

Roles of plant CBL–CIPK systems in abiotic stress responses

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Abstract: Plants evolved from long-term adaptation to form regulatory mechanisms of perception, transduction, and response to stresses. The CBL–CIPK signaling system is a basic calcium sensor that plays an important role in sensing adverse environmental stimuli. CBLs can perceive and bind Ca²⁺ under adversity and then specifically interact with CIPKs. The activated CBL–CIPK complex phosphorylates downstream target proteins (such as ion channels and transporters), or regulates transcription factors and stress responsive genes. Important progress has been made in the study of CBL–CIPK signaling pathways in response to high salt, low N, low K, high Mg, and high pH. This review summarizes the structural features of CBL and CIPK families and the research progress of CBL–CIPK complexes under environmental stresses, and forecasts the important future direction in studies of the CBL–CIPK signaling system.

Key words: CBL–CIPK, calcium signaling, abiotic stress, signal transduction

1. Introduction

Plants have to endure various abiotic and biotic stresses as they cannot move to favorable environments. Stresses, including salt, drought, cold, low nutrition, viruses, and other pathogen attacks, have a great impact on seed germination, seedling growth, photosynthesis, and biomass accumulation (Zhou et al., 2014). Fortunately, plants have acquired the ability to sense, deliver, and respond to stresses at the molecular, cellular, and physiological levels during evolution (Li et al., 2009). External stimuli could change the concentration of calcium ion (Ca²⁺), an acknowledged ubiquitous second messenger, which can be perceived by sensor proteins. Following sensing, a series of molecular, physiological, and biochemical reactions are triggered to cope with the stimuli. There are mainly three Ca²⁺ sensor protein families: calmodulins (CaMs), calcineurin B-like proteins (CBLs), and calcium-dependent protein kinases (CDPKs) (Snedden and Fromm, 2001). CBLs interact and activate CBL-interacting protein kinases (CIPKs), forming the CBL–CIPK complex, which could help plants cope with different stresses. Moreover, the CBL–CIPK module plays an important role in plant growth and development (Pandey, 2014; Zhang, 2015).

Comparative analyses have provided detailed information of the structure and function of the CBL/CIPK family in various plants. Recent studies identified 10 CBLs and 26 CIPKs from *Arabidopsis*, 10 CBLs and 33 CIPKs from rice (*Oryza sativa*) (Kolukisaoglu et al., 2004; Xiang et al., 2007; Giong et al., 2015), 8 CBLs and 43 CIPKs from maize (*Zea mays*) (Chen et al., 2011), 10 CBLs and 27 CIPKs from poplar (*Populus trichocarpa*) (Yu et al., 2007; Zhang et al., 2008), 6 CBLs and 32 CIPK-type kinases from sorghum (*Sorghum bicolor*) (Weinl and Kudla, 2009), 8 CBLs and 21 CIPKs from grape (*Vitis vinifera*) (Weinl and Kudla, 2009; Xi et al., 2017), 7 CBLs and 20 CIPKs from wheat (*Triticum aestivum*) (Sun et al., 2015), 5 CBLs and 15 CIPKs from eggplant (*Solanum melongena*) (Li et al., 2016), 7 CBLs and 23 CIPKs from canola (*Brassica napus*) (Zhang et al., 2014), 19 CBLs and 51 CIPKs from turnip (*Brassica rapa* var. *rapa*) (Yin et al., 2017), 41 CIPKs from diploid cotton (*Gossypium raimondii* and *Gossypium arboreum*) (Wang et al., 2016), 25 CIPKs from cassava (*Manihot esculenta*) (Hu et al., 2015), and 1 CBL and 5 CIPKs from the fern *Selaginella moellendorffii* (Weinl and Kudla, 2009), but only 1 CBL and 1 CIPK from several charophytes (*Ostreococcus lucimarinus*, *Bathycoccus prasinos*, *Coleochaete orbicularis*,

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Klebsormidium flaccidum, *Chaetosperidium globosum*, *Penium margaritaceum*, and *Chlorokybus atmophyticus*) (Weinl and Kudla, 2009; Kleist et al., 2014). At the same time, the function of the CBL–CIPK system from different plants is further investigated widely and in depth. In this review, we focus on the function of the CBL–CIPK system in response to abiotic and biotic stresses and in plant growth and development.

