

Research Progress of NAC Transcription Factor Family in Plant Stress Resistance

Qin Liu^{1,3}, Xiang Wang², Guoyun Dong⁴, Jiqian Wei⁵, Yue Huang⁵, Xiaolan Shang⁵, Jinyao Ying⁶, Huaping Zhou⁶, Xiahong Luo¹, Wenlue Li¹, Tingting Liu¹, Lina Zou¹, Changli Chen¹, Shuqing Guo⁷, Xia An¹ ✉

1 Zhejiang Xiaoshan Institute of Cotton & Bast Fiber Crops, Zhejiang Institute of Landscape Plants and Flowers, Zhejiang Academy of Agricultural Sciences, Hangzhou, 311251, China

2 Agricultural Science and Technology Institute of Xiaoshan District of Hangzhou City, Hangzhou, 311200, China

3 Institute of Resource Plants, Yunnan University, Kunming, 650500, China

4 Zhangjiajie Research Institute of Agricultural Science and Technology, Zhangjiajie, 427000, China

5 Hangzhou Agricultural Technology Promotion Center, Hangzhou, 310020, China

6 Hangzhou Xiaoshan District Agricultural (Forestry) Technology Promotion, Hangzhou, 311203, China

7 Yancheng Xinyang Agricultural Experiment Station of Jiangsu Province, Yancheng, 224049, China

✉ Corresponding author email: anxia@zaas.ac.cn

Molecular Plant Breeding, 2023, Vol.14, No.14 doi: [10.5376/mpb.2023.14.0014](https://doi.org/10.5376/mpb.2023.14.0014)

Received: 28 May, 2023

Accepted: 30 Jun., 2023

Published: 07 Jul., 2023

Copyright © 2023 Liu et al., This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Preferred citation for this article:

Liu Q., Wang X., Dong G.Y., Wei J.Q., Huang Y., Shang X.L., Ying J.Y., Zhou H.P., Luo X.H., Li W.L., Liu T.T., Zou L.N., Chen C.L., Guo S.Q., and An X., 2023, Research progress of NAC transcription factor family in plant stress resistance, *Molecular Plant Breeding*, 14(14): 1-9 (doi: [10.5376/mpb.2023.14.0014](https://doi.org/10.5376/mpb.2023.14.0014))

Abstract NAC (NAM, ATAF1/2 and CUC2) transcription factor family is one of the largest transcription factor families in plant genome. NAC transcription factors have a variety of biological functions and play an important role in plant growth and development, plant hormone signal transduction and resistance to stress. This paper mainly reviews the role of NAC transcription factors in plant growth and development and their resistance to abiotic stresses such as drought, high salt and heavy metals, and provides a reference for future research on the resistance of NAC transcription factors.

Keywords NAC transcription factor; Abiotic stress; Plant stress resistance; Progress

Introduction

Transcription factors are a class of protein molecules with special structures that play an important regulatory role (Li et al., 2022b; Wang et al., 2022b), proteins that specifically binds to cis-acting elements in the promoter region, plays a key role in plant stress signal transduction and their interaction can regulate the expression of downstream genes, which can activate or inhibit downstream genes (Chen et al., 2015), which is an important transacting factor involved in plant expression regulation and plays an important role in seed development and grain filling (Huang et al., 2017). Generally, the function and characteristics of transcription factors are determined by four functional regions, namely: transcriptional regulatory region, DNA binding region, oligomerization site and nuclear localization signal region (Wang et al., 2022b). The regulation of NAC transcription factors is divided into three types, namely, transcriptional level regulation, post-transcription regulation and processing level regulation (Jin, 2021). Transcription factors play an important role in the regulation of gene expression in plant growth and development, secondary metabolism and other processes. Especially in response to external stimuli, by regulating the expression of functional genes, external stimuli are transformed into intracellular physiological and biochemical reactions (Ma, 2021).

The NAC transcription factor family is one of the largest gene families, a new type of plant-specific transcription factor and a multifunctional protein containing NAC domain (Wang et al., 2014b), involved in plant growth, development, and biotic and abiotic stress responses (Yu et al., 2014; Yuce et al., 2019), which can regulate the expression of other genes under biotic and abiotic stresses (Meng et al., 2022). It can also regulate the synthesis of secondary metabolites in plants (Li et al., 2022a). It plays an important regulatory role in plant growth and development and in abiotic stresses such as low temperature, drought and heavy metals (Li et al., 2022b). NAC transcription factor family can participate in the following aspects of plant growth: lateral root formation, shoot

apical meristem, leaf senescence, flower development, fruit ripening and softening, etc., and can also participate in hormone signaling pathways in various stress responses in plants (Chen et al., 2022; Wang et al., 2022b). NAC transcription factors are a class of transcriptional regulators with multiple biological functions (Ma, 2021), which are involved in plant secondary growth, hormone regulation and signal transduction, and biological stress defense responses (Ma, 2021). The expression levels of NAC transcription factors in different organs of plants are different, and most of them have higher expression levels in roots (Li et al., 2022a). Different genes are expressed in different organs. *ThNAC11* is highly expressed in stems, *ThNAC5* and *ThNAC8* are highly expressed in roots, while *ThNAC5*, *ThNAC11*, *ThNAC12*, *ThNAC16* and *ThNAC19* are highly expressed in leaves. The high expression of each gene in different organs indicates that they play different roles in plant growth and development (Wang et al., 2014a). NAC transcription factors are highly expressed in stem xylem, and their expression levels are higher than those in leaves, flowers, shoots, roots and stem bark (Liu et al., 2014).

