Molecular Plant Breeding 2024, Vol.15, No.3, 90-99
http://genbreedpublisher.com/index.php/mpb

Review and Progress **Open Access**

Research Progress of NAC Transcription Factor Family in Plant Stress Resistance

Ziyi Zhu [1,2], Xia An [1] ✉, Xiahong Luo [1], Changli Chen [1], Tingting Liu [1], Lina Zou [1], Guanlin Zhu [1]
1 Zhejiang Institute of Landscape Plants and Flowers (Zhejiang Xiaoshan Cotton and Hemp Research Institute), Zhejiang Academy of Agricultural Sciences, Hangzhou, 311251, Zhejiang, China
2 College of Environment and Resources, College of Carbon Neutrality, Zhejiang A&F University, Hangzhou, 311300, Zhejiang, China
✉ Corresponding email: anxia@zaas.ac.cn

Molecular Plant Breeding, 2024, Vol.15, No.3 doi: 10.5376/mpb.2024.15.0011
Received: 27 May., 2024
Accepted: 20 Jun., 2024
Published: 25 Jun., 2024

Preferred citation for this article:
Zhu Z.Y., An X., Luo X.H., Chen C.L., Liu T.T., Zou L.N., and Zhu G.L., 2024, Research progress of NAC transcription factor family in plant stress resistance, Molecular Plant Breeding, 15(3): 90-99 (doi: 10.5376/mpb.2024.15.0011)

Abstract NAC (NAM, ATAF1/2, and CUC2) transcription factors are a class of plant specific transcription factor genes with numerous family members, commonly found in higher plants, and also found in moss plants. The N-terminus of these genes has a highly conserved NAC domain. It plays a crucial role in the growth and development of plants, as well as in their response to biotic stress (such as insects and plant pathogens) and abiotic stress (such as drought, salinity, temperature, and heavy metals). This article introduces the basic characteristics of the NAC transcription factor family and briefly elaborates on its research in plant stress resistance in recent years, providing some reference for future research on the stress resistance of NAC transcription factors.

Keywords Transcription factors; *NAC* gene; Resistance to adversity; Plant

1 Introduction

Plants, as primary producers in ecosystems, have been exposed to a number of unfavorable environments during their long evolution, mainly including biotic stresses and abiotic stresses. Studies have shown that annual yield losses due to biotic stresses are estimated to be about 35% and abiotic stresses can lead to more than 50% yield losses (Mukhtar and Stockle, 2016). In order to survive and reproduce, plants have evolved complex mechanisms to sense environmental changes and respond adaptively, in which transcription factors play an extremely important regulatory role.

Transcription factors are a crucial component of gene regulation; they are a set of protein molecules that specifically bind to particular sequences upstream of the 5' end of genes, ensuring the expression of target genes in precise temporal and spatial patterns. In plant systems, such molecules play an indispensable role in regulating plant growth and development as well as adaptive responses to environmental stresses, and NAC, WRKY, MYB, MYC, bZIP, DREB, and CBF are some of the more common transcription factors. Among them, the NAC transcription factor family is one of the important transcription factor families in plants, and the name of this transcription factor family comes from the *NAM* gene in the *Petunia* × *hybrida* hort. ex Vilm, the *ATAF1* and *ATAF2* genes in *Arabidopsis thaliana*, and the *CUC2* gene.

In this paper, the basic structural features of the NAC transcription factor family are described in detail, and the related research progress in plant stress tolerance is sorted out and analyzed in the hope of providing a certain theoretical basis for the study of stress tolerance of the NAC transcription factor family. There are many members of the NAC transcription factor family, and each of the members plays a unique function in the response to a specific biotic or abiotic stress. In recent years, the research on NAC transcription factors has made remarkable progress in plant stress tolerance. The following table summarizes the functions of different NAC transcription factors in response to abiotic (Table 1) and biotic (Table 2) stresses in different plants.

2 Characterization of the NAC Transcription Factor Family

The NAC family of transcription factors has a distinctive structural feature (Figure 1), the amino acid-terminal-containing NAC structural domain, consisting of 150~160 amino acid residues, which is responsible for DNA binding and is the basis for the NAC proteins to recognize and bind specific DNA sequences. The domain contains five subdomains (A to E), including conserved subdomains A, C, and D, and diverse subdomains B and E. Based on differences in sequence homology, this family can be systematically classified into two major categories: the first integrates 14 unique subclassifications, counting TERN, ONAC022, SENU5, NAP, AtNAC3, ATAF, OsNAC3, NAC2, ANAC011, TIP, OsNAC8, OsNAC7, NAC1, and NAM. Different subfamilies of NAC proteins showed functional specificity. For instance, the ATAF subfamily, also known as subfamily III-1, has been substantiated through research to have its members extensively involved in various biotic and abiotic stress responses (Ou et al., 2024); the second group, on the other hand, encompasses four subclassifications, namely ANAC001, ONAC003, ONAC001 and ANAC063 (Lu et al., 2024).

