

Mini-Review

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Survival mechanisms to selective pressures and implications

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Abstract: Organisms have evolved a spectrum of strategies that facilitate survival in the face of adverse environmental conditions. In order to make full use of the unfavorable resources of nature, human beings usually impose selective pressures to breed phenotypic traits that can survive in adverse environments. Animals are frequently under attack by biotic stress, such as bacterial and viral infections, while plants are more often subjected to abiotic stress, including high salinity, drought, and cold. In response to these diverse stresses, animals and plants initiate wide-ranging changes in gene expression by altering regulation of transcriptional and post-transcriptional activities. Recent studies have identified a number of key responsive components that promote survival of animals and plants in response to biotic and abiotic stresses. Importantly, with recent developments in genome-editing technology based on the CRISPR/Cas9 system, manipulation of genetic elements to generate stress-resistant animals and plants has become both feasible and cost-effective. Herein, we review important mechanisms that govern the response of organisms to biotic and abiotic stresses with the aim of applying our understanding to the agriculture and animal husbandry industries.

Keywords: selective pressures; immune system; salinity; chilling; drought; genome editing

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1 Introduction

Our world is characterized by broad biodiversity [1, 2], present even in niches with unfavorable environmental conditions [3-8]. Organisms living in these environments have evolved a variety of adaptive mechanisms to respond to biotic and abiotic stresses [9, 10]. For example, animals have developed sophisticated immune systems to respond to the biotic stresses they frequently encounter, such as bacterial or viral infections [11-13]. In contrast, plants more often respond to abiotic stresses through regulation of transcriptional and post-transcriptional activities that affect gene expression [14-20]. Abiotic stresses, which include high salinity [21-25], extreme temperature [20, 26-28], drought [18, 29, 30], heavy metal toxicity [17, 31, 32], ozone [33-37], irradiation [30, 38], carbon dioxide [19, 36, 37, 39-41], sulfur dioxide [42-44], and variations in soil pH [4, 45-47], severely constrain plant growth and development, leading to loss of crop production [48-53]. Thus, one strategy for improvement of crop yields is to cultivate crops that are tolerant to the abiotic stresses. Clearly, genetic variation plays a principal role in adaptation. However, natural selection is long-term process with constant mutation rate. To fuel the adaption processes, stress-stimulated adaption is usually applied for the rapid generation of phenotypic traits (Figure 1).

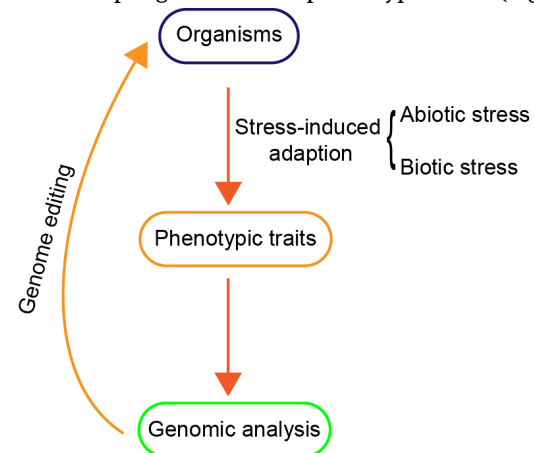


Figure 1. Stress-induced adaption strategy adopted for the generation of phenotypic traits.

Broadening our understanding of the molecular mechanisms governing the responses of animals and plants to stressful conditions would provide substantial benefits for animal husbandry and plant domestication [31, 54-59]. With recent developments in genome-editing technology, carrying out genetic manipulations to generate novel genotypic species resistant to biotic and abiotic stresses has become technically feasible and economically viable [60-66]. In this review, we discuss the molecular mechanisms that contribute to resistance to biotic stresses in animals and abiotic stresses in plants, highlighting key pathways responsible for stress resistance. Genetic manipulation of these pathways may be used in future studies to facilitate development of stress-resistant animals and plants for application in animal husbandry and agriculture [67].

