



INTERORGANELLE COMMUNICATION IN PLANT STRESS ADAPTATION: MEMBRANE CONTACT SITES, RETROGRADE SIGNALING, AND METABOLIC REPROGRAMMING

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ABSTRACT

Environmental stress requires plants to communicate between chloroplasts, mitochondria, the endoplasmic reticulum, peroxisomes, vacuoles, and the nucleus in a well-coordinated manner to keep cells in homeostasis. In this review, the role of interorganelle communication, involving membrane contact sites, retrograde signaling and metabolic reprogramming processes, in plant stress adaptation is discussed. Membrane contact sites convey the exchange of lipids, ions, metabolites and signaling molecules, and retrograde pathways convey the status of organelle function to the nucleus and redirect gene expression. These processes are mediated by major molecular messengers, such as reactive oxygen species, redox signals, calcium, lipids, metabolites and phytohormones. Interorganelle crosstalk also drives coordinated adjustments in photosynthesis, respiration, photorespiration, carbon and nitrogen metabolism, membrane composition, antioxidant systems, and osmoprotective pathways. These responses are particularly important under drought, salinity, temperature extremes, high light, hypoxia, and combined stresses, where cellular energy and redox balance are frequently challenged. New technologies, such as live-cell imaging, genetically encoded biosensors, proximity labelling, organelle-resolved multi-omics and functional genomics, are advancing the spatial and temporal resolution of these networks. However, there are significant gaps in identification of plant-specific contact site components, signal specificity and field-level relevance. A systems-level understanding of organelle communication could help develop new approaches to engineering crops that are more metabolically flexible and resilient under increasingly variable environmental conditions without sacrificing growth, development, or productivity.

Keyword: Interorganelle communication; membrane contact sites; retrograde signaling; metabolic reprogramming; abiotic stress; plant stress resilience

Introduction

Environmental variability always constitutes a problem for plants, such as drought, salinization, high light, heat, cold, hypoxia and oxidative stress, which can affect cellular homeostasis and limit growth and productivity. Rapid detection of stress signals and coordinated regulation across different compartments of the cell are required for adaptation to these conditions. Organelles are not metabolic islands but are part of a complex network of signaling centers which share information through direct contact, redox signals, metabolites, proteins, and gene regulatory networks. This communication allows plant cells to coordinate the regulation of cellular metabolism, energy production and gene expression in response to the environmental information (Mielecki et al., 2020).

Chloroplasts, as key parts of this network, are involved in photosynthetic metabolism and environmental sensing. Adjustments in light intensity, redox conditions, production of reactive oxygen species, and chloroplast gene expression may release signals that modulate the expression of nuclear genes and the broader cellular responses (Zhang et al., 2020). Under harsh environmental conditions, organellar RNA-binding proteins also play roles in RNA processing, RNA stability, translation, and organelle function by regulating them (Lee & Kang, 2020). In addition to their photosynthetic functions, chloroplasts also contribute to hormone signaling, antioxidant regulation, and metabolic changes involved in stress acclimation and protecting the cell (Song et al., 2021).

Mitochondria represent another major regulatory node by linking respiration, cellular energy status, and redox homeostasis. In response to environmental perturbations, mitochondrial activity alters metabolic flux and stress signaling, which enables coordination of energy needs and response to environmental changes (Van Aken, 2021). The coupling between chloroplast and mitochondrial functions is more and more revealed, especially under stress conditions where photosynthetic and respiratory processes need to be tightly synchronized for energy and redox homeostasis (He et al., 2023). The dynamics of organelles like chloroplasts and mitochondria play a role in intracellular communication, aiding in metabolic and signaling interactions within plant cells (Koenig et al., 2023).

Perception of stress by mitochondria may trigger downstream events affecting mitochondrial reactive oxygen species, metabolites, mitochondrial transcriptional regulators and retrograde signals that will change the expression of nuclear genes and metabolism (Selinski et al., 2024). Other organelles are also involved in the control of cellular quality and homeostasis. The degradation of damaged or dysfunctional organelles by the vacuolar degradation pathways is linked to cellular remodeling and recovery from stress, as well as organelle turnover (Otegui et al., 2024). Retrograde signaling from the plastid also involves coordination of developmental processes with environmental responses, thereby continuously communicating the status of plastid function back to the nucleus to coordinate cellular responses (van Veen et al., 2025).

One of the current key ideas in plant stress biology is the communication between different organelles, which is mediated by structural and biochemical mechanisms. The creation of membrane contact sites leads to the formation of regions in close proximity of membranes, thereby allowing the transfer of lipids, ions, metabolites and signaling molecules without membrane fusion. At the same time, retrograde signals are carried back to the nucleus from the organelles, causing changes in transcription and therefore in the functions of the cell. These mechanisms are tightly linked to metabolic reprogramming such as changes in photosynthesis, respiration, photorespiration, lipid metabolism, antioxidant activity, and carbon–nitrogen balance. Therefore, it is crucial to understand the processes involved in these interactions in order to elucidate how plant cells maintain functional stability and metabolic flexibility under environmental stress.