Table 1 Non biological stress-related NAC transcription factors

NAC gene	Stress resistance function	Species	Literature
ANAC096	Positive regulation of drought tolerance	*Arabidopsis thaliana*	(Xu et al., 2013)
OsNAC3	Positive regulation of salt and alkaline tolerance	*Oryza sativa*	(Zhang et al., 2021a)
ZmNAC074	Positive regulation of heat resistance	*Arabidopsis thaliana*	(Xi et al., 2022)
GmNAC20	Positive regulation of salt and cold tolerance	*Arabidopsis thaliana*	(Hao et al., 2011)
CaNAC2	Positive regulation of cold tolerance	*Capsicum annuum*	(Guo et al., 2015)
AmNAC24	Positive regulation of cold tolerance	*Ammopiptanthus mongolicus*	(Dorjee et al., 2024)
MsNAC001 *MsNAC058*	Positive regulation of salt alkaline and drought resistance	*Medicago sativa* L.	(Min et al., 2020)

Table 2 NAC transcription factors related to biological stress

NAC gene	Stress resistance function	Species	Literature
ANAC019 *ANAC055*	Changing resistance to gray mold	*Arabidopsis thaliana*	(Bu et al., 2008)
GhNAC100	Changing resistance to Dahlia wilt pathogen	Cotton	(Hu et al., 2019)
TaNAC069	Enhancing resistance to leaf rust fungus	Wheat	(Zhang et al., 2021b)

The carboxyl-terminus (C-terminus), on the other hand, is the transcriptional activation domain (TAD), which is less conserved and has a high degree of diversity, and plays a decisive role in the functional specificity of transcription factors such as activation or repression of gene expression. For example, the five sub-structural domains (A-E) in Arabidopsis, which are differently conserved, contain multiple chemical modification sites and hydrophobic regions. Subdomain D may be related to DNA binding and nuclear localization, while the C-terminal F and G regions may be related to transcriptional activation functions and secondary growth NAC subfamily delineation (Chen et al., 2009).

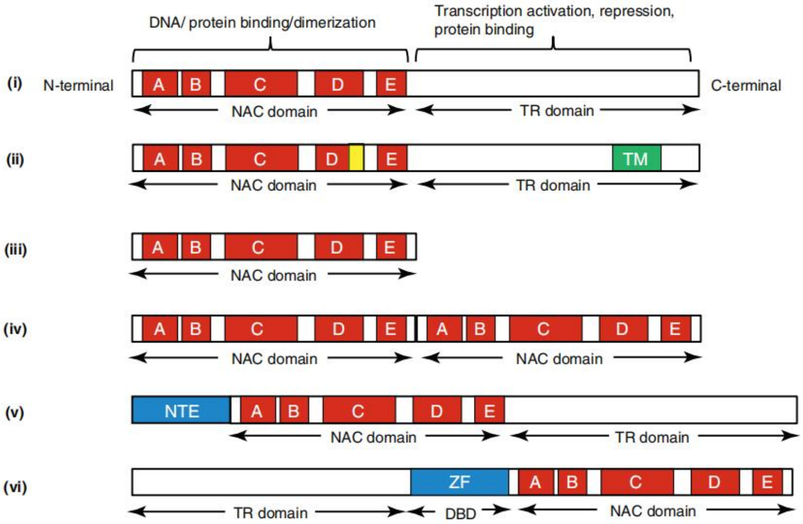

Figure 1 Structural characteristics of NAC transcription factors (Adopted from Puranik et al., 2012)

NAC transcription factors are a family of transcription factors unique to plants and not found in animals or microorganisms, and the NAC family is one of the largest families of transcription factors in plants, with the number of members varying greatly among plant species. For example, in *Arabidopsis thaliana*, about 150 NAC transcription factors are known; in rice, there are more than 300 NAC family members; and in soybean there are 152 each (Sun et al., 2012); and 163 genes in poplar (Han et al., 2023). The variation in the number of NAC transcription factor families in different plants not only reflects the differences in genome size and complexity, but also plays different roles in plant stress response.

3 Role of NAC Transcription Factors in Abiotic Stresses

NAC transcription factors play an important role in abiotic stresses, which mainly include environmental stresses, including drought, salinity, low temperature, high temperature, heavy metal pollution, ultraviolet radiation, and nutrient deficiency.

3.1 Drought stress

Drought stress is a phenomenon that affects normal plant growth and development due to a severe shortage of water content in the soil or a reduction in plant-available water caused by environmental conditions. Studies have shown that NAC transcription factors play an important role in regulating plant responses to drought stress.

For example, when rice is subjected to drought stress during its reproductive period, overexpression of the stress responsive gene *SNAC1* (STRESS-RESPONSIVE NAC1) can improve the drought tolerance of transgenic rice and increase the seed setting rate by 22%~34%. During the nutritional growth period, genetically modified rice also showed excellent drought resistance. Compared to wild-type rice, genetically modified rice has significantly increased sensitivity to abscisic acid (ABA), and research has found that, The *SNAC1* gene is mainly induced and expressed in guard cells under drought conditions, and its encoded protein is a transcriptional activating NAM ATAF and CUC (NAC) transcription factors effectively slow down water loss and improve plant drought resistance by closing stomatal pores more frequently, but this process did not significantly affect their photosynthesis rate (Hu et al., 2006). And in sweet potatoes, there is a pressure induced IbNAC3, which is a transcription activator located in the nucleus and contains a unique activation domain that can interact with ANAC011 The interaction between ANAC072, ANAC083, ANAC100, and NAP enhances plant tolerance to drought environments in Arabidopsis by overexpressing IbNAC3 (Meng et al., 2022). In addition, SlNAC6 (SlNAC6-RNAi) plays an important role in tomato development, drought stress response, and fruit ripening. Studies have shown that some of its effects may be achieved through the regulation of ABA mediated pathways. Overexpression of SlNAC6 leads to a decrease in water loss rate and degree of oxidative damage in tomatoes, as well as an increase in proline content and antioxidant enzyme activity, thereby improving plant drought resistance (Jian et al., 2021).

