Journal of the Korean Society of Grassland and Forage Science 44(3): 197~203, 2024
https://doi.org/10.5333/KGFS.2024.44.3.197
ISSN 2287-5824 (Print)
ISSN 2287-5832 (Online)

Research Article

NAC Transcription Factor *ANAC032* Negatively Regulates Abscisic Acid and Sugar Responses

Netty Ermawati[1,†], Ade Citra Aulia[2,†], Daeyoung Son[3,*] and Joon-Yung Cha[2,*]

[1]Department of Agricultural Production and Central Laboratory for Biosciences, State Polytechnic of Jember, Jember 68101, Indonesia

[2]Dvision of Applied Life Science (BK21 four), Research Institute of Life Sciences, Gyeongsang National University, Jinju 52828, Republic of Korea

[3]Department of Plant Medicine, Institute of Agriculture and Life Science, Gyeongsang National University, Jinju 52828, Republic of Korea

ABSTRACT

This study investigates the role of the NAC transcription factor *ANAC032* in regulating abscisic acid (ABA)-dependent stress responses and its involvement in sugar signaling pathways. Arabidopsis seedlings with overexpressed or knock-out *ANAC032* were examined for their sensitivity to ABA, glucose, and fluridone to elucidate the functional role of *ANAC032* in ABA and high glucose-mediated growth retardation. Our results showed that *ANAC032* negatively regulates ABA responses, as *ANAC*-overexpressing plants exhibited higher ABA sensitivity, while *anac032* mutants were less sensitive. Under high glucose conditions, *anac032* mutants demonstrated hyposensitivity, with germination rates higher than wild-type and *ANAC032*-overexpressing plants. Additionally, yeast two-hybrid screening identified three NAC proteins, ANAC020, ANAC064, and ANAC074, interact with ANAC032. These findings highlight ANAC032's role in stress signaling pathways and its potential interactions with other NAC proteins, contributing to a better understanding of transcriptional regulation in plant stress responses and possibly expanding to forage crop development.

(Key words: Abscisic acid, *ANAC032*, Sugar, Transcription factor)

Ⅰ. INTRODUCTION

Grasslands consist of a complex interaction of various living organisms, including animals, plants, and microorganisms, as well as the surrounding ecological environments. Among these, forage and feed crops, central to the livestock industry, are directly exposed to dynamic external environments and undergo cycles of development and dormancy throughout the year. Additionally, recent climate change issues due to global warming have not only altered grassland vegetation but also decreased productivity (Hart et al., 2022). Plants regulate the development of various organs and tissues and their adaptability to stressful environments, through a various of phytohormones and interactions. This plays a crucial role in helping the plant maintain proper growth and development even under adverse stress conditions (Verma et al., 2016).

The phytohormone abscisic acid (ABA) plays a crucial role in regulating various developmental processes and stress responses, particularly in response to environmental challenges such as drought and salinity (Rai et al., 2024). ABA is also intricately involved in seed germination, post-germination growth, and root development (Ali et al., 2022). Interestingly, photosynthetic products, sugars, interplay with ABA in its diverse processes as similar functions or antagonistic effects (Finkelstein and Gibson, 2002). In this context, transcription factors from the NAC (NAM, ATAF, and CUC) family have been shown to regulate stress responses and growth processes in plants (Souer et al., 1996; Duval et al., 2002; Hegedus et al.,

†These authors equally contributed this work.
*Corresponding author: Daeyoung Son, Department of Plant Medicine, Institute of Agriculture and Life Science, Gyeongsang National University, Jinju 52828, Republic of Korea
Tel: +82-55-772-1926, E-mail: dyson@gnu.ac.kr
Joon-Yung Cha, Dvision of Applied Life Science (BK21 four), Research Institute of Life Sciences, Gyeongsang National University, Jinju 52828, Republic of Korea
Tel: +82-55-772-0092, E-mail: jycha@gnu.ac.kr

