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REVIEW

Structural and functional insights into NAC transcription factors in tomato stress responses and development

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Abstract

Plants inevitably encounter biotic and abiotic stresses during growth and development. NAC transcription factors, as a plant-specific regulatory family, play a pivotal role in various stress responses and developmental processes. This study systematically reviews the structural characteristics, functional classifications, and recent advances in the research on NAC transcription factors in tomato, highlighting their potential mechanisms and regulatory networks in stress responses. The findings provide theoretical foundations and research insights for further functional elucidation of NAC transcription factors and for optimizing genetic improvement of tomato stress adaptability.

Keywords: growth and development, NAC transcription factor, stress response, tomato.

Introduction

In natural environments, the growth and development of plants are frequently impeded by a variety of stresses. These can be categorized into biotic stresses, such as those caused by fungi and bacteria, and abiotic stresses, including factors like low temperature, drought, and salinity (Zhu, 2016). These stresses impact plant photosynthesis, osmotic adjustment, and nutrient uptake, thereby inhibiting plant growth and ultimately resulting in a reduced crop yield and quality. To adapt to the dynamic changes in the environment, plants have evolved a series of complex defense mechanisms that are precisely regulated at the molecular, cellular, biochemical, and physiological levels to respond to various stresses. Among them, transcription factors (TFs) are key regulators that control the majority

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Abbreviations: ABA - abscisic acid; ABC - ATP-binding cassette; CAT - catalase; CUC2 - cup-shaped cotyledon; ETI - effector-triggered immunity; JA - jasmonic acid; MDA - malondialdehyde; NAM - no apical meristem; NLP4 - NAM-like protein; POD - peroxidase; *Pst* DC3000 - *Pseudomonas syringae* pv. *tomato* DC3000; PTI - pattern-triggered immunity; ROS - reactive oxygen species; SA - salicylic acid; SOD - superoxide dismutase; TF - transcription factor; TLCV - tomato leaf curl virus; ToBRFV - tomato brown rugose fruit virus; ToCV - tomato chlorosis virus; TSWV - tomato spotted wilt virus; TYLCV - tomato yellow leaf curl virus; VIGS - virus-induced gene silencing.

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of stress response genes and signal transduction pathways. They are activated by different pathways of signal transduction and can directly or indirectly combine with *cis*-acting elements to modulate the transcription efficiency of target genes, which play a crucial role in the regulation of plant response to biotic and abiotic stresses.

Hundreds of genes encoding plant transcription factors have been discovered, such as WRKY, NAC, MYB, and AP2/ERF, and have been shown to regulate gene expression in response to abiotic and biotic stresses. Among them, the NAC (NAM, CUC, and ATAF) family is one of the most abundant and plant-specific, playing pivotal roles in physiological processes related to plant development and stress tolerance. The NAC transcription factor family derives its name from the acronym of three founding members: NAM (No Apical Meristem) from *Nicotiana tabacum*, ATAF1/2 (*Arabidopsis* Transcription Activation Factor 1/2), and CUC2 (Cup-Shaped Cotyledon 2) from *Arabidopsis thaliana* (Souer et al., 1996; Aida et al., 1997). NAM regulates apical meristem development, ATAF1/2 participates in stress responses, and CUC2 controls organ boundary formation. These three proteins collectively represent the core functions of this family in plant development, stress adaptation, and morphological establishment. With the development of genomic sequencing, several NAC genes have been identified in various species. For example, whole-genome studies have identified 117 NAC genes in *Arabidopsis thaliana* (Kikuchi et al., 2000), 158 in indica rice (Singh et al., 2021), 70 in grape (Mohanta et al., 2020) and 154 in tobacco (Mohanta et al., 2020).

Tomato (*Solanum lycopersicum* L.) is one of the most widely cultivated vegetable crops globally, rich in vitamin C, folic acid, and other nutrients. In China, the cultivation area and yield of tomatoes are accounting for approximately 30% of the global tomato production, thereby holding a significant commercial value in the vegetable industry (Liu et al., 2023). In tomato, the first reported NAC transcription factor functioned in regulating the leaf morphogenesis and lateral bud development (Berger et al., 2009). As research progresses, the roles of an increasing number of tomato NAC transcription factors in response to biotic and abiotic stresses have been unveiled. This review synthesizes the advancements in understanding their functions and regulatory mechanisms under various stress conditions.

