

Low-Temperature Signaling Pathways and Their Signaling Factors in Plant

Jianping Li^{1,2} , Zhiqing Liu^{2,3}, Xiaoyan Hao^{1,2}, Xiaochun Chang^{1,2}, Zhun Zhao^{1,2}, Guo Chen^{1,2}, Wenran Hu^{1,2}, Shengqi Gao^{1,2}, Quansheng Huang^{1,2*}

¹Institute of Nuclear Technology and Biotechnology, Xinjiang Academy of Agricultural Sciences, Urumqi, China

²Xinjiang Key Laboratory of Crop Biotechnology, Urumqi, China

³Institute of Economic Crops, Xinjiang Academy of Agricultural Sciences, Urumqi, China

Email: *hquansheng@126.com

How to cite this paper: Li, J.P., Liu, Z.Q., Hao, X.Y., Chang, X.C., Zhao, Z., Chen, G., Hu, W.R., Gao, S.Q. and Huang, Q.S. (2023) Low-Temperature Signaling Pathways and Their Signaling Factors in Plant. *Agricultural Sciences*, **14**, 256-268.

<https://doi.org/10.4236/as.2023.142017>

Received: January 18, 2023

Accepted: February 24, 2023

Published: February 27, 2023

Copyright © 2023 by author(s) and Scientific Research Publishing Inc. This work is licensed under the Creative Commons Attribution International License (CC BY 4.0).

<http://creativecommons.org/licenses/by/4.0/>



Open Access

Abstract

Low temperature as abiotic stress adversely impacts plant growth and development, and limits the ecological distribution of plants as well. Throughout their long evolutionary history, plants have developed a range of complicated and precise molecular regulatory mechanisms to deal with low-temperature stress, involving the activation of signal transduction pathways and the regulation of related genes. In this review, we provide a systematic summary of the most recent research findings regarding three hypotheses of cellular perception of low-temperature signals and two major intracellular low-temperature signaling pathways, including CBF-dependent signaling pathways and CBF-independent signaling pathways. Focus is placed on the functions of each component of the ICE-CBF-COR signaling cascade as well as their interrelationships. This review concludes that although some progress has been made in the identification, function, and mechanism of low-temperature response genes, their roles in the low-temperature regulatory network and molecular mechanisms still need to be studied in detail, which will be of great significance for improving the low-temperature tolerance of plants and adapting to climate change.

Keywords

Low Temperature, Signaling, CBF, COR, Signaling Factors

1. Introduction

Temperature, as one of the important environmental factors, always accompanies the whole life cycle of plants, influencing their growth and development and limiting their ecological distribution. Low temperature can negatively affect plant

growth and development, which is one of the abiotic stresses, called low-temperature stress. Throughout their long evolutionary history, plants have developed a variety of physiological and molecular mechanisms to adapt to the low-temperature environment and increase their tolerance to low temperatures [1]. With the advent of molecular biology, it has been found that low-temperature stress signal from perception involves different regulatory networks, which are complex and refined. Significant progress has been made in understanding the regulatory networks involved in cold tolerance over the past ten years. In many plants, a large number of transcription factors have been found that mediate cold signaling and regulate the expression of cold regulons [2]. It is composed of many proteins known as Cold-Regulated (COR) proteins and the essential transcriptional factors ICE (Inducer of CBF Expression) and CBF (C-repeat-Binding Factor). Other activators or repressors, in addition to the fundamental components of the *ICE*, *CBF*, and *COR* genes, are engaged in this pathway, and either directly or indirectly, contribute to cold tolerance [3]. Additionally, it has been demonstrated that plant hormones, the circadian clock, and light play significant roles in the response to cold stress. Although the ICE-CBF-COR pathway is the best-studied and important for plants' ability to tolerate low temperatures and homologous genes from this pathway have been identified in a diversity of cold-tolerant and sensitive plants, there are still many questions regarding the regulation and function of these genes, our knowledge of the regulation network involving *CBF* genes is still insufficient.

In this paper, we review the most recent research findings on low-temperature signaling pathways in recent years, focusing on the functions and interrelationships of each component of the low-temperature ICE-CBF-COR signaling cascade.

2. Plant Perception of low-Temperature Signals

When plants are exposed to low temperatures, they must first detect the signal for low temperatures. It is unclear, however, how plants perceive the low-temperature signal and transmit it to the nucleus to activate transcription factors that regulate gene expression and initiate a series of physiological and biochemical responses. There is no direct evidence to support the notion that membrane-based proteins serve as signal receptors for the perception of low-temperature signals, and few new forms of signal receptors have been described. Three hypotheses exist about the perception of low-temperature stress signals: 1) Ca^{2+} channel hypothesis, which proposes that temperature changes affect cell membrane fluidity, which in turn affects the structure and/or activity of membrane-localized proteins such as Ca^{2+} channels, resulting in changes in Ca^{2+} concentration on both sides of the cell membrane and generating calcium ion flow, a process that induces the expression of temperature-responsive genes [4]. It was found that the G-protein regulators COLD1 (Chilling-Tolerance Divergence 1) and RGA1 (Rice G-protein Alpha subunit 1) in rice can control the perception of low-temperature signals