2. The structure of CBLs and CIPKs

The C-terminus of CBL proteins contains two spherical regions, which are connected by a short connecting domain. The PFPF domain, which is the binding site of CIPKs, is also located at the C-terminus. Each CBL protein contains four aligned and spaced high-affinity calcium binding EF-hand domains. Based on the number of typical EF-hand sites, 10 *Arabidopsis* CBL proteins are divided into three groups: the group with two typical sites (CBL1 and CBL9), the group with one typical site (CBL8 and

CBL10), and the group with no typical sites (CBL2, CBL3, SOS3, CBL5, CBL6, and CBL7). Each binding site consists of 12 relatively conserved amino acids (Batistic and Kudla, 2009; Sánchez-Barrena et al., 2013). In addition to EF hands, another notable structural feature of CBL proteins is the presence of the N-terminal sequence of palm acylation and cardamom acylation sites that participate in subcellular localization of the CBL–CIPK complex (Batistic et al., 2008).

The molecular structure of CIPKs includes an N-terminal catalytic domain and a C-terminal regulatory domain. The catalytic domain is a typical serine/threonine protein kinase domain, similar to the SNF1 protein kinase domain, containing an ATP binding site and an activation loop, which could phosphorylate downstream proteins, such as transporters, transcription factors (TFs), channels, enzymes, and phosphatases (Figure 1). The regulatory domain is functionally and structurally divided into a 21-amino-acid FISH (also known as NAF) domain and

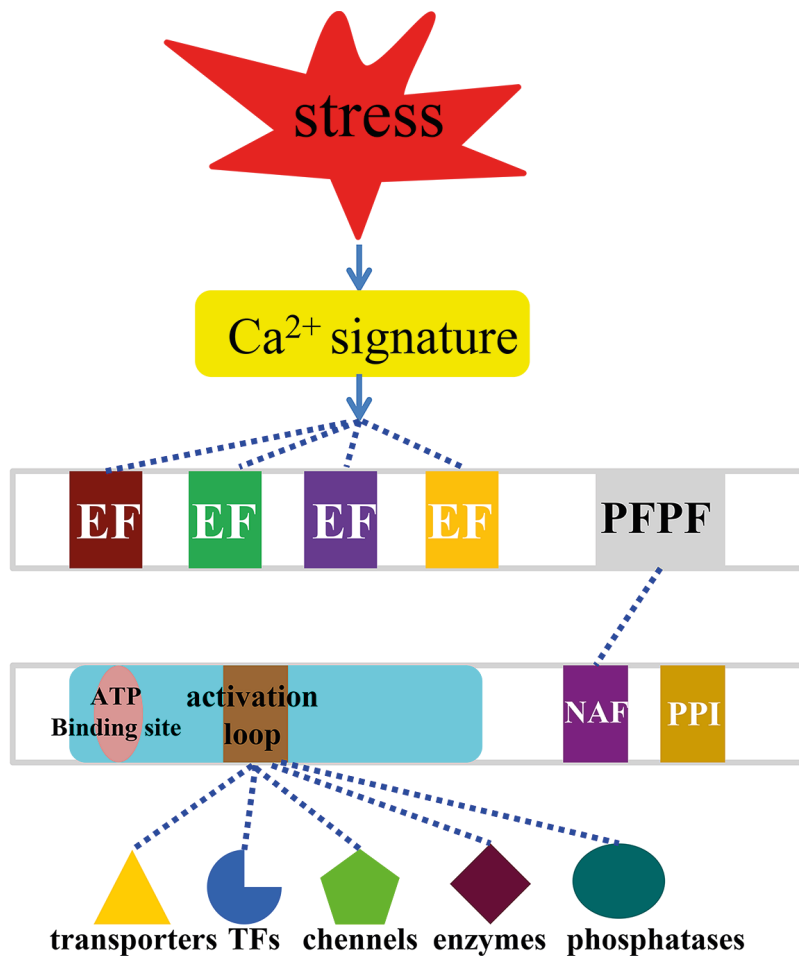


Figure 1. General structure of the Ca²⁺ sensor protein calcineurin B-like (CBL) proteins and CBL-interacting protein kinases (CIPKs).

a PPI region (Figure 1), which is a domain necessary for mediating interactions between CIPKs and CBLs (Guo et al., 2001).

