

MINI REVIEW

Molecular mechanisms underlying stress response and adaptation

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Abstract

Environmental stresses are ubiquitous and unavoidable to all living things. Organisms respond and adapt to stresses through defined regulatory mechanisms that drive changes in gene expression, organismal morphology, or physiology. Immune responses illustrate adaptation to bacterial and viral biotic stresses in animals. Dysregulation of the genotoxic stress response system is frequently associated with various types of human cancer. With respect to plants, especially halophytes, complicated systems have been developed to allow for plant growth in high salt environments. In addition, drought, waterlogging, and low temperatures represent other common plant stresses. In this review, we summarize representative examples of organismal response and adaptation to various stresses. We also discuss the molecular mechanisms underlying the above phenomena with a focus on the improvement of organismal tolerance to unfavorable environments.

Introduction

Animals, plants, and microorganisms are all exposed to a broad range of environmental stresses, leading to the development of a wide variety of stress responses and adaptations.^{1–3} Responses include changes in gene expression, as well as morphological and physiological changes.^{4–6} A wide variety of adaptations have evolved, as they impact the survival and distribution of species.^{7,8} For example, in response to diverse genotoxic stresses, such as ionizing and ultraviolet (UV) radiation, oxidative stress, and chemotherapeutic agents, the genotoxic stress response system is activated to repair DNA damage; in the case of irreparable damage, apoptosis is induced in favor of organismal survival.^{9–11} Dysregulation of the genotoxic stress response system has been implicated in the development of human cancer, and stress-induced responses have been utilized for the development of new anti-cancer therapies.^{9,10,12}

Biotic stresses that affect all organisms include bacteria, viruses, and biological competition. Bacteria are ubiquitous and are present on, in, and around organisms. Gut

microbiota is important for human and animal physiology.^{13,14} Similarly, rhizosphere microbes facilitate plant growth or destroy their root systems.^{15,16} Organisms have also developed stringent and complicated immune responses to combat viruses. Biological competition describes the ability of organisms with superior stress adaptations to outgrow or overcome other organisms in the same environment.

Plants experience a number of abiotic stresses, including cold, drought, waterlogging, high salt concentration, and phosphate starvation.^{4,5,17–20} These stresses can affect nutrient uptake and utilization; therefore, plants have developed a wide variety of structural, morphological, and regulatory adaptations to address these environmental stresses.^{3,21–23} In particular, multi-level regulatory mechanisms involved in salt tolerance have been well characterized in halophytes, such as *Suaeda salsa*,^{5,24–26} *Thellungiella salsuginea*,^{27,28} and *Limonium bicolor*.^{29–33} Adaptations to cold stress, drought, and UV radiation have also been reported to a lesser degree.

Antiviral and antibacterial immunity

Bacterial infections are among significant infectious diseases.^{34,35} Despite the advent of vaccines and antibiotics, the activation of direct immunity enables more rapid and efficient responses to pathogens.^{36–40} *Cyprinus carpio*, an economically valuable commercial farming fish species, has a complicated innate immune system.^{41–43} Regulatory factors, such as interferon regulatory factors (IRFs), the Rig-I-like receptor Mda5, IRAK1, IgM-binding protein, and the cysteine-rich cationic antimicrobial peptide LEAP-2, play important roles in the immune defense system.^{44–48}

IRF1 is constitutively expressed in different organs. When stimulated by poly(I:C), a molecular species associated with viral infection, peripheral blood leukocytes exhibit upregulation of IRF1.⁴⁹ IRF5 is a key molecule in antiviral and antibacterial immunity. Expression of *irf5* has been shown to be upregulated in immune-related tissues, including the liver, spleen, head kidney, foregut, hindgut, skin, and gills, after stimulation with poly(I:C) and lipopolysaccharide, suggesting that IRF5 may play an important role in antiviral and antibacterial immunity in fish.⁵⁰ Similarly, after *Vibrio anguillarum* and poly(I:C) challenge, *irak1* expression is upregulated, especially in the liver and spleen.⁵¹ *mda5* is expressed at high levels in the gills and spleen and at lower levels in the gonad and blood. The addition of poly(I:C) and *Aeromonas hydrophila* stimulates *mda5* expression in the foregut, hindgut, gills, and skin.⁵²

The gut microbiome is important for the response of most organisms to pathogens, and *Blattella germanica* is no exception.^{13,14,53,54} *Bacillus subtilis* BGI-1 and *Pseudomonas reactans* BGI-14 were isolated from the gut of conventional *Blattella germanica*. Both strains inhibit the growth of *Beauveria bassiana*. Microbes with anti-entomopathogenic fungi activity promote resistance to infection with pathogenic fungi in *Blattella germanica*.^{14,53} Similarly, bovine mastitis has been associated with specific types and distributions of *Staphylococcus aureus*.^{55–59}

