

Biological roles of NAC transcription factors in the regulation of biotic and abiotic stress responses in solanaceous crops

Solomon Tweneboah · Sang-Keun Oh

Received: 6 February 2017 / Revised: 19 March 2017 / Accepted: 20 March 2017
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Abstract Evolutionary studies conducted on NAC (NAM, ATAF1&2, and CUC2) genes for all major groups of land plants, indicate the presence of the NAC subfamilies, even in the early land plants. The varied roles played by NAC proteins in plant growth and development range from the formation of shoot apical meristem, floral organ development, reproduction, lateral shoot development, and defense responses to biotic and abiotic stresses. Considering the value and importance of solanaceous crops, the study of NAC proteins in these plants needs to be intensified. This will help to identify and functionally characterize their promoters, which will subsequently aid in engineering plants with improved performance under stressful conditions. In this review, the functionally characterized NAC transcription factors specific to tomato, potato, tobacco, chili pepper and eggplant (aubergine) are summarized, clearly indicating their biological functions in the defense mechanism of the plants, against biotic and abiotic stresses.

Keywords NAC transcription factors, Solanaceous crops, Biotic and abiotic stresses

Introduction

Living things encounter lots of biotic and abiotic stresses in their environment which impact negatively on their growth, development and functioning. When animals encounter such stresses in one environment they easily migrate to new environments where conditions are more conducive for their continued survival and functioning. Plants, on the contrary, are sessile; thus, they are not able to move away from suboptimal conditions in their environment. Plants need to

endure all the effects of harsh environmental and biotic stresses they are faced with. To prevent extinction of their species, plants have evolved a network of robust and densely interconnected systems for rapid signal perception, reaction and adaptation to suboptimal environmental conditions (Smékalová et al. 2013). In these physiological and biochemical network systems, plants utilize a number of hormones, secondary messengers, and enzymes which activate various genes to confer stress tolerance to the plants. Among the numerous stress tolerance and defense response genes in the body of plants are the families of transcription factors. Transcription factors are grouped into many different classes based on the domains that bind to specific DNA sequences in the regulatory regions of downstream target genes (Kikuchi et al. 2000). The role of transcription factors in activating and suppressing gene expression is largely modulated through gene promoters and their associated *cis*-acting elements (Zou et al. 2011; Hernandez-Garcia and Finer 2014). The gene promoters containing multiple *cis*-acting elements are located upstream of the gene coding regions; the *cis*-acting elements serving as specific binding sites for proteins involved in transcription initiation and regulation (Hernandez-Garcia and Finer 2014). Contained in the promoter region, near the transcription initiation site, are the core promoter and the promoter-proximal *cis*-acting sequences (Griffiths et al. 2000). TATA-box and *cis*-elements contained in the core promoter are, respectively, the binding sites for TATA-box-Binding Protein (TFIID TBP) – a transcription initiation factor, and RNA polymerase II – the basic transcriptional machinery (Griffiths et al. 2000; Hernandez-Garcia and Finer 2014). The promoter-proximal *cis*-acting sequences bind to proteins that in turn assist in the binding of RNA polymerase II to its promoter (Griffiths et al. 2000). At a considerable distance – about 50 kb upstream or downstream from the promoter that they control, are the distal *cis*-acting sequence containing enhancers and silencers. Enhancers are regulatory sequences that increase

Solomon Tweneboah · Sang-Keun Oh (✉)
(Department of Applied Biology, College of Agriculture & Life Sciences, Chungnam National University, Daejeon, 34134, Republic of Korea)
e-mail: sangkeun@cnu.ac.kr

the rate of transcription while silencers reduce the rate of transcription (Griffiths et al. 2000).