3. Salt stress

Salt stress is caused by high concentrations of salt in soil. Plants respond to salt stress by restricting Na^+ uptake to maintain the cellular ion homeostasis (Tester and Davenport, 2003). The salt overly sensitive (SOS) pathway, SOS3/CBL4-SOS2/CIPK24-SOS1, was first identified in *Arabidopsis* (Wu et al., 1996; Liu and Zhu, 1997; Liu and Zhu, 1998; Zhu et al., 1998; Halfter et al., 2000; Quintero et al., 2002). The structure, function, and mechanism of this pathway are well elucidated (Lu et al., 1998; Ishitani et al., 2000; Shi et al., 2000; Elphick et al., 2001; Qiu et al., 2002, 2004; Zhu, 2002; Gong et al., 2004; Guo et al., 2004; Sanchez-Barrena, 2005, 2007; Quan et al., 2007; Fujii and Zhu, 2009; Ye et al., 2013). The CBL4-CIPK24 complex activates SOS1, which is a Na^+/H^+ antiporter located in the plasma membrane (Figure 2a). The activated SOS1 could pump redundant Na^+ back into soil (Zhu, 2003). As mentioned by Thoday-Kennedy et al. (2015), a number of SOS pathway members have been identified. Recently, another SOS pathway, SiCBL4-SiCIPK24, has been verified to be involved in salt stress tolerance in foxtail millet (*Setaria italica*) (Zhang et al., 2017).

Besides CBL4, CBL1 and CBL10 can also recruit SOS2/CIPK24 to plasma and the vacuole membrane, respectively, under salt stress (Kolukisaoglu et al., 2004; Kim et al., 2007; Quan et al., 2007). The complexes CBL4-CIPK24 and CBL10-CIPK24 protect roots and shoots from salt stress, respectively (Quan et al., 2007). CIPK24 can also regulate the vacuolar Na^+/H^+ exchange (AtNHX) by interacting with a vacuolar membrane-localized CBL protein (Qiu et al., 2004). Therefore, we speculate that the CBL10-CIPK24 complex can activate AtNHX (Figure 2a). Formation of the CBL2/CBL3-CIPK21 complex in the vacuolar membrane is enhanced by salt stress. The complex may target unknown Na^+ -channels/transporters (Pandey et al., 2015). Overexpression of *CIPK6* and *CIPK16* in *Arabidopsis* improves salt tolerance and knockdown of *CIPK14* and *CIPK16* attenuates tolerance to salt stress (Xu et al., 2008; Tripathi et al., 2009; Chen et al., 2013; Roy et al., 2013).

Many studies describe the roles of *CIPK* genes in salt tolerance from other plant species. Li et al. (2012) demonstrated that HbCIPK2 regulates salt tolerance by maintaining K^+/Na^+ homeostasis in *Hordeum brevisubulatum*. Overexpression of *MdCIPK6L* confers tolerance to salt, drought, and chilling in transgenic tomato. The interaction between *MdCIPK6L* and SOS3 indicates that *MdCIPK6L* may be involved in the SOS pathway (Wang et al., 2012). Autophosphorylation of cowpea

(*Vigna unguiculata* (L.) Walp.) VuCIPK1, a homologue of CIPK3, is induced by sodium chloride, suggesting that CIPK3 is involved in salt tolerance regulation (Imamura et al., 2008). The TaCBL3-TaCIPK29 complex plays a positive role under salt stress by regulating transporter genes and the antioxidant system in wheat (Deng et al., 2013). PeCBL1 interacts with PeCIPK24, PeCIPK25, and PeCIPK26 to maintain the homeostasis of the Na^+/K^+ ratio in *Populus euphratica* (Zhang et al., 2013). Overexpression of *AmCBL1* from *Ammopiptanthus mongolicus* improves the tolerance of salt and heat in transgenic tobacco (Chen et al., 2011). *PeCBL1* and *AmCBL1* are homologous genes of *CBL1*, and they show similar functions in drought, salt, and cold stress (Albrecht et al., 2003; Yong et al., 2003). Overexpression of *SjCBL1* from *Sedirea japonica* in *Arabidopsis cbl1* mutant not only complements the hypersensitive phenotype to salt and osmotic stress, but also significantly enhances tolerance to salt and osmotic stress (Cho et al., 2018). It is demonstrated that the BnCBL1-BnCIPK6 complex is required in salt stress in *Brassica napus* (Chen et al., 2012).

