawaz et al., 2024; Shi & Liu, 2021).

Stress can activate:

Phenylalanine → PAL → cinnamic acid → phenylpropanoid intermediates → flavonoids/phenolics/lignin

Flavonoids and related compounds can:

- absorb UV radiation,
- scavenge ROS,
- stabilize membranes,
- protect photosynthetic structures,
- modify cell walls, and
- participate in signalling.

This pathway is therefore particularly important when drought, heat and high radiation occur simultaneously.

Pigmented traditional crop varieties may provide valuable genetic resources because naturally elevated phenolic, flavonoid or anthocyanin levels can contribute to environmental resilience.

Transcription Factors: Converting Signals into Defense

Stress signals ultimately need to alter gene expression.

Major transcription factor families include:

- WRKY,
- NAC,
- MYB,
- bZIP,
- AP2/ERF,
- DREB,
- HSF, and
- bHLH.

Different transcription factors can integrate signals from multiple pathways. (Zhu, 2016; Li et al., 2019; Gan et al., 2025).

For example, DREB proteins are strongly associated with dehydration and temperature responses, whereas HSFs regulate heat-shock responses. WRKY and MYB proteins frequently connect hormonal, redox and secondary-metabolite pathways.

The regulatory network can therefore be represented as:

Environmental stress → Ca²⁺/ROS → kinase cascades → hormones → transcription factors → defense genes

This hierarchical organization allows plants to convert multiple environmental signals into coordinated gene-expression programs.

Epigenetic Regulation and Stress Memory

Plants are capable of retaining information about previous stress exposure.

This phenomenon is generally described as **stress priming or stress memory**. (Jisha et al., 2013; Hemenway & Gehring, 2023; Kovalchuk, 2023; Sharma et al., 2022).

Priming may involve:

- DNA methylation,
- histone modification,
- chromatin remodelling,
- nucleosome repositioning,
- non-coding RNAs,
- altered transcription-factor activity,
- metabolic memory, and
- persistent redox changes.

A previously stressed plant may respond more rapidly or strongly when exposed to a subsequent stress.

For example:

mild drought → priming → improved response to subsequent drought/heat

This phenomenon can sometimes extend into cross-stress tolerance, although the strength and stability of such effects depend on genotype, stress intensity, developmental stage and environmental conditions.



Stress memory is therefore an attractive concept for crop management and breeding. (Jisha et al., 2013; Kovalchuk, 2023; Sharma et al., 2022).

Cross-Tolerance: The Hidden Advantage of the Defense Web

Cross-tolerance occurs when exposure to one stress improves tolerance to another stress. (Mittler, 2006; Prasch & Sonnewald, 2015; Nadeem et al., 2023).

Examples include:

- drought priming → improved heat tolerance,
- mild salinity → improved osmotic stress tolerance,
- UV-B exposure → enhanced antioxidant and phenylpropanoid defense,
- temperature acclimation → improved oxidative stress tolerance.

The underlying explanation is that different stresses may activate overlapping protective mechanisms.

A simplified cross-tolerance pathway is:

Primary stress

↓

ROS + Ca²⁺ + hormonal signaling

↓

Antioxidants + osmolytes + transcription factors

↓

Primed physiological state

↓

Enhanced tolerance to secondary stress

This mechanism may become increasingly important as climate change produces recurrent and overlapping environmental stress.

Growth–Defense Trade-Off

Plant survival comes at a cost.

Stress defense requires:

- ATP,
- reducing power,
- carbon skeletons,
- nitrogen,
- minerals,
- transcriptional resources, and
- metabolic investment.

Therefore, activation of strong defense responses may reduce growth.

A successful stress-resilient genotype should not simply activate maximum defense. Instead, it should achieve:

efficient defense with minimum growth penalty.

This distinction is particularly important for crop improvement.

The ideal crop should be able to:

1. detect stress early,
2. activate protection rapidly,
3. maintain photosynthesis,
4. preserve reproductive development,
5. minimize unnecessary defense,
6. recover quickly after stress removal.