and extracellular calcium ion influx in a synergistic manner [5]. OsCIPK7 (*Oryza sativa* Calcineurin B-like interacting protein kinases 7) detects low-temperature signals by adjusting its protein structure in response to variations in calcium ion concentration [6]. By controlling calcium ion concentration, CNGCs (Cyclic Nucleotide-Gated Ca²⁺ Channels), a crucial regulator of plant growth and development and stress response, can increase the cold tolerance of *Arabidopsis* and *Moss* [7] [8]. However, it is unclear how COLD1 or CNGCs regulate calcium ion influx during low-temperature stress. Therefore, determining which Ca²⁺ channels are involved in the perception of low-temperature signals remains to be deeply explored. The prevailing view is that Ca²⁺ acts as a second messenger mediating the transmission of cryogenic signals from extracellular to intracellular via calcium-binding proteins such as Calmodulin (CaM), Calcium-Dependent Protein Kinase (CDPK), CBL-Interacting Protein Kinase (CIPK) and proteins of the B subunit of Calcineurin-B Like (CBL) protein. It has been shown that CDPKs antagonist (W7) suppresses low-temperature response gene expression in *alfalfa* and *Arabidopsis* [9] [10]; while low-temperature stress significantly increases autophosphorylation and kinase activity of rice CIPK7, suggesting that low-temperature stress is involved in post-translational regulation of CIPK [6]. Similarly, *Arabidopsis* CBL and CIPK proteins were found to participate in low-temperature signaling in a Ca²⁺-dependent manner [11]. These primary groups of calcium-binding proteins bind calcium ions and undergo conformational changes to effectively regulate the expression of target genes.

2) MAPKs hypothesis, Mitogen-Activated Protein Kinases (MAPKs) are a class of intracellular serine/threonine protein kinases with diverse signaling functions in eukaryotic cells. A typical MAPK module consists of three protein kinases: MAPase Kinase Kinase (MKKK or MEKK), MAPase Kinase (MKK or MEK), and MAP Kinase (MAPK or MPK), which are mutually activated by cascade reactions phosphorylation to transmit signals of adversity stress including low temperature, high salt, and drought [12]. In plants, many MAPK family members respond to low-temperature stress such as the kinase activity of *alfalfa* MMK4 is increased under low temperature stress [13]; the expression of *Arabidopsis* MPK3, MPK4 and MPK6 genes can reach very high levels within a very short time after low-temperature stress [14]. In *Arabidopsis*, under low-temperature induction, CRLK1 activates MEKK1, which in turn activates MPK4 by phosphorylating MKK2 to form the MEKK1-MKK2-MPK4 cascade signaling pathway, and the activation of the MEKK1-MKK2-MPK4 signaling pathway inhibits the activation of the MKK4/5-MPK3/6 cascade signaling pathway, resulting in enhanced low-temperature tolerance in *Arabidopsis* [15].

3) Phosphatase hypothesis, despite the limited number of phosphatases identified to date that can detect low-temperature signals, members of this group play crucial roles in the low-temperature signal transduction pathway. It was found that *Arabidopsis* histidine kinase AtHK1 is up-regulated by low-temperature induction and transmits low-temperature stress signals to the nucleus through phosphorylation [16]; *Bacillus subtilis* histidine kinase K acts as a temperature recep-

tor to regulate the expression of desaturase [17]; Phosphoprotein phosphatase PP2A and PP2B regulate low-temperature signaling by activating or inactivating MAP kinases and CDPKs [18]; *Arabidopsis* CRLK1, a Ca²⁺/CaM receptor kinase, enhances low-temperature tolerance in *Arabidopsis* by positively regulating *COR* gene expression through phosphorylation of MEKK1 [19].

3. Low-Temperature Signaling Pathways

It is a complicated signaling process from receiving the low-temperature signal to producing the corresponding response, which generates a multi-branched signaling regulatory network in the cell. Numerous studies have demonstrated the involvement of the transcription factors CBF (C-repeat Binding Factor) as a significant regulatory factor. Based on the roles of CBFs in the regulation network of low-temperature signaling, the intracellular transduction of signals has been divided into two pathways: CBF-dependent and CBF-independent pathways.

3.1. The CBF-Dependent Signaling Pathway

Among the CBF-dependent signaling pathways, the ICE-CBF-COR signaling pathway is one of the most thoroughly investigated CBF-dependent pathways. ICE (Inducer of CBF Expression), CBF, and many Cold-Regulated (COR) proteins are its core components, of which the most critical component is CBF. Besides ICE, CBF, and COR, many related activators and repressors are as well engaged in this pathway and play crucial roles in the cold response [20]. *Arabidopsis* contains four members of the *CBF* gene family: *CBF1/DREB1B*, *CBF2/DREB1C*, *CBF3/DREB1A*, and *CBF4*. *CBF1-CBF3* expression is induced by low temperature. Regardless *CBF4* expression is not induced by low temperature, overexpression of *CBF4* improves plant cold and drought resistance [21]. The *CBF* single, double, and triple mutants all exhibit a low-temperature sensitive phenotype, with the *cbf123* triple mutant being the most sensitive to low temperature [22]. Upon low-temperature stimulation, *CBF1-CBF3* stimulates *COR* gene expression by binding directly to the CRT/DRE cis-acting region of the *COR* promoters [23]. Overexpression of *CBF1* upregulates *COR* expression, as indicated by an increase in cold tolerance in *Arabidopsis* [24]. Recently, it was also found that low-temperature-induced CBF interacts with PIF3 to enhance the stability of PHYB, which in turn enhances the low-temperature tolerance of *Arabidopsis* [25]. *CBF* homologs in rice, tomato, wheat, barley, and maize have been identified and demonstrated that their transcripts are induced by low temperature [26], and *PtCBF1*, *PtCBF2*, *PtCBF3*, and *PtCBF4* gene expression levels are upregulated in poplar leaves under low-temperature conditions [27].

