

Plant Adaptation Networks: Physiology, Signaling, and Systemic Responses

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ABSTRACT

Plants, as sessile organisms, are continuously exposed to diverse abiotic stresses (e.g., drought, salinity, and extreme temperatures) and biotic challenges that compromise growth and global food security. To withstand these pressures, plants have evolved highly coordinated stress perception and signaling networks that integrate local and systemic responses. This review analyzes the recent advances in understanding stress sensing, signal transduction, and whole-plant adaptive mechanisms. Central components of these networks include phytohormones (ABA, SA, JA), reactive oxygen species (ROS), Ca^{2+} fluxes, electrical signals, and hydraulic waves, which collectively mediate rapid long-distance communication and systemic acquired acclimation. Strong interaction between these signaling pathways helps plants carefully regulate their responses to both single and combined stresses, often leading to different physiological outcomes. Furthermore, stress priming and memory contribute to enhanced resilience in subsequent exposures. Elucidating these integrated signaling frameworks provides a mechanistic basis for developing climate-resilient crops through genome editing and multi-omics strategies.

Keywords: Integrated Plant Physiology, Systemic Signaling, Phytohormones, Reactive Oxygen Species, Crosstalk, Combined Stresses, Stress Priming, Climate-Resilient Crops.

1. Introduction

Plants are sessile organisms and cannot escape unfavorable conditions. They are continuously exposed to fluctuating abiotic stresses, such as drought, salinity, extreme temperatures, high light, and flooding, as well as biotic stresses including pathogens, herbivores, and insect pests. These stresses often occur simultaneously or sequentially, severely affecting growth, development, reproduction, and yield, thereby threatening global food security under accelerating climate change [1]. To deal with these unfavourable conditions, plants have developed highly integrated and dynamic response systems that allow them to detect stresses early, transmit signals rapidly across tissues, and activate coordinated physiological, biochemical, and molecular adjustments for acclimation and survival [2,3].

During plant stress responses, signaling networks are mainly phytohormones such as abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA), and ethylene together with reactive oxygen species (ROS), calcium ions (Ca^{2+}), electrical signals, and hydraulic waves. These interconnected mediators initiate local responses at the site of stress perception and propagate rapid systemic signals, ensuring coordinated whole-plant adaptation [4-6]. For example, ABA predominantly regulates abiotic stress responses, including drought and salinity, by inducing stomatal closure and osmotic adjustment, whereas SA and JA are central to defense against pathogens and herbivores [7,8]. Importantly, extensive hormonal crosstalk enables dynamic prioritization between growth and defense and optimizes resource allocation under concurrent or sequential stress conditions [9,10].

In natural condition, stresses rarely act in isolation; combined stresses often elicit unique responses that cannot be predicted from single-stress studies. Drought paired with heat, for instance, induces distinct transcriptional signatures compared to either stress alone, highlighting the need for integrated signaling to achieve optimal acclimation [3,11]. ROS play a pivotal role here, acting both as damaging agents at high levels and as key signaling molecules that propagate as autopropagating "ROS waves" from the stressed site to distant tissues, integrating with Ca^{2+} waves and electrical signals to drive systemic acquired acclimation (SAA) to abiotic stresses or systemic acquired resistance (SAR) to biotic ones [6,12,13]. This rapid systemic signaling, often occurring within minutes, primes unstressed tissues for enhanced resilience, involving massive but transient transcriptome reprogramming [1,3].

Further complexity arises from hormonal and signal crosstalk between abiotic and biotic pathways. Abiotic stresses can suppress or enhance biotic defenses, and vice versa, through shared nodes like ROS, mitogen-activated protein kinases (MAPKs), and transcription factors (TFs) [14,15]. Emerging roles for small peptides, liquid-liquid phase separation in cellular compartmentalization, and cell wall integrity sensors add layers to this integration, enabling precise tuning of responses [16,17]. Additionally, stress priming and memory mechanisms, where prior mild stress exposure "trains" the plant for stronger future responses, underpin cross-tolerance, with epigenetic modifications, sustained metabolite changes, and transcriptional memory contributing to somatic or even transgenerational inheritance [18-20].

This review integrates recent advances (primarily 2020–2025) in understanding these interconnected processes, from initial stress perception and local signaling to systemic propagation and whole-plant adaptive adjustments. We cover key signaling molecules and pathways, with emphasis on phytohormone crosstalk, ROS and Ca^{2+} integration, local versus systemic responses, and morphological, physiological, and molecular adaptations. By addressing both individual and combined abiotic/biotic stresses, along with priming and memory effects, we aim to illuminate how integrated plant physiology fosters resilience. These insights hold promise for biotechnological applications in breeding climate-resilient crops to sustain agriculture amid escalating environmental challenges.

2. Stress Perception and Initial Signaling in Plants

Plants, as sessile organisms, are perpetually exposed to a dynamic array of environmental stressors, ranging from abiotic factors like drought, salinity, temperature fluctuations, and excessive light to biotic threats such as pathogens and herbivores. The ability to swiftly perceive these challenges at the cellular interface and convert them into actionable intracellular signals is fundamental to their survival and adaptation. This initial phase of stress response encompasses the detection by specialized sensors and receptors, primarily located on the plasma membrane, cell wall, or within organelles, followed by the generation of rapid secondary messengers. Prominent among these are cytosolic calcium ions (Ca^{2+}), reactive oxygen species (ROS), and electrical signals, which collectively form a sophisticated signaling network that decodes environmental cues with remarkable specificity and speed. Recent advancements have illuminated how these elements interact in root-specific contexts and across species, highlighting divergent dynamics and species-specific signatures that refine our understanding of early plant responses [21–23].