The NAC domain is composed of three gene acronyms, which are named according to the common sequence of *NAM* (No apical meristem) gene, *ATAE1/2* (Arabidopsis transcription factor) gene and *CUC2* (Cup-shaped cotyledon) gene (Chen et al., 2015; Jin, 2021; Chen et al., 2022). NAC transcription factors contain a highly conserved N-terminal DNA binding domain and a diverse C-terminal domain (i.e.: transcriptional regulatory region) (Du et al., 2020; Jin, 2021). The N-terminal is a highly conserved protein sequence with about 150 amino acids (Zhu et al., 2021), The C-terminal structure is highly variable and diverse (Dai et al., 2020), rich in proline, serine, threonine and some acidic amino acid simple repeat sequences. The diversity of amino acid sequences determines the diversity of proteins. Amino acid sequences are related to transcriptional regulation (Ma, 2021). NAC transcription factors have transcriptional activation or inhibition activity and participate in the regulation of various signal networks (Chen et al., 2022). NAC domains are usually divided into five subdomains (A-E), in which A, C, D subdomains are conserved, B and E are not conserved (Wu and Zhang, 2022). Most NAC genes contain three exons and two introns. The first two exons encode the N-terminal and the latter encodes the C-terminal (Wang et al., 2014b). Most NACs contain only one NAM domain, and a few contain two NAM domains (Yang et al., 2022). NAC proteins can be divided into two categories: class I has 14 subfamilies, class II has 4 subfamilies (Xing et al., 2012; Wang et al., 2023).

With the rapid development of molecular biology and high-throughput sequencing technology, a large number of NAC members have been found and identified in a variety of plants, and a large number of NAC transcription factors have been identified. 105 *NAC* genes have been identified in *Arabidopsis thaliana* (Ooka et al., 2003), 152 *NAC* genes have been identified in soybean (Le et al., 2011), 151 *NAC* genes have been identified in rice (Nuruzzaman et al., 2010), 74 *NAC* genes have been identified in grape (Wang et al., 2013), and 91 *NAC* genes have been identified in castor (Dai et al., 2020). 57 *NAC* transcription factors were identified in spinach (Tan et al., 2022), and 172 *RsNAC* genes were identified in radish (Karanja et al., 2017). 58 *NAC* genes have been identified in tomato (Jin, 2021) and 72 *NAC* genes have been identified in ryegrass (Nie et al., 2020). These transcription factors play an important role in regulating growth and development, organ formation and biotic and abiotic stress (Chen et al., 2014). The living environment is very important for the growth of plants. Abiotic stresses such as drought, salt and heavy metals can inhibit the growth of plants, and severe stress can lead to plant death (Zhu et al., 2021). Plants sense stress signals through the signal transduction network to transmit signals to transcription factors, and then resist stress through gene expression (Wang et al., 2014b; Wang and Zhang, 2018). The response of plants to adversity is mainly manifested in physiological processes such as chlorophyll content, relative water content, and cell membrane. NAC transcription factors play a key role in abiotic stress (Yuce et al., 2019). The expression of NAC transcription factors in various plants is tissue-specific. Tissue-specific transcription factors play an important role in plant growth and development. NAC transcription factors play a role in abiotic stress response by activating multiple signaling pathways (Yuce et al., 2019). NAC transcription factors may be regulated by abscisic acid-dependent and-independent pathways (Erpen et al., 2018). NAC transcription factors regulate the process of plant response to stress through complex regulatory networks (Ma, 2021).

At present, most of the studies on NAC transcription factors in plant adversity are focused on saline-alkali, drought, cold stress, etc., while the studies on NAC in heavy metal stress is relatively rare. This paper reviews the research of NAC transcription factor family in abiotic stress such as drought, salt and heavy metal, so as to provide a reference for the future research of NAC transcription factor family in adversity stress.

1 The Role of NAC Transcription Factors in Drought and High Salt Stress

1.1 Effects of NAC transcription factors on plant growth

NAC transcription factors play an important role in plant growth. There are many members of NAC transcription factor family, which play different roles in different developmental stages and various environmental factors (You et al., 2022). NAC transcription factors play an important biological functions by activating the target protein, or play an important role in regulating plant growth and development by participating in growth regulation and hormone signal transduction (Chen et al., 2015; Wang and Zhang, 2018; You et al., 2022). NAC may be involved in many functions such as transmembrane transport or regulation of downstream gene expression in plants. NAC is widely involved in plant growth and development and stress response, because most of the NAC transcription factors are located in the nucleus of plants, and also in other organelles (Li et al., 2022b). It plays a role in seed development, meristem growth, secondary wall and xylem formation, root formation and senescence, and synergistically regulates plant tissue development and stress response (You et al., 2022). *NAC* gene can delay plant growth by regulating cell division (Wang et al., 2014b). Among them, *LcNAC1* in litchi can promote fruit senescence. When *GhNAC20* gene is silenced in cotton, the leaf senescence of plants is prolonged, which is a positive regulator of leaf senescence, while the transgenic *Arabidopsis thaliana* of *GhNAC18* gene shows delayed senescence and plays a role in inhibiting senescence (Wang and Zhang, 2018). For example, *SLNAC* in tomato is considered to be a positive regulator of fruit ripening, which can regulate plant growth, leaf senescence and lateral root formation (Tan et al., 2022). Secondly, *NAC* genes play an important role in regulating and controlling the secondary growth of plants, *NAC* is involved in the formation of xylem, the *NAC* genes related to xylem include *VND6 (NAC-DO MAIN6)* and *VND7 (NAC-DO MAIN7)*, which play an inhibit the formation of xylem (Chen et al., 2015). *NAC* transcription factors have a dual role in the growth of secondary walls (Wang et al., 2014b). *AdNAC36* in *Angelica dahurica* can regulate leaf cell death and response to salt stress, *AdNAC20*, *AdNAC42*, *AdNAC43*, *AdNAC45* and *AdNAC70* in *Angelica dahurica* were the highest expressed in the phloem of the root, followed by the xylem of the root (Huang et al., 2021).

