biologia plantarum
an international journal for experimental botany

BIOLOGIA PLANTARUM (2022) 66: 240-254 DOI: 10.32615/bp.2022.030

REVIEW

Transcriptomic and proteomic mechanisms underlying cold tolerance in plants

K. JAMSHIDI GOHARRIZI[1,2,+,*], S. KARAMI[3,+,*], T. BASAKI[3], M. MOSTAFAEI DEHNAVI[4], M.A. NEJAT[3], M.M. MOMENI[2], and G. MERU[5]

[1] *Department of Plant Pathology, University of California, Davis, CA 95616, USA*
[2] *Department of Plant Breeding, Yazd Branch, Islamic Azad University, Yazd, 8915813135, Iran*
[3] *Department of Agriculture, Payame Noor University (PNU), Tehran 19395-4697, Iran*
[4] *Department of Plant Sciences, University of California, Davis, CA 95616, USA*
[5] *Horticultural Sciences Department and the Tropical Research and Education Center, University of Florida, Homestead, FL, 33031, USA*

[*] Corresponding author: E-mail: kjamshidigoharrizi@ucdavis.edu; soraya.karami@pnu.ac.ir

Abstract

Abiotic stress is one of the major challenges facing crop production globally. Abiotic stress resulting from low temperature is a major limitation to crop production, especially in the temperate regions of the world. Cold stress not only influence crop development and reduce yields, but also curtail the efficient distribution of agricultural products worldwide. An understanding of the molecular mechanisms underlying cold stress tolerance is important for the development of strategies to manage crop loss and improve yield. In this review, we explore the major molecular mechanisms involved in plant cold tolerance, including recent discoveries on interrelated gene networks and regulatory mechanisms for cold stress adaptation in crops. Further, we highlight the role of proteomics in the discovery of proteins involved in key signaling pathways, including late embryogenesis-abundant proteins, antifreeze proteins, cold-regulated proteins, heat shock proteins, and pathogenesis-related proteins. The role of these proteins, and their relative abundance in physiological-biochemical reactions, are discussed and key candidate proteins for plant genetic enhancement are suggested.

Keywords: molecular mechanisms; proteomics; physiological-biochemical reactions; plant cold stress, regulatory mechanisms.

Received 19 May 2022; *last revision* 30 June 2022; *accepted* 14 July 2022.

Abbreviations: ABA - abscisic acid; ABRE - ABA-responsive element; ABF - ABRE binding factor; AGC - ascorbate-glutathione cycle; AP2/ERF - APETALA2 and ethylene-responsive element-binding factor; AREB - ABA-responsive element binding protein; APX - ascorbate peroxidase; bHLH - basic-helix-loop-helix; bZIP - basic leucine zipper; CaM - calmodulin; CAMTA3 - calmodulin-binding transcription activator 3; CAT - catalase; CBF - C-repeat binding factor; CBF/DREB1 - C-repeat binding factor/dehydration-responsive element binding protein 1; CBL - calcineurin B-like proteins; AFGPs - antifreeze glycoproteins; AFPs - antifreeze proteins; CE1 - coupling element 1; CE3 - coupling element 3; CIPKs - cross-protein kinases; COR - cold-regulated; CRT - C-repeat; CSPs - cold shock proteins; CYP - cytochrome P450; Cys - conserved cysteine; DRE - dehydration-responsive element; DREB1 - dehydration-responsive element binding protein 1; DRIP1 - DREB2A-interacting protein 1; DRIP2 - DREB2A-interacting protein 2; ERD10 - early reaction to dehydration 10; GOLGA5 - golgin subfamily A member 5; GR - glutathione reductase; GSH - glutathione; GSSG - glutathione disulfide; HSPs - heat shock proteins; ICE - inducer of *CBF* expression; IRI - ice recrystallization; JA - jasmonate; LEA - late embryogenesis abundant; MaMYC2 - *Musa acuminata- Myelocytomatosis 2;* miRNAs - microRNAs; NADPH - nicotinamide adenine dinoclutiotide phosphate; NF-Y - nuclear factors-Y; ObTLP1 - *Ocimum basilicum* thaumatin-like protein; P5CR - pyrroline-5-carboxylate reductase; P5CS - Δ1-pyrroline-5-carboxylate synthetase; POD - peroxidase; PR - pathogen-related; RAD- Radialis; RDR - ribonucleoside-diphosphate reductase; RNAi - RNA interference; ROS - reactive oxygen species; siRNAs - small interfering RNAs; SOD - superoxide dismutase; TFs - transcriptional factors; TH - thermal hysteresis; VRN-1 - vernalization gene; ZNF - Zinc-finger.

Acknowledgements: The present study was supported by Grant No. 291/1/2132, thankful to Payame Noor University (PNU).

[+] These authors contributed equally.

Conflict of interest: The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Introduction

Drought, salinity, heat, and cold are major sources of abiotic stress that have a direct influence on the development and production of plants (Mboup *et al.* 2012, Hasanuzzaman *et al.* 2019, Jamshidi Goharrizi *et al.* 2020a,c,d, Chen *et al.* 2021). Cold stress, which is defined as chilling stress (< 20 °C) (Sales *et al.* 2017) or freezing stress (< 0 °C), is one of the most dangerous stressors that higher plants face (Theocharis *et al.* 2012, Zhou *et al.* 2017). Cold stress greatly limits the spatial distribution of plants and impacts plant growth (Mickelbart *et al.* 2015, Guo *et al.* 2017, Liu and Zhou 2018, Shi *et al.* 2018).

Plants native to temperate climates can survive freezing conditions after being subjected to non-freezing temperatures for a certain length of time, a phenomenon known as cold acclimation (Chinnusamy *et al.* 2007). During early spring and winter, plants that grow in temperate climates are more resistant to seasonal variations in temperature and can withstand cold stress. On the other hand, plants in the tropics and subtropics are not subject to regular cold conditions and lack the ability to acclimate. Plants that are susceptible to chilling and incapable of cold acclimation include many economically important agronomic and horticultural crops such as rice, maize, soybean, potato, cotton, and tomato (Ritonga and Chen 2020). Interestingly, some tropical species such as *Santalum album* have a wide temperature tolerance (4.5 to 38 °C) and can withstand chilling (Zhang *et al.* 2017a). Many plant species, including *Arabidopsis*, winter wheat, and barley lack the ability to acclimate under freezing temperatures (Zhao *et al.* 2015). Even for temperate species, such as the *Betula utilis*, that dominates cold environments; seasonal weather patterns resulting from monsoon winds can cause susceptibility to temperature regimes during the growing season (Pandey *et al.* 2018). The biochemical mechanisms of response and adaptation to cold stress can vary in the duration of exposure to low-temperature extremes. For example, in tea plants, early periods of cold stress are marked by elevated activity of biological processes, cellular components, and molecular functions. In contrast, the latter stages of cold stress are characterized by enhanced metabolism of amino acids (glutamate and aspartate), nucleotide sugars, as well as accelerated protein (*e.g.* alanine) export (Hao *et al.* 2018). In recent years, transcriptome profiling, proteomics, and studies of cold-resistant mutants have increased our knowledge regarding the genes, signaling pathways, and processes related to cold acclimation (Janda *et al.* 2014). Transcriptome studies in the model species *Arabidopsis thaliana* first identified multiple genes involved in response to cold stress (Nordin *et al.* 1991, Welin *et al.* 1995, Medina *et al.* 1999). Transcriptome approaches have been applied to study cold stress responses in *Juglans regia* and *Pinus koraiensis*, for the development of a gene co-expression network in maize, and also for researching wheat flowering and shade-avoidance pathways (Trapnell *et al.* 2010, Da Maia *et al.* 2017, Zhang *et al.* 2017b). Proteomics approaches have been employed to study the cold tolerance of many plants, including *Chorispora bungeana*, *Oryza sativa*, *Musa nana*, *Buchloe dactyloides*, and desert woody plants; desert shrub (*Ammopiptanthus mongolicus*) and desert poplar (*Populus euphratica*) (Yue *et al.* 2010, Kurdrid *et al.* 2011, Zhao *et al.* 2013, Wang *et al.* 2017). Collectively, these studies have revealed the complexity of the mechanisms involved in cold stress adaptation in plants (Tolosa and Zhang 2020).

In this review, we provide a detailed overview of the transcriptomic and proteomic profiles of plants under cold stress.

Transcriptomic profile under cold stress

Cold acclimation can be achieved by either up- or down-regulation of a specific set of genes (Hannah *et al.* 2005). In this phenomenon, multiple gene expression pathways and gene networks of cold-induced genes (regulons) are stimulated (Thomashow 2001). However, it should be noted that these gene networks also mediate response to other abiotic stresses (Thomashow 1999, Seki *et al.* 2003, Zhao and Zhu 2016, Jamshidi Goharrizi *et al.* 2020b,e, Nazari *et al.* 2019) through a common signal transduction pathway (Heidarvand and Amiri 2010).

The signaling pathway starts with low-temperature perception by cells (sensing), which activates signal transduction mechanisms (Denesik 2007). During the acclimation process in response to cold stress, free Ca^{2+} rapidly increases in the plant cell cytoplasm, thus likely plays an important role in signal initiation (Eckardt 2009). Indeed, transient cytosolic calcium ($[Ca^{2+}]$cyt) elevation is a ubiquitous denominator of the signaling network when plants are subjected to every known stress (abiotic and biotic) (Eckardt 2009). These stress-induced $[Ca^{2+}]$ cyt elevations differ in frequency, shape, and magnitude, depending on the severity of the stress as well as the type of stress experienced (Bose *et al.* 2011). Rapid calcium inflow is facilitated by physical alterations in the cell membrane resulting from modified lipid stoichiometry (Knight and Knight 2000). For example, cytosolic Ca^{2+} can accumulate in the cell within 5 - 10 s of exposure to cold stress (Miura and Furumoto 2013). Elevated cytosolic Ca^{2+} induces the C-repeat Binding Factor (CBF), an Apetela 2 domain-containing transcriptional factor that regulates many cold-induced genes (Gopal and Chanakya 2012). Furthermore, Ca^{2+} influx acts as a sensor for protein activation and accumulation during cold stress (Jenks and Wood 2009). In plants, three major categories of Ca^{2+}-dependent proteins have been identified (Jenks and Wood 2009): Ca^{2+}-dependent protein kinases, calmodulin (CaM), and calcineurin B-like proteins (CBL). Calmodulin is a Ca^{2+} cytosolic sensor, which is highly conserved among eukaryotes (Rudd and Franklin-Tong 2001). On the other hand, calmodulin genes regulate calcium fluxes. Calcium-bound calmodulin proteins interact with an element of the promoter of the *CBF2* gene, which controls the CBF regulon and freezing resistance (Doherty *et al.* 2009). Moreover, CAMTA3 (Calmodulin-binding transcription activator 3) (also called SR1) has a major function in the transformation of cytosolic Ca^{2+} signals caused by low temperatures into downstream gene expression regulation (Eckardt 2009). In addition to calmodulin, CBL proteins and their cross-protein kinases (CIPKs) can form functional sets that transmit downstream signals to membrane effectors helping in their adaptation to adverse environmental conditions (Shabala *et al.* 2021). In response to abiotic stress (*e.g.*, cold and salinity), Ca^{2+} is also involved in oxidative stress signaling and detoxification of reactive oxygen species (ROS) (Tyystjärvi 2013). Briefly, an oxidative burst (the transient, rapid generation and accumulation of ROS even at a low level) caused by abiotic stresses elevates the cytoplasmic influx of Ca^{2+} (Rao *et al.* 2006). Afterwards, NADPH (nicotinamide adenine dinucleotide phosphate) oxidase is activated by Ca^{2+} to generate ROS by yielding O^{-2}, which is then transformed to H_2O_2 by superoxide dismutase (SOD). Thus, ROS development is related to Ca^{2+} influx whose levels are mediated by the activation of Ca^{2+} channels in the plasma membrane by the content of ROS (Kwak *et al.* 2003). The function of various proteins regulating the expression of particular protection-related genes is modulated by an interaction of Ca^{2+} and ROS in the nucleus (Rao *et al.* 2006). Moreover, there is evidence that protein phosphorylation requires calcium in response to cold temperatures (Monroy *et al.* 1998). In fact, cold treatment greatly reduces the calcium-dependent activity of protein phosphatase, and on the other hand, low calcium is assumed to limit the phosphorylation potential of phosphatase 2A in response to cold stress (Monroy *et al.* 1998).

