MINI-REVIEW

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Role of SERK genes in plant environmental response

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In plants, cell signaling connects the environmental input to the intracellular responses in plants. Exogenous signals play an important role in cell metabolism leading to growth and defense responses. Some of these stimuli induce anatomical and physiological modifications that are generally modulated by gene expression. *SERK* belongs to a small family of genes that code for a transmembrane protein involved in signal transduction and that have been strongly associated with somatic embryogenesis and apomixis in a number of plant species. Recent studies corroborate its role in somatic embryogenesis and suggest a broader range of functions in plant response to biotic and abiotic stimuli. This mini-review aims to present new data on SERK and discuss its involvement in plant development as well as in response to environmental stress.

Role of SERK in Plant Tissue Organogenesis and Somatic Embryogenesis

During somatic embryogenesis, biochemical and morphological changes occur throughout the development of induced tissues, which is closely related to alterations in gene expression. Several genes are differentially expressed during somatic embryogenesis induction, while others are expressed during differentiation from embryo maturation up to full plant development. Among the genes involved in the induction of somatic embryogenesis, the *Somatic Embryogenesis Receptor Kinase* (*SERK*) gene is claimed to have an important role. *SERK* gene was first isolated from carrot embryogenic cells, hailed as a molecular marker for somatic embryogenesis[1,2] and associated with somatic embryogenesis (SE) in a number of species including *Dactylis glomerata*,[2] *Arabidopsis thaliana*,[3] *Medicago truncatula*,[4] *Helianthus annuus*,[5] *Ocotea catharinensi*,[6] *Citrus unshiu*[7] and *Theobroma cacao*[8] and lately for apomixes.[9,10] SERK is a leucine-rich repeat (LRR) transmembrane protein kinase that enhances the ability of the apical meristem in Arabidopsis to form somatic embryos.[3] LRR kinases transmit their signal by forming homodimers or heterodimers with other RLKs, in response to binding by a ligand. This ligand-induced dimerization causes phosphorylation of the intracellular kinase domains of the receptor-like kinases (RLKs), which activates the next stages of the signal transduction pathway (**Fig. 1**). There is potential for different levels of complexity in the signaling through variation in the binding partners of different RLKs.[11]

In sunflower, *SERK* expression is correlated to induction of two different developmental pathways, somatic embryogenesis and shoot organogenesis.[5] In spite of its role in plant development, different genes from the family showed a different expression pattern during somatic or zygotic embryogenesis[12] and the expression of these genes was differentially detected in different tissues in several plant species, such as in the apical meristem, root and leaves,[5,8,11,13,14] suggesting additional roles for this gene. T-DNA mutational insertions showed the redundancy of two *SERK* homologs and its role in male sporogenesis in Arabidopsis.[15,16]

Somatic embryogenesis is an artificial simulation of natural embryogenesis and may be induced by different signalling stresses such as osmotic pressure, ABA induction and SA pathway, which are generally activated by auxin, mainly 2,4-D, which promotes oxidative stress in plants or similar molecules. The *SERK* pattern of expression in cultures suggests that it is part of a signaling pathway that mediates developmental changes in cells in response to culture conditions. These developmental changes involve the initiation of cell division and cellular reprogramming. Cell fate involving organogenesis or somatic embryogenesis might be conditioned by the status of *SERK* gene expression, and it is supposed to be a key factor in differentiation.[5,11] *SERK* gene expression was strongly related to auxin elicitation, a known somatic embryogenesis inducer.[4,17,18]

Brassinosteroid is an essential class of plant growth regulator involved in signal transduction during different plant growth events[19] that include salinity stress,[20] osmotic stress during seed germination[21] or disease resistance.[22] It was shown that BRASSINOSTEROID-INSENSITIVE1 (BRI1) receptor coprecipitates and interacts in vivo with SERK1.[23] SERK autophosphorylates in the threonine serine site[24] and is involved in transphosphorylation of BRI, which is enhanced under brassinosteroid treatment.[25] Although *SERK* gene belongs to a family that may show redundant roles and differential expression, some evolutionary changes in protein function were observed and differences in spatial expression may not be the only way to control its role.[26]

SERK as a Broader Signal in Response to Biotic and Abiotic Stress

In addition to the study of plant development and totipotency of cells, studies have been carried out with plants exposed to