The perception of stress often commences with membrane-bound sensors and receptor-like kinases (RLKs) that act as the first line of detection. In abiotic stress scenarios, such as osmotic imbalances from drought or salinity, mechanosensitive channels and osmosensors are pivotal. For example, the hyperosmolality-gated calcium-permeable channel OSCA1 directly responds to osmotic shifts by facilitating Ca^{2+} influx, which is essential for osmotic adjustment in guard cells and broader cellular homeostasis [21]. Similarly, the leucine-rich repeat receptor kinase HPCA1 serves as a direct hydrogen peroxide (H_2O_2) sensor, undergoing oxidative modifications to activate downstream Ca^{2+} channels during ROS-mediated signaling [22]. The FERONIA (FER) receptor kinase further exemplifies this by preserving cell wall integrity under salt stress through modulation of Ca^{2+} dynamics, illustrating how physical and chemical cues are integrated at the membrane level [24]. Emerging research underscores the role of hydraulic and electrical signals in drought perception, where reduced root turgor generates xylem tension that precedes hormonal responses, often coupled with multisensor systems involving photoreceptors and membrane fluidity changes [25].

For biotic stresses, pattern recognition receptors (PRRs), predominantly RLKs, identify microbe-associated molecular patterns (MAMPs) or damage-associated molecular patterns (DAMPs). Well-characterized examples include Flagellin-sensing 2 (FLS2) and the elongation factor Tu receptor (EFR), which bind bacterial flagellin or EF-Tu, respectively, to initiate swift immune cascades [26].

Herbivore-induced cues, such as insect oral secretions, are similarly detected by dedicated PRRs, triggering analogous early signaling events [27]. Recent studies in crop species like potato (*Solanum tuberosum*) reveal that biotic PAMPs, such as flg22 and Pep-13, elicit slower Ca^{2+} transients compared to abiotic stressors, with delayed peaks that vary by species, highlighting evolutionary adaptations in perception mechanisms [28].

A defining feature of initial signaling is the rapid elevation in cytosolic Ca^{2+} concentration ($[\text{Ca}^{2+}]_{\text{cyt}}$), often termed the "calcium signature." This signature, defined by its amplitude, duration, frequency, and spatial distribution, encodes stressor-specific information, enabling tailored responses [29]. Ca^{2+} influx is orchestrated by diverse channels, including cyclic nucleotide-gated channels (CNGCs), glutamate receptor-like proteins (GLRs), and two-pore channel 1 (TPC1). GLRs, for instance, are crucial for wound-induced Ca^{2+} waves and electrical propagation, as seen in systemic responses to mechanical damage [30,31]. Annexins, such as AtANN1, further regulate these transients under temperature extremes, facilitating heat- or cold-induced Ca^{2+} spikes [32,33]. In root systems, early Ca^{2+} signaling under osmotic stress or PAMP exposure involves mechanosensitive channels like MSL9, which undergo rapid phosphorylation and interact with kinases (e.g., CPK8), actins (ACT2, ACT7), and antioxidant enzymes (APX1–3, CAT1–3) to fine-tune influx and ROS interplay [23]. Dose-dependent analyses in potato show distinct signatures for abiotic stressors like NaCl and mannitol, with biphasic patterns under oxidative stress, influenced by basal redox states [28].

Interwoven with Ca^{2+} dynamics is the generation of ROS, primarily via plasma membrane-bound respiratory burst oxidase homologs (RBOHs), such as AtRBOHD. At low levels, ROS function as signaling molecules, while excess amounts cause oxidative damage. Stress perception activates RBOHs through Ca^{2+} binding to EF-hand motifs and kinase-mediated phosphorylation, establishing a feedback loop where ROS amplify Ca^{2+} influx [34,35]. This synergy underpins propagating ROS waves that facilitate systemic acclimation, traveling cell-to-cell at rates conducive to whole-plant coordination [36,37]. In abiotic contexts, chloroplast-derived ROS enable retrograde signaling to the nucleus, while root-specific H_2O_2 accumulation exhibits patterns distinct from Ca^{2+} waves, emphasizing compartmentalized responses [23,25].

Electrical signals, encompassing variation potentials (VPs) and action potentials (APs), add another dimension to rapid initial signaling. These depolarizations, induced by wounding, salinity, or thermal stress, disseminate via vascular bundles or plasmodesmata. They are intrinsically linked to Ca^{2+} influx through mechanosensitive channels (e.g., MSL10) and GLRs, and often converge with ROS bursts [38,39]. Wound responses, for instance, depend on GLR3.3 and GLR3.6 for coordinating Ca^{2+} and ROS waves across distances [30]. Recent models integrate these with glutamate signals for long-range wound responses, underscoring their role in systemic defense [25].

These early signals— Ca^{2+} spikes, ROS bursts, and electrical changes operate synergistically rather than independently, forming a robust network. Ca^{2+} activates RBOHs to boost ROS, which in turn oxidizes channels to enhance Ca^{2+} entry, while electrical shifts facilitate ion fluxes [34,35]. This interconnectedness ensures signal specificity and amplification, bridging local perception to global plant coordination prior to the engagement of slower hormonal pathways like abscisic acid (ABA) or jasmonate (JA).

Species-specific variations, such as those observed in potato versus *Arabidopsis*, suggest that basal oxidative states and channel kinetics modulate these interactions, offering insights into crop resilience [28].

Insights into these mechanisms not only reveal the elegance of plant sensory systems but also pave the way for biotechnological interventions, such as engineering enhanced sensors for stress-tolerant crops in an era of climate variability.

3. Important Signaling Molecules and Pathways

Plants rely on a sophisticated network of signaling molecules to perceive environmental stresses and coordinate adaptive responses. These molecules operate through interconnected pathways, allowing the integration of multiple signals for precise regulation of physiological and molecular adjustments.

Phytohormones in Stress Signaling

Phytohormones are central orchestrators of plant stress responses, with abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA), and ethylene playing prominent roles. ABA is often regarded as the primary stress hormone, particularly for abiotic challenges like drought and salinity, where it triggers stomatal closure, osmotic adjustment, and the expression of stress-responsive genes. SA is crucial for defense against biotrophic pathogens, activating systemic acquired resistance (SAR), while JA and ethylene dominate responses to necrotrophic pathogens and herbivory, inducing defenses such as wound healing and volatile compound production.

