



CBL10 – A MASTER CALCIUM SENSOR REGULATING ION HOMEOSTASIS AND STRESS TOLERANCE IN PLANTS

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ABSTRACT: Salinity and drought stress are primary constraints on global agricultural productivity, particularly in arid and semi-arid regions. The calcineurin B-like protein 10 (CBL10) serves as a critical calcium-sensing molecular switch, playing a pivotal role in plant adaptation to ionic and osmotic stresses. Unlike other members of the CBL family, CBL10 localizes to vacuolar and endomembrane compartments where it recruits the CIPK24 kinase to facilitate sodium sequestration, thereby maintaining low cytoplasmic sodium levels.

This review synthesizes current knowledge on the structural architecture of CBL10, focusing on its conserved EF-hand calcium-binding motifs and the post-translational modifications, such as S-acylation and phosphorylation, that regulate its membrane association. Furthermore, we examine the evolutionary significance of CBL10, noting that gene duplication events in halophytes often correlate with enhanced salt tolerance. Finally, we discuss how emerging gene-editing technologies, including CRISPR/Cas systems, enable the rational modification of CBL10-mediated pathways to develop climate-resilient crops and support global food security.

Keywords: Calcium signalling, CBL10 protein, Gene editing, Ion homeostasis, Plant biotechnology, Salt tolerance, Stress resilience

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INTRODUCTION

The world's growing population, coupled with climate change-induced intensification of drought cycles, desertification, and soil salinization, poses unprecedented challenges to global food security (Singh *et al.*, 2022). Approximately 20% of irrigated agricultural land worldwide suffers from salt-induced degradation, with particularly acute impacts in South Asian agroecosystems, including India's arid and semi-arid regions (Kumar and Sharma, 2020). In such regions, agricultural productivity decline directly threatens the

livelihood of farming communities and rural populations dependent on agricultural income.

Traditional crop improvement approaches, relying primarily on phenotypic selection and conventional breeding, require 8–15 years to develop improved varieties, a temporal luxury unavailable given accelerating environmental change (Krishna *et al.*, 2023). Consequently, molecular and biotechnological strategies targeting conserved stress-response genes have emerged as essential complements to conventional breeding. Among the diverse

regulatory pathways controlling plant stress responses, the calcineurin B-like (CBL) protein family has garnered increasing research attention as a molecular hub integrating calcium signalling with ion homeostasis and stress adaptation (Kim *et al.*, 2007; Chen *et al.*, 2024b; Sun *et al.*, 2025).

The CBL protein family represents a class of evolutionarily conserved calcium-binding proteins that function as molecular sensors interpreting stress-induced calcium signatures into specific cellular responses (Mohanta *et al.*, 2015; Chen *et al.*, 2024b; Sun *et al.*, 2025). Within this family, CBL10 occupies a unique functional niche. Unlike most CBL members that localize to the plasma membrane and regulate sodium extrusion from the cell, CBL10 positions itself at intracellular compartments, particularly the tonoplast (vacuolar membrane), where it directs sodium sequestration into vacuoles—a spatially and functionally distinct mechanism of salt tolerance (Kim *et al.*, 2007; Yang *et al.*, 2019).

This review synthesizes comprehensive understanding of CBL10's structural features, molecular mechanisms of action, species-specific variations, and practical applications in crop improvement. We emphasize research conducted at India's Arid Forest Research Institute (AFRI) on CBL10 orthologs from naturally stress-adapted plants, demonstrating the synergistic value of combining traditional ecological knowledge with contemporary molecular science (Unpublished Data). Furthermore, we elaborate on how next-generation gene editing technologies can accelerate the development of stress-resilient crops, supporting agricultural adaptation to climate change while advancing India's biotechnology sector (Gaj *et al.*, 2013; Kumar *et al.*, 2023; Chen *et al.*, 2024a).

STRUCTURAL ARCHITECTURE AND MOLECULAR FEATURES OF CBL10

OVERVIEW OF EF-HAND CALCIUM-BINDING MOTIFS

The defining structural feature of CBL proteins is

the presence of EF-hand motifs - evolutionarily conserved helix-loop-helix structural domains serving as calcium-binding sites (Denessiouk *et al.*, 2014; Sun *et al.*, 2025). Each EF-hand consists of a 12-14-amino acid calcium-coordinating loop flanked by two alpha-helices that undergo conformational changes upon calcium binding (Sanyal *et al.*, 2020). Most canonical EF-hand motifs utilize amino acids at positions 1, 3, 5, 7, 9, and 12 of the loop sequence for calcium coordination, creating a coordination geometry that accommodates Ca^{2+} ions with high affinity and specificity (Li *et al.*, 2009; Sanyal *et al.*, 2020).