Other key genes, such as kinases, and transcription factors play an important role in activating signaling cascades for modulating responses to abiotic stresses including cold, salinity, and drought (Rao *et al.* 2006). For example, in the ascorbate-glutathione cycle (AGC), glutathione has a substantial function in the regulation of hydrogen peroxide content in plants (Kocsy *et al.* 2001). Deposition of H_2O_2 typically results from the reduction of oxygen to superoxide radical (O^{2-}) by extra electrons originating from the photosynthetic and respiratory electron transfer chains (Kocsy *et al.* 2001). The O^{2-} is then transformed to H_2O_2 by SOD. Therefore, the generation of the oxidized form of glutathione (GSH) from its reduced form (glutathione disulfide: GSSG), provides plants with an important mechanism for eliminating excess of H_2O_2. Generally, high content of GSH and NADPH-dependent glutathione reductase (GR) are found in cold-stressed (0 - 15 °C) plants and are a reliable indicator of response to cold stress (Kocsy *et al.* 2001). In addition, the GSH/GSSG ratio and alterations in the content of H_2O_2 have been reported to play a crucial function during cold acclimation by modulating the redox status of cells. The observation of many defensive genes having antioxidant-responsive regions or GSSG-binding elements in their regulatory zones has confirmed this hypothesis (Kocsy *et al.* 2001).

In both plants and animals, the role of micro-RNAs (*miRNAs*) and small interfering *RNAs* (*siRNAs*) in the suppression of gene expression has been proven (Ghildiyal and Zamore 2009). Using bioinformatics tools, numerous *miRNAs* in multiple plant species have been identified, cloned, and sequenced (Zhou *et al.* 2008, Zhang *et al.* 2009, Lv *et al.* 2010, Chen *et al.* 2012). However, little information is available regarding the *miRNA*-controlled target genes in cold stress conditions (Miura and Furumoto 2013). Table 1 summarizes the major cold stress-responsive genes.

CBF pathway for cold stress response

The C-repeat Binding Factor (CBF) transcriptional factors play an important function in cold stress adaptation. *CBF* regulatory genes have been reported across major agronomic and horticultural crops and natural herbaceous and woody plants (Sanghera *et al.* 2011, Mizoi *et al.* 2012). Extensive research in *Arabidopsis* has led to the discovery of a family of CBF/DREB1(C-repeat binding factor/dehydration-responsive element binding protein 1) transcription factors involved in cold acclimation (Gilmour *et al.* 1998). In the promoters of cold and dehydration-responsive genes, these transcription factors interact with specific regulatory regions. These sequences are C-repeats (CRT: TGGCCCGAC) and elements which are dehydration-responsive (DRE: TACCGACAT). They include a core 5-bp sequence (CCGAC), which is highly conserved and functions to regulate the transcription of genes involved in response to drought, salinity, and cold stress (Baker *et al.* 1994, Yamaguchi-Shinozaki and Shinozaki 1994, Gao *et al.* 2007). The expression of cold-responsive genes (*COR* genes) is thus induced by *CBF*, hence indicating its pivotal role in the cold tolerance of plants (Mizoi *et al.* 2012).

The function of the CBF/DREB1 pathway under cold stress was verified in soybean (Yamasaki and Randall 2016); however, evaluations have shown that the downstream genes in this pathway are inefficient in cold response. This inefficiency leads to the inability of soybean to significantly acclimate to freezing/cold stress, which could result from insufficient amounts of *GmCBF/DREB1* transcripts and/or proteins, as well as deficiency in relevant cofactors or the presence of negatively acting promoters (Yamasaki and Randall 2016). On the other hand, in *Arabidopsis*, three distinct cold-responsive *CBF/DREB1* genes have been reported and defined as: *CBF/DREB1B*, *CBF2/DREB1C*, and *CBF3/DREB1A* (Thomashow 2001). More recently, Monroe *et al.* (2016) analyzed *CBF* genes among 477 wild accessions of *Arabidopsis* and reported that variation in *CBF* sequences is closely correlated with winter temperatures. Gery *et al.* (2011) used RNA interference (RNAi) to target the expression of three *CBF* genes across eight accessions of *Arabidopsis thaliana* and reported that observed polymorphisms were correlated with freezing tolerance. In addition, a close co-regulation between *CBF1* and *CBF3* was observed in the study of the interaction between the different forms of *CBFs*, with the expression of *CBF2* and *CBF1* or *CBF3* being influenced by the genetic background in which the RNAi constructs were expressed (Gery *et al.* 2011). Although three strongly linked *CBF* genes have been identified in *Arabidopsis*, an expansion of this gene family has taken place in wheat and some other cereals (Pearce *et al.* 2013), so that in each of the three hexaploid wheat genomes, there are at least 15 *CBF* genes (Badawi *et al.* 2007). An over-expression study of *CBF/DREB1* in transgenic plants revealed that about 12 % of *COR* genes in *Arabidopsis* are regulated by *CBF/DREB1*. In contrast, no clear target was observed among the three *CBF* orthologs. In warm temperatures, the expression of these genes in transgenic plants triggers the expression of downstream *COR* genes, increasing the cold resistance of these plants (Liu *et al.* 1998, Kasuga *et al.* 1999).

In many plant species, the *CBF/DREB1* pathway has been identified and described, suggesting that *CBF* transcriptional pathway under cold stress in the plant kingdom is strongly conserved (Jaglo *et al.* 2001). The expression of *CBFs/DREBs* has been shown to be associated with temperature variations, suggesting the lower the temperature, the greater the expression of these genes. However, temperature-shift experiments have shown that the cold response becomes desensitized at a particular low-temperature point, thus requiring an interval of warm temperature to reset (Zarka *et al.* 2003). This phenomenon implies the presence of a low-temperature 'thermometer' and a high-temperature 'transducer' signal that controls the expressions of *CBFs* (Zarka *et al.* 2003). For instance, Gilmour *et al.* (1998) showed that a transcription factor, referred to as inducer of *CBF* expression (*ICE*), is expressed in warm temperatures, and that, *ICE* recognizes DNA-regulatory elements,

Table 1. A list of differentially expressed genes in response to cold stress.

Gene name	Family	Species	Reference
FtbHLH2	*bHLH*	*Fagopyrum tataricum*	(Yao *et al.* 2018)
BpUVR8	*UVR*	*Betula platyphylla*	(Zhao *et al.* 2016)
FAD2-3	*FAD2*	*Gossypium hirsutum*	(Kargiotidou *et al.* 2008)
FAD2-4	*FAD2*	*Gossypium hirsutum*	(Kargiotidou *et al.* 2008)
FAD8	*FAD*	*Arabidopsis thaliana*	(Matsuda *et al.* 2005)
Sb08g007310	*GST*	*Sorghum bicolor*	(Ortiz *et al.* 2017)
Sb06g018220	*ZEP*	*Sorghum bicolor*	(Hu *et al.* 2015)
AtGRXS17	*Trx*	*Arabidopsis thaliana*	(Hu *et al.* 2015)
AtCBF3	*AP2/ERF*	*Arabidopsis thaliana*	(Yao *et al.* 2018)
VaERF080	*AP2/ERF*	*Vitis amurensis*	(Yao *et al.* 2018)
VaERF087	*AP2/ERF*	*Vitis amurensis*	(Yao *et al.* 2018)
SiDHN	*DHN*	*Saussurea involucrata*	(Yao *et al.* 2018)
OsGH3-2	*GH3*	*Oryza sativa*	(Guo *et al.* 2017)
MYBS3	*MYB*	*Oryza sativa*	(Du *et al.* 2012)
RDM4	-	*Arabidopsis thaliana*	(Mickelbart *et al.* 2015)
OsMADS57	*MIKC*^{c}	*Oryza sativa*	(Chan *et al.* 2016)
GHDREB1	*DREB*	*Gossypium*	(Arora *et al.* 2007)
PUB25/26	*U-box E3 ligases*	*Arabidopsis thaliana*	(Wang *et al.* 2019b)
AtHAP5A	*HAPs (NF-Ys)*	*Arabidopsis thaliana*	(Cao *et al.* 2019)
AtXTH21	*GH16*	*Arabidopsis thaliana*	(Cao *et al.* 2019)
AtPIP2-7	*AQP*	*Arabidopsis thaliana*	(Xu *et al.* 2020)
MaPIP2-7	*AQP*	*Musa acuminata*	(Xu *et al.* 2020)
CsCPKs	*CPK*	*Camellia sinensis*	(Ding *et al.* 2019)
COR413	*COR*	*Camellia sinensis*	(Guo *et al.* 2019)
SET, JmjC	*HKMTases,HDMases*	*Saussurea involucrata, Brassica rapa*	(Liu *et al.* 2019a)
TaTPS11	*TPS*	*Triticum aestivum*	(Liu *et al.* 2019b)
TaSMT1, TaSMT2	*SMT*	*Triticum aestivum*	(Valitova *et al.* 2019)
RCI1A, RCI1B	*14-3-3 proteins*	*Arabidopsis thaliana*	(Visconti *et al.* 2019)
MdMYB108L	*MYB*	*Malus domestica*	(Wang *et al.* 2019c)
MdHY5	*bZIP*	*Malus domestica*	(Wang *et al.* 2019c)
CsLEA	*LEA*	*Camellia sinensis*	(Wang *et al.* 2019a)
DlICE1	*bHLH*	*Dimocarpus longan*	(Yang *et al.* 2019)
ZjICE1	*bHLH*	*Zoysia japonica*	(Zuo *et al.* 2019)
VvCBF	*DREB*	*Vitis vinifera*	(Rubio and Pérez 2019)
AtGLR1.2AtGLR1.3	*GLR*	*Arabidopsis thaliana*	(Zheng *et al.* 2018)
STCH4/ REIL2	*Zinc-finger proteins (ZNFs)*	*Arabidopsis thaliana*	(Schmidt *et al.* 2013)

called '*ICE* boxes', in *CBF* promoters. Indeed, *ICE1*, a nuclear gene encoding an MYC-like bHLH protein, plays an important role in controlling certain *CBF* genes (Chinnusamy *et al.* 2003). In numerous plant species, the function of the *ICE1-CBF/DREB1* network in enhancing cold resistance has been evaluated. In wheat, two *ICE1* homologues, *TaICE141* and *TaICE187*, up-regulated *CBF* group IV genes (Badawi *et al.* 2008). The presence of *CBF/DREB* homologs and their functions in enhancing the cold resistance of rice plants have been documented in several studies (Ito *et al.* 2006, Zhang *et al.* 2009). For example, expression of *OsICE1* and *OsICE2* in rice is caused by cold stress, resulting in *OsDREB1B*, *OSHsfA3* and *OsTPP1B* up-regulation (Nakamura *et al.* 2011). Zhao *et al.* (2013) reported that through the expression of *Musa acuminata-Myelocytomatosis 2* (*MaMYC2*), the chilling resistance of banana plants (*Musa acuminate*) was enhanced by jasmonate (JA). However, *MaMYC2* also interacts with *MaICE1*, activating the CBF-dependent pathway for cold-tolerance signaling. Soltész *et al.* (2013) indicated that in the cold resistance mechanism of wheat, *TaCBF14* and *TaCBF15* play important roles. In addition, these genes have been documented to enhance cold resistance of transgenic plants by various degrees compared to normal plants. Both apples and peaches have at least five *CBF* genes that show a spectrum of expression patterns in response to low temperatures (Wisniewski *et al.* 2014). On the other hand, upregulation of *ICE2*, an *ICE1* homolog, increases cold resistance and *CBF/DREB1B* expression in *Arabidopsis* (Fursova *et al.* 2009). This indicates that the over-expression of *CBF/DREB1 via ICE1* could result in chromatin remodeling. However, besides ICE proteins, other proteins like LOS4, HOS1, and LOS1 show positive regulation of *CBF* expression (Matthew and Jenks 2005).