4. Low N/P/K stress

Nitrogen is a key limiting factor in plant growth. Nitrate (NO_3^-) is the main nitrogen source for plants. At present, the molecular mechanism of NO_3^- signal transduction has been revealed in *Arabidopsis*. Three nitrate transporter families, NRT1, NRT2, and CLC, have been identified in *Arabidopsis* (De Angeli et al., 2009). Among them, four plasma membrane-localized transporter members of the NRT1 and NRT2 families absorb NO_3^- in root cells (Tsay et al., 1993). NRT1.1 (CHL1) is an amphiphilic transporter and NRT1.2 is a low affinity transporter. CHL1 shows high affinity for nitrates when the threonine residue at position 101 (T101) is phosphorylated; otherwise, it has low affinity for nitrates when dephosphorylated; NRT2.1 and AtNRT2.2 are high affinity transporters (Li et al., 2007; Ho et al., 2009). The *Arabidopsis* CBL1/9-CIPK23 complex mediates the phosphorylation of CHL1 (Figure 2d), thereby responding to nitrate at a high affinity level (Vert and Chory, 2009). Transcriptome studies show that *CIPK8* acts as a positive regulator in nitrate low-affinity responses under low nitrogen stress (Hu et al., 2009).

Chen et al. (2012) reported that the expression of *BnCBL1* and *BnCIPK6* is upregulated under low-phosphorus conditions. Yeast two-hybrid results show that the two proteins interact with each other. Under low phosphorus conditions, *Arabidopsis thaliana* plants overexpressing *BnCBL1* or *BnCIPK6* show more vigorous lateral root growth and more biomass accumulation than wild type. Therefore, BnCBL1 and BnCIPK6 may be involved in plant response to low phosphorus stress.