Some *NACs* affect plant growth and development by regulating plant hormone levels. *NAC* transcription factors can affect anther development through hormone pathways such as jasmonic acid, auxin, and abscisic acid. *CUC1* and *CUC2* are key genes regulating floral organ development, affecting the development of stamens and pistils. These two genes can also cooperate with *miRNA164* to regulate inflorescence, petal and stamen development (Wang et al., 2022b). *NAC* transcription factors regulate gibberellin metabolism and signaling pathways, *OsNAC109* regulates plant growth, development and senescence, which may be related to multiple hormone metabolic pathways such as abscisic acid, gibberellin and ethylene (Ma, 2021). Overexpression of *CiNAC1* in *Arabidopsis* can promote root growth (Wang and Zhang, 2018), and activate the expression of downstream auxin response genes by mediating auxin and other signals, thereby promoting lateral root development (Wang et al., 2014b). *LpNAC019*, *LpNAC022* and *LpNAC050* in ryegrass were up-regulated under stress, and all of them were abscisic acid-induced genes (Nie et al., 2020).

1.2 Effects of NAC transcription factors in abiotic stress

NAC transcription factors play a key role in transcriptional regulation in plant response to environmental stress, such as drought, high salt, heavy metals and other abiotic stresses (Zhu et al., 2021). *NAC* can induce other pathways in plants under abiotic stress, combined with the expression of related genes, so that plants have different tolerances (Figure 1) (Singh et al., 2021). Under high salt, drought, heavy metal and abscisic acid treatments, *ThNAC2*, *ThNAC8*, *ThNAC13*, *ThNAC15*, *ThNAC18* and *ThNAC20* in *Tamarix hispida* were highly induced in roots, stems and leaves, indicating that these *NAC* genes play an important role in response to abiotic stress and are regulated by abscisic acid-dependent stress signaling pathways (Wang et al., 2014a). Transgenic

Arabidopsis plants with wheat gene *TaNAC67* have high tolerance to drought, high salt and cold stress (Wang and Zhang, 2018). The overexpression of *SmNAC* in eggplant can reduce the resistance of eggplant, and this gene can reduce resistance to bacterial wilt by inhibiting the expression of salicylic acid synthesis genes (Wang and Zhang, 2018). The *HvNAC6* transcription factor in barley can enhance the resistance of barley to powdery mildew (Wang and Zhang, 2018). *TaNAC1* in wheat plays a negative regulatory role in the response to stripe rust. This gene may regulate the resistance of wheat to stripe rust by affecting the expression of synthetic genes such as jasmonic acid and salicylic acid (Wang and Zhang, 2018).

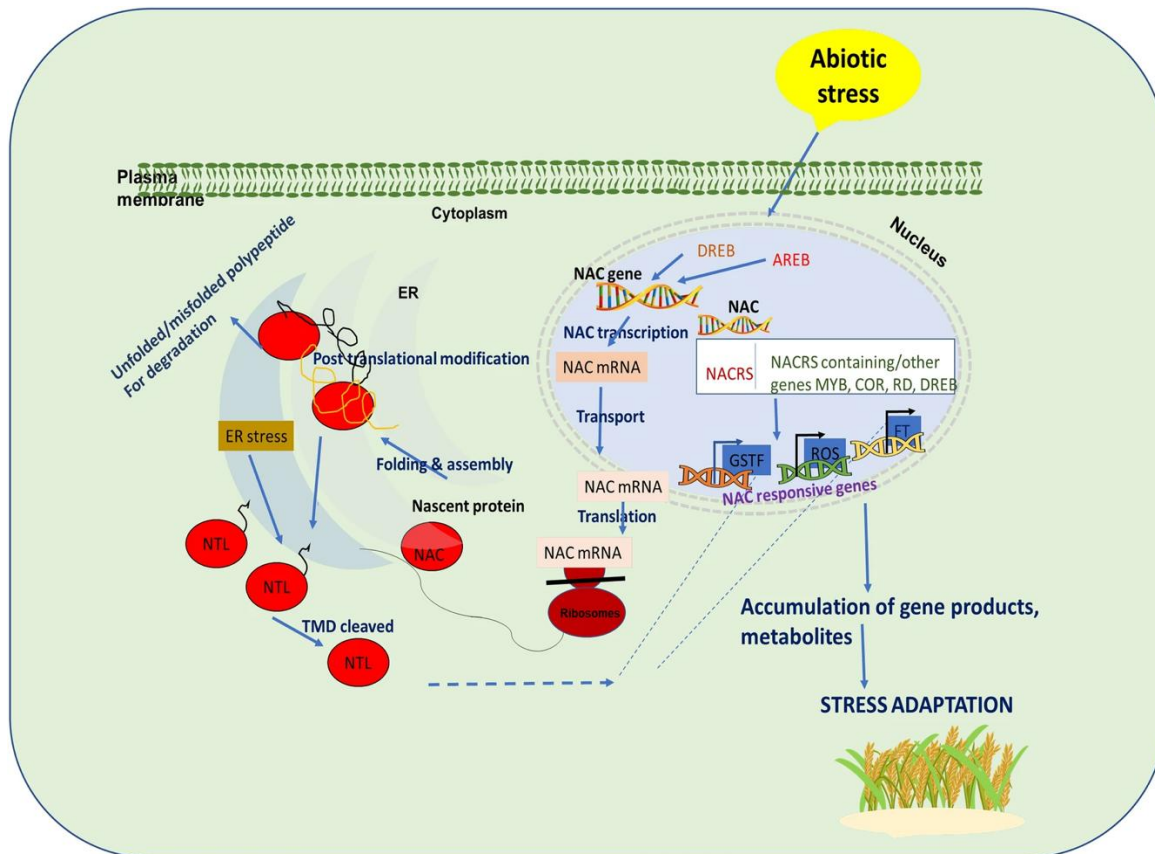


Figure 1 Schematic representation of *NAC* regulation in plant abiotic stress tolerance (Singh et al., 2021)