2003; Fujita et al., 2004; Tran et al., 2004; Lu et al., 2007; Bu et al., 2008; Jensen et al., 2008). Among the NAC transcription factors, members of the ATAF subfamily are believed to function in ABA-dependent stress signaling pathways (Tran et al., 2004; Bu et al., 2008). Interestingly, ABA pathways are overlapped with high glucose responses to repress the photosynthesis in retrograde signaling (Arenas-Huertero et al., 2000). Furthermore, we recently reported two NAC transcription factors, *ANAC032* and *ANAC083*, which are responsible for multi-abiotic stresses, and *ANAC032* positively regulates salinity and droght stress responses (Ermawati et al., 2021; Ermawati et al., 2023).

Previous studies have demonstrated that transcription factors such as ANAC032 can act as both positive and negative regulators of various stress responses, depending on the environmental and hormonal context (Mahmood et al., 2016a; Mahmood et al., 2016b; Maki et al., 2019). This study provides new insights into the functional role of ANAC032 in ABA-dependent stress responses, as well as its involvement in sugar signaling and transcriptional regulation through protein-protein interactions. By elucidating the molecular mechanisms underlying ANAC032 function, this research aims to contribute to the broader understanding of how transcription factors mediate plant responses to environmental stress, potentially offering new strategies for enhancing crop stress tolerance.

Ⅱ. MATERIALS AND METHODS

1. Plant materials and stress treatments

Arabidopsis thaliana (ecotype Columbia) was used for all experiments. Plants were grown on germination medium MS agar plates for a week under a 16-h-light/8-h-dark condition. An Arabidopsis *ANAC032* T-DNA insertion lines (SALK_087702 and SALK_012253) was obtained from the Arabidopsis Biological Resource Center (Columbus, OH). Insertion mutant information was obtained from the Salk Institute Genomic Analysis Laboratory's website (http://signal.salk.edu) and reported in Ermawati et al. (2023). For the ABA sensitivity test, 5-day-old wild-type, *ANAC032*-overexpression (ANAC032-OX) and *anac032* mutant seedlings were transferred to MS plates with or without 100 μM ABA, and grown for 7 days.

2. Germination assay

Germination assay was carried out by planting the seeds of wild-type, *ANAC032*-overexpressing and knockout mutants lines on MS medium supplemented with glucose, sucrose, and ABA at various concentrations (0.25, 0.5, 1.0 μM for ABA) or 1 μM fluridone.

3. Total chlorophyll content

To measure the total extractable chlorophyll, 100 mg of 3-weeks old leaf tissues were collected and extracted with 8 mL of 80% acetone for 24 h. The absorptions of the extracts were determined at 645 and 663 nm using the Ultrospec II UV/Visible Spectrophotometer (Pharmacia LKB, Uppsala, Sweden). The concentrations of total chlorophyll were calculated (Arnon, 1949).

4. Yeast two-hybrid analysis

Yeast two-hybrid analysis was performed using a GAL4-based two hybrid system (Invitrogen, Carlsbad, CA). The screening was conducted by cloning the full-length *ANAC032* and *ANAC083* cDNAs into the GAL4 DNA binding domain (BD) of the pDEST32 gateway vector to generate the *pBD-032* and *pBD-083* constructs. The clones were then transformed into the pJ69-4A yeast strain containing *His3* and *LacZ* reporter genes by the lithium acetate method. To find the interaction partner of ANAC032 protein with other TFs, the Arabidopsis transcription factor (TF) library, which contains full-length cDNAs of 1200 TFs (constructed in pAD-GAL4), was transformed into yeast bait containing BD-032 and BD-083 fusions. The transformant yeast cells bearing both the plasmids were spread on the synthetic complete medium (SD) lacking histidine, tryptophan, leucine or adenine then grown at 30℃ for 4 days. Hy5::STO and pBD::pAD constructs were used as positive and negative controls, respectively. Transformants grown on a medium lacking histidine or adenine was assayed for β-galactosidase activities using X-gal (5-bromo-5-chloro-3-indolyl-β-D-galactoside) as a substrate. The filter lift assay performed by placing the 3M Whatman paper on the surface of the plate of colonies to be assayed then gently rub the filter to help colonies absorb the filter paper. When the filter has been wetted (approximately 2 min), carefully lift it off from the plate and freeze it in liquid