The DNA-regulatory element *CRT/DRE* in the *COR* gene promoter is recognized by CBF proteins. By this mechanism, CBF proteins regulate the expression of the *COR* genes (Baker *et al.* 1994, Yamaguchi-Shinozaki and Shinozaki 1994). Three *CBF* genes found in tandem on chromosome 4 of *Arabidopsis* encode proteins with masses of approximately 24 kDa. These proteins share about 90 % amino acid sequence identity and have a conserved DNA-binding motif with almost 60 APETALA2 and ethylene-responsive element-binding factor (AP2/ERF) domain-designated amino acids (Riechmann and Meyerowitz 1998). In contrast, 144 *AP2/ERF* genes have been identified in *Arabidopsis* (Riechmann *et al.* 2000) and categorized into 5 subgroups according to their DNA-binding domain similarities: *AP2* subfamily (14 genes), *RAV* subfamily (6 genes), *DREB/CBF* subfamily (55 genes), *ERF* subfamily (65 genes), and a 5th group consisting of 4 genes (Sakuma *et al.* 2002). Increased expression of *COR* genes by activation of CRT/DRE elements in their CBF protein promoters is known as a part of the *CBF* regulon. Extensive expression profiling studies of *CBF* genes have recorded and assigned 109 genes to the *CBF* regulon (Fowler and Thomashow 2002, Vogel *et al.* 2005), and divided *CBF* regulon-assigned genes into four groups based on the nature of the encoded proteins (Matthew and Jenks 2005). The first main group contains more than 50 % of proteins with uncertain functions; the second group is comprised of cryoprotective proteins that include COR proteins, the third group consists of regulating proteins, while the fourth consists of biosynthetic proteins (Matthew and Jenks 2005). For these groups, *COR* genes are of particular importance as they encode highly hydrophilic proteins such as dehydrins and LEA proteins (Close 1997). It is proposed that LEA proteins are necessary for membrane stabilization and avoidance of protein aggregation (Hundertmark and Hincha 2008). Most functions of COR proteins, however, are only speculative. Several studies indicate that the CORa protein, one of the most extensively researched COR proteins, helps the stabilization of cell membranes against freezing disruption (Lin and Thomashow 1992, Artus *et al.* 1996, Steponkus *et al.* 1998). In addition, COR proteins have been shown to reduce membranes' propensity to construct hexagonal-II structures, a damaging non-bilayer structure owing to cellular dehydration associated with freezing (Thomashow 1999). Moreover, COR proteins play a role in shielding other proteins from *in vitro* freeze-thaw inactivation (Bravo *et al.* 2003, Hara *et al.* 2003), as well as functioning as dehydration buffers, and protease inhibitors (Bray 1993). In addition, studies have shown that up-regulation of *COR15a* in transgenic *Arabidopsis* (non-acclimated plants) increased chloroplast freezing resistance by around 2 °C (Artus *et al.* 1996). Besides *COR* genes, the expression of heat shock proteins can be caused by low-temperature stress (Timperio *et al.* 2008). Studies have also shown that bacterial cold shock proteins (CSPs) increase stress adjustment in plants such as maize and rice (Castiglioni *et al.* 2008, Guddimalli *et al.* 2021). Cold resistance in transgenic *Arabidopsis* increased with the expression of bacterial CSPs (Karlson and Imai 2003, Nakamura *et al.* 2008). Different PR (pathogen-related) proteins including PR1, PR2, PR5, PR10, PR11, and PR14 have also been shown to be upregulated by exposure to low temperature (Seo *et al.* 2008).

A possible link exists between cold adjustment processes and other physiological pathways in plants. As an example, an association between low-temperature adjustment and vernalization has been reported in temperate cereals since both processes involve exposure to low non-freezing temperature (Dhillon *et al.* 2010). In addition, it was found that the major vernalization gene (*VRN-1*) plays an important role in decreasing the cold acclimation potential of plants (Fowler and Limin 2004). On the other hand, *CBF* gene mRNA is comparatively decreased once the vrn-1 allele-carrying winter genotype is vernalized *versus* non-vernalized plants (Stockinger *et al.* 2007). In wheat, *Fr-1* and *Fr-2*, have been reported to be the primary loci regulating low-temperature tolerance (Vágújfalvi *et al.* 2000). It has been documented that the *Fr-1* locus is closely related to the *Vrn1* locus that is well recognized to be the primary regulator of the transition from vegetative to reproductive meristem under cold stress (Laudencia-Chingcuanco *et al.* 2011). Moreover, it has been confirmed that *Vrn-1* and *Fr-1* are genetically linked (Båga *et al.* 2007). The pleiotropic features of the *Vrn-1* locus explain much of the associated temperature and winter resistance habit of temperate cereals (Dhillon *et al.* 2010).

In reference to the *FR-2* locus, evidence shows that it contains a known group of *CBFs* that play a crucial function in increasing the expression of *COR* genes in various plant species (Campoli *et al.* 2009, Knox *et al.* 2010). Increases in metabolites are followed by changes in gene expression as a reaction to low-temperature stress, some of which have been shown to play a protective role against low-temperature stress damage (Sanghera *et al.* 2011). However, when experiencing low-temperature stress, plants encounter alterations in their gene expression patterns and protein products, and the modification of *CBF* genes has demonstrated utility in breeding for cold-resistant crops adapted to moderate environments (Sanghera *et al.* 2011).

In summary, whole genomes and transcriptomes can provide detailed knowledge about the physiological condition of plant species in a given situation; however, global transcriptions are not always associated with translated proteins. Furthermore, transcript analysis does not screen certain important post-translational changes. In this regard, proteomic research has the ability to offer a detailed picture of plant stress responses at the protein level. Plants use specific signaling and transcriptome control to acclimate to cold stress. An inducer of dehydration responsive elements or C-repeat binding factor expression-1 and dehydration-responsive elements or C-repeat binding factors are two transcription factors that play important functions in the control of cold-responsive genes and plant cold resistance. These genes and transcription factors could be targeted to enhance cold resistance and productivity in agricultural crops through genetic modification.

Proteomic profile of cold stress

Cold stress triggers the expression of a significant number of protein-encoding genes that contribute to plant chilling tolerance (Hughes and Dunn 1996). The cold response proteins, including LEA, antifreeze, cold-regulated, and dehydrins, are encoded by these stress-inducible genes. Under cold stress, they have a crucial function in plant adaptation.

LEA proteins are water-soluble proteins that accumulate during seed desiccation and under different stresses such as low temperature, drought, or salinity (Liu *et al.* 2016). These proteins act as a dehydration buffer, sequestering ions and stabilizing chromatin structures, membranes, and other proteins, thus defending the cells from desiccation and low temperature (Amara *et al.* 2013, Battaglia and Covarrubias 2013, Yang *et al.* 2015). They stop the aggregation of proteins and are essential for membrane stability throughout cold conditions (Hundertmark and Hincha 2008). For example, the overexpression of the citrus LEA gene *CuCOR19* increases the chilling tolerance of transgenic tobacco plants (Hara *et al.* 2003). In barley, the LEA group III protein (LEA D7 protein) encoding by the *HVA1* gene showed up-regulation following exposure to cold stress (Thomashow 1998). On the other hand, the expression of LEA D113 encoding by the tomato *LE25* gene in yeast cells improved their freezing tolerance (Thomashow 1998). Over-expression of transcriptional factors (TFs) such as DREB1A and DREB2A has been found to contribute to the increased aggregation of various enzymes and kinases besides LEA proteins, and ultimately to cold adaptation in *Arabidopsis* (Maruyama *et al.* 2009). In addition, increased deposition of Cor15am, an LEA-related protein in *Arabidopsis*, has been found to attenuate stromal protein aggregation under various stress conditions (Nakayama *et al.* 2007).

Dehydrins are a category of heat stable, membrane stabilizing LEA proteins and denaturation defense proteins during cytoplasm dehydration (Hara 2010). They are hydrophilic proteins containing polar amino acids and glycine, distinguished by the presence in the cell of a K-segment and lysine-rich amino acid motif that acts as chaperones or emulsifiers (Kosová *et al.* 2007). A predicted amphiphilic a-helix domain causing an interaction between hydrophilic and hydrophobic dehydrins is characterized by the inclusion of the K-segment (lysine-rich amino acid sequence). These dehydrins stick and mask with a coherent water layer with the intracellular molecules, preventing their coagulation during desiccation/dehydration (Xu *et al.* 2014). In addition to different developmental mechanisms, dehydrins are major dehydration-inducible proteins aggregated and often caused by cold stress (Hanin *et al.* 2011, Shi *et al.* 2016). They function as molecular chaperones that avoid the disaggregation of denatured proteins (partly) and interact by electrostatic force with phospholipid vesicles (Miura and Furumoto 2013, Graether and Boddington 2014). The primary dehydrins that are induced in plants during cold stress are LTI30 and COR47 (Kosová *et al.* 2007). Several dehydrins have been documented to increase during cold stress including Y2SK4 in apple (Garcia-Bañuelos *et al.* 2009) and PpDHN1 in peach (Artlip *et al.* 2016). These, and other dehydrins such as PCA60 in peach (Wisniewski *et al.* 1999), DHN5 in rye, WCOR410 in wheat, and CuCOR19 in citrus (Miura and Furumoto 2013), function as antifreeze proteins in response to low temperature by avoiding intracellular ice formation. In addition, wheat dehydrin DHN5, which has a pleiotropic effect on stress responses in *Arabidopsis*, either changes the expression of abiotic stress-responsive genes (*LEA*, *RD29B*, *RAB18*, and *LTI30*) or controls the protein-related defense response genes expression. More importantly, DHN5 also controls the signaling of jasmonate (JA) by downregulating the negative regulator (jasmonate-ZIM domain) gene expression (Hanin *et al.* 2011). Cold tolerance proteome research in *Trifolium pratense* has recently revealed the existence of dehydrins as the most notable improvement in proteome composition in cold-acclimated crowns (Bertrand *et al.* 2016). Increased amount of the wheat dehydrin WCS19 in transgenic *Arabidopsis* enhances the resistance to cold stress (NDong *et al.* 2002), while an increased wheat dehydrin WCO410 in transgenic strawberry leaves increases cold resistance of the strawberry plant (Houde *et al.* 2004).

In addition, some dehydrin and Radialis (RAD) homologous proteins have been recognized in the plasma membrane following cold stress. RAD23 is thought to be active in proteolysis due to proteasome 26S (Chen and Madura 2002), indicating the role of RAD23 for increased cryostability in response to cold stress in plasma membrane protein reorganization. In addition, the ERD10 (early reaction to dehydration 10) and ERD14 proteins, which are from the dehydrin-type acidic SK family and mimic COR47, associate with phospholipid vesicles and function like molecular chaperones (Miura and Furumoto 2013). On the other hand, the presence of phosphorylated ERD14 with a calcium-binding is found in the cytosol near the plasmalemma. The phosphorylated and calcium-bound ERD14 can act like a sugar chaperone or ionic buffer in response to low temperature, in a similar manner to calnexin or calreticulin binding Ca^{2+} in the endoplasmic reticulum (Kosová *et al.* 2007).

Antifreeze proteins (AFPs) are one of the significant types of proteins that confer cold resistance to overwintering plants, *i.e.* cold acclimated plants. They include a category of binding proteins that inhibit further development of ice crystals (Gupta and Deswal 2012). Although first isolated as macromolecules from Antarctic fish having the capacity to prevent blood ice development during cold stresses, these proteins are also recognized in plants, fungi, bacteria, vertebrates, and invertebrates (Wen *et al.* 2016). Conversion of the water in the extracellular space into ice occurs at freezing temperatures, *i.e.* below 0 °C, since the extracellular fluid shows a higher freezing temperature relative to the intracellular fluid (Atıcı and Nalbantoğlu 2003). In extracellular space, AFPs are able to adsorb these ice crystals, inhibit their development, and reduce the freezing temperature (Atıcı and Nalbantoğlu 2003, Griffith *et al.* 2005). This protein family protects plants from freezing stress by displaying two distinct properties: thermal hysteresis (TH) and inhibition of ice recrystallization (IRI). In TH, AFPs attach to the ice crystals and avoid the aggregation of water molecules. AFPs decrease the cell sap's freezing temperature as well as freezing point and avoid the development of ice crystals in plants, if it is frozen outside (Zachariassen and Kristiansen 2000). Moreover, AFPs block IRI, as well as the development of tiny ice molecules into larger ones, as these phenomena can cause physical injury and rupture of the plasma membrane, as well as cell death. With the exception of *Prunus persica* and *Forsythia suspensa*, which contain intracellular AFPs, AFPs extracted from eleven other plants are largely apoplastic, suggesting their function in inhibiting intracellular ice nucleators (Simpson *et al.* 2005, Gupta and Deswal 2014). In addition, glycoproteins (AFGPs) offer antifreeze protection in plants. AFGPs have been extracted from numerous plants, including *Daucus carota*, *Lolium perenne*, and *Hippophae rhamnoides* (Sidebottom *et al.* 2000, Pudney *et al.* 2003, Gupta and Deswal 2012). In AFGPs, the sugar moiety has a key function in attaching and stopping the growth of ice crystals (Gupta and Deswal 2014). On the other hand, different studies have indicated that different hormones such as JA and ethylene influence the antifreeze function. An increased antifreeze activity was seen in *Secale cereale* under ACC (an ethylene precursor) application, suggesting the function of ethylene in regulating antifreeze activity.