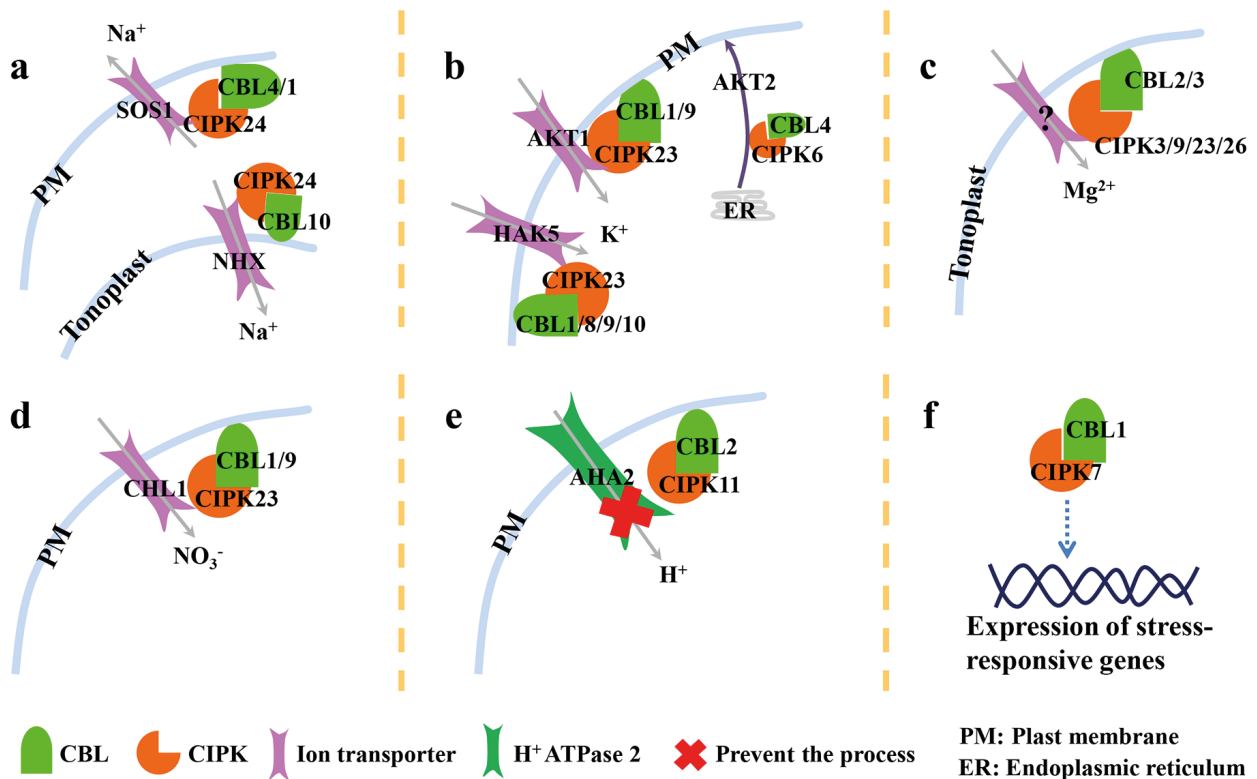


Figure 2. Schematic representation of the functions of calcineurin B-like (CBL) proteins interacting with CBL-interacting protein kinases (CIPKs) in regulating plant (*Arabidopsis*) response to abiotic stress. a, high Na^+ ; b, low K^+ ; c, high Mg^{2+} ; d, low N; e, high pH; f, cold stress.

Potassium ion (K^+) is one of the most abundant cations in plant cells and has important physiological functions in organisms. Potassium acquisition, redistribution, and homeostasis are mainly regulated by potassium channels and secondary potassium transporters (Xu et al., 2006). Many studies describe the link between the CBL–CIPK system and potassium channels and transporters. Almost at the same time, two studies reported that the CBL1/9–CIPK23 complex interacts and phosphorylates AKT1 (Figure 2b), an inward K^+ channel taking up K^+ under low- K^+ conditions (Li et al., 2006; Xu et al., 2006). Cheong et al. (2007) confirmed that the pathway exists in both roots and stomatal guard cells. Lee et al. (2007) also examined other CBL–CIPK complexes (CBL1/2/3/9–CIPK6/16/23) that interact with AKT1. Furthermore, AIP1 negatively regulates the activity of AKT1 (Lee et al., 2007; Lan et al., 2011). However, instead of the CBL–CIPK complex, Ren et al. (2013) found that CBL10 regulates the AKT1 activity directly. The activity of another potassium channel, AKT2, is regulated by CBL4–CIPK6 through mediating translocation from the endoplasmic reticulum membrane to the plasma membrane (Figure 2b) (Held et al., 2011). CIPK9 and CIPK23 are also reported to be involved in low K^+ stress (Pandey et al., 2007; Xue et al., 2016). The

upstream component of CIPK9 in low K^+ regulation is CBL3, since CIPK9 interacts with CBL3 in *Arabidopsis* mesophyll protoplasts by BiFC assays, overexpression of CIPK9 and CBL3 exhibits a similar low K^+ -sensitive phenotype, and *cbl3* and *cipk9* mutants show a similar low K^+ -tolerant phenotype (Liu et al., 2013). By interacting with CBL1/8/9/10, CIPK23 activates HAK5 (Figure 2b), a high-affinity K^+ transporter (Ragel et al., 2015). The relationship between CBL–CIPK complexes and K^+ channels is also uncovered in other plants. Zhang et al. (2010) isolated two shaker-like potassium channels PeKC1 and PeKC2 in *Populus euphratica*, which could complement the *Arabidopsis akt1* mutant and could be phosphorylated by PeCIPK10, PeCIPK17, and PeCIPK24. Similarly, Cuéllar et al. (2013) identified a K^+ channel VvK1.2 from grape (*Vitis vinifera*), which could be activated by the VvCBL01–VvCIPK04 and VvCBL02–VvCIPK03 complex.