Structural features and classification of NAC transcription factors

The most typical structural feature of NAC transcription factors is the presence of a highly conserved N-terminal NAC domain and a highly variable C-terminal transcriptional regulatory region (Mohammed et al., 2020). The NAC domain is a highly twisted antiparallel β-sheet and α-helix structure wrapped on both sides, generally consisting of about 150 amino acids (Ernst et al., 2004), and encompassing five conserved substructures (Fig. 1). Using statistical analysis of the amino acid sequence patterns of the five substructures their conservation was ranked from least to most conserved as follows: E < B < D < C < A (Ooka et al., 2003). Substructure A may participate in the formation of functional dimers; substructures C and D are highly conserved and contain essential positively charged amino acids necessary for binding to DNA. Furthermore, substructure D contains a nuclear localization signal mediated by lysine residues, which is crucial for the nuclear localization and recognition of specific *cis*-elements in the promoter region of target genes by NAC transcription factors. A few NAC proteins have a negative regulatory domain within substructure D, which can suppress transcription activity. Substructures B and E exhibit high variability, potentially contributing to the functional diversity of NAC genes (Singh et al., 2021). The C-terminal transcriptional regulatory region of NAC transcription factors is composed of simple amino acid repeat sequences with high frequency occurrences, displaying significant diversity and conferring either transcriptional activation or repression activity (Rong et al., 2020).

The NAC transcription factor family is indeed widely distributed and numerous, with a complex classification system that lacks a unified standard across different species. NAC transcription factors were initially classified into NAM, ATAF, and CUC subfamilies, based on their structural characteristics (Kikuchi et al., 2000). This classification was a foundational step in understanding the diversity within the NAC family. Subsequently, 105 NAC transcription factors from *Arabidopsis thaliana* and 75 from rice were further divided into group I and group II, based on the degree of similarity in the amino acid sequences of their N-terminal structural domains (Ooka et al., 2003). Group I consisted of 14 subgroups, while group II had 4 subgroups, providing a more detailed framework for NAC classification. In tomato, 104 NAC transcription factor genes were identified through bioinformatics analysis (Jiang et al., 2016). Although functional annotation of tomato NAC transcription factors remains limited, a comprehensive phylogenetic analysis of the entire tomato genome was performed to classify this family, providing a foundation for further research. The phylogenetic tree was constructed using the Neighbor-Joining (NJ) method in *MEGA 11* software, based on the sequence homology of the NAC domain, with 1 000 bootstrap replicates for statistical support. This analysis revealed that the NAC transcription factor family

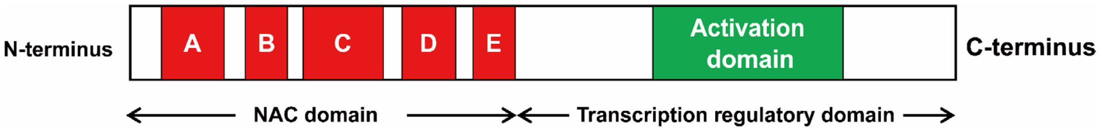

Fig. 1. Structural characterization of plant NAC transcription factors.