Note: Upon encountering stress, the *NAC* gene is induced by ABA dependent/independent pathway, which in turn binds to the promoter sequences of other genes (COR, DREB etc.), thereby regulating ROS, GSTF, FT expression; on the other hand, accumulation of unfolded/misfolded proteins triggers unfolded protein response (UPR) in the ER; thus, membrane bound *NAC* domain proteins (NTLs) are activated by ER stress and undergo conformational changes (TMD cleavage) to modulate the expression of stress-induced gene; NTLs thus, plays important role in communicating ER stress signaling from PM to nucleus to mitigate the ER stress; NACRS: *NAC* recognition site/sequence, COR: Cold regulated, RD: responsive to desiccation, ER: endoplasmic reticulum, NTL: *NAC* with Transmembrane Motif 1" Like, TMD: transmembrane domain, AREB: abscisic acid-responsive element-binding protein, DREB: drought-responsive element-binding, ROS: reactive oxygen species, GSTF: glutathione S-transferase; FT: flowering locus T; UPR: unfolded protein response, PM: plasma membrane (Singh et al., 2021)

1.2.1 Drought stress

The response pathways of *NAC* transcription factors in plants to drought stress include the following four aspects: one is to activate the antioxidant enzyme system by regulating the expression of downstream transcription factors involved in drought stress; second, it can maintain the osmotic balance of plant cells by participating in osmotic adjustment substances, prevent the death of plant cells due to excessive water loss, and improve the survival rate of plants under drought stress. The third is to control the degree of closure of plant guard cells, which can weaken the transpiration of plants and enable plants to maintain high water content; fourth, it can regulate the expression of response genes related to plant drought stress, thereby reducing the damage caused by drought stress to plants

(Ma, 2021). *RtNAC055* in *Reaumuria trigyna* can improve the drought tolerance of plants by regulating the dynamic balance of antioxidant system and reactive oxygen species level in plants, regulating the stomatal size in plants and reducing transpiration (Ma, 2021). Under drought stress, the induced expression of *SNAC1* gene in rice guard cells can promote stomatal closure, thereby improving the drought resistance of rice (Xing et al., 2012). The *BraNACs* genes in *Brassica campestris* winter rapeseed contain elements related to drought stress, cold stress and endogenous hormone regulation, among them, *BraNAC012*, *BraNAC015*, *BraNAC068*, *BraNAC066*, *BraNAC027* and *BraNAC034* can be used as candidate genes to improve crop drought resistance, *BraNAC0127* and *BraNAC012* can be used as candidate genes to improve crop cold resistance (Wang et al., 2022a). Most NAC transcription factors have transcriptional activation activity. The expression of *GmNAC4* gene in soybean can improve the germination rate of Arabidopsis plants, promote root growth and improve drought resistance (Nie et al., 2022). *GmNAC2* in tobacco can make plants more sensitive to drought, salt and low temperature stress (Nie et al., 2022). Overexpression of *ANAC019*, *ANAC055* and *ANAC072* genes in *Arabidopsis thaliana* can improve the drought tolerance of plants and regulate the expression of other genes induced by drought, high salt and abscisic acid stress (Jin, 2021). The NAC transcription factor *ATAF1* in Arabidopsis can participate in plant osmotic stress response as a negative regulator, which can improve the drought resistance of plants (Xing et al., 2012). The overexpression of *AtNAC019*, *AtNAC055* and *AtNAC072* in Arabidopsis can improve the drought resistance of transgenic plants (Xing et al., 2012). The overexpression of *ANACs* in *Arabidopsis thaliana* under different stresses can induce the expression of *ANAC055* in drought, *ANAC072* in deacidification, and *ANAC019* in salt. The overexpression of the three can improve the drought tolerance of *Arabidopsis thaliana* (Baillio et al., 2019). *OsNAC9* and *OsNAC10* in rice seeds can enhance the drought resistance of rice plants and increase the yield of rice by changing the root structure of rice (Huang et al., 2017). *RtNAC100* in Arabidopsis plants promotes ROS and Na⁺ accumulation by breaking the dynamic balance of plant antioxidant system and ion transport system, and activates the corresponding channels to induce PCD-related gene expression. *RtNAC055* in *Arabidopsis thaliana* regulates stomatal closure, reduces transpiration rate and improves plant drought tolerance by maintaining the dynamic balance of antioxidant system and ROS level in plants (Ma, 2021). *OsNAC2* in rice is a negative regulatory transcription factor for drought and high salt stress. This gene can participate in the metabolic pathway of auxin and gibberellin, and can affect the drought resistance of plants by regulating root development (Wang and Zhang, 2018). The genes related to drought resistance in *Kentucky bluegrass* were *PpNAC1*, *PpNAC6*, *PpNAC10* and *PpNAC13* (Zhu et al., 2021).