nitrogen. Thaw the filter paper at room temperature. Placed the filter paper in the plate that contains filter paper-wetted by Z buffer/X-gal solution (Z buffer contains 16g/L of $Na_2HPO_4.7H_2O$, 5.5g/L of $NaH_2PO_4.H_2O$, 0.75g/L KCl, 0.246g/L $MgSO_4.7H_2O$ pH 7.0), 16.7 mL/L of 20 mg/mL X-gal solution and 2.7 mL/L of β-mercaptoethanol. The filters were incubated at 30℃ and periodically checked for the appearance of blue colonies.

Ⅲ. RESULTS AND DISCUSSION

1. *ANAC032* negatively regulates ABA response

The ABA hormone is involved in various developmental processes and adaptation to abiotic stresses (Leung and Giraudat, 1998). Fujita et al. (2004) reported that only members of the ATAF subfamily might function in the ABA-dependent stress-signaling pathway, among other NAC subfamilies. To investigate the stage specificity of the ABA response, we examined seed germination on media containing various concentrations of ABA (0.25, 0.5, 1.0 and 1.5 μM ABA) (Fig. 1A). ANAC032-OX seedlings exhibited a marked sensitivity to ABA. A low concentration of ABA (0.25 μM) was sufficient to reduce the germination efficiencies of ANAC032-OX plants to 30%. In contrast, WT and *anac032* mutant plants maintained 50% and 75% germination efficiencies, respectively, under the same conditions. These results suggest that ABA treatment suppressed seed germination across all genotypes. However, the *anac032* mutant seeds were less sensitive to ABA compared to the WT and ANAC032-OX plants (Fig. 1B). Mutants that have an altered response to ABA either decreased or increased sensitivity, revealed the involvement of ABA in stress signal transduction (Finkelstein, 1994). These results also indicate that the germination and post-germination growth of *ANAC032* transgenic plants were sensitive to ABA.

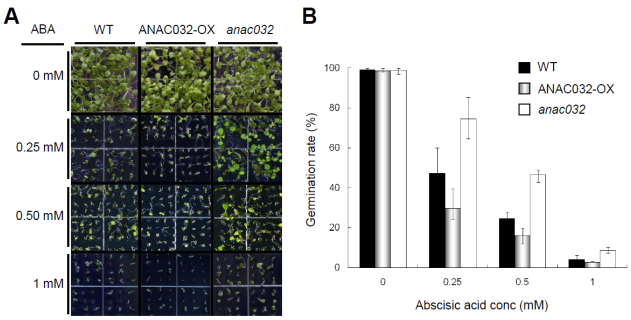

Fig. 1. ABA sensitivity of *ANAC032*-overexpressing plants (A) Phenotypic analysis of ABA sensitivity. Seeds were germinated and grown on the medium containing varying concentrations of ABA for 7 days. (B) Germination rate. The percentage of seeds that successfully germinated in the presence of varying concentrations of ABA was scored after 7 days. Data represent the means with SD values as error bars calculated using five biological independent experiments.

2. *ANAC032* negatively regulates ABA and high glucose

Sugars regulate key processes and influence the expression of many genes in plants. Studies on *Arabidopsis* mutants with altered ABA sensitivity have highlighted the role of sugar signaling in ABA responses (Arenas-Huertero et al., 2000; Dekkers et al., 2004; Dekkers et al., 2008). To determine whether the increased sensitivity of ANAC032-OX in seed germination to ABA observed in this experiment is modulated by sugar signaling, we examined their response to exogenous glucose, which has a strong inhibitory effect on growth compared to other sugars (Jang et al., 1997), and to fluridone, an ABA biosynthesis inhibitor (Saab et al., 1990).