Research has found that six *ZmNAC* genes found in maize can significantly enhance plant drought tolerance (Wang et al., 2020a). For example, the *ZmNAC48* gene in maize has been shown to enhance drought tolerance in Arabidopsis. However, this gene has a natural antisense transcript cis NATZmNAC48, which has a negative regulatory effect on ZmNAC48. When cis-NATZmNAC48 is overexpressed, it interferes with the normal function of ZmNAC48, thereby affecting the normal closure of maize stomata, leading to a decrease in maize drought resistance (Mao et al., 2021). In addition, overexpression of the apple *MdNAC29* gene reduces the drought resistance of apple plants, callus tissues, and tobacco, and exhibits higher relative conductivity, malondialdehyde (MDA) content, and lower chlorophyll content under drought stress (Li et al., 2023). Another study found that under drought conditions, overexpression of LpNAC13 in lily bulbs in tobacco resulted in a decrease in plant antioxidant enzyme activity, proline, and chlorophyll content, The MDA content increased, while the results under salt conditions were opposite to those under drought conditions. Overexpression of LpNAC13 in tobacco reduces its drought resistance and enhances its salt tolerance (Wang et al., 2020b).

3.2 Salt stress

Salt stress is one of the major abiotic stresses that constrain plant growth and development, and to cope with these unfavorable factors, plants adopt a series of strategies, such as synthesizing osmoregulatory substances, increasing the activity of antioxidant enzymes, and maintaining ionic homeostasis, in order to mitigate the negative effects of saline stress on their growth and development.

Some of the NAC transcription factors depend on the ABA pathway to regulate salt tolerance in plants. For example, rice OsNAC3 is an important regulator of ABA signaling response and salt tolerance. the expression of genes such as *Os HKT1;4*, *Oshkt1;5*, *Oslea3-1*, *Ospm-1*, *Ospp2C68*, and *Osrab-21* reduced its sensitivity to abscisic acid and improved plant tolerance to salt stress (Zhang et al., 2021a). Overexpression of GmSIN1 in soybean promoted root growth and increased yield under salt stress. Its response to salt stress requires rapid induction of ABA (abscisic acid) and ROS (reactive oxygen species). Further studies revealed that GmSIN1, GmNCED3s and GmRbohBs synergistically formed a positive feed-forward regulatory mechanism, which significantly accelerated the process of ABA and ROS accumulation, thereby amplifying salt stress signals and enabling the plant to respond to and adapt to the salt-stressed environment more rapidly (Li et al., 2019).

Some NAC transcription factors do not rely on the ABA pathway and regulate plant salt tolerance. Overexpression of *Pennisetum glaucum* PgNAC21 in Arabidopsis enhances GSTF6 (glutathione s-transfer 6), The expression of COR47 (cold regulated 47) and RD20 (responsive to dehydration 20) enhances plant salt tolerance (Shinde et al., 2019). Overexpression of *Ts NAC1* gene in *Thellungiella salsuginea* and Arabidopsis can enhance plant tolerance to drought, cold, and salt stress, thereby delaying plant growth rate (Liu et al., 2018a). A high salt environment can also induce the expression of OsNAC071 in rice, thereby improving plant salt tolerance (Liu, 2023).

In addition, salt stress and alkali stress are two different abiotic stresses, but they are often collectively referred to as salt stress, and alkali stress tends to cause more significant damage to plants (Wang et al., 2017). However, these two stresses often occur together, and high concentrations of salt and alkaline environments can cause multiple adverse effects on plant root cells. It was found that LpNACl3 and LpNAC5 could enhance the seed germination rate under saline and alkaline stress to a certain extent, and significantly enhance the salt and alkali tolerance of transgenic tobacco seedlings, but would reduce their drought tolerance to a certain extent (Wang, 2020). The transgenic tobacco seedlings were found to be more tolerant to salt and alkali. And this phenomenon was also reflected in LpNAC6, where antioxidant enzymes (SOD, POD, CAT) activities, chlorophyll content, proline content and photosynthetic capacity were increased in LpNAC6 transgenic tobacco, while MDA, H_2O_2 and O_2-contents were reduced, which enhanced alkali tolerance, but showed the opposite effect under drought stress (Yan et al., 2022).

3.3 Temperature stress

Temperature stress refers to environmental temperatures that exceed the optimal growth range of plants, and includes two main forms of low-temperature stress and high-temperature stress, which can adversely affect plant growth, development, physiology, and survival. Low-temperature stress is also divided into cold damage (0 ℃~15 ℃) and freezing damage (below 0 ℃), both of which can cause different degrees of damage to plants, but the mechanisms are different, with freezing damage involving the formation of ice crystals directly physically damaging the cells, whereas cold damage leads to damage more through disruption of physiological processes Cold damage is more likely to result in injury through disruption of physiological processes (Lu et al., 2024).

Overexpression of LlNAC2 in *Arabidopsis thaliana* enhances the resistance of *Lilium lancifolia* to cold stress by participating in the DREB/CBF-COR and ABA signaling pathways in cold stress (Yong et al., 2019). CaNAC064 isolated from pepper leaves has transcriptional activation activity at a critical region of 691~1 071 bp, which can interact with low-temperature-induced monomeric-type proteases to positively regulate cold resistance in plants (Hou et al., 2020). At 0 ℃~15 ℃, overexpression of MdNAC104 enhanced the antioxidant enzyme activities of apple plants and attenuated the damage of PSII, thereby enhancing the cold tolerance of the plants. In addition, below 0 ℃, overexpression of MdNAC104 in apple plants affected the accumulation pattern of osmoregulatory substances in the stem and leaves, and improved cold tolerance (Mei, 2023).

