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编号	内容	备注
1	Genome-wide identification and expression analysis of calmodulin-like (CML) genes in Chinese cabbage (<i>Brassica rapa</i> L. ssp. <i>pekinensis</i>)	论文 1
2	论文 1 检索报告	-
3	Transcriptomic analysis identifies critical signaling components involved in the self-incompatibility response in Chinese cabbage	论文 2
4	论文 2 检索报告	-
5	大白菜自交不亲和类钙调蛋白 BrCML 关键基因筛选与功能鉴定	国家自然科学基金-青年项目

RESEARCH

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Genome-wide identification and expression analysis of *calmodulin-like* (CML) genes in Chinese cabbage (*Brassica rapa* L. ssp. *pekinensis*)

Shanshan Nie, Minjuan Zhang and Lugang Zhang*

Abstract

Background: Calmodulin-like (CML) proteins are a primary family of plant-specific Ca^{2+} sensors that specifically bind to Ca^{2+} and deliver a Ca^{2+} signal. CML proteins have been identified and characterized in many plant species, such as the model plant *Arabidopsis* and rice. Based on considerable evidence, the roles of CML proteins are crucial in plant growth and development and in the response to various external stimuli. Nevertheless, the characterization and expression profiling of CML genes in Chinese cabbage (*Brassica rapa* L. ssp. *pekinensis*) remain limited.

Results: In this study, a genome-wide search and comprehensive analysis were performed, and a total of 79 *BrCML* genes were identified in Chinese cabbage. Gene structure analysis revealed that these *BrCML* genes contained two to four conserved EF-hand motifs. Phylogenetic analysis showed that CML homologs between Chinese cabbage and *Arabidopsis* shared close relationships. The identified *BrCML* genes were located across ten chromosomes and three different subgenomes of Chinese cabbage. Moreover, 126 pairs of orthologous CML genes were found among Chinese cabbage, *Arabidopsis* and *Brassica oleracea*. Expression analysis revealed that the expression of some *BrCML* genes was tissue-specific and that of some was susceptible to temperature stress. A putative interaction network of *BrCML* proteins was proposed, which suggested that *BrCML2*, *BrCML6*, *BrCML15* and *BrCML25* were co-expressed and might play roles in flower development and other relevant biological processes of Chinese cabbage.

Conclusions: The results of this study increased the understanding and characterization of *BrCML* genes in Chinese cabbage, and will be a rich resource for further studies to investigate *BrCML* protein function in various developmental processes of Chinese cabbage.

Keywords: CML gene, Chinese cabbage, Expression profiling, Stress response, Interaction network

Background

Calcium (Ca^{2+}), an essential secondary messenger in eukaryotic cells, plays major roles in many aspects of plant growth and development [1–3]. A variety of internal stimuli and external abiotic and biotic stresses, including temperature, light, drought, salinity, plant hormones and disease [1, 4], can induce variation in the level of cytoplasmic free Ca^{2+} and affect the movements of Ca^{2+} in plant cells. The stress signalling is sensed by

unique Ca^{2+} sensors or Ca^{2+} -binding proteins [3, 5, 6]. Ca^{2+} -binding proteins binding to Ca^{2+} trigger their conformational changes, and the modulation of activity subsequently regulates downstream targets, thereby transmitting the Ca^{2+} signals [3, 7, 8].

Ca^{2+} -binding proteins, which contain the conserved EF-hand motif of a characteristic helix-loop-helix motif, have been identified extensively in plant genomes [7–9]. Calmodulin-like proteins (CMLs) are a large subgroup of plant-specific Ca^{2+} sensors and are the key components in Ca^{2+} signal transduction [7, 8]. CMLs are restricted to plants and differ from Calmodulin (CaM), which is the highly evolutionarily

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检索报告

根据委托人聂姗姗委托,通过网络检索,聂姗姗发表的 1 篇论文被《科学引文索引》扩展版 (SCI-Expanded) 数据库收录。数据库检索结果如下:

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Transcriptomic analysis identifies critical signaling components involved in the self-incompatibility response in Chinese cabbage

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ABSTRACT

Self-incompatibility (SI) is a genetic mechanism in plants to prevent inbreeding, promote outcrossing and thereby increase genetic diversity. Although current studies have well revealed the pathway of SI recognition specificity underlying interaction of female and male determinants in *Brassica*, the inhibition mechanism of incompatible pollen germination and tube growth is still deficient. In this study, histological analysis showed that the pollen germination and tube growth were obviously suppressed after self-pollination in self-incompatible Chinese cabbage. Furthermore, RNA-seq and gene expression analysis were performed to identify the differentially expressed genes (DEGs) involved in SI response of Chinese cabbage. A total of 59 DEGs belonging to known SI signaling factors and Ca^{2+} -binding proteins were identified in Chinese cabbage after incompatible self-pollination. QRT-PCR analysis found that several genes were significantly differentially expressed during SI response. Chromosomal localization and potential duplicated genes were also predicted. Additionally, spatial-temporal expression profiling revealed that 15 DEGs were specifically expressed in the floral organ, some of which exhibited higher expressions in the anther and style. These findings will provide insights into the functional exploration of SI signaling factors in Chinese cabbage, and promote the further understanding of SI signaling networks in *Brassica*.

1. Introduction

Self-incompatibility (SI) is one of the important genetic mechanism and widely distributed in flowering plants to promote outcrossing and maintain genetic diversity by preventing self-fertilization (Nasrallah, 2000; Takayama and Isogai, 2005). The SI response is based on the ability of the pistil to discriminate between self-pollen and non-self-pollen (Takayama and Isogai, 2005; Ivanov et al., 2010). According to the incompatibility phenotype feature of plant that is determined by either haploid genotype or diploid genotype, SI can be classified into two major types (Tantikanjana et al., 2010; Iwano and Takayama, 2012): gametophytic SI (GSI) and sporophytic SI (SSI). Brassicaceae plants belong to the SSI system which is genetically controlled by a single multiallelic S-locus, the highly polymorphic S alleles called S-haplotype within species (Tantikanjana et al., 2010). When the stigma recognizes the pollen that carrying the identical S-haplotype, the SSI reaction occurs rapidly in the stigma papilla cells and the plant stigma immediately exhibits the inhibition of pollen hydration, pollen

germination or pollen tube elongation (Nasrallah, 2000; Iwano et al., 2007).

Molecular and genetic studies of SSI in the Brassicaceae have identified three important S-locus genes, among which the stigma-specific S-locus receptor kinase (*SRK*) and pollen-specific S-locus cysteine-rich protein (*SCR*) genes are considered the female and male determinants, respectively (Takasaki et al., 2000; Shiba et al., 2001). Although another S-locus glycoprotein gene (*SLG*) is not the key SI determinant, *SLG* is tightly linked with *SRK* and *SCR* and seems to enhance the recognition reaction of *SRK* (Takayama et al., 2001; Tantikanjana et al., 2010). Increasing evidences reveal the molecular mechanisms involved in SSI reaction. The specific recognition of *SRK-SCR* after self-pollination causes the autophosphorylation of *SRK* (Ivanov et al., 2010; Tantikanjana et al., 2010), and meanwhile M-locus protein kinase (*MLPK*) interacts with *SRK* to generate a protein complex triggering the downstream signal transduction (Ivanov et al., 2010). Then, arm-repeat containing 1 (*ARC1*) binds to the activated *SRK* and is phosphorylated, which will promote the degradation of a negative

Abbreviations: SI, self-incompatibility; RNA-seq, RNA sequencing; qRT-PCR, quantitative real-time PCR; *SRK*, S-locus receptor kinase; *SCR*, S-locus cysteine-rich protein; *SLG*, S-locus glycoprotein gene; *CaM*, calmodulin; *CML*, calmodulin-like protein; *CPK*, calcium-dependent protein kinase; *CBL*, calcineurin B-like protein

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