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Molecular Response Mechanisms of Plants under Adversity Stresses

Mofei Li

College of Agriculture and Biotechnology, Zhejiang University, Hangzhou, China
breathtrap@foxmail.com

Abstract. Throughout the whole growth and development process, plants are frequently challenged by a variety of abiotic stresses including high temperature, low temperature, drought, iron deficiency, heavy metal toxicity and acid soil. These adverse factors induce plants to activate a series of complex and highly coordinated molecular response mechanisms to improve their adaptability and survivability in changing environments. This paper systematically reviews recent research progress on plant responses to various abiotic stresses. It mainly elaborates on regulatory modules covering multiple dimensions, such as hormone signaling pathways including ethylene, jasmonic acid and salicylic acid, key transcription factor families represented by NAC and WRKY, RNA regulatory mechanisms involving miRNA and lncRNA, protein interaction networks such as the MAPK cascade, as well as inter-organelle signal transduction. By integrating regulatory mechanisms at different levels, this study aims to illustrate the systematic response strategies of plants against adversity stresses, and provide theoretical basis and references for the subsequent molecular breeding and genetic improvement of stress-tolerant crops.

Keywords: abiotic stress, hormone signal, stress tolerance mechanism, plant stress physiology

1. Introduction

Against the backdrop of worsening global climate change and soil degradation, plants are exposed to an increasing variety and intensity of abiotic stresses, which seriously threaten agricultural production security and the stability of crop yields. Environmental factors such as high temperature, low temperature, drought, iron deficiency, heavy metal stress and acid soil prevail in farmland ecosystems worldwide, and directly affect plant physiological metabolism, cellular homeostasis and growth and development. To cope with these adverse stresses, plants have evolved a highly sophisticated and well-coordinated molecular response system involving multiple layers, including gene transcriptional regulation, hormone signal modulation, non-coding RNA-mediated expression regulation, protein interaction networks, and signal transduction among subcellular organelles.

Plant hormones play core regulatory roles in responses to abiotic stresses. Among them, ethylene, jasmonic acid and salicylic acid not only act as key regulators in stress perception and signal transduction, but also interact with other hormones to form complex signaling networks that finely modulate the expression of defense-related genes. Meanwhile, multiple transcription factor families

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such as NAC and WRKY serve as mediators in activating stress-induced genes and coordinate the initiation of downstream response programs. In recent years, the functions of non-coding RNAs, especially miRNAs and lncRNAs, in stress regulation have been gradually uncovered. They participate in plant stress response networks via mechanisms including targeted mRNA degradation, post-transcriptional regulation and chromatin modification. In addition, protein interaction pathways such as the MAPK cascade perform irreplaceable functions in the amplification and transmission of stress signals. Notably, signal communication among organelles including chloroplasts, mitochondria and nuclei is critical for coordinating the overall stress response.

This review integrates the latest research findings in hormone signaling, transcription factors, RNA regulation, protein interaction networks and inter-organelle signal transduction, and summarizes the functional patterns of these mechanisms when plants respond to diverse abiotic stresses including high temperature, low temperature, drought, iron deficiency, heavy metal toxicity and acid soil. A systematic analysis of plant stress response networks from the perspective of multi-dimensional molecular regulation provides theoretical references and research directions for the subsequent molecular design breeding and targeted improvement of stress-tolerant crops.

2. Temperature stress

Temperature stress is mainly divided into two categories: high temperature stress and low temperature stress. As a major environmental limiting factor, high temperature stress exerts remarkable adverse effects on plant growth, development and yield formation. It generally triggers a series of physiological disorders such as destabilization of membrane systems, protein denaturation, inhibition of photosynthesis and accumulation of reactive oxygen species (ROS). To adapt to high temperature environments, plants initiate a set of rapid and sophisticated molecular regulatory mechanisms, which cover hormone signal modulation, transcription factor-mediated gene expression regulation, non-coding RNA regulation, protein interaction networks and inter-organelle signal transduction.

