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Review Article

The SnRK Protein Kinase Family and the Function of SnRK1 Protein Kinase

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ABSTRACT

The sucrose non-fermenting 1 (SNF1) protein kinase plays important roles in process of biotic growth and development. In yeast (*Saccharomyces cerevisiae*) and mammals, it regulates the protein-protein interaction, activity regulation and the gene expression of the substrate in response to changing nutrient sources or energy demands and SNF1-related kinase (SnRK1) proteins are present in plants. The sucrose non-fermenting 1-related protein kinase (SnRK) is homologous of SNF1 and AMP-activated protein kinase (AMPK), which widely exists in plant and involves in a variety of signaling pathways. SnRK has been divided into three sub-families: SnRK1, SnRK2 and SnRK3. SnRK is the key switches in plant sugar signal, stress, seed germination and seedling growth. In this review, we summarized the progress of SnRK protein kinase family and the structure, substrate, regulation and gene expression of SnRK1. © 2012 Friends Science Publishers

Key Word: SnRK; Protein kinase family; SnRK1; Signaling pathway; ABA

INTRODUCTION

Protein kinase and protein phosphatase are ubiquitous in organism. They catalyze the processes of protein phosphorylated and dephosphorylated. A series of physiological and biochemical activities including metabolism, mitosis, amitosis, signal transduction are regulated by protein phosphorylation and dephosphorylation. They play important roles in growth and development (Ruben *et al.*, 2011).

SNF1 of yeast, AMPK of mammal and SnRK1 of plant are homologous, belonging to the SNF1 protein kinase superfamily. SNF1 was found in yeast (*Saccharomyces cerevisiae)* originally (Alderson *et al*., 1991). The low intracellular glucose level can be perceived by SNF1. In yeast, glucose regulates the protein-protein interaction, substrate specificity and subcellular localization of the SNF1 subunit that modulates SNF1 kinase activity, resulting in the phosphorylation of activators and repressors that control transcription of multiple genes in metabolic pathways required for the utilization of alternative energy sources. In mammals, activation of AMPK due to increases in the AMP to ATP ratio during metabolic stress results in the enhancement of ATP-producing pathways and the inhibition of ATP consuming pathways (Bradford *et al*., 2003). AMPK complex is directly relevant to obesity and type II diabetes (Rune *et al*, 2009). In the eukaryote, SNF1 protein kinase is very strongly conservative. Many SNF1 analogues have been identified in plants (Alderson *et al*., 1991). Through conservative amino acid sequence analysis, it is divided into three subfamilies, SnRK1, SnRK2, SnRK3, respectively. They participate in a variety of metabolic activities of plants; especially play important roles in the physiological resistance.

The SnRK is a class of Ser/Thr protein kinase, which widely exists in plant and involves in a variety of signaling pathways. They play a pivotal role in plant stress physiology. SnRK family is classified into three subfamilies: SnRK1, SnRK2 and SnRK3. In this review, we summarized the progress of research on SnRK protein kinase family and the structure, substrate, regulation and gene expression of SnRK1.

Protein kinase superfamily of SnRK: Structure of SnRK protein kinase family: A self-regulation kinase domain in the N-terminal is the common structural characteristic of SnRK protein kinase family. The region is a highly variable, and can interact with other protein. Compared with other protein kinase, there is a conserved amino acid-threonine in the activation region. SnRK is composed of α, β and γ composed of three structural domains. The α-domain has a

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N-terminal with Ser/Thr protein kinase domain, C-terminal has regulatory sequences of self-inhibitory function (Jiang & Carlson, 1996). β-domain can combine with α-and γ-domain, so β-domain can regulate shape of heterologous trimer complexes (Jiang & Carlson, 1997). Three sub-families have their own structural characteristics, as shown in Fig. 1 (Wang *et al*., 2010).

