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REVIEW ARTICLE

Beyond Survival: The Unique Salt Secretion and Ion Homeostasis Mechanisms in *Limonium bicolor* Under Salt Stress

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Abstract: Soil salinization poses a significant threat to global agriculture. *Limonium bicolor*, a recretohalophyte, has evolved a unique and efficient salt tolerance mechanism centered on epidermal salt glands for secreting excess salts. This review systematically synthesizes the multilevel salt tolerance strategies in *Limonium bicolor*, covering the structural basis of its multicellular salt glands, the molecular regulatory networks governing their development including core transcription factors (e.g., WD40, bHLH, MYB) and signaling pathways (e.g., cytokinin, MAPK cascades, Ca^{2+}, NO) and the precise ion transport mechanisms for salt secretion. Furthermore, it elaborates on the supportive physiological adaptations, such as osmotic regulation and antioxidant defense, alongside the reprogramming of photosynthesis and secondary metabolism. The identification of key genes with potential for enhancing salt tolerance in other species underscores the translational value of this model halophyte. This integrated overview highlights the synergistic operation of structural, molecular, regulatory, and physiological layers, providing insights for future research and the breeding of salt-tolerant crops to utilize saline lands.

Keywords: *L. bicolor,* Salt Gland, Salt Tolerance, Recretohalophyte, Physiological Adaptations

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Introduction

Soil salinization represents a grave and growing global environmental concern, which poses a significant threat to the sustainability of agricultural production and global food security. According to the Food and Agriculture Organization of the United Nations (FAO), over 1 billion hectares of land worldwide are affected by salinization, accounting for approximately 11% of the Earth's total land area [1, 2]. Due to climate change (such as sea level rise causing seawater intrusion), improper irrigation practices (including high-salinity irrigation water and poor drainage), and excessive fertilizer use, the area of secondary salinized soils continues to expand. Approximately 20% of the world's irrigated farmland is affected by salinization, yet these areas contribute to over one-third of the global food supply. Consequently, yield losses caused by salt stress pose a direct threat to food security.

It has been demonstrated that elevated levels of sodium chloride in soil have a detrimental effect on the water potential of the soil, thereby impeding the process of water absorption by plant roots and inducing a state of physiological drought. Despite the presence of soil moisture, plants manifest symptoms consistent with drought, including wilting and stunted growth. The influx of Na+ and Cl- ions into plant tissues disrupts cellular ion homeostasis, thereby inhibiting the uptake and function of essential nutrients such as K+ and Ca2+. Na+ directly damages cell membranes, enzyme systems, and organelles, thereby impairing fundamental metabolic processes such as photosynthesis and protein synthesis [3, 4]. Salt stress induces the production of significant quantities of Reactive Oxygen Species (ROS) in plants, including hydrogen peroxide (H_2O_2) and superoxide anion (O2-), which have been observed to result in membrane lipid peroxidation, protein denaturation, and DNA damage. In essence, this phenomenon leads to diminished crop growth, diminished leaf area, diminished photosynthetic efficiency, and aberrant flowering and fruiting. Consequently, crop yields are significantly reduced, and fruit or grain quality (e.g., protein content, taste) is markedly diminished [5].

Plants have evolved multiple strategies over long-term evolution to cope with salt stress, which can be broadly categorized into two main types: Salt Avoidance and Salt Tolerance [6-10]. The crux of salt avoidance strategies pertains to the prevention or reduction of salt uptake into plants, with a particular focus on sensitive above-ground tissues [11-13]. One proposed approach involves the selective absorption of K+ by the root system, while simultaneously rejecting Na+, through the regulation of ion absorption channels [14]. This process is intended to impede the entry of excessive Na+ into the xylem. This strategy carries the cost of potentially limiting water uptake, leading to osmotic stress. Plants have been observed to reduce internal salt concentrations through two distinct mechanisms: firstly, through rapid growth, for example, stems and leaves absorbing large amounts of water; and secondly, through increased succulence, for example, enlarged leaves with high water content. Salt tolerance strategies involve plants utilizing internal physiological and biochemical mechanisms to withstand salinity. The most critical mechanism is ion compartmentalization, whereby plants transport excess Na+ and Cl- absorbed into the cytoplasm and store them within vacuoles [14]. This approach reduces ion concentration in the cytoplasm, preventing enzyme system toxicity, while simultaneously utilizing the stored salts in vacuoles for osmotic regulation, aiding cells in absorbing water from the external environment [15]. Salt secretion represents a highly unique and efficient strategy, positioned between salt avoidance and salt tolerance but leaning more toward active salt avoidance. Its core principle involves plants allowing salt uptake through roots and transport to the aboveground parts, while simultaneously expelling excess salts through specialized organs salt glands or salt vesicles to maintain internal ionic homeostasis.

The secretion of salt is an exceptionally unique and efficient strategy, positioned between salt avoidance and salt tolerance, but leaning more towards an active form of salt avoidance [17]. Salt secretion is an exceptionally efficient strategy. Mechanistically, roots absorb salt and transport it to aboveground organs, where specialized salt glands or vesicles actively expel the surplus ions to maintain internal ionic homeostasis [16]. Concurrently, these plants possess specialized organs, designated as salt glands or salt vesicles, which function to expel surplus salts. This process contributes to the maintenance of internal ionic homeostasis within the plant organism.

As a representative species that has evolved this strategy, *Limonium bicolor* differentiates a highly specialized multicellular structure the salt gland in its outer epidermis [17]. These unique salt-secreting organs act like energy-consuming "micro-pumps," efficiently expelling excess toxic ions that are taken up by the roots and transported to the above-ground parts. In doing so, they fundamentally prevent long-term salt accumulation in the plant and reduce potential risks such as vacuolar leakage or tissue senescence. This trait of "turning passive tolerance into active removal" makes *L. bicolor* an ideal model organism for studying the evolution and physiological regulation of recretohalophytes [18].

As documented in the Flora of China*, L. bicolor* is a perennial herb belonging to the genus Limonium. It is primarily distributed in two regions: Firstly, in Xinjiang, and secondly, in the Yellow River basin of China. It is a typical halophyte, possessing epidermal salt glands through which it is able to secrete excess Na+ via specialized structures in its salt glands, leaves, and stem epidermis. This enables it to grow normally and complete its life cycle in high-salinity environments. Its salt tolerance mechanisms have been extensively studied, with thorough investigations into gene identification and salt tolerance regulation, establishing it as a model halophyte [19]. In comparison with conventional glycophyte models (e.g., A. thaliana), it offers distinctive value and environmental versatility. As shown in Figure 1.