The *ICE* gene family was discovered later than the *CBF* family, and in 2003, Chinnusamy *et al.* found that *ICE1* activates *CBF* gene expression by binding directly to the promoter of the *CBF* gene. The *ice1* mutant exhibits reduced tolerance with suppressed expression of the *CBF* gene at low temperatures [28]. *ICE2* was found to similarly function as a positive regulator of *CBF* with low-temperature

induction [29]. *ICE* homologs including *CbICE53* in caper [30], *CsICE1* in tea [31], *CdICE1* in chrysanthemum [32], *SlICE1* in tomato [33], *VaICE1* and *VaICE2* in grape [34], *RscICE1* in radish [35] and *ZmICE1* in maize [36] were found to be responsive to low-temperature stress. In *Arabidopsis*, Overexpression of wheat *TaICE41* and *TaICE87*, which are highly homologous to *Arabidopsis ICE1*, stimulated the expression of *AtCBF2* and *AtCBF3* and enhanced *Arabidopsis*' tolerance to low temperatures [37]. Meanwhile, recent studies indicate that the MAPK signaling pathway modulates the transcription of *CBFs* via regulating the expression of *ICE1*, thus supporting the possibility of multiple regulatory networks upstream of *CBF* [38].

In the early 1990s, a group of genes, namely *COR* genes, were found to play key roles in plant response to low-temperature stress [39], and further studies revealed that the ability of plants to tolerate low temperatures was largely dependent on the regulation of *COR* gene expression [40]. It is notable that the term “*COR* genes” broadly refers to all genes that are responsive to cold, including the cold-regulated gene *COR*, the low-temperature-inducible gene *LTI*, and the cold-inducible gene *KIN* [41]. The expression products of these “*COR* genes” are various types of proteins or biomolecules, including enzymes, molecular chaperones, and antifreeze proteins related to plant respiration, glucose metabolism, lipid metabolism, etc. Certain of these proteins and biomolecules restore cell metabolism at low temperatures, maintain cell membrane stability, and act directly as antifreeze proteins to protect cells from low-temperature injury [23]. *COR* genes in the narrow concept refer to cold regulated genes, which share the common feature of containing a *CRT/DRE* cis-acting element in the promoter that can bind directly to *CBF* genes. The *COR* genes described in this review are genes in the narrow sense of the concept. The expression of *COR* components, which are located downstream of the *ICE1-CBF-COR* pathway are crucial for low-temperature defense [40]. Studied have demonstrated that the *COR47* [42], *COR78* [43], *COR6.6* [44], and *COR15a* [45] genes act as positive regulators in *Arabidopsis*, and *Arabidopsis COR27* and *COR28* negatively regulate the plant's response to cold temperatures [46]. Expression of *COR* homologs from other species such as *BN28* (*BnaAnng37980D*, *Kin1*) and *BN115* (*COR15*) in oilseed rape [47], *COR14b* in barley, *WCOR410* and *WCOR14* in wheat, *CsCOR1* in tea, *BpCOR25* gene in Chinese cabbage [48] and *COR27* in cotton [49] are all mediated by low-temperature induction. Furthermore, *COR* genes are also involved in other aspects of plant development and growth. *Arabidopsis COR27* and *COR28* induced by blue light and low temperature positively control flowering time and biological rhythm [46], and interact with light signaling factors COP1 (Constitutively Photomorphogenic 1) SPA1 (Suppressor of PHYA-105) or HY5 (Elongated Hypocotyls 5) to inhibit photomorphogenesis promoting hypocotyl elongation in response to light [50]. Thus, it was suggested that *COR* genes not only act in the low-temperature signaling pathway but also in other signaling pathways.

Likewise, *CRT* (C-Repeat)/*DRE* (Dehydration Response Element) elements both

containing CCGAC core sequences are of interest as important low-temperature response components, which were found as dehydration response elements by Shinozaki and Baker in 1994 [41]. *CRT/DRE* elements identified from the promoters of *COR* members of *Arabidopsis KINI*, *COR6.6* [44], and *RD29A* (Responsive to Dehydration 29 of *Arabidopsis*) [51], oilseed rape *BN115* [52], wheat *WCSI20* [53] were found to respond to abiotic stresses such as low temperature, drought, and salt. It was also discovered that the *Arabidopsis RD29A* promoter regulates the *AtSOCl* (*Arabidopsis* Suppressor of Cytokine signaling 1) gene to promote early flowering in Chrysanthemum upon induction of drought stress [54].

Interestingly, the CBF signaling pathway is also modulated by post-transcriptional regulation of genes, including pre-mRNA processing, translocation, and translation. Pre-mRNA splicing is an essential process for gene function. For instance, low-temperature induced STA1 (Stabilized 1) protein selectively splice the *COR* gene intron thereby regulating *COR* gene expression [55]. NUPs (Nucleoporins) proteins mediate the translocation of RNAs and proteins between the nucleus and cytoplasm and alter the accumulation of CBF and other low-temperature-responsive mRNAs in the nucleus in response to low-temperature stimulation [56]. *Arabidopsis HOS1* (High expression of Osmotically responsive gene 1) gene promotes the ubiquitinated degradation of phosphorylated ICE1 by binding with phosphorylated ICE1, consequently repressing the transcription of CBF and its downstream genes [57]. Kinases such as MAPKs, CDPKs, and RLKs (Receptor-Like Kinases) exert regulatory functions on the CBF signaling pathway through phosphorylation [58].

3.2. The CBF-Independent Signaling Pathway

Not all *COR* genes are directly regulated by CBF proteins. Analysis of the *Arabidopsis* transcriptome revealed that only 12% of *COR* genes are regulated by CBF [59]. Studies on the promoters of *COR* genes activated by CBF in *Arabidopsis* showed that approximately 38% of genes do not have a *CRT* in a region 1000 bp upstream of the ATG start codon [60]. Despite the involvement of *HSFC1* (Heat Shock Factor 1), *ZAT12* (Zinc finger of Arabidopsis Thaliana 12), and *CZF1* (Phytophthora infestans CFZ1-like protein) in regulating *COR* gene expression, their expression in the *cbf123* triple mutant was not affected, indicating that the regulation of *COR* genes by *HSFC1*, *ZAT12*, and *CZF1* is not dependent on CBF but is functional in low-temperature signaling [3]. Further, CBF expression was not altered in *Arabidopsis esk1* (*Eskimo 1*) mutants, but the mutants showed a constitutive cold-tolerant phenotype [61]; Gigantea (GI), a group of proteins controlling nuclear localization, participated in the modulation of flowering and circadian rhythms in a cold-induced manner independent of the CBF pathway, and *gi-3* mutants showed a reduced capability for cold tolerance [62].