In 0.5 μM ABA, WT, ANAC032-OX, and *anac032* plants showed different germination rates. While WT and ANAC032-OX seeds had 40% and 30% germination rates, respectively, *anac032* seeds exhibited about 70% germination, indicating reduced sensitivity to ABA (Fig. 2A). When treated with 1 μM fluridone, germination in ANAC032-OX seeds was more strongly induced than WT, resulting in seedlings with a white or pink appearance (Fig. 2B). In contrast, germination in the *anac032* mutant was unaffected by fluridone treatment after 5 days incubation (Fig. 2A). In the presence of ABA and fluridone, the inhibitory effect of exogenous ABA on seed germination was alleviated, resulting in similar germination rates across all three genotypes. When seeds were grown on a medium containing 3% glucose, no obvious differences were observed in the germination and post-germination stage between WT, ANAC032-OX and *anac032* seeds (Fig. 2). Higher glucose concentrations had inhibitory effects on seed germination, with different genotypes showing varying sensitivities (Lin et al., 2007). At a high glucose concentration of 6%, around 50% of WT, ANAC032-OX, and *anac032* seeds were able to germinate within 5 days. However, after 2 weeks of incubation in 6% glucose, germination was

arrested entirely in all genotypes, except for about 20% of *anac032* mutant seeds, which contributed to grow and developed true leaves (Fig. 2B). This result suggests that the seed germination in the *anac032* mutant is insensitive to glucose. Fluridone treatment significantly reduced the inhibitory effect of glucose on seed germination, diminishing the differences in glucose sensitivity between WT, ANAC032-OX, and *anac032* (Fig. 2). These results suggest that *anac032* seed germination is less sensitive to both ABA and glucose and that the differential responses of the three genotypes to exogenous ABA or glucose were likely due to the varying levels of endogenous ABA.

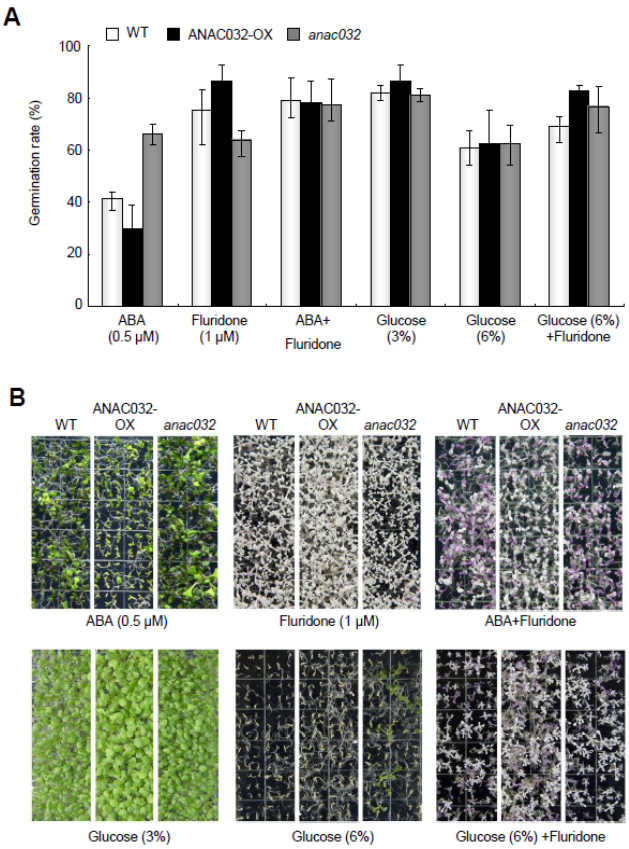

Fig. 2. Effects of ABA and glucose in germination of *ANAC032*-overexpression and knockout mutants. (A) Germination of wild-type, *ANAC032*-overexpression, and knockout mutant seeds in the indicated concentration of ABA (0.5 μM), glucose (3 or 6%) and fluridone (1 μM) 5 days after treatments. (B) The phenotype of wild-type, *ANAC032*-overexpression, and knockout mutant plants in the presence of ABA, glucose and fluridone after 2 weeks of treatments. Data in A represents the means ± SD using three independent biological replicates, and a representative image shown in B.