The present study aims to provide a comprehensive review of the multi-level mechanisms underlying *L. bicolor*'s salt tolerance. In order to achieve this objective, the study will integrate recent advances in the fields of physiology, biochemistry, and molecular biology, and it will also provide perspectives for future research.

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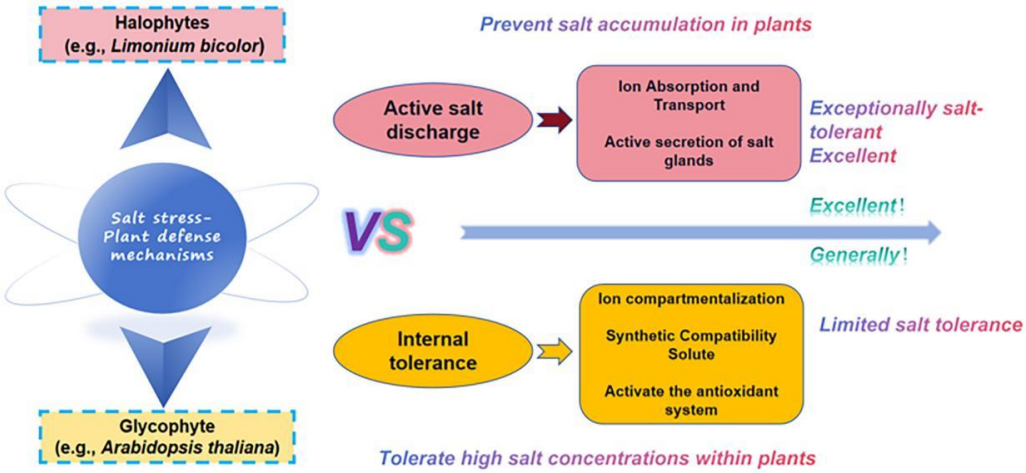

Fig. 1: Comparative analysis of salt tolerance mechanisms in glycophytes and halophytes

Literature Search and Selection Strategy

To ensure the comprehensiveness, objectivity, and rigor of this review, a systematic literature search and screening method was employed. The literature search was primarily conducted across four major academic databases: Web of Science, PubMed, Google Scholar, and the China National Knowledge Infrastructure (CNKI). The search strategy revolved around the following core keywords and their combinations: "*Limonium bicolor*", "salt gland", "recretohalophyte", "salt tolerance", and "ion homeostasis". The search timeframe for each database was from its inception to January 2026. The review focused on peer-reviewed original research papers and high-quality review articles addressing the multicellular salt gland structure, molecular regulatory network of salt secretion, ion transport mechanisms, or related physiological defense systems of *L. bicolor*. Comparative biology studies exploring the evolutionary history of salt tolerance between halophytes and glycophytes were also included. Excluded were studies that only mentioned the species incidentally in field ecological surveys without addressing any microscopic mechanisms, physiological processes, or molecular mechanisms; studies with duplicate data publication, obvious methodological flaws, or non-peer-reviewed brief reports lacking experimental evidence. Through this rigorous screening process, this review ultimately performed an in-depth integration and systematic analysis of the selected core high-quality studies, thereby ensuring the scientific validity and representativeness of the constructed "blueprint for salt tolerance."

Multilevel Mechanisms of Salt Tolerance in *Limonium bicolor*

To transcend the fragmentation inherent in conventional literature, this review establishes a comprehensive "Four-Layer Integrated Conceptual Framework". The elite salt tolerance of *L. bicolor* is conceptualized not as a collection of isolated traits, but as a closed-loop multi-tiered system driven by four tightly interwoven logical layers:

Layer 1: Structural Foundation: Operates via the precise epidermal spatial arrangement of the 16-cell multicellular salt gland as the physical vehicle, deploying a three-stage division of labor collection, transportation, and excretion to directionally clear toxic ions, which serves as the morphological basis of the entire defense network.

Layer 2: Molecular Execution: Driven by the chromosome-expanded LbTTG1-LbHLH-LbMYB48 core transcriptional activation complex, post-transcriptionally fine-tuned by long non-coding RNAs, and micro-geographically calibrated by the TRIPTYCHON-Lb7G34824 unit to precisely govern the epidermal cell fate transition.

Layer 3: Systemic Regulation: Motivated by developmental "cytokinin waves" linked with adversarial/complementary networks of ABA, JA, and SA to establish the hormonal command centers; while simultaneously utilizing MAPK cascades, gaseous NO signals, and Ca2+ flux to transform transient physical stresses into nuclear transcriptional inputs.

Layer 4: Physiological Support: Concurrently reinstates whole-plant osmotic homeostasis via proline and soluble sugar accumulation; neutralizes Reactive Oxygen Species (ROS) via the LbGST1 and LbCAT2 enzymatic scavenging chain; and

reprograms phenylpropanoid/flavonoid secondary metabolic pathways alongside non-photochemical quenching to cushion the long-term metabolic costs of active excretion.

Existing papers typically constrain their scope within traditional "transcription factor-promoter" linear pathways. We systematically emphasize the weights of lncRNA axes, alternative splicing profiles, and polyadenylation shifts, mapping a comprehensive post-transcriptional landscape previously absent in halophyte genetics. Rather than concluding with generic claims about "breeding potential", this review critically dissects the "yield penalty" a major barrier in cross-species translation and proposes a precision route utilizing high-sensitivity, low-background inducible/tissue-specific promoters, bridging basic science directly with agronomic reclamation of saline-alkali wastelands.

Multilevel Mechanisms of Salt Tolerance in *Limonium bicolor*

The core salt tolerance mechanism of L. *bicolor* centers on specialized salt-secreting structures on its leaf surfaces, which are known as salt glands. These glands constitute a complex unit comprising 16 cells arranged with precision [20]. Under the scrutiny of fluorescence microscopy, these glands manifest as blue ring-shaped structures with four prominent autofluorescent spots, driven by the inherent chemical properties of their cell walls. From a functional perspective, these 16 cells can be categorised into four distinct types, with four cells per type arranged symmetrically [21].

The secretory cells sit at the base of the salt gland complex, right next to the surrounding mesophyll cells. Their most striking anatomical feature is the highly folded inner plasma membrane, which greatly increases the cell's surface area. This specialized structure gives them the main spatial framework and physical boundary needed to take up, concentrate, and pass along large amounts of toxic ions (Na^+ and Cl^-) from nearby mesophyll cells [22, 23]. Auxiliary cells are located above the secretory cells. It has been hypothesised that these cells may provide energy support (due to their high mitochondrial content) or perform regulatory functions. Consequently, the inner and outer cup cells form a "cup-like" structure that encloses the inner secretory and auxiliary cells, thereby creating a sealed collection cavity.