In plants, transcription factors regulate their target genes through binding to the *cis*-acting elements located on the promoters or interacting with other transcription factors thereby inducing or repressing the related gene expression (Ma et al. 2010; 2013). Basically, plant transcription factors are critical regulatory factors in modulating the temporal and spatial expression of the genes involved in defense response (Liu et al. 2014). Among plant transcription factors are the families of AP2/EREBP (APETALA2/Ethylene-Responsive Element Binding Protein), bZIP (Basic Leucine Zipper), zinc finger, NAC (NAM, ATAF1&2, CUC2), MYB (myeloblastosis) (Ulm et al. 2004; Hirota et al. 2007), and WRKY (Rushton et al. 2010). Among these, plant-specific NAC transcription factors constitute one of the largest families of transcription factors in plants (Nuruzzaman et al. 2013; Li et al. 2016) and they are known for their roles in many plant growth and developmental processes as well as abiotic and abiotic stress responses (Nakashima et al. 2012).

NAC gene expression responses are largely related to their promoters and every NAC gene contains at least one *cis*-element type in their promoter sequences (Lv et al. 2016). In their study to identify putative stress-responsive *cis*-elements in the promoter regions of *Brachypodium distachyon* NAC (*BdNAC*) genes, 1 kb upstream promoter sequences of the *BdNAC* genes were examined by You et al. (2015) using PlantCARE database search. In this examination, You et al. (2015) found 101 *BdNAC* genes that contained at least one *cis*-element related to stress or hormone response, with 44 of them having more than 5 *cis*-elements, giving the indication that *BdNAC* genes might be involved in the stress-response or hormones-response processes. Additionally, 135 ABA-responsive elements (ABREs), 107 MeJA-responsiveness elements (CGTCA-motifs), 99 MYB binding sites, 64 TCA-elements (SA-responsiveness) and 51 TC-rich repeats were detected in the promoters of *BdNAC* genes, suggesting that *BdNAC* genes have important roles in the responses to ABA, MeJA, drought, SA and defense responses (You et al. 2015).

Many other recent reports demonstrate that NAC proteins often act as regulators in various stress signaling pathways which may include both biotic and abiotic stimuli in plants (Olsen et al. 2005; Kleinow et al. 2009; Puranik et al. 2012). Effects on plant defense responses under both biotic and abiotic stresses have significantly shown the importance of overexpression or knockdown of specific NAC genes in crops such as tomato, potato, tobacco, chili pepper and

eggplant (aubergine). Therefore, in this review we summarize the recent reports on characterized NAC transcription factors specific to solanaceous crops, clearly showing their functions as defense regulators against various biotic and abiotic stresses.

NAC transcription factors in plants

The NAC transcription factor family is divided into several subfamilies such as the NAM, ATAF, and OsNAC3 (Kikuchi et al. 2000). The name NAC is originally derived from the names of three proteins containing similar DNA-binding domains, and these proteins are *Petunia* NAM, *Arabidopsis* ATAF1&2, and CUC2 (Aida et al. 1997). NAM (no apical meristem) proteins are plant development proteins responsible for shoot apical meristem development (Souer et al. 1996; Sablowski and Meyerowitz, 1998). *ATAF1* and *ATAF2* (*Arabidopsis* transcription activation factor 1&2) genes have the ability to activate the CaMV 35S promoter in yeast (Souer et al. 1996; Kikuchi et al. 2000; Duval et al. 2002). Overexpression of *ATAF1* and *ATAF2* respectively regulates drought tolerance (Wu et al. 2009), and negatively regulates resistance to *F. oxysporum* and also represses pathogenesis-related proteins (Delessert et al. 2005). *CUC2* (cup-shaped cotyledon 2) is an essential gene for shoot meristem initiation as well as the formation and stable positioning of carpel margin meristems (Liu et al. 2014).