Plant hormones exhibit regulatory effects on signaling and downstream gene

expression during the low-temperature stress. JAZs (Jasmonate ZIM-domains) interact with EIN3/EIL1 (Ethylene-Insensitive 3/Ethylene-Insensitive 3-Like 1) to mediate JA (Jasmonic Acid), ETH (Ethylene), and CBF signaling, whereas the competitive binding of DELLA (RGA-like protein) to PIF4-BRZ1 (Phytochrome-Interacting Factor 4-Brassinazole Resistant 1) modulates the GA (Gibberellin Acid), BR (Brassinosteroid), and CBF signaling pathways [11]. Among the CBF-independent low-temperature regulatory mechanisms, ABA (Abscisic Acid)-dependent signaling transduction pathways have been investigated for many years, and studies of the *Arabidopsis* transcriptome indicated that 10% of ABA-responsive genes also respond to low-temperature stress [63]. Some *COR* genes, such as *RD29A*, *RD22*, *COR15A*, and *COR47*, contain ABA-responsive (ABRE) *cis*-elements activated by ABRE-binding proteins/factors (AREBs/ABFs) in addition to *CRT/DRE*-acting elements in their promoters [64]. Numerous regulatory factors in ABA biosynthesis and signaling pathways play crucial roles in *COR* gene expression, according to genetic research [62]. ABI3 (ABA Insensitive 3) as an ABRE-binding protein overexpressed in *Arabidopsis* resulted in enhanced *COR* gene expression in asexual tissues [65]. *PHYA* (*Phytochrome A*) and *PHYB* (*Phytochrome B*) negatively regulate the low-temperature response in *Arabidopsis* in an ABA-dependent manner [66].

4. Conclusion and Future Perspectives

Even though remarkable progress has been made in recent years in elucidating the molecular mechanisms of plant responses to low-temperature stress, the question of how plants perceive low-temperature signals has not yet been fully answered, and the various hypotheses proposed need to be supported by more evidence. Upon low-temperature perception, plants activate different types of complicated low-temperature signaling pathways in a CBF-dependent and CBF-independent manner, and despite the fact that CBF-dependent signaling pathways have been well explored, a number of crucial issues remain to be investigated. Many CBF-regulated low-temperature response genes, for instance, are functional in enhancing low-temperature tolerance in plants, but further studies are required to identify which of these genes play a crucial role and how they function. In addition, more signaling factors have been identified in both CBF-mediated and non-CBF-mediated signaling pathways, and these newly identified signaling factors play key or essential roles in other aspects of plant growth and development besides responding to low-temperature stress such as *Arabidopsis* *COR27* and *COR28* genes were found to be involved in the regulation of low-temperature response, photomorphogenesis, flowering time, and biological rhythms [49] [50]. The photoreceptors *PHYA* and *PHYB*, as well as *COP1*, *SPA1*, and *HY5*, which are major signaling components in the light signaling pathway, have been successively identified as being involved in the low-temperature response [50] [66]. The key roles of plant hormones in the low-temperature response have been proven, but the crosstalks between low-temperature signaling and phytohormones signaling, which are ne-

necessary for activating downstream genes essential for plant development and response to low temperature, and potential mechanisms of hormone signaling in the regulation of the low-temperature response still require investigation. We believe it will be the focus of ongoing studies, triggering the consideration of whether there is a balance between the regulatory network of plant development and the regulatory network of adversity to stabilize the whole regulatory network. In conclusion, even though there are still many remaining questions regarding how plants respond to low-temperature stress, these will be eventually addressed with continuous exploration.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (Grant nos.32260449) and the Science and Technology Innovation Base Construction Program of Xinjiang Uygur Autonomous Region—Resource Sharing Platform Construction (Grant nos.PT2222).

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

References

- [1] Huang, G.T., Ma, S.L., Bai, L.P., Zhang, L., Ma, H., Jia, P., Liu, J., Zhong, M. and Guo, Z.F. (2012) Signal Transduction during Cold, Salt, and Drought Stresses in Plants. *Molecular Biology Reports*, **39**, 969-987. <https://doi.org/10.1007/s11033-011-0823-1>
- [2] Zhang, H., Zhu, J., Gong, Z. and Zhu, J.K. (2022) Abiotic Stress Responses in Plants. *Nature Reviews. Genetics*, **23**, 104-119. <https://doi.org/10.1038/s41576-021-00413-0>
- [3] Liu, Y., Dang, P., Liu, L. and He, C. (2019) Cold Acclimation by the CBF-COR Pathway in a Changing Climate: Lessons from *Arabidopsis thaliana*. *Plant Cell Reports*, **38**, 511-519. <https://doi.org/10.1007/s00299-019-02376-3>
- [4] Zhu, J.K. (2016) Abiotic Stress Signaling and Responses in Plants. *Cell*, **167**, 313-324. <https://doi.org/10.1016/j.cell.2016.08.029>
- [5] Ma, Y., Dai, X., Xu, Y., Luo, W., Zheng, X., Zeng, D., Pan, Y., Lin, X., Liu, H., Zhang, D., Xiao, J., Guo, X., Xu, S., Niu, Y., Jin, J., Zhang, H., Xu, X., Li, L., Wang, W., Qian, Q., *et al.* (2015) COLD1 Confers Chilling Tolerance in Rice. *Cell*, **160**, 1209-1221. <https://doi.org/10.1016/j.cell.2015.01.046>
- [6] Zhang, D., Guo, X., Xu, Y., Li, H., Ma, L., Yao, X., Weng, Y., Guo, Y., Liu, C.M. and Chong, K. (2019) OsCIPK7 Point-Mutation Leads to Conformation and Kinase-Activity Change for Sensing Cold Response. *Journal of Integrative Plant Biology*, **61**, 1194-1200. <https://doi.org/10.1111/jipb.12800>
- [7] Finka, A., Cuendet, A.F., Maathuis, F.J., Saidi, Y. and Goloubinoff, P. (2012) Plasma Membrane Cyclic Nucleotide Gated Calcium Channels Control Land Plant Thermal Sensing and Acquired Thermotolerance. *The Plant Cell*, **24**, 3333-3348. <https://doi.org/10.1105/tpc.112.095844>
- [8] Gao, F., Han, X., Wu, J., Zheng, S., Shang, Z., Sun, D., Zhou, R. and Li, B. (2012) A Heat-Activated Calcium-Permeable Channel—*Arabidopsis* Cyclic Nucleotide-Gated