Classification and Related Function of SnRK

SnRK1 subfamily: The SnRK1 was discovered initially in the rye (*Secale cereale* L.). The rye *SnRK1* encodes a polypeptide with a relative molecular mass of 57.7 kDa and 502 amino acids. The identities of yeast *SNF1* and mammalian *AMPK* were up to 42-45% (Alderson *et al*., 1991). At present, some members of the SnRK1 subfamily have been found to form a variety of model plant and some important crops, such as *Arabidopsis thaliana*, rye, barley (*Hordeum vulgare*), potatoes (*Solanum tuberosum*), tobacco and beet, and so on. It may exist in all plants (Halford & Hardie, 1998; Halford *et al*., 2003). According to the similarity of amino acid sequences, SnRK1 is divided into SnRK1a and SnRK1b. *SnRK1a* expressed throughout the developmental period of the plant. But expression of *SnRK1b* in seeds is very high quality, and other parts of the plant are relatively low. This gene exists only in dicotyledon (Halford & Hardie, 1998). Studies have shown that SnRK1 is the key switches in plant sugar signal. And the regulation of glucose metabolism, hormonal regulation and sugar signal are directly related to signal transduction (Mathieu *et al*., 2009; Kleinow *et al*., 2009).

SnRK2 subfamily: SnRK2 sub-family is unique in plants. SnRK2 is a relatively small plant-specific protein family. It is activated by osmotic stress (Sandra *et al*., 2010). According to the similarity of amino acid sequence, SnRK2 is divided into SnRK2a and SnRK2b. Comparing with SnRK1, SnRK2 protein contains a relatively short C-terminal, characterized of the C-terminal acidic with a short "patch." In gaoliang (*Sorghum vulgare*), SnRK2 contains a kinase domain, binding domain, ATP binding domain, Ser/Thr active site and four N-fourteen sites. The acidic patch of SnRK2a is rich in aspartic acid residues, while that of SnRK2b enriches in glutamic acid residues (Zhang *et al*., 2011).

The *SnRK2* was first isolated from wheat embryo cDNA library by ABA treatment that is *PKABA1* (Anderberg & Walker-Simmons, 1992). *PKABA1* is induced by ABA and hypertonic stress. The transient overexpression of *PKABA1* gene in barley aleurone inhibits GA-induced promoter activity, indicating that the ABA signal transduction inhibits the GA signal transduction (Johnson *et al*., 2002). Under drought stress, the expression of *PKABA1* and intracellular level both were increased, and the former was found in roots and skin scales (Laurie & Halford, 2001). Another study found that *PKABA1* could combine with ABA-responsive element factor-TaABF. This combination could regulate the level of expression of the ABA. Meanwhile, studies have shown that SnRK2 sub-family members regulate ABA signaling, for example, SnRK2.6 can regulate ABA signaling in guard cells (Yoshida *et al*., 2002). Ten members of SnRK2 have been discovered, namely SnRK2.1-SnRK2.10 in the Arabidopsis. Boudsocq studies (2004) showed that 10 SnRK2 members in Arabidopsis, in addition to SnRK2.9, the other SnRK2 members can be mannose and NaCl-induced activation. SnRK2.2, SnRK2.3, SnRK2.6, SnRK2.7 and SnRK2.8 can be activated by ABA (Boudsocq *et al*., 2004). Meanwhile, SnRK2 family members have a very important role in plant stress resistance. *SnRK2.4* overexpression in Arabidopsis plants, compared with the control group, revealed that the abilities to salt resistance, drought resistance and frost resistance have greatly improved (Man *et al*., 2010). The overexpression of *SnRK2.8* improved a certain ability of resisting drought intimidation. Under nutritional deficiency, the growth conditions of transgenic plant were better than the control group in Arabidopsis (Shin *et al*., 2007).

SnRK3 subfamily: SnRK3 is a rare protein kinase in plant, called calcineurin B-like calcium sensor-interacting protein kinases (calcineurin B-like calcium sensor-interacting protein kinases, CIPK) (Kim *et al*., 2000). CIPK interacts with calcium-binding protein SOS3, SCaBPS and CBL (calcineurin B-like calcium sensor, CBL). The interaction region is called NAF/FISL motif, which is made up of 22 amino acid residues (Albrecht *et al*., 2001; Guo *et al*., 2001). CIPK kinase region contains a binding site, calcium-binding proteins and calcium-sensitive CBL in the C-terminal inhibitory, which combine to activate protein kinase (Guo *et al*., 2001). Studies have shown that CIPK and CSLs complex of upstream interactions protein involved in salt stress, sucrose and ABA signal transduction (Imamura *et al*., 2008).

