Differential expressions of citrus CAMTAs during fruit development and responses to abiotic stresses


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Abstract

Calmodulin-binding transcription activators (CAMTAs) play important roles in plant growth, developmental processes, and responses to abiotic and biotic factors. Recently, five CAMTA members were identified in *Citrus sinensis*, however, very little is known about the molecular regulation of these CAMTAs in citrus during fruit development and under abiotic stresses. In this study, the different expression profiles of *CsCAMTA* genes were found in different tissues and different fruit developmental stages. The *CsCAMTA* genes also displayed distinct expression patterns after heat, cold, salt, and drought stresses. Furthermore, the expressions of *CsCAMTA* genes were significantly induced by treatments with salicylic acid, methyl jasmonate, or abscisic acid. The green fluorescent protein gene fused with *CsCAMTA* was specifically expressed in the nucleus of *Nicotiana benthamiana* cells. Additionally, CsCAMTA proteins can activate or suppress DNA transcription in yeast. These findings provide helpful information for further studies of stress signals in citrus.

Additional key words: abscisic acid, *Citrus sinensis*, cold, drought, heat, jasmonic acid, *Nicotiana benthamiana*, salicylic acid, salinity, yeast.

Introduction

Calcium is a ubiquitous cellular regulator involved in a wide range of physiological processes and in response to both biotic (pathogens and insect feeding) and abiotic stresses (low temperature, salt, and drought) (Liu et al. 2015, Gilroy et al. 2016, Cao et al. 2017, Wei et al. 2017). In plant cells, calcium is perceived by the EF-hand domain containing protein families, including calmodulin (CaM)/CaM-like proteins, calcium dependent protein kinase (CDPK), and calcineurin B-like proteins (CBL; Tsuda and Somssich 2015, Ranty et al. 2016, Mohanta et al. 2017, Xiao et al. 2017). Among these proteins, CaM is a well characterized Ca$^{2+}$-binding protein, and it functions as a modulator in metabolism, ion transport, transcriptional regulation, protein phosphorylation, and other critical functions. Calmodulin modulates the activity of a certain CaM-binding proteins, which after binding to Ca$^{2+}$, generate physiological responses to various stimuli (Leng et al. 2015). To date, over 90 transcription factors have been identified as CaM-binding proteins including calmodulin-binding transcription activators (CAMTAs, also known as signal regulators) (Fromm and Finkler 2015, Yang et al. 2015).

The CAMTAs are well characterized by a CG-1 DNA-binding domain that binds to CCGG or CGTG core motifs at the N terminus and are found in all multicellular eukaryotes (Bouché et al. 2002). Apart from the CG-1 DNA-binding domain, the structural analysis also shows that CAMTA proteins contain other conserved regions arranged in the same colinear order such as a TIG domain (involved in a nonspecific contact with DNA and in the dimerization of transcription factors), two ankyrin (ANK)
DISTRIBUTION OF CITRUS CAMTA genes and their roles in stress responses

Materials and methods

Domain analyses of CsCAMTA proteins: Protein sequences of CsCAMTA were downloaded from the Phytozone (http://www.phytozone.net) and the Citrus Genome databases (https://www.citrusgenomedb.org). Multiple sequence alignments of the full-length CsCAMTA proteins were conducted using the Clustal X program and were viewed by GeneDoc (http://www.nrbsc.org/gfx/genedoc/). Domain analyses of CsCAMTA proteins were predicted using the Pfam (http://pfam.sanger.ac.uk/) and the Motif Scan (http://myhits.isb-sib.ch/cgi-bin/motif_scan) programs.

Plants and treatments: Citrus sinensis Osbeck cv. Gannanzao was grafted on trifoliate orange and grown in plastic pots containing a mixture of sand, soil, and plant ash (1:1:1, v/v/v) under fluorescent tubes (an irradiance of 200 µmol m⁻² s⁻¹), a 14-h photoperiod, a temperature of 22 ± 2 °C, and a relative humidity of 65 %. For tissue and organ-specific expressions of CsCAMTA genes, mature leaves, stems, and lateral roots were collected from seedlings approximately two months after grafting. Flowers at full bloom and fruits at 110, 140, 160, 180, and 200 d after full blossom (DAFB) were collected from 4-year-old citrus trees grown in a glasshouse. Tissue material was frozen in liquid nitrogen and stored at -80 °C until use.