Low temperature inhibits cellular metabolism, disrupts membrane structures, ion homeostasis and photosynthetic functions of plants. In severe cases, it may even lead to growth arrest and plant death. To cope with chilling injury, plants activate multi-layered signaling networks, including stress perception mechanisms, signal cascade reactions, transcription factor regulation and synergistic modulation by plant hormones.

2.1. Transcription factor-mediated signal transduction

Heat shock proteins (HSPs) and heat shock factors (HSFs) jointly form the core regulatory network for plant responses to high temperature. Relevant studies have demonstrated that HSFA1 transcription factors are rapidly activated at the early stage of high temperature stress, thereby triggering the expression of genes encoding HSP70, HSP90 and small heat shock proteins (sHSPs). Acting as molecular chaperones, these HSPs assist in protein folding and repair, preventing protein aggregation and inactivation caused by high temperature [1]. High temperature stress is also accompanied by massive accumulation of reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2). Excessive ROS can cause membrane lipid peroxidation, DNA damage and programmed cell death. To mitigate oxidative injury, plants upregulate the expression of genes encoding antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX), and accumulate non-enzymatic antioxidants including glutathione (GSH) and ascorbic acid (AsA). For example, overexpression of OsAPX1 in rice can markedly enhance plant thermotolerance [2].

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In the signal transduction of low temperature stress, the C-repeat binding factor (CBF) signaling pathway is widely recognized as a core mechanism governing plant cold tolerance. Cold stimuli rapidly trigger the accumulation of inducer of CBF expression 1 (ICE1). ICE1 further activates the expression of CBF1, CBF2 and CBF3, which in turn induce a set of cold-responsive (COR) genes such as COR15A and RD29A. The proteins encoded by these genes stabilize cell membranes, regulate cellular osmotic pressure and scavenge reactive oxygen species, thereby improving plant freezing tolerance [3]. In addition, low temperature enhances cold resistance by modulating endogenous hormone balance. The level of abscisic acid (ABA) generally rises under cold conditions, which promotes the activation of the CBF pathway and induces the expression of various protective proteins [4]. Calcium signals and reactive oxygen species also act as early signaling molecules involved in cold sensing and responses, jointly regulating the downstream transcriptional networks.

2.2. Regulation by plant hormones

Plant hormones also play vital roles in regulating plant responses to heat stress. The biosynthesis of abscisic acid (ABA) increases under high temperature. It helps plants close stomata to reduce transpiration and heat loss, and interacts with heat shock factors (HSFs) to modulate the expression of heat-resistant genes. Ethylene, salicylic acid (SA) and jasmonic acid (JA) also jointly participate in the regulatory network of plant thermotolerance by regulating reactive oxygen species (ROS) levels or activating downstream transcription factors.

2.3. Regulation at the translational level

To maintain intracellular protein homeostasis under high temperature, plants implement regulation at the translational level. They selectively express key genes such as those encoding heat shock proteins (HSPs), and eliminate denatured or misfolded proteins via the ubiquitin-proteasome system [5].

2.4. Adaptive regulation of cell membranes

High temperature exerts a profound impact on cell membranes. Plants adjust the unsaturation degree of fatty acids to sustain the fluidity and functional stability of cell membranes [6]. Low temperature causes membrane lipids to transform from a liquid state to a gel state, which reduces membrane fluidity and impairs the functions of transmembrane proteins and signal perception. To adapt to low temperature, plants enhance the flexibility and stability of cell membranes by increasing fatty acid unsaturation, for example, by upregulating the expression of fatty acid desaturase genes such as FAD8 [6].

In summary, the molecular mechanisms underlying plant tolerance to high temperature constitute an integrated network involving multiple layers including transcriptional regulation, signal transduction, protein homeostasis modulation and membrane adaptation. These mechanisms reflect plants' strong capacity to sense adverse environments and lay a theoretical foundation for breeding heat-tolerant crop varieties. The response mechanisms of plants to low temperature stress form a dynamic and highly coordinated molecular network covering membrane lipid remodeling, CBF signal regulation, as well as the coordination of hormone and ROS signals. In-depth elucidation of these mechanisms can provide important molecular targets for improving cold tolerance in crops.