The proteins of the NAC gene family contain a highly conserved N-terminal DNA-binding domain and a variable C-terminal domain (Olsen et al. 2005, Fang et al. 2008) (Fig. 1). The N-terminal region, which is involved in DNA binding and formation of homodimers or heterodimers with other NAC domain proteins (Olsen et al. 2005; Cenci et al. 2014), consists of approximately 150–160 amino acids with five subdomains A–E (Olsen et al. 2005; Nuruzzaman et al. 2013). Each subdomain is distinguishable by blocks of heterogeneous amino acids or gaps (Kikuchi et al. 2000). Subdomains C and D, rich in basic amino acids, contain putative nuclear localization signals (Kikuchi et al. 2000; Duval et al. 2002). Subdomains D and E contain a 60 amino acid region where the DNA-binding domain is located (Duval et al. 2002). The C-terminal region, which is highly diversified in length and sequence (He et al. 2005), is implicated in transcriptional activation or repression activity (Puranik et al. 2012; Ma et al. 2013; Cenci et al. 2014). Nuruzzaman et al. (2013) explained that the C-terminal region is large and possesses protein-binding activity.

According to Zhu et al. (2012), evolutionary studies conducted on NAC genes for all major groups of land

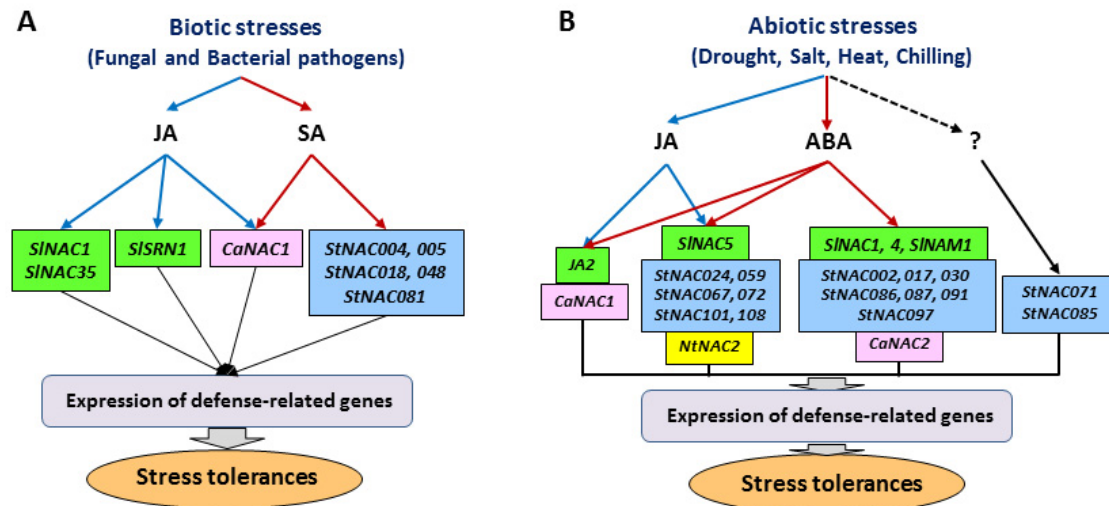


Fig. 2 A model showing the role of specific NAC transcription factors in defense responses during biotic and abiotic stress conditions. (A) During pathogen attack, NAC transcription factors SINAC1, SINAC35, SmNAC, SISRN1, StNAC004, 005, 018, 048, 081, and CaNAC1 elicit plant defenses through SA or JA (and their cross-talk) signaling pathways. (B) Under abiotic stress conditions, a large number of NAC transcription factors activate the expression of defense-related genes through the JA or ABA signaling pathways. Color keys: tomato (green); pepper (pink); potato (blue); and tobacco (yellow)

termed TNAC genes, which are unique to Solanaceae species. Specific NAC transcription factors have been implicated in the formation of shoot apical meristem, floral organ development, reproduction, lateral shoot development, defense against insect pests and pathogens, regulation of programmed cell death, abiotic stress responses, and responses to hormones (Olsen et al. 2005; Rushton et al. 2008; Hu et al. 2010). Essentially, NAC transcription factors are central components of several plant innate immune systems, basal defense, as well as systemic acquired resistance (Nuruzzaman et al. 2013).