In Arabidopsis, PKS3, PKS18 and CIPK3 of SnRK3 family can regulate plant growth, stomatal opening and closing and seed germination treated by ABA (Kim *et al*., 2003). AtCIPK1 of Arabidopsis form complexes with AtCBL1 and AtCBL9 regulates ABA-independent and ABA-dependent pathways, respectively (Angelo *et al*., 2006). AtCIPK3 regulates ABA and cold signal transduction pathways (Kim *et al*., 2003). Girdhar's study showed that CBL9 interacted with CIPK3 to regulate the ABA pathway, and this point got validation in the yeast two-hybrid experiment (Pandey *et al*., 2008). Comparing with *cbl9/cipk3* double mutant plant and single mutant of two genes, three mutants could response to ABA signaling. Under salt and mannitol stress, seed germination and seedling growth of three mutants are inhibited (Pandey *et al*., 2004).

Structure and Function of Snrk1

SnRK1 structure: The AMPK/SNF1/SnRK1 protein kinase functions as heterotrimeric complexes require α-, β-subunit and γ-subunits. For example, in yeast (*Saccharomyces cerevisiae*), SNF1 contains a catalytic subunit (Snf1), three β-subunits (Sip1, Sip2 & Gal83)

and a γ-subunit (Snf4). All of these three subunits also exist in the animal, namely AMPKα, AMPKβ and AMPKγ. In plant, SnRK1 complex contains three subunits (Fig. 2). In Arabidopsis, Snf1 and AMPK α are KIN10/KIN11 with a similar structure and function, while there may be a pseudogene of KIN12 (Gustavo *et al.*, 2011). Other three genes KINβ1/KINβ2/KINβ of Arabidopsis 3 and β-subunit of yeast and mammalian are sharing the same feature. Meanwhile, a SNF4/AMPKγ homologue called AtSNF4 has been cloned from Arabidopsis by complementation of a snf4 mutant (Kleinow *et al*., 2000).

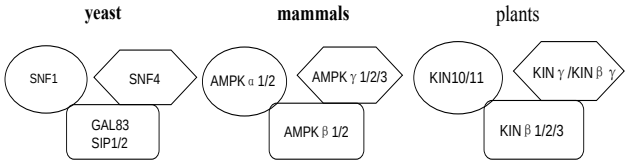
SnRK1 substrates and activity regulation: The first plant protein identified as a substrate for SnRK1 was HMG-CoA reductase in Arabidopsis (Dale *et al.*, 1995). At the same time, sucrose phosphate synthase, nitrate reductase and trehalose-5-phosphate synthase had been identified as SnRK1 substrates (Harthill *et al.*, 2006; Eleazar *et al.*, 2011). SnRK1 can directly phosphorylate HMG-CoA reductase and sucrose phosphate synthase resulting in loss of activity. But the inactivation of NR and TPS5 also requires the binding of a 14-3-3 protein to the phosphorylation site (Harthill *et al.*, 2006). By regulating the activity of these four enzymes, SnRK1 achieve the metabolism of plants, development and regulation of stress reactions.

The enzyme 3-hydroxy-3-methyl glutaryl coenzyme A. (HMG-CoA) reductase (HMGR) catalyzes the conversion of HMG-CoA into mevalonate (MVA), which is the limiting step in the biosynthesis of isopentenyl pyrophosphate. SPS is a key enzyme in the pathway of sucrose biosynthesis in plants. Nitrate reductase is molybdoenzymes that reduce nitrate (NO_3^-) to nitrite (NO_2^-). It plays an important role in synthesis nitro-organic compounds. The achievement as follows about interaction of sugar and nitrogen signal: as mentioned above, sucrose synthase, the key enzyme in carbon metabolism is controlled by SnRK1 protein kinases, at the same time the kinase also regulates the activity of NR. When tobacco (*Nicotiana tabacum*) leaves were fed with sucrose *in vitro*, NR activity, nitrogen assimilation and amino acids were significantly enhanced. These results showed that the SnRK1 kinase plays an important role in carbon-nitrogen interactions (Halford *et al.*, 2004; Li *et al.*, 2010). SnRK1 can regulate the activity of those important physiological effects of substrate, which gives us a new way of thinking about the co-regulation of sugar, nitrogen compounds and the variety of secondary metabolites. SnRK1 can also control the activity of other enzymes. ADP-glucose pyrophosphorylase (AGPase) is a key enzyme in starch synthesis in growing potato tubers. AGPase activity depends on the redox regulation, to make own cells to respond to sucrose, but AGPase oxidation does not occur in the antisense expression of potato tubers.

