

The *SnRK* gene family in passion fruit: evolution, abscisic acid signaling, and roles in abiotic stress responses

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Abstract

Drought, salinity, high temperatures, and cold are major constraints to crops' productivity worldwide. In tropical and subtropical fruit crops like passion fruit (*Passiflora edulis*), the increasing climate variability exacerbates the yield's instability and threatens sustainable production. Plants have evolved complex signaling networks to perceive environmental cues and activate adaptive responses. Among these, protein kinases are central regulators. One of the conserved gene families of serine/threonine kinases is the Sucrose nonfermenting-1-related protein kinase (SnRK) family that integrates energy status, hormonal signaling, and stress responses. The *SnRK* family is divided into three subfamilies: *SnRK1*, *SnRK2*, and *SnRK3* (also known as calcineurin B-like [CBL]-interacting protein kinase genes [CIPKs]). Each of these subfamilies has distinct but interconnected biological functions. Among the three subfamilies, *SnRK2* kinases are core components of the abscisic acid (ABA) signaling pathway and play pivotal roles in the regulation of stomatal movement, transcriptional reprogramming, and physiological adaptation in response to abiotic stress. Though extensive functional and genome-wide studies of *SnRK* genes have been carried out in model plants and major crops, integrated syntheses regarding this aspect in passion fruit are presently sparse. This review aims to summarize the current knowledge and gaps on the classification, evolution, structural features, and molecular functions of the *SnRK* gene family, with a particular emphasis on *SnRK2*-mediated ABA signaling and abiotic stress responses. We integrate evidence from mechanistic studies, genome-wide analyses, and comparative research across plant species for relevance in passion fruit biology.

Keywords: Sucrose non-fermenting-1-related protein kinases, Passion fruit (*Passiflora edulis*), Abscisic acid (ABA), Abiotic stress responses, *SnRK2* kinases, Stress signaling networks

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Introduction

passion fruit (*Passiflora edulis*) is an important horticultural crop valued for its unique flavor, nutritional value, and commercial opportunities^[1–3]. Cultivated widely in many tropical and subtropical regions, passion fruit is severely affected by abiotic stresses^[4]. Drought, salinity, high temperature, low temperature, and hyperosmotic stresses severely affect its vegetative growth, flowering, fruit set, and yield stability^[4–6]. Because of the alarming rate of climate change, the frequency and intensity of such stresses are increasing, and there will be a definite need for cultivars with enhanced resilience against abiotic stresses.

In plants, the perception of abiotic stresses and the occurrence of adaptive responses are governed by complex signaling networks, each providing the potential for very rapid perception of the environmental change^[7–10]. The ability of a protein kinase to transmit signals in phosphorylation cascades is at the core of these networks. It regulates downstream transcription factors (TFs), ion channels, metabolic enzymes, and stress-responsive genes. Among these, the Sucrose nonfermenting-1-related protein kinase (SnRK) family has emerged as a master regulator that integrates energy homeostasis, hormonal signaling, and environmental stress responses^[11–13].

The *SnRK* family is evolutionarily conserved in plants and includes three major subfamilies: *SnRK1*, *SnRK2*, and *SnRK3* (calcineurin B-like [CBL]-interacting protein kinase genes [CIPKs])^[14,15]. *SnRK1* functions

as a core metabolic sensor coordinating growth and carbon allocation under energy-limiting conditions^[16–18]; in contrast, *SnRK2* and *SnRK3* are more directly involved in abiotic stress and hormone-mediated signaling cascades^[15,19]. *SnRK2* kinases, in particular, represent core positive regulators of the abscisic acid (ABA) signaling pathway, a phytohormone that plays a vital role in plant responses to abiotic stresses, e.g., drought, salinity, and osmotic stress.

Emerging transcriptomic evidence in *P. edulis* indicates that key components of ABA-responsive signaling pathways, including ABA-regulated TFs and stress-inducible genes, are differentially expressed under drought, temperature, and osmotic stress conditions, suggesting that ABA-mediated signaling is an important regulatory mechanism in passion fruit's stress adaptation. Given the conserved role of *SnRK2* kinases as central mediators of ABA signal transduction in plants, it is highly plausible that *SnRK*-dependent pathways contribute to abiotic stress resilience in passion fruit.

Genome-wide characterization and functional identification of the *SnRK* genes have been performed in a variety of plant species in recent decades, including *Arabidopsis thaliana*, rice (*Oryza sativa*), maize (*Zea mays*), bamboo (*Phyllostachys edulis*), poplar (*Populus* sp.), and barley (*Hordeum vulgare*)^[14,20–23]. Despite an available chromosome-scale reference genome for passion fruit and an increase in the associated transcriptomic resources, a review synthesis of *SnRK*-related knowledge in the context of passion fruit has not been

published^[24]. This review aims to summarize the current understanding of the *SnRK* gene family's structure, signaling mechanisms, and roles in abiotic stress responses, with a focus on their potential relevance to improving passion fruit.

Overview of the *SnRK* gene family

Classification of *SnRK* gene family

The *SnRK* family derives its name from the yeast sucrose non-fermenting-1 (SNF1) kinase and its mammalian homolog, AMP-activated protein kinase (AMPK), reflecting evolutionary conservation across eukaryotes. They have subsequently diversified into three distinct subfamilies in plants, namely *SnRK1*, *SnRK2*, and *SnRK3/CIPKs*^[11,15,25].

SnRK1 is an ancestral branch that shares functional features with SNF1/AMPK in acting as a central energy sensor regulating metabolic balance under carbon starvation/stress conditions^[18]. In contrast, the subfamilies *SnRK2* and *SnRK3* have expansions predominantly in plants and mostly function in environmental stress and hormone signaling. Phylogenetic analyses across various species have established lineage-specific expansions of *SnRK2* and *SnRK3* genes, which demonstrates adaptive diversification towards the challenges of the terrestrial environment^[20,26]. The details of *SnRK* gene family are given in Table 1.

Phylogenetic classification of the *SnRK* gene family across crop species

Comparative phylogenetic analysis (Fig. 1) of *SnRK* family members in passion fruit, together with representative crop and model species including^[41], *Citrus sinensis*^[42], *Carica papaya*, *Vitis vinifera* (grape)^[43], *Musa acuminata* (banana), *Mangifera indica* (mango), and *A. thaliana*^[36,44,45], revealed a conserved subdivision of the *SnRK* gene family into three major subfamilies: *SnRK1*, *SnRK2*, and *SnRK3 (CIPKs)*. Phylogenetic analysis was performed using the maximum likelihood method in MEGA11 with 1,000 bootstrap replicates, based on ClustalW-aligned full-length *SnRK* protein sequences. *SnRK1* members formed a tightly conserved clade across all analyzed species, consistent with their central role in energy sensing and metabolic regulation. *SnRK2* proteins clustered into distinct stress-activated protein kinase (SAPK) groups within the phylogenetic tree, supporting their functional specialization in ABA signaling and abiotic stress responses in crops. In contrast, *SnRK3* genes displayed broader and more diverse clade expansion, which was particularly evident in perennial fruit crops such as passion fruit, grape, banana, and mango, reflecting lineage-specific diversification associated with calcium-dependent signaling pathways. The presence of all three *SnRK* subfamilies in both monocot and dicot crops indicates that *SnRKs'* diversification occurred early in plants' evolution, with subsequent species-specific expansion patterns observed in the phylogenetic tree during the adaptation and domestication of crops.