Characterization of AFP revealed that they consist of a zinc finger motif available in WRKY proteins, a class of TFs that govern the aggregation of proteins associated with pathogenesis in plants (Griffith *et al.* 2005). AFP has a unique function in that it has 10 consecutive 13-mer repeats at the C-terminus, which is a typical animal antifreeze protein characteristic (Huang and Duman 2002). Interestingly, AFPs' constitutive activities have not been recorded to date, however, studies have shown that the outputs of *AFP* genes (*mRNA* and protein) accumulate during cold adaptation (Griffith and Yaish 2004). Thermal hysteresis and ice recrystallization suppression in transgenic plants containing an *AFP* gene was observed in overwintering plants (Griffith and Yaish 2004). In addition, the *AFPs* demonstrated antifreeze behavior in rye by modifying the structure of ice crystals and showing very high thermal hysteresis activity (Thomashow 1998). PR-proteins like class I and class II chitinases, β-1,3-glucanase, and thaumatin-like proteins are homologous to AFPs (Hon *et al.* 1995). These proteins can inhibit intracellular ice production by suppressing the intercellular ice recrystallization in apoplastic areas, because extracellular freezing induces cell dehydration (Janská *et al.* 2010).

Cold regulated (COR) proteins are water soluble and have a key function toward plant low-temperature resistance (Kazuoka and Oeda 1992). Not only in cold acclimation but also in chilling resistance, COR accumulation in plants has been found to be significant (Miura and Furumoto 2013). Dehydrins encoding by *COR6.6*, *COR15a*, *COR47*, and *COR78/RD29A* are caused by cold stress in *Arabidopsis* and other plants (Thomashow 1998). By reducing the hexagonal II phase lipids synthesis, COR15a aggregation prevents membrane damage and improves the freezing resistance of plants (Uemura and Steponkus 1997). Moreover, to reduce freezing damages, COR15a is able to form enzyme-binding oligomers in *Arabidopsis* and avoid chloroplast stromal protein aggregation (Nakayama *et al.* 2007). The COR15 aggregation detected in *Citrus paradise* enhances chilling resistance in mature fruits (Porat *et al.* 2002). Furthermore, increased COR14b aggregation enhances the freezing resistance of barley (Crosatti *et al.* 2008). Numerous heat-stable COR proteins from cold-adjusted spinach were isolated by Kazuoka and Oeda (1992), but there were no similar proteins in non-adjusted spinach. In contrast, during cold acclimation, functional chloroplasts are necessary, because up-regulation of transcription factor CBF1-3 in mutant results in down-regulation of the downstream genes, *COR47*, *COR15a*, and *COR78*, in comparison with wild type (Kindgren *et al.* 2015). Increased accumulation of COR protein in the chloroplast, such as COR15a, has been found to improve the chloroplasts' chilling resistance in non-acclimated plants by almost 2 °C (Artus *et al.* 1996). CuCOR19 enhances the resistance to stress *via* clearing free radicals created during low temperature conditions in *Citrus unshiu*. Moreover, this study has demonstrated that free radical-clearing action of dehydrin can stop lipid peroxidation and enhance cold tolerance (Hara *et al.* 2003). It has been reported that CuCOR19 is a protein rich in histidine, glycine, and lysine and it can scavenge peroxyl and hydroxyl radicals (Hara *et al.* 2004). Another histidine-rich protein has been documented in *Citrus unshiu* namely metal-binding CuCOR15, which has a strong antioxidant capability. Because free metal ions serve like effective catalytic compounds to produce radicals in cells, by binding these free metal ions under low-temperature conditions, CuCOR15 stops oxidation of proteins and peroxidation of lipids (Hara *et al.* 2005). Furthermore, WCOR14 and WCOR15 are chloroplastic COR proteins that are correlated with cold resistance in wheat, while as WCS120 and WCOR410 were found to be strongly increased under low temperature conditions in *Arabidopsis* and other plants (Fowler *et al.* 2001, Takumi and Nakamura 2005, Shimamura *et al.* 2006). WCS120 protects plants against low temperature by accumulation in the meristematic tissue; and its maintenance is extremely necessary for the low-temperature maintenance of the entire plant (Kosová *et al.* 2007). On the other hand, WCOR410 protects plant cells against freezing damage by accumulating near the plasma membrane (Xu *et al.* 2014).

Heat shock proteins (HSPs): These proteins mediate response to low-temperature conditions and are a significant part of the early response to cold stress (Timperio *et al.* 2008, Janmohammadi *et al.* 2015). They are molecular chaperones that inhibit the accumulation of denatured proteins and prevent membrane degradation under cold stress by being highly cryo-protective (Renaut *et al.* 2006, Timperio *et al.* 2008). Five large HSP families are recognized: HSP40, HSP70, HSP90, HSP100, and another tiny HSP based on their molecular mass (Gupta *et al.* 2010). HSP40 or J-protein (J-domain containing protein) as a part of HSP70, enhances the affinity of HSP70 to different substrates in stressed plant cells (Kampinga and Craig 2010). The HSP70, which represents the highly conserved family of HSPs, inhibits misfolding of proteins and ensures accurate folding of proteins under stress conditions (Kosakivska *et al.* 2008, Park and Seo 2015). In response to environmental stress, HSP90 is the most frequent cytosolic HSP. The HSP90 recruits different proteins, like tubulin, actin, calmodulin, receptor proteins and kinases, and reacts with several other co-chaperones, like tetratricopeptide repeat to control different cellular processes under cold stress (Park and Seo 2015). By resolving non-stable protein aggregations and destroying weakened polypeptides, HSP100 retains the functional integrity of multiple essential polypeptides (Gupta *et al.* 2010). Moreover, small HSPs stabilize protein conformation in conjunction with other HSPs by blocking the assembly of faulty folded or denatured proteins and facilitating the denaturation of disaggregated proteins under low-temperature stress (Gupta *et al.* 2010). Small HSPs play a vital function in plant adjustment to low temperature by promoting refolding of HSP70- and HSP100-directed proteins (Sun *et al.* 2002, Mogk *et al.* 2003, Janmohammadi *et al.* 2015). This collective evidence indicates the important role of HSPs for cold acclimation in plants (An *et al.* 2016). For example, in *Manihot esculenta*, in response to dehydration, HSPs simplify protein folding, block cellular injury, and enhance plant stress resistance (Fu *et al.* 2016). Similarly, different HSPs have been reported to be over-expressed in leaves of winter barley under low temperatures (Janská *et al.* 2011). Small HSPs (class I and II) are reported to accumulate in seeds throughout mid-maturation and have been found to be extremely common in dry seeds, indicating their function in resistance to desiccation (Hara 2010).

Pathogenesis-related (PR) proteins induced by pathological conditions are a large group of proteins that are classified in 17 families (Almeida-Silva and Venancio 2022). The increased expression of certain PR proteins, like PR-2 (β-1,3-glucanase), PR-3, PR-4, PR-5 (thaumatin-like protein), PR-8, PR-10, PR-11 (chitinase), and PR-14 (lipid transport protein), can also be caused by low temperature stress (Janská *et al.* 2010). Among these, the overwintering monocots can synthesize thaumatin-like protein, β-1,3-glucanase, and chitinases, which have antifreeze action that inhibit intracellular ice formation and prevent ice recrystallization in the apoplastic space (Yu *et al.* 2001, Griffith and Yaish 2004, Renaut *et al.* 2006). In winter rye, maize, wheat, and bermudagrass frost causes chitinase and thaumatin-like protein aggregation (Yu *et al.* 2001). Low temperature triggers the initiation of endogenous ethylene development in winter rye, which results in the expression of the *AFP* gene and aggregation of thaumatin-like proteins, chitinases and glucanases (Yu *et al.* 2001). Proteins with a low molecular mass containing conserved cysteine (Cys) residues, are thaumatin-like proteins. These Cys residues regulate intra-molecular disulfide bonds and give stability to proteins. Misra *et al.* (2016) demonstrated that ObTLP1 supplies resistance to abiotic stress in transgenic *Arabidopsis* while in *Ocimum basilicum* thaumatin-like protein (ObTLP1) can function as the target of various hormone signaling mechanisms in regulating reaction of plants to abiotic stress. However, there is no definite biological role of thaumatin-like proteins (Misra *et al.* 2016). In overwintering grasses, glucanases and chitinases with the capacity to attach to ice crystals enhance cold tolerance (Hon *et al.* 1995). Glucanases, along with chitinases adsorbed on the ice crystal surface, have a combined impact, enhancing the ice crystal potency alteration and growth suppression (Hon *et al.* 1995, Nakamura *et al.* 2008). There is an elevated accumulation of PR proteins in the leaf apoplast of winter rye during acclimation to low temperature (Hon *et al.* 1995). Two PR-10 proteins (ZmPR-10 and ZmPR-10.1) are known to be induced by various stresses, including cold stress (Jain *et al.* 2012). Interestingly, a protein related to pathogenesis (PR1b1) was found to cause disease tolerance in tomato fruit in response to cold stress (Goyal *et al.* 2016). Furthermore, extensive genomic analysis of the *PR-1* gene family and its involvement in defense response in *Musa* spp. revealed its potential for conferring resistance to multiple stresses in novel banana varieties

(Anuradha *et al.* 2022).

Protein profiles of numerous plant species in response to low-temperature conditions, in particular, have sparked a lot of scientific interest, culminating in the discovery of differentially expressed proteins that have greatly enhanced our understanding of the cold response. These data shed new light on the reaction of plants against low-temperature conditions and could pave a way for further studies into the molecular processes that decide how plant cells react to environmental change. Nonetheless, it should be stated that a considerable proportion of the discovered proteins to-date remained largely unexplained in terms of probable function. This is due in part to lack of high-quality protein-coding gene annotations for several plant species. The experimental confirmation of these un-annotated proteins would help close the knowledge gap between protein profile of stress-induced molecules and their actual function. Such information could facilitate isolation of potential candidates involved in cold stress adaptation *via* plant genetic engineering.

Conclusions

In this review, the molecular concepts underlying plant response to low temperatures were introduced. Moreover, the significant function of cold acclimation and the ensuing molecular alterations were discussed. This review highlighted cold-regulated genes and the mechanisms that govern their regulation. In addition, the important role of *CBF* genes in the overexpression of COR proteins were discussed. The beneficial role of various molecular mechanisms in conferring resistance to low temperatures in plants has been shown by recent studies. Proteomics offers an important platform for understanding the molecular processes in various plants adapted to cold stress. The latest proteomics research revealing protein-amount response to cold stress have been examined here, with special focus to changes at organ and organelle levels. There are numerous classes of proteins that accumulate during low-temperature stress, such as dehydrins, antifreeze proteins, and late embryogenesis abundant proteins. These proteins have roles in various processes, such as free radical scavenging, ice crystal inhibition, ion binding, and antifreeze functions during plant exposure to cold stress. Even with these advancements, more comprehensive molecular methods are urgently required to decipher the structural predictions based on genome sequence data and to explore protein modifications and their correlations with cold-resistant genotypes.

References

Almeida-Silva, F., Venancio, T.M.: Pathogenesis-related protein 1 (*PR-1*) genes in soybean: Genome-wide identification, structural analysis and expression profiling under multiple biotic and abiotic stresses. - Gene **809**: 146013, 2022.

Amara, I., Capellades, M., Ludevid, M.D., Pages, M., Goday, A.: Enhanced water stress tolerance of transgenic maize plants over-expressing *LEA Rab28* gene. - J. Plant Physiol. **170**: 864-873, 2013.

An, F., Li, G., Li, Q.X., Li, K., Carvalho, L.J., Ou, W., Chen, S.: The comparatively proteomic analysis in response to cold stress in cassava plantlets. - Plant mol. Biol. Rep. **34**: 1095-1110, 2016.