Accordingly, the objectives of this review are to:

- Elucidate the roles of membrane contact sites and retrograde signaling in coordinating interorganelle communication during plant stress.
- Examine how organelle crosstalk regulates metabolic reprogramming and cellular homeostasis under environmental stress.
- Identify major knowledge gaps and emerging strategies for improving plant stress resilience through interorganelle signaling networks.

2. Interorganelle Communication as a Coordinated Stress-Response Network

2.1 Organelles as Stress-Sensing and Signaling Hubs

Plant organelles act as complementary stress-sensing hubs. Peroxisomes modulate reactive oxygen and nitrogen species that coordinate intracellular signaling, while mitochondria coordinate respiratory, energetic, redox, and metabolic changes in response to environmental stress (Sandalio et al., 2021; Barreto et al., 2022). The endoplasmic reticulum detects misfolded proteins or any disruption of membrane homeostasis, triggering the unfolded protein response in order to maintain proteostasis, and maintaining the balance between stress tolerance and growth (Y. Liu et al., 2022).

2.2 Modes of Interorganelle Communication

Interorganelle communication is mediated by diffusible signals such as ROS, Ca²⁺, redox equivalents and metabolites, as well as membrane contacts. Chloroplast–mitochondrial cooperation coordinates electron transport, respiration, and cellular redox balance (Igamberdiev & Bykova, 2023), while the endomembrane system supports vesicular trafficking, membrane remodeling, and organelle organization (Zhuang et al., 2024).

2.3 Spatial and Temporal Integration of Stress Signals

Temporal regulation also occurs in interorganelle signaling. In addition, chloroplast quality-control pathways respond to stress levels by making adjustments to the photosynthetic components (Fu et al., 2022), whereas ER responses make protective adjustments or broader transcriptional reprogramming, depending on the level of stress (Kim et al., 2022). These mechanisms help plants to distinguish between temporary and long-term stress.

3. Membrane Contact Sites as Structural Platforms for Stress Signaling

3.1 Molecular Organization and Dynamics of Membrane Contact Sites

Membrane contact sites (MCSs) are areas where two organelles come into close proximity with membranes that do not fuse, allowing for rapid molecular sharing and signaling. These interfaces are important in plants for lipid, ion, metabolite and regulatory molecule transport, organelle positioning, dynamics and quality control in plant cells. Involved in their formation are complexes of proteins and membrane-associated complexes that are essential for the stabilization of interaction between neighbouring compartments and are sensitive to shifting cellular state. MCSs also play their role in autophagic processes, influencing the remodeling of membranes and communication among organelles of degradation and recycling pathways (Ye et al., 2020). The abundance and distribution of plant MCSs is dynamic and has been confirmed by live cell reporter systems under different cellular conditions (Baillie et al., 2020; Li et al., 2020).

3.2 ER-Centered Contact Sites

The ER exists in almost every cell and is involved in numerous interactions with other cell components, particularly with the plasma membrane, the chloroplasts, the mitochondria and the vacuoles, which make it one of the most widespread contact networks in plant cells. ER–plasma membrane contact sites play a crucial role in lipid composition and membrane homeostasis in stressed cells. These interfaces contain synaptotagmins that control distribution of the diacylglycerols and play a role in maintaining membrane stability under stress conditions (Ruiz-Lopez et al., 2021). Structural studies of Arabidopsis SYT1 have revealed that the highly flexible membrane-binding regions enable dynamic engagement with lipid bilayers, which provides a molecular mechanism for regulated formation of contact sites (Benavente et al., 2021). ER contact sites are more broadly involved in the organization of membranes and the trafficking of lipids, calcium exchange, positioning of organelles, and non-vesicular transport, which all contribute to cellular signaling and homeostasis (Bian et al., 2023).

3.3 Chloroplast–Mitochondria–Peroxisome Contact Networks

The functional interactions among chloroplasts, mitochondria, and peroxisomes are of particular importance as these organelles together control metabolism of photosynthesis, respiration, photorespiration, redox balance, metabolism of reactive oxygen species. As they are organized in close proximity physically they can improve the exchange of metabolites and coordination of pathways involved in energy production and detoxification. ER contacts also affect plastid morphology and movement, suggesting that the morphology of organelles is closely tied with intracellular communication (Mathur et al., 2023). VAP27 proteins are found at the ER-plastid interface where they facilitate lipid transfer and membrane organization between the two organelles (Renna et al., 2024). Contact networks are thus able to give structural continuity to metabolic pathways that need to be rapidly coordinated when environmental perturbations occur.

3.4 Stress-Induced Remodeling of Membrane Contact Sites

Because the abundance, architecture and molecular composition of MCS can change in response to environmental stresses, plant cells are able to restructure the communication between them in response to changing physiological demands. Recently, VAP27-1 was found to control the architecture of ER and plasma membrane contacts and to impact resistance to ER stress, providing direct evidence that reorganization of physical contacts may directly affect stress tolerance (Man et al., 2024). ER–plastid contact sites are also becoming a growing focus of interest in the regulation of plastid lipid biosynthesis and in the adaptation of the plastid membranes structure in response to stress conditions and lipid demand (Huercano et al., 2025). Dynamic remodeling of MCSs may therefore enhance lipid redistribution, calcium signaling, redox coordination, and metabolite exchange among organelles, allowing cellular structures and metabolic pathways to respond synchronously. The interfaces are a key structural level of plant stress signalling, linking physical proximity with biochemical communication and adaptive cellular reorganization. Environmental stress can remodel contacts and interactions among chloroplasts, mitochondria, the endoplasmic reticulum, and peroxisomes to enable lipid, Ca^{2+} , metabolite, and redox signal exchanges as illustrated in Figure 1.

