



Review

Post-translational regulation of cold acclimation response

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ABSTRACT

Cold acclimation is an adaptive response whereby plants from temperate regions increase their capacity to tolerate freezing in response to low-nonfreezing temperatures. Numerous studies have unveiled the large transcriptome re-programming that takes place during cold acclimation in diverse species, and a number of proteins have been identified as important regulators of this adaptive response. Post-translational mechanisms regulating the function of proteins involved in cold acclimation have been, however, much less studied. Several components of the signal transduction pathways mediating cold response have been described to be post-translationally modified. These post-translational modifications, including protein phosphorylation and dephosphorylation, ubiquitination, SUMOylation, N-glycosylation and lipid modification, determine key aspects of protein function such as sub-cellular localization, stability, activity or ability to interact with other proteins. Integrating these post-translational mechanisms within the appropriate spatio-temporal context of cold acclimation is essential to develop new crops with improved cold tolerance. Here, we review available evidence regarding the post-translational regulation of cold acclimation, discuss its relevance for the accurate development of this response, and highlight significant missing data.

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1. Introduction

Post-translational modifications are a common strategy to regulate protein function. More than 200 types of modifications determine critical facets of protein function, including turnover, subcellular localization, activity, or interaction with other proteins [1,2]. The importance of post-translational regulation in plants is suggested by the observation that 10% of the Arabidopsis genome is dedicated to protein phosphorylation and ubiquitination, two of

the most frequent post-translational modifications [3,4]. Furthermore, the protein kinase superfamily has been demonstrated to be larger in plants than in other eukaryotes [3], indicating the relevance of protein post-translational modifications in plants. The higher number of protein kinases in plants may be related to the need of plants to adapt to ever-changing environmental conditions [5].

Low temperature is one of the most important environmental challenges that plants face during their life cycle. Plants from temperate climates increase their freezing tolerance after a brief exposure to low non-freezing temperatures, an adaptive response termed cold acclimation [6,7]. During the last 20 years, significant progress has been made in understanding the molecular

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mechanisms leading to cold acclimation [8,9]. Low temperature is signaled by a swift rise in cytosolic free Ca^{2+} that is subsequently transduced by phosphorylation and transcriptional cascades resulting in a large re-programming of the plant transcriptome. As a consequence, an array of cellular adjustments takes place protecting the photosynthetic machinery, cellular membranes and other cellular structures from cold-induced reactive oxygen species and dehydration [10,11]. A number of proteins have been established as important regulators or effectors of cold acclimation [8]. Thus, an interesting picture is emerging in which cold acclimation is a very complex response that is tightly regulated at all levels, *i.e.* transcriptionally, post-transcriptionally, translationally and post-translationally [12]. Our current knowledge of these regulatory levels, however, is not uniform. Many papers have addressed the regulation of cold acclimation at transcriptional and post-transcriptional levels but data concerning the translational and post-translational regulation of this response are quite scarce. Here, we review and discuss results that have been reported on the post-translational mechanisms implicated in regulating freezing tolerance and cold acclimation, and highlight the relevance of post-translational modifications in plant response to low temperature. Most data discussed have been obtained from the model plant *Arabidopsis thaliana* and, in some cases, are difficult to extrapolate to other species such as cereals. We will not consider the post-translational regulation of histones, since this subject has been recently reviewed in the context of the epigenetic control of the cold acclimation response [13,14].

2. Post-translational modifications regulating freezing tolerance and cold acclimation

2.1. Phosphorylation

Phosphorylation mediated by kinases is one of the most ordinary mechanisms by which environmental cues are transduced and protein function is regulated in eukaryotic cells. Approximately, 1–2% of eukaryotic genes encode protein kinases [3], which indicates the significance of phosphorylation when considering the different types of post-translational modifications. Phosphorylation is largely a reversible protein modification, with the level of phosphorylation of a particular substrate depending on the balance of specific kinase and phosphatase activities. Protein phosphorylation may affect several aspects of protein function such as catalytic activity, subcellular localization, stability and/or interaction with other proteins [15].