High temperature stress occurs when the ambient temperature reaches or exceeds the maximum temperature threshold for plant growth. This stress may lead to problems such as reduced photosynthetic efficiency, altered protein structure, and increased membrane lipid peroxidation in plants, which in turn affects flowering and fruiting and may cause tissue damage, such as standing wilt in seedlings. It has been found that in response to high-temperature stress, plants synthesize heat-stimulated proteins (HSPs), which are usually regulated by heat-stimulated transcription factors (HSFs). NAC019 overexpressed in *Arabidopsis thaliana* was able to bind to the promoters of HSFA1b, HSFA6b, HSFA7a, and HSFC1, increasing the heat tolerance of plants (Guan et al., 2014). Under high-temperature treatment, by transferring the *TaNAC2* gene from wheat to Arabidopsis, the hypocotyl growth length of transgenic TaNAC2L Arabidopsis significantly exceeded that of wild-type plants, and expression levels of six thermally induced genes in Arabidopsis notably surpassed those in the wild type, implying that *TaNAC2L* enhances thermal resistance by orchestrating the expression of stress-related genes (Guo et al., 2015). When overexpressed in transgenic Arabidopsis, *ZmNAC074* isolated from corn significantly enhances plant tolerance to high-temperature environments by regulating various stress metabolites such as reactive oxygen species (ROS), malondialdehyde (MDA), proline, soluble protein, chlorophyll, and carotenoids (Xi et al., 2022). The involvement of NAC transcription factors can appropriately regulate the mechanism of plant response to temperature stress, helping plants to adapt and resist these adverse environmental factors to a certain extent.

In addition, ATAF1 in *Arabidopsis thaliana* is negatively regulated under high-temperature environment. ATAF1 knockout mutants exhibited better heat tolerance compared to the wild type in the experiment (Alshareef et al., 2022).

3.4 Heavy metal stress

Heavy metal stress refers to the presence of heavy metal ions in the environment, such as Cd Mn, Pb, Cd, and Hg, etc, present in the environment at too high a concentration, negatively affect organisms (especially plants). When these heavy metal ions enter the plant body, they interfere with normal physiological and biochemical processes and induce a series of defense responses.

Research has found that NAC transcription factors from *Aegilops markkrafii* can reduce cadmium concentration in transgenic wheat. Under excessive cadmium treatment, the transcription of AemNAC2 and AemNAC3 is upregulated approximately 150 times, Overexpression of AemNAC2 in the wheat variety "Bobwhite" leads to a decrease in cadmium concentration in roots, aboveground parts, and grains (Du et al., 2020). In addition, IDEF2 (Iron deficiency responsive cis acting element 2) in the rice NAC family can maintain Fe stability in rice tissues (Walker and Connolly, 2008). Another study found that SiNACs in willows exhibit two significant Pb positive reaction patterns (early and late), both containing 10 SiNACs (Xin et al., 2023). In addition, Overexpression of TdNAC8470 in rice increased grain starch concentration but decreased grain Fe The content of Zn and Mn may be involved in regulating grain protein content, starch synthesis, etc. (Gong et al., 2022).

3.5 Others

In addition to the aforementioned abiotic stresses, plants may also face mineral nutrient stress, light stress, oxidative stress, and mechanical and physical damage. For example, research has found that after dark treatment, more than 1/4 of NAC expression is increased in Arabidopsis leaves (Lin and Wu, 2004); And under strong light, ANAC078 can induce genes related to flavonoid biosynthesis, increase the accumulation of anthocyanins, and cope with high light stress (Morishita et al., 2009). At 0.1% oxygen, the decrease in ANAC102 expression significantly reduces germination efficiency, but the increase in expression has no effect on germination. Arabidopsis ANAC102 is an important regulatory factor for seed germination under flooded conditions (Christianson et al., 2009). Under low phosphorus stress, soybean transcription factor GsNAC1 can regulate the expression of genes in plant roots, stems, and leaves, enhancing soybean tolerance to low phosphorus soil (Xiong et al., 2024).

4 Role of NAC Transcription Factors in Biotic Stresses

Biotic stress is the combined effects of various biological factors that are detrimental to the survival and development of an organism. These effects usually originate from the activities of other organisms, including diseases caused by pathogens (e.g., viruses, bacteria, fungi), pest infestation, disturbance by parasitic organisms, and damage by competing species (e.g., weeds), etc. NAC can be involved in different pathogen stresses in different plants (Figure 2). There are fewer reports in the existing literature related to the involvement of the NAC transcription factor family in the biological responses of plants, and there are either positive or negative regulatory roles of NAC transcription factors in biotic stresses.

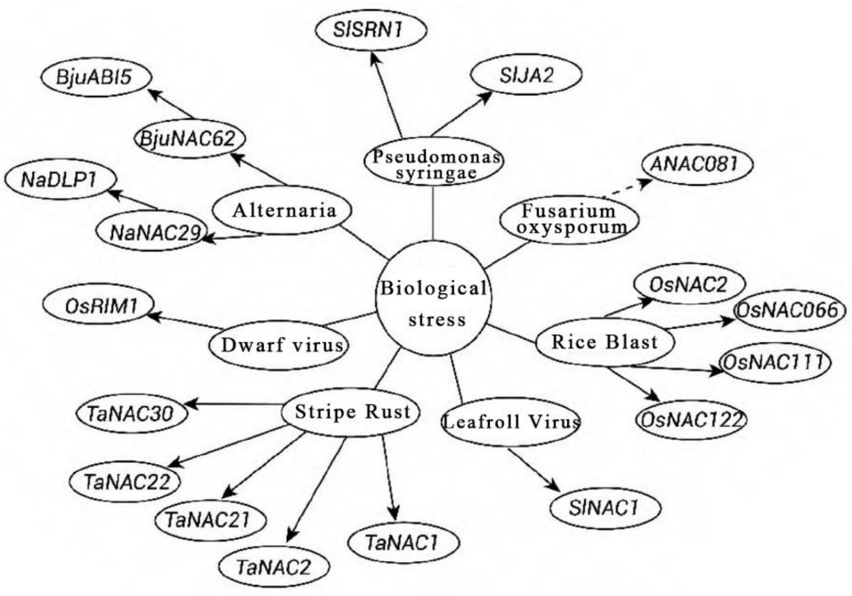

Figure 2 The role of NAC transcription factors in biological stress (Adopted from Lu et al., 2024)

