



Global insights of protein responses to cold stress in plants: Signaling, defence, and degradation

Seyyede-Sanam Kazemi-Shahandashti, Reza Maali-Amiri*

Department of Agronomy and Plant Breeding, University College of Agriculture and Natural Resources, University of Tehran, 31587-77871, Karaj, Iran



ARTICLE INFO

Keywords:

Cold stress
Defense
Degrading
Gene expression reprogramming
Proteins
Signaling
Tolerance

ABSTRACT

Cold stress (CS) as one of the unfavorable abiotic tensions proceeds different aspects of plant responses. These responses are generated through CS effects on crucial processes such as photosynthesis, energy metabolism, ROS homeostasis, membrane fluidity and cell wall architecture. As a tolerance response, plants apply proteins in various strategies such as transferring the message of cold entrance named as signaling, producing defensive and protective molecules against the stress and degrading some unfavorable or unnecessary proteins to produce other required ones. A change in one part of these networks can irritate alternations in others. These strategies as acclimation mechanisms are conducted through gene expression reprogramming to provide a new adjusted metabolic homeostasis dependent on the stress severity and duration and plant species. Investigating protein alterations in metabolic pathways and their role in adjusting cellular components from upstream to downstream levels can provide a profound knowledge of plants tolerance mechanism against the damaging effects of CS. In this review, we summarized the activity of some cold-responsive proteins from the perception phase to tolerance response against CS.

1. Introduction

Plants on earth are constantly threatened by diverse abiotic stresses including drought, waterlogging, extremes of temperatures, salinity, mineral deficiency, and toxicity through restricting their cultivation, growth, productivity, survival and also geographical distribution. Cold stress (CS), defined as chilling (0–20 °C) and freezing (< 0 °C), imposes destructive impacts on plants life in different situations like cold climates at high latitudes or altitudes, fluctuations in global temperatures, cold snaps that occur on average every three to four years and, finally, the undeniable role of global climate change. In spite of the expected temperature increase followed by climate change, the arbitrary weather patterns will create detrimental spring frosts demonstrating the influential role of cold tolerance (CT) in plants. It is also revealed that plant responses to CS can be influenced negatively by high atmospheric CO₂ concentrations so that plants susceptibility to frost damage may be boosted in these inappropriate conditions (Gu et al., 2008). In addition, according to the climate change effects, more periods of frequently

flooding are predicted in the Northern Hemisphere, indicating the importance of CT in parallel with flooding that can enforce plants to tolerate freezing (Jurczyk et al., 2016a). So future changes in climate may cause incredible challenges for agriculture worldwide; for instance, the unprecedented damages of many economically important crops that will eventually obligate negative effects on commercial crops industry.

In many world regions, the precipitation index shows lower amount of rainfall while cold injuries which are induced by daily temperature fluctuations, increased exceedingly, indicating the climate change impact on plants. The inevitable policy of providing the increasing nutritional demands through plant protein sources is completely obvious that can persuade researchers to focus more and more on new strategies in plants against CS.

CS may cause burden in a plant through series of processes as the damaging line, consisting of micro-organelle disruption, dehydration of cells and tissues, phase transition in cell membrane lipids, reactive oxygen species (ROS) production and its concomitant oxidizing potential, including degradation of essential macromolecules such as

Abbreviations: ABA, Abscissic acid; AFPs, Antifreeze proteins; AGPs, Arabinogalactan proteins; ATG, Autophagy; CDPKs, Ca²⁺-dependent protein kinases; CIPKs, CBL-interacting protein kinases; CAX, Ca²⁺/H⁺ exchangers; ICE1, Inducer of CBF expression 1; CBFs, C-repeat binding factors; CBL, Calcineurin B-like proteins; CaM, Calmodulin; CMLs, CaM-like proteins; CA, Cold acclimation; COR, cold-regulated; CSD, Cold shock domain; CS, Cold stress; CT, Cold tolerance; ER, Endoplasmic reticulum; ETC, Electron transfer chain; ET, Ethylene; GPI-APs, GPI-anchored proteins; HSPs, Heat shock proteins; HKs, Histidine kinases; JA, Jasmonic acid; NO, Nitric oxide; MAPK, Mitogen-activated protein kinase; NR, nitrate reductase; OST1, Open stomata1; HOS1, Osmotically responsive gene; PEPC, Phosphoenolpyruvate carboxylase; PA, Phosphatidic acid; PLD, Phospholipase D; ROS, Reactive oxygen species; RLKs, Receptor-like kinases; RCA, Rubisco activase; Ub, Ubiquitin; WAKs, wall-associated kinases

* Corresponding author.