CBL10-SPECIFIC STRUCTURAL CHARACTERISTICS

CBL10 is distinguished from other CBL family members by a distinctive elongated N-terminus containing a predicted transmembrane domain (TMD) spanning amino acids 17–35 (Batistič *et al.*, 2010). This TMD differs fundamentally from the N-terminal myristoylation signal present in other CBLs (particularly CBL1, CBL4, CBL5, CBL9), which targets these proteins to the plasma membrane (Batistič *et al.*, 2008). The CBL10 TMD, in contrast, functions as an intracellular targeting signal directing CBL10 to the tonoplast and associated endomembrane compartments rather than the plasma membrane (Kim *et al.*, 2007; Yang *et al.*, 2019).

Within the core protein structure, CBL10 contains four conserved EF-hand motifs arranged in tandem array (Denessiouk *et al.*, 2014; Sanyal *et al.*, 2020). Each EF-hand displays distinct calcium-binding affinity and cooperativity characteristics, creating a sophisticated calcium-sensing apparatus capable of decoding complex calcium signals generated during stress conditions (Ikura, 1996). This structural arrangement with four EF-hands organized with defined spacing and flanking helical domains generates a molecular platform uniquely suited to calcium-dependent conformational changes that expose CIPK-binding interfaces (Plasencia *et al.*, 2021).

POST-TRANSLATIONAL MODIFICATIONS REGULATING CBL10 LOCALIZATION AND FUNCTION

Beyond the core polypeptide structure, CBL10 undergoes critical post-translational modifications that dynamically regulate its membrane association and signalling capacity (Plasencia *et al.*, 2021).

S-acylation (Palmitoylation): CBL10 undergoes S-acylation at specific cysteine residues, predominantly at Cysteine-38 (Chai *et al.*, 2020). This reversible lipidation is catalyzed by PAT10 (protein acyltransferase 10) and similarly acting acyltransferases (PATs), which attach saturated fatty acids (typically palmitic acid, C16) to cysteine thiol groups via thioester bonds (Chai *et al.*, 2020). S-acylation increases CBL10 hydrophobicity, enhancing its insertion into the tonoplast lipid bilayer and stabilizing its association with the vacuolar membrane.

Phosphorylation: CBL10 undergoes phosphorylation at multiple serine and threonine residues. Notably, Serine-237 in *Arabidopsis* CBL10 exhibits phosphorylation during salt stress, representing a hallmark of CIPK24-mediated activation (Quan *et al.*, 2007; Lin *et al.*, 2009; Hashimoto *et al.*, 2012). Additionally, CBL10 undergoes calcium-dependent phosphorylation that modulates CIPK24 recruitment and kinase activation, creating a positive feedback loop where calcium-activated CIPK24 phosphorylates CBL10, enhancing CIPK24 recruitment and signal amplification (Hashimoto *et al.*, 2012; Chaves-Sanjuan *et al.*, 2014).

MOLECULAR MECHANISMS OF CBL10 IN CALCIUM SIGNALLING

CALCIUM INCREASE AND SIGNAL TRANSDUCTION AT THE TONOPLAST

The mechanistic basis of CBL10 function begins with its strategic positioning at the tonoplast membrane (Kim *et al.*, 2007; Yang *et al.*, 2019). Under normal conditions, cytoplasmic calcium

concentration remains at basal levels (~100–200 nM) (Igamberdiev and Hill, 2018). Upon salt stress, plants generate a characteristic calcium signature manifesting as rapid, transient increases in cytoplasmic calcium concentration reaching 1.0 μ M (Pottosin and Schönknecht, 2007). This calcium elevation occurs through multiple routes: influx from the extracellular space via plasma membrane calcium channels, release from intracellular calcium stores via IP₃ -receptors and ryanodine-like channels on the endoplasmic reticulum, and calcium mobilization from vacuolar stores via tonoplast calcium release channels (Santulli *et al.*, 2017; Demidchik *et al.*, 2018). CBL10 localized at the tonoplast directly senses calcium increases in the cytoplasm-tonoplast interfacial region and further signal is transduced by the CBL10-CIPK24 complex (Yang *et al.*, 2019; Plasencia *et al.*, 2021; Hunpatin *et al.*, 2023).

CBL10-CIPK24 COMPLEX FORMATION AND FUNCTIONAL SPECIFICITY

The CBL10-CIPK24 interaction represents a central molecular module in salt tolerance signalling (Yang *et al.*, 2019; Plasencia *et al.*, 2021; Hunpatin *et al.*, 2023). CIPK24, also designated SOS2 (salt overly sensitive 2), is a serine/threonine protein kinase containing an N-terminal kinase catalytic domain and a C-terminal regulatory domain (Chaves-Sanjuan *et al.*, 2014; Ding *et al.*, 2022). Elevated calcium binding to EF-hand motifs induces conformational changes in CBL10 that expose a protein-protein interaction surface (PFPF motif) to enable binding of CIPK (Cho *et al.*, 2017; Ding *et al.*, 2022). The regulatory domain of CIPK24 contains the NAF domain critical for CBL interaction. This NAF domain serves as a high-affinity binding site for the C-terminal regulatory domain of CIPK24, recruiting the kinase to the tonoplast membrane (Ding *et al.*, 2022). Upon recruitment by calcium-activated CBL10, CIPK24 undergoes conformational changes that optimally position its catalytic domain for substrate phosphorylation. This leads to the activation of CIPK24 catalytic activity by relieving

the self-inhibition, directing its serine/threonine kinase domain toward tonoplast-localized substrate proteins (Chaves-Sanjuan *et al.*, 2014; Yang *et al.*, 2019; Ding *et al.*, 2022).