5. Cold stress

To date several studies have revealed the association between the CBL–CIPK system and cold stress. Cheong et al. (2003) demonstrated that CBL1 negatively regulates the cold stress response. Huang et al. (2011) discovered that the expression of *CIPK7* is influenced by *CBL1* under

cold stress. Both in vitro and in vivo interactions between CBL1 and CIPK7 indicate that the CBL1–CIPK7 complex may play an important role in cold stress response (Figure 2f) (Huang et al., 2011). The expression of cold- and salt-responsive genes (such as *RD29A*, *KINI1*, and *KIN2*) is different between wild type and *cipk3* mutant, suggesting *CIPK3* may be involved in the regulation of cold stress response (Kim et al., 2003). In other plants, overexpression of *MdCIPK6L* confers tolerance to chilling stress in transgenic tomato (Wang et al., 2012). Ectopic expression of *BdCIPK31* improves ROS detoxification and osmoprotectant biosynthesis in transgenic tobacco under cold stress (Luo et al., 2018).

6. Drought stress

Very few CBLs and CIPKs are implicated in drought stress. In *Arabidopsis*, only CBL1 and CBL5 are proven positive regulators in drought stress (Albrecht et al., 2003; Cheong et al., 2003, 2010). In rice, suppression of *OsCIPK23* expression leads to hypersensitive response to drought stress, but enhanced cold resistance is found in *OsCIPK23*-overexpressing plants. Moreover, expression induction of drought-related genes is also observed in *OsCIPK23*-overexpressing plants (Yang et al., 2008). In wheat (*Triticum aestivum*), heterologous expression of *TaCIPK2*, *TaCIPK23*, or *TaCIPK27* enhances the drought resistance of the transgenic plants in an ABA-dependent pathway (Wang et al., 2016, 2017; Cui et al., 2018). In addition, overexpression of *BdCIPK31* in tobacco reduces water loss under dehydration conditions and maintains the homeostasis of Na^+/K^+ and root K^+ loss under salt stress (Luo et al., 2017). *MdCIPK6L* from apple (*Malus domestica*), a homologue of *CIPK6*, plays a positive regulatory role in drought stress responses in transgenic tomato plants (Wang et al., 2012).

7. High Mg and pH stress

An adequate and balanced supply of mineral nutrients is essential for plant growth and development. Magnesium (Mg^{2+}) is essential for chlorophyll synthesis, enzyme activation, and cation balance (Gao et al., 2015). However, a high level of Mg^{2+} in soil does harm plants. Tang et al. (2015) demonstrated that the *Arabidopsis cbl2cbl3* double mutant and *cipk3cipk9cipk23cipk26* quadruple mutant plants retain lower Mg^{2+} content than WT under normal and high Mg^{2+} conditions and exhibit similar Mg^{2+} hypersensitivity phenotypes. However, the two double mutants *cipk9cipk23* and *cipk3cipk26* show slight sensitivity to a high level of Mg^{2+} . Furthermore, CBL2/CBL3 could recruit CIPK3/CIPK9/CIPK23/CIPK26 on the vacuole membrane. It is speculated that the CBL2/CBL3–CIPK3/CIPK9/CIPK23/CIPK26 complex targets tonoplast-localized Mg^{2+} transporters, which contribute to vacuolar Mg^{2+} uptake (Figure 2c) (Tang and Luan, 2017).

Plant cells are under changing pH conditions. They use phosphorylation and dephosphorylation of H^+ -ATPase to regulate the concentration changes of intracellular and extracellular ions. The CBL2–CIPK11 complex can phosphorylate the plasma membrane H^+ -ATPase AHA2 at Ser-931. Phosphorylation inhibits the activity of AHA2 (Figure 2e) and then impedes the interaction with 14-3-3 proteins, resulting in loss of capacity of 14-3-3 proteins to transport protons. However, in the *cipk11* mutant, the dephosphorylated AHA2 interacts with 14-3-3 proteins and enhances the ability of 14-3-3 proteins to transport protons, thus promoting intracellular H^+ efflux (Fuglsang et al., 2007). It is reported that J3, a chaperone, can interact with and repress the kinase activity of CIPK11 and then activate the activity of AHA2 (Yang et al., 2010).

