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Review

Some advances in plant stress physiology and their implications in the systems biology era

Hong-Bo Shao [a,b,c,*], Shui-Yuan Jiang [f], Feng-Mei Li [b], Li-Ye Chu [b], Chang-Xing Zhao [e,**], Ming-An Shao [a,d], Xi-Ning Zhao [g], Feng Li [f]

[a] *State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Centre of Soil and Water Conservation and Eco-environmental Research, The Chinese Academy of Sciences, Northwest A&F University, Yangling 712100, China*
[b] *Key Laboratory of Biological Sciences, College of Molecular and Chemical Engineering, Qingdao University of Science and Technology, Qingdao 266042, China*
[c] *Key Laboratory of Molecular Biology, Bio-informatics College, Chongqing University of Posts & Telecommunications, Chongqing 400065, China*
[d] *Institute of Geographical Sciences and Resources, The Chinese Academy of Sciences, Beijing 100101, China*
[e] *College of Plant Science and Technology, Laiyang Agricultural University, Qingdao 266199, China*
[f] *Guangxi Institute of Botany, Guangxizhuangzu Autonomous Region, The Chinese Academy of Sciences, Guilin 541006, China*
[g] *Center of National Water-saving and Irrigation at Yangling, Centre of Soil and Water Conservation and Eco-environmental Research, The Chinese Academy of Sciences, Northwest A&F University , Yangling 712100, China*

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Abstract

The study for biointerfaces at different scales in the past years has pricked up the march of biological sciences, in which biomembrane concept and its characteristics, receptor proteins, ion channel proteins, LEA proteins, calcium and newly recognized second messengers, ROS, MAPKs and their related sensors and new genes in osmoregulation, signal transduction, and other aspects have been understood fully, widening area of understanding the extensive interactions from biosystem and biointerfaces. The related discipline, plant stress physiology, especially, crop stress physiology has gained much attention world widely, the important reason of which is from the reducing quality of global ecoenvironment and decreasing food supply. This short review will place a stress on the recent progresses in plant stress physiology, combined with the new results from our State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau.

Keywords: Crop; Stress physiology; Biointerfaces; Signal transduction; Combination of stresses; Transgenic plants

Contents

1. Introduction

Our modern world is at the stage of concerning about the health of humankind itself and quality of its survival ecoenvironment on the basis of satisfied food supply [3,8,12,26], owing to which the concept of sustainable development was put forward, and many big projects emerged, including Human Genome Project, FACE Project, *Arabidopsis* Genome Plan, Rice

Abbreviations: LEA, late-embryogenesis abundant protein; MAPKs, mitogen-activated protein kinases; ROS, reactive oxygen species; ABA, abscisic acid; PA, phosphatidic acid; POD, peroxidase; CAT, catalase; SOD, superoxide dismutase; MDA, malondialdehyde

* Corresponding author. Tel.: +86 23 62477654.
** Corresponding author.
E-mail addresses: shaohongbochu@126.com, shaohongbochu@hotmail.com (H.-B. Shao), changxingzhao@hotmail.com (C.-X. Zhao).

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Genome Project, Western Development of China, related Space Projects and others [8,9,27–33,45–48]. These projects stimulate development of biological sciences in extensive aspects, including molecular biology and plant stress physiology [34–44]. Plants realize their productivity beneficial for humankind by the different ways of metabolism and physiology, which are controlled spatio-temperally by the corresponding genes in field environment [8,12,19,26,55,58]. So, the final essence of molecular biology is to make its progress serve for humankind benefits timely and efficiently [23–33,55]. From this context, plant stress physiology is increasing its importance and gaining its attention on the globe under global climate change [1–12,19–33]. Some major advances in plant stress physiology and their extensive implications in the systems biology era will be focused below.

2. Osmotic signaling mediated by second messengers and kinases families in plants

One of the most important abiotic stresses for crop yields concerns about plant dehydration [8,12,23]. Plants suffer from dehydration under the condition of drought, high salinity, and low-temperatures, all of which cause hyper-osmotic stress characterized by a decreased turgor pressure and water loss [9–11,20,28–31,36–39,42–44,49–55,58]. Dehydration triggers the biosynthesis of the ABA hormone and it has been known for a long time that a set of genes, induced by drought, salt, and cold stresses, are also activated by ABA [20,21,23,31]. The application of common components and pathways in plant responses to related stresses allows plants (crops) to acclimate partially to a wide range of adverse conditions after exposure to only one specific stress [23]. In addition to these common signaling elements, highly specific signaling mechanisms occur and newly recognized related genes can also act in the process, allowing precise plant adaptation [13–18,56]. For instance, several genes induced by salt, drought, UV-B radiation, and cold stress are not responsive to exogenous ABA treatment, indicating the existence of ABA-independent signal transduction cascades besides the ABA-mediated pathways [23].