Anuradha, C., Chandrasekar, A., Backiyarani, S., Thangavelu, R., Giribabu, P., Uma, S.: Genome-wide analysis of pathogenesis-related protein 1 (*PR-1*) gene family from *Musa* spp. and its role in defense response during stresses. - Gene **821**: 146334, 2022.

Arora, R., Agarwal, P., Ray, S., Singh, A.K., Singh, V.P., Tyagi, A.K., Kapoor, S.: MADS-box gene family in rice: genome-wide identification, organization and expression profiling during reproductive development and stress. - BMC Genomics **8**: 242, 2007.

Artlip, T.S., Wisniewski, M.E., Arora, R., Norelli, J.L.: An apple rootstock overexpressing a peach *CBF* gene alters growth and flowering in the scion but does not impact cold hardiness or dormancy. - Hort. Res. **3**: 1-9, 2016.

Artus, N.N., Uemura, M., Steponkus, P.L., Gilmour, S.J., Lin, C., Thomashow, M.F.: Constitutive expression of the cold-regulated *Arabidopsis thaliana COR15a* gene affects both chloroplast and protoplast freezing tolerance. - Proc nat. Acad. Sci. USA **93**: 13404-13409, 1996.

Atıcı, Ö., Nalbantoğlu, B.: Antifreeze proteins in higher plants. - Phytochemistry **64**: 1187-1196, 2003.

Badawi, M., Danyluk, J., Boucho, B., Houde, M., Sarhan, F.: The *CBF* gene family in hexaploid wheat and its relationship to the phylogenetic complexity of cereal CBFs. - Mol. Genet. Genom. **277**: 533-554, 2007.

Badawi, M., Reddy, Y.V., Agharbaoui, Z., Tominaga, Y., Danyluk, J., Sarhan, F., Houde, M.: Structure and functional analysis of wheat *ICE* (inducer of CBF expression) genes. - Plant Cell Physiol. **49**: 1237-1249, 2008.

Båga, M., Chodaparambil, S.V., Limin, A.E., Pecar, M., Fowler, D.B., Chibbar, R.N.: Identification of quantitative trait loci and associated candidate genes for low-temperature tolerance in cold-hardy winter wheat. - Funct. Integr. Genomics **7**: 53-68, 2007.

Baker, S.S., Wilhelm, K.S., Thomashow, M.F.: The 5′-region of *Arabidopsis thaliana cor15a* has cis-acting elements that confer cold-, drought-and ABA-regulated gene expression. - Plant mol. Biol. **24**: 701-713, 1994.

Battaglia, M., Covarrubias, A.A.: Late embryogenesis abundant (LEA) proteins in legumes. - Front. Plant Sci. **4**: 190, 2013.

Bertrand, A., Bipfubusa, M., Castonguay, Y., Rocher, S., Szopinska-Morawska, A., Papadopoulos, Y., Renaut, J.: A proteome analysis of freezing tolerance in red clover (*Trifolium pratense* L.). - BMC Plant Biol. **16**: 1-18, 2016.

Bose, J., Pottosin, I., Shabala, S.S.S., Palmgren, M.G., Shabala, S.: Calcium efflux systems in stress signaling and adaptation in plants. - Front. Plant Sci. **2**: 85, 2011.

Bravo, L.A., Gallardo, J., Navarrete, A., Olave, N., Martínez, J., Alberdi, M., Close, T.J., Corcuera, L.J.: Cryoprotective activity of a cold-induced dehydrin purified from barley. - Physiol. Plant. **118**: 262-269, 2003.

Bray, E.A.: Molecular responses to water deficit. - Plant Physiol. **103**: 1035, 1993.

Campoli, C., Matus-Cádiz, M.A., Pozniak, C.J., Cattivelli, L., Fowler, D.B.: Comparative expression of *Cbf* genes in the *Triticeae* under different acclimation induction temperatures. - Mol. Genet. Genom. **282**: 141-152, 2009.

Cao, J., Lv, Y., Li, X.: Interspaced repeat sequences confer the regulatory functions of AtXTH10, important for root growth in *Arabidopsis*. - Plants **8**: 130, 2019.

Castiglioni, P., Warner, D., Bensen, R.J., Anstrom, D.C., Harrison, J., Stoecker, M., Abad, M., Kumar, G., Salvador, S., D'Ordine, R.: Bacterial RNA chaperones confer abiotic stress tolerance in plants and improved grain yield in maize under water-limited conditions. - Plant Physiol. **147**: 446-455, 2008.

Chan, Z., Wang, Y., Cao, M., Gong, Y., Mu, Z., Wang, H., Hu, Y., Deng, X., He, X.J., Zhu, J.K.: RDM 4 modulates cold stress resistance in *Arabidopsis* partially through the CBF-mediated pathway. - New Phytol. **209**: 1527-1539, 2016.

Chen, L., Madura, K.: Rad23 promotes the targeting of proteolytic substrates to the proteasome. - Mol. cell. Biol. **22**: 4902-4913, 2002.

Chen, L., Zhang, Y., Ren, Y., Xu, J., Zhang, Z., Wang, Y.: Genome-wide identification of cold-responsive and new microRNAs in *Populus tomentosa* by high-throughput sequencing. - Biochem. biophys. Res. Commun. **417**: 892-896, 2012.

Chen, T., Shabala, S., Niu, Y., Chen, Z.-H., Shabala, L., Meinke, H., Venkataraman, G., Pareek, A., Xu, J., Zhou, M.: Molecular mechanisms of salinity tolerance in rice. - Crop J. **9:** 506-520, 2021.

Chinnusamy, V., Ohta, M., Kanrar, S., Lee, B.-H., Hong, X., Agarwal, M., Zhu, J.-K.: ICE1: a regulator of cold-induced transcriptome and freezing tolerance in *Arabidopsis*. - Genes Dev. **17**: 1043-1054, 2003.

Chinnusamy, V., Zhu, J., Zhu, J.-K.: Cold stress regulation of gene expression in plants. - Trends Plant Sci. **12**: 444-451, 2007.

Close, T.J.: Dehydrins: a commonalty in the response of plants to dehydration and low temperature. - Physiol. Plant. **100**: 291-296, 1997.

Crosatti, C., Pagani, D., Cattivelli, L., Stanca, A., Rizza, F.: Effects of growth stage and hardening conditions on the association between frost resistance and the expression of the cold-induced protein COR14b in barley. - Environ. exp. Bot. **62**: 93-100, 2008.

Da Maia, L.C., Cadore, P.R., Benitez, L.C., Danielowski, R., Braga, E.J., Fagundes, P.R., Magalhães, A.M., De Oliveira, A.C.: Transcriptome profiling of rice seedlings under cold stress. - Funct. Plant Biol. **44**: 419-429, 2017.

Denesik, T.J.: Quantitative expression analysis of four low-temperature-tolerance-associated genes during cold acclimation in wheat (*Triticum aestivum* L.). University of Saskatchewan, 2007.

Dhillon, T., Pearce, S.P., Stockinger, E.J., Distelfeld, A., Li, C., Knox, A.K., Vashegyi, I., Vágújfalvi, A., Galiba, G., Dubcovsky, J.: Regulation of freezing tolerance and flowering in temperate cereals: the *VRN-1* connection. - Plant Physiol. **153**: 1846-1858, 2010.

Ding, C., Lei, L., Yao, L., Wang, L., Hao, X., Li, N., Wang, Y., Yin, P., Guo, G., Yang, Y.: The involvements of calcium-dependent protein kinases and catechins in tea plant [*Camellia sinensis* (L.) O. Kuntze] cold responses. - Plant Physiol. Biochem. **143**: 190-202, 2019.

Doherty, C.J., Van Buskirk, H.A., Myers, S.J., Thomashow, M.F.: Roles for *Arabidopsis* CAMTA transcription factors in cold-regulated gene expression and freezing tolerance. - Plant Cell **21**: 972-984, 2009.

Du, H., Wu, N., Fu, J., Wang, S., Li, X., Xiao, J., Xiong, L.: A GH3 family member, OsGH3-2, modulates auxin and abscisic acid levels and differentially affects drought and cold tolerance in rice. - J. exp. Bot. **63**: 6467-6480, 2012.

Eckardt, N.A.: CAMTA proteins: a direct link between calcium signals and cold acclimation? - Plant Cell **21**: 697-697, 2009.

Fowler, D., Limin, A.: Interactions among factors regulating phenological development and acclimation rate determine low-temperature tolerance in wheat. - Ann. Bot. **94**: 717-724, 2004.

Fowler, D.B., Breton, G., Limin, A.E., Mahfoozi, S., Sarhan, F.: Photoperiod and temperature interactions regulate low-temperature-induced gene expression in barley. - Plant Physiol. **127**: 1676-1681, 2001.

Fowler, S., Thomashow, M.F.: *Arabidopsis* transcriptome profiling indicates that multiple regulatory pathways are activated during cold acclimation in addition to the CBF cold response pathway. - Plant Cell **14**: 1675-1690, 2002.

Fu, L., Ding, Z., Han, B., Hu, W., Li, Y., Zhang, J.: Physiological investigation and transcriptome analysis of polyethylene glycol (PEG)-induced dehydration stress in cassava. - Int. J. mol. Sci. **17**: 283, 2016.

Fursova, O.V., Pogorelko, G.V., Tarasov, V.A.: Identification of *ICE2*, a gene involved in cold acclimation which determines freezing tolerance in *Arabidopsis thaliana*. - Gene **429**: 98-103, 2009.

Gao, J.P., Chao, D.Y., Lin, H.X.: Understanding abiotic stress tolerance mechanisms: recent studies on stress response in rice. - J. integr. Plant Biol. **49**: 742-750, 2007.

Garcia-Bañuelos, M.L., Gardea, A.A., Winzerling, J.J., Vazquez-Moreno, L.: Characterization of a midwinter-expressed dehydrin (*DHN*) gene from apple trees (*Malus domestica*). - Plant mol. Biol. Rep. **27**: 476-487, 2009.

Gery, C., Zuther, E., Schulz, E., Legoupi, J., Chauveau, A., McKhann, H., Hincha, D.K., Téoulé, E.: Natural variation in the freezing tolerance of *Arabidopsis thaliana*: effects of RNAi-induced CBF depletion and QTL localisation vary among accessions. - Plant Sci. **180**: 12-23, 2011.

Ghildiyal, M., Zamore, P.D.: Small silencing RNAs: an expanding universe. - Nat. Rev. Genet. **10**: 94-108, 2009.

Gilmour, S.J., Zarka, D.G., Stockinger, E.J., Salazar, M.P., Houghton, J.M., Thomashow, M.F.: Low temperature regulation of the *Arabidopsis* CBF family of AP2 transcriptional activators as an early step in cold-induced *COR* gene expression. - Plant J. **16**: 433-442, 1998.

Gopal, C., Chanakya, N.K.: Induction of a C-repeat binding factor gene by calcium to resist low temperature stress in rice. - Int. J. Plant Physiol. Biochem. **4**: 142-145, 2012.

Goyal, R.K., Fatima, T., Topuz, M., Bernadec, A., Sicher, R., Handa, A.K., Mattoo, A.K.: Pathogenesis-related protein 1b1 (PR1b1) is a major tomato fruit protein responsive to chilling temperature and upregulated in high polyamine transgenic genotypes. - Front. Plant Sci. **7**: 901, 2016.

Graether, S.P., Boddington, K.F.: Disorder and function: a review of the dehydrin protein family. - Front. Plant Sci. **5**: 576, 2014.

Griffith, M., Lumb, C., Wiseman, S.B., Wisniewski, M., Johnson, R.W., Marangoni, A.G.: Antifreeze proteins modify the freezing process in planta. - Plant Physiol. **138**: 330-340, 2005.

Griffith, M., Yaish, M.W.: Antifreeze proteins in overwintering plants: a tale of two activities. - Trends Plant Sci. **9**: 399-405, 2004.

Guddimalli, R., Somanaboina, A.K., Palle, S.R., Edupuganti, S., Kummari, D., Palakolanu, S.R., Naravula, J., Gandra, J., Qureshi, I.A., Marka, N.: Overexpression of RNA-binding bacterial chaperones in rice leads to stay-green phenotype, improved yield and tolerance to salt and drought stresses. - Physiol. Plant. **173**: 1351-1368, 2021.