The specificity of the CBL10-CIPK24 module distinguishes it from other CBL-CIPK combinations (Kim *et al.*, 2007). Whereas CBL4 (also designated SOS3) functions at the plasma membrane to activate CIPK24-mediated phosphorylation of SOS1 (a sodium/proton antiporter mediating Na^+ extrusion), CBL10 directs CIPK24 toward vacuolar membrane substrates, regulating sodium sequestration (Kim *et al.*, 2007; Li *et al.*, 2009; Yang *et al.*, 2019).

REGULATION OF VACUOLAR CATION TRANSPORTERS

The primary substrates of CBL10-CIPK24 complexes are proposed to be tonoplast-localized cation/proton transporters, particularly those involved in vacuolar Na^+ sequestration (Yang *et al.*, 2019; Plasencia *et al.*, 2021). It has been suggested that the CBL10-CIPK24-mediated phosphorylation may regulate Na^+/H^+ exchangers (NHXs), thereby inducing conformational changes that enhance their sodium transport capacity and drive sodium sequestration into the vacuolar lumen (Plasencia *et al.*, 2021). This mechanism maintains high vacuolar Na^+ concentrations supporting osmotic balance and cellular turgor, while simultaneously maintaining low cytoplasmic sodium levels that protect sensitive metabolic enzymes and photosynthetic machinery from sodium toxicity (Kim *et al.*, 2007; Yang *et al.*, 2019).

CROSSTALK BETWEEN SALT AND DROUGHT STRESS SIGNALLING

The CBL10-mediated salt stress signalling pathway exhibits significant overlap with drought stress responses. Both salt and water stress activate the same calcium-signalling apparatus through mechanistically distinct initial triggers: salt stress activates calcium channels through accumulation through the hallmark SOS pathway,

whereas drought stress activates calcium mobilization majorly through abscisic acid (ABA)-dependent mechanisms and osmotic sensing (Zhu, 2002; Seifikalhor *et al.*, 2019; Bachani *et al.*, 2022). Despite the different initiating signals, both stresses converge on calcium elevation and activation of CBL10-mediated ion homeostasis pathways. However, CBL10 signalling may function differently in response to the two stressful conditions. While it acts as a positive regulator of salt stress, CBL10 has been proposed to have an opposite effect during drought, where it has been implicated as a negative regulator of the stress resistance response (Kang and Nam, 2016; Yang *et al.*, 2019; Plasencia *et al.*, 2021).

CBL IN REGULATING GROWTH VERSUS STRESS TOLERANCE TRADE-OFFS

Under salt stress, plants exhibit considerably diminished growth as resources are allocated to survival. CBL10 has been implicated in positively regulating plant growth under salt stress through maintenance of a low $\text{Na}^+/\text{Ca}^{2+}$ ratio in the growing plant tissues (Egea *et al.*, 2018). It regulates the Na^+ and Ca^{2+} fluxes in the vacuole, working in cooperation with the Two-Pore Channel 1 (TPC1). This discovery came with the observation that *cb10* mutants exhibit reduced Na^+ accumulation in leaves and impaired Ca^{2+} release from vacuolar deposits. The mutant phenotype manifests as severe alterations in the shoot apex and reproductive organs under salinity. This abnormal growth is attributed to the reduced uploading of Na^+ from the xylem in leaves, causing the Na^+ to reach the apical and floral meristems.

Furthermore, recent research has revealed that the Target of Rapamycin Complex (TORC) signalling, a nutrient-sensing pathway regulating growth versus stress tolerance trade-offs, reciprocally regulates CBL10-CIPK24 interaction strength (Li *et al.*, 2025). CIPK24 modulates the TORC activity by physically interacting with RAPTOR1B (a subunit of TORC) through conditional phosphorylation of

RAPTOR1B at Serine-897 residue under salt stress. This phosphorylation event promotes the dissociation of RAPTOR1B, eventually inhibiting TORC. Hence, under "too salty" conditions, repression of TORC causes strengthening of the CBL10-CIPK24 interaction, thereby promoting salt tolerance at the expense of growth. During the recovery phase ("just right" conditions), RAPTOR1B disrupts CBL10-CIPK24 interaction and blocks CIPK24 phosphorylation, deactivating the SOS pathway and allowing growth resumption.

TISSUE-SPECIFIC EXPRESSION AND FUNCTIONAL SPECIALIZATION OF CBL10

SHOOT-SPECIFIC EXPRESSION PATTERN

In contrast to CBL4, which functions primarily in roots to exclude sodium uptake, CBL10 exhibits predominant expression in shoot tissues where salt toxicity symptoms most severely manifest (Kim *et al.*, 2007; Quan *et al.*, 2007; Yang *et al.*, 2019). This tissue-specific expression pattern reflects evolutionary specialization: shoots face unavoidable sodium accumulation from transpirational water loss and phloem recirculation, requiring specialized mechanisms for sodium management. Root tissues prioritize sodium exclusion through active uptake limitation, rendering CBL10 largely unnecessary in roots. This shoot-specific functional specialization explains why *cb10* mutants display severe salt sensitivity with substantially wilted, chlorotic shoots under moderate salt concentrations, while root growth initially remains relatively preserved (Kim *et al.*, 2007; Quan *et al.*, 2007).