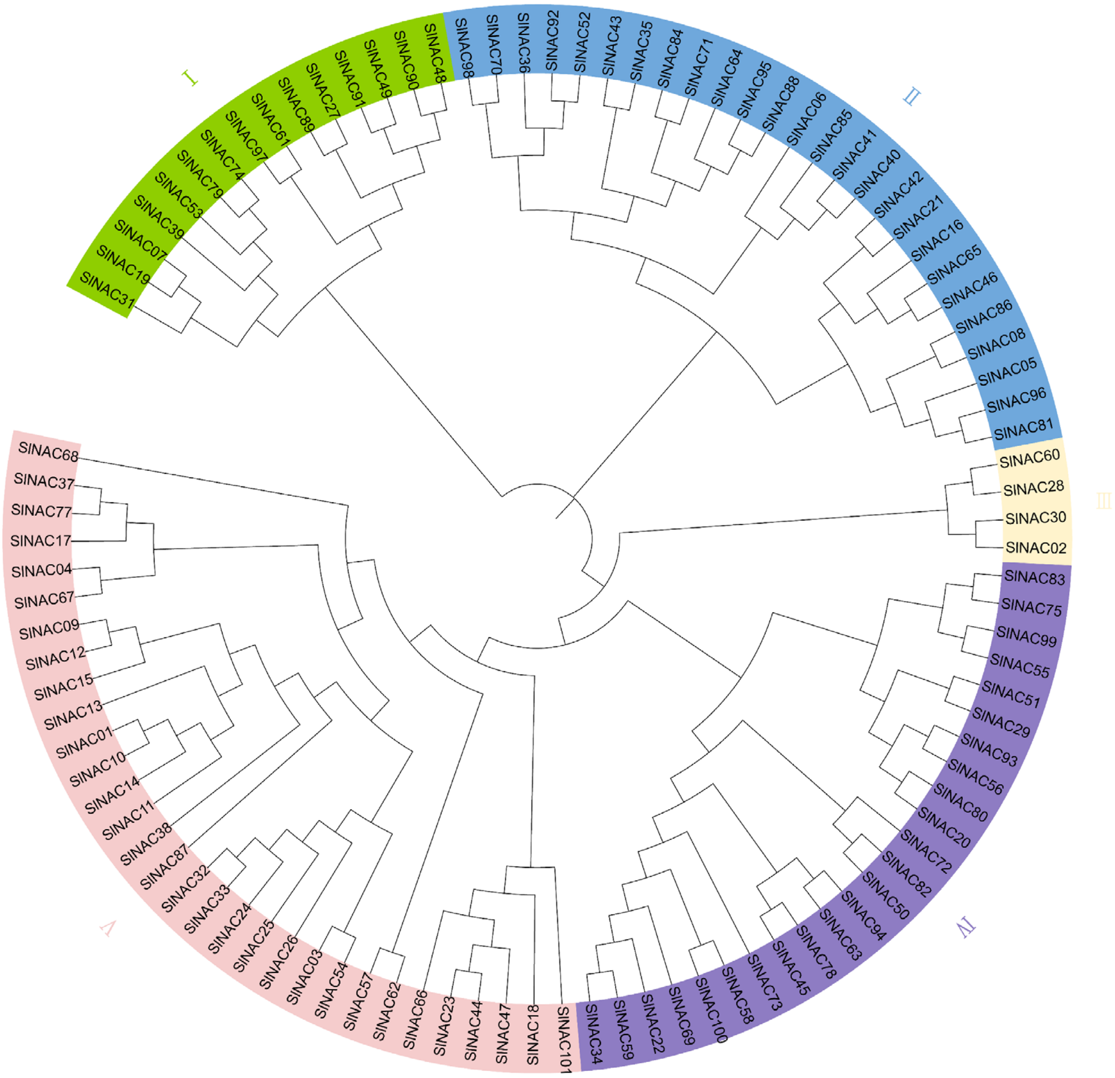

Fig. 2. Phylogenetic tree of the tomato NAC family. I - V represent different clades of the NAC family in tomato.

was classified into five groups. Notably, Class III contained the fewest members, with only four genes, whereas Class V had the largest number, comprising 31 genes (Fig. 2).

The regulatory role of NAC transcription factors in tomato growth and development

Plant growth and development is a complex, multi-tiered process that unfolds across various stages, and NAC transcription factors play an important role in tomato growth and development, such as root development, flower organ formation, leaf senescence, and fruit ripening (Fig. 3).

Studies have shown that *Solanum lycopersicum NAC1* (*SlNAC1*) plays a key regulatory role in tomato fruit ripening and lateral root development. Overexpression of *SlNAC1* can increase the number of lateral roots and regulate tomato fruit ripening through ethylene-dependent and abscisic acid-dependent pathways (Ma et al., 2014). SlNAC1 forms a regulatory complex with transcription factor *SlERF109*-like, which regulates the degradation of chlorophyll, the accumulation of carotenoids, the synthesis of ethylene, and the metabolism of cell wall genes, negatively regulating the tomato fruit ripening process (Sun et al., 2024). In addition, compared with the wild type, *SlNAC1* mutants show delayed ripening, deeper red fruit color, increased total carotenoid and lycopene content, slower fruit softening, enhanced cell wall metabolism and abscisic acid (ABA) synthesis, and ultimately yellow or orange fruit (Ma et al., 2014). This reveals that SlNAC1 plays a multi-level role in the fruit ripening process by regulating pigment metabolism, cell wall degradation, and hormone synthesis. *SlNAC3* is highly expressed in tomato flower and root tissues, suggesting that it may play an important role in the growth and development of flowers and roots (Jing et al., 2018). *SlNAM2* participates in the establishment of the boundary between the cyclical whorls and the calyx, and in plant aging responses (Hendelman et al., 2013). Similarly, the NAC transcription factor *SlNAM1* also positively regulates tomato fruit maturation