Guo, X., Zhang, L., Dong, G., Xu, Z., Li, G., Liu, N., Wang, A., Zhu, J.: A novel cold-regulated protein isolated from *Saussurea involucrata* confers cold and drought tolerance in transgenic tobacco (*Nicotiana tabacum*). - Plant Sci. **289**: 110246, 2019.

Guo, X., Zhang, L., Zhu, J., Liu, H., Wang, A.: Cloning and characterization of *SiDHN*, a novel dehydrin gene from

Saussurea involucrata Kar. et Kir. that enhances cold and drought tolerance in tobacco. - Plant Sci. **256**: 160-169, 2017.

Gupta, R., Deswal, R.: Low temperature stress modulated secretome analysis and purification of antifreeze protein from *Hippophae rhamnoides*, a Himalayan wonder plant. - J. Proteome Res. **11**: 2684-2696, 2012.

Gupta, R., Deswal, R.: Antifreeze proteins enable plants to survive in freezing conditions. - J. Biosci. **39**: 931-944, 2014.

Gupta, S.C., Sharma, A., Mishra, M., Mishra, R.K., Chowdhuri, D.K.: Heat shock proteins in toxicology: how close and how far? - Life Sci. **86**: 377-384, 2010.

Hanin, M., Brini, F., Ebel, C., Toda, Y., Takeda, S., Masmoudi, K.: Plant dehydrins and stress tolerance: versatile proteins for complex mechanisms. - Plant Signal. Behav. **6**: 1503-1509, 2011.

Hannah, M.A., Heyer, A.G., Hincha, D.K.: A global survey of gene regulation during cold acclimation in *Arabidopsis thaliana*. - PLoS Genet. **1**: e26, 2005.

Hao, X., Wang, B., Wang, L., Zeng, J., Yang, Y., Wang, X.: Comprehensive transcriptome analysis reveals common and specific genes and pathways involved in cold acclimation and cold stress in tea plant leaves. - Sci. Hort. **240**: 354-368, 2018.

Hara, M.: The multifunctionality of dehydrins: an overview. - Plant Signal. Behav. **5**: 503-508, 2010.

Hara, M., Fujinaga, M., Kuboi, T.: Radical scavenging activity and oxidative modification of citrus dehydrin. - Plant Physiol. Biochem. **42**: 657-662, 2004.

Hara, M., Fujinaga, M., Kuboi, T.: Metal binding by citrus dehydrin with histidine-rich domains. - J. exp. Bot. **56**: 2695-2703, 2005.

Hara, M., Terashima, S., Fukaya, T., Kuboi, T.: Enhancement of cold tolerance and inhibition of lipid peroxidation by citrus dehydrin in transgenic tobacco. - Planta **217**: 290-298, 2003.

Hasanuzzaman, M., Shabala, L., Brodribb, T.J., Zhou, M., Shabala, S.: Understanding physiological and morphological traits contributing to drought tolerance in barley. - J Agron. Crop Sci. **205**: 129-140, 2019.

Heidarvand, L., Amiri, R.M.: What happens in plant molecular responses to cold stress? - Acta Physiol. Plant. **32**: 419-431, 2010.

Hon, W.-C., Griffith, M., Mlynarz, A., Kwok, Y.C., Yang, D.S.: Antifreeze proteins in winter rye are similar to pathogenesis-related proteins. - Plant Physiol. **109**: 879-889, 1995.

Houde, M., Dallaire, S., N'Dong, D., Sarhan, F.: Overexpression of the acidic dehydrin WCOR410 improves freezing tolerance in transgenic strawberry leaves. - Plant Biotechnol. J. **2**: 381-387, 2004.

Hu, Y., Wu, Q., Sprague, S.A., Park, J., Oh, M., Rajashekar, C., Koiwa, H., Nakata, P.A., Cheng, N., Hirschi, K.D.: Tomato expressing *Arabidopsis* glutaredoxin gene *AtGRXS17* confers tolerance to chilling stress *via* modulating cold responsive components. - Hort. Res. **2**: 1-11, 2015.

Huang, T., Duman, J.G.: Cloning and characterization of a thermal hysteresis (antifreeze) protein with DNA-binding activity from winter bittersweet nightshade, *Solanum dulcamara*. - Plant mol. Biol. **48**: 339-350, 2002.

Hughes, M.A., Dunn, M.A.: The molecular biology of plant acclimation to low temperature. - J. exp. Bot. **47**: 291-305, 1996.

Hundertmark, M., Hincha, D.K.: LEA (late embryogenesis abundant) proteins and their encoding genes in *Arabidopsis thaliana*. - BMC Genomics **9**: 1-22, 2008.

Ito, Y., Katsura, K., Maruyama, K., Taji, T., Kobayashi, M., Seki, M., Shinozaki, K., Yamaguchi-Shinozaki, K.: Functional analysis of rice DREB1/CBF-type transcription factors involved in cold-responsive gene expression in transgenic rice. - Plant Cell Physiol. **47**: 141-153, 2006.

Jaglo, K.R., Kleff, S., Amundsen, K.L., Zhang, X., Haake, V., Zhang, J.Z., Deits, T., Thomashow, M.F.: Components of the *Arabidopsis* C-repeat/dehydration-responsive element binding factor cold-response pathway are conserved in *Brassica napus* and other plant species. - Plant Physiol. **127**: 910-917, 2001.

Jain, S., Kumar, D., Jain, M., Chaudhary, P., Deswal, R., Sarin, N.B.: Ectopic overexpression of a salt stress-induced pathogenesis-related class 10 protein (PR10) gene from peanut (*Arachis hypogaea* L.) affords broad spectrum abiotic stress tolerance in transgenic tobacco. - Plant Cell Tissue Organ Cult. **109**: 19-31, 2012.

Jamshidi Goharrizi, K., Amirmahani, F., Salehi, F.: Assessment of changes in physiological and biochemical traits in four pistachio rootstocks under drought, salinity and drought + salinity stresses. - Physiol. Plant. **168**: 973-989, 2020a.

Jamshidi Goharrizi, K., Baghizadeh, A., Kalantar, M., Fatehi, F.: Assessment of changes in some biochemical traits and proteomic profile of UCB-1 pistachio rootstock leaf under salinity stress. - J. Plant Growth Regul. **39:** 608-630, 2020b.

Jamshidi Goharrizi, K., Baghizadeh, A., Kalantar, M., Fatehi, F.: Combined effects of salinity and drought on physiological and biochemical characteristics of pistachio rootstocks. - Sci. Hort. **261**: 108970, 2020c.

Jamshidi Goharrizi, K., Moosavi, S.S., Amirmahani, F., Salehi, F., Nazari, M.: Assessment of changes in growth traits, oxidative stress parameters, and enzymatic and non-enzymatic antioxidant defense mechanisms in *Lepidium draba* plant under osmotic stress induced by polyethylene glycol. - Protoplasma **257**: 459-473, 2020d.

Jamshidi Goharrizi, K., Riahi-Madvar, A., Rezaee, F., Pakzad, R., Bonyad, F.J., Ahsaei, M.G.: Effect of salinity stress on enzymes' activity, ions concentration, oxidative stress parameters, biochemical traits, content of sulforaphane, and *cyp79f1* gene expression level in *Lepidium draba* plant. - J. Plant Growth Regul. **39**: 1075-1094, 2020e.

Janda, T., Majláth, I., Szalai, G.: Interaction of temperature and light in the development of freezing tolerance in plants. - J. Plant Growth Regul. **33**: 460-469, 2014.

Janmohammadi, M., Zolla, L., Rinalducci, S.: Low temperature tolerance in plants: changes at the protein level. - Phytochemistry **117**: 76-89, 2015.

Janská, A., Aprile, A., Zámečník, J., Cattivelli, L., Ovesná, J.: Transcriptional responses of winter barley to cold indicate nucleosome remodelling as a specific feature of crown tissues. - Funct. Integr. Genomics **11**: 307-325, 2011.

Janská, A., Maršík, P., Zelenková, S., Ovesná, J.: Cold stress and acclimation – what is important for metabolic adjustment? - Plant Biol. **12**: 395-405, 2010.

Jenks, M.A., Wood, A.J.: Genes for Plant Abiotic Stress. John Wiley & Sons, New York 2009.

Kampinga, H.H., Craig, E.A.: The HSP70 chaperone machinery: J proteins as drivers of functional specificity. - Nat. Rev. mol. cell. Biol. **11**: 579-592, 2010.

Kargiotidou, A., Deli, D., Galanopoulou, D., Tsaftaris, A., Farmaki, T.: Low temperature and light regulate delta 12 fatty acid desaturases (FAD2) at a transcriptional level in cotton (*Gossypium hirsutum*). - J. exp. Bot. **59**: 2043-2056, 2008.

Karlson, D., Imai, R.: Conservation of the cold shock protein of *Escherichia coli*. - Plant Physiol. **131**: 12-15, 2003.

Kasuga, M., Liu, Q., Miura, S., Yamaguchi-Shinozaki, K., Shinozaki, K.: Improving plant drought, salt, and freezing tolerance by gene transfer of a single stress-inducible transcription factor. - Nat. Biotechnol. **17**: 287-291, 1999.

Kazuoka, T., Oeda, K.: Heat-Stable COR (Cold-Regulated) proteins associated with freezing tolerance in spinach. - Plant Cell. Physiol. **33**: 1107-1114, 1992.

Kindgren, P., Dubreuil, C., Strand, Å.: The recovery of plastid function is required for optimal response to low temperatures in *Arabidopsis*. - PloS ONE **10**: e0138010, 2015.

Knight, H., Knight, M.R.: Imaging spatial and cellular characteristics of low temperature calcium signature after cold acclimation in *Arabidopsis*. - J. exp. Bot. **51**: 1679-1686, 2000.

Knox, A.K., Dhillon, T., Cheng, H., Tondelli, A., Pecchioni, N., Stockinger, E.J.: *CBF* gene copy number variation at Frost Resistance-2 is associated with levels of freezing tolerance in temperate-climate cereals. - Theor. appl. Genet. **121**: 21-35, 2010.

Kocsy, G., Galiba, G., Brunold, C.: Role of glutathione in adaptation and signalling during chilling and cold acclimation in plants. - Physiol. Plant. **113**: 158-164, 2001.

Kosakivska, I., Klymchuk, D., Negretzky, V., Bluma, D., Ustinova, A.: Stress proteins and ultrastructural characteristics of leaf cells of plants with different types of ecological strategies. - Gen. appl. Plant Physiol. **34**: 405-418, 2008.

Kosová, K., Vítámvás, P., Prášil, I.: The role of dehydrins in plant response to cold. - Biol. Plant. **51**: 601-617, 2007.

Kurdrid, P., Senachak, J., Sirijuntarut, M., Yutthanasirikul, R., Phuengcharoen, P., Jeamton, W., Roytrakul, S., Cheevadhanarak, S., Hongsthong, A.: Comparative analysis of the *Spirulina platensis* subcellular proteome in response to low-and high-temperature stresses: uncovering cross-talk of signaling components. - Proteome Sci. **9**: 1-17, 2011.

Kwak, J.M., Mori, I.C., Pei, Z.M., Leonhardt, N., Torres, M.A., Dangl, J.L., Bloom, R.E., Bodde, S., Jones, J.D., Schroeder, J.I.: NADPH oxidase *AtrbohD* and *AtrbohF* genes function in ROS-dependent ABA signaling in *Arabidopsis*. - EMBO J. **22**: 2623-2633, 2003.

Laudencia-Chingcuanco, D., Ganeshan, S., You, F., Fowler, B., Chibbar, R., Anderson, O.: Genome-wide gene expression analysis supports a developmental model of low temperature tolerance gene regulation in wheat (*Triticum aestivum* L.). - BMC Genomics **12**: 1-20, 2011.

Lin, C., Thomashow, M.F.: DNA sequence analysis of a complementary DNA for cold-regulated *Arabidopsis* gene *cor15* and characterization of the COR 15 polypeptide. - Plant Physiol. **99**: 519-525, 1992.

Liu, G., Khan, N., Ma, X., Hou, X.: Identification, evolution, and expression profiling of histone lysine methylation moderators in *Brassica rapa*. - Plants **8**: 526, 2019a.