Within shoot tissues, CBL10 displays particularly high expression in upper mature leaves where it plays a critical role in both vegetative growth and reproductive development under saline conditions (Monihan *et al.*, 2016; Egea *et al.*, 2018). CBL10 ensures proper Na⁺ and Ca²⁺ distribution within the shoot apical meristem to facilitate maintenance of a low Na⁺/Ca²⁺ ratio (Kim *et al.*, 2007; Quan *et al.*, 2007; Egea *et al.*, 2018). The maintenance of this ion homeostasis directly

influences meristematic activity and developmental plasticity (Egea *et al.*, 2018). CBL10 deficiency impairs not merely stress tolerance but also basal growth capacity, indicating CBL10's fundamental role in maintaining cellular homeostasis, supporting both normal development and stress adaptation.

DEVELOPMENTAL REGULATION OF CBL10 EXPRESSION

CBL10 expression undergoes developmental regulation, with expression levels increasing in tissues approaching developmental maturity and displaying reduced growth rates (Kim *et al.*, 2007; Mohanta *et al.*, 2015; Egea *et al.*, 2018). While the young leaves and stems also display an increased CBL10 expression in response to salt stress, its expression is highest in the mature adult leaves. This developmental pattern aligns with the principle that stress tolerance and growth represent competing physiological priorities: young, rapidly growing tissues prioritize growth allocation, while mature tissues increasingly allocate resources to stress tolerance and cellular maintenance.

EVOLUTIONARY CONSERVATION AND SPECIES-SPECIFIC VARIATION OF CBL10

DEEP EVOLUTIONARY CONSERVATION ACROSS PLANT DIVERSITY

CBL10 exhibits remarkable evolutionary conservation across more than 100 plant species spanning monocots, eudicots, and basal angiosperms, a degree of conservation spanning over 400 million years of plant evolution. Phylogenetic analysis reveals CBL10 orthologs cluster into species-specific monophyletic groups, with the highest sequence identity to CBL10 orthologs from species within the same clade, yet fundamental functional properties are preserved across deep evolutionary distances (Lu *et al.*, 2017; Mohanta *et al.*, 2015).

The evolutionary conservation of CBL10 confirms its primary function in salt tolerance, which is

conserved across these evolutionary lines (Plasencia *et al.*, 2021). It can also be speculated that this evolutionary conservation demonstrates that salt and osmotic stress have represented consistent selective pressures throughout plant evolutionary history, a sobering reminder that such stresses are not recent phenomena but rather ancient constraints shaping plant development and physiology.

ORTHOLOG ANALYSIS ACROSS MODEL AND CROP SPECIES

Detailed phylogenetic and functional analyses have identified *CBL10* orthologs in economically important crops, including rice (*Oryza sativa*, *OsCBL10*), wheat (*Triticum aestivum*, *TaCBL10*), tomato (*Solanum lycopersicum*, *SlCBL10*), soybean (*Glycine max*, *GmCBL10*), grapevine (*Vitis vinifera*, *VvCBL10A* and *VvCBL10B*), canola (*Brassica napus*, *BnaCBL10*), cabbage (*Brassica oleracea*, *BoCBL10A*), eggplant (*Solanum melongena*, *SmCBL10*), maize (*Zea mays*, *ZmCBL10*), sugarcane (*Saccharum spontaneum*, *SsCBL10*), cotton (*Gossypium arboreum*, *GaCBL10-1* and *GaCBL10-2*; *G. raimondii*, *GrCBL10-1* and *GrCBL10-2*; and *G. hirsutum*, *GhCBL10-1*, *GhCBL10-2*, *GhCBL10-3*, and *GhCBL10-4*) and numerous other species (Zhang *et al.*, 2014; Sun *et al.*, 2015; Li *et al.*, 2016; Zhang *et al.*, 2016; Lu *et al.*, 2017; Xi *et al.*, 2017; Xu *et al.*, 2017; Egea *et al.*, 2018; Jiang *et al.*, 2020; Feng *et al.*, 2021; Jiao *et al.*, 2024). Comparative sequence analysis reveals these orthologs maintain the core structural features essential for CBL10 function, the characteristic TMD targeting to internal membranes, four EF-hand domains, and conserved CIPK-interaction interfaces, despite divergence in regulatory regions and tissue-specific expression patterns reflecting crop-specific stress responses (Mohanta *et al.*, 2015).