The structure of salt glands is highly specialised, forming a multicellular composite tissue whose fundamental architecture underpins its highly efficient salt secretion capacity. Scanning Electron Microscopy (SEM) observations demonstrate the presence of four distinct secretory pores on the apical cuticle of each salt gland, corresponding to the locations of four secretory cells [24]. These pores function as the final exit points for salt excretion. The utilisation of Environmental Scanning Electron Microscopy (ESEM) in conjunction with Energy Dispersive Spectroscopy (EDS) analysis has substantiated that the "rice-grain-like" secretions observed above these pores are predominantly composed of crystalline sodium chloride. This finding directly demonstrates salt excretion through these pores. It has been demonstrated that sodium chloride (NaCl) can only be eliminated via this specific pathway, rather than diffusing randomly through the epidermis. This process prevents unnecessary energy expenditure during secretion and avoids counter-diffusion of ions. It is therefore hypothesised that salt glands achieve efficient salt secretion through a three-stage functional division of labour: Collection, transport, and excretion, as illustrated in Figure 2. First, during the collection stage, the secretory cells located immediately adjacent to the mesophyll cells act as pumping stations. The plasma membranes of these cells are highly folded inward, and these folded membranes are enriched with (Proton-translocating Adenosine Triphosphatase) H^+-ATPase and SOS1 transporters. By means of these transporters, the secretory cells actively take up and concentrate Na^+ and Cl^- ions against the concentration gradient. Second, during the transport stage, the subsidiary cells situated above the secretory cells contain a large number of mitochondria. These mitochondria release substantial amounts of ATP, which continuously provides energy for Golgi-mediated vesicular transport, driving the salt-loaded vesicles to move toward the cell center. Finally, during the excretion stage, the inner and outer cup-shaped cells together enclose a sealed collection chamber. This chamber directs the ions toward the salt gland apex, where they are expelled through four secretory pores in the cuticle. The positions of these four pores correspond exactly to the apices of the four secretory cells. The excreted salt crystallizes in the air, forming "rice-grain-like" sodium chloride particles visible to the naked eye. This precise cellular division of labor prevents random ion diffusion and counter-diffusion.

The salt glands of the wild-type *L. bicolor* specimen under scrutiny via fluorescence microscopy manifest as a blue fluorescent ring and four strong autofluorescent spots. A rare mutant of the lb23 gene has been identified, characterised by variable numbers of salt gland cells, ranging from 20 to 32, corresponding to five to eight fluorescent spots [25, 26]. The rate of salt secretion per gland increases in proportion to the number of cells. This expansion provides a larger ion-absorbing surface area, more ion transporters, and broader secretion outlets, thereby enhancing salt excretion efficiency. The autofluorescent substance in salt glands was identified as ferulic acid [27], present in the cuticle layer. The correlation between its concentration and both fluorescence intensity and Na^+ secretion rate is positive, with the enzyme directly participating in

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salt secretion. It is notable that salt glands represent the earliest differentiated structures in leaves, preceding both stomatal and epidermal cells. The density of these cells peaks during the early phase of leaf expansion, subsequently declining due to epidermal cell expansion . In mature leaves, salt glands are more abundant in the middle and apical regions than at the base. As the leaves pass through the various stages of development, the density of the salt glands decreases linearly during the initial phase of leaf expansion. This is due to the rapid enlargement of the epidermal cells. Thereafter, the density of the salt glands remains relatively constant. Conversely, the total number of glands in leaves exhibits an inverse trend compared to salt gland density. As salt accumulation increases in saline-alkali soils, salt gland density demonstrates a positive correlation with leaf age and leaf area [28].

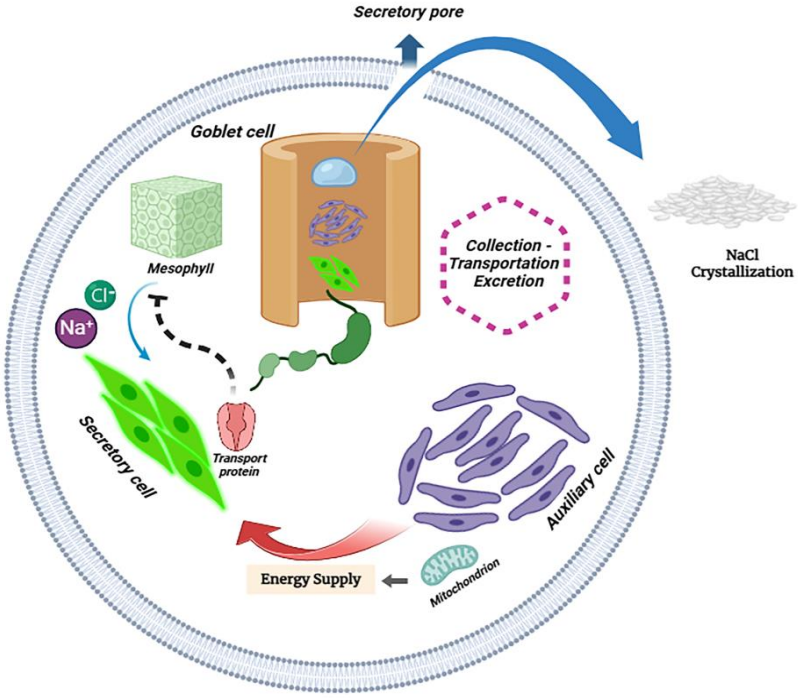

Fig. 2: Potential mechanisms of salt secretion in salt glands: collection, transport, and excretion

Molecular Regulatory Network of Salt Gland Development

Core Transcription Factor Family

The core transcription factor cluster primarily comprises the WD40 protein family, bHLH transcription factor family, MYB (Myeloblastosis family) transcription factor family, and other core transcription factors. Among these, the entire genome of *L. bicolor* identified 367 LbWD40 genes, a number far exceeding that of Arabidopsis thaliana, indicating significant lineage-specific expansion. Key genes LbTTG1, Lb1G05968, and Lb3G17197 have been confirmed to positively regulate the initiation and differentiation of salt glands by interacting with their partner protein LbHLH. Silencing these genes resulted in a substantial decrease in salt gland density (up to 66%), reduced total salt secretion, and diminished salt tolerance [29].