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3. Drought stress

Drought stress is one of the major abiotic stresses that restrict plant growth and development and reduce crop yield. It usually leads to a series of adverse physiological effects such as cellular water loss, stomatal closure, inhibited photosynthesis and accumulation of reactive oxygen species (ROS). To adapt to water-deficient environments, plants establish complex molecular regulatory networks, which involve hormone signal-mediated response pathways (especially abscisic acid), transcription factor-regulated gene expression reprogramming, post-transcriptional regulation mediated by non-coding RNAs, dynamic adjustment of cell wall and membrane lipid components, accumulation of osmoregulatory substances and activation of antioxidant systems. These mechanisms enable plants to rapidly sense and efficiently adapt to drought conditions.

3.1. Regulation at the genetic level

Drought stress induces massive accumulation of abscisic acid (ABA) in plant roots and leaves. ABA binds to PYR/PYL receptors to activate SnRK2 protein kinases, which further regulate transcription factors such as AREB/ABF and trigger the expression of a variety of drought-resistant genes. The products of these genes include osmoregulatory proteins such as late embryogenesis abundant (LEA) proteins and dehydrins, as well as aquaporins including PIPs and TIPs. They help plants maintain intracellular water balance and protein stability [7].

Drought stress also triggers excessive production of reactive oxygen species (ROS), such as superoxide anion (O_2^-) and hydrogen peroxide (H_2O_2). Excess ROS are toxic to cells, while appropriate levels of ROS act as signaling molecules to modulate plant drought responses. Plants upregulate antioxidant enzymes including superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX), as well as non-enzymatic antioxidants such as glutathione (GSH) and ascorbic acid (AsA) to keep ROS in check and prevent cells from oxidative damage [8, 9].

At the transcriptional level, multiple drought-related transcription factor families including DREB (especially DREB2A), NAC, MYB and bZIP are activated. These transcription factors can directly bind to drought-responsive elements such as DRE and ABRE to initiate the transcription of downstream drought-resistant genes. Overexpression of certain transcription factors such as OsNAC10 and AtDREB2A in crops can significantly improve plant drought tolerance [10].

3.2. Other regulatory mechanisms

In addition, plants enhance structural stability and metabolic adaptability under drought stress through cell wall remodeling, lipid metabolism adjustment and signal transduction reprogramming [11, 12]. For example, increased lignin synthesis strengthens the cell wall, and changes in membrane lipid composition modulate the permeability and stability of cell membranes.

To sum up, plant drought response is centered on the ABA signaling pathway, with ROS, osmoregulation, transcription factors and structural remodeling functioning collaboratively to form a multi-layered regulatory network. An in-depth understanding of these mechanisms can provide abundant molecular tools for breeding highly drought-tolerant crops.

4. Iron deficiency stress

Iron is an essential trace element for plant growth and participates in many vital physiological processes, including photosynthesis, respiratory chain reactions and nitrogen assimilation. In soil,

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iron mainly exists in the form of insoluble ferric iron (Fe^{3+}), which is hardly available for plant uptake. When exposed to iron deficiency stress, plants rapidly activate regulatory networks for iron absorption and redistribution. Plants primarily adopt two distinct strategies to cope with iron shortage, namely Strategy I for non-graminaceous plants and Strategy II for graminaceous plants.