SnRK1 plays important roles in the transcription regulation of gene expression. In the developing tuber of potato, the expression level of *SnRK1* was higher, lower in stem and lowest in leaf. The experiment on potato provided evidence for SnRK1 to regulate the transcription.

Fig. 1: Structure of SnRK protein kinase family (Wang *et al.*, 2010). Vertical lines represent the length of the variable and function region of N-terminalor and C-terminal. Dashed lines represent the main regulatory area of subfamily SnRK1; structure of subfamily SnRK2 has a D/E acidic patch; hachures represent a depressing area of subfamily SnRK3

Fig. 2: The variable composition of the heterotrimeric SNF1/AMPK/SnRK1 complexes among different organisms (Ghillebert *et al.*, 2011). The AMPK/SNF1/SnRK1 protein kinases function as heterotrimeric complexes require α-subunit (circle), a β-subunit (rectangular) and a γ-subunit (polygon)

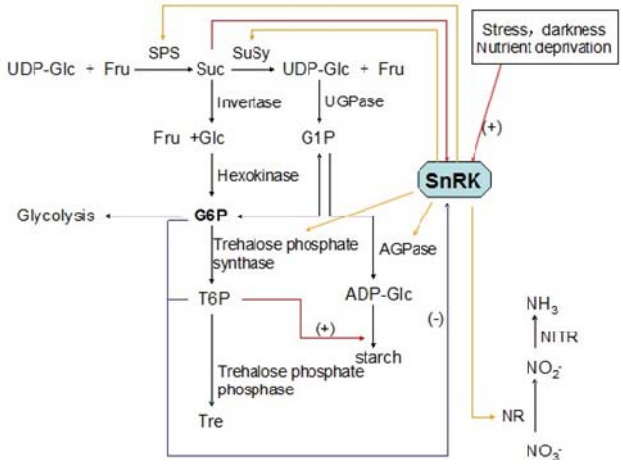


The activity of SnRK1 in young tuber was 40 times than in mature tuber (Man *et al*., 1997). The regulation of SnRK1 gene expression and the pure natural signal of kinase activity are not clear. SnRK1 gene dephosphorylation can be inhibited by low concentration 5'-AMP, and SnRK1 activity can also be inhibited by glucose 6-phosphate. The relationship between the induced or inhibited activity of SnRK1 and metabolism is still an assumptive construct. The evidence is that SnRK1 may be activated by the high concentration of intracellular sucrose, and a low concentration intracellular sucrose can bring response too (Halford & Dickinson, 2001).

SnRK1 regulation of gene expression: The results showed that SnRK1 can directly regulate the regulation of sucrose synthase at the transcriptional level. In wild potato tuber, sucrose synthase gene expression was normal and it was induced by external sucrose. Antisense expression of *SnRK1* made SnRK1 activity of potato tubers decrease, coupling with the decrease of sucrose synthase activity. However, antisense genes in the leaves could not be induced by sucrose. Sucrose synthase is one of the important enzymes on glucose metabolism in potato tubers. Sucrose and starch in storage organs play an important role in metabolism (Halford & Hardie, 1998).

Meanwhile, SnRK1 could regulate the expression of other genes, which can encode carbohydrate metabolism enzymes. For instance, they are useful as a transient expression system for the proving that antisense SnRK1

Fig. 3: SnRK1 is at the heart of the control of carbon/nitrogen partitioning in plants, regulating the activity of important enzymes by affecting their activation state or the activity of the genes that encode them (Adriano *et al*., 2010). The black arrows indicate reactions; yellow arrows indicate increases in expression of SnRK1. Red arrows is positive sign, symbolize protein activation and in blue, with negative sign, protein inhibition. Glc, glucose; Fru, fructose; Suc, sucrose; G6P, glucose-6-phosphate; G1P, glucose-1-phosphate; T6P, trehalose-6-phosphate; Glu, glutamate; Gln, glutamine; AGPase, ADP-glucose pyrophosphorylase; UGPase, UDP-glucose pyrophosphorylase; SPS, sucrose phosphate synthase; SuSy, sucrose synthase; NR, nitrate reductase; NITR, nitrite transporter. For simplification, neither sub-cellular compartmentalization nor mechanistic information is presented



expression inhibits a-amylase promoter activity in the wheat germ (Laurie *et al.*, 2003). These accounts for that SnRK1 influence starch biosynthesis via regulating the expression of sucrose synthase and the activity of AGPase. SnRK1 activity can respond to sucrose appropriately (Halford & Paul, 2003). According to the studies, currently, SnRK1 family is a key switch in sugar signal transduction and metabolic pathways of plant (Fig. 3) (Polge & Thomas, 2007).