A large set of defense-related genes are activated by NAC genes to elicit multiple immune responses when plants encounter stresses (Nakashima et al. 2012). Under biotic stresses, at least three signaling mediators, specifically, salicylic acid (SA), jasmonic acid (JA) and ethylene are generally harmonized to generate plant defenses (Glazebrook, 2001; Oh et al. 2005), and NAC transcription factors such as SINAC1, SINAC35, SmNAC, SISRN1, StNAC004, 005, 018, 048, 081, and CaNAC1 are involved in complex network of signaling pathways to induce local and systemic disease resistance (Fig. 2A). JA is also induced to mediate responses under certain abiotic stresses such as drought and salinity while abscisic acid (ABA) mediates most responses under abiotic stresses (Fig. 2B) (Nakashima et al. 2012).

Roles of NAC transcription factors in tomato (*Solanum lycopersicum*)

About 101 NAC transcription factors are found in the tomato plant as seen in the Plant Transcription Factor Database (Jin et al. 2014). In the characterization and expression analysis of tomato genes, Song et al. (2015) identified 10 TNAC genes which were expressed in tomato under various forms of abiotic stresses (Table 1). *Solanum lycopersicum* NAC1 (SINAC1), an ATAF subfamily transcription factor, abundantly expresses in the nuclei of root, flower, green fruit as well as seed cells to confer salt stress tolerance to tomato plants during salt stress (Yang et al. 2011). SINAC1 is also accumulated during chilling stress (4°C), heat stress (40°C), osmotic stress and mechanical wounding aiding the plant's tolerance against these stresses (Ma et al. 2013; Liang et al. 2015; Meng et al. 2016). Although *Pseudomonas syringae* pv. *tomato* (*Pst*) DC3000 has evolved mechanisms to suppress PAMP-triggered basal defense, the induction of SINAC1 was not repressed by *Pst* DC3000 resulting in more protein production, triggering protection against *Pst* DC3000 (Huang et al. 2013). In their work, Ma et al. (2013) induced the expression of SINAC1 in tomato plants through the application of abscisic acid (ABA), methyl jasmonate (MeJA), salicylic acid (SA), gibberellin (GA₃), ethylene, methyl viologen and hydrogen peroxide (H₂O₂). Ripening fruits overexpressing SINAC1 displayed yellow/orange color instead of red pigmentation and this was coupled with reduced fruit firmness due to the accumulation of ABA (Ma et al. 2014). Infection of tomato by tomato leaf curl virus (TLCV) also induced SINAC1 expression, however, SINAC1 overexpression corresponded with increased TLCV

Table 1 Functionally characterized NAC transcription factors in tomato

Genes	Sub-family	Stress inducing transcription	Methods	References
SINAC1*	ATAF	Salt stress	Salt stress tolerance	Yang et al. (2011)
		Tomato leaf curl virus (TLCV) infection	Increased TLCV replication	Selth et al. (2005)
		Chilling stress (4°C), Heat stress (40°C), Osmotic stress, Mechanical wounding, Application of ABA, MeJA, SA, GA ₃ , ethylene, methyl viologen and H ₂ O ₂	Chilling stress tolerance, Heat stress tolerance, Fruit ripening, Altered fruit pigmentation and early fruit softening	Ma et al. (2013); Liang et al. (2015); Meng et al. (2016); Ma et al. (2014)
		<i>Pseudomonas</i> infection	Defense against <i>Pseudomonas</i> infection	Huang et al. (2013)
SINAM1	NAM	Chilling stress (4°C), Treatment of PEG, NaCl, ABA, MeJA	Chilling stress tolerance in tomato, increased germination rate and higher photosynthetic rate under chilling stress in tobacco	Yang et al. (2011); Li et al. (2016)
SISRNI	NAM	<i>B. cinerea</i> or Pst DC3000 infection, SA, Jasmonic acid (JA), 1-amino cyclopropane-1-carboxylic acid, Drought stress	Defense against <i>B. cinerea</i> and Pst DC3000	Liu et al. (2014)
SINAC4	NAM	Mechanical wounding, Treatment of NaCl and MeJA, Dehydration, Low temperature (4°C)	Salt and drought tolerance, Fruit ripening and carotenoid accumulation	Zhu et al. (2014b, 2014c)
SINAC3	NAM	Suppressed by salt stress, drought stress and ABA treatment	Young embryo and endosperm development	Han et al. (2012; 2014)
SINAC5–SINAC10		NaCl stress, wounding, dehydration, and high/low temperature. All except SINAC6 are induced by ABA, ACC, GA ₃ , MeJA, and IAA**	SINAC5 improves NaCl stress tolerance	Zhu et al. (2014a)
SINAC35		Drought stress, Salt stress, Bacterial pathogen	Root growth and development, Resistance to bacterial pathogen	Wang et al. (2016)
JA2		ABA	Stomatal closure	Du et al. (2014)
JA2L		JA and coronatine	Stomatal reopening	Du et al. (2014)