The disruption of phosphorylation has a significant effect on the ability of plants to acclimate to low temperature [16]. Several protein kinases belonging to diverse families, including mitogen activated protein kinases (MAPKs), Ca^{2+} -dependent protein kinases (CDPKs), calcineurin-B-Like interacting protein kinases (CIPKs), and receptor-like kinases (RLKs) are involved in regulating cold acclimation. Signaling pathways mediated by MAPKs have long been recognized as key molecular switches for transduction of environmental and developmental signals. The mechanistic paradigm of a typical MAPK pathway is that plasma-membrane receptors activate MAP kinase kinase kinases (MAP3Ks) that, in turn, elicit a phosphorylation cascade involving other downstream MAPKs culminating in the phosphorylation of effector proteins, which usually are either enzymes or transcription factors [17]. MAPKs have been implicated in plant responses to abiotic stresses including low temperature. For instance, the over-expression of a constitutively active form of OsMPKK6 in rice increases chilling tolerance [18]. MAPKs also have an important role in cold acclimation in freezing tolerant plants such as *Arabidopsis*. In this way, different lines of evidence

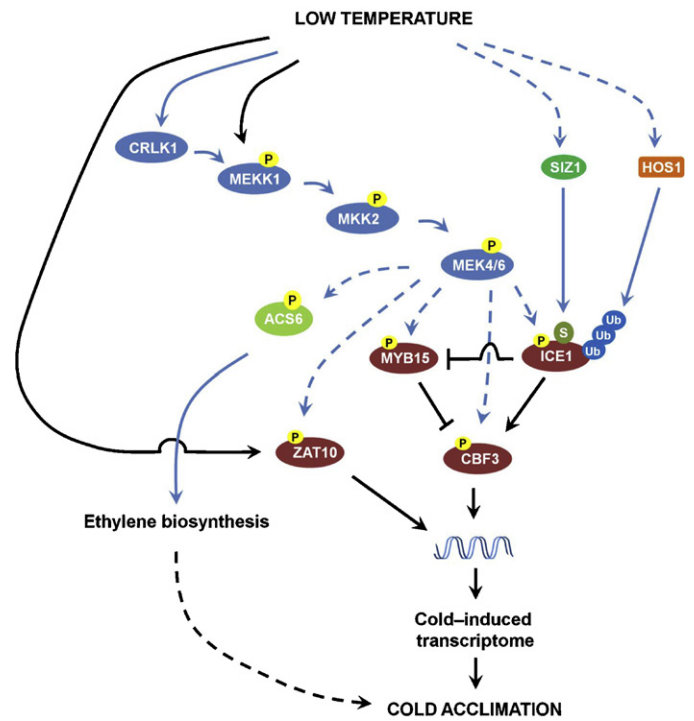


Fig. 1. Multiple post-translational mechanisms overlap with transcriptional regulation of gene expression to fine-tune the development of cold acclimation response. After low temperature perception, cold stress is signaled by kinase-mediated pathways resulting in the phosphorylation of an array of transcription factors that are central to the transcriptome re-programming leading to cold acclimation. Further post-translational modifications, including protein ubiquitination, SUMOylation, N-glycosylation and lipid modification, converge over these factors creating an intricate network of regulatory mechanisms. The modulation of ICE1 activity is a paradigmatic example of the complexity with which the function of transcription factors with important roles in cold acclimation may be post-translationally regulated. Low temperature elicits a MAPK pathway that culminates with the phosphorylation of ICE1. SUMOylation and ubiquitination also contribute to adjust ICE1 activity during the development of cold acclimation. In addition to transcription factors, other signaling components mediating this adaptive response are also regulated at the post-translational level. Thus, ACS6 is phosphorylated following MAPK activation, which results in ethylene biosynthesis that contributes to the hormonal regulation of cold acclimation. Solid lines represent established pathways while dashed lines represent theoretical pathways. Black arrows indicate transcriptional regulations and blue arrows represent post-translational regulations. Arrowheads denote positive regulation and endlines represent negative regulation.

link the *Arabidopsis* MAPK pathway mediated by MEKK1-MKK2-MPK4/6 to cold acclimation (Fig. 1). First, MEKK1 expression is induced by cold [19] and a N-terminal truncated MEKK1 can interact *in vitro* with MKK2 increasing its activity [20]. Second, *mkk2* mutants have enhanced sensitivity to freezing temperature in both non-acclimated and cold-acclimated plants whilst over-expression of constitutively active MKK2 increases freezing tolerance even without previous exposure to cold [20]. Finally, MKK2 activity is enhanced by low temperature upregulating MPK4 and MPK6 activity as well as the expression of several cold-regulated genes, which links MAPK signaling to the large transcriptome re-programming that leads to cold acclimation [20]. Nevertheless, the specific downstream proteins targeted by MPK4 and MPK6 in response to low temperature remain to be elucidated. High-throughput phosphoproteomic analysis [21] and yeast-two-hybrid screens [22] have allowed the identification of a collection of putative MPK4 and MPK6 targets that include key transcription factors in cold acclimation in *Arabidopsis* like ICE1, CBF1, CBF3 and MYB15 (Fig. 1). These proteins represent good candidate targets of MPK4 or MPK6 activity during cold acclimation development. Furthermore, a 1-aminocyclopropane 1-carboxylate synthase isoform that regulates

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