- Ion Channel 6—Is Involved in Heat Shock Responses. *The Plant Journal: For Cell and Molecular Biology*, **70**, 1056-1069. <https://doi.org/10.1111/j.1365-313X.2012.04969.x>
- [9] Dhindsa, R.S., Monroy, A.F., Sangwan, V., Kawczynski, W. and Labbé, E. (1997) Low Temperature Signal Transduction during Cold Acclimation of Alfalfa. In: Li, P.H. and Chen, T.H.H., Eds., *Plant Cold Hardiness*, Springer, Boston, MA, 15-28. https://doi.org/10.1007/978-1-4899-0277-1_2
- [10] García-Cerdán, J.G., Sveshnikov, D., Dewez, D., Jansson, S., Funk, C. and Schröder, W.P. (2009) Antisense Inhibition of the PsbX Protein Affects PSII Integrity in the Higher Plant *Arabidopsis thaliana*. *Plant & Cell Physiology*, **50**, 191-202. <https://doi.org/10.1093/pcp/pcn188>
- [11] Ding, Y., Shi, Y. and Yang, S. (2020) Molecular Regulation of Plant Responses to Environmental Temperatures. *Molecular Plant*, **13**, 544-564. <https://doi.org/10.1016/j.molp.2020.02.004>
- [12] Kumar, K., Raina, S.K. and Sultan, S.M. (2020) *Arabidopsis* MAPK Signaling Pathways and Their Cross Talks in Abiotic Stress Response. *Journal of Plant Biochemistry and Biotechnology*, **29**, 700-714. <https://doi.org/10.1007/s13562-020-00596-3>
- [13] Jonak, C., Kiegerl, S., Ligterink, W., Barker, P.J., Huskisson, N.S. and Hirt, H. (1996) Stress Signaling in Plants: A Mitogen-Activated Protein Kinase Pathway Is Activated by Cold and Drought. *Proceedings of the National Academy of Sciences of the United States of America*, **93**, 11274-11279. <https://doi.org/10.1073/pnas.93.20.11274>
- [14] Kovtun, Y.I., Chiu, W.L. and Tena, G. (2000) Functional Analysis of Oxidative Stress-Activated Mitogen-Activated Protein Kinase Cascade in Plants. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 2940-2945. <https://doi.org/10.1073/pnas.97.6.2940>
- [15] Yang, T., Shad Ali, G., Yang, L., Du, L., Reddy, A.S. and Poovaiah, B.W. (2010) Calcium/Calmodulin-Regulated Receptor-Like Kinase CRLK1 Interacts with MEKK1 in Plants. *Plant Signaling & Behavior*, **5**, 991-994. <https://doi.org/10.4161/psb.5.8.12225>
- [16] Urao, T., Yakubov, B., Satoh, R., Yamaguchi-Shinozaki, K., Seki, M., Hirayama, T. and Shinozaki, K. (1999) A Transmembrane Hybrid-Type Histidine Kinase in *Arabidopsis* Functions as an Osmosensor. *The Plant Cell*, **11**, 1743-1754. <https://doi.org/10.1105/tpc.11.9.1743>
- [17] Ardito, F., Giuliani, M., Perrone, D., Troiano, G. and Lo Muzio, L. (2017) The Crucial Role of Protein Phosphorylation in Cell Signaling and Its Use as Targeted Therapy. *International Journal of Molecular Medicine*, **40**, 271-280. <https://doi.org/10.3892/ijmm.2017.3036>
- [18] Sharma, P., Sharma, N. and Deswal, R. (2005) The Molecular Biology of the Low-Temperature Response in Plants. *BioEssays: News and Reviews in Molecular, Cellular and Developmental Biology*, **27**, 1048-1059. <https://doi.org/10.1002/bies.20307>
- [19] Yang, T., Chaudhuri, S., Yang, L., Du, L. and Poovaiah, B.W. (2010) A Calcium/Calmodulin-Regulated Member of the Receptor-Like Kinase Family Confers Cold Tolerance in Plants. *The Journal of Biological Chemistry*, **285**, 7119-7126. <https://doi.org/10.1074/jbc.M109.035659>
- [20] Verma, V., Ravindran, P. and Kumar, P.P. (2016) Plant Hormone-Mediated Regulation of Stress Responses. *BMC Plant Biology*, **16**, Article No. 86. <https://doi.org/10.1186/s12870-016-0771-y>
- [21] Haake, V., Cook, D., Riechmann, J.L., Pineda, O., Thomashow, M.F. and Zhang, J.Z. (2002) Transcription Factor CBF4 Is a Regulator of Drought Adaptation in *Arabidop-*