Salt stress

Saline-alkaline soil is widespread in many areas of the world, and salt stress negatively affects plant growth and productivity.⁶⁰ As a result of the high NaCl concentrations and high pH, many grain crops cannot grow.^{61–63} Halophytes are a group of plants that have developed targeted adaptation for living under high salt conditions.^{64,65} For example, *Suaeda salsa* is a halophyte that produces dimorphic seeds in response to differing salt conditions;^{24,66,67} seeds are black under low salt and brown under high salt concentrations.^{66,68,69} A series of *Suaeda salsa* genes

important for salt tolerance have been identified, including *SsNHX1*, *SsHKT1*, *SsAPX*, *SsCAT1*, *SsCHLAPXs*, *SsP5CS*, and *SsBADH*.^{25,70–72} Specific NaCl concentrations have been shown to improve *Suaeda salsa* seed vitality by increasing seed weight and levels of stored protein, starch, and fatty acids.^{26,73–77} In the related organism, *Suaeda physophora*, cotyledons play an important role in seedling establishment by generating oxygen and compartmentalizing Na⁺ under salt stress.^{78,79} Based on research of salt-tolerance mechanisms in *Suaeda salsa*, overexpression of the related genes in tobacco^{80,81} and *Arabidopsis thaliana* can increase salt tolerance.^{82–87} This is a type of coevolution. NaCl treatment results in resistance to photoinhibition and increased concentrations of unsaturated fatty acids in the halophyte *Thellungiella salsuginea*. Both these changes enhance the tolerance of photosystem II to salt stress.^{88,89} A total of 26 microRNAs are known to participate in regulation of the salt stress response in *Thellungiella salsuginea*.²⁷

Retreohalophytes have developed specialized salt-secreting structures to remove excess salts from plant tissues.^{90–97} For example, *Limonium bicolor* is a typical retreohalophyte that lives in saline environments.^{30,33} The salt gland is the first differentiated epidermal structure in *Limonium bicolor*, differentiating two days earlier than the stomata.^{98–100} These salt glands have four secretory pores in the center of the cuticle that secrete NaCl.³² Using high-throughput RNA sequencing, candidate genes have been identified in the *Limonium bicolor* salt gland that are highly associated with salt secretion.^{29,101} In addition, an efficient method has been developed to screen for mutants capable of adapting to abnormal salt gland density.³¹ In addition to the morphology of these specialized structures, the K⁺/Na⁺ ratio has been shown to play an important role in *Limonium bicolor* salt tolerance.^{102–107} Accumulation of K⁺ in the cytoplasm and nucleus of salt gland cells is a key factor in salt secretion.¹⁰⁸

In addition to halophytes, many other plants also exhibit adaptations to protect against salt stress.¹⁰⁹ For example, in cotton (*Gossypium hirsutum* L.), high NaCl concentrations induce leaf senescence.¹¹⁰ Nitric oxide (NO) has been found to delay salt-induced leaf senescence in cotton through regulation of *SOS1*, *NHX1*, *NCED2*, *NCED9*, and *IPT1* expression.^{110–112} Changes in expression of these genes decrease intracellular Na⁺ levels and abscisic acid (ABA) contents and increase intracellular K⁺ levels and cytokinin expression.^{110,113,114} Similar to the effects of NO in cotton, exogenous hydrogen sulfide production enhances salt tolerance by decreasing Na⁺ content in wheat seedlings.^{115,116} During salt acclimation in *Arabidopsis thaliana*, cell wall remodeling, ethylene biosynthesis, and signaling pathways play crucial roles.^{117–120} K⁺ and Ca²⁺ homeostasis are also important.^{121,122} Some transgenic *Arabidopsis thaliana* strains exhibit higher salinity tolerance and osmotic

stress.^{123–126} For example, overexpression of AtZFP1, a CCH-type zinc finger protein, enhances salt tolerance by maintaining ionic balance and limiting oxidative and osmotic stress.^{127,128} Overexpression of TsGOLS2, a galactinol synthase in *Thellungiella salsuginea*,¹²⁹ increases levels of galactinol, raffinose, and alpha-ketoglutaric acid in *Arabidopsis thaliana*, thereby promoting salt tolerance and resistance to osmotic stress.^{130,131}