The bHLH transcription factor family was identified as comprising 187 Lb bHLH genes. Among these, Lb1G07934 was demonstrated to be a key negative regulator: CRISPR-Cas9 knockout lines exhibited increased salt gland numbers, enhanced salt secretion capacity, and improved salt tolerance, while overexpression produced the opposite effects [30, 31]. Another gene, LbHLH, expressed in salt glands, has been demonstrated to promote trichome formation and inhibit root hair development through interaction with the AtGL1 protein. During heterologous expression, this interaction has been shown to significantly enhance salt tolerance [32].

The most central member of the MYB transcription factor family is LbMYB48, which encodes a 195-amino acid protein containing a SANT domain and belongs to the R1-MYB transcription factor class [33]. As a predominant member of the MYB family, LbMYB48 encodes a nuclear transcription activator. Its silencing leads to a 30% reduction in salt gland density

compared to the control, significantly compromising salt tolerance. In the LbMYB48-silenced lines, a total of 2,158 differentially expressed genes were identified (1,212 downregulated and 946 upregulated). These included genes associated with salt gland development (e.g., LbCPC-like, LbDIS3); salt stress response genes (e.g., LbSOS2, LbSOS3, LbRLK5, LbGST5); ABA signalling pathway genes (e.g., LbABI5, LbNCED1); and ROS scavenging-related genes (e.g., LbAPX3, LbPHGPx). In contrast, LbCPC functions as a negative regulator. Its expression has been shown to inhibit salt gland development and reduce salt gland density, while its silencing has been demonstrated to promote salt gland development, increasing both the number of salt glands and salt secretion [34]. LbCPC has been identified as a "braking" gene in salt gland formation.

It has been observed that other core transcription factors, including LbAP2/ERF32 [35], LbNAC54 [36], and LbbZIP28 [37], demonstrate an uneven distribution across eight chromosomes. The functional loss of these factors has been shown to result in a consistent reduction in salt gland density, leaf salt excretion, and overall salt tolerance. This indicates their positive roles in salt gland development. The mechanism of core transcription factors is shown in Figure 3.

Figure 3 presents a panoramic view of the transcriptional regulatory network, organized into three interconnected layers: core activation, peripheral regulation, and downstream response. At the center of the network lies the core activation complex, composed of the positive regulators LbTTG1 (a WD40 family member), LbHLH, and LbMYB48. This complex serves as the decisive switch that directs epidermal cells toward salt gland fate. Surrounding this core, the network exhibits a complex peripheral checkpoint mechanism: on the left side, plant hormones such as cytokinin and positive transcription factors (e.g., LbAP2/ERF32) strongly promote and drive the activity of the core complex. In contrast, negative regulators the "brake genes" LbCPC and Lb1G07934- strongly inhibit the assembly and activation of the core complex. Ultimately, upon activation, the core complex precisely directs the transcriptional reprogramming of four key downstream response modules on the right side. These include the induction of salt-gland-specific genes (LbCPC-like), activation of a salt stress-responsive kinase (LbRLK5), mediation of Abscisic Acid (ABA) signaling pathway responses, and activation of an antioxidant enzyme (LbAPX3) for Reactive Oxygen Species (ROS) scavenging.

Signaling Pathways and Transcriptional Regulation of Non-Coding RNAs

Transcriptome and gene function studies reveal that salt gland development shares a core regulatory pathway with trichome development in Arabidopsis, namely the TTG1-bHLH-MYB module (e.g., LbTTG1, LbGL3/EGL3, LbMYB) [38]. This provides robust molecular evidence supporting the evolutionary hypothesis of "salt glands and trichomes being homologous." High-quality genome sequencing has revealed that *L. bicolor* possesses homologous genes for trichome development, but lacks key trichome fate-determining genes such as GLABRA3 and GLABRA2.

For a long time, academic circles have debated two competing ideas about the origin of salt-secreting organs: the "trichome homology hypothesis" and the "independent convergent evolution hypothesis." The molecular evidence reported in this section specifically, the shared TTG1-bHLH-MYB module strongly supports the former view. However, a closer critical look reveals clear differences in findings across recretohalophyte species. For instance, studies on salt gland development in grasses (such as wild rice or Puccinellia) and mangroves (such as Avicennia marina) have not detected such a highly conserved trichome regulatory module. Instead, the formation of their salt-secreting structures tends to correlate more with genes involved in stomatal lineage regulation. These contrasting observations suggest that the evolution of salt-secreting structures in plant epidermis may not have a single origin.

The recruitment of the trichome pathway in *L. bicolor* likely reflects a neofunctionalization event following Whole-Genome Duplication (WGD) and subsequent subfunctionalization-rather than a general rule shared by all recretohalophytes. This comparative analysis serves as a reminder: when building models of halophyte epidermal development, one must critically assess evolutionary heterogeneity across species and avoid over-extending conclusions based on a single species.

This genetic explanation accounts for the "hairless" phenotype, which is replaced by salt glands. It is hypothesised that a single whole-genome duplication event provided the genetic material for this adaptive evolution [39, 40].

During the initial and differentiation stages of salt gland development, extensive and specific alternative splicing and polyadenylation events occur [41]. This finding suggests that salt gland development is not solely governed by gene expression status, but is also subject to the precise regulation of distinct transcript variants. This post-transcriptional regulation is a critical mechanism that enables precise control over salt gland differentiation. It is evident from the analysis of Iso-seq (Isoform Sequencing) data that the long non-coding RNA Btranscript_153392 plays a pivotal role in the regulation of normal salt gland numbers [42], salt secretion function, and plant salt tolerance. The functional loss of this non-coding RNA was

achieved through the implementation of gene editing and virus-induced gene silencing techniques [43]. Studies conducted in this field have demonstrated that the absence of the non-coding RNA Btranscript_153392 is associated with a substantial decrease in the number of salt glands present within the leaf epidermis. This decline in salt gland quantity consequently led to diminished salt secretion capacity, ultimately resulting in decreased overall plant salt tolerance. This finding indicates that Btranscript_153392 plays a pivotal role in regulating normal salt gland numbers, salt secretion function, and overall plant salt tolerance.