1.2.2 Salt stress

NAC transcription factors play an important role in plant response to salt stress (Yu et al., 2014). The response pathways of NAC transcription factors under high salt stress include the following aspects: First, by regulating the expression of ion transport-related proteins, the Na⁺/K⁺ ratio in plant cells is maintained, thereby affecting the salt tolerance of plants; secondly, by activating the expression of stress response-related genes, such as antioxidant enzyme genes, antioxidant genes and other related response genes, the relative homeostasis of the intracellular environment can be maintained. The third is to promote the accumulation of small molecule osmotic regulators, which can maintain the osmotic balance of plant cells, thus protecting the stability of cell structure. Fourth, by regulating signal molecules, etc., the degree of opening and closing of plant guard cells is controlled, thereby affecting plant transpiration (Ma, 2021). Overexpression of *SNAC1* gene in rice can improve the salt tolerance of rice in vegetative stage, while overexpression of *OsNAC6* and *OsNAC2* can improve the salt tolerance of rice in seedling development stage (Yu et al., 2014; Baillio et al., 2019). The *AtNAC2* gene in Arabidopsis can participate in the ethylene and auxin signaling pathways in response to salt stress, and the expression of *CmNAC1* gene is stimulated by drought, salt, abscisic acid and hydrogen peroxide (Yuce et al., 2019). The overexpressed *RtNAC100* gene in Arabidopsis is sensitive to high salt stress (Ma, 2021). Zhu et al. (2021) found that *PpNAC10* and *PpNAC24* genes in *Kentucky bluegrass* were related to salt tolerance. *PpNAC10* in *Kentucky bluegrass* is highly expressed under heavy metal, drought, high salt and low temperature stress, and *PpNAC18* is highly expressed under heavy metal, drought and low temperature stress. Both of them can be used as candidate genes in abiotic stress (Zhu et al., 2021). *PpNAC1*, *PpNAC10* and *PpNAC18* in *Kentucky bluegrass* are related to cold

resistance, and *PpNAC20* is a gene related to high temperature resistance (Zhu et al., 2021). The *SoNACs* genes in spinach can participate in the regulation of high temperature and salt stress tolerance (Tan et al., 2022). Under salt stress, *RsNAC008*, *RsNAC027* and *RsNAC038* genes in radish were significantly up-regulated, and these *RsNACs* genes could improve the tolerance of radish to salt (Karanja et al., 2017).

2 The Role of NAC Transcription Factors in Heavy Metal Stress

2.1 Cadmium stress

Heavy metals can seriously affect the growth and development of plants, and even lead to plant death. Heavy metal cadmium is a non-essential metal element for plant growth and development. Cadmium has strong toxicity. When it accumulates too much in plants, it will affect the growth of plants. NAC transcription factors in plants play an important role in heavy metal cadmium stress (Wu and Zhang, 2022). Under cadmium stress, 22 NAC family transcription factors were found in potato, among which 10 NAC transcription factors were found to have the resistance to heavy metal cadmium in the core genes, and the resistance of these *NAC* to cadmium increased with the increase of heavy metal cadmium stress concentration, resulting in the increase of the expression of these transcription factors (Fu, 2019). *OsNAC300* in rice is induced by cadmium stress. The gene is located in the nucleus and has a certain cadmium concentration dependence. It has strong expression in lateral roots, vascular bundles and embryos of rice. It can enhance the tolerance of rice to cadmium by regulating the expression of functional genes. *OsNAC300* can positively regulate the tolerance of rice plants to cadmium under cadmium stress (Hu, 2017; Hu et al., 2021). Under cadmium treatment the expression levels of *OsNAC3*, *OsNAC5* and *OsNAC6* in rice leaves increased first and then decreased with time. When the cadmium treatment was 50 μ m, the three genes were up-regulated each other. The phenomenon indicates that cadmium stress can induce the expression of these three genes in rice leaves and has a certain tolerance to cadmium (Jiang, 2015). In cadmium stress, the expression of *CsNAC019* gene in cucumber was significantly up-regulated, indicating that the expression of this gene was induced by cadmium, transcription factors can initiate the expression of stress response genes, and can also resist drought and salt stress by activating abscisic acid and other pathways (Li et al., 2017). *TaNAC22* in wheat plays an important role in cadmium stress response and growth and development, *TaNAC22* is a positive regulator that can regulate the expression of stress-responsive genes by increasing the enzymatic antioxidant defense system, thereby improving the tolerance of transgenic wheat to cadmium (Wu and Zhang, 2022). Overexpression of *AemNAC2* gene in transgenic wheat inhibited the absorption and transport of heavy metal cadmium in wheat under cadmium stress, which could lead to the decrease of cadmium concentration in roots, shoots and grains, indicating that *AemNAC2* gene is an important transcription factor for cadmium tolerance in wheat (Du et al., 2020). *AemNAC2* and *AemNAC3* in *Aegilops markgrafii* enhanced the cadmium tolerance of transgenic wheat and reduced the cadmium concentration in grains (Du et al., 2020). The up-regulated expression of *RsNAC058* gene in radish under heavy metal cadmium stress indicated that *RsNAC058* gene had high tolerance to heavy metal cadmium (Karanja et al., 2017). Under cadmium stress, *LpNACs* in ryegrass changed with cadmium treatment time, and the expression of different genes was different at different treatment time. Most *LpNACs* genes were significantly down-regulated during cadmium treatment, while *LpNAC045*, *LpNAC054* and *LpNAC065* were significantly up-regulated at cadmium treatment 12 h, 48 h and 6 h, respectively, indicating that these three genes had certain resistance to cadmium (Nie et al., 2020). The *ANAC004* gene in *Arabidopsis thaliana* plays a major role in the response of *Arabidopsis thaliana* to cadmium stress, the gene modification enhances the cadmium resistance of *Arabidopsis thaliana* plants by the following ways: First, it can induce cadmium stress and participate in plant regulation of cadmium resistance, enhance the fixation of cadmium by cell wall hemicellulose, and reduce the flow of cadmium to other cells such as roots; second, it can regulate the expression of genes related to cadmium detoxification; third, it can down-regulate the expression of genes related to cadmium transport; fourthly, it can lead to the accumulation of abscisic acid and the enhancement of antioxidant capacity, thus enhancing the tolerance of *Arabidopsis* plants to cadmium (Meng et al., 2022).

