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Role of calmodulin in thermotolerance

Lixiu Jia[1], Hongye Chu[1], Dan Wu[1], Mei Feng[2], and Liqun Zhao[1,*]

[1]School of Life Sciences; Hebei Normal University; Shijiazhuang, PR China; [2]Hebei Chemical and Pharmaceutical College; Shijiazhuang, PR China

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Nitric oxide (NO) and hydrogen peroxide (H_2O_2) are 2 key elements in heat shock (HS) signaling pathway. Our experiments indicate the existence of a cross talk among H_2O_2, NO, Ca^{2+} channels, and the activation of calmodulin (CaM) to stimulate the DNA-binding activity of HS transcription factors as well as the accumulation of HS proteins so as to confer thermotolerance. CaM can bind to target proteins to alter their function, acting as part of a calcium signal transduction pathway. However, only a few of its target proteins had been reported by now. Herein we are discussing them and conclude that in order to obtain a more profound understanding of CaM signaling, further research will be needed in the future.

CaM, a ubiquitous intracellular calcium sensor, plays an important role in plant responses to various biotic and abiotic stresses, by modulating the activity of a variety of downstream target proteins. It has been also considered as the key signaling connection in thermotolerance; however, its signal pathway is little known by now.[1] Therefore, many unknown target proteins need our detailed and continuous work to find to enrich our knowledge about heat resistance. According to our analyses, 4 types of protein might be used as candidates in the research.

Transcription Factors (TFs)

TFs can bind to specific DNA sequences of other proteins to control related genes to turn on or off in the genome. According to the structure of their DNA-binding domain, they have been divided into several families. Among them, bZIP, WRKY, AP2/ERF, and MYB ones were reported to be involved in plant responses to biotic and abiotic stresses. According to high-density *Arabidopsis* protein microarrays a large number of TFs were believed to interact with CaM,[2] though the binding of CaM to nuclear factors has been shown to affect their DNA-binding characteristics.[3] Consistent with these findings, the direct interaction of a divergent CaM isoform and the transcription factor, MYB2, enhances salt tolerance in *Arabidopsis*.[4] So, we infer that there should be direct or indirect interaction between CaM and some TFs in the heat signal pathway.

Protein Kinases

Protein kinases can phosphorylate other proteins by chemically adding the phosphate group from ATP. This modification will rapidly change the function of their target proteins, and, thus, mediate the signal transduction. So far, many protein kinases have been reported to play important roles in various biotic and abiotic stress responses. For example, mitogen-activated protein kinases (MAPKs), calcium-dependent protein kinases (CDPKs), and receptor-like kinases (RLKs) were reported to be involved in drought, high salinity, and low temperature signaling. Some of them containing CaM-binding sequence also reply to high temperature stimulation, whereas only 2 CaM-binding protein phosphatases, CBK3 and PP7, were reported as the CaM downstream components of the HS signaling transduction.[5,6] So it is reasonable to consider that more ones are activated and interact to induce thermotolerance according to their binding to CaM.

Cyclic Nucleotide-Gated Ion Channel (CNGCs)

CNGCs are nonselective cation channels in plasma membrane that function in response to the binding of cyclic nucleotides. They have been found to play important roles in signal transduction. In *Arabidopsis*, CNGC gene family has 20 members, which have both distinct and collaborative biological activities in different defense responses. Ca^{2+} entry has been shown to be essential to the specific heat activation of original signaling element. Several CNGCs were believed to control land plant thermal sensing and acquired thermotolerance through mediating Ca^{2+} influx. Indeed, 3 heat-activated Ca^{2+}-permeable channels, CNGC2, CNGC6, and CNGC16, were recently found to be involved in HS responses.[7-9] What's more, the CNGC proteins contain a CaM-binding site and can interact with CaM,[10] thus, their relationship in heat shock pathway is one ongoing subject in our group.

Cytoskeleton

The cytoskeleton, an indispensable component of the cell structure, is made up of proteins which assemble themselves into actin filaments, intermediate filaments, and microtubules. Their important functions are to help the cell with support, shape, and movement. Though there is little report about the involvement of the cytoskeleton in abiotic stress,[11] but it's well-known that the change of stomatal conductance is a very important measure for plants to adapt abiotic stress, and the stomatal movement depends on the cytoskeleton. Recently, cytoskeleton was reported to response to high temperature according to cell reconstruction.[12] Also, it many components contain the CaM-binding domain. So we deduce that the interaction between CaM and cytoskeleton might be a potential key subject for plant adaptation to heat stress.

Apart from upon these proteins, there are still some important issues awaiting further studies such as metabolic

*Correspondence to: Liqun Zhao; Email: zhaolq70@163.com
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enzymes, regulatory factors, etc. We expect the emergence of some novel findings at this aspect in the future.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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