Plant Signaling: Mechanisms, Pathways, and Emerging Insights (Expanded Review)

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SUMMARY
Plants continuously monitor their surroundings using sophisticated signaling networks that allow them to detect environmental changes, coordinate development, and respond to stress. Unlike animals, plants cannot relocate, and thus their survival depends on the rapid and precise integration of diverse signals—chemical, electrical, peptide-based, hormonal, and RNA-mediated. This expanded review synthesizes advances in plant signaling research, emphasizing perception mechanisms, hormone crosstalk, secondary messenger dynamics, electrical signaling, long-distance communication, and rhizosphere-mediated interactions. Emerging technologies such as multi-omics integration, biosensors, single-cell profiling, and computational modeling are discussed, highlighting future opportunities for engineering climate-resilient crops.

INTRODUCTION
Plants thrive in highly variable ecosystems, facing fluctuations in temperature, light, water availability, soil composition, and biotic threats. To cope with these stresses, they have evolved intricate signaling networks capable of sensing external and internal cues and translating them into adaptive physiological responses. Signal perception is highly specific and depends on precise receptor–ligand interactions, while downstream pathways often involve phosphorylation, secondary messengers, gene expression changes, and long-distance systemic signaling.

Plant signals can be classified as:
Biochemical (hrmones, peptides, metabolites)
Electrical (action potentials, variation potentials)
Mechanical (touch, turgor pressure)
Light-based (photoreceptor-regulated)
RNA and protein mobility (phloem-translocated regulators)
Microbe-derived cues (VOCs, Nod/Myc factors)

These systems do not act independently; instead, they form a highly integrated network where one pathway modulates another—often through feedback loops and hormonal crosstalk. Understanding this interconnectivity is increasingly essential for designing stress-resilient crops, especially under climate change conditions.

SIGNAL PERCEPTION MECHANISMS
Receptor-Like Kinases (RLKs) and Receptor-Like Proteins (RLPs)
RLKs represent one of the largest receptor families in plants, with over 600 members in Arabidopsis. Their extracellular leucine-rich repeat (LRR) or LysM domains bind diverse ligands.

Key examples include:
FLS2 detecting bacterial flagellin
EFR sensing EF-Tu peptides
PEPRs recognizing damage-associated peptides (PEPs)
BRI1 functioning as a receptor for brassinosteroids

Upon ligand perception, RLKs form complexes with co-receptors (e.g., BAK1), initiating phosphorylation cascades that activate MAPKs and transcription factors.

RLPs lack intracellular kinase domains but partner with RLKs like SOBIR1. They play major roles in disease resistance, recognizing pathogen effectors and cell wall degradation fragments.

Intracellular NLR Receptors
Nucleotide-binding leucine-rich repeat proteins (NLRs) detect pathogen effectors inside cells.

Two classes are common:
TIR-NLRs (TNLs) involving TIR-domain signaling
CC-NLRs (CNLs) involving coiled-coil domains

Activation of NLRs can trigger effector-triggered immunity (ETI), often culminating in hypersensitive cell death at infection sites.

Mechanical and Chemical Receptors
Plants also perceive mechanical stimuli (e.g., wind, touch, gravity) via mechanosensitive channels (MSL, MCA).

Chemical perception includes:
nutrient sensing (nitrate via NRT1.1)
CO_2 and O_2 sensing
pH-sensing receptors
Collectively, these receptors form a first line of perception integrating environmental signals.

HORMONAL SIGNALING AND CROSSTALK
Plant hormones act as long-distance chemical signals, regulating nearly all stages of plant life. However, they rarely act independently; their pathways integrate through crosstalk and feedback loops.

Auxin
Auxin gradients control root development, tropisms, and branching. Transport is highly directional due to PIN proteins. Auxin perception occurs via the TIR1/AFB–Aux/IAA complex, leading to regulated gene expression.

Cytokinins
Cytokinins regulate cell division, shoot meristem activity, and nutrient signaling. Their perception relies on a two-component phosphorelay system involving histidine kinases.

Gibberellins (GA)
GA promotes stem elongation and seed germination. GA perception triggers degradation of DELLA repressors, enabling growth-promoting transcription factors.

Abscisic Acid (ABA)
ABA is central to abiotic stress responses, especially drought.

Key components:
PYR/PYL receptors
PP2C phosphatases
SnRK2 kinases

Activation of ABA signaling closes stomata, regulates osmotic balance, and induces stress-protective genes.
Brassinosteroids (BRs)
BRs regulate cellulose synthesis, photomorphogenesis, and stress adaptation through BRI1–BAK1 co-receptor complexes.
Salicylic Acid (SA)
SA is essential for systemic acquired resistance (SAR) and defense against biotrophic pathogens. The master regulator NPR1 activates defense gene transcription.

Jasmonates (JA)
JA regulates herbivory responses, wounding, and necrotrophic pathogen defenses.
COI1–JAZ complexes regulate JA-responsive gene activation.

Ethylene
Ethylene regulates fruit ripening, senescence, stress adaptation, and mechanical responses.

Hormone Crosstalk
Examples include:
SA and JA antagonism in pathogen defense
Auxin and BR synergy in cell elongation
ABA and GA antagonism in seed dormancy
Cytokinin–auxin balance in root vs. shoot development

This hormonal network allows plants to fine-tune responses based on multiple simultaneous signals.