* *SINAC*; *Solanum lycopersicum* NAC, ** ACC; 1-aminocyclopropane-1-carboxylic acid, GA₃; Gibberellic acid, IAA; Indole-3-acetic acid

replication (Selth et al. 2005).

SINAM1, SISRNI, SINAC3&4 belong to the NAM subfamily. SINAM1, mostly induced by chilling stress (4°C), treatment of polyethylene glycol (PEG), salt (NaCl), ABA and MeJA, confers chilling stress tolerance to both growing tomato plants as well as germinating seeds (Yang et al. 2011; Li et al. 2016). SISRNI transcription factor defends the plant against *Botrytis cinerea* and *Pst* DC3000 infection (Liu et al. 2014). SINAC3 and SINAC4 encourage embryo development and enhance salt and drought stress tolerance respectively (Han et al. 2012; 2014; Zhu et al. 2014b, 2014c). SINAC5-10 range of transcription factors improve salt stress tolerance of tomato plants (Zhu et al. 2014a). SINAC35 not only encourages root growth and development but also enhances resistance against bacterial pathogens (Wang et al. 2016). According to Du et al. (2014)

JA2 and JA2L transcription factors regulate the opening and closure of stomata preventing excessive plant water loss during water stress conditions.

Roles of NAC transcription factors in potato (*Solanum tuberosum*)

Genome-wide analysis conducted by Singh et al. (2013) identified 110 NAC genes in potato encoding for 136 proteins, including 36 putative TNAC proteins. The potato NAC genes were designated as StNAC followed by numbers 1–110 based on the position of their corresponding genes on chromosomes 1–12 and from top to bottom. NAM domain was present in all the StNAC proteins except for StNAC034, which contained additional tyrosine kinase domain (PF07714) (Singh et al. 2013). The biology of potato NAC genes is

Table 2 Functionally characterized NAC transcription factors in potato

Genes	Sub-family	Stress inducing transcription	Methods	References
<i>StNAC017, 030, 086, 097</i>	NAM	Salt and heat stresses, mannitol treatment	Salt and heat stress tolerance	Singh et al. (2013)
<i>StNAC002, 025, 087, 091</i>	NAM	<i>P. infestans</i> infection, wounding, salt stress, drought stress, salicylic acid, ABA	Salt and drought tolerance	Zu et al. (2014); Singh et al. (2013)
<i>StNAC073</i>	NAM	nd	nd	Singh et al. (2013)
<i>StNAC082</i>	"	nd	nd	Singh et al. (2013)
<i>StNAC024, 059, 067, 072, 108, 101</i>	"	NaCl stress	Salt stress tolerance	Singh et al. (2013)
<i>StNAC053, 072, 080, 101</i>	"	Manitol treatment	nd	Singh et al. (2013)
<i>StNAC071, 085</i>	"	Heat stress	Heat stress tolerance	Singh et al. (2013)
<i>StNAC072, 101</i>	"	ABA	Nd	Singh et al. (2013)
<i>StNAC004, 005, 018, 048, 081</i>	"	<i>P. infestans</i> infection	Resistance to <i>P. infestans</i> infection	Collinge and Boller (2001)
<i>StNAC004, 051</i>	"	Mechanical wounding	nd	Collinge and Boller (2001)
<i>StNAC017, 072, 090, 097, 101, 110</i>	"	BABA treatment ***	nd	Singh et al. (2013)
<i>StNAC007, 090, 094</i>	"	BTH treatment ****	"	Singh et al. (2013)
<i>StNAC005, 090,</i>	"	IAA treatment	"	Singh et al. (2013)
<i>StNAC016, 059, 090,</i>	"	BAP and GA3 treatments	"	Singh et al. (2013)
<i>StNAC090</i>	"	ABA treatment	"	Singh et al. (2013)
<i>StNAC034*, 075</i>	"	nd	"	