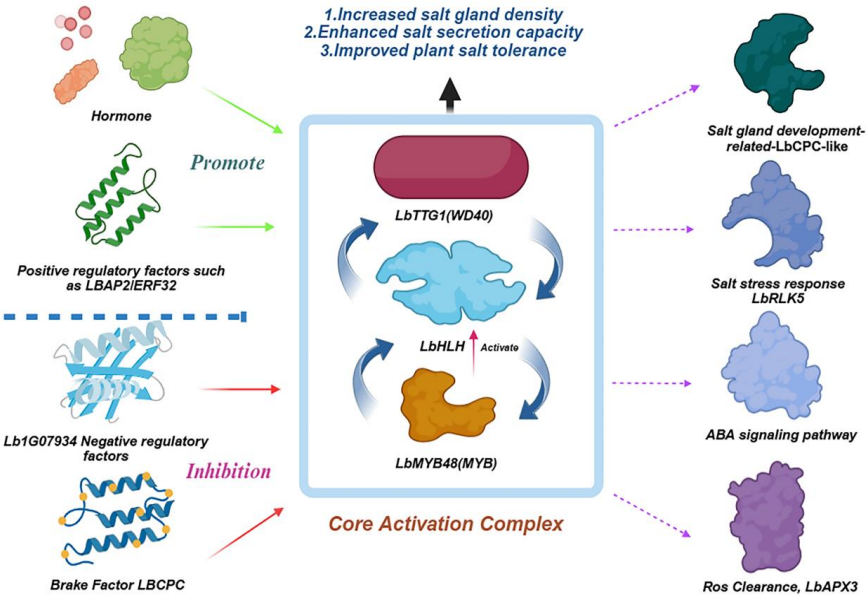

Fig. 3: The mechanism of core transcription factors

Molecular Mechanisms of Protein Complex Regulation Identified by Single-cell RNA Sequencing

High-throughput single-cell RNA sequencing technology was employed to identify gene expression profiles [44]. A total of 19 cell clusters were identified in *L. bicolor*, primarily grouped into four categories [45]. The meristematic tissue cluster, rich in genes related to cell cycle and DNA replication, represents the growth center of the leaf [46]. The epidermis and its precursor cell cluster highly express genes for cutin synthesis, wax production, and cell wall proteins, forming the outer barrier of the leaf [47]. The mesophyll cell cluster contains key photosynthesis genes, while the vascular tissue cell cluster harbors genes related to substance transport and lignin synthesis, responsible for conducting water and nutrients [48]. Cytokinin signaling plays an “engine” role in the salt gland development pathway [49]. Along the differentiation pathway from progenitor cells to mature salt gland cells, cytokinin biosynthesis, metabolism, and signaling genes exhibit significant dynamic changes, forming a precise “hormone wave” that drives and maintains cellular differentiation. At the molecular level, a key protein complex responsible for finely regulating cytokinin homeostasis during this process has been identified. This complex comprises the protein TRIPTYCHON and its interacting partner Lb7G34824. The TRIPTYCHON-Lb7G34824 complex likely functions as a central regulatory unit. By directly or indirectly modulating a series of cytokinin metabolic genes and signaling genes, it ensures cytokinin concentrations within the differentiation microenvironment remain within an “optimal window.” Crucially, this complex was demonstrated to directly activate the expression of GIS2, a key gene in salt gland development. GIS2 is a known upstream master transcription factor whose expression directly determines whether cells can transition to a salt gland fate. This demonstrates that the protein complex receives and integrates developmental signals, precisely initiates and advances the salt gland differentiation program by fine-tuning cytokinin levels, and activates core downstream effectors, thereby ensuring salt glands develop correctly in the right locations and in the correct numbers [50].

To make this complex molecular network easier to follow, the cell fate regulation mediated by this complex can be broken down into the following three clear, linear steps: Step 1: Hormonal fine-tuning (microenvironmental flow control). The TRIPTYCHON protein binds with Lb7G34824 to form a central regulatory unit. This complex, either directly or indirectly,

modulates downstream genes involved in cytokinin metabolism (e.g., oxidases) and signaling responses, thereby strictly limiting local cytokinin concentration to an "optimal dosage window" that favors development. Step 2: Gene activation (trigger switch). Once the hormone concentration in the cell differentiation microenvironment stabilizes, the TRIPTYCHON–Lb7G34824 complex binds specifically to and directly activates the transcription of the upstream master regulator gene GIS2. Step 3: Fate determination (precise differentiation). As a core transcription factor, successful expression of GIS2 serves as the "final switch" for cell fate transition, directly committing precursor cells to enter the salt gland differentiation program. This ensures, at the genetic level, that salt glands develop with the correct number and morphology at specific epidermal positions. This stepwise regulatory mechanism indicates that *L. bicolor* achieves precise remodeling of spatial epidermal structures through a layered strategy-first fine-tuning hormone concentration, then activating core genes mediated by the above protein complex.

Precise Regulation of Ion Homeostasis and Salt Secretion

Salt Secretion Transport Pathways and Active Mechanisms

Relevant studies have confirmed that salt secretion by the salt glands of *L. bicolor* is highly dependent on Golgi-mediated exocytosis and vesicle transport. Pharmacological experiments showed that treating leaves with brefeldin A (BFA), a classic specific inhibitor of exocytosis, rapidly disassembles the stacked Golgi network, thereby blocking the directional transport of salt-loaded vesicles to the plasma membrane and causing a sharp drop in salt secretion rate. This pharmacological result closely matches the genetic knockdown/silencing phenotype of LbSYP61, a vesicle fusion-related SNARE protein. Loss of LbSYP61 function leads to a marked reduction in total salt secretion and plant salt tolerance. Together, these two lines of evidence one from chemical pharmacological blockade and the other from endogenous gene manipulation demonstrate that the Golgi-mediated vesicle trafficking pathway is an indispensable active core mechanism for *L. bicolor* to expel Na^+ and Cl^- toxins and maintain cellular ion homeostasis. *L. bicolor* has been shown to facilitate the transportation of Na^+ to salt glands with a high degree of efficiency, subsequently excreting the ions through a precise regulation of ion transport. Relevant studies confirm that salt secretion by salt glands depends on vesicular transport mediated by the Golgi apparatus [51]. The silencing of the key SNARE protein LbSYP61 led to a significant reduction in salt secretion capacity, thereby demonstrating the central role of vesicular transport in this process [52].

LbHKT1;1 localises to the plasma membrane and was shown to play a negative regulatory role [53]. This finding contradicts conventional understanding. LbHKT1;1 exhibits a deficiency in K^+ transport capacity; however, it demonstrates a higher level of tolerance in comparison to its AtHKT1;1 counterpart from the same genus when subjected to elevated Na^+ concentrations [54]. Its function was confirmed to be that of a negative regulator of salt gland secretion and plant salt tolerance.