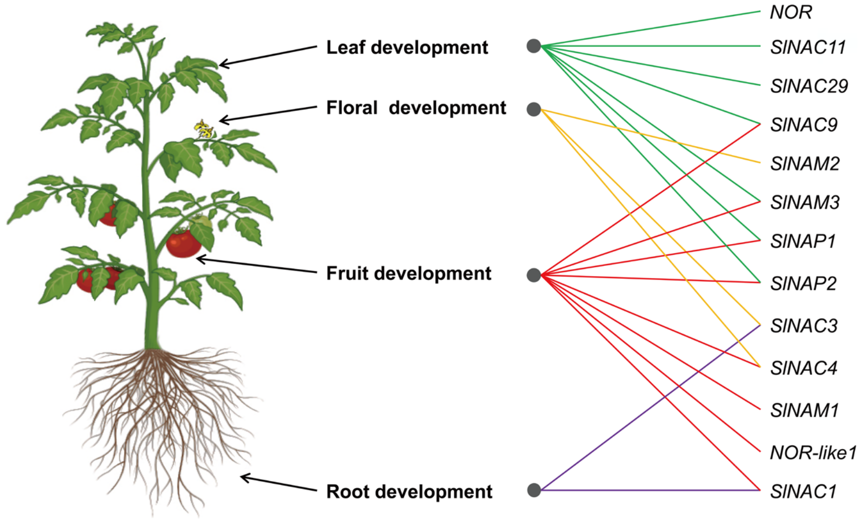

Fig. 3. NAC transcription factors involved in tomato growth and development.

by regulating the synthesis of ethylene (Gao et al., 2021). Additionally, *SlNAP1* is a key NAC transcription factor that positively regulates tomato fruit development. Overexpression of *SlNAP1* has been shown to suppress overall plant growth while concurrently enhancing fruit yield (Wang et al., 2020). This dual effect is mediated through the activation of *SlGA2ox1* and *SlGA2ox5*, which are key genes involved in the degradation of gibberellins, thereby hastening the maturation process of the fruit. Furthermore, CRISPR/Cas9 knockout mutants of SlNAP1 exhibit delayed ethylene production and fruit maturation, and the interaction between SlNAP1 and gibberellin (GA) receptor SlGID1 may amplify SlNAP1's regulatory influence, suggesting a complex interplay in the hormonal control of fruit development (Li et al., 2024). SlNAP2 regulates tomato fruit maturity and yield by directly regulating the expression of ABA synthesis gene *SlNCED* and ABC (ATP-binding cassette) transporter gene *SlABCG40* (Ma et al., 2018). The NAC transcription factor *NOR-like1* affects tomato fruit size by regulating the number of cell layers and cell area, and its overexpression in plant causes the fruit to become smaller, while knockout plant leads to an increase in fruit size. The mechanism of *NOR-like1* regulation mechanism includes inhibiting the expression of *SlGRAS2*, *SlFW3.2*, and *SlFW11.3* and activating the expression of *ARF9* (Peng et al., 2024). During fruit softening, NOR-like1 regulates the metabolism of cell wall-related genes to accelerate cell wall degradation, increase water-soluble pectin and ionic-soluble pectin, and reduce the amount of covalently bound pectin and hemicellulose (Peng et al., 2024). During epidermal tissue development, NOR-like1 activates *SlGPAT6* and *SlCD2* to promote cuticle deposition, while inhibiting the expression of *SlKCS1* and other wax-related genes to reduce wax accumulation (Liu et al., 2024). Additionally, NOR-like1 positively regulates fruit maturity, and mutants exhibit reduced ethylene production, delayed softening, slower chlorophyll degradation, and reduced lycopene accumulation, indicating the crucial role of NOR-like1 in fruit maturity (Gao et al., 2018).