2.2 Other heavy metals

NAC transcription factors play an important role in heavy metal stress. NAC transcription factors were studied in other heavy metal stresses such as aluminum, chromium, copper and lead.

SINACs in tomato play an important role in response to aluminum stress, *SINAC063* can be specifically up-regulated in tomato roots under aluminum stress, especially in root tips, among them, the up-regulated expression induced by aluminum is proportional to the concentration and treatment time of aluminum stress. The gene can negatively regulate the aluminum tolerance of tomato, thus affecting the expression of the gene in tomato roots (Jin, 2021). *SINAC0064* in tomato can participate in the response of tomato to aluminum stress by regulating *SLAEE3-1*, thus playing a negative regulatory role in roots and a positive regulatory role in leaves (Jin, 2021). Under chromium stress, the growth and development of plants are affected by changing the physiological processes of plants. For example, the NAC transcription factor in sunflower is up-regulated in roots under chromium stress and identified as a heavy metal response gene (Yuce et al., 2019). In copper stress, 453 NAC transcription factors are involved in the process of *Vetiveria zizanioides* response to copper stress, of which 268 are up-regulated and 185 were down-regulated.

These *NACs* play an important role in signal transduction, osmotic regulation, ion transduction, functional proteins and transcriptional regulation in plants (Wang, 2021). Among the 21 representative radish *RsNACs* genes, *RsNAC023* and *RsNAC080* were found to respond to all stresses such as heavy metals, salt, heat, and abscisic acid (Karanja, 2017). The expression of *RsNAC027*, *RsNAC038* and *RsNAC062* in radish was stably up-regulated under heavy metal lead and cadmium stress, indicating that these genes had certain tolerance to heavy metal lead and cadmium, while other *RsNACs* had down-regulated expression under heavy metal stress (Karanja, 2017). Under lead stress, the process of ROS-dependent programmed cell death in kenaf cells is regulated by the differential expression of *NAC* transcription genes (An et al., 2020). *PpNAC10*, *PpNAC18*, *PpNAC19* and *PpNAC24* genes in *Kentucky bluegrass* are all related to heavy metal stress (Zhu et al., 2021).

3 Conclusion

NAC transcription factor is one of the most abundant transcription factor families in plants. NAC has been found and identified in many plants. At present, there are some research bases on its structure and functional characteristics, but there are still many unknown on *NAC* genes under stress, especially in heavy metal stress. With the development of molecular technology, *NAC* can be used to improve crop quality and improve stress resistance (Wang and Zhang, 2018). Secondly, the research on regulatory genes of NAC transcription factors and corresponding target gene promoters should be strengthened to determine the expression of corresponding genes. Through more in-depth study of the molecular mechanism of NAC transcription factors, it has important significance for plant stress resistance.

Authors' contributions

LQ and AX were the designers and executors of the review, completed the collection and analysis of relevant literature and the writing of the first draft of the paper. WX, DGY, WJQ, HY, SXL, YJY, ZHP, LXH, LWL, LTT, ZLN, CCL, GSQ participated in the analysis and collation of literature materials. All authors read and approved the final manuscript.

Acknowledgements

This research was funded by Zhejiang Provincial Basic Public Welfare Research Plan (LGN20C150007), China Agriculture Research System of MOF and MARA, China Agriculture Research System for Bast and Leaf Fiber Crops (CARS-16-S05), the National Natural Science Foundation of China (32202506) and International Cooperation Fund of ZAAS (2022).

References

An X., Chen J., and Jin G.R., 2020, Transcriptome profiling of kenaf (*Hibiscus cannabinus* L.) under plumbic stress conditions implies the involvement of NAC transcription factors regulating reactive oxygen species-dependent programmed cell death, *PeerJ*, 8: e8733.