It is worth in-depth discussion that the aforementioned finding regarding LbHKT1;1 as a negative regulator exhibits significant phenotypic divergence from the widely established conclusion observed in conventional glycophytic model plants such as Arabidopsis (AtHKT1;1) or rice (OsHKT1;5), where these transporters function positively in mediating Na^+ unloading and facilitating root salt tolerance. This discrepancy among research findings cannot be simply attributed to experimental error; rather, it reflects a fundamental divergence in long-distance ion transport strategies between recretohalophytes and non-secretory glycophytes. From a critical perspective: First, differential tissue-specific expression emerges as a key factor. AtHKT1;1 is predominantly expressed in xylem parenchyma cells to restrict Na^+ translocation to the shoots. In contrast, in *L. bicolor*, which requires efficient Na^+ delivery to the leaves to meet the demand for active salt secretion by the shoot epidermal salt glands, excessive Na^+ reflux or inhibition mediated by LbHKT1;1 would instead compromise the salt secretion pathway. Second, mutations in key amino acid residues within the pore region of the protein may alter its sensitivity to high Na^+ concentrations and modulate its transport flux. This divergence highlights that HKT1-family genes have undergone profound functional differentiation and remodeling during the terrestrial evolution of higher plants. Silencing this gene has been shown to enhance salt secretion capacity, improve ion homeostasis, and increase salt tolerance. The expression of this gene is directly regulated by the transcription factor LbbZIP52 through binding and activation.

Other Transporters and Channel Proteins Involved in Salt Tolerance

The transmembrane protein LbRSG is localized to the plasma membrane of cells. Gain-of-function (overexpression) experiments demonstrate that this protein significantly enhances plant salt tolerance. Related studies reveal that a highly negatively charged region exists within a ring-shaped area on the outer side of the cell membrane where this protein resides [55]. Functional validation methods, including site-directed mutagenesis, confirm that this unique structural feature constitutes

a critical domain essential for its salt tolerance function. It is hypothesized that this region may sense or respond to ionic environment changes under salt stress through electrostatic interactions. LbRSG interacts with proteins such as PGK1 and BGLU18. PGK1, a key enzyme in glycolysis, suggests LbRSG may counteract the energy demands of salt stress by influencing cellular energy metabolism [56]. BGLU18, a β-glucosidase, may participate in cell wall polysaccharide metabolism or signal molecule activation, which relates to maintaining cell wall integrity and signal transduction [57]. LbRSG may function as a regulatory hub located on the plasma membrane. It senses environmental signals through its highly negatively charged extracellular domain and, by interacting with diverse downstream functional proteins, synergistically regulates energy metabolism and cell structure, thereby collectively mediating enhanced salt tolerance [55].

Phytohormone-Mediated Systemic Regulatory Networks

In *L. bicolor*'s response to salt stress and its unique salt gland development, plant hormones form a precise and synergistic core regulatory network. Systematic studies have revealed that different hormones, through distinct signalling pathways, collectively shape the final epidermal structure and stress resistance of the plant. Cytokinin has been demonstrated to play a pivotal driving role within this network. The exogenous application of its analogue, Exogenous 6-BA, has been shown to significantly upregulate a series of core salt gland development genes, including LbTTG1, LbGIS, LbZFP5, and LbGL3 [58]. This process of transcriptional reprogramming has been observed to have no effect on the secretion efficiency of individual salt glands; however, it has been demonstrated to result in a significant increase in their number. The augmented number of salt glands considerably enhances the overall salt-excretion capacity of the leaf, thereby fundamentally boosting the plant's salt tolerance. This process is complemented by the action of abscisic acid (ABA) [59]. Furthermore, it has been demonstrated that ABA activates antioxidant enzymes such as SOD and POD whilst concomitantly promoting the accumulation of osmotic regulators such as proline [60]. This, in turn, establishes an effective physiological defence system that enhances plant salt tolerance through multiple pathways. Jasmonic acid and salicylic acid have been shown to reveal distinct aspects of hormonal regulation. The exogenous application of methyl jasmonate and salicylic acid has been shown to effectively alleviate growth inhibition under salt stress conditions [61]. The primary function of MeJA is to improve photosynthetic parameters and maintain intracellular ion homeostasis. In contrast, SA significantly promotes seed germination under salt stress by finely regulating the biosynthesis and signalling pathways of gibberellins and abscisic acid, thereby breaking seed dormancy [62]. Further research has revealed intricate synergistic and antagonistic relationships among various hormones in the regulation of epidermal development. Systems biology analyses indicate that salicylic acid and brassinolide promote the development of epidermal structures, such as salt glands and stomata, at low concentrations [63]. Conversely, jasmonic acid, gibberellin, and abscisic acid generally inhibit the formation of these structures. This precise hormonal balance ensures that plants can optimise resource allocation according to environmental conditions. It is noteworthy that the developmental processes of three key epidermal structures – salt glands, stomata, and pavement cells – exhibit high synergy, suggesting that they may share an upstream developmental programme regulated by multiple hormones.

Intracellular Second Messenger and Kinase-Mediated Cascade Signaling

In the intricate network that governs *L. bicolor*'s response to salt stress and the regulation of salt gland development, beyond the core directives of plant hormones, second messenger and kinase systems form the rapid, precise hubs for signal transduction and execution, translating upstream signals into specific physiological and developmental responses. The Mitogen-Activated Protein Kinase (MAPK) cascade is considered to be one of the core signalling pathways. Research has identified 20 LbMAPK genes, which collectively form a complex signalling network [64]. Among these, LbMAPK2 has been demonstrated to play a pivotal role, exhibiting highly specific expression during the early stages of salt gland development.

Functional studies indicate that silencing LbMAPK2 leads to a reduction in salt gland numbers, decreased salt secretion capacity, and a significant decline in plant salt tolerance. Nitric Oxide (NO), acting as a gaseous signaling molecule, enhances salt efflux efficiency through a sophisticated dual mechanism. On one hand, treatment with the NO donor sodium nitroprusside directly increases salt gland numbers, providing more “exits” for salt efflux. More importantly, NO significantly enhances the Na^+ accumulation capacity of individual salt gland cells. The molecular mechanism involves NO activating H^+-ATPases on the plasma and vacuolar membranes, establishing a proton motive force [65]. This, in turn, activates Na^+/H^+ countertransporters, utilizing the proton gradient to either sequester excess cytoplasmic Na^+ into the vacuole or directly pump it out of the cell. This dual strategy of “increasing supply” (enhancing salt gland number) and “conserving flow” (boosting

individual gland function) collectively elevates the plant's overall salt excretion efficiency. Calcium ions (Ca^{2+}) also play an indispensable role in salt gland development and salt tolerance [66]. Exogenous application of Ca^{2+} has been shown to effectively promote salt gland development and increase their diameter. This not only expands the surface area for salt secretion but also directly increases the rate of salt excretion. Furthermore, Ca^{2+} stabilizes the structure of cell membranes and cell walls, reducing electrolyte leakage under salt stress and maintaining cellular integrity. Thus, it synergistically enhances plant salt tolerance at both structural and functional levels.