CBL10 ORTHOLOGS FROM HALOPHYTIC SPECIES

Particularly valuable insights emerge from analyzing CBL10 orthologs from plants naturally

adapted to extreme salt stress—facultative and obligate halophytes (Unpublished Data). These plants, evolving under selection pressures favoring enhanced salt tolerance, have accumulated functional variants of CBL10 and associated components of the CBL10-CIPK24 pathway optimizing performance under chronic high-salinity conditions (Unpublished Data). The characterization of CBL10 orthologs from such halophytic species, particularly from plants like *Salvadora persica* native to India's arid regions, offers unparalleled opportunities to identify and harness naturally evolved mechanistic enhancements (Unpublished Data).

Salvadora persica, a facultative halophyte native to the Thar Desert, thrives in soils with salt concentrations far exceeding typical agricultural thresholds. The CBL10 ortholog from this species (*SpCBL10*) likely contains functional variants enhancing salt-stress tolerance, accumulated through natural selection over millennia. Research at AFRI Jodhpur has undertaken a comprehensive characterization of *SpCBL10*, including analysis of its structural organization, divergence from reference orthologs, and functional validation through transgenic expression in model systems (Unpublished Data).

CBL10-MEDIATED MOLECULAR MECHANISMS OF SALT AND OSMOTIC STRESS TOLERANCE

MAINTENANCE OF CELLULAR ION HOMEOSTASIS

The primary mechanism by which CBL10 confers enhanced stress tolerance involves maintenance of cellular ion homeostasis under conditions of excess salt or osmotic stress (Kim *et al.*, 2007; Yang *et al.*, 2019). Through CBL10-CIPK24-mediated phosphorylation and possible activation of tonoplast Na^+/H^+ antiporters and related transporters, plants sequester excessive Na^+ into the vacuolar lumen, maintaining the cytoplasm as a low-sodium compartment. This compartmentalization prevents sodium-induced

enzyme inhibition, photosynthetic impairment, and cell division disruption that would otherwise occur with cytoplasmic Na^+ accumulation.

The quantitative outcome of this compartmentalization proves substantial: vacuolar Na^+ concentrations may reach several hundred millimolar, while cytoplasmic concentrations remain below 50 mM despite external salt concentrations of 200+ mM

(Isayenkov and Maathuis, 2019). This 4 to 10-fold concentration gradient between vacuole and cytoplasm, maintained through ATP-driven tonoplast transporters whose activity CBL10 regulates, represents a critical determinant of salt tolerance (Kim *et al.*, 2007). The Figure 1 portrays the mechanism of action of CBL10 in coordination with other ion channels during stress induced signal transduction.