The effectiveness of these hormones stems from their extensive crosstalk, which fine-tunes responses to specific stressors or combinations thereof. For instance, ABA and JA often synergize in abiotic stress, with JA enhancing ABA-mediated stomatal regulation through pathways involving reactive oxygen species (ROS) and nitric oxide. In contrast, SA and JA pathways frequently antagonize each other to prioritize biotic defense types SA suppressing JA in biotrophic infections and vice versa in necrotrophic cases. Ethylene modulates these interactions, sometimes amplifying JA effects in wound responses or antagonizing ABA in seed germination under stress. This hormonal interplay ensures resource allocation between growth and defense, with recent insights highlighting epigenetic and transcriptional nodes as integration points [7,8,40].

Reactive Oxygen Species (ROS) and Redox Signaling

ROS, including hydrogen peroxide (H_2O_2), superoxide, and singlet oxygen, were once viewed primarily as damaging byproducts of metabolism. However, they are now recognized as essential signaling molecules in stress adaptation. Produced mainly in chloroplasts, mitochondria, and peroxisomes via enzymes like respiratory burst oxidase homologs (RBOHs), ROS accumulate rapidly upon stress perception, acting as secondary messengers. At low levels, ROS modulate redox-sensitive proteins, transcription factors, and kinases, activating antioxidant systems and stress genes. H_2O_2 , being relatively stable and diffusible, propagates systemic signals, such as ROS waves that coordinate whole-plant acclimation. ROS interplay with phytohormones is bidirectional: ABA and JA stimulate ROS production, while ROS in turn amplify hormonal signaling. This redox hub integrates abiotic and biotic cues, balancing oxidative damage with protective responses through antioxidant enzymes like superoxide dismutase and ascorbate peroxidase [6,41].

Calcium and Electrical Signaling

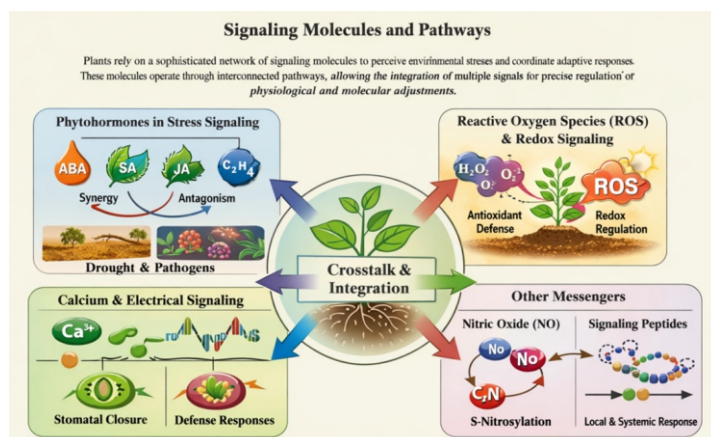
Calcium (Ca^{2+}) serves as a universal second messenger, with stress-induced transients in cytosolic Ca^{2+} levels known as Ca^{2+} signatures encoding stimulus-specific information. These signatures arise from influx through channels (e.g., glutamate receptor-like proteins) and release from internal stores, decoded by sensors like calmodulins, calcineurin B-like proteins, and Ca^{2+} -dependent protein kinases.

Ca^{2+} waves propagate systemically, often coupled with electrical signals such as variation potentials or action potentials, enabling rapid long-distance communication during wounding or abiotic stress. Electrical signals depolarize membranes, activating Ca^{2+} channels and ROS production, forming a self-amplifying loop with phytohormones. For example, Ca^{2+} integrates with ABA in stomatal closure and with JA/SA in immune responses, highlighting its role in signal convergence [13,31,42].

Other Messengers

Additional messengers, including nitric oxide (NO) and signaling peptides, further enrich the network. NO, a gaseous radical, acts via post-translational modifications like S-nitrosylation, influencing protein function and gene expression. It crosstalks extensively with ROS (forming peroxynitrite for signaling) and hormones, enhancing ABA effects in stomatal regulation or synergizing with JA in defense.

Signaling peptides, such as systemin or rapid alkalization factors, amplify local and systemic responses, often interacting with JA pathways in wound signaling. These messengers provide fine-tuned, rapid adjustments, bridging early perception with downstream adaptations [43,44]. These molecules form an integrated web where crosstalk ensures robust, context-dependent responses, enabling plants to thrive amid fluctuating environments.



4. Local Responses to Stress

When plants first encounter environmental stresses, whether abiotic, like drought or salinity, or biotic, such as pathogen attack, the initial reactions occur right at the site where the stress is perceived. These local responses involve rapid physiological adjustments and molecular changes that help stabilize the affected cells and tissues, preventing immediate damage while buying time for broader plant-wide adaptations. One of the earliest events is the generation of reactive oxygen species (ROS), such as hydrogen peroxide and superoxide. These molecules accumulate quickly in stressed cells, acting not just as harmful byproducts but as important signaling agents that trigger protective mechanisms [45].

For instance, in leaves exposed to high light or drought, ROS production in chloroplasts helps activate antioxidant defenses locally, reducing oxidative damage to proteins and membranes [46].

Almost simultaneously, a rise in cytosolic calcium levels occurs, creating specific "calcium signatures" unique to the type of stress. This calcium influx is detected by sensor proteins like calmodulins and calcium-dependent protein kinases, which then phosphorylate targets to alter cell functions [47]. In root cells facing salinity, for example, this calcium signal rapidly closes ion channels to limit sodium uptake at the local site [48].

Phytohormones also play a key role locally. Absciscic acid (ABA) is often synthesized on-site in response to osmotic stresses, leading to quick stomatal closure in guard cells to conserve water [49]. For biotic stresses, jasmonic acid and salicylic acid accumulate rapidly at infection sites, inducing defense compounds like phytoalexins and reinforcing cell walls [50].

At the molecular level, these signals converge to reprogram gene expression. Transcription factors, such as those from the WRKY or NAC families, bind to promoters of stress-responsive genes, upregulating protective proteins like heat shock proteins, osmoprotectants, and enzymes for ROS scavenging [51]. This local transcriptional burst ensures immediate production of tools needed for cell survival, such as proline for osmotic adjustment or pathogenesis-related proteins during pathogen encounters [52].

Overall, these immediate local changes—spanning seconds to hours—form the foundation of plant resilience, limiting damage at the point of impact and often generating mobile signals for systemic coordination.