- sis. *Plant Physiology*, **130**, 639-648. <https://doi.org/10.1104/pp.006478>
- [22] Zhao, C., Zhang, Z., Xie, S., Si, T., Li, Y. and Zhu, J.K. (2016) Mutational Evidence for the Critical Role of CBF Transcription Factors in Cold Acclimation in Arabidopsis. *Plant Physiology*, **171**, 2744-2759. <https://doi.org/10.1104/pp.16.00533>
- [23] Wang, P., Cui, X., Zhao, C., Shi, L., Zhang, G., Sun, F., Cao, X., Yuan, L., Xie, Q. and Xu, X. (2017) COR27 and COR28 Encode Nighttime Repressors Integrating Arabidopsis Circadian Clock and Cold Response. *Journal of Integrative Plant Biology*, **59**, 78-85. <https://doi.org/10.1111/jipb.12512>
- [24] Jaglo-Ottosen, K.R., Gilmour, S.J., Zarka, D.G., Schabenberger, O. and Thomashow, M.F. (1998) Arabidopsis CBF1 Overexpression Induces COR Genes and Enhances Freezing Tolerance. *Science*, **280**, 104-106. <https://doi.org/10.1126/science.280.5360.104>
- [25] Jiang, B., Shi, Y., Peng, Y., Jia, Y., Yan, Y., Dong, X., Li, H., Dong, J., Li, J., Gong, Z., Thomashow, M.F. and Yang, S. (2020) Cold-Induced CBF-PIF3 Interaction Enhances Freezing Tolerance by Stabilizing the phyB Thermosensor in Arabidopsis. *Molecular Plant*, **13**, 894-906. <https://doi.org/10.1016/j.molp.2020.04.006>
- [26] Benedict, C., Skinner, J.S., Meng, R., Chang, Y. and Hurry, V. (2010) The CBF1-Dependent Low Temperature Signalling Pathway, Regulon and Increase in Freeze Tolerance Are Conserved in *Populus* spp. *Plant Cell & Environment*, **29**, 1259-1272. <https://doi.org/10.1111/j.1365-3040.2006.01505.x>
- [27] Zhang, H., Gong, Y., Sun, P., Chen, S. and Ma, C. (2022) Genome-Wide Identification of CBF Genes and Their Responses to Cold Acclimation in *Taraxacum kok-saghyz*. *PeerJ*, **10**, e13429. <https://doi.org/10.7717/peerj.13429>
- [28] Chinnusamy, V., Ohta, M., Kanrar, S., Lee, B.H., Hong, X., Agarwal, M. and Zhu, J.K. (2003) ICE1: A Regulator of Cold-Induced Transcriptome and Freezing Tolerance in Arabidopsis. *Genes & Development*, **17**, 1043-1054. <https://doi.org/10.1101/gad.1077503>
- [29] Fursova, O.V., Pogorelko, G.V. and Tarasov, V.A. (2009) Identification of ICE2, a Gene Involved in Cold Acclimation Which Determines Freezing Tolerance in *Arabidopsis thaliana*. *Gene*, **429**, 98-103. <https://doi.org/10.1016/j.gene.2008.10.016>
- [30] Zhou, M., Wu, L., Liang, J., Shen, C. and Lin, J. (2012) Cold-Induced Modulation of *CbICE53* Gene Activates Endogenous Genes to Enhance Acclimation in Transgenic Tobacco. *Molecular Breeding*, **30**, 1611-1620. <https://doi.org/10.1007/s11032-012-9744-5>
- [31] Wang, Y., Jiang, C.J., Li, Y.Y., Wei, C.L. and Deng, W.W. (2012) CsICE1 and CsCBF1: Two Transcription Factors Involved in Cold Responses in *Camellia sinensis*. *Plant Cell Reports*, **31**, 27-34. <https://doi.org/10.1007/s00299-011-1136-5>
- [32] Chen, Y., Jiang, J., Song, A., Chen, S., Shan, H., Luo, H., Gu, C., Sun, J., Zhu, L., Fang, W. and Chen, F. (2013) Ambient Temperature Enhanced Freezing Tolerance of *Chrysanthemum dichrum* CdICE1 Arabidopsis via miR398. *BMC Biology*, **11**, Article No. 121. <https://doi.org/10.1186/1741-7007-11-121>
- [33] Feng, H.L., Ma, N.N., Meng, X., Zhang, S., Wang, J.R., Chai, S. and Meng, Q.W. (2013) A Novel Tomato MYC-Type ICE1-Like Transcription Factor, SLICE1a, Confers Cold, Osmotic and Salt Tolerance in Transgenic Tobacco. *Plant Physiology and Biochemistry*, **73**, 309-320. <https://doi.org/10.1016/j.plaphy.2013.09.014>
- [34] Xu, W., Jiao, Y., Li, R., Zhang, N., Xiao, D., Ding, X. and Wang, Z. (2014) Chinese Wild-Growing *Vitis amurensis* ICE1 and ICE2 Encode MYC-Type bHLH Transcription Activators That Regulate Cold Tolerance in Arabidopsis. *PLOS ONE*, **9**,