This represents productive resilience, rather than merely survival.

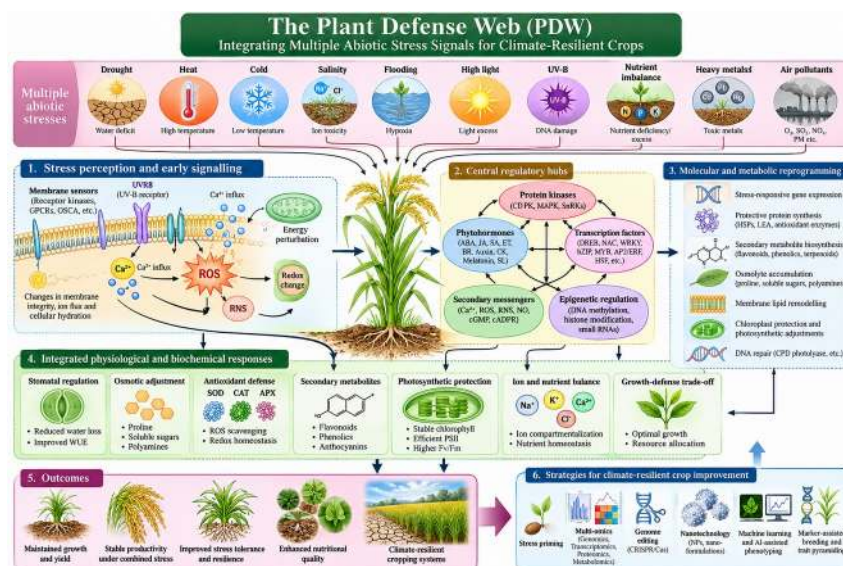


Figure 1: Integrated Plant Defense Web (PDW) Model for Multiple Abiotic Stress Tolerance

Central hypothesis of the model

The model proposes that **multiple abiotic stresses do not activate completely independent defense pathways**. Instead, they converge on a limited number of signalling and metabolic hubs.

The most important hubs are:

$\text{Ca}^{2+} \rightarrow \text{ROS} \rightarrow \text{MAPKs/CDPKs} \rightarrow \text{phytohormones} \rightarrow \text{transcription factors} \rightarrow \text{antioxidants/osmolytes/secondary metabolites} \rightarrow \text{physiological protection}$ (Zhu, 2016; Baxter et al., 2014; Kovalchuk, 2023). These connected layers are represented in Figure 1.

Stress memory subsequently modifies the sensitivity of this network during future stress episodes.

A New Concept: The Stress Defense Threshold

An important extension of the Plant Defense Web is the concept of a **stress defense threshold**.

At low stress intensity:

Stress $\rightarrow$ acclimation

At moderate stress intensity:

Stress $\rightarrow$ defense activation $\rightarrow$ metabolic adjustment

At high stress intensity:

Stress $\rightarrow$ excessive ROS $\rightarrow$ cellular injury $\rightarrow$ growth inhibition

Therefore, plant resilience depends not only on the strength of defense mechanisms but also on how efficiently a plant detects when to switch between acclimation, protection, recovery and programmed cell death.

The proposed relationship can be summarized as:

Environmental pressure

$\rightarrow$ **signal perception**

$\rightarrow$ **defense threshold**

$\rightarrow$ **acclimation OR injury**

This threshold is likely controlled by genotype, developmental stage, previous stress history and environmental context.

Multi-Omics Approaches for Decoding Multiple-Stress Tolerance

Understanding combined stress responses requires integration of multiple biological levels.

Genomics

Genomics can identify:

- stress-associated genes,
- allelic variation,
- QTLs,



- candidate genes, and
- genomic regions associated with resilience.

Transcriptomics

RNA sequencing can identify:

- differentially expressed genes,
- stress-specific genes,
- common stress-responsive genes,
- transcription-factor networks, and
- pathway enrichment.

Proteomics

Proteomics provides information on the actual proteins accumulating or disappearing during stress.

This is important because transcript abundance does not always predict protein abundance or activity.