The role of SnRK1 in signaling and plant development: Antisense gene expressions in different plant indicate that SnRK1 has very important roles in plant growth and development processes. For instance, sprouting process of potato tuber was inhibited by the *SnRK1* antisense gene (Halford *et al.*, 2003). Barley pollen development can be inhibited by antisense *SnRK1* and Pollen is very small, pear shaped, containing little or no starch and no life. But antisense *SnRK1* gene cannot be passed to the next generation. Also it inhibited the ovule development. Pollen dysplasia is related to the lack of starch accumulation and non-active sugar (Zhang *et al.*, 2001). Male sterility in rice and wheat caused the decrease of activity of acid instead of non-sucrose synthase activity. SnRK1 and the invertase regulation have not discovered the positive connection but in tobacco's anthers. Antisense *SnRK1* of transgenic barley was similar to that antisense expression of invertase in extracellularly causes abnormal pollen (Goetz *et al.*, 2001). Currently, there are evidences on the SnRK1 involving in cell metabolism and circulation. The overexpression of plant *SnRK1* in yeast could make the body of yeast decrease in size significantly. It implied that SnRK1 makes cell cycle completely earlier in yeast. The possible reason is that the normal function of the SnRK1 or SNF1 is coupled with the interaction between metabolism and cell cycle signals. However, the overexpression of exogenous *SnRK1* can cause system disturbance of yeast. On the basis of the above resolution, we can conjecture that SnRK1 family is a key switch in sugar signal transduction and metabolic pathways of plant. At present, we need further study in order to clarify the operation of carbon and nitrogen metabolites, and their signal perception and transduction.

CONCLUSION

As the SNF1 function research work went further and more detailed, especially SNF1 is related with sugar metabolism and sugar signaling, which has become hot area of research. But there is little attention for the research on SnRK1 in plant. With the discovery of new *SnRK1* and the isolation of more substrates, more and more studies suggest that SnRK1 plays an important role in the plant growth and signal transduction pathway. At present, the majority of researchers is focused on SnRK1 in plant distribution, physical and chemical properties, physiological substrates, correlation between protein kinase and the position of the signal transduction and so on. At the same time, the application of transgenic technology and antisense RNA technology, SnRK1 determines the enzyme in the position of plant regulatory networks, regulation mechanisms. Development of effective products was applied to agricultural production, the promotion of plant growth and development, enhancing plant stress resistance and improving crop quality and yield, which is very significant.

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REFERENCES

Adriano, N., R. Alisdair, Fernie and S. Mark, 2010. Metabolic and Signaling Aspects Underpinning the regulation of Plant Carbon Nitrogen Interactions. *Mol. Plant,* 3: 973–996

Albrecht, V., O. Ritz and S. Linder, 2001. The NAF domain defines a novel protein-protein interaction module conserved in Ca^{2+}-regulated kinases. *EMBO J.*, 20: 1051–1063

Alderson, A., P.A. Sabelli, J.R. Dickinson and D. Cole, 1991. Complementation of snf1, a mutation affecting global regulation of carbon metabolism in yeast, by a plant protein kinase cDNA. *Proc. Natl. Acad. Sci*., 88: 8602–8605

Anderberg, R.J. and M.K. Walker-Simmons, 1992. Isolation of a wheat cDNA clone for an abscisic acid-inducible transcript with homology to protein kinases. *Proc. Natl. Acad. Sci.,* 89: 10183–10187

Angelo, C.D., S. Weinl and O. Batistic, 2006. Alternative complex formation of the Ca2+ regulated protein kinase CIPK1 controls abscisic acid-dependent and independent stress responses in Arabidopsis. *Plant J*., 48: 857–872

Boudsocq, M., H. Barbier-Brygoo and C. Laurière, 2004. Identification of nine sucrose non-fermenting 1-related protein kinases 2 activated by hyperosmotic and saline stresses in Arabidopsis thaliana. *J. Biol. Chem*., 279: 41758–41766