5. Systemic Signaling Mechanisms

Plants, as sessile beings anchored in their environments, have evolved intricate mechanisms for long-distance communication to synchronize responses across their entire body. When a stress is detected in one area, such as a root encountering drought or a leaf facing herbivore attack, systemic signals propagate to distant tissues, priming them for defense or adaptation. This coordination relies on the vascular system—primarily the phloem and xylem—as conduits for chemical messengers, alongside faster wave-like signals that integrate electrical, hydraulic, and biochemical cues. Recent research has highlighted how these pathways not only respond to single stressors but also integrate multiple environmental inputs, enhancing plant resilience in dynamic ecosystems [53]. Understanding these mechanisms is crucial for advancing crop improvement strategies amid climate change.

Mobile Signals and Long-Distance Communication (e.g., via Phloem/Xylem)

The phloem and xylem form the backbone of plant long-distance transport, acting like a circulatory system that moves water, nutrients, and signals. The phloem, composed of sieve elements and companion cells, enables bidirectional flow driven by pressure gradients, ideal for distributing photoassimilates and signals from source leaves to sinks like roots or fruits. In contrast, the xylem conducts unidirectional upward flow of water and minerals via transpiration pull, often carrying root-sensed signals to shoots. This dual system allows plants to relay information about soil conditions, nutrient availability, or biotic threats over meters in large trees or centimeters in herbs, with speeds varying from hours to days depending on plant size and environmental factors [53,54].

Core mobile signals include phytohormones such as absciscic acid (ABA) for drought signaling, salicylic acid (SA) for pathogen responses, and jasmonic acid (JA) for wounding, which can accumulate systemically and trigger gene expression changes in remote tissues [55]. Peptides play a starring role in nutrient-related communication; for instance, C-TERMINALLY ENCODED PEPTIDES (CEPs) are synthesized in roots under nitrogen starvation, travel via xylem to shoots, and bind receptors like CEP RECEPTOR (CEPR) to induce downstream phloem-mobile polypeptides such as CEP DOWNSTREAM (CEPD) 1 and 2, which return to roots to upregulate nitrate transporters like NRT2.1 [56,57]. Similarly, CLAVATA3/EMBRYO-SURROUNDING REGION-RELATED (CLE) peptides, one of the largest peptide families in plants, mediate responses to mineral deficiencies—under low nitrogen, CLE1, CLE3, CLE4, and CLE7 suppress lateral root growth by interacting with phloem-localized receptors like CLAVATA1 (CLV1) [58,59]. These peptide relays exemplify root-shoot crosstalk, optimizing nutrient uptake.

Beyond hormones and peptides, macromolecules like proteins, mRNAs, and small RNAs traverse the phloem, often loaded via companion cells acting as signaling hubs. For example, FLOWERING LOCUS T (FT) protein moves from leaves to shoot apices to induce flowering, while microRNAs like miR399 relocate from shoots to roots during phosphate limitation, suppressing PHOSPHATE 2 (PHO2) to enhance phosphate loading into the xylem [60-62]. Recent studies emphasize how lipids, metabolites, and even long non-coding RNAs (lncRNAs) contribute, such as INDUCED BY PHOSPHATE STARVATION 1 (IPS1) acting as a miR399 mimic under low phosphate [63]. In pathogen contexts, mobile signals include peptides and chemicals transmitted through phloem for systemic immunity [64]. Advances in 2024 highlight how companion cells synthesize and translocate these molecules, with tools like phloem exudate analysis from "bleeding" plants (e.g., cucurbits) revealing diverse signal repertoires [65]. This complexity ensures plants adapt holistically, balancing growth and stress tolerance.

Rapid Systemic Signals (e.g., ROS Waves, Calcium Waves, Variation Potentials)

Complementing slower vascular transport, plants employ rapid, wave-like signals that spread systemically in seconds to minutes, integrating reactive oxygen species (ROS), calcium (Ca^{2+}), electrical potentials, and hydraulic changes. These waves often originate at the stress site and propagate through vascular bundles or cell-to-cell via plasmodesmata, enabling near-instantaneous whole-plant alerts to threats like wounding, salinity, or light stress.

ROS waves, spearheaded by apoplastic bursts of hydrogen peroxide (H_2O_2) and superoxide, are generated by enzymes like RESPIRATORY BURST OXIDASE HOMOLOG D (RBOHD) and propagate at speeds of up to 8.4 cm/min [36]. They trigger systemic acquired acclimation (SAA), enhancing antioxidant defenses in distant leaves against abiotic stresses. Recent reviews underscore ROS's dual role as stressors and signals, balancing growth, development, and immunity through interactions with phytohormones, gasotransmitters (e.g., nitric oxide), and protein kinases [66,67]. For instance, under multiple stressors, ROS waves evolve to target specific cellular components, fine-tuning responses [68].

Intertwined with ROS are Ca^{2+} waves, where cytosolic Ca^{2+} spikes, mediated by channels like GLUTAMATE RECEPTOR-LIKE (GLR) 3.3/3.6 and TWO PORE CHANNEL 1 (TPC1), amplify signals [69,70]. These waves travel alongside ROS, with mutual reinforcement—ROS activates Ca^{2+} influx, and Ca^{2+} boosts ROS production via RBOHD. Hydraulic signals, such as pressure drops from wounding, initiate these via mechanosensitive channels, leading to electrical waves like variation potentials (VPs) [71]. VPs, slower than action potentials, involve membrane depolarization propagating through xylem or phloem, often attenuated in RBOHD mutants, illustrating crosstalk [37]. A 2024 study elucidates VP specificity: different stimuli (e.g., burning vs. cutting) elicit unique VP patterns due to varying ion fluxes and hydraulic components, allowing stimulus-specific responses [72].

Integration of these signals—ROS, Ca^{2+} , electrical, and hydraulic—occurs via shared hubs like GLRs and RBOHDs, enabling multi-stress decoding [3,34]. Recent work shows even non-vascular plants like *Marchantia polymorpha* propagate Ca^{2+} waves, suggesting ancient origins [73]. In 2025, studies emphasize how electrical- Ca^{2+} signaling mediates systemic defense, with ROS as a bridge between local perception and distant acclimation [74,75]. This rapid network ensures swift, tailored adaptations, preventing overreactions that could hinder growth.