Structural features

The members of all *SnRKs* contain a well-conserved N-terminal serine/threonine kinase domain, which possesses catalytic activity^[34,46]. Nevertheless, their C-terminal domains display considerable variation among subfamilies, which exhibit specialized functions^[47,48]. The domain structures with conservation and variation among *SnRK* subfamilies are graphically represented in Fig. 2, which

specifies the specialized motifs underlying the distinct functions. The regulatory domains of *SnRK1* play pivotal roles in complex formations and metabolic regulations. The *SnRK2* kinase enzymes possess special motifs within their C-termini, which include the *SnRK2* box and ABA box, which are vital for the activation and interactions of *SnRK2* with regulatory phosphatases. *SnRK3* or *CIPKs* are differentiated by the existence of a special Asparagine-alanine-phenylalanine/Phenylalanine-isoleucine-serine-leucine (NAF/FISL) motif within their C-terminal domain, which is responsible for interactions between calcineurin B-like calcium sensors and is instrumental in coupling calcium signaling with stress responses^[21,39].

Functional roles of *SnRK* subfamilies

SnRK1: energy sensing and stress adaptation

SnRK1 is a key player in energy homeostasis; it regulates metabolic pathways under conditions of energy deficiency. On activation, *SnRK1* suppresses anabolic processes while stimulating catabolic pathways to restore energy homeostasis under stress conditions. Though *SnRK1* is not strictly a stress-specific protein, it indirectly aids tolerance to abiotic stresses by coordinating growth-stress trade-offs and interactions with hormone signaling networks^[49].

SnRK3 (CIPKs): calcium-mediated stress signaling

SnRK3/CIPKs, along with their interacting CBL calcium sensors, decode stress-induced calcium signatures^[20]. Upon stress, calcium influx causes the association of CBLs with *CIPKs*, which results in the recruitment of *CIPKs* to specific cellular membranes, where they modulate the activity of ion transporters and channels. Numerous recent studies have reported the roles of *CIPKs* in salt tolerance, potassium homeostasis, and ionic balance^[49,50]. Specific functional analyses, including transgenic studies, demonstrate that some *CIPKs* confer salinity tolerance by maintaining Na⁺/K⁺ homeostasis and modulating the activity of transporters^[39].

SnRK2: central regulators of ABA and abiotic stress responses

Among the *SnRK* subfamilies, *SnRK2* kinases are the most directly implicated in abiotic stress signaling. *SnRK2s* are classified into two groups, namely ABA-dependent (Subclasses II and III) and ABA-independent (Subclass I), on the basis of their activation profiles and structural features (e.g., the presence of the ABA box in Subclass III)^[51]. ABA-responsive *SnRK2s*, particularly Subclass III *SnRK2s*, are positive regulators of ABA signaling and become rapidly activated under osmotic stress and drought conditions^[31].

ABA signaling pathway is mediated by *SnRK2*

Core ABA signaling module

The ABA signaling pathway represents a central regulatory network through which plants perceive and respond to diverse abiotic stresses, including drought, salinity, cold, and osmotic stress (Fig. 3). Under nonstress conditions, intracellular ABA levels remain low, and Subclass III *SnRK2s* such as *OST1/SnRK2.6* are maintained in an inactive state via direct interaction with Clade A protein phosphatase 2Cs (PP2Cs), including ABI1 and ABI2^[52,53]. These PP2Cs

Table 1. Classification, structural features, and core functions of the *SnRK* gene family in plants

<i>SnRK</i> subfamily	Alternative name	Conserved structural features	Primary biological functions	Representative genes
<i>SnRK1</i> ^[13,16–18,20,25]	SNF1-related kinase 1	N-terminal kinase domain; regulatory C-terminal region	Energy sensing; carbon metabolism; growth–stress balance	<i>AtSnRK1.1</i> , <i>AtSnRK1.2</i>
<i>SnRK2</i> ^[12,15,19,27–38]	Stress-activated protein kinases (SAPKs)	Kinase domain; <i>SnRK2</i> box; ABA box	ABA signaling; drought and osmotic stress response; transcriptional regulation	<i>OST1/SnRK2.6</i> , <i>SAPK8</i>
<i>SnRK3</i> ^[13,20,21,39,40]	CIPKs (CBL-interacting protein kinases)	Kinase domain; NAF/FISL motif for CBL binding	Calcium signaling; ion homeostasis; salinity tolerance	<i>CIPK23</i> , <i>CIPK16</i>