The citrus seedlings two-month-old after grafting were subjected to various treatments. For drought and salinity stresses, seedlings were transferred from hydroponic cultivation to a layered filter for rapid dehydration or kept in a liquid medium with 200 mM NaCl, respectively. For cold or heat treatment, culture tubes were transferred to incubators maintained at 4 ± 1 °C or 42 ± 1 °C for 8, 24, and 48 h, respectively. Citrus seedlings kept at 28 ± 1 °C were used as a negative control. For hormone treatments, leaves were sprayed with 100 mM SA, 100 µM MeJA, or 100 µM ABA solutions containing 0.1 % (v/v) ethanol and 0.02 % (v/v) Tween-20 and kept under the normal growth conditions. Plants that were sprayed with a solution containing only 0.1 % ethanol and 0.02 % Tween-20 were used as a negative control. All leaf samples harvested at indicated times were stored at -80 °C until future use.

Extraction of RNA and cloning CsCAMTA genes: Total RNA was extracted from treated and control samples using a TRIZOL reagent (Invitrogen, Shanghai, China) and treated with RNase-free DNase I (TaKaRa, Dalian, China). Approximately 1 µg of the total RNA was used to synthesize first-strand cDNA using a Superscript III RT Reagent kit (Invitrogen, Shanghai, China) according to the manufacturer’s instructions. The full open reading frame of CsCAMTA genes was amplified based on the predicted sequence using special primers listed in Table 1 Suppl. The amplified cDNA fragments were cloned and sequenced.

Reverse transcription quantitative PCR (RT-qPCR)
was used to test the expression patterns of CsCAMTAs. The RT-PCR reactions were conducted in a total volume of 25 mm₃ containing 1 μg of cDNA, 12.5 mm₃ of SYBR Green Master Mix (TaKaRa) and specific primers (3 μM). The RT-qPCR was performed on a 96-well plate (BIORAD CFX96 q-PCR system, Hercules, CA, USA) under following conditions: an initial denaturation at 95 °C for 10 min followed by 40 cycles at 95 °C for 15 s and at 57 °C for 60 s. Quantification analysis was conducted using by the CFX Manager software. Three independent biological replicates were used for analyses, and the relative expressions were calculated using the 2⁻ΔΔCT method. Primers used are listed in Table 1 Suppl. Citrus CsActin (Gene ID: 102577980) was used as an internal control with primers CsActin-F and CsActin-R (Xie et al. 2014), and the relative expressions of the target genes were shown as a fold of the expression of the actin gene (Table 1 Suppl.).

Subcellular localization: The coding sequences of CsCAMTA genes were amplified by PCR with specific primers (Table 1 Suppl.). The PCR products were digested with XbaI and SamI restriction enzymes and inserted into the corresponding XbaI/SamI site of a vector pFGC-Egfp to obtain pFGC-Egfp:CsCAMTA1-5. The sequence-verified constructions and pFGC-Egfp were transformed into Agrobacterium tumefaciens GV3101. Four-week-old Nicotiana benthamiana Domin plants were inoculated with the transformed Agrobacterium cultures and then grown at 25 °C for 48 h. Fluorescence signals were excited at 488 nm and detected using a 500 - 530 nm emission filter performed with a confocal laser scanning microscope (Zeiss LSM 510 META, Oberkochen, Germany).

Transcription activation assay in yeast: The full open reading frame sequence of CsCAMTA genes was amplified using the primers listed in Table 1 Suppl. The amplicons were cut with restriction enzymes and inserted into the appropriate site of a pBD-GAL4Cam vector, resulting in pBD-CsCAMTAs. The recombinant plasmids and the pBD empty vector (negative control) were transformed into yeast strain AH109 and cultivated on SD/-Trp and SD/-Trp/-His media followed by supplementation with β-D-galactopyranoside (X-α-galactose) at 28 °C for 3 d.

Statistical analysis: The SAS statistical software package v. 9.4 was used for statistical analysis. Experiments were repeated three times, and three replicates were included in each experiment. Data obtained from the three independent experiments were analyzed by the Dunnett t-tests, taking $P < 0.05$ as a significant difference.