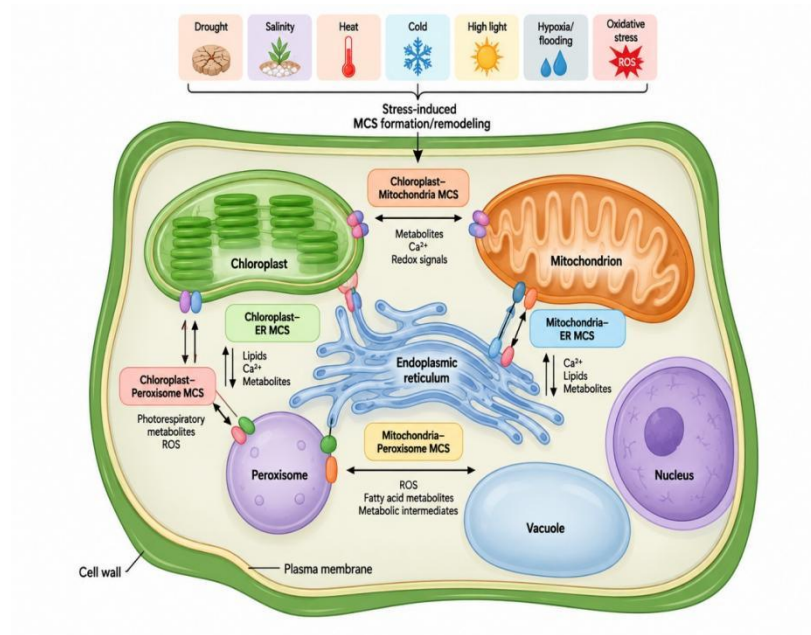


Figure 1. Stress-Responsive Membrane Contact Site Network in Plant Cells

Table 1 summarizes the major membrane contact sites in plant cells, their principal functions, and their relevance to environmental stress responses.

Table 1. Major membrane contact sites and their functions in plant stress responses

Membrane contact/interface	Major functions	Principal processes exchanged/coordinated	Stress relevance
ER–plasma membrane	Membrane organization and signaling	Lipids, Ca^{2+} , membrane-associated signals	Osmotic, salt, and ER stress
ER–chloroplast	Lipid transfer and plastid membrane maintenance	Phospholipids, lipid precursors, membrane remodeling	Temperature and oxidative stress
ER–mitochondria	Metabolic and membrane coordination	Lipids, Ca^{2+} , metabolites	Energy and redox imbalance
Chloroplast–mitochondria	Coordination of photosynthesis and respiration	Reducing equivalents, organic acids, energy signals	High light, drought, heat
Chloroplast–peroxisome	Photorespiratory exchange	Glycolate/glycerate, ROS-related metabolites	High light and oxidative stress
Mitochondria–peroxisome	Redox and metabolic coordination	ROS, fatty-acid-derived metabolites	Oxidative and metabolic stress

4. Retrograde Signaling and Nuclear Reprogramming

4.1 Chloroplast Retrograde Signaling

The chloroplast retrograde signal pathway allows the plastid to send signals to the nucleus that inform it of the metabolic status and activity of the plastid, resulting in a coordination of nuclear gene expression with photosynthetic activity and environmental conditions. The pathways are of specific relevance in stressful situations, when alterations in electron transport, redox balance, tetrapyrrole biosynthesis and ROS production provide signals for the initiation of transcriptional adjustment. The communication between chloroplast and mitochondrial retrograde pathways is becoming more apparent and is likely not a distinct process but a coordinated response across organelles of cellular energy state and/or redox state (Wang et al., 2020). This may be useful for understanding how disruptions in plastid metabolism can generate operational signals that are specific to stress, impacting on the nuclear response (Unal et al., 2020).

The GENOMES UNCOUPLED (GUN) network couples plastid biogenesis and tetrapyrrole metabolism with nuclear gene expression (Page et al., 2020; Shimizu & Masuda, 2021). GUN1 also links plastid RNA regulation and protein homeostasis with broader metabolic responses (Tadini et al., 2020; Richter et al., 2020). Oxylipins represent another link between plastid oxidative status and stress-responsive transcription in a parallel pathway with the metabolic status (Muñoz & Munné-Bosch, 2020).

4.2 Mitochondrial Retrograde Signaling

Mitochondrial retrograde signaling transmits information about disturbances in respiration, redox balance, and energy metabolism to the nucleus. One of the key regulators of this response is ANAC017, an endoplasmic-reticulum-associated transcription factor that is induced by mitochondrial dysfunction and then regulates nuclear gene expression. Under reductive stress, ANAC017-mediated signaling enhances mitochondrial respiratory capacity and contributes to protection of ER homeostasis, demonstrating direct functional integration between mitochondrial and ER stress pathways (Fuchs et al., 2022). Mitochondrial dysfunction also triggers MAP kinase, ethylene and auxin signaling pathways via ANAC017, allowing stress adaptation to be balanced against growth and development (He et al., 2022).