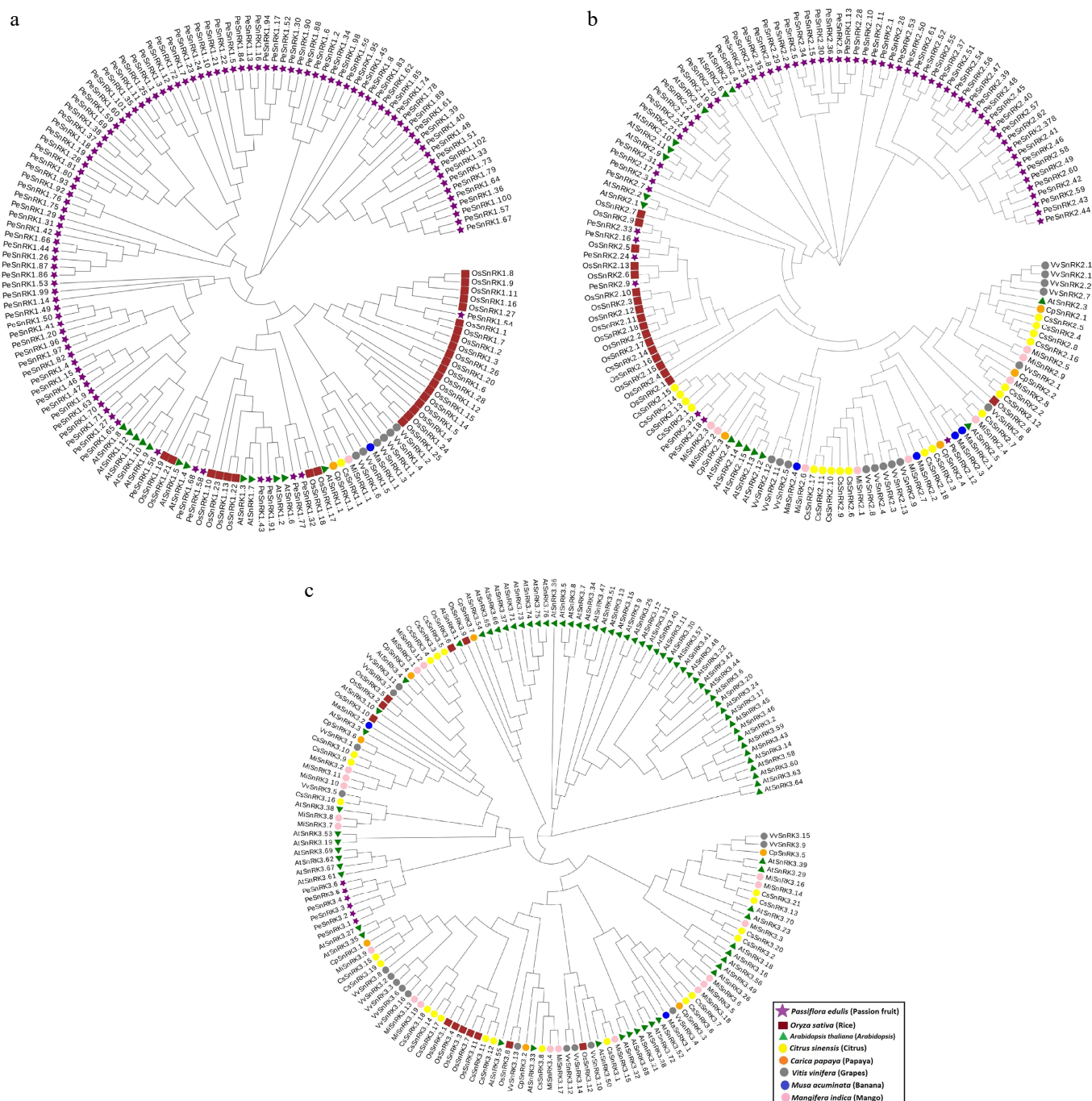


Fig. 1 *SnRK* proteins' phylogeny across plant lineages. Phylogenetic trees of *SnRK* proteins were constructed using the maximum likelihood method based on full-length amino acid sequences and visualized in a circular layout. The *SnRK* gene family is divided into three distinct subfamilies: (a) *SnRK1* (SNF1-related kinases), (b) *SnRK2* (stress-activated protein kinases, SAPKs), and (c) *SnRK3* (CBL-interacting protein kinases, CIPKs). Each panel represents one subfamily: (a) *SnRK1*, (b) *SnRK2*, and (c) *SnRK3*. Distinct colors and symbols denote different plant species as follows: *P. edulis* (purple stars), *O. sativa* (red squares), *A. thaliana* (green triangles), *C. sinensis* (yellow circles), *C. papaya* (orange circles), *V. vinifera* (gray circles), *M. acuminata* (blue circles), and *M. indica* (pink circles). The clustering pattern reveals clear subfamily segregation and highlights both conserved evolutionary relationships and lineage-specific expansion of *SnRK* genes across monocot and dicot species.

Domain architecture of SnRK subfamilies

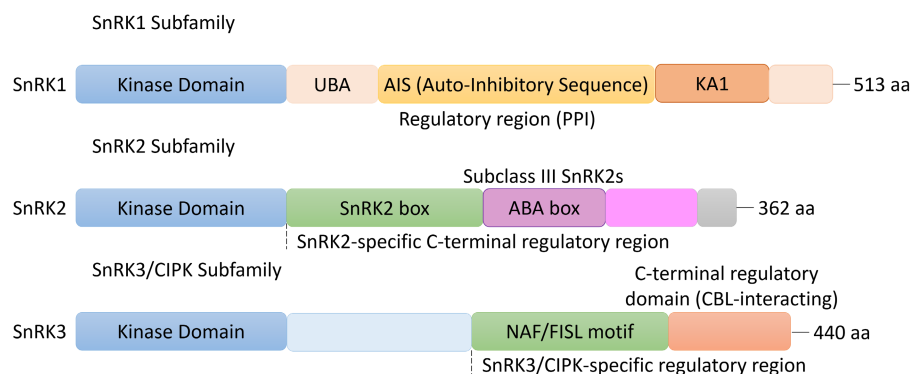


Fig. 2 Schematic representation of the conserved domain organization of plant Sucrose nonfermenting-1-related protein kinase (SnRK) family. All subfamilies share a conserved N-terminal serine/threonine kinase domain but differ markedly in their C-terminal regulatory regions. *SnRK1* contains a ubiquitin-associated (UBA) domain, an autoinhibitory/ regulatory sequence (AIS), and a kinase-associated 1 (KA1) domain involved in protein–protein interactions and complex assembly. *SnRK2* proteins possess a *SnRK2*-specific C-terminal regulatory region containing the *SnRK2* box required for kinase activation and, in Subclass III *SnRK2*, an ABA box mediating the interaction with PP2C phosphatases during ABA signaling. *SnRK3/CIPKs* harbor a conserved NAF/FISL motif within a *SnRK3/CIPK*-specific regulatory region that facilitates interactions with calcineurin B-like (CBL) calcium sensors and regulates kinase activity. Approximate protein lengths are indicated for each subfamily.

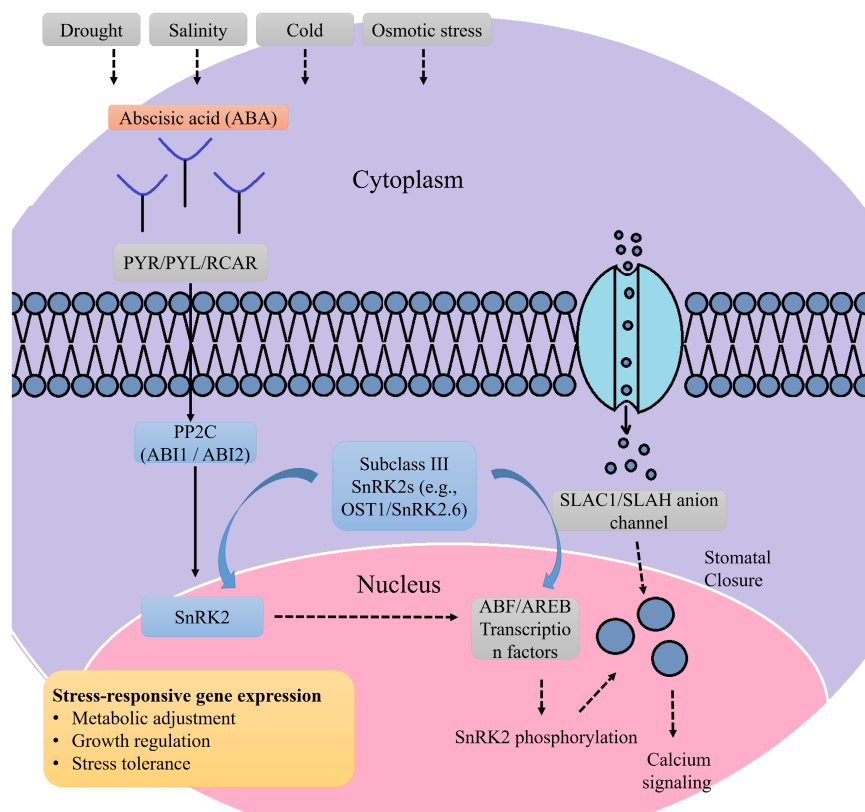


Fig. 3 Schematic overview of the ABA–PP2C–SnRK2 signaling cascade under abiotic stress conditions. Abiotic stresses, including salinity, cold, drought, and osmotic stress, promote the accumulation of ABA. ABA is perceived by PYR/PYL/RCAR receptor proteins, which subsequently inhibit Clade A protein phosphatases 2C (PP2Cs; ABI1/ABI2). Relief of PP2C-mediated repression enables the activation of Subclass III SnRK2 kinases (e.g., OST1/SnRK2.6). Activated SnRK2s phosphorylate plasma membrane anion channels, such as SLAC1/SLAH, leading to anion efflux and stomatal closure. In parallel, SnRK2 translocates to the nucleus, where they phosphorylate ABA-responsive bZIP TFs (ABF)/ABA-responsive element binding (AREB) transcription factors, inducing the expression of ABA-responsive genes involved in metabolic adjustment, growth regulation, and stress tolerance. Calcium signaling acts as an additional regulatory component, integrating with ABA–SnRK2 signaling to fine-tune downstream responses.

effectively dephosphorylate the activation loop residues of SnRK2, thereby repressing the expression of ABA-responsive genes.

