Chapter 5

CBF-Dependent and CBF-Independent Transcriptional Regulation of Cold Stress Responses in Plants

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5.1 Introduction

The world's population will reach 9.1 billion by 2050, which will have to be feed. Since the 1960s, crop production has seen a very important increase through plant improvement. However, due to climate change, urbanization, as well as pollution, the total area of arable land is close to maximum utilization, with a direct effect on the increase of human undernourishment. It is imperative that other plant breeding tools in which biotechnological engineering of economically and nutritionally important traits should be critically and thoroughly examined. The major abiotic stresses worldwide causing risks to food security are high salinity, drought, submergence and extreme temperature including heat and cold (Wani and Sah 2014).

Plants are often confronted with unfavourable environmental conditions that can be called 'stress' and which results in decreased growth and yield of crops. Invariably subjected to all kinds of environmental stresses of biotic origin (aggressions by pathogens) or abiotic (excess or lack of light, abrupt fluctuations in temperature, hypoxia, water stress, salinity, etc.), plant developed varied and ingenious strategies to defend themselves and adapt to their changing environment, triggering sometimes very complex spectra of molecular, metabolic and morphogenetic responses (Fig. 5.1).

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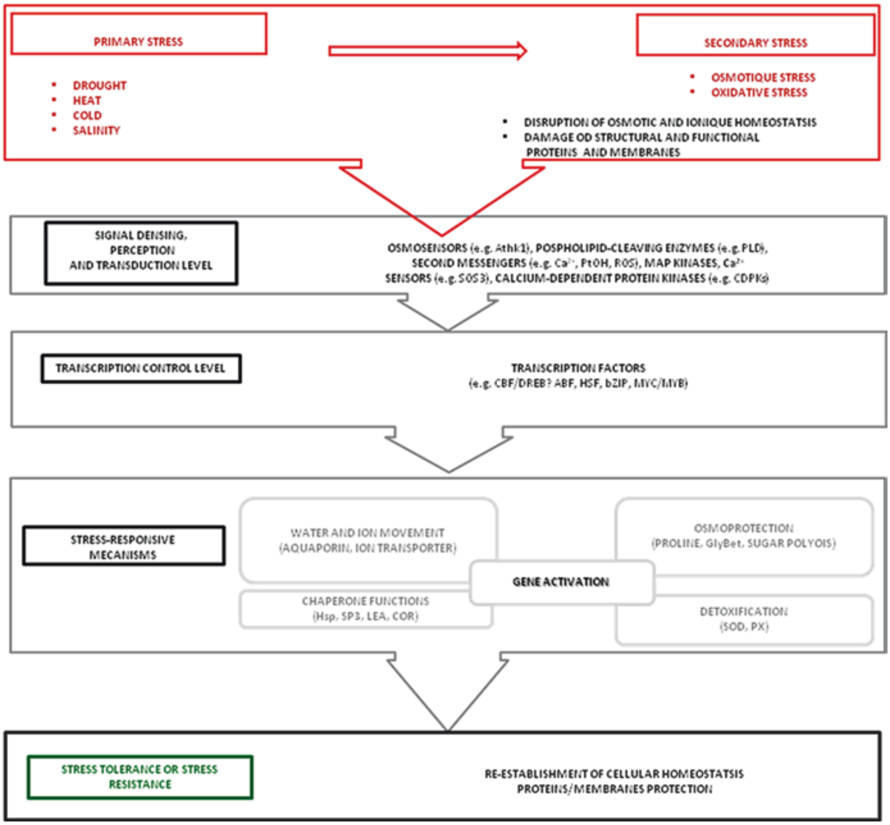

Fig. 5.1 Plant responses to abiotic stresses. Primary stresses are interrelated and provoke cellular damage as well as secondary stresses. The initial stress signal causes activation of signalling process as well as transcription control. Consequence of this is initiation of stress-responsive mechanism to restoration of cellular homeostasis, accompanied by the protection and repair of damaged proteins and membranes. Finally, plant gained tolerance or resistance to stress. ABF ABRE binding factor, Athk1 *Arabidopsis thaliana* histidine kinase-1, bZIP basic leucine zipper transcription factor, CBF/DREB C-repeat binding factor/dehydration-responsive binding protein, CDPK calcium-dependent protein kinase, COR cold-responsive protein, Hsp heat-shock protein, LEA late embryogenesis abundant, MAP mitogen-activated protein, PLD phospholipase D–PtdOH, phosphatidic acid, PX peroxidase, ROS reactive oxygen species, SOD super dismutase, SP1 stable protein 1. (Source: Gerszberg and Hnatuszko-Konka 2017)