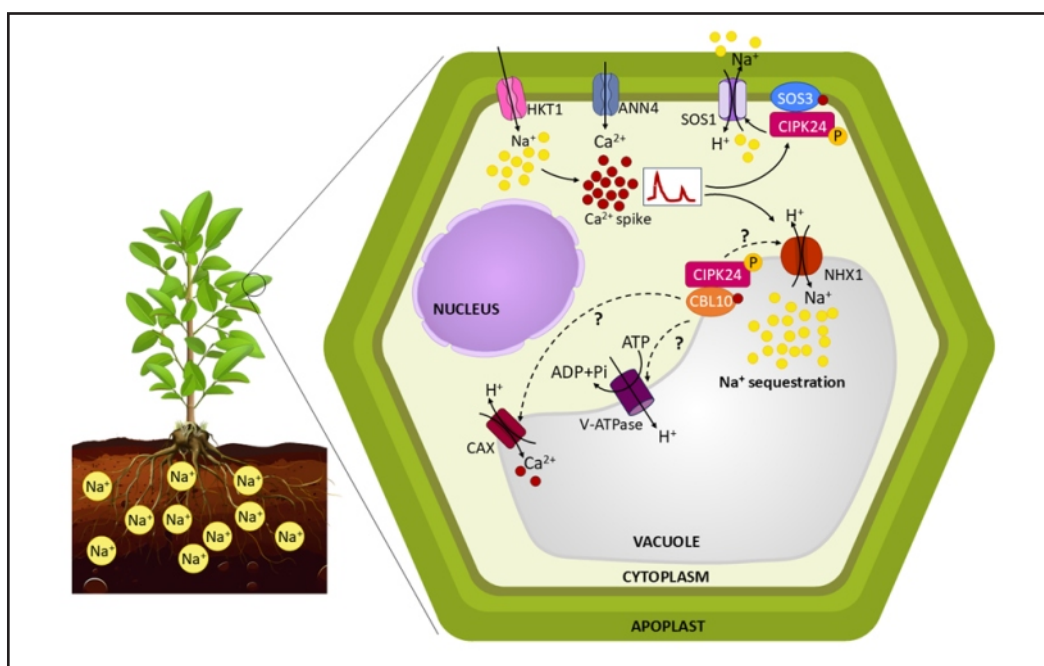


Fig. 1. Illustration depicting the model for CBL10 function. Excess Na^+ present in the transpiration stream is unloaded into the shoot tissues and enters the surrounding parenchyma cells via HKT1 (and other channels), thereby reducing the amount of Na^+ reaching the growing apex. Build-up of Na^+ in the cells triggers a spike of Ca^{2+} , which is decoded by specialized Ca^{2+} sensors within the cell. While the SOS1 pathway at the plasma membrane facilitates Na^+ extrusion to the apoplast following phosphorylation by the SOS2-SOS3 complex (SOS2 essentially being CIPK24), the Ca^{2+} wave at the level of the vacuole is perceived by CBL10, a master regulator in Na^+ homeostasis and salt stress signaling. CBL10 interacts with CIPK24 (SOS2) while being tethered to the tonoplast. Together, the CBL10-CIPK24 module may interact with the vacuolar H^+ pumps and NHX1 by yet unknown mechanisms, facilitating Na^+ sequestration into the vacuole. It may also modulate the activity of vacuolar CAX essential for cytoplasmic Ca^{2+} efflux, thus preventing excessive $[\text{Ca}^{2+}]_{\text{cyt}}$.

[Abbreviations- ANN4: Annexin 4; ADP: Adenosine diphosphate; ATP: Adenosine triphosphate; CAX: $\text{Ca}^{2+}/\text{H}^+$ exchanger; CBL10: Calcineurin B-like protein 10; CIPK24: CBL-interacting serine/threonine-protein kinase 24; HKT1: High-Affinity K^+ Transporter 1; NHX1: Na^+/H^+ exchanger 1; Pi: Inorganic phosphate; SOS1/2/3: Salt overly sensitive 1/2/3; V-ATPase: Vacuolar-type ATPase or proton pump]

MAINTENANCE OF CELLULAR OSMOTIC BALANCE AND TURGOR

By sequestering Na^+ into vacuoles, CBL10-mediated mechanisms may sustain high vacuolar osmotic potential, thereby reducing cellular water potential to drive water uptake under saline conditions (Zhang *et al.*, 2025). This, in turn, can help maintain cellular turgor pressure essential for cell growth, stomatal opening, and photosynthetic function. Without this osmotic balance maintenance, cells lose turgor, growth arrests, stomata close, photosynthesis ceases, and the plant rapidly enters a senescence-like state under continued stress. CBL10's role in turgor maintenance thus extends beyond toxic ion avoidance to active support of physiological function under stress conditions.

CALCIUM HOMEOSTASIS AND SIGNALLING

Beyond sodium sequestration, CBL10-CIPK24 complexes regulate calcium homeostasis through phosphorylation of tonoplast-localized calcium transporters. Proper calcium signalling functions require maintenance of basal cytoplasmic calcium around 100–200 nM, with stress-induced elevations reaching 0.5–1.0 μM (Igamberdiev and Hill, 2018; Pottosin and Schönknecht, 2007). CBL10-mediated regulation of tonoplast calcium transporters modulates calcium fluxes across both the plasma membrane and the tonoplast (Plasencia *et al.*, 2021). This aids in appropriate Ca^{2+} partitioning in plants and fruits by mobilizing Ca^{2+} reservoirs (Egea *et al.*, 2018). Without functional CBL10, Ca^{2+} is retained in the mature leaves, thus preventing it from being mobilized to the developing tissues and fruits in adequate concentration.

ROLE OF CBL10 IN MULTIPLE PHYSIOLOGICAL CONTEXTS

IMMUNE SIGNALLING AND PLANT-PATHOGEN INTERACTIONS

Beyond abiotic stress responses, emerging evidence indicates CBL10 participates in plant

immune signalling through calcium-dependent mechanisms (Cui *et al.*, 2014; Plasencia *et al.*, 2021). In tomato, it has been revealed that CBL10 interacts with CIPK6 (rather than CIPK24), forming distinct signalling modules activated during pathogen-associated molecular pattern (PAMP) recognition and effector-triggered immunity (ETI) (de la Torre *et al.*, 2013). These CBL10-CIPK6 complexes regulate production of ROS essential for antimicrobial defense through phosphorylation of membrane-bound NADPH oxidases, i.e. the Respiratory Burst Oxidase Homolog proteins (RBOHs) (de la Torre *et al.*, 2013). This, in turn, could lead to the ROS-induced Ca^{2+} release through regulation of the activity of TPC essential for the plant systemic signalling (Choi *et al.*, 2017). This functional diversity, whereby CBL10 associates with different CIPK partners to generate context-specific responses, exemplifies a sophisticated signalling economy where conserved sensors generate multiple distinct outputs through combinatorial association with different effectors.

NUTRIENT STRESS RESPONSES

Apart from CBL10-mediated salt tolerance, it has been revealed that CBL10 influences the Arabidopsis K^+ transporter 1 (AKT1) and thereby aids in the maintenance of K^+ homeostasis, hinting at its possible role in ion homeostasis (Ren *et al.*, 2013). Furthermore, under K^+ deprivation, it has been shown that expression of CBL10 in cotton (*GhCBL10-3*) is reduced in early phases (6 h), which later increased at 2 and/or 5 days of deficiency (Lu *et al.*, 2017). It is interesting to note that the refeeding of K^+ leads to decrease in *GhCBL10-3* expression. The differential modulation of CBL10 thus implicates it, along with other CBLs, in the response to K^+ starvation (Lu *et al.*, 2017). Despite these revelations, direct involvement of CBL10 in nutrient stress has not been studied in much detail yet. Nonetheless, it would be an interesting line of research to reveal the roles of CBL10 beyond Na^+ and K^+ homeostasis.