Bradford, 2003. Abscisic Acid and Gibberellin Differentially Regulate Expression of Genes of the SNF1-Related Kinase Complex in Tomato Seeds. *Plant Physiol.,* 132: 1560–1576

Dale, S.W.A. and A.M. Edelman, 1995. Similar substrate recognition motifs for mammalian AMP activated protein kinase, higher plant HMG-CoA reductase kinase-A, yeast SNF1, and mammalian calmodulin-dependent protein kinase. *FEBS Lett.,* 361: 191–195

Eleazar, M.B. and D. Thierry, 2011. Wheat grain development is characterised by remarkable trehalose 6-phosphate accumulation pre-grain filling, tissue distribution and relationship to SNF1-related protein kinase1 activity. *Plant Physiol. Preview,* 10: 111–140

Goetz, M., D.E. Godt, A. Guivarch, U. Kahmann, D. Chriqui and T. Roitsch, 2001. Induction of male sterility in plants by metabolic engineering of the carbohydrate supply. *PNAS,* 98: 6522–6527

Guo, Y., U. Halfter and M. Ishitani, 2001. Molecular characterization of functional domains in the protein kinase SOS2 that is required for plant salt tolerance. *Plant Cell,* 13: 1383–1400

Gustavo, T.D., C.M. Cleverson and P.T. Juarez, 2011. The Arabidopsis b-ZIP Gene AtbZIP63 is a sensitive integrator of transient abscisic acid and glucose signals. *Plant Physiol.,* 157: 692–705

Halford, N.G. and J.R. Dickinson, 2001. Sugar sensing and cell cycle control: evidence of cross-talk between two ancient signaling pathways. *Plant Cell Cycle Interfaces,* 35: 87–107

Halford, N.G. and D.G. Hardie, 1998. SNF1-related protein kinases, global regulators of carbon metabolism in plants? *Plant Mol. Biol.,* 37: 735–748

Halford, N.G., S. Hey, D. Jhurreea and S. Laurie, 2003. Metabolic signalling and carbon partitioning, role for Snf1-related (SnRK1) protein kinase. *J. Exp. Bot.,* 54: 467–475

Halford, N.G., S. Hey, D. Jhurreea and S. Laurie, 2004. Highly conserved protein kinases involved in the regulation of carbon and amino acid metabolism. *J. Exp. Bot.,* 394: 35–42

Halford, N.G. and M.J. Paul, 2003. Carbon metabolite sensing and signaling. *Plant Biotechnol. J*., 1: 381–398

Harthill, J.E., S.E.M. Meek and N. Morrice, 2006. Phosphorylation and 14-3-3 binding of Arabidopsis trehalose- phosphate synthase response to 2-deoxyglucose. *Plant J*., 47: 211–223

Imamura, M., T. Yuasa and T. Takahashi, 2008. Isolation and characterization of a cDNA coding cowpea (*Vigna unguiculata* (L.) Walp) calcineurin B-like protein interacting protein kinase, VuCIPK1. *Plant Biol.,* 25: 437–445

Jiang, R. and M. Carlson, 1996. Glucose regulates protein interactions with in the yeast Snf1 protein kinase complex. *Genes Dev.,* 10: 3105–3115

Jiang, R. and M. Carlson, 1997. The Snf1 protein kinsae and its activating subunit Snf4 interact with distinct domains of the Sip1/Sip2/Gal83 component in the kinase complex. *Mol. Cell Biol.,* 17: 2099–2106

Johnson, R. and R. Wagner, 2002. The ABA-responsive kinase PKABA1 interacts with a seed specific response element binding factor, TaABF, and phosphorylates TaABF peptide sequences. *Plant Physiol.,* 130: 837–846

Kim, K.N., Y.H. Cheong and R. Gupta, 2000. Interaction specificity of Arabidopsis calcineurin B-like calcium sensors and their target kinases. *Plant Physiol.,* 124: 1844–1853

Kim, K.N., J.S. Lee, H. Han, S.A. Choi, S.J. Go and I.S. Yoon, 2003. Isolation and characterization of a novel rice Ca2+-regulated protein kinase gene involved in responses to diverse signals including cold, light, cytokinins, sugars and salts. *Plant Mol. Biol.,* 52: 1191–202

Kleinow, T., R. Bhalerao, F. Breuer and M. Umeda, 2000. Functional identification of an Arabidopsis snf4 ortholog by screening for heterologous multicopy suppressors of snf4 deficiency in yeast. *Plant J.,* 23: 115–122