Abiotic stresses induce, separately or in combination, general and specific adverse impacts on plant growth and development, ultimately leading to significant crop yield losses. The main abiotic stresses (drought, salinity, frost) lead to reduced water availability for essential cellular functions and maintenance of turgor pressure. However, beyond these common and well- characterized mechanisms, the response to these stresses has specificities. Most plants have developed various coping mechanisms and intricate detoxification strategies to overcome these stress conditions (Guy et al. 1985; Yahia and Fyad-Lameche 2003; Gosal et al. 2009; He et al. 2015; Yahia et al. 2015; Wani and Kumar 2015; Touati et al. 2016; Wani et al. 2016; Joshi et al. 2016).

The increased knowledge of all the metabolites formed (or metabolomics), the corresponding genes and the transcription factors (TFs) controlling their expression in response to stress conditions has bettered chances for deciphering these underlying responsive mechanisms and to target them for producing stress-tolerant plants. In the initial attempts, Guy et al. (1985) observed changes in gene expression during cold acclimatization and concluded that cold-responsive genes can achieve the biochemical and physiological changes necessary for growth and development. A large number of cold-induced genes have been isolated since then and characterized corresponding to fatty acids, chaperone proteins, proteins involved in the biosynthesis of osmoprotectants, antifreeze proteins and gene regulation components such as TFs, kinases and phosphatases, but many remain unknown. Chinnusamy et al. (2010) argued that the degree of chilling or frost tolerance of a plant therefore depends on its ability to maintain the expression of cold-inducible genes at a high level during the acclimation period.

In the initial stage of cold stress, the plants highlight changes in the expression of genes leading to synthesis of common or specific proteins. In addition, these changes in the gene expression were often accompanied by elevated levels of metabolites such as osmoprotective agents against the adverse effects of low-temperature stress (Sanghera et al. 2011). Indeed, under low temperature, multitude inducible genes have been isolated from several plants, and the expression of some of them is regulated by C-repeat binding factor/dehydration-responsive element binding (CBF/DREB1) TFs. These TFs (*bZip*, *MYC*, *MYB*, *DREB*, *NACs NAM*, *ATAF*, *CUC*, *MAP* kinase, CDP kinase, etc.) regulate gene expression, and signal transduction and function under stress responses may be useful for improving the abiotic stress tolerance in plants (Gosal et al. 2009).

Plant species react in various ways to cold stress. They modify their physiology, metabolism and growth by reprogramming gene expression. Cold stress signals in plants are transmitted to activate CBF-dependent and CBF-independent transcriptional pathways, of which the earlier one activates CBF regulon. Transcriptional cascades are next players which operate through ABA-dependent and ABA-independent pathways to induce cold-regulated (COR) gene expression, resulting in increasing levels of hundreds of metabolites, some of them being known to have protective effects against the damaging impacts of cold stress (Heidarvand and Amiri 2010). CBF TF genes are induced by the constitutively expressed ICE1 (inducer of CBF expression 1) by binding to the *CBF* promoter. ICE1–CBF cold response pathway is conserved in diverse plant species (Fig. 5.1). The cold-inducible genes are regulated mainly via transcriptional regulation. This regulation is largely modulated by proteins that bind to specific sites in the promoter regions of the genes. The CCGAC (or CRT for C-repeat) pattern forms the pattern of a low-temperature-responsive element or dehydration-responsive element (DRE). CBFs are TFs that regulate the expression of several genes in relation to abiotic stress (Chinnusamy et al. 2006; Zhao et al. 2011; Guo et al. 2011). CBF genes were also referred to as DRE-binding factor genes that code for the transcription of conserved sequences of COR (CCGAC [C-repeat (CRT)/dehydration element (DRE)]) genes at the promoter level of several genes. Responses to stress include genes for early dehydration stress responses and cold stress (Stockinger et al. 1997; Liu et al. 1998; Thomashow 2001; Shinozaki and Yamaguchi-Shinozaki 2007).