In response to these stresses, the accumulation of ABA is very swift and sensed by Pyrabactin Resistance/Pyrabactin Resistance

1-Like/Regulatory Component of ABA Receptor (PYR/PYL/RCAR) soluble receptors in the cytoplasm and nucleus. Binding of ABA triggers a conformational change in PYR/PYL receptors and allows them to establish stable ternary complexes with PP2Cs. This

encounter results in a reduction in the activity of PP2C phosphatase through masking of their catalytic sites, causing derepression of SnRK2 proteins. Without dephosphorylation by PP2Cs, SnRK2 proteins undergo autophosphorylation or *trans*-phosphorylation and become fully activated^[52,53].

Activated SnRK2 proteins function as central hub modules, which phosphorylate various downstream targets. In guard cells, SnRK2 proteins phosphorylate slow-anion channel proteins like Slow Anion Channel-Associated 1 (SLAC1) and SLAC1 Homologue (SLAH) proteins, leading to the efflux of anions, depolarization, secondary Ca^{2+} influx, and consequent stomatal closure, which is an important adaptive mechanism that prevents water loss in drought conditions^[54]. Concurrently, SnRK2s modulate calcium signaling pathways, further amplifying ABA responses and integrating hormonal and ionic signals.

In the nucleus, activated SnRK2 phosphorylates ABA-responsive bZIP TFs (ABFs), which interact with the ABA-responsive elements (ABREs) in the promoter regions of the target gene, thereby triggering the transcriptional reprogramming^[30]. The transcriptional response regulates a broad spectrum of stress adaptation functions such as the biosynthesis of osmoprotectants and antioxidants, growth regulation, and enhancement of stress tolerance. The PYR/PYL–PP2C–SnRK2 module forms a very conserved ABA-dependent pathway that allows plants to quickly transform environmental stresses into physiological or molecular responses^[29].

SnRK-centered ABA signaling and transcriptional regulation under abiotic stress

To provide a conceptual synthesis of the molecular function of SnRK signaling pathways in abiotic stress response, we developed a conceptual regulatory map (Fig. 4). Abiotic stresses, drought, salt, cold, or osmotic stress trigger the production of ABA, which is sensed by the PYR/PYL/RCAR receptor complex, resulting in the inhibition of Class A PP2Cs. Relieving the inhibition of PP2Cs relief leads to the activation of Subclass III SnRK2s^[52]. Activated SnRK2 phosphorylates downstream targets, which include ion channel-regulating factors, as well as ABA-regulated TFs, such as ABF/ABA-responsive element binding (AREB), NAC, MYB, and basic helix–loop–helix (bHLH), which mediate large-scale transcriptomic changes^[31]. Concurrent with these responses, Ca^{2+} -mediated signaling pathways trigger the activation of the CBL–CIPK (SnRK3) complex, which regulates Na^+/K^+ transporters, among other ion transport mechanisms, in response to salinity. These signaling pathways provide upstream inputs to stress-responsive genes encoding osmoprotectants, reactive oxygen species detoxification enzymes, late embryogenesis abundant (LEA) proteins, and aquaporins, which ultimately culminate in increased stress tolerance in plants. The conceptual model helps to inform prioritization strategies related to candidate SnRK genes, which may be used as targets in passion fruit^[39,49].

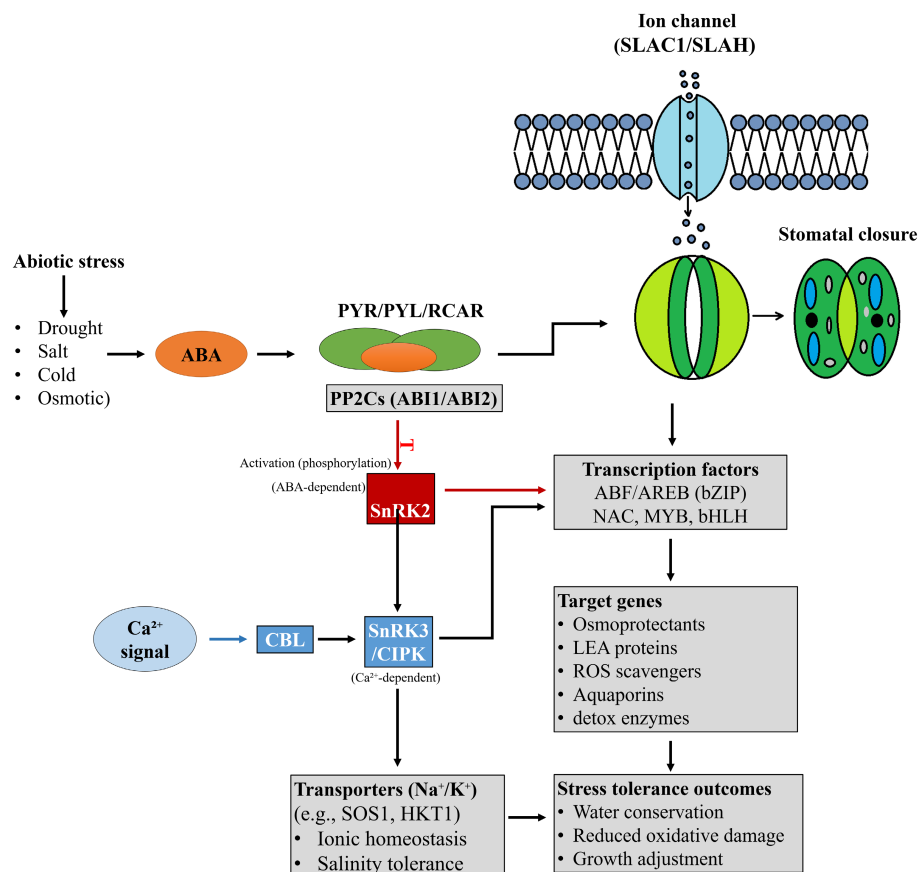


Fig. 4 SnRK2-mediated regulatory network integrating the ABA pathway with the regulation of abiotic stress responses at the transcriptional level. ABA accumulation is caused by abiotic stress, leading to the activation of SnRK2 protein kinases through the inhibitory effect of PYRs/PYLS on the activity of PP2Cs. SnRK2 act on ion channels and ABA-responsive TFs, whereas the Ca^{2+} -regulated CBL–CIPK pathway is responsible for the regulation of ion homeostasis.