Metabolomics

Metabolomics can reveal changes in:

- amino acids,
- sugars,
- flavonoids,
- phenolics,
- organic acids,
- lipids,
- hormones, and
- antioxidants.

Phenomics

High-throughput phenotyping can quantify:

- canopy temperature,
- chlorophyll fluorescence,
- vegetation indices,
- plant architecture,
- biomass,
- water-use efficiency, and
- recovery rate.

The future of multiple-stress research will increasingly depend on connecting these datasets.

Machine Learning and Artificial Intelligence in Stress Biology

Multiple-stress responses generate extremely complex datasets.

Machine learning can help identify relationships among: (Nawaz et al., 2024; Choudhury et al., 2017).

genotype × environment × stress × phenotype × metabolite × gene expression

Potential applications include:

- predicting stress tolerance,
- identifying biomarker metabolites,
- classifying tolerant genotypes,
- predicting yield under stress,
- identifying gene–metabolite relationships,
- integrating spectral information,
- identifying stress-specific signatures.

A particularly promising approach is to combine hyperspectral or chlorophyll-fluorescence imaging with biochemical and molecular measurements.

For example:

Spectral phenotype → machine learning → biochemical prediction → tolerant genotype identification the translational workflow from traditional germplasm screening through multi-omics, machine-learning integration and field validation is summarized in Figure 2.

This could substantially accelerate screening of traditional crop germplasm.

Traditional Crop Diversity as a Reservoir of Multiple-Stress Tolerance

Modern breeding has frequently prioritized yield under favourable conditions. However, traditional and indigenous crop varieties have evolved under heterogeneous environments and may contain valuable alleles associated with stress adaptation. (Mittler & Blumwald, 2010).

Traditional germplasm may possess combinations of:

- deeper root systems,



- efficient water use,
- antioxidant capacity,
- osmotic adjustment,
- pigmentation,
- phenylpropanoid accumulation,
- stable photosynthesis,
- efficient nutrient acquisition, and
- flexible phenology.

Therefore, traditional varieties should not merely be regarded as historical resources. They can function as **living reservoirs of stress-adaptive genetic diversity**.

A promising breeding strategy is:

traditional germplasm → stress phenotyping → molecular characterization → candidate genes/markers → pre-breeding → elite cultivar development

Nanotechnology and Exogenous Priming (Nawaz et al., 2024; Jisha et al., 2013).

External application of signalling compounds and nanoparticles represents another emerging strategy.

Potential priming agents include:

- melatonin,
- salicylic acid,
- jasmonates,
- silicon,
- proline,
- selenium,
- nanoparticles, and
- beneficial microorganisms.

These treatments can potentially stimulate antioxidant systems, improve nutrient acquisition, stabilize membranes and alter stress-responsive gene expression.

However, application should be carefully optimized because concentration, particle size, formulation, genotype and environmental conditions strongly influence plant responses.

Therefore, future research should move from “more treatment” toward **precision priming**.

From Defense to Recovery: An Understudied Component

Most stress studies measure plant responses during stress. However, recovery after stress removal may be equally important. Recovery capacity should therefore be evaluated alongside stress injury and tolerance (Mittler, 2006; Prasch & Sonnewald, 2015).

Two genotypes can show similar damage during stress but differ dramatically in their recovery capacity.

A resilient genotype may rapidly:

- restore photosynthetic activity,
- remove excess ROS,
- repair damaged proteins,
- restore membrane integrity,
- re-establish growth,
- recover reproductive development.

Therefore, **recovery rate should become an important phenotype in stress-resilience screening**.

A proposed resilience index could integrate:

Stress tolerance + damage avoidance + recovery capacity + yield stability

rather than relying on a single physiological measurement.

Future Research Priorities

The following research priorities emerge from the Plant Defense Web concept.

Study realistic stress combinations

Experiments should increasingly examine:

- drought + heat,
- drought + UV-B,
- drought + salinity,
- heat + salinity,
- flooding + salinity,
- heat + high light,
- drought + nutrient deficiency.