5.2 Perception and Transduction of the Cold Stress Signals

For a plant to implement effective cold tolerance mechanisms, it is necessary first to perceive the low temperatures followed by signal transmission in order to regulate the appropriate genes, and finally the proteins are synthesized to limit the damage caused by the cold (Navarro 2009). Cold stress induces immediate changes (known as primary events) in the cell balance. These primary events are the cause of the damage of the cell but also inform the cell of the existence of a stress. It is well established that the cell membrane systems are the main sites of gel injury in plants. Cell membranes are fluid structures; membrane fluidity depends on temperature but also on the lipid composition and degree of saturation of the fatty acids of the membranes (Steponkus 1984; Murata and Los 1997). The signal induced by low temperature is initially perceived by the plasma membrane either by the membrane fluidity or through membrane sensors such as Ca^{2+}, kinases, histidine kinase receptors and phospholipases. Subsequently, cytoskeletal reorganization and cytosolic Ca^{2+} influx take place. The increase of cytosolic Ca^{2+} is captured by CDPKs, phosphatases and MAPKs, whose role is signal transduction to activate the transcriptional cascade (Knight and Knight 2001; Vergnolle et al. 2005). Cold temperatures can reduce their fluidity, causing increased stiffness, and negative temperatures cause damage due to the formation of ice crystals. The presence of ice in the extracellular space reduces its water potential. This results in dehydration and contraction of the cell volume, which will destabilize the plasma membrane. When crystallization reaches the intracellular medium, it results in cell destruction and therefore tissue death (Guy 1990).

The major difference between acclimated and non-acclimated plant membranes is that the membrane material remains intact during the freeze-thaw cycle in the tolerant cells. The cells of the tolerant plants are able to modify their wall and the plasma membrane to protect the plant from injury caused by freezing. Indeed, the protoplasts of acclimated plants do not form an endocytotic vesicle that would inevitably lead to a loss of surface. On the other hand, exocytotic extrusions are formed that allow the membrane to recover its original surface without tearing during the thaw period. Freezing or frost tolerance, therefore, was closely related to the mechanisms by which plant cells avoid injury to their cellular membranes. Several studies have shown that, during cold stress, the levels of sterols and phospholipids in the plasma membrane increase. On the other hand, the levels of acetylated glucosides and cerebrosides (CER) decrease. These changes were observed in *Arabidopsis*, rye and oats during cold acclimatization. These changes would have a role in the cryostability of the plasma membrane during freezing (Uemura et al. 1995, 2006; Yamazaki et al. 2009). In the similar vein, Zhu (2016) reported that the mechanisms of cold-sensing in plants are that cold shock leads to changes in membrane fluidity and rearrangement of the cytoskeleton that trigger Ca^{2+} influx; consequently it activates the induction of COR genes.

Ma et al. (2015) showed that COLD1 gene plays a key role in enhancing chilling tolerance in rice line. It stimulates intracellular Ca^{2+} influx by associating with the α-subunit of the G protein and accelerates the activity of the G-GTPase protein, to ultimately up-regulate the expression of the COR genes, under cold stress. Furthermore, abscisic acid (ABA) and reactive oxygen species (ROS) can also induce Ca^{2+} signatures that influence cold signalling (Chinnusamy et al. 2007). If the input of Ca^{2+} ions is inhibited, the low-temperature tolerance decreases (Sung et al. 2003).

Among the main molecules involved in signal transduction are ABA (Leung and Giraudat 1998) and ROS (Lamb and Dixon 1997). ABA is a stress hormone that regulates many aspects of plant development such as seed germination, dormancy and tolerance to seed desiccation, but it also plays a major role in the response to biotic and abiotic stresses (Chinnusamy et al. 2004). ABA improves antioxidant defence and slows ROS accumulation caused by low temperatures (Liu et al. 2011). Thus, it regulates the expression of many genes involved in resistance to cold, osmotic shock or dehydration (Xiong et al. 2001).

Some symptoms observed under stress of biotic or abiotic origin are the consequence of a strong accumulation of oxygen free radicals and an alteration of cellular homeostasis. Plants exposed to low temperatures produce reactive forms of oxygen that damage membrane lipids, proteins, chlorophyll and nucleic acids. Although reactive forms of oxygen are formed during the normal metabolism of the plant, increasing their intracellular concentration is often synonymous with stress. In addition to their effect on calcium signatures, they are also involved in the signalling cascades responsible for the induction and regulation of many defence genes. Thus, ROS serves as a second messenger for activation of stress response and defence mechanisms (Mittler 2002; Apel and Hirt 2004).