E-mail address: rmamiri@ut.ac.ir (R. Maali-Amiri).

<https://doi.org/10.1016/j.jplph.2018.03.022>

Received 29 March 2018; Accepted 30 March 2018

Available online 04 May 2018

0176-1617/ © 2018 Elsevier GmbH. All rights reserved.

polysaccharides, lipids, photosynthetic pigments, denaturation of enzymes, nucleic acids and the disturbed operation of electron transfer chain (ETC) (Kazemi-Shahandashti et al., 2013; Heidarvand and Maali, 2013). Besides the products that appear in cells as a result of the interrupted homeostasis, cellular signal transduction molecules are produced as the initial alarm line of cells reactions opposed to CS and involved in mediating the acclimation response. Another line of cell responses against CS that can be categorized as the defense mechanism is the adjustment of plant metabolic pathways; a phenomenon known as cold acclimation (CA). This process is created by exposing plants to low but non-freezing temperatures before CS (Kazemi-Shahandashti et al., 2014). As a multigenic, quantitative trait in temperate species, CA induces processes such as cellular osmotic stabilization, cell compartmentalisation, changing lipid and fatty acids membrane compositions, increasing antioxidative activities, energy metabolism and the activation of primary and secondary metabolites. These responses are due to the expression reprogramming of stress-related genes, resulting in a new adjusted metabolic homeostasis which may inhibit growth-related genes and eventually protect cellular phenotype regarding growth rate and stress tolerance (Amini et al., 2017). The exact CA temperatures and its related molecular alterations in cells are species-dependent. The up- or down-regulation of different genes during CS have been identified in many studies but there is always a divergence between transcripts and proteins followed by some post-transcriptional and post-translational modifications. So in contrast with transcripts, proteins are more impressive products in response to CS.

Along with notable fixed indices like chlorophyll fluorescence for detecting stress tolerance degree in plants, researchers assay damage indices as both a sign for the amount of damage and a signal for the cells in order to induce acclimation responses. As the most effective macromolecules and by changing their concentration, type and activity, proteins play a unique role in cellular responses since they are present in almost all cellular processes, including plant growth, development, defense and the synthesis/degradation/inhibition of all other macromolecules even themselves. In spite of these functional similarities, proteins show diverse activities in species, genotypes and organelles as well as in critical phases such as growth and development, dependent on the stress severity and duration; the issue that confirms the complexity of their acclimation responses. In order to understand these changes, there are various comparative protein analyses of commonly divided into two groups of comparison; first between stressed and non-stressed (control) plants and second between two plant species/genotypes to measure their tolerance (Kazemi-Shahandashti et al., 2013).

Being detected and analyzed through proteins approach, cold-responsive proteins may be categorized and described in three groups: signaling molecules and regulatory proteins, degrading proteins and, finally, defensive and protective proteins that are explained in this review paper.

2. Cold signaling molecules and regulatory proteins

One of the major fundamental biological questions is about the processes through that plants sense stress signals. Recent studies have illustrated some crucial signal pathways that may be connected to plant defense response against abiotic stresses like CS. Because of the multiplicity, continuity and complicated nature of connections among cellular components, identifying particular sensors as the stress signal remain poorly understood (Murata and Los, 1997; Suzuki et al., 2000). Cell membranes as the entrance section of the cells are the first stress affected line, change their fluidity, permeability, stretching and interactions with cell wall. So, perceiving CS by signaling receptors usually means change on plasma membrane surface irritating various pathways in diverse organelles like endoplasmic reticulum (ER), chloroplast, mitochondrion, peroxisome, and etc. So the beginning section is devoted to signals in membranes.