4.3 ER and Peroxisome-to-Nucleus Signaling

Intracellular stress can be also spread to nuclear regulatory networks via the ER and peroxisomes. ER perturbations trigger unfolded protein response pathways that upregulate molecular chaperones and protein quality control and restore secretory homeostasis (Y. Liu et al., 2022). Peroxisomes have roles in contributing to changes in hydrogen peroxide production, redox balance, and metabolic signaling (Sandalio et al., 2021). Peroxisomal redox status is highly sensitive to environmental changes and such changes can affect the expression of genes involved in antioxidant defense, metabolism, and cell recovery.

4.4 Convergence of Retrograde Signals in the Nucleus

The information from the organelles is integrated with developmental, hormonal, circadian, and environmental signals within nuclear transcriptional networks, all of which are connected to retrograde pathways. Communication between the nucleus and the chloroplast allows the plastid function to be dynamically modulated via retrograde and anterograde regulation in a coordinated way (Jan et al., 2022). The GUN pathway and the associated signalling pathways also show that retrograde signalling is not a linear pathway but rather comprises overlapping metabolic, redox and transcriptional processes (Richter et al., 2023). Mitochondrial signaling is similarly integrated with circadian regulation, with clock-associated factors modulating ANAC017-dependent responses and thereby linking organelle status to temporal control of gene expression (Zhu et al., 2023). Convergence enables plant cells to prioritize competing signals, coordinate organellar functions and orchestrate transcriptional responses that are suitable for the type, duration and severity of the environmental stress. Figure 2 shows that retrograde signals from chloroplasts, mitochondria, the endoplasmic reticulum, and peroxisomes converge on the nucleus to control stress-related gene expression, antioxidant defenses, proteostasis, metabolic adjustment and acclimation.

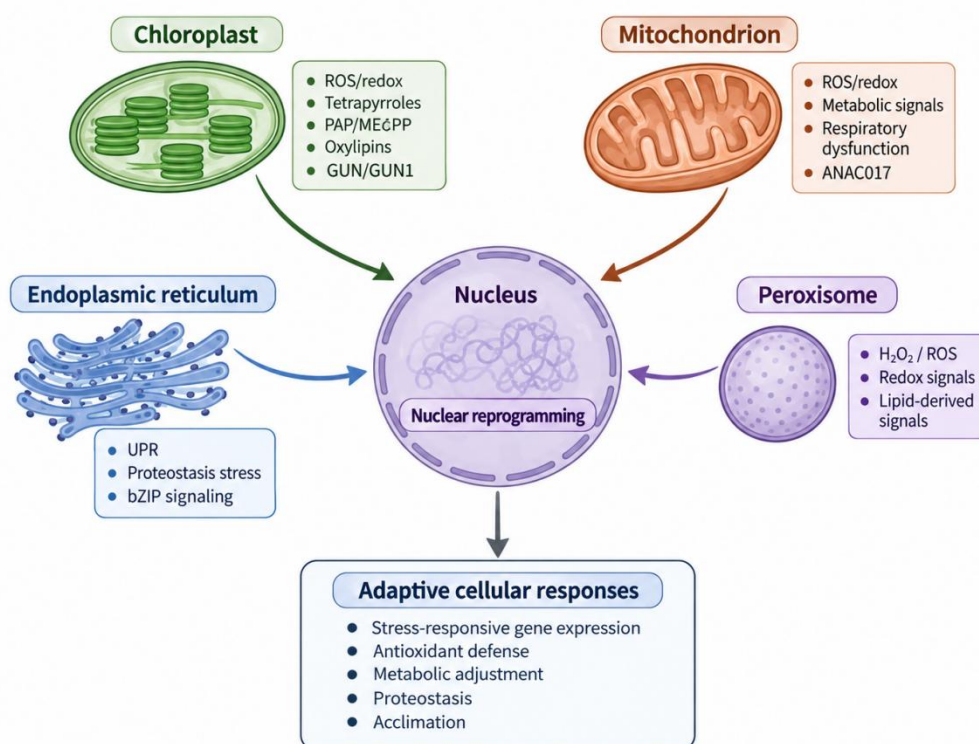


Figure 2. Convergence of Organelle-Derived Retrograde Signals on Nuclear Reprogramming during Plant Stress

5. Molecular Mediators of Interorganelle Communication

5.1 Reactive Oxygen Species and Redox Signals

During environmental stress, reactive oxygen species (ROS) serve as key messengers between chloroplasts, mitochondria, peroxisomes and the nucleus. Singlet oxygen, superoxide and hydrogen peroxide are produced as by-products of photosynthetic electron transport by chloroplasts and provide information on cellular redox state and metabolic imbalance when produced in a controlled fashion. These signals can alter the expression of nuclear genes, the level of antioxidants and energy metabolism, and thus result in an orchestrated response to stress from organelle perturbations (Foyer & Hanke, 2022). Redox regulation within chloroplasts further depends on thioredoxin-associated systems and electron-transfer networks that adjust enzyme activity and metabolic flux according to prevailing conditions (Yoshida & Hisabori, 2023). Under heat stress, excessive electron pressure can lead to an imbalance in cellular homeostasis, thus requiring coordination between chloroplast and mitochondrial ROS, redox state, and energy metabolism (Suzuki, 2023). In addition, proton motive force across thylakoid membranes has the ability to regulate redox processes by regulating photosynthetic electron transport and lumenal processes (Hoh et al., 2024).