5.3 Regulation of Gene Expression in Response to Low Temperatures

The expression of gene cascades in plants is regulated by abiotic environmental stresses including cold (Thomashow 1999; Shinozaki et al. 2003; Shi et al. 2018a, b). Sensitive or cold tolerant, acclimated or not acclimated, all plants are generally capable of experiencing low temperatures and modifying gene expression in response to these conditions, though with a varying degree. Large modifications at the transcriptome scale are noted each time (Carvallo et al. 2011; Maruyama et al. 2012), leading to modifications of the proteome and the metabolome. Recently, Kumar and Wigge (2010) showed that temperature can have a direct effect on chromatin remodelling and thus on the activation of transcription of many genes.

Many abiotic inducible genes are controlled by ABA, but not all, indicating that both ABA-dependent and independent ABA regulation systems are involved in the expression of stress-sensitive genes (Thomashow 1999; Shinozaki et al. 2003). In response to cold stress, the independent ABA pathway leads to the activation of a family of TF genes called DREBs or CBFs, in turn inducing effector genes by binding to the cis CRT/DRE element (C-repeat/dehydration element) located in their promoter region (Stockinger et al. 1997). At the same time, the cold induces an accumulation of the ABA hormone, which leads to the expression of the ABA-responsive element binding factor which can also induce the effector genes but via another cis sequence: the ABA-responsive element (ABRE) (Liu et al. 1998).

5.3.1 CBF Pathway

CBF/DREB1 genes are key players in the control of the cold acclimatization process in plants (Thomashow 2010; Shi et al. 2018a, b). They regulate the expression of a set of target genes that are involved in transcription by binding to the cis element LTRE/CRT/DRE (low-temperature-responsive element/C-repeat/dehydration element) located on their promoter sequence. This set of genes was generally referred to as the CBF regulon. Thus, CBFs regulate the expression of genes that are involved in phosphoinositide metabolism, osmolyte biosynthesis, ROS detoxification, membrane transport, hormone metabolism, signalling and many others with known or suspected cellular protection (Lee et al. 2005; Fowler and Thomashow 2002; Maruyama et al. 2004). CBFs appear to be involved in growth control, leaf surface area, cell volume, leaf thickness, stomatal density and anthocyanin synthesis (Gilmour et al. 2004; Savitch et al. 2005; Pino et al. 2008). Overexpression of AtCBF1 and AtCBF3 enhanced frost tolerance in non-acclimated plants and induced soluble sugars and proline accumulated in plants under warm conditions (Jaglo-Ottosen et al. 1998).

The number of CBF/DREB1 genes varies from one species to another but also at the intraspecific scale. Generally, it was considered that the genomes of monocotyledons (especially Triticeae) have more CBF/DREB1 genes than those of dicotyledons. In monocotyledonous plants such as barley and wheat, the family has up to 25 members (Badawi et al. 2007), whereas in dicotyledonous plants, the literature reports a maximum of six sequences as in *Arabidopsis* and poplar (Haake et al. 2002; Benedict et al. 2006). CBF genes are highly conserved between species and even more so between members of the same family as is the case in the vine or the *V. vinifera*. CBF4 sequence is 99% identical to that of *V. riparia* (Xiao et al. 2008).

CBF/DREB1 genes generally respond to cold stress in cold-acclimatizing monocot plants as demonstrated in wheat, barley (Choi et al. 2002; Marozsán-Tóth et al. 2015), ryegrass (Xiong and Fei 2006), rice (Dubouzet et al. 2003), maize (Qin et al. 2004) or dicotyledons such as rapeseed (Gao et al. 2002) or tomato (Jaglo et al. 2001). Similarly, the results showed that the EguCBF1a, EguCBF1b, EguCBF1c and EguCBF1d genes isolated from *E. gunnii* respond strongly to cold shocks in

E. gunnii and *E. gunnii* × *E. dalrympleana* but also for species more sensitive to cold as *E. urophylla* × *E. grandis*.

Since the *Arabidopsis* genome sequenced, six CBF/DREB1 genes have been isolated. The initial investigations on *Arabidopsis* were focused on cold-induced CBF1, 2 and 3, arranged in tandem with chromosome 4 (Gilmour et al. 1998; Medina et al. 1999). Isolated AtCBF4 gene was induced by drought and is located on chromosome 5 (Haake et al. 2002). On the other hand, the CBF5 and 6 genes, named AtDDF1 and AtDDF2 induced by salt stress, were mainly located on chromosome 1 (Magome et al. 2004). The CBF pathway accounts for 5–15% of the transcript changes in response to cold in *Arabidopsis* (Hannah et al. 2006). DNA sequencing and result mapping indicated that the CBF1, CBF2 and CBF3 genes are present in the direct repeat genome, CBF1-CBF3-CBF2, on chromosome 4 at 72.8 cM, closely related to molecular markers PG11 and m600 (Gilmour et al. 1998).