FLOODING AND HYPOXIA

CBL10 is also likely involved in response to hypoxic conditions resulting from flooding, as has been reported in rice (Ye *et al.*, 2018). The study reported that the divergent flooding resistance in 8 rice cultivars at the germination stage is contingent upon their respective expression levels of CBL10. It has been shown that a steady low CBL10 expression and a lower cytoplasmic Ca^{2+} influx in cultivars corresponds to flood-tolerance, in contrast to the cultivars exhibiting flood-sensitivity. In concert with this, the lines overexpressing *CBL10* showcase an increased sensitivity to flooding and an enhanced Ca^{2+} influx in the cytoplasm.

WHY *CBL10* BASED GENE TRANSFER IS A BETTER STRATEGY FOR DEVELOPING ABIOTIC STRESS-TOLERANT PLANTS

By cloning and transferring *CBL10* gene, we are not just adding a pump (like *NHX1* or *SOS1*), but we are providing the plant with a superior 'decision-making' capability. This allows the transgenic plant to perceive salt stress more efficiently and coordinate a multifaceted defence that protects the vital meristematic tissues, which is essential for survival in arid and saline environments in particular.

THE "MASTER SWITCH" FOR NON-LINEAR SIGNAL AMPLIFICATION

Overexpressing a single transporter like *NHX1* directly is like adding one more exhaust fan to a hot room. Overexpressing a sensor like CBL10 is like upgrading the entire thermostat system. One CBL10 molecule, upon binding Ca^{2+} can activate multiple CIPK24 (*SOS2*) kinases. Each kinase can then phosphorylate and activate hundreds of *NHX1* and *V-ATPase* pumps. This provides a non-linear amplification of the stress response that a single transporter cannot match.

SPATIOTEMPORAL PRECISION FOR PROTECTION OF SHOOT APICAL MERISTEM (SAM)

CBL10 is not a generic sensor. It is a specialized Shoot/SAM architect. In arid-zone forestry species, survival depends on protecting the Shoot Apical Meristem (SAM). Because CBL10 has a unique transmembrane domain that anchors it specifically to the tonoplast in shoot tissues, its overexpression will ensure that Na^+ sequestration is prioritized in the most sensitive growing tips. This will maintain the developmental potential of the plant under saline conditions, which is far more critical than simply reducing total salt content.

METABOLIC EFFICIENCY AND RESOURCE MANAGEMENT

Constant overexpression of a transporter coding gene (like *NHX1*) creates a metabolic drain because the plant spends energy (ATP) pumping ions even when stress is low. *CBL10* is signal-dependent. It only recruits the Na^+ sequestration machinery when it senses a Ca^{2+} spike (the stress signal). This "smart" regulation prevents the plant from wasting energy on defence during favourable growth periods, avoiding the yield penalty often seen with constitutively expressed transporters.

ORCHESTRATION OF MULTI-COMPONENT HOMEOSTASIS

Salt tolerance is never the result of one protein. It requires a balance of Na^+ , H^+ , and Ca^{2+} . *CBL10* does not just influence *NHX1*. As a central hub, it coordinates – (i) Na^+ Sequestration: Via *NHX1*, (ii) Energy Provision: Via *V-ATPase* activation, (iii) Signal Resetting: Via *CAX* proteins to restore Ca^{2+} levels.

Therefore, by transferring *CBL10* gene to a plant, we would be transferring the coordinator that manages the entire jigsaw puzzle, rather than just one piece of it.

POTENTIAL APPLICATIONS OF *CBL10*-ENHANCED CROPS TO AGRICULTURAL CHALLENGES AND CLIMATE CHANGE ADAPTATION

SALT-AFFECTED SOIL RECLAMATION AND SUSTAINABLE INTENSIFICATION

Approximately 1.5 billion hectares of salt-affected soils globally, with 20-50% of irrigated soils across the globe, undergo continuous productivity decline as salinization intensifies (Singh *et al.*, 2022; FAO, 2024). CBL10-enhanced crop varieties would enable the cultivation of previously marginal or abandoned salt-affected lands, dramatically expanding the land resource base available for food production. In regions like Rajasthan, where saline groundwater and surface salt crusts constrain agricultural productivity, CBL10-enhanced varieties could unlock productivity from extensive otherwise-barren lands.

FORESTRY AND AGROFORESTRY APPLICATIONS

Beyond annual crops, CBL10-enhanced salt tolerance has applications in forestry and agroforestry systems. Tree species engineered with enhanced CBL10 function could be established on degraded salt-affected sites, providing fuel wood, timber, and non-timber forest products while simultaneously rehabilitating degraded lands. This is particularly relevant in India's arid regions, where tree establishment on saline sites remains economically challenging despite ecological and social benefits.