Leaf senescence is an essential physiological process in plant growth and development. In tomato, *SlNAC11* has the highest expression in young leaves, and its expression decreases in mature leaves and senescent leaves, suggesting that this gene may participate in the regulation of leaf development (Wang et al., 2017). *SlNAP2* is upregulated in senescent leaves, and inhibiting its expression in tomato can prevent leaf senescence and improve fruit yield and sugar content, which may be due to the prolonged photosynthesis time in aging tomato plants (Ma et al., 2018). SlNAM3 regulates the expression of important mature-related genes to participate in the regulation of tomato leaf senescence and fruit ripening (Lin et al., 2022). Furthermore, NAC transcription factor *NOR* regulates the expression of related aging genes such as *SlSAG15*, *SlSAG113*, *SlSGR1*, and *SlYLS4* to regulate plant aging. Gao et al. (2020) and Ma et al. (2018) found that SlNAP2 acts upstream of NOR to regulate the expression of NOR. *SlNAC29* is highly expressed in aging and senescent leaves but low in young and mature leaves. Overexpressing *SlNAC29* reduces plant height, decreases chlorophyll content and photosynthesis, and accelerates leaf senescence. In contrast, *SlNAC29* mutants show delayed senescence, no visible yellowing, three times higher chlorophyll levels, and reduced expression of senescence and chlorophyll degradation genes, indicating that *SlNAC29* negatively regulates aging (Wang et al., 2021).

The regulatory role of NAC transcription factors in tomato abiotic stress response

Abiotic stress refers to environmental stress caused by non-biotic factors such as drought, temperature, salinity, and heavy metals, which poses a serious threat to plant growth and development and agricultural production. These environmental stresses can cause plants to stunted plant growth, early senescence, reduce yield, and even die. To adapt to abiotic stress, plants have evolved complex molecular regulatory mechanisms to regulate the expression of stress-related genes, thereby enhancing their stress tolerance. Within this regulatory network, NAC transcription factors play a crucial regulatory role in tomato's response to abiotic stress.

Drought stress: Drought is one of the most severe non-biological stresses that affect agricultural production, inhibiting plant growth and development and limiting crop yield and quality. Under drought stress, tomato plant growth is significantly inhibited, and fruit yield is greatly reduced. Research has shown that NAC transcription factors play an important role in tomato's response to drought stress. In tomato, *SlNAC4* is induced by jasmonic acid and has a positive regulatory role in tomato's response to drought stress. The *SlNAC4*-RNAi silenced line showed higher leaf water loss rate, lower water content, and lower chlorophyll content compared to the wild-type, indicating that *SlNAC4* positively regulates drought stress response in tomato (Zhu et al., 2014). Silencing of *SlSRN1* (*Solanum lycopersicum* stress-related NAC1) enhances tomato's tolerance to drought stress, indicating that *SlSRN1* negatively regulates tomato's response to drought stress (Liu et al., 2014). Overexpression of NAC gene *SlNAP1* significantly enhances tomato's drought resistance (Wang et al., 2020). Drought stress can induce the expression of *SlNAC35*, and overexpression of tomato *SlNAC35* gene in tobacco enhances its drought resistance by affecting growth hormone signaling and the expression of several growth hormone response factor genes (Wang et al., 2016). Drought stress also promotes the expression of *SlNAC6*, and *SlNAC6*-RNAi tomato lines exhibit reduced growth, shorter stature, and lower drought tolerance compared to wild-type plants. Conversely, overexpression of *SlNAC6* enhances drought resistance, indicating that *SlNAC6* positively regulates tomato's response to drought stress (Jian et al., 2021). In *Arabidopsis thaliana*, overexpression of *SlNAC2* has been shown to modulate glutathione metabolism, thereby improving tolerance to both salt and drought stress (Borgohain et al., 2019). Similarly, in tobacco, overexpression of *SlNAC2* enhances drought resistance by delaying leaf senescence, maintaining relative water content, regulating glutathione metabolism, and increasing proline content (van Beek et al., 2021). Additionally, Wang et al. (2017) found that *SlNAC11* expression is induced by drought, cold, and heat stress, and that *SlNAC11*-RNAi plants exhibit reduced drought tolerance compared to wild-type plants. Moreover, Thirumalaikumar et al. (2018) demonstrated that the NAC gene *JUNGBRUNNEN1* (*SlJUB1*) plays a crucial role in drought tolerance in tomato by regulating the expression of drought-related genes, including *SlDREB1*, *SlDREB2*, and *SlDELLA*. *SlNAC3*, which is associated with stress responses, shows reduced expression under both drought and salt stress in tomato (Han et al., 2012). Although these NAC genes have been implicated in regulating tomato's response to drought stress, the specific molecular mechanisms and key genes involved in this process remain largely unexplored.