Although the aforementioned studies have respectively demonstrated the necessity of phytohormones (cytokinin, abscisic acid) and second messengers/protein kinases (MAPK cascade, NO, Ca^{2+}) in the salt tolerance response of *L. bicolor*, an integrative and critical evaluation from a systems biology perspective reveals a clear spatiotemporal hierarchical network.

First tier: Immediate emergency signaling (seconds to minutes). When acute salt stress occurs in roots or leaf epidermis, Ca^{2+} and NO are activated first as the most rapid second messengers. NO quickly activates plasma membrane H^+-ATPase to establish a proton motive force, while Ca^{2+} helps stabilize membrane structure and reduce electrolyte leakage. This tier represents a physical and biochemical "emergency self-rescue" response.

Second tier: Signal cascade and central relay (minutes to hours). The MAPK cascade (e.g., LbMAPK2) acts as a core hub and "signal router" within the signaling network. It converts transient extracellular physicochemical stimuli captured at the first tier into stable intracellular kinase signals through sequential phosphorylation, and precisely transmits these signals to the transcriptional regulatory machinery.

Third tier: Long-term fate remodeling and epidermal reconstruction (hours to days). Classical phytohormones such as cytokinin and abscisic acid play the role of "commanders" of global regulation at this tier. The dynamic "hormonal wave" formed by cytokinin directly initiates and determines the terminal fate of precursor cells differentiating into mature salt gland cells, thereby fundamentally alleviating salt stress damage by remodeling epidermal structure (increasing salt secretion outlets).

Although the outline of the above hierarchical network has emerged, two unresolved implicit contradictions and knowledge gaps remain in this field: The absence of a "salt sensor": The most upstream direct receptor that triggers Ca^{2+} influx or activates LbMAPK2 remains unclear. How plants specifically sense changes in Na^+ concentration across the plasma membrane within seconds represents a theoretical gap connecting the two-stage signaling pathway. The molecular "brake" balance mechanism of antagonistic pathways: Systematic analysis shows that cytokinin promotes epidermal differentiation, whereas jasmonic acid and abscisic acid exhibit inhibitory effects at specific stages. However, how these two classes of signals achieve real-time crosstalk and molecular-level trade-offs in the single-cell microenvironment remains unknown. Elucidating this antagonistic-complementary mechanism is key to breaking through the current bottleneck of descriptive research.

Osmotic Homeostasis and Enzymatic Antioxidant Defenses

In the overall strategy of *L. bicolor* for coping with salt stress, besides relying on the unique “salt-excretion” structure of salt glands, its cells establish a sophisticated “stabilization” system. This system primarily maintains cellular homeostasis through two major physiological and biochemical pathways: osmotic regulation and antioxidant defense [67]. Together, these form the intrinsic foundation of salt tolerance. Confronted with osmotic fluctuations and water imbalance induced by salt stress, *L. bicolor* actively accumulates small-molecule organic solutes to maintain cell turgor pressure, thereby safeguarding essential physiological functions. Among these, proline, soluble sugars, and soluble proteins serve as key osmotic regulators [68]. Their synergistic accumulation not only effectively maintains cellular osmotic balance and hydration, preventing excessive water loss, but also stabilizes the structure and function of biomolecules to a certain extent, providing cells with a protected internal environment. Simultaneously, salt stress inevitably induces oxidative stress, leading to an explosive accumulation of Reactive Oxygen Species (ROS). To address this challenge, *L. bicolor* efficiently activates its intrinsic antioxidant defense system. At the core of this system lies a series of synergistically acting antioxidant enzymes, including Superoxide Dismutase (SOD), Peroxidase (POD), Catalase (CAT), Ascorbate Peroxidase (APX), and Glutathione S-transferase (GST) [69]. Together, they form an efficient scavenging chain: SOD converts superoxide anion into hydrogen peroxide (H_2O_2), while POD, CAT, and APX further transform H_2O_2 into harmless water and oxygen [70]. When effectively activated, this system rapidly eliminates excess ROS, significantly mitigating membrane lipid peroxidation damage. This is evidenced by stable or even reduced malondialdehyde (MDA) levels in stressed cells, indicating well-preserved membrane structural integrity [71]. This highly efficient physiological defense system is driven by key protein molecules. Research reveals that glutathione S-transferase

LbGST1 serves as a multifunctional critical node. Its overexpression not only enhances its own Glutathione S-Transferase (GST) activity but also simultaneously boosts Glutathione Peroxidase (GPX) activity [72]. In transgenic tobacco, this leads to stronger ROS scavenging capacity and salt tolerance, highlighting its central role in the antioxidant network. On the other hand, the function of catalase LbCAT2, a key enzyme in hydrogen peroxide clearance, is finely regulated. Research reveals that LbCAT2 interacts with a zinc finger protein, LbRZF1 [73]. This interaction enhances LbCAT2 stability, fortifying this vital antioxidant defense. Together, LbRZF1 and LbCAT2 form a functional module that positively regulates plant salt tolerance.

Photosynthetic Modulation and Secondary Metabolic Reprogramming

In the overall physiological response of *L. bicolor* to salt stress, photosynthetic regulation exhibits a typical biphasic pattern characterized by “low-concentration promotion and high-concentration inhibition.” Under low-salt conditions (e.g., 100 mM NaCl), *L. bicolor* can moderately enhance photosynthesis, likely reflecting the plant's compensatory response triggered by moderate stress [19]. However, when salt concentration escalates to high stress levels of 300–400 mM, photosynthetic performance is significantly suppressed, manifested as declines in chlorophyll content, maximum photochemical efficiency (Fv/Fm), and photochemical quenching coefficient (qP) [74]. Notably, facing the risk of imbalance in light energy absorption and utilization, *L. bicolor* has evolved an effective protective mechanism: by significantly enhancing non-photochemical quenching (qN) capacity, it safely dissipates excess light energy absorbed by photosynthetic organs as thermal energy. This prevents photodamage and safeguards the structural and functional integrity of photosynthetic organs under adverse conditions.