Systemic Acquired Resistance (SAR) and Induced Systemic Resistance (ISR)

Systemic immunity exemplifies specialized long-distance signaling against biotic invaders, with SAR and ISR as key modes that prime uninfected tissues for enhanced defense. SAR, activated by local infections from biotrophic pathogens, confers broad-spectrum, durable resistance via phloem-mobile signals like pipelicolic acid (Pip), N-hydroxypipelicolic acid (NHP), azelaic acid, glycerol-3-phosphate, and methyl salicylate, orchestrated by SA-dependent pathways [76]. These metabolites accumulate in distal leaves, inducing pathogenesis-related (PR) genes and fortifying cell walls.

ISR, conversely, is induced by root-colonizing beneficial microbes (e.g., *Pseudomonas* or *Bacillus* spp.), relying on JA and ethylene (ET) signaling to prime against necrotrophs and herbivores without immediate PR gene activation [77]. It involves root-to-shoot volatiles or elicitors, enhancing responsiveness via epigenetic modifications like histone acetylation for "memory" [78]. Recent advancements reveal ISR's mechanistic basis, including molecular crosstalk and priming for stress tolerance [79].

Crosstalk between SAR and ISR amplifies protection; ROS and Ca^{2+} waves contribute to SAR initiation, while shared transcription factors like NPR1 integrate SA and JA/ET pathways [80,81]. Triple interactions—plant, pathogen, and beneficial microbes—underscore ISR, with plant growth-promoting rhizobacteria (PGPR) enhancing ISR through siderophores, volatiles, and hormone modulation [82]. A 2025 study shows PGPR boosts ISR against fungal pathogens, improving yield under stress [83]. Epigenetic memory in ISR allows transgenerational resistance, vital for sustainable agriculture [84,85]. These mechanisms highlight how systemic immunity evolves with microbial communities, offering biotech targets for resilient crops.

In summary, systemic signaling intertwines vascular-mobile elements with rapid waves to forge a responsive network, enabling plants to thrive amid adversity.

Ongoing research into multi-signal integration promises breakthroughs in engineering stress-tolerant varieties.

6. Integration of Signals for Whole-Plant Coordination

Plants, as sessile organisms, face a barrage of environmental challenges that demand a sophisticated orchestration of responses across their entire body. The integration of diverse signals—ranging from hormonal cues to environmental stressors—ensures that local perceptions translate into systemic adaptations, maintaining growth, development, and survival. This coordination hinges on intricate crosstalk among signaling pathways, bidirectional communication between shoots and roots, and tailored responses to multiple concurrent stresses. By weaving these elements together, plants achieve a holistic resilience that goes beyond isolated reactions.

Crosstalk among signaling pathways forms the backbone of this integration, allowing plants to process and prioritize inputs from hormones, reactive oxygen species (ROS), and other messengers. For instance, multistep phosphorelay (MSP) signaling serves as a central hub, where histidine kinases (such as AHK2, AHK3, and AHK4) perceive cytokinins and relay phosphate groups through intermediaries to response regulators that modulate gene expression [86]. This pathway intersects with abscisic acid (ABA) and ethylene signaling; under drought, ABA accumulation suppresses cytokinin responses by phosphorylating type-A response regulators, thereby shifting priorities toward stomatal closure and water conservation. Such interactions are not merely additive but often antagonistic or synergistic, as seen in the "gas-and-brake" mechanisms where temperature-induced signals promote stomatal opening, only to be overridden by drought cues via protein kinases like OST1 [87]. Transcription factors, including NAC and WRKY families, further amplify this crosstalk by binding to shared promoter regions, enabling the fine-tuning of gene networks that balance growth and defense. In essence, these overlapping pathways prevent signal overload, ensuring that plants respond coherently to fluctuating conditions.

Shoot-root communication exemplifies how signals traverse the plant to foster whole-organism harmony. Roots, often the first to detect soil-based stresses like salinity or nutrient scarcity, dispatch mobile messengers—such as peptides, hormones, and electrical waves—to inform shoots, while shoots reciprocate with cues about aerial conditions. Auxin redistribution plays a pivotal role here; shade avoidance in shoots redirects auxin away from roots, inhibiting root elongation to favor above-ground growth [88]. Conversely, root-derived peptides like CEP1 travel via the xylem to the shoot, where they trigger auxin biosynthesis that promotes lateral root formation in nutrient-rich zones. This bidirectional dialogue is mediated by the vascular system, with phloem transporting jasmonic acid from wounded shoots to roots, reallocating carbon for storage and defense. ROS waves also facilitate rapid systemic signaling, propagating from roots under salt stress to prepare shoots for osmotic adjustments [87]. Such communication ensures resource allocation aligns with environmental demands, like enhancing root architecture for water foraging during drought while curbing shoot expansion to minimize transpiration.

When plants encounter multiple stresses simultaneously—such as heat combined with drought or salinity—their responses transcend those elicited by individual factors, often yielding unique physiological outcomes. Signal integration under multi-stress scenarios relies heavily on ROS as a quantitative sensor, where the amplitude and signature of ROS

bursts dictate the severity and specificity of the response [87]. For example, combined heat and drought suppress thermomorphogenic traits like petiole elongation, mediated by ABA counteracting auxin-driven growth via transcription factors such as PIF4. Hormonal crosstalk intensifies here, with ABA and jasmonic acid collaborating to upregulate antioxidant systems and osmoprotectants like sucrose, replacing proline to avoid toxicity in high temperatures. MSP contributes by incorporating non-hormonal inputs, such as redox modifications from hydrogen peroxide, to modulate tolerance without relying solely on ABA [86]. Epigenetic mechanisms, including microRNA regulation and histone modifications, add another layer, enabling memory of prior stresses to prime faster acclimation in future multi-stress events. This integrated approach not only enhances survival but also optimizes energy use, as seen in metabolic shifts toward amino acid accumulation for osmotic balance.

In summary, the seamless integration of signals across pathways, organs, and stress types underscores plants' remarkable adaptability. By leveraging crosstalk, shoot-root dialogues, and multi-stress tailoring, plants achieve a unified strategy that bolsters resilience in dynamic environments. Future research into these mechanisms could unlock avenues for engineering crops with enhanced tolerance to climate variability.