<https://doi.org/10.7717/peerj.8733>

PMid:32195056 PMCid:PMC7069409

- Baillo E.H., Kimotho R.N., Zhang Z., and Xu P., 2019, Transcription factors associated with abiotic and biotic stress tolerance and their potential for crops improvement, *Genes* (Basel), 10(10): 771.
<https://doi.org/10.3390/genes10100771>
PMid:31575043 PMCID:PMC6827364
- Chen G.H., Pang X.K., Li G., Wang H., Wu S.W., Wen H.W., Yin Q., Yuan L.Y., Hou J.F., Tang X.Y., and Wang C.G., 2022, Genome-wide identification of NAC gene family in Brassica rapa and its expression analysis of response to vernalization, *Journal of Nanjing Agricultural University*, 45(4): 656-665.
- Chen N., Jiang J., Cao B.H., Lei J.J., and Chen C.M., 2015, The latest progresses on plant NAC transcription factors function, *Molecular Plant Breeding*, 13(6): 1407-1414.
- Chen X.L., Wang A.X., Zhang Z.Z., and Li J.F., 2014, Genome-wide identification and bioinformatics analysis of NAC gene family in tomato, *Plant Physiology Journal*, 50(4): 461-470.
- Dai M.Y., Gao M., and Li W.C., 2020, Identification and bioinformatics analysis of NAC transcription factor family in castor bean, *Molecular Plant Breeding*, 18(6): 1808-1817.
- Du X.Y., He F., Zhu B., Ren M.J., and Tang H., 2020, NAC transcription factors from *Aegilops markgrafii* reduce cadmium concentration in transgenic wheat, *Plant and Soil*, 449: 39-50.
<https://doi.org/10.1007/s11104-019-04419-w>
- Erpen L., Devi H.S., Grosser J.W., and Dutt M., 2018, Potential use of the DREB/ERF, MYB, NAC and WRKY transcription factors to improve abiotic and biotic stress in transgenic plants, *Plant Cell, Tissue and Organ Culture (PCTOC)*, 132: 1-25.
<https://doi.org/10.1007/s11240-017-1320-6>
- Fu D.S., 2019, Transcriptome sequencing and candidate gene mining of potato related gene expression under cadmium stress, Thesis for Ph.D., College of Resources and Environmental Engineering, Guizhou University, Supervisor: He T.B., pp.4-6.
- Hu S.B., 2017, Transcription factors of OsHSF1, OsMYB45 and OsNAC300 involved in regulation of Cd tolerance in rice, Dissertation for Ph.D., College of Life Science, Nanjing Agricultural University, Supervisor: Zheng L.Q., pp.75-92.
- Hu S.B., Shinwari K.I., Song Y.X.R., Xia J.X., Xu H., Du B.B., Luo L., and Zheng L.Q., 2021, OsNAC300 positively regulates Cadmium stress responses and tolerance in rice roots, *Agronomy*, 11(1): 95.
<https://doi.org/10.3390/agronomy11010095>
- Huang J., Deng J., Zhu L.W., and Chen Q.F., 2017, Progress of NAC transcription factor related to plant seed development, *Seed*, 36(11): 51-55.
- Huang W.J., Xu X., Chen J.S., Jiang Y.J., Yao F., Jiang M.Y., Zhang H.H., and Wu W., 2021, Bioinformatics analysis and expression pattern of NAC transcription factor family of *Angelica dahurica* var. *formosana* from Sichuan province, *China Journal of Chinese Materia Medica*, 46(7): 1769-1782.
- Jiang M., 2015, OsNACs were up-regulated by Cd in rice and the function study of OsNACs domain sequence, Thesis for M.S., Life Science and Technology Institute, Nanjing Agricultural University, Supervisor: Tan M.P., pp.7-28.
- Jin J.F., 2021, Study on the roles of two NAC transcription factors in response to aluminum stress in tomato, Dissertation for Ph.D., College of Life Science, Zhejiang University, Supervisors: Yang J.L., and Zheng S. J., pp.8-31.
- Karanja B.K., Xu L., Wang Y., Muleke E.M., Jabir B.M., Xie Y., Zhu X.W., Cheng W.W., and Liu L.W., 2017, Genome-wide characterization and expression profiling of NAC transcription factor genes under abiotic stresses in radish (*Raphanus sativus* L.), *PeerJ*, 5: e4172.
<https://doi.org/10.7717/peerj.4172>
PMid:29259849 PMCID:PMC5733918
- Karanja K.B., 2017, Identification and characterization of WRKY, AP2/ERF and NAC transcription factors and their responses to abiotic stresses in *Raphanus sativus* L., Dissertation for Ph.D., College of Horticulture, Nanjing Agricultural University, Supervisor: Liu L.W., pp.11-12.
- Le D.T., Nishiyama R., Watanabe Y., Mochida K., Yamaguchi-Shinozaki K., Shinozaki K., and Tran L.S.P., 2011, Genome-wide survey and expression analysis of the plant-specific NAC transcription factor family in soybean during development and dehydration stress, *DNA Res.*, 18(4): 263-276.
<https://doi.org/10.1093/dnares/dsr015>
PMid:21685489 PMCID:PMC3158466
- Li H.Y., Liu T.R., Chen J.H., Wang B., and Li H.B., 2022a, Genome-wide identification and expression analysis of the NAC gene family in *Salvia miltiorrhiza*, *Modern Chinese Medicine*, 1-16.
- Li H.Y., Tian C.Y., Zheng Y.Y., and Wu T., 2017, Cloning and expression analysis of Cadmium tolerance related gene CsNAC019 in cucumber, *Scientia Agricultura Sinica*, 50(10): 1852-1861.
- Li L.H., Guo Y.B., and Wei X., 2022b, Phylogenetic evolution of NAC gene families in four poaceae species and expression profile analysis of maize ZmNACs under drought stress, *Agricultural Research in the Arid Areas*, 40(4): 230-237.
- Liu T.M., Zhu S.Y., Tang Q.M., and Tang S.W., 2014, Identification of 32 full-length NAC transcription factors in ramie (*Boehmeria nivea* L. Gaud) and characterization of the expression pattern of these genes, *Molecular Genetics and Genomics*, 289: 675-684.
<https://doi.org/10.1007/s00438-014-0842-4>
PMid:24691727
- Ma B.J., 2021, Molecular mechanisms and functions of RtNAC100 and RtNAC055 in *Reaumuria trigyna* regulating plant response to salt and drought stresses, Dissertation for Ph.D., College of Life Science, Inner Mongolia University, Supervisors: Wang Y.C., pp.6-30.