- e102303. <https://doi.org/10.1371/journal.pone.0102303>
- [35] Man, L., Xiang, D., Wang, L., Zhang, W., Wang, X. and Qi, G. (2017) Stress-Responsive Gene *RsICE1* from *Raphanus sativus* Increases Cold Tolerance in Rice. *Protoplasma*, **254**, 945-956. <https://doi.org/10.1007/s00709-016-1004-9>
- [36] Lu, X., Yang, L., Yu, M., Lai, J., Wang, C., McNeil, D., Zhou, M. and Yang, C. (2017) A Novel *Zea mays* ssp. *mexicana* L. MYC-Type ICE-Like Transcription Factor Gene *ZmmICE1*, Enhances Freezing Tolerance in Transgenic *Arabidopsis thaliana*. *Plant Physiology and Biochemistry*, **113**, 78-88. <https://doi.org/10.1016/j.plaphy.2017.02.002>
- [37] Guo, J., Ren, Y., Tang, Z., Shi, W. and Zhou, M. (2019) Characterization and Expression Profiling of the ICE-CBF-COR Genes in Wheat. *PeerJ*, **7**, e8190. <https://doi.org/10.7717/peerj.8190>
- [38] Adamovich, I., Agarwal, S., Ahedo, E., Alves, L.L., Baalrud, S., Babaeva, N., Bogaerts, A., Bourdon, A., Bruggeman, P.J., Canal, C., Choi, E.H., Coulombe, S., Donkó, Z., Graves, D.B., Hamaguchi, S., Hegemann, D., Hori, M., Kim, H.H., Kroesen, G.M.W., Kushner, M.J., Laricchiuta, A., Li, X., Magin, T.E., Mededovic Thagard, S., Miller, V., Murphy, A.B., Oehrlein, G.S., Puac, N., Sankaran, R.M., Samukawa, S., Shiratani, M., Šimek, M., Tarasenko, N., Terashima, K., Thomas Jr., E., Trieschmann, J., Tsikata, S., Turner, M.M., Van Der Walt, I.J., Van De Sanden, M.C.M. and Von Woedtke, T. (2022) The 2022 Plasma Roadmap: Low Temperature Plasma Science and Technology. *Journal of Physics D: Applied Physics*, **55**, Article ID: 373001. <https://doi.org/10.1088/1361-6463/ac5e1c>
- [39] Baker, S.S., Wilhelm, K.S. and Thomashow, M.F. (1994) The 5'-Region of *Arabidopsis thaliana cor15a* Has *cis*-Acting Elements That Confer Cold-, Drought- and ABA-Regulated Gene Expression. *Plant Molecular Biology*, **24**, 701-713. <https://doi.org/10.1007/BF00029852>
- [40] Zhao, C., Lang, Z. and Zhu, J.K. (2015) Cold Responsive Gene Transcription Becomes More Complex. *Trends in Plant Science*, **20**, 466-468. <https://doi.org/10.1016/j.tplants.2015.06.001>
- [41] Shi, Y., Ding, Y. and Yang, S. (2018) Molecular Regulation of CBF Signaling in Cold Acclimation. *Trends in Plant Science*, **23**, 623-637. <https://doi.org/10.1016/j.tplants.2018.04.002>
- [42] Gilmour, S.J., Artus, N.N. and Thomashow, M.F. (1992) cDNA Sequence Analysis and Expression of Two Cold-Regulated Genes of *Arabidopsis thaliana*. *Plant Molecular Biology*, **18**, 13-21. <https://doi.org/10.1007/BF00018452>
- [43] Horvath, D.P., McLarney, B.K. and Thomashow, M.F. (1993) Regulation of *Arabidopsis thaliana* L. (Heyn) *cor78* in Response to Low Temperature. *Plant Physiology*, **103**, 1047-1053. <https://doi.org/10.1104/pp.103.4.1047>
- [44] Wang, H., Datla, R., Georges, F., Loewen, M. and Cutler, A.J. (1995) Promoters from *kin1* and *cor6.6*, Two Homologous *Arabidopsis thaliana* Genes: Transcriptional Regulation and Gene Expression Induced by Low Temperature, ABA, Osmoticum and Dehydration. *Plant Molecular Biology*, **28**, 605-617. <https://doi.org/10.1007/BF00021187>
- [45] Artus, N.N., Uemura, M., Steponkus, P.L., Gilmour, S.J., Lin, C. and Thomashow, M.F. (1996) Constitutive Expression of the Cold-Regulated *Arabidopsis thaliana* COR15a Gene Affects Both Chloroplast and Protoplast Freezing Tolerance. *Proceedings of the National Academy of Sciences of the United States of America*, **93**, 13404-13409. <https://doi.org/10.1073/pnas.93.23.13404>
- [46] Li, X., Ma, D., Lu, S.X., Hu, X., Huang, R., Liang, T., Xu, T., Tobin, E.M. and Liu, H.