Downstream targets and physiological responses

Activated *SnRK2* phosphorylates a wide array of downstream targets, including ABF/AREB TFs, thereby inducing the induction of stress-responsive genes^[55]. In guard cells, *SnRK2.6* directly phosphorylates the ion channels of SLAC1, thereby facilitating anion efflux and stomatal closure under drought stress. This constitutes a direct mechanistic link between the activation of *SnRK2* and physiological adaptation to drought.

Beyond transcriptional regulation, *SnRK2* take part in post-transcriptional and translational regulation. Recent studies have shown that *SnRK2* regulates the decapping and stability of mRNA under salinity, displaying an ABA-independent function that widens the functional repertoire of *SnRK2* kinases^[31].

Evidence from genome-wide and comparative studies

The *SnRK* gene family has been identified on a genome-wide scale in a number of plant species, exhibiting highly conserved structural features with species-specific expansions. Systematic characterization of *SnRK* gene numbers, their chromosomal distribution, gene duplication events, and expression in response to a series of abiotic stresses has been performed in bamboo^[56], barley^[20], tobacco (*Nicotiana tabacum*)^[38,57], poplar, maize^[58], and rice^[13,21].

These studies consistently illustrate that *SnRK2* genes are strongly induced by drought, salinity, and ABA treatments, whereas *SnRK3* genes respond predominantly to ionic and calcium-related stresses. Such comparative analyses thus provide valuable frameworks for predicting *SnRK* genes' functions in passion fruit, where direct functional studies remain limited. Comparative genome-wide analyses of *SnRK* gene families in diverse crops such as barley, bamboo, and tobacco have established conserved structural features and stress-induced expression patterns that provide a useful framework for investigating *SnRK* genes in passion fruit^[20,24].

Relevance of *SnRK* signaling to passion fruit

The availability of the chromosome-scale reference genome of *P. edulis* has enabled systematic investigation of the gene families involved in abiotic stress responses^[59,60]. Recent genome-wide studies in passion fruit have characterized multiple TF families in stress adaptation, which include the MYB, bHLH, NAC, and basic leucine zipper (bZIP) proteins^[61–63]. Zhang et al. identified stress-responsive MYB transcription factors associated with drought and temperature stresses^[59]. Xu et al. demonstrated that bHLH TFs are involved in regulating cold and osmotic stress responses^[62]. Similarly, NAC TFs in passion fruit were found to participate in cold stress tolerance through transcriptional regulation of downstream genes that are responsive to cold stress. Ma et al. provided integrative evidence at the transcriptomic and metabolomic levels that bZIP TFs play critical roles in the coordination of hormone signals and metabolic adjustment under abiotic stresses^[64]. In other plant systems, *SnRK2* kinases directly phosphorylate ABA-responsive bZIP TFs (ABF/AREB), while also indirectly modulating MYB, NAC, and bHLH TFs' activity through transcriptional reprogramming and stress-responsive signaling cascades, a regulatory mechanism that is likely conserved in passion fruit. Considering the well-documented role of *SnRK* kinases in modulating TF activities in other plant species, these findings strongly point toward the involvement of *SnRK*-mediated signaling networks in the abiotic stress adaptation of passion fruit. A summary of *SnRK*-centered regulatory networks and the associated genes involved in abiotic stress responses across diverse plant species, including downstream TFs and signaling components, is provided in Table 2.

Knowledge gaps and future perspectives

Despite the extensive progress made in other plant species, several gaps still remain regarding *SnRKs'* function in passion fruit. Direct genome-wide identification and functional validation of the *SnRK* genes have not yet been reported in passion fruit. Therefore, a

Table 2. *SnRK*-centered regulatory networks and associated genes involved in abiotic stress responses across plant species.

Species	<i>SnRK</i> gene/subfamily	Abiotic stress	Experimental evidence	Key findings
<i>A. thaliana</i> ^[65]	<i>SnRK2.6</i> (OST1)	Drought	Mutant + kinase assays	Phosphorylates SLAC1; induces stomatal closure
<i>A. thaliana</i> ^[35]	<i>SnRK2</i>	ABA/osmotic stress	Biochemical reconstitution	Core PYR/PYL–PP2C– <i>SnRK2</i> signaling module
<i>A. thaliana</i> ^[66]	<i>SnRK2</i>	ABA signaling	Genetic + molecular studies	PP2Cs act as gatekeepers of <i>SnRK2</i> activity
<i>A. thaliana</i> ^[37]	<i>SnRK2</i> kinases	Stress signaling	Structural biology	<i>SnRK2</i> box and ABA box regulate autoactivation
<i>A. thaliana</i> ^[33]	<i>SnRK2</i>	Salinity	Genetic + transcriptomic	Regulate mRNA decapping and stress adaptation
Rice ^[67]	SAPK family (<i>SnRK2</i>)	Salinity, drought	Expression profiling	Enhanced stress tolerance and ABA response
<i>Populus</i> spp. ^[68]	<i>CIPKs</i> (<i>SnRK3</i>)	Salinity	Genome-wide + expression	Ion homeostasis and stress adaptation
Wheat ^[69]	<i>CIPK16</i>	Salinity	Transgenic validation	Improves Na ⁺ /K ⁺ balance and salt tolerance
Bamboo ^[56]	<i>SnRK</i>	Abiotic stress	Genome-wide + functional analysis	Stress-induced <i>SnRK</i> expression
Tobacco ^[38]	<i>SnRK2</i> family	Salinity	Comparative genomics	Conserved <i>SnRK2</i> expansion patterns
passion fruit ^[59]	Stress-responsive TFs (<i>MYB</i>). No <i>PeSnRK</i> genes characterized to date	Drought, temperature	RNA-seq	TF networks associated with stress
passion fruit ^[62]	<i>bHLH</i> TFs (no <i>PeSnRK</i> genes characterized to date)	Cold, osmotic stress	Genome-wide + expression	TF-mediated stress regulation
passion fruit ^[63]	<i>NAC</i> TFs (no <i>PeSnRK</i> genes characterized to date)	Cold stress	Transcriptomics	Stress-responsive <i>NAC</i> regulation
passion fruit ^[64]	<i>bZIP</i> TFs (no <i>PeSnRK</i> genes characterized to date)	Multiple stresses	Transcriptomics + metabolomics	Hormone and metabolic coordination

This table summarizes both *SnRK* kinases and functionally associated downstream regulatory genes, including TFs and signaling components, which participate in abiotic stress responses.

combination of transcriptomics, proteomics, and functional genomics (e.g., quantitative real-time polymerase chain reaction, yeast two-hybrid assays, clustered regularly interspaced short palindromic repeats [CRISPR]/CRISPR-associated protein 9) will be required to unravel *SnRK*-centered regulatory networks. Given the central role of *SnRK2* in ABA signaling, the targeted manipulation of *SnRK* pathways may offer promising strategies for the improvement of drought and salinity tolerance in passion fruit^[31]. In the future, functional investigations of passion fruit should focus on integrating the identification of *SnRK* genes with TF-associated regulatory networks previously characterized in the same species, such as the *MYB*, *bHLH*, *NAC*, and *bZIP* families, to further illustrate *SnRK*-centered modules of stress signaling^[59,64].