7. Adaptive Mechanisms and Physiological Adjustments

Plants face a myriad of environmental challenges, from fluctuating temperatures and water availability to soil salinity and heavy metal contamination, all of which can severely impact growth, reproduction, and survival. To counter these stresses, plants have evolved sophisticated adaptive mechanisms that integrate morphological, developmental, physiological, and molecular strategies. These adaptations not only allow immediate coping but also enable long-term resilience, often through priming and memory effects that prepare the plant for future stressors. For example, exposure to mild drought can enhance tolerance to subsequent heat or salinity by reprogramming cellular processes. This interconnected response is crucial in the context of climate change, where multiple stresses frequently co-occur, demanding coordinated adjustments across the whole plant.

Morphological and Developmental Adaptations

Morphological and developmental changes represent some of the most tangible ways plants restructure themselves to endure stress. In drought-prone environments, plants often prioritize root system expansion, developing longer primary roots or more lateral branches to penetrate deeper soil layers for water and nutrients. This root plasticity is regulated by hormonal crosstalk, such as abscisic acid (ABA) interacting with auxin to modify root angles and elongation, as seen in species like *Arabidopsis*, where ABA-auxin signaling enhances hydraulic conductivity through aquaporin upregulation [89]. Similarly, under salinity, roots may reduce plasticity but recruit beneficial microbes in the rhizosphere to immobilize toxic ions via organic acid secretion.

Flooding triggers distinct adaptations, including the formation of adventitious roots and aerenchyma spongy tissues that create air channels for oxygen transport in hypoxic conditions [90]. Ethylene plays a key role here, promoting shoot elongation or aerenchyma development to escape waterlogged soils.

In heat stress, thermomorphogenesis leads to hypocotyl elongation and leaf hyponasty, allowing better air circulation and cooling, mediated by transcription factors like PIF4 [91]. Cold stress, conversely, may inhibit root growth but balance it through CBF3-SHR signaling to maintain meristem activity.

Developmentally, plants exhibit phenological shifts, such as earlier flowering in annuals to evade prolonged drought, a strategy known as drought escape. Leaf modifications, including rolling, thicker cuticles, increased wax deposition, or higher trichome density, further reduce water loss and protect against UV or extreme temperatures [92]. Recent studies highlight how combined stresses, like drought and heat, induce unique morphological responses, such as differential biomass allocation to reproductive organs to safeguard seed production [93]. These adaptations not only provide physical barriers but also optimize resource allocation, ensuring survival in dynamic environments.

Physiological Responses (e.g., Stomatal Regulation, Osmotic Adjustment, Antioxidant Systems)

Physiological adjustments allow plants to maintain homeostasis under stress by fine-tuning essential processes like water relations, ion balance, and redox status. Stomatal regulation is pivotal: during drought or salinity, ABA signaling rapidly closes stomata via pathways involving SnRK2 kinases and SLAC1 ion channels, minimizing transpiration while inevitably reducing CO₂ intake and photosynthesis [94]. In combined stresses like heat and drought, a "gas-and-brake" mechanism emerges, where heat promotes stomatal opening for cooling (via TOT3-AHA1), but drought overrides this through OST1-ABA inhibition, illustrating adaptive trade-offs.

Osmotic adjustment involves accumulating compatible solutes—such as proline, glycine betaine, trehalose, and sugars—to lower osmotic potential, draw water into cells, and stabilize proteins and membranes [95]. Under salinity, this is complemented by ion homeostasis mechanisms, including Na⁺ extrusion via the SOS pathway (SOS1 antiporter) and vacuolar sequestration by NHX transporters, preventing cytosolic toxicity. Heavy metal stress similarly prompts chelation and compartmentalization using phytochelatins and metallothioneins.

Antioxidant systems are essential for mitigating oxidative stress from reactive oxygen species (ROS), which accumulate under various abiotic pressures. Enzymatic antioxidants like superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and the ascorbate-glutathione cycle scavenge ROS, while non-enzymatic ones such as flavonoids and glutathione provide additional protection [96]. Priming enhances these systems; for instance, initial mild stress boosts enzyme activity, enabling faster ROS detoxification in subsequent exposures. In cold stress, membrane lipid remodeling increases unsaturated fatty acids to maintain fluidity, coupled with cryoprotectant accumulation like LEA proteins. These physiological responses are highly integrated, with ROS serving dual roles as damaging agents and signaling molecules that propagate systemic waves for whole-plant coordination.

Molecular Adaptations (e.g., Gene Expression, Transcription Factors, Epigenetic Modifications)

At the molecular core, stress adaptations involve reprogramming gene expression to activate protective pathways.

Thousands of genes are differentially expressed under stress, regulated by transcription factors (TFs) such as DREB/CBF for cold and drought, WRKY and NAC for multiple stresses, and HSFA1a for heat, which bind to promoters of genes encoding osmolytes, chaperones, and transporters [52]. In combined stresses, unique TFs like ELF6 act as hubs, resolving hormonal conflicts (e.g., ABA vs. auxin) to tailor responses.

Epigenetic modifications add a dynamic layer, allowing heritable changes without DNA alterations. DNA methylation, often via RNA-directed pathways, silences transposons while activating stress genes; histone marks like H3K4me3 and acetylation promote open chromatin for rapid gene activation [97]. Stress memory relies on these marks: for example, heat priming sustains H3K4 methylation at HSFA2 loci, enabling quicker reactivation. Small non-coding RNAs, including miRNAs (e.g., miR156 for growth-stress balance), and long non-coding RNAs, guide these processes, contributing to transgenerational tolerance, as observed in rice under heavy metals. Post-transcriptional regulation, such as alternative splicing and stress granules formed by LLPS, further refines protein output. These molecular adaptations underpin physiological and morphological changes, creating a feedback loop that enhances overall resilience. Advances in multi-omics and CRISPR editing are uncovering these networks, paving the way for engineering stress-tolerant crops.

In summary, the seamless integration of these mechanisms equips plants to thrive amid adversity, with implications for agriculture in an era of escalating environmental pressures.