5.2 Calcium and Ion Signaling

Calcium acts as a rapid and versatile intracellular messenger, with changes in its concentration generating different spatiotemporal signatures. Calcium storage, release and uptake takes place in chloroplasts, mitochondria, endoplasmic reticulum, and vacuoles, which allows for organelle-specific calcium dynamics to coordinate cellular responses (Resentini et al., 2021). Downstream responses are mediated by the amplitude, frequency and duration of the signals, and the interaction of Ca^{2+} and ROS is an integral component of ionic and redox signaling (Allan et al., 2022).

5.3 Lipid and Metabolite Signaling

Signaling molecules are produced during the lipid remodeling process that mediate membrane adaptation in response to stress and trigger protective responses. Phospholipid and oxylipin related pathways are, for instance, linked to membrane perturbation and consequent stress signaling, and these pathways are stimulated during drought and heat conditions (Sharma et al., 2023). Other metabolites, such as sugars, organic acids, amino acids and energy related metabolites, can also relay metabolic status between compartments and modify transcriptional and enzymatic regulation.

5.4 Hormonal Integration of Organelle Signals

Phytohormones coordinate responses across the organelle, cell and plant levels. Abscisic acid, salicylic acid, jasmonates, ethylene and auxin engage with redox, metabolic and calcium signals and ROS to coordinate growth, defense, and stress adaptation. Organelles both influence hormone biosynthesis and respond to hormonal cues, forming reciprocal regulatory networks that connect cellular metabolism with

environmental perception (Bittner et al., 2022). The multi-layered integration allows plant cells to cope with stress and carry out metabolic processes and development within a balanced framework.

As shown in Table 2, interorganelle communication is mediated by a diverse set of retrograde, redox, calcium, lipid, metabolic, and hormonal signals that coordinate cellular stress responses.

Table 2. Major retrograde and molecular signals involved in interorganelle communication

Signal/pathway	Major source	Main target/process	Functional consequence
ROS	Chloroplasts, mitochondria, peroxisomes	Redox-sensitive proteins and nuclear transcription	Antioxidant and stress-response activation
Ca ²⁺	ER, vacuole, chloroplasts, mitochondria	Ca ²⁺ sensors and kinases	Rapid stress-signal propagation
GUN signaling	Chloroplast	Nuclear gene expression	Coordination of plastid and nuclear functions
ANAC017 pathway	Mitochondria/ER-associated system	Nuclear stress-response genes	Adjustment of respiration and metabolism
PAP, MEcPP and tetrapyrroles	Chloroplast	Nuclear regulatory pathways	Acclimation and metabolic reprogramming
Lipid-derived signals	Chloroplasts, ER and membranes	Stress and defense pathways	Membrane adaptation and signaling
Metabolites	Multiple organelles	Metabolic enzymes and transcriptional networks	Adjustment of carbon and energy metabolism
Phytohormones	Multiple cellular compartments	Hormonal signaling networks	Integration of growth and stress responses

6. Metabolic Reprogramming Driven by Interorganelle Crosstalk

6.1 Photosynthetic and Respiratory Reconfiguration

When environmental stress is encountered, the balance of carbon fixation, electron transport, respiration, and energy demands of the cell are often upset, and metabolic reprogramming must take place in

chloroplasts and mitochondria. Photosynthetic adjustment involves modification of electron flow, photoprotective mechanisms, carbon assimilation, and redox balance, whereas mitochondria compensate through changes in respiratory activity and alternative electron transport. Photorespiration is a significant metabolic link between these processes as it connects chloroplast and peroxisomal and mitochondrial metabolism, and serves as a link to carbon recycling and redox regulation (Fernie & Bauwe, 2020). The mitochondrial alternative oxidase (AOX) assists in maintaining respiratory flexibility, reducing excessive electron pressure, and limiting oxidative damage under oxygen limitation and reoxygenation (Jayawardhane et al., 2020). In addition, coordination of chloroplast cyclic electron transport and mitochondrial alternative oxidase can help maintain the stability of photosynthesis in response to environmental variations (Chadee et al., 2021).

6.2 Photorespiratory Metabolism and Organelle Cooperation

Photorespiration is also intrinsically linked to interorganelle cooperation due to the requirement of sequential reactions within chloroplasts, peroxisomes and mitochondria. This pathway entails carbon loss, but also contributes to nitrogen recycling, regulates redox status and maintains the viability of the photosynthetic apparatus under stress. Further links between sulfur signaling and metabolic adaptation are created by regulatory modifications (e.g., protein persulfidation) of photorespiratory enzymes (Aroca et al., 2023). Efficient exchange of photorespiratory intermediates, when photosynthetic carbon fixation is reduced, thus helps maintain metabolic stability.

