



Review

Low temperature tolerance in plants: Changes at the protein level

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ABSTRACT

Low temperature (LT) is one of several important environmental stresses influencing plant performance and distribution. Adaptation to LT is a highly dynamic stress-response phenomenon and involves complex cross-talk between different regulatory levels. Although plants differ in their sensitivity to LT, in temperate species low nonfreezing temperatures cause noticeable alterations in various biochemical and physiological processes that can potentially improve freezing tolerance. This adaptation is associated with changes in the expression pattern of genes and their protein products. Proteins are the major players in most cellular events and are directly involved in plant LT responses, thereby proteome analysis could help uncover additional novel proteins associated with LT tolerance. Proteomics is recommended as an appropriate strategy for complementing transcriptome level changes and characterizing translational and post-translational regulations. In this review, we considered alterations in the expression and accumulation of proteins in response to LT stress in the three major cereal crops produced worldwide (wheat, barley, and rice). LT stress down-regulates many photosynthesis-related proteins. On the contrary, pathways/protein sets that are up-regulated by LT include carbohydrate metabolism (ATP formation), ROS scavenging, redox adjustment, cell wall remodelling, cytoskeletal rearrangements, cryoprotection, defence/detoxification. These modifications are common adaptation reactions also observed in the plant model *Arabidopsis*, thus representing key potential biomarkers and critical intervention points for improving LT tolerance of crop plants in cold regions with short summers. We believe that an assessment of the proteome within a broad time frame and during the different phenological stages may disclose the molecular mechanisms related to the developmental regulation of LT tolerance and facilitate the progress of genetically engineered stress-resistant plant varieties.

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1. Introduction

Environmental stresses adversely affect growth and productivity and cause a series of morphological, physiological, biochemical and molecular modifications in plants (Larcher, 2003). Low temperatures (LT), defined as sub-zero to chilling temperatures, are common in nature and impose a major environmental restriction on plant performance, especially in cold climates at high latitudes or altitudes. LT may cause stress in a plant in a twofold manner: (i) by the effects of LT alone, and (ii) by dehydration of cells and tissues when cellular water freezes (Beck et al., 2004). LT tolerance¹ is a multigenic trait involving a large number of LT-inducible genes. These genes mainly encode three protein types: structural proteins, regulatory proteins (e.g. transcription factors, translation elongation factors and signal transduction proteins) and osmoprotectants (Breton et al., 2003) such as dehydrins and late-embryogenesis abundant (Lea) proteins. In studying LT stress, overriding emphasis is placed on the identification of LT-induced proteins and on the regulation of genes that encode these proteins. Plant response to LT stress is a dynamic process which is dependent on different factors, such as the developmental stage, the duration and severity of the stress, the rates of cooling (and rewarming), and whether ice formation takes place intracellularly or extracellularly in the intercellular spaces. During the onset of chilling stress several stages of plant response can be distinguished: an initial alarm phase, an acclimation phase, a maintenance phase, and an exhaustion phase if the stress endures too long (Larcher, 2003). Consistently, plant proteome reveals highly temporal dynamics during development (Kosová et al., 2011) and functional characterization of proteome remodelling during different growth stages can contain a great deal of useful information for breeders. There are significant differences between genotypes in response to LT and LT tolerance is determined by genotype-dependent expression levels of LT-responsive genes. LT-tolerant species have developed different efficient strategies to adapt to cold environments. Overwintering plants can increase their freezing tolerance when they experience low (but not freezing) temperatures, a process known as cold acclimation (Thomashow, 1999). However, even hardy plants are not freezing-tolerant during the all growth stages. Some hardy plants delay transition from vegetative growth to the reproductive stage until they have been exposed to a period of low but non-freezing temperatures, a process called vernalization that allows plants to over-winter as seedlings (Amasino, 2004). However, reduction/loss of freezing tolerance of winter plants often can be started by saturation of vernalization requirements at end of the vegetative phase (Limin and Fowler, 2006).

Acclimation to cold stress is mediated via intense changes in gene expression that translate into alterations in the composition of the transcriptome, proteome and metabolome (Thomashow, 1999; Chinnusamy et al., 2007). Previously, it has been proved that modifications in gene expression at the transcript level frequently do not match with alterations at the protein level (Bogeat-Triboulot et al., 2007). Furthermore, some of the LT-responsive proteins undergo post-translational modifications, including phosphorylation, N-glycosylation, ubiquitination, SUMOylation and lipid

modification (Barrero-Gil and Salinas, 2013); these changes determine key aspects of protein function such as sub-cellular localization, stability, activity or ability to interact with other proteins. Consequently, examining proteome alterations is crucial, since proteins, unlike transcripts, are direct effectors of the plant stress response. In recent years, major advances have been made into discovering the LT signalling and regulatory pathways underlying cold acclimation through proteomics approaches. This review summarizes recent findings achieved by proteomics in plant responses to both chilling and freezing stress. The three major cereal crops produced worldwide (wheat, barley and rice) are given priority treatment in order to help elucidate the main physiological processes that are affected by LT stress, thus impairing food productivity. In addition, we document the current state of knowledge in regards to *Arabidopsis* proteomics response to chilling stress. This model plant provides an exceptional opportunity for tracking and following-up post-genomic tools (such as proteomics) in its full capacity (Weckwerth et al., 2008). Finally, we focus attention on some important proteins that have been identified to be significantly up- or down-regulated during cold acclimation in crop plants.

2. Analysis of the wheat proteome under LT stress

Winter wheat is one of the most important crops in cold areas. In these regions frost injury during winter (winterkilling) and early spring can be particularly destructive. Wheat breeders have long recognized the need to introduce cultivars with greater winter hardiness, but they have had limited success in developing cultivars that exhibit improved tolerance to freezing. This can be due in part to the participation of very different genes in LT tolerance, as well as to the unpredictable nature of frost injury under field conditions where snow and sloped ground both create microclimates. Identification of mechanisms by which wheat copes with LT stress is crucial for breeding new frost-resistant cultivars and decreasing the risk of crop failure in cold areas.

In winter cereals the full expression of LT-tolerance genes only occurs in the vegetative stage. It appears that developmental genes act to control genes affecting the expression of LT-induced genes associated with the acquisition of frost tolerance. This has been proposed as developmental regulation of LT-responsive genes. In winter wheat vernalization requirement play a crucial role in development of LT tolerance by preventing premature transition to the reproductive phase before the ending of the freezing threat. Vernalization constraint in winter wheat is due to a recessive vernalization gene VRN1 of which expression is inhibited by a VRN2 gene product, while a spring growth habit possesses a dominant vernalization gene VRN1 and can initiate the reproductive phase after basic growth under optimal conditions (von Zitzewitz et al., 2005). However, besides experiencing LT, day length as well seems able to affect the transition from the vegetative to reproductive stage. The VRN1 gene is positively regulated by VRN3, which is up-regulated by long days. Overexpression of VRN3 in transgenic winter wheat plants was adequate to induce flowering even in the presence of recessive *vrn1* alleles and the absence of vernalization (Yan et al. 2006). It has been suggested that TaVRT-1 is a key developmental gene in the regulatory pathway that controls the transition from the vegetative to reproductive phase in wheat (Trevaskis, 2010). Although it has been identified that over 2% of

¹ Tolerance refers to the capacity to endure continued subjection to cold stress without adverse reaction. Resistance is a general term that refers to the ability of plants not to be adversely affected by low temperature. Avoidance is a coping mechanism characterized by the effort to avoid dealing with a stress.

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