- Meng Y.T., Zhang X.L., Wu Q., Shen R.F., and Zhu X.F., 2022, Transcription factor ANAC004 enhances Cd tolerance in *Arabidopsis thaliana* by regulating cell wall fixation, translocation and vacuolar detoxification of Cd, ABA accumulation and antioxidant capacity, *J. Hazard Mater.*, 436: 129121.
<https://doi.org/10.1016/j.jhazmat.2022.129121>
PMid:35580499
- Nie G., Yang X.Y., Yang Z.F., Zhong M.Y., Zhu Y.Q., Zhou J., Appiah C., Liao Z.C., Feng G.Y., and Zhang X.Q., 2020, Genome-wide investigation of the NAC transcript factor family in perennial ryegrass (*Lolium perenne* L.) and expression analysis under various abiotic stressor, *Genomics*, 112(6): 4224-4231.
<https://doi.org/10.1016/j.ygeno.2020.06.033>
PMid:32640275
- Nie T.M., Liu C., Ni Z.Y., and Yu Y.H., 2022, Bioinformatics analysis and transcriptional activation of soybean GmNAC120, *Soybean Science*, 1-11.
- Nuruzzaman M., Manimekalai R., Sharoni A.M., Satoh K., Kondoh H., Ooka H., and Kikuchi S., 2010, Genome-wide analysis of NAC transcription factor family in rice, *Gene*, 465(1-2): 30-44.
<https://doi.org/10.1016/j.gene.2010.06.008>
PMid:20600702
- Ooka H., Satoh K., Doi K., Nagata T., Otomo Y., Murakami K., Matsubara K., Osato N., Kawai J., Carninci P., Hayashizaki Y., Suzuki K., Kojima K., Takahara Y., Yamamoto K., and Kuikuschi S., 2003, Comprehensive analysis of NAC family genes in *Oryza sativa* and *Arabidopsis thaliana*, *DNA Res.*, 10(6): 239-247.
<https://doi.org/10.1093/dnares/10.6.239>
PMid:15029955
- Singh S., Koyama H., Bhati K.K., and Alok A., 2021, The biotechnological importance of the plant-specific NAC transcription factor family in crop improvement, *J. Plant Res.*, 134(3): 475-495.
<https://doi.org/10.1007/s10265-021-01270-y>
PMid:33616799 PMCID:PMC8106581
- Tan X.Z., Ge C.H., Dai Y.R., Kong M., Xu C.X., and Wang Q.H., 2022, Genome-wide identification and analysis of spinach SoNAC transcription factor family, *Journal of Shanghai Normal University (Natural Sciences)*, 51(1): 20-31.
- Wang C.Y., and Zhang Q., 2018, Research progress on plant NAC transcription factors, *Biotechnology Bulletin*, 34(11): 8-14.
- Wang H.B., Zhang C., Wu M.X., Li X., Jiang Z.L., Lin R.X., Guo J.L., and Kan Y.X., 2023, Genome-wide identification of NAC transcription factors ATAF subfamily in *Saccharum spontaneum* and functional analysis of its homologous gene ScNAC2 in sugarcane cultivar, *Acta Agronomica Sinica*, 49(1): 46-61.
- Wang H.Q., 2021, Study on tolerance mechanism of vetiver under Cu stress, Thesis for Ph.D., College of Animal Science, Guizhou University, Supervisor: Cheng W., pp.45-50.
- Wang H.W., Fan J.Q., Lu X.M., Zeng R., Wu J.Y., Liu L.J., Ma L., Pu Y.Y., Sun W.C., and Li X.C., 2022a, Identification and expression analysis of NAC gene family in *Brassica rapa* L., *Jiangsu Journal of Agriculture Science*, 38(5): 1315-1329.
- Wang J.L., Wang H.B., Yang H.Q., Hu R.L., Wei D.Y., Tang Q.L., and Wang Z.M., 2022b, The role of NAC transcription factors in flower development in plants, *Shengwu Gongcheng Xuebao*, 38(8): 2687-2699.
- Wang L.Q., Wang C., Wang D.Y., and Wang Y.C., 2014a, Molecular characterization and transcript profiling of NAC genes in response to abiotic stress in *Tamarix hispida*, *Tree Genetics and Genomes*, 10: 157-171.
<https://doi.org/10.1007/s11295-013-0672-2>
- Wang N., Zheng Y., Xin H.P., Fang L.C., and Li S.H., 2013, Comprehensive analysis of NAC domain transcription factor gene family in *Vitis vinifera*, *Plant Cell Rep.*, 32(1): 61-75.
<https://doi.org/10.1007/s00299-012-1340-y>
- Wang R.F., Hu Y.S., Gao W.R., Zhang Y.X., and Song X.S., 2014b, Functions of NAC transcription factors family in stress responses in plants, *Plant Physiology Journal*, 50(10): 1494-1500.
- Wu Y.G., and Zhang L., 2022, The wheat NAC transcription factor TaNAC22 enhances cadmium stress tolerance in wheat, *Seed*, 36(11): 51-55.
- Xing G.F., Zhang Y.M., Zhang W.B., Ma X.Y., and Han Y.H., 2012, Research progress of NAC transcription factors in plant, *Journal of Shanxi Agricultural Sciences*, 40(4): 409-411, 423.
- Yang M.S., Ni Z.Y., and Yu Y.H., 2022, Soybean GmNAC46 bioinformatics, autoactivation, and tissue expression analysis, *Soybean Science*, 1-9.
- You Y.W., Zhang Y., Sun J.Y., and Zhang W., 2022, Genome-wide identification of NAC family and screening of its members related to prickly development in *Rosa chinensis* old blush, *Scientia Agricultura Sinica*, 55(24): 4895-4911.
- Yu Y., Huang W., Chen H., Wu G., Yuan H., Song X., Kang Q., Zhao D., Jiang W., Liu Y., Wu J., Cheng L., Yao Y., and Guan F., 2014, Identification of differentially expressed genes in flax (*Linum usitatissimum* L.) under saline-alkaline stress by digital gene expression, *Gene*, 549(1): 113-122.
<https://doi.org/10.1016/j.gene.2014.07.053>
- Yuce M., Taspinar M.S., Aydin M., and Agar G., 2019, Response of NAC transcription factor genes against chromium stress in sunflower (*Helianthus annuus* L.), *Plant Cell, Tissue and Organ Culture (PCTOC)*, 136: 479-487.
<https://doi.org/10.1007/s11240-018-01529-8>
- Zhu R.T., Niu K.J., Zhang R., and Ma H.L., 2021, Identification of NAC gene family and analysis of its expression pattern under abiotic stress in *Poa pratensis*, *Grassland and Turf*, 41(4): 26-35.