6.3 Carbon and Nitrogen Metabolic Reprogramming

Stress-induced metabolic adjustment also involves substantial redistribution of carbon and nitrogen resources. Modifications in sugar metabolism, glycolysis, tricarboxylic acid cycle, amino-acid biosynthesis and nitrogen assimilation are responsible for maintaining the energy supply and production of protective compounds. Calcium-dependent protein kinases may provide a regulatory link between stress perception and coordination of carbon–nitrogen metabolism, linking the carbon–nitrogen metabolism with signaling pathways (Alves et al., 2021). Metabolomic analysis also indicates that plants alter their primary metabolism during abiotic stress, which results in distinct sugar, organic acid, amino acid and energy related intermediate changes (Xu & Fu, 2022).

6.4 Lipid and Membrane Remodeling

Membrane lipid composition changes rapidly under environmental stress, affecting fluidity, organelle integrity, signaling, and energy metabolism (Kim, 2020). Under drought, salinity and temperature stress, membrane stability and photosynthetic function are changed, thereby necessitating a coordinated remodeling of the lipids in the cellular compartments (Muhammad et al., 2021). These modifications allow to maintain the activity of the organelles and communication between them.

6.5 Antioxidant and Osmoprotective Metabolism

Metabolic reprogramming also boosts antioxidant and osmoprotective properties. The accumulation of proline helps in osmotic adjustment, redox buffering, protein stabilization, and protection from heat-induced oxidative damage (Kavi Kishor et al., 2022). These changes are more interconnected when combined environmental stress occurs, and metabolic networks tend to shift towards energy conservation, antioxidant protection, membrane stabilization and build-up of protective metabolites (Bulut et al., 2025). These changes, taken together, provide evidence that interorganelle crosstalk affects central metabolism to ensure the function of the cell and to enhance stress acclimation.

As shown in Figure 3, interorganelle signaling networks integrate signals from chloroplasts, mitochondria, the endoplasmic reticulum, and peroxisomes, leading to coordinated reprogramming of carbon, nitrogen, lipid, and protective metabolism that supports plant stress adaptation.

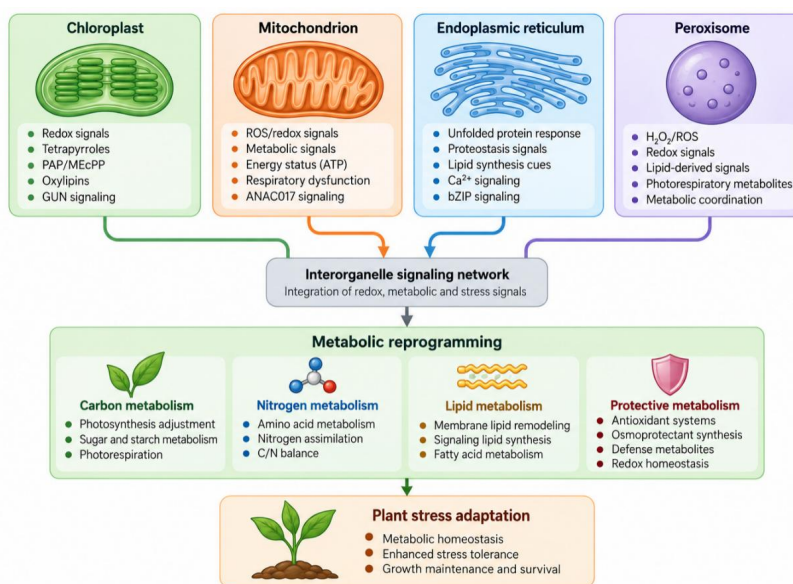


Figure 3. Interorganelle Signaling-to-Metabolism Axis Driving Plant Stress Adaptation

7. Interorganelle Crosstalk under Environmental Stress

7.1 Drought and Salinity Stress

Osmotic, ionic and oxidative constraints due to drought and salinity are responsible for impairing organelle functions and demanding coordinated cellular responses. The chloroplasts are especially susceptible because excess salt can cause changes in the thylakoid structure, pigment content, photosynthetic electron transport, and carbon fixation, which could result in the greater production of ROSs and reduced energy conversion (Hameed et al., 2021). Under water deficit, chloroplasts, mitochondria, peroxisomes, and the endoplasmic reticulum respond to redox changes, respiration, changes in lipid composition and protective metabolism to maintain cellular homeostasis. All these responses are coupled with abscisic acid signaling, calcium flux, accumulation of osmolytes and

antioxidant defenses. Another effect of repeated drought exposure is to induce stress memory, which allows the plant to alter its response to the subsequent drought by physiological, metabolic, and regulatory changes that promote better acclimation to repeated water stress (X. Liu et al., 2022).

7.2 Heat and Cold Stress

The physical and biochemical characteristics of membranes, enzyme stability, protein folding and organelle metabolism are highly sensitive to temperature. Chloroplasts under heat stress have impaired photosystem function, electron transport changes, increased production of ROS, and destabilization of thylakoid membranes. Protective mechanisms include changes in the expression of chloroplast genes, antioxidant activity, protein quality control and coordinated regulation with mitochondrial respiration to regulate energy and redox levels (Zeng et al., 2021). Cold stress also has an impact on membrane fluidity and metabolic rates; it implies the need for lipid composition changes, respiratory activity, accumulation of protective metabolites. Organelle morphology and interactions are also dynamic to facilitate adaptation, redistributing metabolic and signaling capacity in response to temperature stress (Tang & Zhu, 2022).