***SnRK* gene applications in crop improvement (transgenic and gene-edited approaches)**

Transgenic and gene-editing studies in model plants and crops provide practical evidence that *SnRK*-centered pathways can be leveraged to improve abiotic stress resilience^[70]. In multiple species, manipulation of *SnRK2* Subclass III kinases (regulators of the central ABA pathway) has been associated with enhanced drought or osmotic stress tolerance through improved stomatal control, ABA-responsive transcriptional activation (e.g., ABF/AREB modules), and stress-responsive gene expression^[31,65]. Similarly, engineering components of the CBL–CIPK (*SnRK3*) network has been used to modulate ionic homeostasis (Na^+/K^+ balance) and salt tolerance, consistent with the established roles of CIPKs as calcium-decoding kinases that regulate transporters and channels^[39,49]. These examples provide a translational rationale for passion fruit: Once *PeSnRK* candidates are prioritized by stress-inducible expression and phylogenetic placement, functional testing via overexpression or CRISPR-based modulation can be used to validate different drought/salinity phenotypes and downstream transcriptional effects.

For *P. edulis*, a feasible pipeline is to (i) identify *PeSnRK2/PeCIPK* candidates with strong induction under drought/salinity/ABA stress, (ii) confirm their subcellular localization and protein–protein interactions (*PP2C–SnRK2*; *CBL–CIPK*), and (iii) evaluate edited/overexpression lines using standardized physiological endpoints (stomatal conductance, leaf water potential, electrolyte leakage) alongside transcript markers (*ABF/AREB* targets, osmoprotectant and reactive oxygen species-detox genes). Collectively, cross-species application evidence strengthens the argument that *SnRK* engineering is a realistic strategy for developing stress-resilient passion fruit cultivars.

Conclusions

SnRK genes encode a family that has emerged as an important integrative module connecting the plant metabolism, hormones, and abiotic stress adaptations. Recent advances in model and crop plants have confirmed the functional diversification of *SnRK* gene subfamilies: *SnRK1* acts as a core energy sensor, *SnRK3/CIPKs* mediate Ca^{2+} -dependent stress signaling, and Subclass III *SnRK2* kinases function as central hubs in abiotic stress signaling, integrating ABA perception with transcriptional reprogramming and physiological adaptations such as stomatal closure.

Despite these achievements, the bulk of what has been inferred about *SnRK* signaling in passion fruit (*P. edulis*) has come from observations in other plants. The present availability of a reference chromosome-scale genome, as well as growing transcriptomic data, presents an opportune moment in which to help close the gap. Genome-wide gene identification, expression profiling, protein

interaction analyses, and functional validation will be critical for uncovering *SnRK*-related regulatory modules in passion fruit.

As the rising susceptibility of tropical and subtropical fruit crops like passion fruit to stresses triggered by climate change, elucidating the roles of *SnRK*-mediated stress signaling has immense potential and implications for crop improvement programs. The manipulation of stress signaling via the *SnRK2*-mediated ABA signaling pathway and the *SnRK3/CIPK*-mediated ion homeostasis pathway may provide immense potential for the development of passion fruit with high resistance to drought, salt, and osmotic stress. Future research work, therefore, that integrates the fields of genomic research, biotechnology, and passion fruit may provide immense contributions not only towards understanding stress signaling, but also towards the development of stress-tolerant passion fruit varieties.

Author contributions

The authors confirm their contributions to this study as follows: Xu Y and Song S jointly conceived and supervised this study and revised the manuscript. Hussain M was responsible for experimental operations and drafted the manuscript. Ma F and Huang D were responsible for revising the manuscript. Xing W and Wu B were responsible for data verification. All authors reviewed and approved the final manuscript for publication.

Data availability

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

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Conflict of interest

The authors declare that they have no competing interests. The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

- [1] Biswas S, Mishra R, Bist AS. 2021. Passion to profession: a review of passion fruit processing. *Aptisi Transactions on Technopreneurship (ATT)* 3(1):48–56
- [2] He X, Luan F, Yang Y, Wang Z, Zhao Z, et al. 2020. *Passiflora edulis*: an insight into current researches on phytochemistry and pharmacology. *Frontiers in Pharmacology* 11:617
- [3] Thokchom R, Mandal G. 2017. Production preference and importance of passion fruit (*Passiflora edulis*): a review. *Journal of Agricultural Engineering and Food Technology* 4(1):27–30