2.1. Ca^{2+} related signaling molecules and thermosensors

CS signals initially cause plasma membrane rigidification, then induce a reorganization of the cytoskeleton that is finally continuing by the alterations in cytosolic Ca^{2+} concentration. Almost all kinds of abiotic stresses can elevate the cytosolic Ca^{2+} concentration in plants. This increase in Ca^{2+} is moderated by membrane rigidification-activated mechano-sensitive or ligand-activated Ca^{2+} channels that can stimulate the mitogen-activated protein kinase (MAPK) signaling pathway leading to the phosphorylation of transcriptional regulators (Conde et al., 2011). This signal transduction can also be accomplished through phospholipids. Moreover, new evidence identified different channels carrying Ca^{2+} across membranes to some of the influx pathways in plants, including the annexins, glutamate-like receptors, and cyclic nucleotide-gated channels. According to the experiments operated by researchers, ROS set Ca^{2+} channels in motion to regulate other ion channels in the plasma membrane that are influenced by abscisic acid (ABA)-induced stomatal movements. CS signal transduction through Ca^{2+} channels eventually affects the expression of cold-responsive genes and CT response. The relationship among Ca^{2+} , ABA, ROS and MAPK are explained in details in 2.7 Section.

Besides Ca^{2+} channels, there are two major types of Ca^{2+} efflux systems, Ca^{2+} -ATPase pumps and Ca^{2+} / H^{+} exchangers (CAX); both of them work at the plasma membrane and endomembranes. Assaying the activity of Ca^{2+} efflux systems in almost all reported experimental evidences demonstrated the cytosolic Ca^{2+} signatures in response to environmental stimuli. Different researches showed that Ca^{2+} -ATPases are transcriptionally regulated by CS, possessing an important role in CT through the adjustment of Ca^{2+} concentration. Up to now, six CAX genes (*AtCAX1* to *AtCAX6*) have been identified in *Arabidopsis thaliana*; amongst, *CAX1* can play a role in acclimation but other reports claimed that the negative impact of *CAX1* on CT is created as a result of down-regulation of *DREB1* and cold-responsive genes (Shigaki et al., 2006). In addition, the results of different experiments indicated that the interaction between ABA and cold signal transduction in tobacco are affected by GhCAX3 (Xu et al., 2013), indicating CAX species-dependent role.

The increased cytosolic Ca^{2+} concentrations are decoded by Ca^{2+} sensor proteins, including calmodulin (CaM), CaM-like proteins (CMLs), Ca^{2+} -dependent protein kinases (CDPKs), calcineurin B-like proteins (CBL), CBL-interacting protein kinases (CIPKs) that regulate particular responses against stresses through applying precise characteristics in Ca^{2+} -binding affinity, expression patterns, subcellular localization, and interaction partners (Cho et al., 2016). All of the Ca^{2+} sensor protein families are unique to plants except CaM that is the most notable conserved sensor protein in all eukaryotes.

CaM is a well-characterized Ca^{2+} sensor and there is an extended family of CaM isoforms and CMLs in addition to its evolutionarily conserved form. Unlike the cytosolic location of the typical isoform of CaM, several reports of its presence in the nucleus, peroxisome and extracellular matrix have been recorded. CaM and CMLs family members are subjected to different changes in targeting various proteins like kinase, channel proteins, metabolic enzymes and transcription factors (Oh et al., 2012). While the role of CaM and CMLs in plant acclimation to abiotic stresses is characterized in different surveys, genetic studies argued both positive and negative effects of CaM-regulated pathways on stress responses. The overexpression of CaM in *A. thaliana* decreases the cold-responsive gene expression, demonstrating its negative regulation during CS. However, there are many examples of the crucial role of CaM-binding protein kinase and phosphatase in the regulation of gene expression; for instance, the enhanced tolerance to CS by Ca^{2+} /CaM-regulated receptor-like kinase in *A. thaliana* (Virdi et al., 2015).

CDPKs are exclusive among Ca^{2+} sensors because they carry a kinase domain and function as Ca^{2+} responders since they link Ca^{2+} signal to downstream responses. CDPKs express specifically in response to developmental stages and environmental stresses like CS. The

Download English Version:

<https://daneshyari.com/en/article/8386775>

Download Persian Version:

<https://daneshyari.com/article/8386775>

[Daneshyari.com](https://daneshyari.com)