NUTRITIONAL SECURITY AND LIVELIHOOD RESILIENCE

Enhanced crop productivity on previously marginal lands directly translates to improved nutritional security and rural livelihood resilience (Kumar and Sharma, 2020; Singh *et al.*, 2022). Farming communities dependent on marginal lands currently experiencing severe productivity constraints could achieve substantially improved yields through cultivation of CBL10-enhanced varieties, providing food security and economic resilience essential for sustainable development in marginal agroecosystems.

FUTURE RESEARCH DIRECTIONS AND EMERGING TECHNOLOGIES

STRUCTURAL BIOLOGY AND STRUCTURE-GUIDED PROTEIN ENGINEERING

High-resolution crystal structures of CBL10 in complex with calcium ions, CIPK24, and target substrates should enable artificial intelligence (AI)-assisted structure-guided protein engineering (Egea *et al.*, 2025). Rational engineering based on atomic-scale structural information could generate CBL10 variants with enhanced calcium sensitivity, improved CIPK24 binding, or altered regulatory properties. Such engineered CBL10 variants might achieve equivalent stress tolerance with reduced constitutive expression, minimizing metabolic costs.

MULTI-OMICS INTEGRATION AND SYSTEMS-LEVEL UNDERSTANDING

Integration of genomic, transcriptomic, proteomics, and metabolomic approaches examining plant responses to stress in CBL10 overexpression versus null mutant backgrounds would illuminate the complete physiological and metabolic consequences of CBL10 modulation (Yang *et al.*, 2021). This systems-level understanding could identify unexpected side effects or opportunities for synergistic pathway engineering.

FIELD VALIDATION AND AGRONOMIC OPTIMIZATION

Laboratory demonstration of enhanced stress tolerance requires rigorous field validation across diverse agroecologies and multiple growing seasons. Long-term field experiments comparing CBL10-enhanced varieties to conventional cultivars across variable rainfall years, soil types, and management practices would establish agronomic performance and identify any unforeseen interactions between enhanced stress tolerance and other agronomic.

REGULATORY FRAMEWORK DEVELOPMENT AND CONSUMER ACCEPTANCE

As genetically modified or gene-edited CBL10-enhanced crops approach commercialization, the development of science-based regulatory frameworks that ensure safety while facilitating timely market access represents a critical

requirement (Gaj *et al.*, 2013; Kumar *et al.*, 2023; Chen *et al.*, 2024a). Furthermore, consumer education regarding gene editing technologies, distinguishing them from transgenic approaches and highlighting their benefits for sustainable agriculture, will determine market acceptance.

INTEGRATION WITH CLIMATE-SMART AGRICULTURE PRACTICES

CBL10-enhanced varieties in future will represent only one component of comprehensive climate-smart agriculture approaches (FAO, 2022). Optimal benefits emerge through integration with water-harvesting technologies, soil conservation practices, improved agronomic management, and farmer training programs (FAO, 2022). Holistic approaches combining multiple innovations may generate synergistic benefits exceeding those of single technological interventions (FAO, 2022).

CONCLUSION

CBL10 represents a critically important molecular hub integrating calcium signalling with ion homeostasis and stress tolerance mechanisms, particularly for salinity, essential for plant survival in terrestrial environments. The remarkable evolutionary conservation of this protein across plant diversity, combined with evidence of natural functional variants in halophytic species, testifies to its fundamental biological importance and practical utility for crop improvement. Contemporary understanding of CBL10 structural features, calcium-dependent signalling mechanisms, tissue-specific expression patterns, and functional outcomes across diverse plant species provides a solid foundation for rational manipulation of this gene to enhance stress tolerance.

The convergence of sophisticated gene editing technologies with improved understanding of CBL10 biology promises new opportunities to enhance crop stress tolerance with unprecedented precision. CRISPR/Cas9-mediated approaches may further enable not merely overexpression of single genes but rational

reengineering of entire stress-response pathways, creating crops with fine-tuned stress responses appropriately calibrated to agricultural environments. Base editing, prime editing, and related emerging technologies provide complementary capabilities enabling subtle, precise modifications unachievable through conventional genetic engineering.

The urgency of global food security in an era of climate change and expanding populations makes deployment of enhanced stress-tolerance crops increasingly critical. CBL10-enhanced varieties, developed through rational application of contemporary biotechnology to stress-response mechanisms refined through evolutionary processes, represent a scientifically sound and practically feasible approach to improving agricultural resilience and productivity. Particularly in arid and semi-arid regions of India and globally, where marginal agroecosystems support vulnerable farming communities, CBL10-enhanced crops promise substantial benefits for food security, livelihood resilience, and sustainable agricultural intensification.

Future progress requires continued investment in molecular characterization of stress-tolerance genes, field validation of enhanced varieties across diverse agroecologies, development of enabling regulatory frameworks, and farmer-participatory approaches ensuring that biotechnology benefits reach farming communities most affected by stress constraints. The convergence of plant molecular biology, crop genetics, gene editing technology, and agricultural science offers unprecedented potential to develop crops adequate to the challenges of agriculture in the 21st century.

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