* *StNAC*; *Solanum tuberosum* NAC ** nd; not determined, *** BABA treatment; DL- β -amino-n-butyric acid (BABA, 2 mg/ml), **** BTH treatment; acibenzolar-s-methyl (BTH, 100 μ g/ml)

poorly understood but informative reports have been published recently. According to Zu et al. (2014) and Singh et al. (2013) *StNAC002, 025, 087* and *091* confer salt and drought tolerance to potato plant, and they are induced by mechanical wounding, salt stress, drought stress, application of salicylic acid ABA, and *Phytophthora infestans* infection (Table 2). Similarly, *StNAC024, 059, 067, 108, 072, 101* enhance salt stress tolerance (Singh et al. 2013). Collinge and Boller (2001) also indicate that *StNAC004, 005, 018, 048, 051, 081* improves potato plant's ability to resist *P. infestans* infection.

Roles of NAC transcription factors in tobacco (*Nicotiana tabacum*)

Tobacco is one of the most studied higher plant species. Out of the 2500 transcription factors analyzed in tobacco, Rushton et al. (2008) found 203 complete or partial NAC domains and a minimum number of 152 NAC genes. They also identified seven major NAC gene subfamilies, six of which were present in tobacco as well as in other plant species (like rice, *Arabidopsis*, etc.), and a seventh subfamily which contained 50 tobacco NAC (TNAC) genes accounting

for approximately one quarter of all NAC genes in tobacco. The TNAC genes were further subdivided into three major clades – A, B, and C, with members in each clade having clearly different primary amino acid sequences in their NAC domains. Tobacco *NtNAC84, NtNAC176* and *NtNAC156* genes belonged to clade A, B and C respectively while potato CV505554, tomato BI422367, and pepper U204177 genes belonged to TNAC clade C. Besides lacking LPPG and YPNG motifs that are conserved in NAC family members, TNAC genes contain D/ExE motifs instead of the conserved D/EEE motif found in NACs (Rushton et al. 2008; Singh et al. 2013).

Nicotiana tabacum NAC (NtNAC) transcription factors range from NtNAC1 to over NtNAC176, but not much published information is available on their functional characterization. Available information indicates that NtNAC-R1, which is induced by mechanical wounding during topping, increases lateral root development and nicotine content (Fu et al. 2013) while NtNAC2 confers salinity stress tolerance to the tobacco plants (Han et al. 2015) (Table 3).

Table 3 Functionally characterized NAC transcription factors in tobacco, chili pepper and aubergine

Plants	Genes	Sub-family	Stress inducing transcription	Methods	References
Tobacco	<i>NtNAC-R1*</i>	nd	Mechanical wounding during topping	Increased number of lateral roots and nicotine contents	Fu et al. (2013)
	<i>NtNAC2</i>	nd	High level salt stress	Salinity stress tolerance	Han et al. (2015)
	<i>NtNAC151</i>	nd	nd	nd	Rushton et al. (2008)
	<i>NtNAC156</i>	"	nd	nd	Rushton et al. (2008)
	<i>NtNAC176</i>	"	nd	nd	Rushton et al. (2008)
Chili pepper	<i>CaNAC1**</i>	NAM	A non-host pathogen <i>Xanthomonas axonopodis</i> pv. <i>glycines</i> infection, salicylic acid, ethephon treatment	Defense responses resulting in hypersensitive sensitive cell death, Drought stress and BAX tolerance in <i>CaNAC1</i> transgenic tobacco plants (on-going work)	Oh et al. (2005)
	<i>CaNAC2</i>	NAC2	Cold stress, salt stress and ABA treatment	Cold stress tolerance, root growth and seed maturation	Guo et al. (2015)
Eggplant	<i>SmNAC***</i>	NAC	<i>Ralstonia solanacearum</i> infection, MeJA treatment	Increased susceptibility of plant to bacterial wilt	Na et al. (2016)