4.1. Reduction-based mechanism

To improve iron uptake under iron-deficient conditions, plants implement three core steps. First is rhizosphere acidification. The expression of root-localized H^+-ATPases, such as AHA2 in Arabidopsis thaliana and MxHA7 in Malus xiaojinensis, is upregulated to boost proton efflux and lower the pH of the rhizosphere, thereby increasing the solubility of Fe^{3+}. Second is the reduction of Fe^{3+} to Fe^{2+}. Ferric-chelate reductases represented by FRO2 in Arabidopsis thaliana convert Fe^{3+} into bioavailable Fe^{2+}, which acts as the rate-limiting step of iron acquisition in this pathway. Third is the transport of Fe^{2+} into root cells. Iron-regulated transporters such as IRT1 in Arabidopsis thaliana mediate the inward transport of Fe^{2+}. Several metal transporters including NRAMP1 are also involved in iron absorption, though their functional mechanisms remain to be fully elucidated. This strategy has certain limitations. It works inefficiently in calcareous soils with high pH, which frequently leads to iron-deficiency chlorosis in plants [13].

4.2. Chelation-based mechanism

Grasses such as rice and wheat take up iron via two major steps under iron deficiency. Firstly, plants synthesize and secrete phytosiderophores (PS). They produce mugineic acid (MA) and other phenolic phytosiderophores, which are actively secreted into the rhizosphere by the TOM1 protein. The biosynthesis of phytosiderophores requires key enzymes including NAS, NAAT and DMAS, with S-adenosylmethionine (SAM) serving as the reaction substrate. Secondly, plants absorb Fe(III)-PS complexes. Phytosiderophores released into soil bind to Fe^{3+} to form Fe(III)-PS complexes, which are then specifically taken up by plants via transporters of the YS1/YSL family, such as OsYSL15 in rice. A major advantage of this mechanism is that it functions independently of low pH conditions, conferring strong adaptability to calcareous soils [13].

4.3. Other auxiliary adaptive mechanisms

Furthermore, plants employ a variety of auxiliary mechanisms to adapt to iron-deficient environments. On the one hand, they regulate iron redistribution between chloroplasts and mitochondria. Ferritin proteins temporarily store iron and control its release to sustain normal operation of core metabolic activities. On the other hand, plants reshape root architecture, such as increasing root hair density and forming iron plaques, so as to expand the area for iron absorption. Meanwhile, plant hormones including ethylene, nitrate, abscisic acid (ABA) and salicylic acid (SA) interact with iron signaling pathways and modulate iron deficiency responses in roots. Reactive oxygen species (ROS) also participate in this process: moderate ROS facilitates the activation of related transcription factors, while excessive ROS needs to be scavenged by the antioxidant system to prevent oxidative damage to plants.

5. Heavy metal stress

The continuous accumulation of heavy metals such as Cd^{2+}, Pb^{2+}, As^{3+} and Hg^{2+} in soil severely disturbs normal plant metabolism. These substances cause damage to plants mainly by triggering

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oxidative stress, exerting ionic toxicity and competing for absorption sites of nutrient elements. As a critical abiotic stressor that threatens plant growth and crop yield safety, heavy metal stress leads to disordered cellular metabolism and impaired physiological functions via ionic toxicity, competition for nutrient uptake and induced accumulation of reactive oxygen species (ROS). To survive in heavy metal-contaminated environments, plants have developed multi-layered defense and adaptive mechanisms, including metal ion chelation and compartmentalization, regulation of transmembrane transport, activation of antioxidant systems, modulation of hormone and signaling pathways, as well as gene expression regulatory networks involving transcription factors and non-coding RNAs. These mechanisms help plants maintain cellular homeostasis and ensure survival under complex adverse conditions.

5.1. Recognition, chelation and detoxification of metal ions

Heavy metal ions activate signaling cascades such as the Ca^{2+}-ROS-MAPK pathway. Plant hormones including ethylene, abscisic acid (ABA) and jasmonic acid participate in responses to heavy metal stress by regulating root growth and inducing the expression of stress-resistant genes. Zinc finger transcription factors such as ZAT directly promote the synthesis of phytochelatins (PCs) and glutathione (GSH) metabolism, thereby further enhancing plant tolerance to heavy metal stress [14].