3. *ANAC032* interacting partner proteins by yeast two-hybrid.

NAC proteins are functionally redundant in plants, which suggests that overlapping interaction patterns may occur to fulfill specific functions (Riechmann et al., 2000; Olsen et al., 2005). A yeast two-hybrid screen investigated whether ANAC032

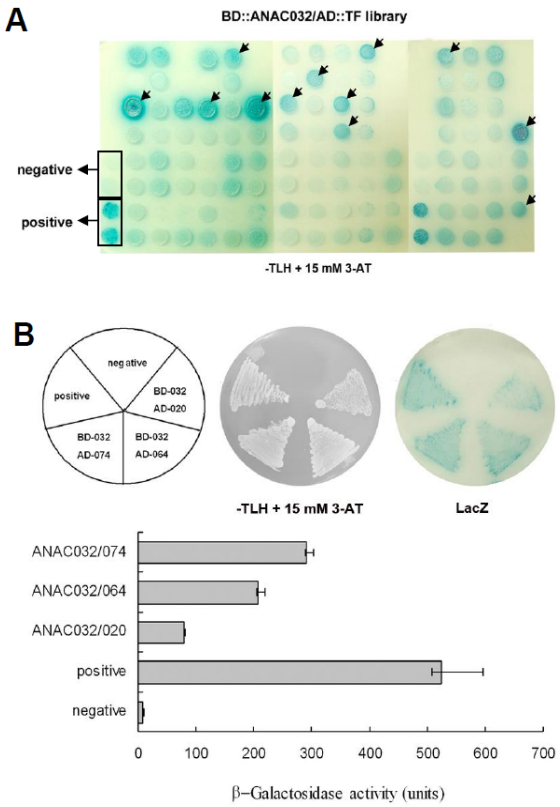

Fig. 3. Screening and interaction analysis of ANAC032 protein using yeast two-hybrid system. (A) ANAC032 was used as bait to screen its partner proteins in a cDNA library of Arabidopsis. Transformats grown on a selective medium were picked and transferred to a selective medium lacking histidine (-H) + 15 mM 3-aminotriazole (3-AT). After 3 days of incubation, the transformant's cell cultures were spotted on selective plates supplemented with X-gal. Arrows indicated the identified interacting clones. (B) Assay the ability of ANAC032 to interact with ANAC020, ANAC064, and ANAC074 by measuring b-galactosidase activities using a filter paper assay and ONPG assay. Data represent the means ± SD using three independent biological replicates.

can recruit partner proteins to the transcription complex. For this purpose, the full-length *ANAC032* was used as bait to screen for interacting proteins in a transcription factor library. To confirm positive interactions, fusion yeast were grown on a selective medium lacking triptophan, leucine, histidine, and adenine supplemented with X-gal. Of approximately 1×10^3 cDNA clones, 14 positive clones were identified as interacting with ANAC032. These clones were subsequently isolated and transformed into *E. coli* for sequencing. All identified clones were members of the NAC family proteins, specifically ANAC020, ANAC064 and ANAC074 (Fig. 3A).

We performed one-on-one interaction analyses to confirm these interactions by co-expressing ANAC020, ANAC064 and ANAC074 with the bait, ANAC032. These three NAC proteins consistenly showed histidine autotrophy and b-galactosidase activity, indicating positive interaction with ANAC032 (Fig. 3B). These results suggest that these proteins interact directly with ANAC032.