Include stress sequence

The order of stress exposure may change plant responses.

For example:

drought → heat

may produce a different response from:

heat → drought

Measure recovery

Recovery should be incorporated into experimental designs.

Integrate multiple biological levels

Future studies should combine:

phenomics + transcriptomics + proteomics + metabolomics + ionomics

Develop stress-resilience biomarkers

Potential biomarkers include:

- Fv/Fm,
- NPQ,
- ROS-scavenging capacity,
- proline,
- flavonoids,
- antioxidant enzyme activity,
- membrane stability,
- canopy temperature,
- specific transcripts,
- metabolites.

Explore stress memory

Priming and epigenetic memory may provide a low-input strategy for improving resilience.

Exploit traditional germplasm

Indigenous crop diversity should be systematically evaluated under combined stress environments.

Integrate artificial intelligence

Machine learning should be incorporated into multi-stress phenotyping and genotype selection.

CONCLUSION

Plant tolerance to environmental stress cannot be adequately explained by isolated stress-response pathways. In natural environments, plants encounter fluctuating combinations of drought, heat, salinity, radiation, flooding, nutrient imbalance and other environmental challenges. These stress combinations generate complex and sometimes unpredictable responses.

The evidence reviewed here supports a network-based model in which multiple environmental stresses converge on a limited set of cellular signalling hubs. Calcium, ROS, MAPKs, phytohormones and transcription factors form the central communication architecture, while antioxidants, osmolytes, flavonoids, phenolics, compatible solutes and protective proteins form the biochemical defense layer. Epigenetic regulation and stress memory extend this network across time, allowing plants to respond differently to recurrent environmental challenges. (Mittler, 2006; Choudhury et al., 2017; Nadeem et al., 2023; Zhu, 2016).

The proposed **Plant Defense Web** provides a conceptual bridge between molecular signalling and whole-plant resilience. Importantly, the objective of crop improvement should not be to maximize the activation of every defense pathway. Excessive defense can suppress growth and yield. Instead, the objective should be to develop plants capable of **rapid perception, precise signalling, efficient protection and rapid recovery with minimal growth penalty**.

Future climate-resilient agriculture will therefore require a shift from single-gene and single-stress thinking toward **network-based, multi-stress and phenotype-driven crop improvement**.

The most promising strategy can be summarized as:

Diverse germplasm → realistic multiple-stress phenotyping → multi-omics → defense-network biomarkers → precision breeding/editing → priming → resilient cultivar

Ultimately, plant resilience should be defined not simply as the ability to survive stress, but as the ability to **maintain photosynthesis, growth, reproduction and yield while continuously adapting to an unpredictable environment**.