Signal perception at the plasma membrane leads to the production of second messengers that initiate cascades of signaling events. Among them, calcium has been extensively studied [42–44,51,52]. It was shown that osmotic stresses induced calcium fluxes characterized by diverse kinetics and magnitudes, causing calcium signatures specific to a particular stress and cell type [1,23,29,33,51,52]. The calcium signal results from extracellular calcium influx and/or calcium release from intracellular pools [51,52]. It has been shown that hyperosmotic stresses induce an increase in inositol 1,4,5-trisphosphate (IP3), which is blocked by phospholipase C inhibitors [51,52]. IP3 is well known to activate vacuolar calcium channels and it was proposed that calcium is released from intracellular pools in response to hyperosmotic stresses as a result of the activation of the IP3 dependent calcium channels [1,8,20,22,23,52].

Other phospholipids, especially phosphatidic acid (PA), seem to have significant roles in osmotic signaling [23,52]. PA was reported to accumulate in response to cold treatment and water deficit [51]. It can be formed directly by phospholipase D or indirectly by phospholipase C after phosphorylation of diacylglycerol [23,42]. It is worth noting that these pathways are involved in PA production in response to osmotic stresses, allowing a refine regulation in PA concentration [22,42–44]. Besides, the stress-activated alfalfa MAPK, was shown to be activated by PA in a dose-dependent manner [8,22,23,42]. A recent study using PA affinity chromatography identified several transduction proteins such as kinases, phophatases, and 14-3-3 proteins as potential PA targets [22,23]. All these information strongly support the viewpoint that PA plays an important role in osmotic transduction pathways [8,51,52,57,58].

It is well known that osmotic stresses induce oxidative damage, which can be reduced by the activation of antioxidant enzymes and the biosynthesis of osmolytes acting as ROS scavengers [3–9,22–26,36–39,42–45]. However, many recent reports suggest that ROS could also play a signaling role, as in response to biotic stresses in which ROS production is partly duo to a plasma membrane NADPH oxidase [36,37]. Although, major ROS production induced by hyperosmotic stresses happens at intracellular sites, it was also shown that a cell wall diamine oxidase and a plasma membrane NADPH oxidase were activated by hyperosmolarity and drought, respectively [36,37,42,50]. Interestingly, the hyperosmotic induction of the catalase gene *CAT*1 was shown to be mediated by H_2O_2 [23]. Moreover, H_2O_2 is able to activate the osmotic-responsive MAPK in *Arabidopsis* cell suspensions [8,25,43]. Future work is needed to understand the extensive roles of second messengers and cross-talk of ROS, H_2O_2, PA and MAPKs in the process of osmotic signaling [23,33,43].

3. Plant stress physiology is a powerful tool for improving crop anti-stress tolerance

A series of work in relation to plant stress biology and molecular biology by our State Key Laboratory has contributed to current plant stress physiology and molecular biology on the globe greatly. Some work related to plant stress physiology has provided important implications for stress biotechnology, dryland farming and water-saving of the world. In addition, the most influencing work from our laboratory is the exploration of wheat stress physiology from the angle of dynamic development and evolution in terms of ROS, biomembrane per-oxidation, osmotic regulation, dynamic photosynthetic physiology, water use physiology [1–11,26,33].

First, our group applied barley matured embryo in vitro system to investigate the widely used osmotic regulator, PEG-6000's effect on hormone content (ABA, GAs, IAA) in barley seeds, embryos, endosperm and regenerated plants [1]. We showed that different ions (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, Fe^{2+}, Zn^{2+}) in culture media had different influence upon plant growth and development. This conclusion is of great help to understanding substance exchange between soil and plant root system, in particular nutrients at soil water deficits. The different ions in soil have obvious effect on physiological functions of upper plant parts.

Second, LEA (late embryogenesis abundant) protein is one type of important proteins mainly involved in plant drought resis-