Salt stress: Salt stress is one of the most common non-biotic stressors and is one of the main environmental factors limiting plant growth and productivity. Soil salinity affects over 20% of the world's cultivated land. It initially triggers osmotic stress, inhibiting seedling growth, followed by ion toxicity, which accelerates leaf senescence and ultimately reduces crop yield (Balasubramaniam et al., 2023). Tomatoes are moderately salt-sensitive plants, and there have been some studies on the role of tomato NAC genes in salt stress. For example, overexpression of *SlNAC2* in *Arabidopsis thaliana* enhances tolerance to salt stress (Borgohain et al., 2019), while *SlNAC11*-RNAi plants show less tolerance to salt stress (Wang et al., 2017). Zhu et al., (2014) found that injury, salt, dehydration, and high/low temperature can induce the expression of *SlNAC4*, and *SlNAC4*-RNAi transgenic plants show lower tolerance to salt stress and drought stress. Wang et al., (2016) reported that overexpression of *SlNAC35* in tobacco promotes root growth and development under salt stress, enhancing the plant's tolerance to salt stress. Han et al. (2012) demonstrated that salt stress significantly inhibits the transcriptional expression of *SlNAC3* in seedlings, indicating that *SlNAC3* plays a key role in salt stress response. Yang et al. (2011) isolated two NAC genes related to salt stress response (*SlNAC1* and *SlNAM1*), and analyzed their expression in tomato, finding that both genes are induced by salt stress and involved in regulating tomato salt tolerance. *SlNAP1* is significantly induced by salt stress, and the antioxidant enzyme activities (SOD, POD, and CAT) of the transgenic plants overexpressing *SlNAP1* are significantly better than those of the wild type under salt stress. The Na^+ content is lower in the transgenic plants and they accumulate less MDA, H_2O_2, and O^{2-}, and the activities of SOD, POD, and CAT, as well as the synthesis of antioxidant enzyme genes, are significantly higher, indicating that SlNAP1 positively regulates tomato's salt tolerance (Du et al., 2023).

Temperature stress: As a key environmental factor, temperature significantly impacts plant growth and development, with both low and high temperature extremes inducing stress responses. Low temperature stress adversely affects plant physiology by compromising cell membrane fluidity and enzyme activity, leading to reduced photosynthetic efficiency, metabolic imbalance, and impaired nutrient transport. Conversely, high temperature stress negatively impacts reproductive processes through suppressed pollen viability, impaired fertilization, and disrupted grain filling or fruit development, while simultaneously inhibiting photosynthetic activity (Arshad et al., 2017). Studies have demonstrated that NAC transcription factors play an important role in response of tomato to temperature stress. The expression of *SlNAC1* is induced by low temperature stress (4°C) and high temperature stress (40°C), and its overexpression in transgenic plants enhances cold tolerance by maintaining higher maximum photochemical efficiency of photosystem II and oxygen evolution activity (Ma et al., 2018). Additionally, the *SlNAC1* gene positively regulates tomato's high-temperature resistance; inhibiting the expression of *SlNAC1* reduces the accumulation of heat shock proteins (HSPs) and osmotic regulators in plants, lowering the activity of antioxidant enzymes and thus diminishing tomato plants' resistance to high temperature stress (Liang, 2015). *SlNAC35* plays a role in plant responses to cold stress, and overexpression of *SlNAC35* in transgenic plants showed higher chlorophyll content, fresh weight, and lower accumulation of reactive oxygen species and membrane damage in cold stress, indicating that *SlNAC35* positively regulates tomatoes' response to cold stress (Wang et al., 2018). Zuo et al. (2014) found that the expression of *LeNLP4* (NAM-like protein) is induced by low temperature stress, and overexpression of *LeNLP4* in plants showed higher growth rate, maximum photochemical efficiency of photosystem II, antioxidant enzyme activity, and lower malondialdehyde (MDA) content and relative electrical conductivity, indicating that the overexpression of *LeNLP4* enhances tomato tolerance to low temperature stress. Under low temperature stress, tobacco overexpressing *SlNAM1* exhibited higher germination and photosynthetic rates, concurrently reducing the content of H_2O_2 and O^{2-}, as well as cell membrane damage, which indicates that the overexpression of *SlNAM1* enhances the cold stress tolerance of transgenic tobacco (Li et al., 2016). In contrast, plants overexpressing *SlNAC73* displayed increased cell membrane damage and reactive oxygen species (ROS) accumulation under high-temperature stress. However, *SlNAC73*-RNAi plants exhibited improved tolerance to heat stress, suggesting that *SlNAC73* acts as a negative regulator of high-temperature stress tolerance (Ming, 2019). Similarly, overexpression of *SlJA2* (*Solanum lycopersicum* Jasmonic Acid 2) in tobacco plants increased stomatal pore size and water loss, exacerbated photosynthetic organ damage, accelerated chlorophyll degradation, and restricted proline synthesis under heat stress. These physiological changes resulted in severe oxidative damage, supporting the role of *SlJA2* as a negative regulator of plant heat tolerance (Liu et al., 2017). Additionally, SlNAC3 has been shown to negatively regulate cold tolerance by modulating ethylene synthesis genes and promoting excessive ethylene release under cold stress. Unlike the conventional CBF-dependent cold tolerance pathway, SlNAC3 primarily functions through a CBF-independent mechanism to influence cold stress responses (Wang et al., 2024).