7.3 High-Light and Oxidative Stress

Photosynthetic electron transport can be overwhelmed by excess irradiance and excess ROS formation can occur inside chloroplasts. Plants respond through non-photochemical quenching, cyclic electron flow, antioxidant systems, repair of photosynthetic components, and redistribution of excess reducing power. Mitochondrial respiration and alternative electron pathways also contribute by dissipating excess reductants and supporting cellular energy balance. High-light acclimation therefore depends on coordinated communication among chloroplasts, mitochondria, peroxisomes, and nuclear regulatory networks rather than on chloroplast responses alone (Zhang et al., 2024).

7.4 Flooding, Hypoxia, and Reoxygenation

Under flooding conditions oxygen is limited and mitochondrial oxidative phosphorylation is quickly inhibited and leads to an energetic crisis with a rapid switch to anaerobic ATP production. Hypoxia also affects the redox homeostasis, the distribution of metabolites and the signaling of ROS. The sudden oxidative burst that can occur during reoxygenation is due to the restoration of mitochondrial and chloroplast electron transport, which should be coordinated with strong antioxidant response to protect against cell damage (León et al., 2021). In brief, communication between the different organelles is crucial for balancing energy conservation during oxygen deficiency with controlled metabolic recovery after reoxygenation.

7.5 Combined and Sequential Stresses

In the natural environment, plants are often exposed to several stresses at once or stresses in succession, resulting in a “stress combination” that is different from a single stress experiment. Drought stress and salinity stress, for instance, exacerbate osmotic stress and cause unique hormonal, metabolic, ionic and

antioxidant responses (Angon et al., 2022). These states need to be prioritized and integrated at the organelle level with conflicting signals. The flexible regulation of photosynthesis, respiration, redox homeostasis, membrane properties, and resource allocation, in addition to stress-specific and shared signaling networks, is essential for acclimation to multiple stresses (Jiang et al., 2025). It is therefore crucial to comprehend these coordinated responses to understand plant resilience under complex and dynamic environmental conditions.

Table 3 presents the major organelles, signaling features, and metabolic adjustments associated with plant responses to individual and combined environmental stresses.

Table 3. Interorganelle crosstalk and metabolic adjustments under major environmental stresses

Stress	Major organelles involved	Dominant communication features	Key metabolic adjustments
Drought	Chloroplast, mitochondria, ER, peroxisome	ROS, Ca ²⁺ , ABA, redox signaling	Osmolyte accumulation, antioxidant activation, respiratory adjustment
Salinity	Chloroplast, mitochondria, ER, vacuole	Ion, ROS and hormonal signaling	Ion homeostasis, lipid remodeling, energy adjustment
Heat	Chloroplast, mitochondria, ER	ROS/redox signaling, unfolded protein response	Membrane remodeling, photoprotection, respiratory adjustment
Cold	Chloroplast, mitochondria, ER	Redox and lipid-mediated signaling	Fatty-acid remodeling, protective metabolite accumulation
High light	Chloroplast, mitochondria, peroxisome	ROS and redox communication	Photoprotection, cyclic electron flow, antioxidant metabolism
Flooding/hypoxia	Mitochondria, chloroplast, peroxisome	Energy and redox signals	Anaerobic metabolism, ATP conservation
Reoxygenation	Mitochondria, chloroplast, peroxisome	Rapid ROS signaling	Antioxidant activation and respiratory recovery
Combined stresses	Multiple organelles	Convergent and antagonistic signals	Integrated resource allocation and metabolic reprogramming

8. Emerging Technologies for Decoding Interorganelle Communication

8.1 Advanced Imaging and Organelle-Specific Biosensors

The capacity to monitor interorganelle communication in real time has greatly improved due to recent developments in live-cell imaging and genetically encoded biosensors. Fluorescent reporters can now track changes in calcium, reactive oxygen species, pH, ATP, redox status, and membrane potential within specific cellular compartments, enabling spatially resolved analysis of stress signaling (Sadoine et al., 2021). Proximity-labeling techniques also enable the identification of proteins that are in proximity to known organelles and/or membrane contact sites, thereby aiding to elucidate transient molecular interactions which cannot be readily captured using conventional biochemical methods (Yang et al., 2021). These methods are useful for the study of transient contacts between organelles that are rapidly changing in composition as well as duration around environmental stress.

8.2 Organelle-Resolved Multi-Omics

Organelle-specific proteomics, transcriptomics, metabolomics, and lipidomics provide a complementary systems-level view of intracellular communication. Combining these datasets can shed light on the nature of the changes in one compartment that affect the metabolic and regulatory responses in other compartments of the cell. Integration of single-cell and spatial technologies is needed to address cell-type-specific organelle organization and molecular states, the Plant Cell Atlas framework emphasizes the need for integrating single-cell and spatial technologies (Birnbaum et al., 2022). These strategies should enhance knowledge of tissue-specific and developmental variations in interorganelle networks that are responsive to stress.

8.3 Functional Genomics and Systems Biology

Functional validation is increasingly supported by CRISPR-based gene editing, reverse genetics, proximity labeling, and network modeling. Advanced proximity-labeling strategies can identify organelle-associated protein complexes and candidate tethering factors with high spatial resolution (Xu et al., 2023). Metabolic imaging, on the other hand, can be used in situ to visualize metabolic fluxes and compartment-specific biochemical changes within intact tissues (Horn & Chapman, 2024). When these technologies are used in combination with computational network analysis, they provide a potent way to distinguish causal regulators from correlated responses and build dynamic signaling pathways from organelle interactions to plant stress adaptation.