Integrated analysis of transcriptomic and metabolomic data revealed that under high-salt stress, the phenylpropanoid biosynthesis and flavonoid biosynthesis pathways were strongly and specifically activated [19]. This led to substantial accumulation of bioactive secondary metabolites, including flavonoids (e.g., kaempferol-3-O-rhamnoside, naringenin) and phenolic acids (e.g., Caffeic acid and rosmarinic acid) [75-77]. These accumulated metabolites are not terminal products; instead, they function as cellular scavengers through their potent antioxidant activity, efficiently assisting in the removal of excess Reactive Oxygen Species (ROS). Thus, they play an indispensable role in mitigating oxidative damage induced by salt stress. This metabolic defense reprogramming is closely linked to expression changes in key genes such as Chalcone Synthase (CHS), confirming that plants actively enhance their antioxidant stress resistance by precisely regulating specific metabolic pathways [78].

Identification and Breeding Applications of Key Genetic Resources in *Limonium bicolor*

In-depth exploration of salt gland development and salt tolerance in *L. bicolor* has successfully identified a series of novel genes with unknown functions, demonstrating significant application potential. Among these, genes such as Lb1G04202 and Lb1G04794 are particularly noteworthy, exhibiting extremely low similarity in other species and thus considered unique to *L. bicolor* [63]. These genes exhibit specific expression in salt glands, and their encoded proteins localize to the cell nucleus, suggesting they may function as novel transcription regulators. Functional studies indicate that heterologous overexpression of these genes in Arabidopsis generally and significantly enhances the salt tolerance of transgenic plants through mechanisms such as improved osmotic regulation (e.g., markedly promoting proline accumulation), demonstrating their direct value as stress-resistant gene resources. Other key genes also demonstrate outstanding efficacy in cross-species applications.

For instance, when LbDREB is introduced into *Populus ussuriensis* Kom. as a transcription factor, it significantly enhances the salt tolerance of transgenic poplar through multiple synergistic mechanisms. These include the comprehensive enhancement of antioxidant capacity, the augmentation of osmotic regulatory substances, and the promotion of root development. In contrast, heterologous expression of LbGST1 in tobacco has been shown to enhance the activity of glutathione S-transferases (GSTs) and glutathione peroxidases (GPXs), thereby conferring enhanced oxidative stress tolerance to the resulting transgenic tobacco plants [79]. Furthermore, the expression of LbRZF1 (a RING-type zinc finger protein) and the LbMYB48 transcription factor in Arabidopsis conferred enhanced salt tolerance to recipient plants, further validating the immense potential for cross-species application of such regulatory genes [80]. It is important to note that related studies also offer profound insights from a negative perspective.

Current limitations and Unresolved Questions

Accumulating evidence confirms that *L. bicolor* efficiently moves Na^+ over long distances to the epidermal salt glands, with plasma membrane H^+-ATPases and Golgi-mediated vesicle trafficking acting as key active mechanisms. However, once

Na^+ leaves the vascular bundle and enters the mesophyll, the exact microscopic path that guides these toxic ions into the base of secretory cells remains largely a black box. Symplastic versus apoplastic dominance remains unclear. It is still debated whether the large ion flow across the mesophyll toward the salt gland base mainly follows a symplastic route (through plasmodesmata) or an apoplastic one (through intercellular spaces). This uncertainty makes it impossible to spatially block or redirect toxic ions in any targeted way. The molecular basis of vesicle loading is also unresolved. While vesicle transport is a known feature of active salt excretion, the machinery that recognizes cytoplasmic Na^+ and loads it into Golgi-derived vesicles such as specific transporters or channels has yet to be identified.

Conclusion and Future Outlook

The salt tolerance of *L. bicolor* is not governed by a single mechanism but rather constitutes an integrated system featuring four tightly interconnected layers structural foundation, functional execution, systemic regulation, and physiological support operating through multi-level synergistic interactions. At the core of this system lies its unique salt gland structure for salt secretion, whose development and operation are driven by a transcriptional regulatory network centered on the TTG1-bHLH-MYB ternary complex. This network undergoes precise fine-tuning by multiple plant hormones, including cytokinins and abscisic acid, and is meticulously regulated by environmental signals mediated through second messenger systems such as MAPK kinase cascades, NO, and Ca^{2+}. Recent studies have further revealed the crucial roles of long non-coding RNAs and post-transcriptional regulation within this network. At the physiological level, plants maintain cellular homeostasis through efficient osmotic regulation and robust antioxidant defense systems before and after salt secretion. They provide solid internal support for salt tolerance by dynamically adjusting photosynthetic machinery and activating secondary metabolic pathways like phenylpropanoid/flavonoid synthesis. This synergistic operation of a multi-tiered system enables Limonium bicolo to thrive in high-salinity environments.

In the future, research in this field is expected to shift focus from component analysis to system integration, indicating a significant potential for practical applications. With regard to the refinement of mechanisms, the next frontier lies in elucidating the complete cellular pathway by which Na^+ is transported from mesophyll cells to salt gland cells and ultimately excreted. A detailed characterisation of the specific membrane transport systems involved (e.g., pumps, channels, and carriers) is required, as well as the precise molecular machinery governing vesicle loading, transport, and exocytosis. With regard to network integration, there is an urgent need to leverage multi-omics data and systems biology approaches to construct a comprehensive global regulatory network spanning from salt stress perception to salt gland development and salt secretion function. The following will serve to elucidate the intricate crosstalk and weighting relationships that exist among the various signalling pathways [81].

The most compelling aspect of this phenomenon lies in its vast potential for practical applications. This study has identified a large number of key genes with well-defined functions. For instance, the knockout of negative regulators such as Lb1G07934 (bHLH) and LbCPC (MYB), or the overexpression of positive regulators like LbMYB48, LbTTG1, and LbDREB, has demonstrated significant potential for enhancing salt tolerance in model plants. These findings have resulted in the establishment of an unparalleled gene resource library and have elucidated precise technical pathways for the breeding of salt-tolerant crops through contemporary biotechnologies such as gene editing and transgenic techniques. The decoding and harnessing of the complex "salt tolerance blueprint" of *L. bicolor* is of profound strategic significance for the purposes of revolutionising crop breeding strategies, safeguarding global food security, and enabling large-scale development and utilisation of saline-alkali wasteland resources.

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Authors Contributions

Linyang Wang: Writing original draft, Writing review and edited.

Pin Chen: Methodology.

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Declaration of Competing Interests

The authors declare no competing financial interests.

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