Heavy metal stress: Human activities and industrial production have made the problem of heavy metal pollution in the environment increasingly serious. Heavy metals not only inhibit plant growth but also reduce the rate of photosynthesis, reduce the accumulation of carbohydrates and proline, and increase malondialdehyde content, thus causing a serious impact on crop yield. However, there is still relatively little research on the role of NAC transcription factors in tomato response to heavy metal stress. NAC genes are involved in the early aluminum stress response of tomato root tips. Jin (2021) screened out two NAC genes related to tomato acid-resistant aluminum tolerance, named *NAC063* and *NAC064*. Under aluminum treatment conditions, *SlNAC063* was specifically upregulated in tomato roots. Plants encounter numerous abiotic stressors during growth and development, while simultaneously facing biotic threats from pathogens such as bacteria, fungi, and viruses. These combined stresses often result in reduced biomass accumulation and plant mortality, ultimately compromising both plant growth and crop yield.

Oxidative stress: Oxygen is one of the essential factors for plant survival, mainly involved in metabolic processes, respiration, and oxidative phosphorylation. However, during metabolic processes, oxygen is activated to produce reactive oxygen species, which causes damage to the plasma membrane permeability, irreversible metabolic dysfunction, and cell death. In tomato, silencing *SlSRN1* (*Solanum lycopersicum* Stress-related NAC1) enhances tolerance to oxidative and drought stress while accelerating reactive oxygen species (ROS) accumulation, indicating that *SlSRN1* is a negative regulator of tomato oxidative stress response (Liu et al., 2014). ABA is a key hormone for plant growth and development, and plays an important role in integrating various stress signals and regulating downstream stress responses. Plants adapt to changing physiological and environmental conditions by regulating ABA. *SlNAC3* may play a potential role in regulating ABA-related drought stress (Han et al., 2012).

The regulatory role of NAC transcription factors in tomato biotic stress

In addition to suffering from various non-biological stresses during plant growth and development, plants are also attacked by bacteria, fungi, viruses, *etc*., leading to a reduction in plant biomass and even death, ultimately affecting plant growth and crop yield (Bigeard et al., 2015). NAC transcription factors not only participate in plant growth and development and abiotic stress, but also participate in regulating the defense response to biotic stresses. Some NAC proteins mainly induce cell death and hypersensitive response in the infected site by activating disease-related genes (Jensen et al., 2007; Kaneda et al., 2009; Seo et al., 2010). In contrast, NAC genes may mainly inhibit disease-related genes (Delessert et al., 2005; Bu et al., 2008). Some NAC proteins interact directly with virus-encoded proteins to enhance or inhibit the spread of the virus (Ren et al., 2000; Selth et al., 2005; Yoshii et al., 2009).