M. truncatula has at least 17 CBF/DREB1 genes (considering MtCBF2a and MtCBF2b) all located in homologous regions (Azar et al. 2011). In cereals, recent studies show that CBF2A in barley and CBF14 and CBF15 in wheat have been directly proven involved in cold acclimatization causing a significant increase in frost tolerance (Soltész et al. 2013; Jeknic et al. 2014).

In woody plants also, CBF genes are identified; the first CBF of isolated woody cherry (*Prunus avium*) is designated PaDREB1 or PaD2B (Kitashiba et al. 2002). EguCBF1a and EguCBF1b are the first isolated and characterized CBF in *Eucalyptus* (*E. gunnii*). They are strongly regulated by the cold, but not so by other abiotic stresses (El Kayal et al. 2006). CBFs were then isolated from other trees such as poplar, apple, birch and grapevine. Among the six CBF genes isolated from *Populus trichocarpa*, only PtCBF1 and PtCBF2 were phylogenetically similar to *Arabidopsis* AtCBF1-4. These genes respond to cold stress and were differently expressed in different plant parts (stems and leaves, Benedict et al. 2006). In addition, four CBFs isolated from birch (*Betula pendula*) respond to cold and exhibit rapid and transient expression in active tissues in long daylight and late, more durable expression in short days in dormant tissues. This suggests the involvement of CBFs in the winter acclimatization of this woody species (Welling and Palva 2008).

Xiao et al. (2006) showed that four CBF are common in *Vitis vinifera* (cold sensitive) and *V. riparia* (cold tolerant). VvCBF1-3 and VrCBF1-3 are induced by cold, dryness and ABA, while the more distinct VvCBF4 and VrCBF4 sequence respond for at least 1 day and only identical way in both species (Xiao et al. 2008). CBF have also been identified in tropical deciduous plants such as *Hevea* (*Hevea brasiliensis*). In tropical evergreen plants closest to *E. gunnii*, a cold-responsive EgCBF1 was isolated from *E. globulus* (Gamboa et al. 2007). Houde et al. (2004), based on the ion leakage experiments, concluded that Wcor410a acidic dehydrin gene from wheat transferred in transgenic strawberry, conferred frost tolerance, and wcor410 protein was expressed in transgenic strawberry at the level comparable with that in cold-acclimated wheat. Further, two cold-induced CBFs were isolated from the tolerant species *Poncirus trifoliata* and the susceptible species *Citrus paradisi* (Champ et al. 2007).

5.3.2 CBF: The Independent Pathway

It is conventionally established that phytohormones such as auxins, cytokinins, ethylene, gibberellins and abscisic acid ABA, in addition to new members, brassinosteroids, jasmonates and strigolactones as it happens, could prove to be potential targets for their engineering for producing abiotic stress tolerance crop plants (Wani et al. 2016). Among these phytohormones, ABA is the most studied in the engineering of abiotic stress tolerance in plants of agronomic interest because of its importance as a stress hormone and for its preponderant role and extensive functions related to environmental stresses (Wani and Kumar 2015). Phytohormones including auxin, cytokinins, ABA, gibberellins, jasmonic acid, ethylene and brassinosteroids are intimately linked in the CBF-independent transcriptional pathway components under cold acclimation (Zhao et al. 2014; Wani et al. 2016; Joshi et al. 2016).

The CRT/DRE motif is a 5 bp CBF/DREB1 binding motif, which forms the conserved central element of a cis-acting regulatory element, in which the CBF TFs bind (Yamaguchi-Shinozaki and Shinozaki, 1994; Stockinger et al. 1997; Liu et al. 1998). Agarwal et al. (2006) showed that DREB proteins are important TFs that induce a set of abiotic stress-related genes to confer stress resistance in the plants. The DREB TFs can be divided in two types, DREB1 and DREB2, which control two different signal transduction pathways, the first for low- temperature stress and the second for dehydration stress. Clusters of CBF/DREB1 genes repeated in tandem have been demonstrated in several species, other than *Arabidopsis* (6 genes) (Gilmour et al. 1998), such as *Triticum monococcum* (14 genes) (Miller et al. 2006) and *Hordeum vulgare* (12 genes) (Skinner et al. 2006). Interestingly, even the ectopic expression of CBFs is reported sufficient to activate the expression of COR genes and induce cold acclimation, even at warm temperatures (Stockinger et al. 1997; Liu et al. 1998; Patel and Franklin 2009; Zhao et al. 2011; Shi et al. 2015; Erimina et al. 2016; Gerszberg and Hnatuszko-Konka 2017).