NtNAC*; *Nicotiana tabacum* NAC, *CaNAC*; *Capsicum annuum* NAC, ****SmNAC*; *Solanum melongena*

Roles of NAC transcription factors in chili pepper (*Capsicum annuum*)

In a recent work on chili pepper genome sequencing, Kim et al. (2014) identified a total of 2,139 genes which were unique to solanaceous plants, with 756 of them being unique to chili pepper. They further explained that pepper genome shared 27 gene families with *Arabidopsis*, 51 with grape and 20 with rice. Also, they found 2,153 transcription factors (6.25% of total genes) and transcriptional regulators in 80 gene families in chili pepper, some of which are involved in disease resistance and cellular functions (e.g. cytochrome P450), and 70 heat shock proteins that were significantly expanded in the pepper genome. In total, 105 putative *Capsicum annuum* NAC (*CaNAC*) transcription factors in pepper genome were identified and *CaNAC* proteins contain the typical NAC domain at the N-terminus including NLS localization, and highly divergent motif at the C-terminus. The predicted pepper NAC transcription factors with higher similarity for sequence and structure as compared to known NAC-proteins were retrieved from the various plants genomes (Fig. 3). Kim et al (2014) indicated that the size of the pepper NAC gene family is slightly expanded compared to the tomato genome. Moreover, they found a Solanaceae-specific NAC subgroup in pepper, tomato, and potato genome. This subgroup contains 33 members in pepper, 25 in tomato, and 35 in potato genome, whereas representatives of *Arabidopsis*- and rice-specific NAC subgroup were found in the *Arabidopsis* and rice genomes (Fig. 3; Kim et al. 2014).

CaNAC1 transcription factor was first discovered and

characterized by Oh et al. (2005). This gene enhanced defense response against non-host pathogens resulting in hypersensitive cell death. According to Oh et al. (2005) the cross-talk between SA and JA signaling pathways might account for the regulation of defense responses by *CaNAC1* transcription factor. In an on-going experiment on *CaNAC1* transgenic *Nicotiana tabacum* plants, overexpression of *CaNAC1* resulted in a higher tolerance of transgenic plants to pathogen infection and drought stress than the wild type (data not shown).

A report on aubergine (*Solanum melongena*) NAC (*SmNAC*) transcription factor expression by Na et al. (2016) indicates that *SmNAC* is induced by *Ralstonia solanacearum* infection and MeJA treatment, and *SmNAC* overexpression resulted in the reduced accumulation of SA which increased bacterial wilt susceptibility of aubergine. Published information on the functional characterization of chili pepper and aubergine NAC transcription factors are so scanty (Oh et al. 2005; Guo et al. 2015) and more study in this area need to be conducted.

Conclusion

A crop's ability to respond appropriately to biotic and abiotic stresses may ultimately increase its chances of survival and may also affect its yields positively. As global food demand continues to increase in the face of climate change, paying more attention to the study of NAC transcription factors in solanaceous plant to identify and functionally characterize their promoters will help to