8. Case Studies: Responses to Specific Stresses

Plants encounter a diverse array of environmental challenges throughout their life cycle, triggering integrated physiological, signaling, and adaptive responses. While individual stresses elicit specific pathways, real-world conditions often involve overlapping or combined stressors, leading to unique whole-plant adjustments. This section examines key examples of plant responses to major abiotic stresses (drought, salinity, and temperature extremes), biotic stresses (pathogens and herbivores), and the interplay in combined stresses, including the role of priming in enhancing resilience.

Abiotic Stresses (e.g., Drought, Salinity, Temperature Extremes)

Drought stress profoundly impacts plant water relations, prompting rapid stomatal closure to conserve water, often mediated by abscisic acid (ABA) accumulation and signaling. Roots sense soil water deficits and transmit hydraulic or chemical signals to shoots, activating ABA-dependent pathways that induce osmotic adjustment through proline and soluble sugar accumulation, alongside antioxidant defenses to mitigate reactive oxygen species (ROS) buildup. These responses enable local and systemic adaptations, such as altered root architecture for deeper water access and reduced leaf growth to minimize transpiration [98]. In crops like rice and maize, long-distance signaling involving peptides and ABA transport integrates organ-level responses for sustained tolerance [99].

Salinity imposes both osmotic and ionic challenges, with excess Na⁺ triggering Ca²⁺ spikes and activation of the Salt Overly Sensitive (SOS) pathway, which excludes Na⁺ via SOS1 transporters and compartmentalizes it in vacuoles. Hormonal crosstalk, particularly ABA and jasmonic acid (JA), coordinates ion homeostasis, osmoprotectant synthesis (e.g., glycine betaine), and redox balance.

Plants also adjust root morphology and enhance antioxidant enzyme activity to counteract oxidative damage, leading to systemic tolerance that limits Na⁺ translocation to shoots [100]. Temperature extremes—heat or cold—disrupt membrane fluidity and protein stability. Heat stress induces heat shock proteins (HSPs) as chaperones, alongside ROS scavenging and altered lipid composition for membrane protection. Brassinosteroids and ABA mediate thermotolerance, often through transcription factors like DREB2A that integrate heat and drought signals [101]. Cold stress rigidifies membranes, eliciting Ca²⁺ influx and the C-repeat binding factor (CBF) pathway, which upregulates cold-regulated (COR) genes for cryoprotectants and antifreeze proteins. Shared regulatory networks between drought and cold, such as convergent gene expression, highlight adaptive overlap [102].

Biotic Stresses (e.g., Pathogens, Herbivores)

Biotic interactions activate distinct defense modules. Pathogen encounters trigger pattern recognition receptors, leading to hypersensitive responses or systemic acquired resistance (SAR), primarily salicylic acid (SA)-dependent, involving pathogenesis-related (PR) proteins and long-distance signals like pipelicolic acid. Necrotrophs or herbivores often engage JA/ethylene pathways, promoting defenses such as protease inhibitors and volatile emissions that attract natural enemies [103].

Induced systemic resistance (ISR), elicited by beneficial rhizobacteria, relies on JA/ethylene signaling without PR gene activation in some cases, providing broad-spectrum protection against necrotrophs and insects. Herbivory induces similar JA-mediated responses, including oxylipin synthesis and systemic volatiles for plant-plant communication. Crosstalk between SA and JA pathways fine-tunes defenses, prioritizing based on attacker type—SA for biotrophs, JA for necrotrophs and herbivores [104].

Combined Stresses and Priming Effects

In nature, stresses rarely occur singly; combinations like drought-heat or salinity-pathogen elicit tailored responses not predictable from individual stresses. Drought-heat synergy exacerbates yield losses through amplified transpiration demands and ROS, but shared hubs like DREB2A and Ca²⁺/ROS signaling integrate cues for unique transcriptomes, favoring sucrose over proline accumulation [101]. Abiotic-biotic overlaps can prime defenses; mild drought may enhance pathogen resistance via ABA-JA crosstalk, while heat priming boosts subsequent biotic tolerance [105].

Priming pre-exposure to mild stress induces "memory" via epigenetic marks, sustained transcription factor activation, or dormant signals, conferring cross-tolerance. Drought priming enhances cold or heat resilience through bolstered antioxidants and osmoprotectants, while chemical agents (e.g., melatonin, H₂O₂) mimic this for multi-stress protection [106]. In crops, priming improves stomatal regulation, photosynthetic efficiency, and yield under fluctuating conditions, underscoring its potential for climate-resilient agriculture [107].

These case studies illustrate how integrated hormonal, redox, and transcriptional signaling underpins plant adaptability, with priming emerging as a key mechanism for navigating complex, concurrent stresses.

9. Applications and Future Perspectives

Implications for Crop Improvement

The integrated framework of plant physiology, signaling cascades, systemic responses, and adaptive strategies serves as a cornerstone for advancing crop resilience in the face of escalating climate variability. With abiotic stresses such as prolonged droughts, extreme heat waves, soil salinization, and flooding increasingly intersecting with biotic pressures like pathogen outbreaks and pest infestations, these holistic systems emerge as vital targets for developing varieties that sustain productivity under multifaceted threats [108,109]. By unraveling the mechanisms through which plants detect stressors at cellular levels and propagate responses via reactive oxygen species (ROS) waves, calcium signaling bursts, electrical variation potentials, and intricate hormonal networks involving abscisic acid (ABA), jasmonic acid (JA), and salicylic acid (SA), researchers can engineer crops that exhibit rapid, coordinated acclimation across the entire plant body. This not only minimizes yield losses but also enhances resource efficiency, such as optimized water and nutrient utilization in marginal lands. For example, in staple crops like maize and sorghum, integrating these insights has led to breeding programs that prioritize traits like deeper root architectures for drought evasion and enhanced photosynthetic efficiency under heat stress, ultimately supporting global food security in a warming world [110,111].