There have been some studies on the response of tomato NAC transcription factors to disease resistance. Tomato leaf spot disease is a bacterial disease caused by *Pseudomonas syringae* pv. *tomato* DC3000 (*Pst* DC3000) (Xin and He, 2013). Tomato *SlNAC1* was upregulated during *Pseudomonas* infection and played a role in the basic defense of tomato against *Pseudomonas* (Huang et al., 2013). Two homologous tomato NAC transcription factors, *JA2* and *JA2L*, regulate *Pst* DC3000-induced stomatal movement through different mechanisms. JA2 regulated ABA biosynthesis gene expression to regulate ABA-mediated stomatal closure, while JA2L regulated salicylic acid (SA) metabolism gene expression to act on the JA/COR-mediated stomatal reopening (Du et al., 2014). *SlNAC35* was induced by bacterial pathogens and overexpression of *SlNAC35* enhanced the resistance of transgenic tobacco to *Pseudomonas* (Wang et al., 2016). NAC transcription factor *NAC29* played an important role in resisting bacterial leaf spot disease, overexpression of the *NAC29* gene could significantly enhance the defense ability of tomato plants against *Pst* DC3000 (Zheng, 2019). NAC29 could specifically recognize the *βCA3* promoter sequence and regulate its transcription to increase βCA3 content, ultimately leading to enhanced defense ability of tomato plants against *Pst* DC3000. Several *SlNAC* genes are involved in the response to *Pst* DC3000 in tomato, among the 20 identified *SlNAC*s genes, 18 were significantly induced in the defense response to *Pst* DC3000, and 13 were responsive to *Pst* DC3000 in the pattern-triggered immunity (PTI) or effector-triggered immunity (ETI) process (Xu et al., 2022). Tomato wilt disease is a bacterial soil-borne disease caused by *Ralstonia solanacearum* that can cause up to 60 - 100% yield loss (Mohammed et al., 2020). Overexpression of tomato NAC gene *SlNAP1* could significantly enhance the plant resistance to leaf spot disease and bacterial wilt disease (Wang et al., 2020). Chen and Shao (2023) used virus-induced gene silencing (VIGS) technology to silence SlNAP2, which reduced the plant resistance to bacterial wilt disease, indicating that SlNAP2 plays a positive regulatory role in tomato resistance to bacterial wilt disease. In addition to bacterial diseases, tomato cultivation is also often threatened by fungal diseases, such as gray mold disease caused by *Botrytis cinerea* (Zhang et al., 2021). NAC gene *SlSRN1* is a positive regulator of the defense response against gray mold disease and *Pst* DC3000 (Liu et al., 2014). Tomato viral disease is one of the important factors limiting tomato industry development, and tomato plants are mainly threatened by tomato yellow leaf curl virus (TYLCV), tomato spotted wilt virus (TSWV), tomato chlorosis virus (ToCV), and tomato brown rugose fruit virus (ToBRFV) in greenhouse cultivation (Mi et al., 2021). Additionally, tomato leaf curl virus (TLCV) could induce the specific expression of *SlNAC1* gene in infected cells and interact with the virus replication enhancer to enhance virus DNA replication (Selth et al., 2005). NAC transcription factors (*SlNAC20*, *SlNAC24*, *SlNAC47*, and *SlNAC61*) could respond to TYLCV infection in tomato, and concluded that SlNAC61 played a positive regulatory role in response to TYLCV infection (Huang et al., 2017). In addition, tomato ubiquitin ligase SlNA3 (SEVEN IN ABSENTIA3) could ubiquitinate a defense-related NAC transcription factor NAC1, promote its degradation, and play a negative regulatory role in defense signal transduction (Miao et al., 2016). NAC089 is essential for endoplasmic reticulum stress-induced immunity and plant resistance to pathogens (Ai et al., 2021). All these studies indicated that NAC transcription factors play an important role in the regulation of plant resistance to biotic stress.

Perspectives

With the global climate change, the frequency and duration of environmental stressors faced by crops in various regions are increasing, leading to significant declines in crop yields and quality. Population growth, limited arable land, and soil degradation have become key bottlenecks restricting agricultural modernization and sustainable development. Plants must adapt to the complex and variable environment during their growth and development, while various biotic and abiotic stresses differentially impact distinct growth stages of crops. To enhance the crops' resistance to environmental stressors, many issues still need to be addressed.

Biotic and abiotic stresses are major factors limiting plant growth and development. Deepening the study of the molecular mechanisms by which plant transcription factors resist stressors will have important practical value in enhancing crop tolerance to adverse conditions. As a key regulatory factor, NAC transcription factors not only participate in the regulation of plant growth and development but also play an important role in response to external stressors. The study of the function of NAC transcription factors provides important theoretical basis for breeding high-yielding and stress-resistant crop varieties. Although the binding sites and the ways in which some transcription factors bind to the promoters of their target genes have been elucidated, the mechanism by which multiple transcription factors coordinate to activate stress-resistant signals still needs further research. At the same time, due to the complexity of the trait of crop stress response involving multiple gene regulation, as well as the long breeding cycle and the influence of various uncertain factors, the breeding efficiency is significantly limited. Therefore, future research needs to integrate the use of genomics, metabolomics, and epigenetics technologies, and introduce single-crop breeding and gene editing to accelerate the development of stress-resistant crop germplasm resources and breeding efficiency.

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