During the long evolutionary process of plants, a fine-tuned system of disease resistance defense has been developed. This system is mainly composed of three disease resistance signaling pathways, namely: a salicylic acid (SA)-dependent signaling pathway, a jasmonic acid (JA)-dependent signaling pathway, and an ethylene-dependent signaling pathway (Zhou et al., 2017). Many NAC proteins regulate plant defense responses to enhance plant disease resistance by activating *PR* genes, inducing hypersensitive response (HR) and cell death at the site of infection (Nuruzzaman et al., 2013).

It was found that ONAC122 and ONAC131 were induced to be expressed under the infestation of *Botrytis cinerea*. And, ONAC122 and ONAC131 were induced by salicylic acid, methyl jasmonate, or 1-aminocyclopropane-1-carboxylic acid (precursor of ethylene) treatment (Sun et al., 2013). ONAC066 positively regulates rice resistance to rice blast and leaf blight, and ONAC0666 exerts its disease resistance function by regulating the ABA signaling pathway, sugar and amino acid accumulation in rice (Liu et al., 2018b). In addition, by overexpressing the *OsNAC60* gene, the transgenic plant exhibit improved resistance to rice blast, whereas when the miR164a/OsNAC60 regulatory module was dysfunctional, rice was significantly susceptible to *Rickettsia* spp. infection. Further studies found that Osa-miR164a, on the other hand, promotes the infection of *B. oryzae* (Wang et al., 2018).

Except for rice, some *NAC* genes of other plants also play an important role in disease resistance response. In *B. juncea*, *BjuNAC62 Δ C* can enhance resistance to the black spot pathogen of Chinese cabbage (Mondal et al., 2022). The *TaNAC069* gene plays a positive regulatory role in the resistance of wheat to leaf rust (Zhang et al., 2021b). The barley leaf rust resistance gene locus *Rph7* has been shown to exhibit abnormally high sequence and haplotype differences, and it shares structural similarities with the N-terminal DNA binding domain of the NAC transcription factor (ANAC019) from Arabidopsis, *Rph7* is presumed to be a NAC transcription factor (Chen et al., 2023).

5 Prospect

Although NAC transcription factors have made significant achievements in the field of plant stress resistance research, there are still many unknown areas waiting to be explored. In order to gain a more comprehensive understanding of the molecular regulatory mechanisms of NAC in plants and provide strong support for growth regulation and stress resistance enhancement, future research can be carried out in the following directions: Firstly, given the numerous and diverse functions of the NAC family, in-depth research on the interactions and synergistic regulatory mechanisms among different members will help us to have a more comprehensive understanding of the role of NAC in plant growth, development, and stress response; Secondly, current research on the role of NAC in stress response mainly focuses on the nutritional growth stage of plants, with limited understanding of its regulatory role in the reproductive stage, which will be an important direction for future research; Finally, by exploring the excellent allele variations of NAC in natural and mutant populations, and exploring their potential applications in improving crop quality, yield, and stress resistance, new strategies and ideas will be provided for genetic improvement of crops.

6 Conclusion

NAC transcription factors play a crucial role in the response mechanisms of plants to biotic and abiotic stresses. They can sense various environmental pressure signals, such as drought, salinity, low temperature, etc., thereby activating or inhibiting the expression of a series of downstream genes, helping plants adapt to adverse environmental conditions. This enables us to accurately cultivate new plants with stronger resistance to disease and stress through transgenic technology.

Authors' Contributions

ZZ, XA, LZ, GZ, and CC originated the conceptual framework; XA supervised the data compilation; ZZ performed the formal analyses; XA secured the financial support. The research was carried out by ZZ and TL, with methodological guidance from ZZ and XL. Resource acquisition was handled by XA and ZZ. The initial draft of the manuscript was prepared by XA and ZZ, and XA led the subsequent drafting, review, and editing process. All authors read and approved the final manuscript.

Acknowledgments

This study is funded by the Ministry of Finance and the Ministry of Agriculture and Rural Affairs: the National Bast Modern Agricultural Industry Technology System (CARS-16-S05).

Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Alshareef N.O., Otterbach S.L., Allu A.D., Woo Y.H., de Werk T., Kamranfar I., Mueller-Roeber B., Tester M., Balazadeh S., and Schmöckel S.M., 2022, NAC transcription factors ATAF1 and ANAC055 affect the heat stress response in Arabidopsis, Sci. Rep., 12(1): 11264.
https://doi.org/10.1038/s41598-022-14429-x
PMid:35787631 PMCid:PMC9253118

Bu Q., Jiang H., Li C.B., Zhai Q., Zhang J., Wu X., Sun J., Xie Q., and Li C., 2008, Role of the *Arabidopsis thaliana* NAC transcription factors ANAC019 and ANAC055 in regulating jasmonic acid-signaled defense responses, Cell Research, 18(7): 756-767.
https://doi.org/10.1038/cr.2008.53

Chen C., Jost M., Outram M.A., Friendship D., Chen J., Wang A., Periyannan S., Bartoš J., Holušová K., Doležel J., Zhang P., Bhatt D., Singh D., Lagudah E., Park R.F., and Dracatos P.M., 2023, A pathogen-induced putative NAC transcription factor mediates leaf rust resistance in barley, Nature Communications, 14(1): 5468.
https://doi.org/10.1038/s41467-023-41021-2
PMid:37673864 PMCid:PMC10482968

Chen Y., Sun X., Hu S., Cao Y., and Lu X.Q., 2009, Analysis of conserved domains of NAC transcription factors related to secondary growth in *Arabidopsis thaliana*, Journal of Northwest A&F University (Natural Science Edition), 37(5): 185-194, 200.

Christianson J.A., Wilson I.W., Llewellyn D.J., and Dennis E.S., 2009, The low-oxygen-induced NAC domain transcription factor ANAC102 affects viability of Arabidopsis seeds following low-oxygen treatment, Plant Physiology, 149(4): 1724-1738.
https://doi.org/10.1104/pp.108.131912

Dorjee T., Cui Y., Zhang Y., Liu Q., Li X., Sumbur B., Yan H., Bing J., Geng Y., Zhou Y., and Gao F., 2024, Characterization of NAC gene family in *Ammopiptanthus mongolicus* and functional analysis of AmNAC24, an osmotic and cold-stress-induced *NAC* gene, Biomolecules, 14(2): 182.
https://doi.org/10.3390/biom14020182
PMid:38397419 PMCid:PMC10886826

Du X., He F., Zhu B., Ren M., and Tang H., 2020, NAC transcription factors from *Aegilops markgrafii* reduce cadmium concentration in transgenic wheat, Plant and Soil, 449(1-2): 39-50.
https://doi.org/10.1007/s11104-019-04419-w

Gong F., Zhang T., Wang Z., Qi T., Lu Y., Liu Y., Zhao S., Liu R., Yi R., He J., Tu B., Zhang T., Zhang L., Hao M., Zheng Y., Liu D., Huang L., and Wu B., 2022, Genome-wide survey and functional verification of the NAC transcription factor family in wild emmer wheat, International Journal of Molecular Sciences, 23(19): 11598.
https://doi.org/10.3390/ijms231911598

Guan Q., Yue X., Zeng H., and Zhu J., 2014, The protein phosphatase RCF2 and its interacting partner *NAC019* are critical for heat stress-responsive gene regulation and thermotolerance in Arabidopsis, The Plant Cell, 26(1): 438-453.
https://doi.org/10.1105/tpc.113.118927
PMid:24415771 PMCid:PMC3963588

Guo W., Zhang J., Zhang N., Xin M., Peng H., Hu Z., Ni Z., and Du J., 2015, The wheat NAC transcription factor TaNAC2L is regulated at the transcriptional and post-translational levels and promotes heat stress tolerance in transgenic Arabidopsis, PLoS One, 10(8): e0135667.
https://doi.org/10.1371/journal.pone.0135667
PMid:26305210 PMCid:PMC4549282

Han K., Zhao Y., Sun Y., and Li Y., 2023, NACs, generalist in plant life, Plant Biotechnology Journal, 21(12): 2433-2457.
https://doi.org/10.1111/pbi.14161
PMid:37623750 PMCid:PMC10651149

Hao Y.J., Wei W., Song Q.X., Chen H.W., Zhang Y.Q., Wang F., Zou H.F., Lei G., Tian A.G., Zhang W.K., Ma B., Zhang J.S., and Chen S.Y., 2011, Soybean NAC transcription factors promote abiotic stress tolerance and lateral root formation in transgenic plants, The Plant Journal, 68(2): 302-313.
https://doi.org/10.1111/j.1365-313X.2011.04687.x

Hou X.M., Zhang H.F., Liu S.Y., Wang X.K., Zhang Y.M., Meng Y.C., Luo D., and Chen R.G., 2020, The NAC transcription factor CaNAC064 is a regulator of cold stress tolerance in peppers, Plant Science, 291: 110346.
https://doi.org/10.1016/j.plantsci.2019.110346
PMid:31928677

Hu G., Lei Y., Liu J., Hao M., Zhang Z., Tang Y., Chen A., and Wu J., 2019, The ghr-miR164 and GhNAC100 modulate cotton plant resistance against *Verticillium dahlia*, Plant Science, 293: 110438.
https://doi.org/10.1016/j.plantsci.2020.110438
PMid:32081275

Hu H., Dai M., Yao J., Xiao B., Li X., Zhang Q., and Xiong L., 2006, Overexpressing a NAM, ATAF, and CUC (NAC) transcription factor enhances drought resistance and salt tolerance in rice, Proc. Natl. Acad. Sci. USA, 103(35): 12987-12992.
https://doi.org/10.1073/pnas.0604882103
PMid:16924117 PMCid:PMC1559740

Jian W., Zheng Y., Yu T., Cao H., Chen Y., Cui Q., Xu C., and Li Z., 2021, SlNAC6, A NAC transcription factor, is involved in drought stress response and reproductive process in tomato, Journal of Plant Physiology, 264: 153483.
https://doi.org/10.1016/j.jplph.2021.153483

Li S., Jing X., Tan Q., Wen B., Fu X., Li D., Chen X., Xiao W., and Li L., 2023, The NAC transcription factor MdNAC29 negatively regulates drought tolerance in apple, Frontiers in Plant Science, 14: 1173107.
https://doi.org/10.3389/fpls.2023.1173107
PMid:37484477 PMCid:PMC10359905