8. Conclusion and future prospects

In summary, the structure and interaction mechanism of CBL and CIPK have been extensively elaborated. Great progress has been made in functional studies on the effects of CBL and CIPK single proteins and complexes on different physiological processes. The research mainly focuses on salt and cold tolerance, nutrient element deficiency, and pH stress as shown in the Table. Recently, several articles report that the CBL–CIPK complex plays important roles in biotic stress resistance (Liu et al., 2017, 2018; Sardar et al., 2017), but the mechanism is still far from understood. In addition to the responses to abiotic and biotic stresses, CBL–CIPK also plays important roles in flower development (Yang et al., 2008; Yuasa et al., 2012; Park et al., 2013), pollen tube germination and growth (Mahs et al., 2013), and root growth and seed development (Tripathi et al., 2009; Piao et al., 2010; Zhao et al., 2011). These studies are mainly conducted in *Arabidopsis*. In other plant species, the research on the CBL and CIPK family is still in its infancy, and the interaction and expression analyses between them are very limited.

Future research should focus on the mechanisms of interaction between CBLs and CIPKs, identifying components in the respective signaling pathways and analyzing the genetic functions, which will enable us to better understand how plants respond to abiotic stresses. The availability of whole genome sequences of more and more species and the advancement of more technologies and methodologies will contribute to the study of the evolution, functional diversity, and interaction networks of CBL–CIPK complexes (Zhou et al., 2014). Therefore, challenges in the future are not only in the functional analysis but also in the clarification of the details of synergistic effects and the molecular mechanism of the complex regulation of target proteins.

Therefore, comprehensive analysis and identification of plant CBL–CIPK signal components and signaling pathways of plant response to stresses, particularly the

Table. Summary of the function of CBLs, CIPKs, and CBL–CIPK complexes.

Gene or CBL–CIPK complex	Localization	Substrate	Function
CBL1	plasma membrane		positively regulates drought and salt stress, negatively regulates cold stress (Albrecht et al., 2003; Cheong et al., 2003; Batistic et al., 2010)
CBL1–CIPK7	?	?	negatively regulates cold stress (Huang et al., 2011)
CBL1/9–CIPK1	plasma membrane	?	ABA-dependent and ABA-independent stress responses (Angelo et al., 2006)
CBL1/9–CIPK23	plasma membrane	AKT1	K ⁺ uptake and transport (Cheong et al., 2007; Li et al., 2006; Xu et al., 2006)
CBL1/8/9/10–CIPK23	?	HAK5	mediates high-affinity K ⁺ uptake in <i>Arabidopsis</i> roots (Ragel et al., 2016)
CBL2–CIPK11	plasma membrane	AHA2	negatively regulates the activity of plasma membrane H ⁺ -ATPase, AHA2 (Fuglsang et al., 2007; Yang et al., 2010)
CBL2/3–CIPK9	tonoplast	?	function in K ⁺ homeostasis under low-K ⁺ stress (Liu et al., 2013)
CBL2/3–CIPK3/9/23/26	tonoplast	unknown tonoplast-localized Mg ²⁺ transporters	protects plants from high Mg ²⁺ poison (Tang et al., 2015)
CBL4–CIPK6	plasma membrane	AKT2	mediates endoplasmic reticulum to plasma membrane translocation of AKT2 (Held et al., 2011)
CBL4–CIPK24	plasma membrane	SOS1	known as SOS pathway, response to salt stress and control long-distance Na ⁺ transport from root to shoot (Lin et al., 2009; Qiu et al., 2002)
CBL5	cytoplasm and nucleus	?	functions as a positive regulator of salt or drought responses (Batistic et al., 2010; Cheong et al., 2010)
CBL10–CIPK24	plasma membrane	SOS1	functions mainly in the shoot response to salt toxicity (Quan et al., 2007)
CIPK6	nucleus, cytoplasm, and cytosol	?	positively regulates salt stress as well as root development (Chen et al., 2013; Tripathi et al., 2009)
CIPK8	?	?	involved in the low-affinity system (Hu et al., 2009)
CIPK16	?	?	positively regulates salt stress (Roy et al., 2013)
CIPK23	protoplast	CHL1	response to low nitrate concentrations (Ho et al., 2009)

excavation of special habitats of plant CBL–CIPK signal components, will provide important insights into quickly and efficiently improving plant stress tolerance through genetic engineering in combination with molecularly designed breeding strategies.

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