- [4] Kondo T, Koyama A. 2023. Physiological responses in passion fruit to drought stress and attempt to reduce the stress by cross-protection with heat treatment. *Acta Horticulturae* (1372):51–56
- [5] Moura RS, Gheyi HR, Coelho Filho MA, Nunes de Jesus O, da Silva Sá FV, et al. 2016. Tolerance of passion fruit species under salt stress. *International Journal of Current Research* 8:37689–37695
- [6] Kishore K, Pathak A, Yadav D, Bujarbaruah K, Bharali R, et al. 2006. Passion Fruit. *Technical bulletin*. Umiam, Meghalaya, India: Director, ICAR Research Complex for NEH Region. doi: [10.13140/RG.2.2.25156.01925](https://doi.org/10.13140/RG.2.2.25156.01925)
- [7] Saijo Y, Loo EP. 2020. Plant immunity in signal integration between biotic and abiotic stress responses. *New Phytologist* 225(1):87–104
- [8] Kollist H, Zandalinas SI, Sengupta S, Nuhkat M, Kangasjärvi J, et al. 2019. Rapid responses to abiotic stress: priming the landscape for the signal transduction network. *Trends in Plant Science* 24(1):25–37
- [9] Zhu JK. 2016. Abiotic stress signaling and responses in plants. *Cell* 167(2):313–324
- [10] Sofia A, de Almeida AM, da Silva AB, da Silva JM, Paula A, et al. 2013. Abiotic stress responses in plants: unraveling the complexity of genes and networks to survive. In *Abiotic stress-plant responses and applications in agriculture*. IntechOpen. pp. 49–101 doi: [10.5772/52779](https://doi.org/10.5772/52779)
- [11] Coello P, Hey SJ, Halford NG. 2011. The sucrose non-fermenting-1-related (SnRK) family of protein kinases: potential for manipulation to improve stress tolerance and increase yield. *Journal of Experimental Botany* 62(3):883–893
- [12] Mao X, Li Y, Rehman SU, Miao L, Zhang Y, et al. 2020. The sucrose non-fermenting 1-related protein kinase 2 (SnRK2) genes are multifaceted players in plant growth, development and response to environmental stimuli. *Plant and Cell Physiology* 61(2):225–242
- [13] Zheng R, Zhao K, Chen J, Zhu X, Peng Y, et al. 2025. Genomic signatures of SnRKs highlighted conserved evolution within orchids and stress responses through ABA signaling in the Cymbidium ensifolium. *BMC Plant Biology* 25(1):277
- [14] Sun H, Yuan Q, Li J, Ma M, Ren H, et al. 2026. Genome-wide identification of the SnRK gene family in willow and expression analysis under abiotic stress. *BMC Plant Biology* in press
- [15] Kulik A, Wawer I, Krzywińska E, Bucholc M, et al. 2011. SnRK2 protein kinases—key regulators of plant response to abiotic stresses. *OMICS: A Journal of Integrative Biology* 15(12):859–872
- [16] Xu Q, Kong F, Yang W. 2025. SnRK1 as the core node integrating energy homeostasis, stress adaptation and hormonal crosstalk in plants. *Plant, Cell & Environment* 48(11):7830–7847
- [17] Han C, Wang H, Shi W, Bai MY. 2024. The molecular associations between the SnRK1 complex and carbon/nitrogen metabolism in plants. *New Crops* 1:100008
- [18] Wurzing B, Nukarinen E, Nägele T, Weckwerth W, Teige M. 2018. The SnRK1 kinase as central mediator of energy signaling between different organelles. *Plant Physiology* 176(2):1085–1094
- [19] Lim CW, Lee SC. 2023. *Arabidopsis* SnRK2.3/SRK2I plays a positive role in seed germination under cold stress conditions. *Environmental and Experimental Botany* 212:105399
- [20] Chen Z, Zhou L, Jiang P, Lu R, Halford NG, et al. 2021. Genome-wide identification of sucrose nonfermenting-1-related protein kinase (SnRK) genes in barley and RNA-seq analyses of their expression in response to abscisic acid treatment. *BMC Genomics* 22(1):300
- [21] Tang RJ, Luan S. 2017. Regulation of calcium and magnesium homeostasis in plants: from transporters to signaling network. *Current Opinion in Plant Biology* 39:97–105
- [22] Zhang Y, Xu Y, Xing W, Wu B, Huang D, et al. 2023. Identification of the passion fruit (*Passiflora edulis* Sims) MYB family in fruit development and abiotic stress, and functional analysis of *PeMYB87* in abiotic stresses. *Frontiers in Plant Science* 14:1124351
- [23] Yu T, Cen Q, Kang L, Mou W, Zhang X, et al. 2022. Identification and expression pattern analysis of the *OsSnRK2* gene family in rice. *Frontiers in Plant Science* 13:1088281
- [24] Xia Z, Huang D, Zhang S, Wang W, Ma F, et al. 2021. Chromosome-scale genome assembly provides insights into the evolution and flavor synthesis of passion fruit (*Passiflora edulis* Sims). *Horticulture Research* 8:14
- [25] Crozet P, Margalha L, Confraria A, Rodrigues A, Martinho C, et al. 2014. Mechanisms of regulation of SNF1/AMPK/SnRK1 protein kinases. *Frontiers in Plant Science* 5:190
- [26] Sanz P, Viana R, Garcia-Gimeno MA. 2016. AMPK in yeast: the SNF1 (sucrose non-fermenting 1) protein kinase complex. In *AMP-activated Protein Kinase*. Cham: Springer International Publishing. pp. 353–374 doi: [10.1007/978-3-319-43589-3_14](https://doi.org/10.1007/978-3-319-43589-3_14)
- [27] Amjad E, Sokouti B, Asnaashari S, Dastmalchi S. 2024. A systematic review on the role of SnRK2 gene in *Arabidopsis thaliana* growth stages under abiotic stresses. *OBM Genetics* 8(4):1–26
- [28] Fàbregas N, Yoshida T, Fernie AR. 2020. Role of Raf-like kinases in SnRK2 activation and osmotic stress response in plants. *Nature Communications* 11:6184
- [29] Fujita Y, Nakashima K, Yoshida T, Katagiri T, Kidokoro S, et al. 2009. Three SnRK2 protein kinases are the main positive regulators of abscisic acid signaling in response to water stress in *Arabidopsis*. *Plant and Cell Physiology* 50(12):2123–2132
- [30] Fujita Y, Yoshida T, Yamaguchi-Shinozaki K. 2013. Pivotal role of the AREB/ABF-SnRK2 pathway in ABRE-mediated transcription in response to osmotic stress in plants. *Physiologia Plantarum* 147(1):15–27
- [31] Hasan MM, Liu XD, Waseem M, Yao GQ, Alabdallah NM, et al. 2022. ABA activated SnRK2 kinases: an emerging role in plant growth and physiology. *Plant Signaling & Behavior* 17:2071024
- [32] Jin H, Li J, Song T, Miao D, Ning Q, et al. 2025. Genome-wide identification of the SnRK2 gene family and its response to abiotic stress in *Populus euphratica*. *International Journal of Molecular Sciences* 26(21):10750
- [33] Kawa D, Meyer AJ, Dekker HL, Abd-El-Halim AM, Gevaert K, et al. 2020. SnRK2 protein kinases and mRNA decapping machinery control root development and response to salt. *Plant Physiology* 182(1):361–377
- [34] Li C, Nong Q, Xie J, Wang Z, Liang Q, et al. 2017. Molecular characterization and co-expression analysis of the SnRK2 gene family in sugarcane (*Saccharum officinarum* L.). *Scientific Reports* 7:17659
- [35] Li GJ, Chen K, Sun S, Zhao Y. 2024. Osmotic signaling releases PP2C-mediated inhibition of *Arabidopsis* SnRK2s via the receptor-like cytoplasmic kinase BIK1. *The EMBO Journal* 43(23):6076–6103
- [36] Nakashima K, Fujita Y, Kanamori N, Katagiri T, Umezawa T, et al. 2009. Three *Arabidopsis* SnRK2 protein kinases, SRK2D/SnRK2.2, SRK2E/SnRK2.6/OST1 and SRK2I/SnRK2.3, involved in ABA signaling are essential for the control of seed development and dormancy. *Plant and Cell Physiology* 50(7):1345–1363
- [37] Righetto GL, Sriranganadane D, Halabelian L, Chiodi CG, Elkins JM, et al. 2019. The C-terminal domains SnRK2 box and ABA box have a role in sugarcane SnRK2s auto-activation and activity. *Frontiers in Plant Science* 10:1105
- [38] Tang Y, Zhang Y, Hu Z, Yan X, Hu R, et al. 2025. Genome-wide identification and evolutionary analysis of the SnRK2 gene family in *Nicotiana* species. *Agriculture* 15(13):1396
- [39] Luan S. 2009. The CBL–CIPK network in plant calcium signaling. *Trends in Plant Science* 14(1):37–42
- [40] Chen Y, Jin YF, Wang Y, Gao Y, Wang Q, et al. 2022. Diverse roles of the CIPK gene family in transcription regulation and various biotic and abiotic stresses: a literature review and bibliometric study. *Frontiers in Genetics* 13:1041078
- [41] Son S, Park SR. 2023. The rice SnRK family: biological roles and cell signaling modules. *Frontiers in Plant Science* 14:1285485