Temperature changes

Cold stress is an important environmental factor that affects plant growth and crop productivity. A number of genes and pathways have been found to contribute to cold stress adaptation, some of which overlap with salt stress resistance pathways. In rice, the casein kinase LTRPK1 plays a key role in cold tolerance by regulating cytoskeletal rearrangements that favor cold adaptation.^{132–134} Recent studies have shown that the light signaling gene *phyB* also participates in a pathway that promotes resistance to chilling.^{135–137} *PhyB* negatively regulates chloroplast structural stability by lowering levels of unsaturated fatty acids present in membrane lipids.^{138–140} *PhyB* deficiency positively regulates *OsPIL16* and *OsDREB1*,¹⁴¹ thereby alleviating chilling-induced photoinhibition and enhancing chilling tolerance.^{142–144} Similar mechanisms have also been characterized in *Suaeda salsa*. Severe photoinhibition occurred in *Suaeda salsa* leaves when exposed to cold stress. Photoinhibition is associated with the accumulation of reactive oxygen species and water–water cycle.^{5,145–147} Increased salinity, such as treatment with high concentrations of NaCl, can also increase chilling tolerance under conditions of low irradiance.¹⁴⁸ By controlling the opening and closing of stomata, *Suaeda salsa* can adapt to a variety of temperatures.^{149–151} RNA-sequencing analysis revealed numerous differentially expressed genes in *Thellungiella salsuginea* under cold treatment.^{152,153} RNA interference lines of the cold-induced gene *TsFtsH8* enhanced *Thellungiella salsuginea* tolerance to cold.^{28,154–156} Similarly, the *Thellungiella salsuginea* salt-induced gene *TsnsLTP4* encodes a non-specific lipid transfer protein that participates in wax deposition and in plant tolerance against abiotic stresses, including salt, ABA, and high and low temperatures.^{157–160}

Distinct pathways mediate stress adaptation

In addition to salt stress and temperature variation, drought and waterlogging also threaten plant growth and survival.^{161–168} In peanut plants, 22 genes were identified as drought-responsive genes by complementary DNA microarray analysis.^{169–171} *DELLA* genes and heat shock

transcription factors were found to promote the survival of plants in adverse environments.^{172–174} In rice, *PhyB* not only contributes to cold stress resistance, but also influences drought tolerance by regulating total leaf area and transpiration per unit leaf area.^{4,175,176} *Suaeda salsa* produces nitric oxide to protect adventitious root formation under waterlogged conditions.^{18,34,91,177–179} Compared to xerophytes, two halophytes were more tolerant to waterlogging and dry-moist cycles during emergence under saline conditions.^{17,180–183}

Because of the availability of molecular approaches, *Arabidopsis thaliana* is an ideal model system to characterize responses to different environmental stresses.^{184–187} When exposed to enhanced UVB radiation, the *sad2-1* mutant *Arabidopsis thaliana* strain accumulates more UV absorption materials and endogenous ABA and activates ROS-scavenging enzymes. These physiological changes enhance tolerance to UV.^{188,189} *Arabidopsis thaliana* responds to low CO₂ stress by altering biomass productivity, thylakoid stacking, and expression of photosynthesis regulators.^{190–192} *AtFes1A* has been shown to play an important role in abiotic stress tolerance.¹⁹³

Conclusions and perspectives

In this review we have summarized multiple regulatory processes that contribute to the response and adaptation to various stresses. Adaptation to salt stress can be induced by NaCl exposure,^{26,73,148} and include the formation of specialized structures,^{29–33,98–101,108} and changes in physiology and gene expression profiles.^{28,71,72,80,120,127,132} Induction makes plants more adaptive to salt tolerance as they complement each other. Similarly, although animals face a more versatile environment, they develop rigorous immune systems to adapt to stresses arising from exposure to viruses or pathogenic bacteria.^{41–44,46–48,50–52,194} Cytoskeleton-associated proteins and cellular events may also play important roles in stress response and adaptation in humans and other animals.^{195,196} In addition to adaptation by the plant or animal itself, resident microbiota also contribute to resistance to pathogens.^{13,14,53,197}

Based on research focused on the mechanisms associated with stress responses, a common set of proteins and regulatory pathways contribute to adaptation. These mechanisms can be used in plants and animals to improve stress tolerance,^{16,81–83,85,119,191,198} and may be beneficial to the adaptation of plants and animals.^{81–83,85,119,191,199} In general, a clearer understanding of the mechanisms that contribute to stress tolerance in different types of organisms would facilitate their application in improving organismal tolerance to unfavorable environments. For example, a better understanding of plant stress tolerance pathways could enhance the number of plants capable of growing in

adverse conditions. From a different perspective, adaptation of different organisms to abiotic and biotic stressors is a form of natural selection that follows the rule of “survival of the fittest.”

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Disclosure

No authors report any conflict of interest.

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