Liu, Q., Kasuga, M., Sakuma, Y., Abe, H., Miura, S., Yamaguchi-Shinozaki, K., Shinozaki, K.: Two transcription factors, DREB1 and DREB2, with an EREBP/AP2 DNA binding domain separate two cellular signal transduction pathways in drought-and low-temperature-responsive gene expression, respectively, in Arabidopsis. - Plant Cell **10**: 1391-1406, 1998.

Liu, X., Fu, L., Qin, P., Sun, Y., Liu, J., Wang, X.: Overexpression of the wheat trehalose 6-phosphate synthase 11 gene enhances cold tolerance in *Arabidopsis thaliana*. - Gene **710**: 210-217, 2019b.

Liu, Y., Liang, J., Sun, L., Yang, X., Li, D.: Group 3 LEA protein, ZmLEA3, is involved in protection from low temperature stress. - Front. Plant Sci. **7**: 1011, 2016.

Liu, Y., Zhou, J.: MAPping kinase regulation of ICE1 in freezing tolerance. - Trends Plant Sci. **23**: 91-93, 2018.

Lv, D.-K., Bai, X., Li, Y., Ding, X.-D., Ge, Y., Cai, H., Ji, W., Wu, N., Zhu, Y.-M.: Profiling of cold-stress-responsive miRNAs in rice by microarrays. - Gene **459**: 39-47, 2010.

Maruyama, K., Takeda, M., Kidokoro, S., Yamada, K., Sakuma, Y., Urano, K., Fujita, M., Yoshiwara, K., Matsukura, S., Morishita, Y.: Metabolic pathways involved in cold acclimation identified by integrated analysis of metabolites and transcripts regulated by DREB1A and DREB2A. - Plant Physiol. **150**: 1972-1980, 2009.

Matsuda, O., Sakamoto, H., Hashimoto, T., Iba, K.: A temperature-sensitive mechanism that regulates post-translational stability of a plastidial omega-3 fatty acid desaturase (FAD8) in *Arabidopsis* leaf tissues. - J. biol. Chem. **280**: 3597-3604, 2005.

Matthew, A., Jenks, P.M.H: Plant Abiotic Stress. - Blackwell, New York 2005.

Mboup, M., Fischer, I., Lainer, H., Stephan, W.: Trans-species polymorphism and allele-specific expression in the *CBF* gene family of wild tomatoes. - Mol. Biol. Evol. **29**: 3641-3652, 2012.

Medina, J., Bargues, M., Terol, J., Pérez-Alonso, M., Salinas, J.: The *Arabidopsis CBF* gene family is composed of three genes encoding AP2 domain-containing proteins whose expression is regulated by low temperature but not by abscisic acid or dehydration. - Plant Physiol. **119**: 463-470, 1999.

Mickelbart, M.V., Hasegawa, P.M., Bailey-Serres, J.: Genetic mechanisms of abiotic stress tolerance that translate to crop yield stability. - Nat. Rev. Genet. **16**: 237-251, 2015.

Misra, R.C., Kamthan, M., Kumar, S., Ghosh, S.: A thaumatin-like protein of *Ocimum basilicum* confers tolerance to fungal pathogen and abiotic stress in transgenic *Arabidopsis*. - Sci. Rep. **6**: 1-14, 2016.

Miura, K., Furumoto, T.: Cold signaling and cold response in plants. - Int. J. mol. Sci. **14**: 5312-5337, 2013.

Mizoi, J., Shinozaki, K., Yamaguchi-Shinozaki, K.: AP2/ERF family transcription factors in plant abiotic stress responses. - Biochim. biophys. Acta, Gene. Regul. Mech. **1819**: 86-96, 2012.

Mogk, A., Schlieker, C., Friedrich, K.L., Schönfeld, H.-J., Vierling, E., Bukau, B.: Refolding of substrates bound to small Hsps relies on a disaggregation reaction mediated most efficiently by ClpB/DnaK. - J. biol. Chem. **278**: 31033-31042, 2003.

Monroe, J.G., McGovern, C., Lasky, J.R., Grogan, K., Beck, J., McKay, J.K.: Adaptation to warmer climates by parallel functional evolution of *CBF* genes in *Arabidopsis thaliana*. - Mol. Ecol. **25**: 3632-3644, 2016.

Monroy, A.F., Sangwan, V., Dhindsa, R.S.: Low temperature signal transduction during cold acclimation: protein phosphatase 2A as an early target for cold-inactivation. - Plant J. **13**: 653-660, 1998.

Nakamura, J., Yuasa, T., Huong, T.T., Harano, K., Tanaka, S., Iwata, T., Phan, T., Iwaya, M.: Rice homologs of inducer of *CBF* expression (*OsICE*) are involved in cold acclimation. - Plant Biotechnol. **28**: 303-309, 2011.

Nakamura, T., Ishikawa, M., Nakatani, H., Oda, A.: Characterization of cold-responsive extracellular chitinase in bromegrass cell cultures and its relationship to antifreeze activity. - Plant Physiol. **147**: 391-401, 2008.

Nakayama, K., Okawa, K., Kakizaki, T., Honma, T., Itoh, H., Inaba, T.: *Arabidopsis* Cor15am is a chloroplast stromal protein that has cryoprotective activity and forms oligomers. - Plant Physiol. **144**: 513-523, 2007.

Nazari, M., Jamshidi Goharrizi, K., Moosavi, S.S., Maleki, M.: Expression changes in the TaNAC2 and TaNAC69-1 transcription factors in drought stress tolerant and susceptible. - Plant Genet. Resour.: Characterisation Utilisation **1**: 9, 2019.

NDong, C., Danyluk, J., Wilson, K.E., Pocock, T., Huner, N.P., Sarhan, F.: Cold-regulated cereal chloroplast late embryogenesis abundant-like proteins. Molecular characterization and functional analyses. - Plant Physiol. **129**:

1368-1381, 2002.

Nordin, K., Heino, P., Palva, E.T.: Separate signal pathways regulate the expression of a low-temperature-induced gene in *Arabidopsis thaliana* (L.) Heynh. - Plant mol. Biol. **16**: 1061-1071, 1991.

Ortiz, D., Hu, J., Salas Fernandez, M.G.: Genetic architecture of photosynthesis in *Sorghum bicolor* under non-stress and cold stress conditions. - J. exp. Bot. **68**: 4545-4557, 2017.

Pandey, S., Carrer, M., Castagneri, D., Petit, G.: Xylem anatomical responses to climate variability in Himalayan birch trees at one of the world's highest forest limit. - Perspect. Plant Ecol. Evol. Syst. **33**: 34-41, 2018.

Park, C.-J., Seo, Y.-S.: Heat shock proteins: a review of the molecular chaperones for plant immunity. - Plant Pathol. J. **31**: 323, 2015.

Pearce, S., Zhu, J., Boldizsár, Á., Vágújfalvi, A., Burke, A., Garland-Campbell, K., Galiba, G., Dubcovsky, J.: Large deletions in the *CBF* gene cluster at the Fr-B2 locus are associated with reduced frost tolerance in wheat. - Theor. appl. Genet. **126**: 2683-2697, 2013.

Porat, R., Pavoncello, D., Lurie, S., Mccollum, T.G.: Identification of a grapefruit cDNA belonging to a unique class of citrus dehydrins and characterization of its expression patterns under temperature stress conditions. - Physiol. Plant. **115**: 598-603, 2002.

Pudney, P., Buckley, S., Sidebottom, C., Twigg, S., Sevilla, M.-P., Holt, C., Roper, D., Telford, J., McArthur, A., Lillford, P.: The physico-chemical characterization of a boiling stable antifreeze protein from a perennial grass (*Lolium perenne*). - Arch. Biochem. Biophys. **410**: 238-245, 2003.

Rao, K., Raghavendra, A., Reddy, K.: Physiology and Molecular Biology of Stress Tolerance. - Springer, Dordrecht, Netherlands 2006.

Renaut, J., Hausman, J.F., Wisniewski, M.E.: Proteomics and low-temperature studies: bridging the gap between gene expression and metabolism. - Physiol. Plant. **126**: 97-109, 2006.

Riechmann, J.L., Heard, J., Martin, G., Reuber, L., Jiang, C.-Z., Keddie, J., Adam, L., Pineda, O., Ratcliffe, O., Samaha, R.: *Arabidopsis* transcription factors: genome-wide comparative analysis among eukaryotes. - Science **290**: 2105-2110, 2000.

Riechmann, J.L., Meyerowitz, E.M.: The AP2/EREBP family of plant transcription factors. - Biol. Chem. **379**: 633-646, 1998.

Ritonga, F.N., Chen, S.: Physiological and molecular mechanism involved in cold stress tolerance in plants. - Plants **9**: 560, 2020.

Rubio, S., Pérez, F.J.: ABA and its signaling pathway are involved in the cold acclimation and deacclimation of grapevine buds. - Sci. Hort. **256**: 108565, 2019.

Rudd, J.J., Franklin-Tong, V.E.: Unravelling response-specificity in Ca^{2+} signalling pathways in plant cells. - New Phytol. **151**: 7-33, 2001.

Sakuma, Y., Liu, Q., Dubouzet, J.G., Abe, H., Shinozaki, K., Yamaguchi-Shinozaki, K.: DNA-binding specificity of the ERF/AP2 domain of *Arabidopsis* DREBs, transcription factors involved in dehydration-and cold-inducible gene expression. - Biochem. biophys. Res. Commun. **290**: 998-1009, 2002.

Sales, E., Viruel, J., Domingo, C., Marqués, L.: Genome wide association analysis of cold tolerance at germination in temperate japonica rice (*Oryza sativa* L.) varieties. - PloS ONE **12**: e0183416, 2017.

Sanghera, G.S., Wani, S.H., Hussain, W., Singh, N.: Engineering cold stress tolerance in crop plants. - Curr. Genom. **12**: 30, 2011.

Schmidt, S., Dethloff, F., Beine-Golovchuk, O., Kopka, J.: The REIL1 and REIL2 Proteins of *Arabidopsis thaliana* are required for leaf growth in the cold - Plant Physiol. **163**: 1623-1639, 2013.

Seki, M., Kamei, A., Yamaguchi-Shinozaki, K., Shinozaki, K.: Molecular responses to drought, salinity and frost: common and different paths for plant protection. - Curr. Opin. Biotechnol. **14**: 194-199, 2003.

Seo, P.J., Lee, A.-K., Xiang, F., Park, C.-M.: Molecular and functional profiling of *Arabidopsis* pathogenesis-related genes: insights into their roles in salt response of seed germination. - Plant Cell. Physiol. **49**: 334-344, 2008.

Shabala, S., Alnayef, M., Bose, J., Chen, Z.-H., Venkataraman, G., Zhou, M., Shabala, L., Yu, M.: Revealing the role of the Calcineurin B-Like Protein-Interacting Protein Kinase 9 (CIPK9) in rice adaptive responses to salinity, osmotic stress, and K^+ deficiency. - Plants **10**: 1513, 2021.

Shi, J., Liu, M., Chen, Y., Wang, J., Lu, C.: Heterologous expression of the dehydrin-like protein gene *AmCIP* from *Ammopiptanthus mongolicus* enhances viability of *Escherichia coli* and tobacco under cold stress. - Plant Growth Regul. **79**: 71-80, 2016.

Shi, Y., Ding, Y., Yang, S.: Molecular regulation of CBF signaling in cold acclimation. - Trends Plant Sci. **23**: 623-637, 2018.

Shimamura, C., Ohno, R., Nakamura, C., Takumi, S.: Improvement of freezing tolerance in tobacco plants expressing a cold-responsive and chloroplast-targeting protein WCOR15 of wheat. - J. Plant Physiol. **163**: 213-219, 2006.

Sidebottom, C., Buckley, S., Pudney, P., Twigg, S., Jarman, C., Holt, C., Telford, J., McArthur, A., Worrall, D., Hubbard, R.: Heat-stable antifreeze protein from grass. - Nature **406**: 256-256, 2000.

Simpson, D.J., Smallwood, M., Twigg, S., Doucet, C.J., Ross, J., Bowles, D.J.: Purification and characterisation of an antifreeze protein from *Forsythia suspensa* (L.). - Cryobiology **51**: 230-234, 2005.

Soltész, A., Smedley, M., Vashegyi, I., Galiba, G., Harwood, W., Vágújfalvi, A.: Transgenic barley lines prove the involvement of *TaCBF14* and *TaCBF15* in the cold acclimation process and in frost tolerance. - J. exp. Bot. **64**: 1849-1862, 2013.