- [42] Lu P, Shi Z, Liu T, Ji J, Li J, et al. 2025. SnRK-PP2C-PYL gene families in *Citrus sinensis*: genomic characterization and regulatory roles in carotenoid metabolism. *Metabolites* 15(9):610
- [43] Wang X, Zheng S, Sun L, Zhao S. 2021. Heterologous expression of *Vitis vinifera* SNF1-related kinase 1.1 gene in *Arabidopsis* akin10 mutant reveals the signaling regulatory network of sucrose metabolism. *Plant Growth Regulation* 94(3):245–259
- [44] Mohannath G, Jackel JN, Lee YH, Buchmann RC, Wang H, et al. 2014. A complex containing SNF1-related kinase (SnRK1) and adenosine kinase in *Arabidopsis*. *PLoS One* 9(1):e87592
- [45] Hrabak EM, Chan CWM, Gribskov M, Harper JF, Choi JH, et al. 2003. The *Arabidopsis* CDPK-SnRK superfamily of protein kinases. *Plant Physiology* 132(2):666–680
- [46] Thirugnanam K, Ramchandran R. 2020. SNRK: a metabolic regulator with multifaceted role in development and disease. *Vessel Plus* 4:26
- [47] Luo Y, Niu Y, Gao R, Wang C, Liao W. 2022. Genome-wide identification and expression analysis of *SnRK* gene family under abiotic stress in cucumber (*Cucumis sativus* L.). *Agronomy* 12(7):1550
- [48] Wu P, Wang W, Duan W, Li Y, Hou X. 2017. Comprehensive analysis of the CDPK-SnRK superfamily genes in Chinese cabbage and its evolutionary implications in plants. *Frontiers in Plant Science* 8:162
- [49] Ma X, Li QH, Yu YN, Qiao YM, Haq SU, et al. 2020. The CBL–CIPK pathway in plant response to stress signals. *International Journal of Molecular Sciences* 21(16):5668
- [50] Nuruzzaman Manik SM, Shi S, Mao J, Dong L, Su Y, et al. 2015. The calcium sensor CBL–CIPK is involved in plant's response to abiotic stresses. *International Journal of Genomics* 2015:493191
- [51] Wei Y, Peng L, Zhou X. 2025. SnRK2s: kinases or substrates? *Plants* 14(8):1171
- [52] Fidler J, Graska J, Gietler M, Nykiel M, Prabucka B, et al. 2022. PYR/PYL/RCAR receptors play a vital role in the abscisic-acid-dependent responses of plants to external or internal stimuli. *Cells* 11(8):1352
- [53] Shivhare R, Lata C. 2026. Structure and function of diverse abscisic acid receptors and coreceptors in modulating developmental and stress responses. In *Plant Receptors in Cellular Signaling*, ed. Roychoudhury A. Amsterdam: Elsevier. pp. 125–142 doi: 10.1016/b978-0-443-30244-2.00027-0
- [54] Zhang XL, Jiang L, Xin Q, Liu Y, Tan JX, et al. 2015. Structural basis and functions of abscisic acid receptors PYLs. *Frontiers in Plant Science* 6:88
- [55] Rai GK, Khanday DM, Choudhary SM, Kumar P, Kumari S, et al. 2024. Unlocking nature's stress buster: Abscisic acid's crucial role in defending plants against abiotic stress. *Plant Stress* 11:100359
- [56] Yin S, Ma H, Ye Q, Lu H, Wang K, et al. 2024. Identification of SnRK2 family and functional study of PeSnRK2.2A and PeSnRK2.2B for drought resistance in *Phyllostachys edulis*. *Industrial Crops and Products* 219:119087
- [57] Li J, Song J, Li C, Ma J, Liu J, et al. 2022. Genome-wide identification and expression profile analysis of the SnRK2 gene family in *Nicotiana glauca*. *Biochemical Genetics* 60(5):1511–1526
- [58] Long T, Xu B, Hu Y, Wang Y, Mao C, et al. 2021. Genome-wide identification of *ZmSnRK2* genes and functional analysis of *ZmSnRK2.10* in ABA signaling pathway in maize (*Zea mays* L.). *BMC Plant Biology* 21(1):309
- [59] Ni Y, Cui Z, Zhang Z, Chen H, Zhou S. 2023. Genome-wide identification and expression analysis of anthocyanin synthesis-related R2R3-MYB gene family in purple passion fruit (*Passiflora edulis*). *Materials Express* 13(3):467–481
- [60] Song S, Zhang D, Ma F, Xing W, Huang D, et al. 2022. Genome-wide identification and expression analyses of the aquaporin gene family in passion fruit (*Passiflora edulis*), revealing PeTIP3-2 to be involved in drought stress. *International Journal of Molecular Sciences* 23(10):5720
- [61] Liang J, Fang Y, An C, Yao Y, Wang X, et al. 2023. Genome-wide identification and expression analysis of the bHLH gene family in passion fruit (*Passiflora edulis*) and its response to abiotic stress. *International Journal of Biological Macromolecules* 225:389–403
- [62] Xu Y, Zhou W, Ma F, Huang D, Xing W, et al. 2023. Characterization of the passion fruit (*Passiflora edulis* Sim) bHLH family in fruit development and abiotic stress and functional analysis of PebHLH56 in cold stress. *Horticulturae* 9(2):272
- [63] Xu Y, Li P, Ma F, Huang D, Xing W, et al. 2023. Characterization of the NAC transcription factor in passion fruit (*Passiflora edulis*) and functional identification of PeNAC-19 in cold stress. *Plants* 12(6):1393
- [64] Ma F, Zhou H, Xu Y, Huang D, Wu B, et al. 2023. Comprehensive analysis of bZIP transcription factors in passion fruit. *iScience* 26(4):106556
- [65] Sirichandra C, Davanture M, Turk BE, Zivy M, Valot B, et al. 2010. The *Arabidopsis* ABA-activated kinase OST1 phosphorylates the bZIP transcription factor ABF3 and creates a 14-3-3 binding site involved in its turnover. *PLoS One* 5(11):e13935
- [66] Umezawa T, Sugiyama N, Mizoguchi M, Hayashi S, Myouga F, et al. 2009. Type 2C protein phosphatases directly regulate abscisic acid-activated protein kinases in *Arabidopsis*. *Proceedings of the National Academy of Sciences of the United States of America* 106(41):17588–17593
- [67] Basu S, Roychoudhury A. 2014. Expression profiling of abiotic stress-inducible genes in response to multiple stresses in rice (*Oryza sativa* L.) varieties with contrasting level of stress tolerance. *BioMed Research International* 2014:706890
- [68] Liu JG, Han X, Yang T, Cui WH, Wu AM, et al. 2019. Genome-wide transcriptional adaptation to salt stress in *Populus*. *BMC Plant Biology* 19(1):367
- [69] Imtiaz K, Ahmed M, Annum N, Tester M, Saeed NA. 2023. AtCIPK16, a CBL-interacting protein kinase gene, confers salinity tolerance in transgenic wheat. *Frontiers in Plant Science* 14:1127311
- [70] Anwar A, Kim JK. 2020. Transgenic breeding approaches for improving abiotic stress tolerance: recent progress and future perspectives. *International Journal of Molecular Sciences* 21(8):2695



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