SECONDARY MESSENGERS

Calcium (Ca^{2+}) Signaling

Ca^{2+} signatures vary by stimulus and act as "frequency-modulated" codes. Sensors include:
calmodulins (CaM)
calcium-dependent protein kinases (CDPKs)
CBL–CIPK complexes
Ca^{2+} waves propagate systemically through plasmodesmata and the phloem.

Reactive Oxygen Species (ROS)

ROS function as both damaging molecules and signaling cues.
NADPH oxidases (RBOHs) initiate ROS bursts crucial for defense and cell wall remodeling.

Nitric Oxide (NO)

NO influences stomatal closure, immunity, and flowering time. It interacts heavily with SA and ROS pathways.

Cyclic Nucleotides

cAMP and cGMP regulate ion channels and stress responses, though their pathways are less understood compared to animals.

Lipid-derived Messengers

Signals such as phosphatidic acid (PA) and jasmonate precursors emerge rapidly during stress and integrate with hormonal pathways.

ELECTRICAL SIGNALING

Plants generate action potentials, variation potentials, and system potentials.

Electrical signals:

propagate faster than chemical ones
coordinate leaf-to-leaf responses
regulate ion channel activity
activate defense-related gene expression
Electrical signaling interacts with Ca^{2+} and ROS, enabling rapid systemic responses to wounding or temperature shock.

PEPTIDE SIGNALING

Plant peptides act as small, precise regulators.

Key groups:
CLE peptides regulate meristems
PSK and RALF peptides regulate growth
Systemin triggers wounding responses
CEP peptides regulate nitrogen uptake
IDA peptides control abscission

Peptides allow highly specialized communication between neighboring cells and tissues.

ENVIRONMENTAL SIGNALING

Light Signaling

Plants use several photoreceptors:
Phytochromes (red/far-red)
Cryptochromes (blue)
Phototropins (phototropism)
UVR8 (UV-B responses)

Light affects circadian rhythms, chloroplast development, stem elongation, and stress tolerance.

Temperature Signaling

Heat stress activates heat shock transcription factors (HSFs), which induce heat shock proteins (HSPs).
Cold stress triggers the CBF/DREB pathway, increasing cold tolerance.

Water and Drought Signaling
Hydraulic signals propagate changes in water potential quickly. ABA-mediated responses induce stomatal closure and osmoprotective gene expression.

ROOT AND RHIZOSPHERE SIGNALING
Volatile Organic Compounds (VOCs)
Microbial VOCs influence:
root branching
hormone levels
systemic immunity
nutrient uptake
Symbiotic Signaling
Legumes detect rhizobia Nod factors, initiating nodule formation.
Mycorrhizal fungi produce Myc factors enhancing nutrient exchange.

Allelopathy
Plants release chemicals that inhibit competitors or attract beneficial organisms.
Root–Shoot Signaling
Roots send long-distance signals under nitrogen, phosphate, or drought stress.
These include peptides (CEP), hormones, and mobile RNAs.

BIOTIC STRESS SIGNALING
Pattern-Triggered Immunity (PTI)
Triggered by recognition of microbial signatures such as flagellin, chitin, or LPS via RLKs.

Responses include:
ion fluxes
ROS bursts
Ca^{2+} spikes
MAPK cascades
transcriptional reprogramming

Effector-Triggered Immunity (ETI)
NLR receptors detect pathogen effectors.
ETI is stronger and often associated with hypersensitive cell death (HR).

Herbivore-Induced Responses
Wounding activates JA signaling.
Plants release green leaf volatiles (GLVs) to attract predators of herbivores.

LONG-DISTANCE SIGNALING
Phloem Mobile RNAs
miRNAs and siRNAs act as systemic regulators of development and stress.

Hydraulic Signals
Water potential changes act as rapid whole-plant warnings.

ROS and Calcium Waves
ROS–Ca^{2+} feedback loops propagate defense signals at high speed.

Systemic Acquired Resistance (SAR)
SA derivatives such as methyl salicylate travel long distances to prime immunity.

TECHNOLOGICAL ADVANCES
Multi-Omics Integration
Combining genomics, transcriptomics, proteomics, and metabolomics reveals system-level signaling networks.

Single-Cell Sequencing
Reveals cell-type specific signaling dynamics.

Biosensors

Genetically encoded fluorescent biosensors monitor:

Ca^{2+}

ROS

hormones (e.g., DII-VENUS for auxin)

pH and ion fluxes

CRISPR-Cas Editing

Used to modify signaling components for improved stress resilience.

Computational Modeling & AI

Models simulate hormonal crosstalk, signaling waves, and whole-plant responses.

APPLICATIONS IN AGRICULTURE

Plant signaling research enables:

engineering drought/heat tolerant crops

optimizing hormonal pathways to enhance yield

designing microbial consortia to boost immunity

developing biosensors for smart farming

manipulating root–shoot signaling for nutrient efficiency

Such innovations are vital for agriculture in a warming climate.

CONCLUSIONS

Plant signaling represents highly interconnected pathways controlling plant behavior and survival. Rapid advances in molecular tools and high-resolution imaging continue to reveal new aspects of signaling. Future opportunities lie in integrating signaling with synthetic biology and microbiome engineering to create climate-adapted, high-performing crops.

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