Steponkus, P.L., Uemura, M., Joseph, R.A., Gilmour, S.J., Thomashow, M.F.: Mode of action of the *COR15a* gene on the freezing tolerance of *Arabidopsis thaliana*. - Proc. nat. Acad. Sci. USA **95**: 14570-14575, 1998.

Stockinger, E.J., Skinner, J.S., Gardner, K.G., Francia, E., Pecchioni, N.: Expression levels of barley *Cbf* genes at the Frost resistance-H2 locus are dependent upon alleles at Fr-H1 and Fr-H2. - Plant J. **51**: 308-321, 2007.

Sun, W., Van Montagu, M., Verbruggen, N.: Small heat shock proteins and stress tolerance in plants. - Biochim. biophys. Acta, Gene Struct. Expression **1577**: 1-9, 2002.

Takumi, S., Nakamura, C.: Abiotic stress signal pathways associated with development of freezing tolerance after cold acclimation in common. - Front. Wheat Biosci., Wheat Info. Serv. **100**: 89-107, 2005.

Theocharis, A., Clément, C., Barka, E.A.: Physiological and molecular changes in plants grown at low temperatures. - Planta **235**: 1091-1105, 2012.

Thomashow, M.F.: Role of cold-responsive genes in plant freezing tolerance. - Plant Physiol. **118**: 1-8, 1998.

Thomashow, M.F.: Plant cold acclimation: freezing tolerance genes and regulatory mechanisms. - Annu. Rev. Plant Biol. **50**: 571-599, 1999.

Thomashow, M.F.: So what's new in the field of plant cold acclimation? Lots! - Plant Physiol. **125**: 89-93, 2001.

Timperio, A.M., Egidi, M.G., Zolla, L.: Proteomics applied on plant abiotic stresses: role of heat shock proteins (HSP). - J.

Proteom. **71**: 391-411, 2008.

Tolosa, L.N., Zhang, Z.: The role of major transcription factors in solanaceous food crops under different stress conditions: current and future perspectives. - Plants **9**: 56, 2020.

Trapnell, C., Williams, B.A., Pertea, G., Mortazavi, A., Kwan, G., Van Baren, M.J., Salzberg, S.L., Wold, B.J., Pachter, L.: Transcript assembly and quantification by RNA-Seq reveals unannotated transcripts and isoform switching during cell differentiation. - Nat. Biotechnol. **28**: 511-515, 2010.

Tyystjärvi, E.: Photoinhibition of photosystem II. - Int. Rev. cell. mol. Biol. **300**: 243-303, 2013.

Uemura, M., Steponkus, P.L.: Effect of cold acclimation on membrane lipid composition and freeze-induced membrane destablization. - In: Li, P.-H., Chen, T.-H.-H (eds.): Plant Cold Hardiness. Pp. 171-179. Springer, Dordrecht 1997.

Vágújfalvi, A., Galiba, G., Dubcovsky, J., Cattivelli, L.: Two loci on wheat chromosome 5A regulate the differential cold-dependent expression of the *cor14b* gene in frost-tolerant and frost-sensitive genotypes. - Mol. gen. Genet. **263**: 194-200, 2000.

Valitova, J., Renkova, A., Mukhitova, F., Dmitrieva, S., Beckett, R.P., Minibayeva, F.V.: Membrane sterols and genes of sterol biosynthesis are involved in the response of *Triticum aestivum* seedlings to cold stress. - Plant Physiol. Biochem. **142**: 452-459, 2019.

Visconti, S., D'Ambrosio, C., Fiorillo, A., Arena, S., Muzi, C., Zottini, M., Aducci, P., Marra, M., Scaloni, A., Camoni, L.: Overexpression of 14-3-3 proteins enhances cold tolerance and increases levels of stress-responsive proteins of *Arabidopsis* plants. - Plant Sci. **289**: 110215, 2019.

Vogel, J.T., Zarka, D.G., Van Buskirk, H.A., Fowler, S.G., Thomashow, M.F.: Roles of the CBF2 and ZAT12 transcription factors in configuring the low temperature transcriptome of *Arabidopsis*. - Plant J. **41**: 195-211, 2005.

Wang, T., Ye, C., Wang, M., Chu, G.: Identification of cold-stress responsive proteins in *Anabasis aphylla* seedlings *via* the iTRAQ proteomics technique. - J. Plant Interact. **12**: 505-519, 2017.

Wang, W., Gao, T., Chen, J., Yang, J., Huang, H., Yu, Y.: The late embryogenesis abundant gene family in tea plant (*Camellia sinensis*): genome-wide characterization and expression analysis in response to cold and dehydration stress. - Plant Physiol. Biochem. **135**: 277-286, 2019a.

Wang, X., Ding, Y., Li, Z., Shi, Y., Wang, J., Hua, J., Gong, Z., Zhou, J.-M., Yang, S.: PUB25 and PUB26 promote plant freezing tolerance by degrading the cold signaling negative regulator MYB15. - Dev. Cell **51**: 222-235.e225, 2019b.

Wang, Y., Mao, Z., Jiang, H., Zhang, Z., Chen, X.: A feedback loop involving MdMYB108L and MdHY5 controls apple cold tolerance. - Biochem. biophys. Res. Commun. **512**: 381-386, 2019c.

Welin, B.V., Olson, Å., Palva, E.T.: Structure and organization of two closely related low-temperature-induced dhn/lea/rab-like genes in *Arabidopsis thaliana* L. Heynh. - Plant mol. Biol. **29**: 391-395, 1995.

Wen, X., Wang, S., Duman, J.G., Arifin, J.F., Juwita, V., Goddard, W.A., Rios, A., Liu, F., Kim, S.-K., Abrol, R.: Antifreeze proteins govern the precipitation of trehalose in a freezing-avoiding insect at low temperature. - Proc. nat. Acad. Sci. USA **113**: 6683-6688, 2016.

Wisniewski, M., Nassuth, A., Teulieres, C., Marque, C., Rowland, J., Cao, P.B., Brown, A.: Genomics of cold hardiness in woody plants. - Crit. Rev. Plant. Sci. **33**: 92-124, 2014.

Wisniewski, M., Webb, R., Balsamo, R., Close, T.J., Yu, X.M., Griffith, M.: Purification, immunolocalization, cryoprotective, and antifreeze activity of PCA60: a dehydrin from peach (*Prunus persica*). - Physiol. Plant. **105**: 600-608, 1999.

Xu, H., Yang, Y., Xie, L., Li, X., Feng, C., Chen, J., Xu, C.: Involvement of multiple types of dehydrins in the freezing response in loquat (*Eriobotrya japonica*). - PloS ONE **9**: e87575, 2014.

Xu, Y., Hu, W., Liu, J., Song, S., Hou, X., Jia, C., Li, J., Miao, H., Wang, Z., Tie, W.: An aquaporin gene MaPIP2-7 is involved in tolerance to drought, cold and salt stresses in transgenic banana (*Musa acuminata* L.). - Plant Physiol. Biochem. **147**: 66-76, 2020.

Yamaguchi-Shinozaki, K., Shinozaki, K.: A novel *cis*-acting element in an *Arabidopsis* gene is involved in responsiveness to drought, low-temperature, or high-salt stress. - Plant Cell **6**: 251-264, 1994.

Yamasaki, Y., Randall, S.K.: Functionality of soybean CBF/DREB1 transcription factors. - Plant Sci. **246**: 80-90, 2016.

Yang, W., Zhang, L., Lv, H., Li, H., Zhang, Y., Xu, Y., Yu, J.: The K-segments of wheat dehydrin WZY2 are essential for its protective functions under temperature stress. - Front. Plant Sci. **6**: 406, 2015.

Yang, X., Wang, R., Hu, Q., Li, S., Mao, X., Jing, H., Zhao, J., Hu, G., Fu, J., Liu, C.: DlICE1, a stress-responsive gene from *Dimocarpus longan*, enhances cold tolerance in transgenic *Arabidopsis*. - Plant Physiol. Biochem. **142**: 490-499, 2019.

Yao, P., Sun, Z., Li, C., Zhao, X., Li, M., Deng, R., Huang, Y., Zhao, H., Chen, H., Wu, Q.: Overexpression of *Fagopyrum tataricum* FtbHLH2 enhances tolerance to cold stress in transgenic *Arabidopsis*. - Plant Physiol. Biochem. **125**: 85-94, 2018.

Yu, X.-M., Griffith, M., Wiseman, S.B.: Ethylene induces antifreeze activity in winter rye leaves. - Plant Physiol. **126**: 1232-1240, 2001.

Yue, N., Zheng, C.-X., BO, X., Hao, J.-Q.: Proteomics analysis of heteromorphic leaves of *Populus euphratica* Oliv. - Chin. Biotechnol. **29**, 2010.

Zachariassen, K.E., Kristiansen, E.: Ice nucleation and antinucleation in nature. - Cryobiology **41**: 257-279, 2000.

Zarka, D.G., Vogel, J.T., Cook, D., Thomashow, M.F.: Cold induction of *Arabidopsis CBF* genes involves multiple ICE (inducer of *CBF* expression) promoter elements and a cold-regulatory circuit that is desensitized by low temperature. - Plant Physiol. **133**: 910-918, 2003.

Zhang, J., Xu, Y., Huan, Q., Chong, K.: Deep sequencing of *Brachypodium* small RNAs at the global genome level identifies microRNAs involved in cold stress response. - BMC Genomics **10**: 1-16, 2009.

Zhang, X., Teixeira da Silva, J.A., Niu, M., Li, M., He, C., Zhao, J., Zeng, S., Duan, J., Ma, G.: Physiological and transcriptomic analyses reveal a response mechanism to cold stress in *Santalum album* L. leaves. - Sci. Rep. **7**: 1-18, 2017a.

Zhang, Z., Li, J., Pan, Y., Li, J., Shi, H., Zeng, Y., Guo, H., Yang, S., Zheng, W., Yu, J.: Natural variation in CTB4a enhances rice adaptation to cold habitats. - Nat. Biotechnol. **8**: 1-13, 2017b.

Zhao, C., Lang, Z., Zhu, J.-K.: Cold responsive gene transcription becomes more complex. - Trends Plant Sci. **20**: 466-468, 2015.

Zhao, C., Mao, K., You, C.-X., Zhao, X.-Y., Wang, S.-H., Li, Y.-Y., Hao, Y.-J.: Molecular cloning and functional analysis of a UV-B photoreceptor gene, *MdUVR8* (UV Resistance Locus 8), from apple. - Plant Sci. **247**: 115-126, 2016.

Zhao, C., Zhu, J.-K.: The broad roles of *CBF* genes: from development to abiotic stress. - Plant Signal. Behav. **11**: e1215794, 2016.

Zhao, M.-L., Wang, J.-N., Shan, W., Fan, J.-G., Kuang, J.-F., Wu, K.-Q., LI, X.-P., Chen, W.-X., He, F.-Y., Chen, J.-Y., Lu, W.-J.: Induction of jasmonate signalling regulators MaMYC2s and their physical interactions with MaICE1 in methyl jasmonate-induced chilling tolerance in banana fruit. - Plant. Cell. Environ. **36**: 30-51, 2013.

Zheng, Y., Luo, L., Wei, J., Chen, Q., Yang, Y., Hu, X., Kong, X.: The glutamate receptors AtGLR1. 2 and AtGLR1. 3 increase cold tolerance by regulating jasmonate signaling in *Arabidopsis thaliana*. - Biochem. biophys. Res. Commun. **506**: 895-900, 2018.

Zhou, M., Chen, H., Wei, D., Ma, H., Lin, J.: *Arabidopsis CBF3* and *DELLAs* positively regulate each other in response to low temperature. - Sci. Rep. **7**: 1-13, 2017.

Zhou, X., Wang, G., Sutoh, K., Zhu, J.-K., Zhang, W.: Identification of cold-inducible microRNAs in plants by transcriptome analysis. - Biochim. biophys. Acta, Gene. Regul. Mech. **1779**: 780-788, 2008.

Zuo, Z.-F., Kang, H.-G., Park, M.-Y., Jeong, H., Sun, H.-J., Song, P.-S., Lee, H.-Y.: *Zoysia japonica* MYC type transcription factor ZjICE1 regulates cold tolerance in transgenic *Arabidopsis*. - Plant Sci. **289**: 110254, 2019.