2 Immune responses to biotic stresses

Animals have developed defense mechanisms to respond to biotic stresses, such as bacteria, viruses, fungi, and parasites [68-74]. The innate immune system acts as the first-line of defense against these invading pathogens through the action of pattern recognition receptors directed against conserved pathogenic molecules, termed pathogen-associated molecular patterns [75-78]. The roles of the insulin, TGF- β , mTOR, and p38 MAPK pathways in the immune response have been well characterized, and a number of other challenge-response genes have also been identified. For example, the alpha-2-macroglobulin gene has been associated with mastitis and has the potential to serve as a biomarker for mastitis susceptibility [26, 79, 80]. Mannose-binding lectin is crucial for the host immune defense against a spectrum of pathogens [81-83]. Melanoma differentiation-associated gene 5, interferon regulatory factor 5, and hepcidin family genes have been shown to be essential for the innate immune response of common carp [84-86].

3 Survival mechanisms to abiotic stresses

During evolution, plants have formed diverse adaptive mechanisms to survive in the adverse environmental conditions. High salinity represents one of most common abiotic stresses faced by plants. Exposure to high salinity markedly limits the growth and production of plants due to induction of osmotic, oxidative, and temperature stresses

[25, 32, 34, 87-89]. Although the molecular mechanisms used by plants to overcome high salinity challenge are not fully understood, recent advances have begun to identify key pathways and molecules [12, 28, 90-95], many of which regulate the ionic balance [16, 21, 24, 38, 77, 96-101]. For example, Na⁺ has been shown to be important for maintenance of intracellular K⁺ concentrations, and Na⁺/K⁺ homeostasis is crucial for plant growth and development. At high salt concentrations, plants reduce Na⁺ influx and/or increase Na⁺ efflux to maintain homeostasis of intracellular Na⁺ concentrations [102]. Genes involved in the response to high salinity stress include the glycosyltransferase *Qua1*, which modulates Ca₂⁺ levels as part of the response to high salinity stress [103]. Overexpression of *AtZFP1*, a CCCH type zinc finger protein, promotes tolerance to high salinity by regulating expression of ion transport proteins [97, 104]. A subset of genes with ion-independent functions have also been shown to be critical for tolerance to high salinity [14, 22, 23, 105-112]. For example, *Arabidopsis* plants overexpressing glutathione S-transferase (*GST*) are more tolerant to high salinity stress [113].

Ionic compartmentalization into vacuoles, salt exclusion and excretion by vesicles are the underlying mechanism of high salinity tolerance. However, the intensively studied plant *Arabidopsis thaliana* is not a true halophyte without salt glands in its epidermis, as such the precise mechanism of high salinity tolerance in *Arabidopsis* to be largely elusive. *Limonium bicolor*, a typical exo-recretohalophyte, has been sequenced to identify the genes involved in salt secretion [114]. Several transcription factors, including MYB, bHLH, C2H2, and NAC, have been identified to be essential for high salinity tolerance, suggesting transcriptional regulation of salt resistant-related gene expression during high salinity stress. Genes encoding proteins that are involved in the modulation of Na⁺ efflux, K⁺ uptake, chloride transport, cation transport, and H⁺-ATPase have been identified, confirming that ion transport is important for salt secretion from salt glands [114]. In addition, four *ascorbate peroxidase* genes, fourteen *glutathione S-transferase (GST)* genes, and four *monodehydroascorbate reductase* genes were differentially expressed under high salinity exposure, indicating the importance of the reactive oxygen species (ROS) scavenging system in high salinity tolerance [114, 115].

In addition to high salinity, chilling stress is another major environmental factor that affects plant growth and development, leading to crop loss [16]. Chilling stress influences seed germination and damages seedlings and root systems by affecting the membrane phase transition,

water absorption, metabolism, and other physiological processes. Tolerance to chilling stress varies across plant species, and variations are associated with changes in epigenetic modifications affecting plant physiology, metabolism, and growth. Ectopic expression of genes that affect these activities can promote resistance to chilling stress [16, 20, 26-28, 109, 116, 117]. For example, glycine betaine enhances the tolerance of tomato to chilling stress by regulating expression of *codA* and synthesis of choline oxidase [118]. Overexpression of peanut acyl carrier protein in tobacco alters the membrane lipid synthesis pathway, promoting resistance to chilling stress [116]. Reactive oxygen species signaling has also been associated with responses to chilling [19, 48, 61, 108, 119, 120].