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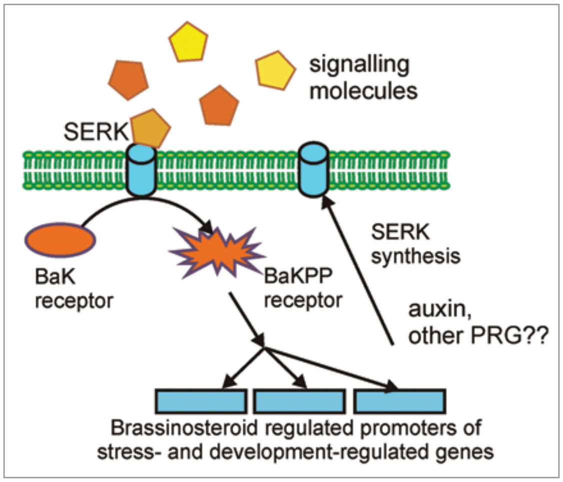

Figure 1. Somatic embryogenic receptor kinase (SERK) signaling. The SERK gene is expressed under auxin or other Plant Growth Regulator (PRG) stimuli. The SERK protein, a membrane receptor, phosphorylates the brassinosteroid receptor under appropriate external signal, to upregulate pathogen-related (PR) genes or disease response genes, increasing plant pathogen tolerance. SERK is involved in the expression of stress-response genes, and developmental pathways such as somatic embryogenesis or shoot organogenesis.

different sources of stress, involving plant growth regulators, elicitors and signal transduction (**Fig. 1**). These plant stresses can be separated into two main classes: biotic stresses including herbivores, fungal and bacterial attack or virus infection, and a second class that includes abiotic stresses such as drought, extreme temperature, salinity, light etc. Environmental interactions are mediated by elicitors signaling molecules through the transduction pathway.[27]

Recent advances in research on gene regulation have led to the emergence of post-transcriptional gene silencing (PTGS) or epigenetic variation as additional levels of gene regulation.[28] In recent work we have produced a stable PTGS silencing state in transgenic lettuce carrying a *SERK* gene antisense cassette.[29] These lettuce plants exhibited *LsSERK* gene silencing, showed reduced somatic embryogenesis ability and became more susceptible to Sclerotinia attack. Thus, the elimination of *LsSERK* via RNA silencing corroborates the hypothesis that *SERK* is involved in somatic embryogenesis and also in plant defence, since these plants had less ability to form somatic embryos or to resist fungus attack.[29]

Similarly, increased somatic embryogenesis ability was induced by overexpressing *OsSERK1*, controlled by the constitutive CaMV35S promoter, in rice plants.[13] These transgenic rice plants showed an increase resistance to *Magnapothe grisea*.[13] Reinforcing the idea that *SERK* is involved in response to biotic stress, transgenic rice expressing the bacterial flagellin (N1141) gene triggered the activation of innate immune response and increased resistance to *M. grisea*.[30] The *OsBISERK* gene showed upregulation under benzothiadiazole (BTH) treatment, which also leads to an increase in rice resistance to *M. grisea*.[31] It has been shown that BTH induces systemic acquired resistance (SAR) and activates the gene involved in disease resistance.[32] In *Vitis vinifera* differential expression of *SERK* genes was observed concomitantly to some PR proteins upregulated by 2,4-D, a known somatic embryogenesis inducer.[14]

On the other hand, it was demonstrated that the auxin naphthalene acetic acid (NAA) was able to upregulate *SERK* gene in *Medicago trucatula*.[4] In rice some defense signaling molecules, such as SA and JA, induced *SERK* upregulation and a slight induction by ABA.[13] SERK3/BAK1 proteins act on BR signaling and were associated as a component of pathogen-associated molecular pattern (PAMP)-triggered immunity by flagellin elicitation (PTI).[33,34]

Concluding Remarks

Current data collectively lead to the idea that *SERK* may be involved in plant signaling and multiple other functions, and not only in plant development. *SERK* is highly expressed in embryogenic tissues and some undifferentiated cells,[35] preceding and coinciding with early somatic embryogenesis.[36] Plant cell pluripotency may be associated with chromatin folding[37] and the pattern of DNA methylation, which determine plant cell differentiation.[38,39] Additional investigation of *SERK* gene methylation patterns during plant development and under biotic and abiotic stress response would increase knowledge on its role in plant environmental response.

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