Results

The Motif Scan program was used to complete domain analyses of CsCAMTA proteins. As predicted, all CsCAMTA proteins contained one CG-1 DNA bind domain in the N-terminus, two ankyrin repeats, two or three IQ motifs, and one Ca²⁺ dependent calmodulin binding domain (Cam-binding domain) in the C-terminus (Fig. 1 Suppl.). Except for CsCAMTA5, all other CsCAMTA proteins contained one TIG domain. Additionally, one or two nuclear localization signals (NLS) domains were identified in all CsCAMTA proteins, consistent with their function in the nucleus (Wang et al. 2015). Analyses of the amino acid sequences indicate that all five CsCAMTAs were genuine homologs belonging to the CAMTA transcription factor family.

To determine the physiological functions of the different members of citrus CAMTA genes, we analyzed their tissue-specific expression patterns in different tissues, including roots, stem, leaves, flowers, and fruits by RT-qPCR. The results show that the five CsCAMTA genes were detectable in all the tested tissues but exhibited different expression patterns (Fig. 1). The CsCAMTA1 and CsCAMTA4 reached high expressions in leaves and
flowers but low in roots. The expression of \textit{CsCAMTA3} in stems was higher than in other tissues. However, \textit{CsCAMTA2} showed low expressions in stems, flowers, fruit peel, and fruit pulp. The \textit{CsCAMTA5} was highly expressed in stems and leaves, but the expressions were relatively low in other organs, particularly in roots. Generally, all the \textit{CsCAMTA} genes had relatively high expressions in stems and leaves and low in roots. The results suggest that \textit{CsCAMTA} genes played various roles in different tissues.

To study the potential role of \textit{CsCAMTA} genes in fruit development and ripening, we evaluated their expression patterns during five different developmental and ripening stages. Four \textit{CsCAMTA} genes (\textit{CsCAMTA1}, 2, 4, and 5) in peel and all \textit{CsCAMTA} genes in pulp were down-regulated at 200 DAFB compared with their expressions at 110 DAFB. Notably, \textit{CsCAMTA3} expression in peel was constant in all the five tested stages (Fig. 2). The \textit{CsCAMTA1} and \textit{CsCAMTA5} expressions in peel increased from 110 to 160 DAFB and then decreased from 180 to 200 DAFB, whereas the expression of \textit{CsCAMTA2} in peel firstly decreased but then increased at 160 DAFB and thereafter decreased gradually (Fig. 2). The expressions of \textit{CsCAMTA2}, 3, 4, and 5 in pulp were relative high at 110 and 140 DAFB but decreased from 160 to 200 DAFB. The expression of \textit{CsCAMTA1} from 140 to 180 DAFB in the pulp was significantly lower than in peel as well as those of \textit{CsCAMTA3} from 160 to 200 DAFB and \textit{CsCAMTA4} at 140 and 160 DAFB (data not shown). In general, the expressions of \textit{CsCAMTA}s were lower at the later stages (160 to 200 DAFB) than in the early stages of fruit development and ripening in pulp, whereas expressions of four \textit{CsCAMTA} genes were down-regulated at 180 and 200 DAFB in peel compared with 110 DAFB.

![Fig. 2. Expression patterns of calmodulin-binding transcription activator (\textit{CAMTA}) genes in fruit peel (A) and pulp (B) during different fruit development and ripening stages. C - Samples used in expression assay of \textit{CAMTA} genes. S1 - 110 days after full blossom (DAFB), S2 - 140 DAFB, S3 - 160 DAFB, S4 - 180 DAFB, and S5 - 200 DAFB. A relative expression to the endogenous control \textit{CsActin}. Means ± SDs, \(n=3\); * - significant differences between treatments at \(P \leq 0.05\).](image)

Drought, salinity and extreme temperature are the primary environmental stresses affecting plant growth/development and ultimately crop yield. To investigate the molecular functions of \textit{CsCAMTA} genes in response to abiotic stress, we analyzed the expressions of the five \textit{CsCAMTA} genes in leaves of citrus seedlings under different stresses including heat (42 °C), cold (4 °C), drought (placing on a lab bench without water supply) and salt (drenching with 200 mM NaCl).