Drought stress is also a common environmental factor affecting plant survival. Drought stress leads to dehydration and reduction of cytosolic and vacuolar volume. Moreover, drought stress typically suppresses the photosynthesis rate and efficiency and can ultimately result in wilting and apoptotic cell death. Mounting evidence shows that stomatal closure plays an essential role in the plant response to drought stress, and genes that are involved in this process are crucial for drought stress resistance [18, 29, 30, 48, 103, 105, 121, 122]. Recent studies have implicated casein kinase 1-like protein 2 and stomatal closure-related actin binding protein 1 in hypersensitivity to drought stress and these proteins drive actin filament reorganization to regulate stomatal closure [121, 122]. *PhyB* regulates plant sensitivity to drought stress by suppressing expression of cell expansion-associated genes, including putative *erecta* family genes and *expansin* family genes [29]. A wide variety of drought-responsive genes have been identified in different species, including genes encoding stress-responsive proteins, auxin-responsive proteins, transcription factors, Na^+/H^+ transporters, and chloroplast photosynthetic oxygen-evolving protein subunits [18].

4 Crosstalk between biotic and abiotic stress responses

In addition to abiotic stress, plants are often simultaneously challenged by biotic stress, such as pathogen attack [123, 124]. Interestingly, a widely observed phenomenon seen in plants is resistance to multiple stress exposure, termed as cross-tolerance, and this phenomenon suggests that a powerful regulatory mechanism allows plants to adapt rapidly to a varying environment. Multiple lines of evidence reveal that hormones, transcription factors, kinase cascades, and ROS are the major regulatory factors controlling crosstalk between biotic and abiotic

stress responses [125, 126]. Abscisic acid (ABA), an endogenous phytohormone associated with abiotic stress responses to drought and low temperature, plays a negative role in pathogen resistance through down-regulation of the expression of key biotic stress-responsive genes, such as jasmonic acid (JA) and ethylene (ET) [125]. ROS, as toxic by-products of aerobic metabolism, must be tightly controlled; on the other hand, ROS behave as an important signaling modulator in a diversity of cellular events. Emerging evidence reveals that ROS produced by NADPH-dependent respiratory burst oxidase homolog genes (*AtrbohD* and *AtrbohF*) might connect ABA-related signaling pathways and pathogen-response signaling pathways [123, 125]. In addition, a number of transcription factors, such as the dehydration responsive element binding proteins (DREB), C-repeat binding factors (CBF), and cup-shaped cotyledon (CUC), induce the expression of a number of biotic and abiotic stress-responsive genes, leading to plant resistance to abiotic stress and pathogen infection [126].

5 Concluding Remarks and Future Perspectives

Biotic and abiotic stresses continue to represent a major threat to animal and agriculture husbandry. As a result of exposure to stressful conditions, animals and plants have evolved a wide range of defense mechanisms that promote survival in adverse environments. Increasing our understanding of the diverse mechanisms that promote resistance to biotic and abiotic stresses will provide valuable insight into selection and generation of desirable traits important for future innovations in animal husbandry and agriculture [127-134]. Simultaneous manipulation of multiple genes with precise specificity is required for effective crop breeding and animal husbandry, since abiotic stress usually involves multiple gene responses, which coordinately regulate metabolic pathways so that the organism can adapt to the stressful conditions [135]. Fortunately, with recent advances in genome-editing technology, such as discovery and optimization of the CRISPR/Cas9 system, combinatorial introduction of stress-response genes into animals and plants has become feasible, raising the possibility of the development of stress-resistant species [136, 137]. Advances in high-throughput sequencing technologies, functional genomics analyses, and integrated 'omics' analyses, especially integrated metabolomics [138], have additionally facilitated many ongoing studies characterizing the complex interactomes associated

with stress tolerance. Application of genome-editing technology to modify the expression of key proteins associated with challenge tolerance could accelerate the development of stress-resistant animals and crop plants, thereby benefiting the animal husbandry and agriculture industries.

Conflict of interest: Authors state no conflict of interest.

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