5.2. Responses of hormone and signaling networks

Plants synthesize cysteine-rich phytochelatins (PCs) and metallothioneins (MTs) to bind heavy metal ions. They also utilize ABC transporters such as ABCC1 and ABCC2 to transport metal-chelate complexes into vacuoles for compartmental storage, which reduces the concentration of free heavy metal ions in the cytoplasm [15]. In terms of transport regulation, proteins including ZIP, NRAMP and HMA function as transmembrane channels for metal ions. They coordinate heavy metal uptake by roots, rhizosphere transport and vascular distribution, and minimize the accumulation of toxic heavy metals in above-ground plant tissues [16]. In conclusion, plants cope with heavy metal stress comprehensively through the synergistic action of metal chelation and compartmentalization, antioxidant protection, transport regulation, as well as signaling and hormone networks.

6. Acid soil stress

When growing in acid soils, plants are exposed to multiple stresses, including proton toxicity, aluminum (Al^{3+}) and manganese (Mn^{2+}) toxicity, as well as reduced bioavailability of nutrients such as calcium (Ca^{2+}), magnesium (Mg^{2+}) and phosphorus (P). To adapt to such complex environments, plants activate a comprehensive set of molecular response mechanisms.

6.1. Organic acid secretion and aluminum ion chelation

Upon sensing aluminum toxicity in acid soils, root tip cells actively secrete organic acids such as malic acid and citric acid into the rhizosphere via transporters including ALMT (e.g., AtALMT1) and MATE (e.g., OsFRDL4). These organic acids chelate Al^{3+} to form complexes that cannot be absorbed by plant cells, thereby blocking the entry of Al^{3+} and alleviating aluminum toxicity [17].

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6.2. Adaptive remodeling of cell walls

Al^{3+} tends to bind to carboxyl groups of pectin in cell walls. Accordingly, plants modulate the expression of cell wall-related genes such as XTH, expansin and pectin methylesterase. This process alters the degree of pectin methylation and polysaccharide structures, reduces the binding sites for Al^{3+} and decreases its accumulation in cell walls [18, 19].

6.3. Regulatory networks of transcription factors

Multiple transcription factors work synergistically to initiate plant resistance mechanisms against acid stress. STOP1 in Arabidopsis thaliana and ART1 in rice act as core regulators, which control the expression of transporter genes such as ALMT1 and MATE. Their activities are co-regulated by pH sensing, ROS and hormone signals, serving as key hubs that integrate diverse stress signals [20]. In summary, plant adaptation to acid soils is a sophisticated systematic regulatory process involving metabolic modulation, substance transport, antioxidant protection and signal regulation. An in-depth interpretation of these mechanisms provides an important theoretical basis and molecular targets for improving the adaptability of crops to acid soils.

7. Conclusion

When confronted with various abiotic stresses including high temperature, low temperature, drought, heavy metal toxicity, iron deficiency and acid soil, plants activate highly complex and dynamic molecular regulatory networks. These response mechanisms cover stress perception and signal transduction pathways such as the Ca^{2+}-ROS-MAPK cascade, transcription factor-mediated gene expression reprogramming involving HSFs, DREB, WRKY and STOP1, as well as adaptive metabolic adjustments including antioxidant system activation, chelator synthesis, organic acid secretion, membrane lipid remodeling and synergistic regulation of hormone networks. Relying on these mechanisms, plants can not only maintain cellular homeostasis, but also effectively remodel their physiological functions and structural characteristics to enhance stress adaptability.

Nevertheless, distinct differences exist among various stress types, and multiple stresses frequently occur simultaneously. For instance, aluminum toxicity and nutrient deficiency coexist in acid soils, resulting in intricate interactive effects during plant stress responses. Future research should place greater emphasis on deciphering the crosstalk mechanisms between different stresses, conducting integrative analysis of key regulatory factor networks, and screening target genes for crop resistance breeding based on molecular genomics. These efforts will provide theoretical support and practical strategies for improving the sustainable productivity of agricultural systems amid global climate change and soil degradation.

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