- (2016) Blue Light- and Low Temperature-Regulated COR27 and COR28 Play Roles in the Arabidopsis Circadian Clock. *The Plant Cell*, **28**, 2755-2769. <https://doi.org/10.1105/tpc.16.00354>
- [47] Weretilnyk, E., Orr, W., White, T.C., Iu, B. and Singh, J. (1993) Characterization of Three Related Low-Temperature-Regulated cDNAs from Winter *Brassica napus*. *Plant Physiology*, **101**, 171-177. <https://doi.org/10.1104/pp.101.1.171>
- [48] Wani, S.H., Sah, S.K., Sanghera, G., Hussain, W. and Singh, N.B. (2016) Genetic Engineering for Cold Stress Tolerance in Crop Plants. *Plants*, **4**, 173-201. <https://doi.org/10.2174/9781681081731116040010>
- [49] Li, J.P., Hao, X.Y., Tuerxun, Z., Chang, X.C., Gao, S.Q., Hu, W.R., Chen, G. and Huang, Q.S. (2020) GhCOR27, Which Encodes a Cold-Related Gene, Is Involved in Cotton Tolerance to Cold Stress. *International Journal of Applied Agricultural Sciences*, **6**, 1-6. <https://doi.org/10.11648/j.ijaas.20200601.11>
- [50] Zhu, W., Zhou, H., Lin, F., Zhao, X., Jiang, Y., Xu, D. and Deng, X.W. (2020) COLD-REGULATED GENE27 Integrates Signals from Light and the Circadian Clock to Promote Hypocotyl Growth in Arabidopsis. *The Plant Cell*, **32**, 3155-3169. <https://doi.org/10.1105/tpc.20.00192>
- [51] Kasuga, M., Miura, S., Shinozaki, K. and Yamaguchi-Shinozaki, K. (2004) A Combination of the Arabidopsis DREB1A Gene and Stress-Inducible *rd29A* Promoter Improved Drought- and Low-Temperature Stress Tolerance in Tobacco by Gene Transfer. *Plant & Cell Physiology*, **45**, 346-350. <https://doi.org/10.1093/pcp/pch037>
- [52] Jiang, C., Iu, B. and Singh, J. (1996) Requirement of a CCGAC *cis*-Acting Element for Cold Induction of the *BN15* Gene from Winter *Brassica napus*. *Plant Molecular Biology*, **30**, 679-684. <https://doi.org/10.1007/BF00049344>
- [53] Ouellet, F., Vazquez-Tello, A. and Sarhan, F. (1998) The Wheat *wcs120* Promoter Is Cold-Inducible in Both Monocotyledonous and Dicotyledonous Species. *FEBS Letters*, **423**, 324-328. [https://doi.org/10.1016/S0014-5793\(98\)00116-1](https://doi.org/10.1016/S0014-5793(98)00116-1)
- [54] Jin, Z., Yu, X. and Pei, Y. (2020) Ectopic Expression of *AtSOC1* Gene Driven by the Inducible Promoter *rd29A*, Causes Early Flowering in Chrysanthemum. *Scientia Horticulturae*, **261**, Article ID: 109051. <https://doi.org/10.1016/j.scienta.2019.109051>
- [55] Lee, B.H., Kapoor, A., Zhu, J. and Zhu, J.K. (2006) STABILIZED1, a Stress-Upregulated Nuclear Protein, Is Required for Pre-mRNA Splicing, mRNA Turnover, and Stress Tolerance in Arabidopsis. *The Plant Cell*, **18**, 1736-1749. <https://doi.org/10.1105/tpc.106.042184>
- [56] Dong, C.H., Agarwal, M., Zhang, Y., Xie, Q. and Zhu, J.K. (2006) The Negative Regulator of Plant Cold Responses, HOS1, Is a RING E3 Ligase That Mediates the Ubiquitination and Degradation of ICE1. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 8281-8286. <https://doi.org/10.1073/pnas.0602874103>
- [57] Dong, C.H., Hu, X., Tang, W., Zheng, X., Kim, Y.S., Lee, B.H. and Zhu, J.K. (2006) A Putative Arabidopsis Nucleoporin, AtNUP160, Is Critical for RNA Export and Required for Plant Tolerance to Cold Stress. *Molecular and Cellular Biology*, **26**, 9533-9543. <https://doi.org/10.1128/MCB.01063-06>
- [58] Mann, M. and Jensen, O.N. (2003) Proteomic Analysis of Post-Translational Modifications. *Nature Biotechnology*, **21**, 255-261. <https://doi.org/10.1038/nbt0303-255>
- [59] Wang, D.Z., Jin, Y.N., Ding, X.H., Wang, W.J., Zhai, S.S., Bai, L.P. and Guo, Z.F. (2017) Gene Regulation and Signal Transduction in the ICE-CBF-COR Signaling

- Pathway during Cold Stress in Plants. *Biochemistry*, **82**, 1103-1117. <https://doi.org/10.1134/S0006297917100030>
- [60] Fowler, S. and Thomashow, M.F. (2002) Arabidopsis Transcriptome Profiling Indicates That Multiple Regulatory Pathways Are Activated during Cold Acclimation in Addition to the CBF Cold Response Pathway. *The Plant Cell*, **14**, 1675-1690. <https://doi.org/10.1105/tpc.003483>
- [61] Browse, J. and Xin, Z. (2001) Temperature Sensing and Cold Acclimation. *Current opinion in Plant Biology*, **4**, 241-246. [https://doi.org/10.1016/S1369-5266\(00\)00167-9](https://doi.org/10.1016/S1369-5266(00)00167-9)
- [62] Cao, S.Q., Song, Y.Q. and Su, L. (2007) Freezing Sensitivity in the Gigantea Mutant of Arabidopsis Is Associated with Sugar Deficiency. *Biologia Plantarum*, **51**, 359-362. <https://doi.org/10.1007/s10535-007-0073-1>
- [63] Kreps, J.A., Wu, Y., Chang, H.S., Zhu, T., Wang, X. and Harper, J.F. (2002) Transcriptome Changes for Arabidopsis in Response to Salt, Osmotic, and Cold Stress. *Plant Physiology*, **130**, 2129-2141. <https://doi.org/10.1104/pp.008532>
- [64] Uno, Y., Furihata, T., Abe, H., Yoshida, R., Shinozaki, K. and Yamaguchi-Shinozaki, K. (2000) Arabidopsis Basic Leucine Zipper Transcription Factors Involved in an Abscisic Acid-Dependent Signal Transduction Pathway under Drought and High-Salinity Conditions. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 11632-11637. <https://doi.org/10.1073/pnas.190309197>
- [65] Penfield, S. (2008) Temperature Perception and Signal Transduction in Plants. *The New Phytologist*, **179**, 615-628. <https://doi.org/10.1111/j.1469-8137.2008.02478.x>
- [66] Wang, F., Guo, Z., Li, H., Wang, M., Onac, E., Zhou, J., Xia, X., Shi, K., Yu, J. and Zhou, Y. (2016) Phytochrome A and B Function Antagonistically to Regulate Cold Tolerance via Abscisic Acid-Dependent Jasmonate Signaling. *Plant Physiology*, **170**, 459-471. <https://doi.org/10.1104/pp.15.01171>