To further explore the regions required for interaction between ANAC032 and its target proteins, two deletion constructs were created: ANAC032N-term (amino acids 1-163) and ANAC032C-term (amino acids 164-253). The full length *ANAC032* and these two deletion constructs were fused to ANAC020, ANAC064 and ANAC074 to determine which regions are necessary for interaction. The analyses revealed that the N-terminal domain of ANAC032 is crucial for the interaction, as deletion of the NAC domain abolished interactions with its target proteins (Fig. 4).

Ⅳ. CONCLUSIONS

In conclusion, this study demonstrates that the NAC transcription factor *ANAC032* plays a crucial role in regulating ABA-dependent stress responses and sugar signaling in plants. *ANAC032* regulates the ABA sensitivity, particularly in seed germination and post-germination stages. These results suggest that *ANAC032* negatively regulates ABA responses, influencing the plant's adaptability to abiotic stress. Additionally, the interplay between ABA and glucose was highlighted, with *ANAC032* involved in heightened sensitivity to both ABA and high glucose concentrations. ingThe findings suggest that ANAC032 acts as a negative regulator in ABA and sugar signaling, offering insights into its role in plant stress tolerance mechanisms, which is essential genetic materials for generating forage crop variety.

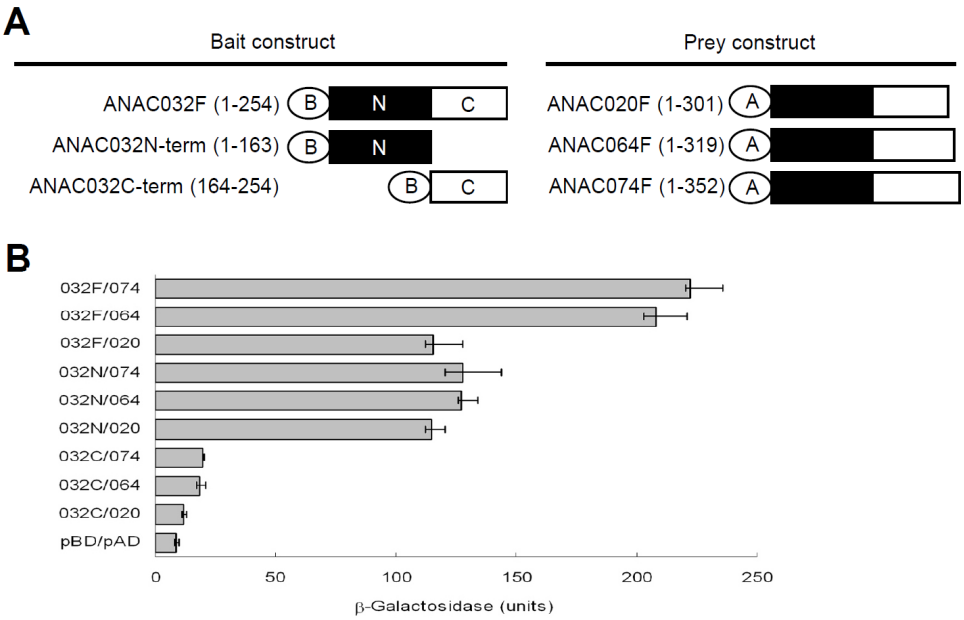

Fig. 4. Yeast two-hybrid assay using ANAC truncation with ANAC020, ANAC064, and ANAC074. (A) Diagram representation of ANAC032 (bait) and target proteins (prey) tested for interaction. (B) β-galactosidase assay using ANAC truncation. Three bait were prepared to find the interaction regions of ANAC032 with its binding proteins and measure the activities of interacting proteins. Data represent the means ± SD using three independent biological replicates.

Ⅴ. ACKNOWLEDGEMENTS

This work was supported by the National Research Foundation of Korea (NRF) grant funded by the Korean Government (MOE-2022R1I1A1A01070257), Republic of Korea.

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(Received : September 11, 2024 | Revised : September 26, 2024 | Accepted : September 26, 2024)