Figure 2: Translational Pipeline for Developing Climate-Resilient Crops

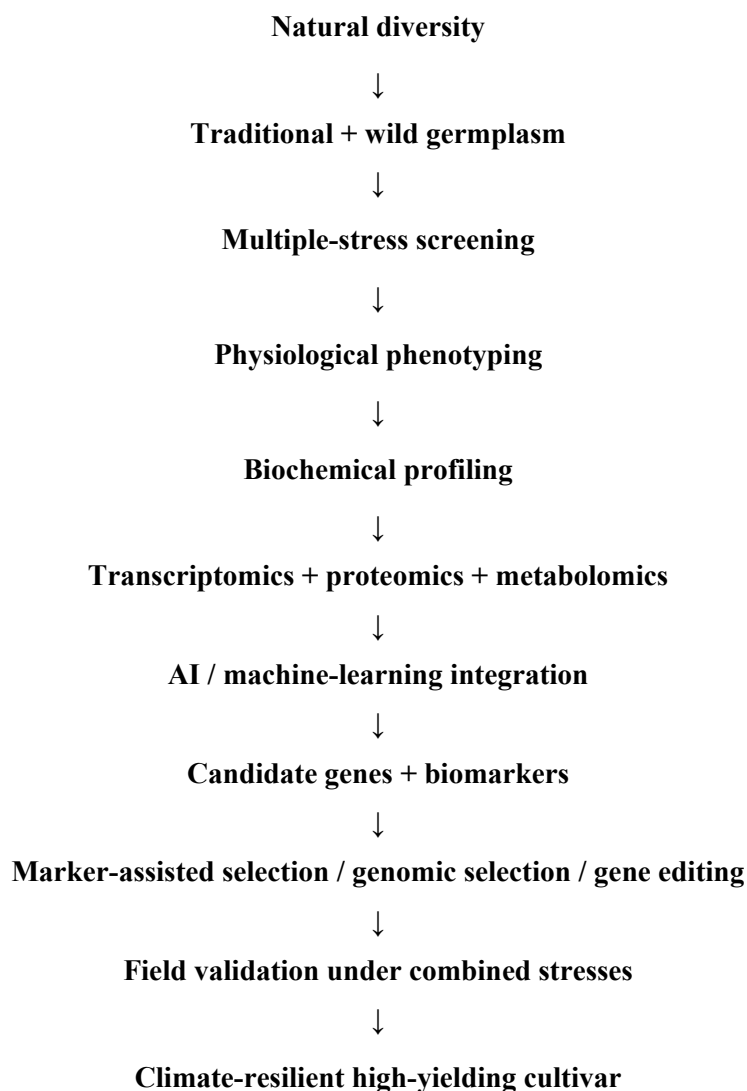


Table 1: Major Abiotic Stresses and Their Principal Defense Responses

Stress	Primary disturbance	Major signalling components	Important defense mechanisms
Drought	Water deficit	ABA, Ca ²⁺ , ROS, MAPKs	Stomatal closure, osmolytes, antioxidants
Salinity	Osmotic + ionic stress	ABA, Ca ²⁺ , ROS, SOS pathway	Na ⁺ exclusion, K ⁺ retention, osmotic adjustment
Heat	Protein/membrane instability	Ca ²⁺ , ROS, HSFs, ABA	HSPs, antioxidants, membrane stabilization
Cold	Reduced membrane fluidity	Ca ²⁺ , ROS, CBF/DREB	Cryoprotection, unsaturated lipids, osmolytes
Flooding	Hypoxia/anoxia	Ethylene, ROS, Ca ²⁺	Fermentation, aerenchyma, carbohydrate management
UV-B	DNA/photosynthetic damage	UVR8, ROS, Ca ²⁺	Flavonoids, DNA repair, antioxidants
High light	Photoinhibition	ROS, Ca ²⁺	NPQ, carotenoids, antioxidant defense
Heavy metals	Oxidative + ionic toxicity	ROS, Ca ²⁺ , hormones	Chelation, sequestration, antioxidant defense

Stress	Primary disturbance	Major signalling components	Important defense mechanisms
Nutrient deficiency	Metabolic limitation	Hormones, ROS, nutrient sensors	Root remodeling, transporter activation
Combined stress	Multiple disturbances	Integrated signaling network	Cross-tolerance, metabolic plasticity, priming

Table 2: Major Components of the Plant Defense Web

Layer	Components	Principal function
Perception	UVR8, membrane sensors, ion channels	Detect environmental changes
Early signaling	Ca ²⁺ , ROS, NO	Rapid information transfer
Kinases	MAPKs, CDPKs, SnRKs, CIPKs	Signal amplification
Hormones	ABA, JA, SA, ET, BR, auxin, melatonin	Signal integration
Transcription factors	WRKY, NAC, MYB, DREB, HSF, bZIP	Gene regulation
Antioxidants	SOD, CAT, APX, GR, GPX	Redox protection
Osmolytes	Proline, sugars, glycine betaine	Osmotic protection
Secondary metabolites	Flavonoids, phenolics, anthocyanins	ROS/UV protection
Molecular repair	DNA repair, HSPs, proteostasis	Damage recovery
Memory	DNA methylation, histone modification, ncRNA	Stress priming
Phenotype	Photosynthesis, water-use efficiency, growth	Whole-plant adaptation
Outcome	Survival + recovery + yield	Agricultural resilience

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