We first analyzed the expressions of the \textit{CsCAMTA} genes in leaves of citrus seedlings after heat and cold treatments. In the heat treatment group, the expressions of four of the \textit{CsCAMTA} genes (\textit{CsCAMTA1}, 2, 4, and 5) increased and displayed the highest expression (1.9- to 3.4-fold higher than in the control) at 24 h after heat treatment (Fig. 3). However, the expression level of \textit{CsCAMTA3} did not show significant changes under the heat stress conditions. In the cold treatment assay, the expressions of all the five \textit{CsCAMTA} genes was up-regulated and increased at 24 h, ranging from a 1.8- to 4.1-fold increase compared with control plants. Notably, \textit{CsCAMTA2} was strongly induced at all time-points following treatment.

In response to drought stress, the expressions of the five
CsCAMTA genes were significantly affected. The expressions of three of the CsCAMTA genes (CsCAMTA3, 4, and 5) increased rapidly after drought treatment, resulting in 3.3- to 6.5-fold increase compared with the control. By contrast, CsCAMTA1 and CsCAMTA2 were down-regulated at all the tested time points (Fig. 4), the expression of CsCAMTA1 was down-regulated significantly by >7-fold at 24 h after drought treatment. In the salt treatment group, three of the CsCAMTA genes (CsCAMTA1, 3, and 5) were affected after NaCl treatment (Fig. 4). The expression of CsCAMTA1 gradually decreased and peaked at 24 h after salt treatment,
resulting in a 3.5-fold decrease compared with the control, whereas the expressions of CsCAMTA3 and CsCAMTA5 decreased significantly only at 24 h after treatment. The other two CsCAMTA genes showed no apparent changes in expressions under the salt stress conditions.

To examine the effects of SA, JA, and ABA on CsCAMTA expressions, we analyzed the expressions of these genes after the plants were sprayed with 100 mM SA, 100 µM MeJA, or 100 µM ABA (Fig. 5). The JA significantly increased the expressions of CsCAMTA1 and 5 at 24 and 48 h after spraying, leading to a 1.6- to 2.2-fold increase in expressions compared with the control. However, no significant change occurred in the expressions of the other three CsCAMTA genes ($P < 0.05$). The expressions of CsCAMTA1, 4, and 5 were induced by SA treatment with an increase of 1.6-, 4.5-, and 1.6-fold at 24 h after treatment, respectively. Among these three genes, the expression of CsCAMTA4 exhibited a continuous increase and showed a significant up-regulation by 10.1-fold at 48 h after SA treatment. Furthermore, for all the CsCAMTA genes, the expressions increased from 1.5- to 2.8-fold at 24 and 48 h in ABA-treated plants (Fig. 5). The CsCAMTA genes responded to phytohormones by differential expression patterns, which might indicate biological functions in relation with stress hormone-mediated signalling.

![Expression of calmodulin-binding transcription activator (CsCAMTA) genes in response to application of phytohormones.](image)

To investigate the subcellular localization of CsCAMTA proteins, the coding sequences of CsCAMTA genes were amplified and fused to the N-terminal of green fluorescent protein (GFP) under control of the CaMV 35S promoter, and then transiently expressed in N. benthamiana leaves. Subcellular localization of GFP in N. benthamiana leaves was examined by confocal microscopy. The results show that CsCAMTA-GFPs were exclusively localized to the nucleus, whereas the GFP alone was detected in both the nucleus and the cytoplasm (Fig. 6). These results demonstrate that CsCAMTA proteins were nuclear-targeted proteins.

Most transcription factors, such as *Oryza sativa* OsERF3, act as activators that positively regulate the transcriptions of their target genes (Lu *et al.* 2011). The five CsCAMTA genes were transformed into yeast cells. As shown in Fig. 7, yeast cells, harboring plasmids pBD-CsCAMTA and a pBD empty vector (as a negative control) grew normally on an SD/-Trp medium. However, the pBD-CsCAMTAs-containing yeast cells grew well also on an SD/-His/-Trp medium and produced a blue pigment after supplementation with x-α-galactose, excluding transformants containing the pBD empty vector (Fig. 7). These results suggest that CsCAMTA proteins functioned as transcriptional activators.