Kleinow, T., S. Himbert and B. Krenz, 2009. NAC domain transcription factor ATAF1 interacts with SNF1-related kinases and silencing of its subfamily causes severe developmental defects in Arabidopsis. *Plant Sci.,* 177: 360–370

Laurie, S. and N.G. Halford, 2001. The role of protein kinases in the regulation of plant growth and development. *Plant Growth Regul.,* 34: 253–265

Laurie, S., R.S. Mckibbin and N.G. Halford, 2003. Antisense SNF-related (SnRK1) protein kinase gene represses transient activity of an a-amylase (a-Amy2) gene promoter in cultured wheat embryos. *J. Exp. Bot.,* 54: 739–747

Li, G.J., F. Peng and L. Zhang, 2010. Cloning and characterization of a SnRK1- encoding gene from Malus hupehensis Rehd and heterologous expression in tomato. *Mol. Biol. Rep.,* 37: 947–954

Man, A.L., P.C. Purcell, U. Hannappel and N.G. Halford, 1997. Potato SNF1-related protein kinase, molecular cloning, expression analysis and peptide kinase activity measurements. *Plant Mol. Biol.,* 34: 31–43

Man, X., H. Zhang, S. Tian, X. Chang and R. Jing, 2010. TaSnRK2.4 an SNF1-type serine/threonine protein kinase of wheat, confers enhanced multistress tolerance in Arabidopsis. *J. Exp. Bot.,* 61: 683–396

Mathieu, J., P. Jean and P.M. Bouly, 2009. SnRK1 (SNF1-related kinase 1) has a central role in sugar and ABA signalling in Arabidopsis thaliana. *Plant J.,* 59: 316–328

Pandey, G.K.C., Y.H. Heong and K.N. Kim, 2004. The calcium sensor calcineurin B-like 9 modulates abscisic acid sensitivity and biosynthes is in Arabidopsis. *Plant Cell,* 16: 1912–1924

Pandey, G.K., J.J. Grant and Y.H. Cheonga, 2008. Calcineurin B-like protein CBL9 interacts with target kinase CIPK the regulation of response in seed germination. *Mol. Plant,* 1: 238–248

Polge, C. and M. Thomas, 2007. SNF1/AMPK/SnRK1 kinases, global regulators at the heart of energy control? *Trends Plant Sci.,* 12: 20–28

Ruben, G.B., S. Erwin and W. Jing, 2011. The AMPK/SNF1/SnRK1 fuel gauge and energy regulator: structure, function and regulation. *FEBS J.,* 278: 3978–3990

Rune, A., M.E. Osier, T. Fritz and J.R. Zierath, 2009. Regulation of skeletal muscle sucrose Non- fermenting 1/AMP- activated protein kinase-related kinase (SNARK) by metabolic Stress and diabetes. *Diabetologia,* 52: 2182–2189

Sandra, J.H., B. Edward and G. Nigel, 2010. The interface between metabolic and stress signaling. *Annl. Bot.,* 105: 197–203

Shin, R., A.Y. Burch, K.A. Huppert, S.B. Tiwari, A.S. Murphy, T.J. Guilfoyle and D.P. Schachtman, 2007. The Arabidopsis transcription factor MYB77 modulates auxin signal transduction. *Plant Cell,* 19: 2440–2453

Wang, Y.B., S.Q. Gao and Y.M. Tang, 2010. Advance of the Sucrose Non-fermenting 1 related protein in kinase family in plants. *Bio. Technol. Bull.,* 11: 7–17

Yoshida, R., T. Hobo and K. Ichimura, 2002. ABA-activated SnRK2 protein kinase is required for dehydration stress signaling in Arabidopsis. *Plant Cell Physiol.,* 43: 1473–1483

Zhang, H.Y., X.G. Mao and R.L. Jing, 2011. SnRK2 acts within an intricate network that links sucrose metabolic and stress signaling in wheat. *Plant Signal. Behav.,* 6: 652–654

Zhang, Y., P.R. Shewry, H. Jones, P. Barcelo, P.A. Lazzeri and N.G. Halford, 2001. Expression of antisense SnRK1 protein kinase sequence causes abnormal pollen development and male sterility in transgenic barley. *Plant J.,* 28: 431–441

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