Li S., Wang N., Ji D., Zhang W., Wang Y., Yu Y., Zhao S., Lyu M., You J., Zhang Y., Wang L., Wang X., Liu Z., Tong J., Xiao L., Bai M., and Xiang F., 2019, A GmSIN1/GmNCED3s/GmRbohBs feed-forward loop acts as a signal amplifier that regulates root growth in soybean exposed to salt stress, The Plant Cell, 31(9): 2107-2130.
https://doi.org/10.1105/tpc.18.00662
PMid:31227558 PMCid:PMC6751118

Lin J., and Wu S., 2004, Molecular events in senescing Arabidopsis leaves, The Plant Journal, 39(4): 612-628.
https://doi.org/10.1111/j.1365-313X.2004.02160.x
PMid:15272878

Liu C., Wang B., Li Z., Peng Z., and Zhang J., 2018a, TsNAC1 is a key transcription factor in abiotic stress resistance and growth, Plant Physiology, 176(1): 742-756.
https://doi.org/10.1104/pp.17.01089

Liu Q., Yan S., Huang W., Yang J., Dong J., Zhang S., Zhao J., Yang T., Mao X., Zhu X., and Liu B., 2018b, NAC transcription factor ONAC066 positively regulates disease resistance by suppressing the ABA signaling pathway in rice, Plant Molecular Biology, 98(4-5): 289-302.
https://doi.org/10.1007/s11103-018-0768-z
PMid:30387038

Lu H., Li N., Jiang K., Wang Y., and Jiang J., 2024, Research advance on NAC transcription factors regulating plant development and stress responses, Plant Physiology Journal, 60(2): 271-283.

Mao Y., Xu J., Wang Q., Li G., Tang X., Liu T., Feng X., Wu F., Li M., Xie W., and Lu Y., 2021, A natural antisense transcript acts as a negative regulator for the maize drought stress response gene *ZmNAC48*, J. Exp. Bot., 72(7): 2790-2806.
https://doi.org/10.1093/jxb/erab023

Mei C., 2023, Functional study and regulatory mechanism of MdNAC104 transcription factor in apple cold stress, Dissertation for Ph.D., Northwest A&F University, Supervisor: Ma F.W., pp.117.

Meng X., Liu S., Zhang C., He J., Ma D., Wang X., Dong T., Guo F., Cai J., Long T., Li Z., and Zhu M., 2022, The unique sweet potato NAC transcription factor IbNAC3 modulates combined salt and drought stresses, Plant Physiol., 191(1): 747-771.
https://doi.org/10.1093/plphys/kiac508
PMid:36315103 PMCid:PMC9806649

Min X., Jin X., Zhang Z., Wei X., Ndayambaza B., Wang Y., and Liu W., 2020, Genome-wide identification of NAC transcription factor family and functional analysis of the abiotic stress-responsive genes in *Medicago sativa* L., Journal of Plant Growth Regulation, 39(1): 324-337.
https://doi.org/10.1007/s00344-019-09984-z

Mondal B., Mukherjee A., Mazumder M., De A., Ghosh S., and Basu D., 2022, Inducible expression of truncated NAC62 provides tolerance against *Alternaria brassicicola* and imparts developmental changes in Indian mustard, Plant Science, 324: 111425.
https://doi.org/10.1016/j.plantsci.2022.111425
PMid:36007630

Morishita T., Kojima Y., Maruta T., Nishizawa-Yokoi A., Yabuta Y., and Shigeoka S., 2009, Arabidopsis NAC transcription factor, ANAC078, regulates flavonoid biosynthesis under high-light, Plant and Cell Physiology, 50(12): 2210-2222.
https://doi.org/10.1093/pcp/pcp159

Mukhtar A., and Stockle C.O., eds., 2016, Quantification of climate variability, adaptation and mitigation for agricultural sustainability, Springer, Cham., pp.165-180.

Nuruzzaman M., Sharoni A.M., and Kikuchi S., 2013, Roles of NAC transcription factors in the regulation of biotic and abiotic stress responses in plants, Frontiers in Microbiology, 4: 248.
https://doi.org/10.3389/fmicb.2013.00248
PMid:24058359 PMCid:PMC3759801

Ou X., Sun L., Chen Y., Zhao Z., and Jian W., 2024, Characteristics of NAC transcription factors in Solanaceae crops and their roles in responding to abiotic and biotic stresses, Biochemical and Biophysical Research Communications, 709: 149840.
https://doi.org/10.1016/j.bbrc.2024.149840
PMid:38564941

Puranik S., Sahu P.P., Srivastava S.P., and Prasad M., 2012, NAC proteins: regulation and role in stress tolerance, Trends in Plant Science, 17(6): 369-381.
https://doi.org/10.1016/j.tplants.2012.02.004
PMid:22445067

Shinde H., Dudhate A., Tsugama D., Gupta S.K., Liu S., and Takano T., 2019, Pearl millet stress-responsive NAC transcription factor PgNAC21 enhances salinity stress tolerance in Arabidopsis, Plant Physiology and Biochemistry, 135: 546-553.
https://doi.org/10.1016/j.plaphy.2018.11.004
PMid:30447941

Sun L., Li D., Zhang H., and Song F., 2012, The role of NAC transcription factors in plant disease resistance and abiotic stress response, Heredity, 34(8): 993-1002.
https://doi.org/10.3724/SP.J.1005.2012.00993
PMid:22917904