Table 4 outlines the principal experimental and computational approaches currently used to investigate interorganelle communication, together with their major applications and limitations.

Table 4. Emerging approaches for resolving plant interorganelle communication

Approach	Information obtained	Major application	Key limitation
Live-cell fluorescence imaging	Organelle position and dynamics	Visualization of contact-site behavior	Limited molecular identification
Super-resolution microscopy	Fine spatial organization	Resolving membrane contact architecture	Technical complexity
Genetically encoded biosensors	ROS, Ca ²⁺ , ATP, pH and redox dynamics	Real-time compartment-specific signaling	Sensor calibration and interference
Proximity labeling	Proteins within local molecular environments	Identification of contact-site components	May capture transient neighboring proteins
Organelle proteomics	Compartment-specific protein composition	Discovery of signaling regulators	Organelle purification challenges
Metabolomics/lipidomics	Metabolic and lipid changes	Mapping stress-induced metabolic exchange	Limited spatial resolution
Spatial/single-cell omics	Cell- and tissue-specific molecular states	Resolving heterogeneous stress responses	High analytical complexity
CRISPR and functional genomics	Causal gene functions	Validation and engineering of signaling networks	Pleiotropic effects
Systems biology	Integrated pathway relationships	Network reconstruction and prediction	Dependent on data quality

9. Knowledge Gaps and Future Perspectives

9.1 Unresolved Mechanisms of Organelle Communication

Despite rapid progress, major aspects of interorganelle communication remain unresolved. The identities of many of the tethers that contact membranes, the directionality of the signal exchange and the

mechanisms that determine stress-specific communication are still poorly defined. Many contact configurations are not known to have a specific function while plant organelles are highly dynamic in structure and association (Kang et al., 2022). The overall composition and regulation of contact sites need to be better understood, with particular attention to the role of NETWORKED and VAP27 proteins as examples of cytoskeletal and membrane-associated proteins that regulate contact-site organization (Duckney et al., 2025). Peroxisomal signalling is also not fully incorporated in existing models, as the interactions with the response of chloroplast and mitochondria in relation to the production of peroxisomal ROS and RNS are not fully understood (Molina-Moya et al., 2025).

9.2 From Model Plants to Crops and Field Conditions

Many of the mechanisms of organelle communication have been deduced in Arabidopsis and in controlled laboratory systems. The mechanisms described here need to be tested in other important crops and under realistic field conditions. Emphasis should be placed on tissue specificity, developmental stage, duration of stress and multiple stresses. Seamless integration of spatial imaging, organelle-resolved omics and physiological measures under field-relevant conditions will be critical to translate molecular insights to crop level resilience.

9.3 Engineering Interorganelle Networks for Stress-Resilient Crops

Emerging biotechnology offers opportunities to manipulate organelle communication for improved stress tolerance. New strategies are emerging for chloroplast genome engineering and chloroplast transformation for the modification of organelle-specific pathways and regulatory networks (Narra et al., 2025). The engineering of protective chloroplast functions has already been demonstrated by enhanced drought resistance by increasing the photoprotection and ABA-related responses (Niu et al., 2025). Coordinated signaling and the consideration of potential trade-offs between stress resilience, growth, development, and productivity should be the focus of future approaches.

10. Conclusion

Interorganelle communication is fundamental to the ability of plants to perceive environmental disturbances, coordinate cellular responses, and maintain metabolic stability under stress. The chloroplasts, mitochondria, endoplasmic reticulum, peroxisomes, vacuoles, and the nucleus operate as a coordinated network rather than as isolated compartments. They act in concert to facilitate the transfer of information on stress via membrane contact sites, redox changes, calcium dynamics, metabolites, lipids, hormones, and retrograde signaling pathways.

Membrane contact sites provide structural platforms that facilitate rapid transfer of molecules and support dynamic interactions among organelles. Retrograde signaling complements these physical connections by conveying organelle functional status to the nucleus, where transcriptional programs are adjusted according to cellular requirements. Together, these mechanisms enable coordinated regulation of

photosynthesis, respiration, photorespiration, carbon and nitrogen metabolism, lipid remodeling, antioxidant defenses, and osmoprotective pathways. It is important to note that this metabolic reprogramming is vital for maintaining energy balance, redox homeostasis, membrane integrity and cell viability during drought, salinity, temperature extremes, high light, hypoxia and combined stresses.

Recent breakthroughs in live-cell imaging, biosensors, proximity labeling, organelle-resolved omics and functional genomics are increasingly providing insights into the spatiotemporal complexity of these interactions. The molecular composition of many contact sites, the mechanism of control over the specificity of signals and the integration of information from the organelles under combinations of stress conditions relevant to the field, however, are not yet fully understood. In the future, more progress will be made by linking mechanistic information from model systems with crop physiology and environmental factors. A systems-level understanding of interorganelle communication thus provides a promising basis for engineered plants to more flexibly adapt to environmental changes and stress via improved metabolic capacity.

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