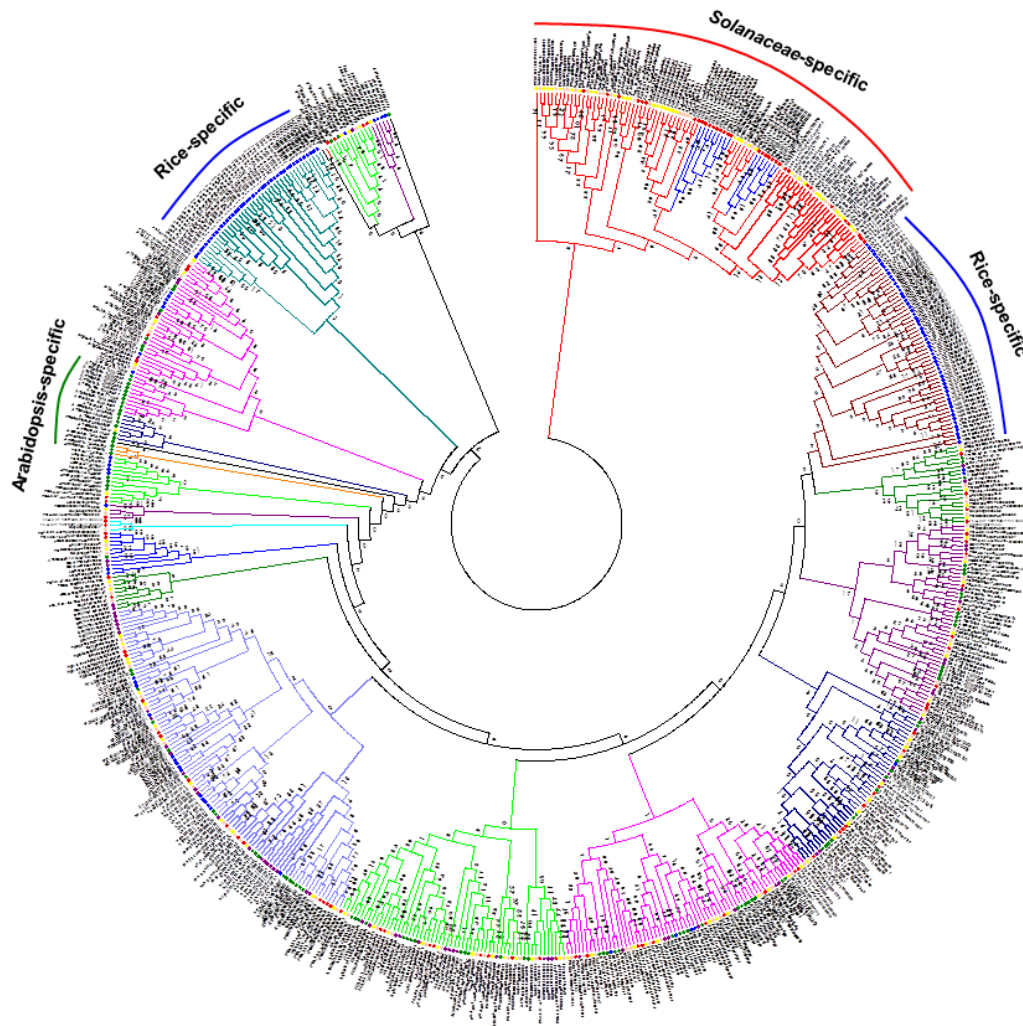


Fig. 3 Phylogenetic tree between tomato, potato and pepper, grape, rice, and Arabidopsis NAC genes. The deduced full-length amino acid sequences of 101 tomato (Solyc), 109 potato (PGSC), 106 pepper (PGA), 71 grape (GSVIVT), 140 rice (LOC_Os), and 113 Arabidopsis NAC genes, were aligned by Clustal W. The evolutionary relationship was inferred with the MEGA 5 program (Tamura et al. 2011) using the Neighbor-Joining method with 500 bootstrap replicates (Modified from Kim et al. 2014). Each NAC subgroup is indicated in a specific color circle. Tomato (pale pink), potato (yellow), pepper (red), grape (brown), rice (blue), and Arabidopsis (green)

engineer crops with improved performance under stressful conditions. A lot of transcription factors in solanaceae are characterized yet several TNAC transcription factors remain unknown (Rushton et al. 2008). Considering the involvement of NAC transcription factors in plant growth, development and defense, further experimental investigation into NAC transcription factors is indispensable.

Acknowledgement

This work was supported by research fund of Chungnam National University.

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