**Discussion**

The calmodulin-binding transcription activator is a universal family of multifunctional transcription factors, which has been identified in various eukaryote species. Comprehensive gene expression analysis of CAMTA

![Expression diagram](image)
family genes revealed that CAMTAs have distinct expression patterns in various tissues of several plant species (Yang and Poovaiah 2002, Yang et al. 2012, 2013, Wang et al. 2015, Leng et al. 2015, Yue et al. 2015, Rahman et al. 2016a). Some members of the CAMTA family exhibit organ-specific expression patterns or are not expressed in some tissues, e.g., AtCAMTA1 is specifically expressed in pollen (Mitsuda et al. 2003). Expressions of SISR3L and SISR4 are only detected in tomato fruit (Yang et al. 2012), whereas BnCAMTA3A2, A3C2 are nearly undetectable in all tested tissues of Brassica napus (Rahman et al. 2016a). By contrast, some members of CAMTAs have high expressions in special organs such as FaCAMTA3 and FaCAMTA4 in young berries of strawberry (Leng et al. 2015). The expression patterns of CAMTA genes vary greatly among different plant species. In this study, the CsCAMTA genes were expressed in all tested tissues, but they exhibited differential expression patterns (Fig. 1) suggesting that they play different roles in different tissues.

Fig. 6. Localization of calmodulin-binding transcription activator (CsCAMTA) proteins to the nucleus. Nicotiana benthamiana leaves were transiently transformed by agroinfiltration with constructs harboring pFGC-Egfp:CsCAMTAs or pFGC-Egfp. Fluorescence of target proteins was observed with confocal microscopy after 48 h.

The CAMTAs are likely found exclusively in multicellular organisms suggesting their involvement in cell-cell communication and developmental processes (Bouché et al. 2002). In mammals, CAMTAs are involved in controlling growth and cell proliferation (Song et al. 2006). However, no direct evidence has been provided for the role of the plant CAMTA family in these processes. Yang et al. (2012) reported that SISR2 is scarcely expressed at two critical developmental stages of tomato fruit, whereas SISR3L and SISR4 are expressed in fruit tissues exclusively. Moreover, SISR2L expression is dramatically altered in a ripening mutant rin compared with a wild type fruit. In Gossypium hirsutum, GhCAMTA2A.2 and GhCAMTA7A have high expressions in initiation and secondary cell wall synthesis stages, respectively. Additionally, several genes encoding, e.g., fatty acid desaturase, fatty acid desaturase linked oxidase, kinesin, protein kinase, auxin/indole-3-acetic acid (AUX/IAA) protein, ABC transporter-like, DNA-binding WRKY, MYB, homeodomain, zinc finger, leucine-rich repeat, and cellulose synthase protein families, which have imperative roles in cotton fiber development, are positively or negatively co-expressed with GhCAMTA2A.2 and GhCAMTA7A (Pant et al. 2018). In the present study, the expressions of all the five CsCAMTAs were lower in mature fruit peel and pulp than in early fruit development.
and ripening stages except the expression of CsCAMTA1 (Fig. 2). Collectively, these data indicate that citrus CAMTA genes may be involved in regulating citrus fruit development and ripening processes.

Drought, salt, low temperature, and heat stress can result in water deficit in plant tissues (Aroca et al. 2007, Wahid and Close 2007). The CAMTA gene expressions can respond to these abiotic stresses in many species (Pandey et al. 2013). In Arabidopsis, CAMTA1 shows an increased sensitivity to drought with a reduced survivability (Pandey et al. 2013). Silencing SIR1L in tomato leads to a decrease in drought stress tolerance, acceleration of leaf water loss, reduction of root biomass, and attenuation of expressions of drought stress responsive genes (Li et al. 2014). The AtSRI1/CAMTA3 demonstrates the role of CAMTA in salinity; a mutant shows more tolerance to salt stress because of the repressed expression of salt-responsive genes (Prasad et al. 2016). Many stress-responsive genes encode proteins to protect cells from a water stress and regulate gene expression for signal transduction in water stress response. The AtCAMTA1 positively induces the expression of transcription factors (such as AP2, bZIP, MYB, WRKY, and GRAS) most likely by binding to CGCG and CGTG boxes in the promoter region of these target genes. The regulated expressions of these transcription factors restrict the expression of various genes and control regulatory proteins for maintaining the homeostasis of plants channelled through various adaptive and stress responsive genes (Pandey et al. 2013). The AtCAMTA3 is a positive regulator of C-repeat-binding factor 2 expression, and double camtai/3 mutant plants are impaired in freeze tolerance, establishing a role for CAMTAs in the regulation of plant responses to cold (Doherty et al. 2009). The expressions of CAMTAs response to both environmental stresses (drought, salt, low temperature, and heat stresses) and ABA, by inducing a series of signalling cascades (Yue et al. 2015). The results presented in this study show that members of the CsCAMTA family were responsive to various environmental stresses (Fig. 3, 4, and 5). For example, the expression of CsCAMTA5 was induced under all the tested stresses and the ABA treatment. However, the expressions of CsCAMTA1 and CsCAMTA3 were downregulated by the drought and the salt stresses but upregulated by ABA. The expression profiles of CsCAMTA5 and CsCAMTA3 were similar to the results observed in the At/GmCAMTA family and ZmCAMTA4a/7b, respectively (Yang and Poovaiah 2002, Wang et al. 2015, Yue et al. 2015). The expressions of CAMTAs in response to abiotic stresses and ABA indicate their important role in the signal transduction of plant water deficit by both ABA-dependent and ABA-independent pathways (Yamaguchi-Shinozaki and Shinozaki 2006). Furthermore, we observed the induction or the suppression of CsCAMTA family genes in response to tested stresses suggesting a crosstalk between different stress signalling pathways.