Sun L., Zhang H., Li D., Huang L., Hong Y., Ding X.S., Nelson R.S., Zhou X., and Song F., 2013, Functions of rice NAC transcriptional factors, ONAC122 and ONAC131, in defense responses against *Magnaporthe grisea*, Plant Molecular Biology, 81(1-2): 41-56.
https://doi.org/10.1007/s11103-012-9981-3
PMid:23103994

Walker E.L., and Connolly E.L., 2008, Time to pump iron: Iron-deficiency-signaling mechanisms of higher plants, Current Opinion in Plant Biology, 11(5): 530-535.
https://doi.org/10.1016/j.pbi.2008.06.013
PMid:18722804

Wang G., Yuan Z., Zhang P., Liu Z., Wang T., and Wei L., 2020a, Genome-wide analysis of NAC transcription factor family in maize under drought stress and rewatering, Physiology and Molecular Biology of Plants, 26(4): 705-717.
https://doi.org/10.1007/s12298-020-00770-w

Wang Q., Liu Q., Gao Y., and Liu X., 2017, Research progress on the response mechanism of plants to salt alkali stress, Journal of Ecology, (16): 5565-5577.

Wang Y., 2020, Study on stress tolerance of transgenic tobacco overexpressing *Lilium pumilum* LpNAC5 and LpNAC13, Thesis for M.S., Northeast Forestry University, Supervisor: Zhang Y.N., pp.93.

Wang Y., Cao S., Guan C., Kong X., Wang Y., Cui Y., Liu B., Zhou Y., and Zhang Y., 2020b, Overexpressing the NAC transcription factor LpNAC13 from *Lilium pumilum* in tobacco negatively regulates the drought response and positively regulates the salt response, Plant Physiology and Biochemistry, 149: 96-110.
https://doi.org/10.1016/j.plaphy.2020.01.036
PMid:32058898

Wang Z., Xia Y., Lin S., Wang Y., Guo B., Song X., Ding S., Zheng L., Feng R., Chen S., Bao Y., Sheng C., Zhang X., Wu J., Niu D., Jin H., and Zhao H., 2018, Osa-miR164a targets OsNAC60 and negatively regulates rice immunity against the blast fungus *Magnaporthe oryzae*, The Plant Journal, 95(4): 584-597.
https://doi.org/10.1111/tpj.13972
PMid:29775494

Xi Y., Ling Q., Zhou Y., Liu X., and Qian Y., 2022, ZmNAC074, a maize stress-responsive NAC transcription factor, confers heat stress tolerance in transgenic Arabidopsis, Frontiers in Plant Science, 13: 986628.
https://doi.org/10.3389/fpls.2022.986628
PMid:36247610 PMCid:PMC9558894

Xin Y., Huang R., Xu M., and Xu L., 2023, Transcriptome-wide identification and response pattern analysis of the *Salix integra* NAC transcription factor in response to Pb stress, International Journal of Molecular Sciences, 24(14): 11334.
https://doi.org/10.3390/ijms241411334
PMid:37511094 PMCid:PMC10379125

Xiong C., Guo Z., Zhou Q., Cheng Y., Ma Q., Cai Z., and Nian H., 2024, Function analysis of the soybean transcription factor NAC1 in tolerance to low phosphorus, Scientia Agricultura Sinica, 57(3): 442-453.

Xu Z.Y., Kim S.Y., Hyeon D.Y., Kim D.H., Dong T., Park Y., Jin J.B., Joo S.H., Kim S.K., Hong J.C., Hwang D., and Hwang I., 2013, The Arabidopsis NAC transcription factor ANAC096 cooperates with bZIP-Type transcription factors in dehydration and osmotic stress responses, The Plant Cell, 25(11): 4708-4724.
https://doi.org/10.1105/tpc.113.119099
PMid:24285786 PMCid:PMC3875745

Yan H., Liu B., Cui Y., Wang Y., Sun S., Wang J., Tan M., Wang Y., and Zhang Y., 2022, LpNAC6 reversely regulates the alkali tolerance and drought tolerance of *Lilium pumilum*, Journal of Plant Physiology, 270: 153635.
https://doi.org/10.1016/j.jplph.2022.153635
PMid:35124291

Yong Y., Zhang Y., and Lyu Y., 2019, A stress-responsive NAC transcription factor from tiger lily (LlNAC2) interacts with LlDREB1 and LlZHFD4 and enhances various abiotic stress tolerance in Arabidopsis, International Journal of Molecular Sciences, 20(13): 3225.
https://doi.org/10.3390/ijms20133225
PMid:31262062 PMCid:PMC6651202

Zhang X., Long Y., Chen X., Zhang B., Xin Y., Li L., Cao S., Liu F., Wang Z., Huang H., Zhou D., and Xia J., 2021a, A NAC transcription factor OsNAC3 positively regulates ABA response and salt tolerance in rice, BMC Plant Biology, 21(1): 546.
https://doi.org/10.1186/s12870-021-03333-7
PMid:34800972 PMCid:PMC8605558

Zhang Y., Geng H., Cui Z., Wang H., and Liu D., 2021b, Functional analysis of wheat NAC transcription factor, TaNAC069, in regulating resistance of wheat to leaf rust fungus, Frontiers in Plant Science, 12: 604797.
https://doi.org/10.3389/fpls.2021.604797
PMid:33790919 PMCid:PMC8005738

Zhou H., Huang H., Xu B., Su X., Deng R., Hong Y., Jiang M., Song F., and Zhang H., 2017, Functions of NAC transcription factors in plant responses to biotic and abiotic stresses, Plant Physiology Journal, 53(8): 1372-1382.