Biotechnology and Genome Editing Advances

Biotechnological innovations, particularly those leveraging CRISPR/Cas9 and its derivatives, have dramatically accelerated the pace of targeted genetic enhancements for stress tolerance in crops. These tools facilitate precise alterations in key regulatory genes, such as those encoding dehydration-responsive element-binding (DREB) proteins, C-repeat binding factors (CBF), or ion transporters like NHX1 and HKT1, which collectively bolster resistance to environmental adversities including drought, salinity, and temperature extremes without introducing foreign DNA [112,113]. Recent developments in multiplex genome editing allow simultaneous modifications of multiple loci, addressing polygenic traits that govern complex stress responses, such as osmotic adjustment and antioxidant defense systems. In rice and wheat, for instance, CRISPR-edited lines have demonstrated up to 30% higher yields under combined drought-heat conditions by fine-tuning ABA signaling pathways and reducing susceptibility to oxidative damage [114,115]. Furthermore, base editing and prime editing variants of CRISPR expand the toolkit, enabling subtle nucleotide changes that mimic natural adaptations observed in resilient wild relatives, thus avoiding the regulatory hurdles associated with traditional transgenics. These advancements also extend to enhancing biotic defenses through edits that amplify SAR and ISR pathways, creating broad-spectrum resistance while preserving growth vigor in diverse agroecosystems [110].

Harnessing Priming and Plant-Microbe Interactions

Eco-friendly approaches like stress priming and symbiotic associations with beneficial microbes represent a shift toward sustainable agriculture by exploiting innate plant mechanisms without genetic alteration. Priming involves exposing plants to sub-lethal stressors or elicitors, which establishes a "stress memory" that primes distant tissues for amplified, expedited responses to subsequent challenges, often mediated by

epigenetic changes and systemic signals like ROS and electrical waves [76,109]. In practical terms, applying chemical primers such as beta-aminobutyric acid or microbial consortia in seed treatments has proven effective in field settings, yielding crops with heightened tolerance to abiotic stresses and reduced reliance on chemical inputs. Plant-microbe interactions, particularly with plant growth-promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi, and endophytes, further augment this resilience by modulating root exudates, hormonal balances, and nutrient acquisition pathways under climate-induced stresses [109,116]. For crops facing drought and salinity in arid regions, these microbes enhance water retention through biofilm formation and improve ion homeostasis, leading to measurable gains in biomass and grain quality. Emerging research highlights how climate change alters these interactions, prompting the selection of heat-tolerant microbial strains that sustain benefits in warmer, drier conditions, thus integrating microbial engineering into broader crop improvement strategies [117].

Emerging Tools: Multi-Omics and Systems Approaches

The future of plant stress research is increasingly reliant on multi-omics platforms that fuse genomics, transcriptomics, proteomics, metabolomics, and phenomics to decode the layered complexities of stress networks under realistic, combined scenarios [108,111]. These integrative analyses reveal dynamic interactions, such as the crosstalk between ABA-mediated stomatal closure and JA-induced defense priming, enabling predictive modeling of whole-plant behaviors. Machine learning algorithms, trained on vast omics datasets, can forecast optimal gene targets for editing, accelerating the breeding of multi-stress-tolerant cultivars. Nanotechnology complements this by delivering targeted biostimulants that modulate signaling pathways at the nanoscale, enhancing traits like photosynthetic resilience in high-light stress [115]. Systems biology approaches further simulate environmental fluctuations, identifying hubs in regulatory networks that could be leveraged for synthetic biology designs, such as engineered signaling circuits for rapid acclimation.

Open Questions and Challenges

Despite these strides, several fundamental questions persist in the realm of integrated plant responses. How do plants hierarchically prioritize and reconcile divergent long-distance signals such as conflicting ROS waves, hydraulic cues, and hormonal gradients amid simultaneous multi-stress exposures? The role of epigenetic modifications, including DNA methylation and histone acetylation, in forging durable stress memories and facilitating transgenerational inheritance remains incompletely understood, with implications for breeding stable, heritable resilience [76,111]. Additionally, translating findings from model organisms like *Arabidopsis* to polyploid field crops poses challenges, including unintended pleiotropic effects that could compromise yield or nutritional quality in variable environments. Bridging these gaps requires robust field validation and interdisciplinary collaboration, incorporating climate modeling to anticipate future stress regimes.

Through concerted interdisciplinary efforts, these advancements will foster climate-resilient agriculture, where crops not only endure but thrive amid global changes, bolstering ecological sustainability and food sovereignty.

10. Conclusion

Plants, as sessile organisms, have evolved a remarkably sophisticated and integrated system to perceive, transduce, and respond to environmental challenges, ensuring survival and reproduction in ever-changing conditions. This review has highlighted how stress perception at the cellular level rapidly triggers local signaling cascades involving calcium ions, reactive oxygen species, electrical signals, and phytohormones, which are then propagated systemically to coordinate whole-plant responses. The intricate crosstalk among pathways such as abscisic acid-driven stomatal regulation, jasmonic and salicylic acid-mediated defenses, and redox balancing enables plants to mount precise, energy-efficient adaptations that extend from immediate physiological adjustments to long-term morphological and developmental reprogramming.

Central to this integration is the ability of plants to achieve systemic acquired acclimation and resistance, where localized stress exposure primes distant tissues for enhanced resilience, often through rapid long-distance signals like ROS waves and hydraulic cues. These mechanisms not only mitigate damage from individual abiotic or biotic stresses but also confer cross-tolerance to combined stresses, a critical feature in the context of climate change, where drought, heat, salinity, and pathogens frequently coincide.

The practical implications of these insights are profound. Advances in genome editing, multi-omics approaches, stress priming, and beneficial plant-microbe interactions offer powerful tools to translate fundamental knowledge into resilient crop varieties that maintain productivity under adverse conditions. By targeting key nodes in signaling networks and harnessing natural adaptive strategies, we can develop sustainable agricultural systems that reduce reliance on chemical inputs while supporting global food security.

Ultimately, the study of integrated plant physiology underscores a unifying principle: plants do not respond to stresses in isolation but as dynamic, interconnected systems capable of remarkable plasticity and foresight. Continued interdisciplinary research bridging molecular mechanisms with field-scale applications and addressing remaining questions on signal prioritization, epigenetic memory, and multi-stress integration will be essential to fully unlock this potential. In doing so, we move closer to engineering and cultivating crops that not only endure but thrive in an increasingly unpredictable world, contributing to resilient ecosystems and sustainable agriculture for future generations.

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