The gene products of the AP2/EREBP family are characterized by a conserved domain of DNA binding (Okamuro et al. 1997; Zhao et al. 2014) which is of the order of 60 amino acids: the AP2/ERF domain which is the domain of DNA binding (Jofuku et al. 1994; Ohme-Takagi and Shinshi 1995). The AP2/ERF domain also presumably contains the address signal to the kernel (Canella et al. 2010). The CBF/DREB1 genes have a simple structure with an average 700 bp coding region not including introns. Recent report by Erimina et al. (2016) showed that it is clear that hormones act as central regulators of cold stress responses in plant. Shi et al. (2015) reported that hormonal components play important roles in regulating plant freezing tolerance by either CBF-dependent or CBF-independent pathways.

5.4 Conclusion

Stress conditions induce signalling reactions that can lead to the establishment of defences or trigger programmed cell death. Cold induce osmotic stress and oxidative stress, which ultimately leads to an imbalance of homeostasis and weakening of

Table 5.1 Examples of genes exploited for enhanced tolerance to cold stress

Plant	Gene	Effect of gene engineering	References
Pyrus betulaefolia	*PbrMYB5*	PbrMYB5 overexpression contributes to the improvement of cold tolerance in transgenic plant	Xing et al. (2018)
Camellia sinensis	*KCSs, NAC080, SWEETs, and ENOs*	Regulates cold tolerance in tea plant leaves	Hao et al. (2018)
Arabidopsis thaliana	*AtMYB14*	Regulates cold tolerance in *Arabidopsis*	Chen et al. (2013)
A. thaliana	*AtMYB14*	AtMYB14 participates in freezing tolerance in *Arabidopsis* by affecting expression of CBF genes. Encodes a nuclear protein that functions as an R2R3-MYB transcription activator	Chen et al. (2013)
Dendranthema grandiflorum	*DEG genes*	Cold-responsive genes related to low-temperature sensing and signal transduction, membrane lipid stability, ROS scavenging and osmoregulation	Wang et al. (2018)
Lycopersicon esculentum	*Osmotin*	Enhanced tolerance to cold	Patade et al. (2013)
Oryza sativa	*OsNAC*	OsNAC regulates the expression NACRS target gene to increase cold tolerance	Zang et al. (2017)
Medicago falcata	*MfTIL1*	MfTIL1 confer elevated survival rate in response to freezing in transgenic tobacco plants	He et al. (2015)
Oryza sativa	OsmiR156k	OsmiR156k is suggested a negative regulator of plant tolerance to cold stress	Cui et al. (2015)
Solanum melongena L.	*POD and CAT genes*	POD and CAT relative gene expression enhances chilling tolerance and reduces damage in cold-stored eggplant	Shi et al. (2018a, b)
Artemisia annua	*Aa547*	Aa 547 peroxidase gene overexpression under cold stress	Nair et al. (2018)
Medicago truncatula	*CBF/DREB1*	CBF/DREB1 genes located in a major freezing tolerance QTL region on *Medicago truncatula* chromosome 6	Tayeh et al. (2013)
Oryza sativa	*COLD1*	Transmembrane protein regulates GTPase activity under chilling stress	Ma et al. (2015)

membranes and proteins. The perception and the transduction of the signal leads to the altered expression of regulatory genes which in turn controls the expression patterns of effector genes allowing the establishment of stress responses and tolerance mechanisms. During cold acclimation, several molecular and physiological factors are involved and are crucial. The TF CBFs/DREBs play crucial roles in the regulation of genes involved in tolerance to low-temperature stress; once the plants sense low temperature, they activate a complex cold acclimation process and activation of CBF-dependent and CBF-independent pathways. With regard to CBF-independent, more than 80% components of cold-responsive genes are not controlled directly by

CBFs. Transcriptome analyses have indicated that only ~12% of the cold-responsive genes are controlled by CBFs. During cold stress, a cascade of phosphorylation triggered by the influx of cytosolic Ca^{2+} and the induction of CBF genes gets underway. In the future, it is interesting to focus on studies targeting the role of phytohormones, small RNAs, as well as the effects of overexpression of CBF genes for the improvement of agronomic species and in order to better understand the cold stress response mechanisms (Table 5.1).

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