In addition, defence against different biotic stresses is specified by antagonism between the SA and JA/ET signalling pathways (Atkinson and Urwin 2012, Laluk et al. 2012). The ET and SA are often involved in CAMTA regulations of pathogenesis-related protein expression, leading to plant defence against pathogens (Dempsey et al. 2011). The AtSRI1/CAMTA3, which are significantly up-regulated in response to MeJA, negatively regulates plant...
defense against pathogens, insect attack, and wounded through JA- and SA-mediated pathways (Laluk et al. 2012, Qiu et al. 2012). By contrast, SA, MeJA, ET, and pathogen infection lead to up-regulation of SISR1 in tomato fruit, whereas SISR3L is induced by SA, ET, and pathogen infection (Yang et al. 2012, 2013). Silencing SISR1 and SISR3L in tomato confers an increased resistance to B. cinerea and P. syringae pv. tomato DC3000 through modulating the SA- and ET-signalling pathways (Li et al. 2014). In our study, SA and JA significantly induced the expressions of CAMTA1, 4, and 5. These findings are similar to those of previous studies in Arabidopsis and tomato (Yang and Poovaiah 2002, Yang et al. 2013) suggesting a potential role of CAMTAs in regulation of biotic stress.

Proteins targeted to the nucleus contain amino acid targeting sequences called nuclear localization signal NLS (Liu et al. 1999, Lange et al. 2007). The AtCAMTA1, 3, and 5 contain an NLS region, and they are located in the nucleus (Bouché et al. 2002, Yang and Poovaiah 2002, Mitsuda et al. 2003). Almost all the CAMTAs contain a NLS region in the CG-1 domain. We also found a NLS region in the CG-1 domain of CsCAMTAs (Fig. 1 Suppl.). In the present study, we examined the subcellular localization of CsCAMTAs, and the results indicate that the members of this family were nucleus-targeted proteins (Fig. 6), which is consistent with that of AtCAMTA1, 3, and 5. Additionally, transcription activation domains have been mapped in Arabidopsis AtCAMTA1 and human HsCAMTA2, and both transcription activation domains map to a region between the CG-1 and TIG domains (Finkler et al. 2007). The CAMTA participates in transcriptional regulation of downstream genes by recognizing and binding to a specific cis-element (G/A/C)CGCG(C/G/T), and thereby leading to physiological responses (Yang and Poovaiah 2002, Galon et al. 2008, Leng et al. 2015, Shen et al. 2015). The AtSRI1/CAMTA3 bind to the core vCGCGb motif of several genes including EDS1 (enhanced disease susceptibility1) and NDR1 (non-race-specific disease resistance1) and the EIN3 (ethylene insensitive3) promoter region in vivo (Doherty et al. 2009, Du et al. 2009, Nie et al. 2012). In our study, all the five CAMTA genes of citrus also acted as transcriptional activators (Fig. 7). This result correlates with a fact that tomato SISR1/3L, Arabidopsis AtCAMTA1/AtCAMTA5, and human HsCAMTA1/2 also function as activators (Bouché et al. 2002, Mitsuda et al. 2003, Li et al. 2014).

References

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