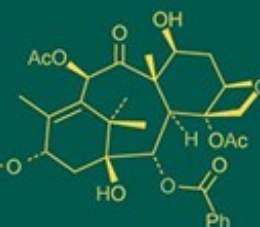
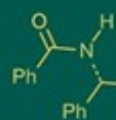


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Promoter analysis revealed multifunctional role of ALDH superfamily in soybean

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ABSTRACT

The aldehyde dehydrogenase (ALDH) superfamily plays a crucial role in plant growth, development, and environmental stress adaptation by detoxifying reactive aldehydes generated during cellular metabolism. Understanding the transcriptional regulation of these genes is essential for targeted crop improvement. In this study, we conducted a comprehensive *in silico* analysis of the *cis*-acting regulatory elements in the promoter regions of *Glycine max* ALDH (GmALDH) genes. Analysis of the 1500 bp upstream sequences using the PlantCARE database revealed a dense and complex distribution of regulatory motifs, which were categorized into abiotic stress-responsive, biotic stress-responsive, and phytohormone-responsive groups. The extensive presence of core elements such as ABRE, MYB, GATA-motifs, and WUN-motifs suggests a highly integrated regulatory network governing GmALDH expression. These findings provide a critical foundation for understanding the hormone and stress-mediated transcriptional regulation of ALDHs in soybean, ultimately identifying promising targets for precise genome editing to develop stress-resilient cultivars.

Keywords: *Glycine max*, Aldehyde dehydrogenase, *Cis*-acting regulatory elements, Promoter analysis, Transcriptional regulation

1. Introduction

Environmental fluctuations, including drought, extreme temperatures, salinity, and pathogen attacks, disrupt cellular homeostasis and induce the overproduction of reactive oxygen species (ROS) and toxic lipid-derived aldehydes in plants (Kirch *et al.*, 2005) [1]. If left unchecked, these aldehydes cause severe damage to cellular membranes and macromolecules (Kotchoni *et al.*, 2003) [2]. The aldehyde dehydrogenase (ALDH) superfamily acts as a primary enzymatic detoxification mechanism, irreversibly oxidizing various endogenous and exogenous aldehydes into corresponding, less toxic carboxylic acids. Specific members of this family have multifunctional role.

While the structural characteristics and enzymatic functions of ALDHs have been extensively documented, their precise transcriptional regulation in response to multi-stress environments remains a complex challenge in crop biotechnology. Gene expression is largely controlled by the promoter region, which contains specific *cis*-acting regulatory elements that act as binding sites for transcription factors (Wang *et al.*, 2016) [3]. Identifying these molecular switches in the promoter regions of soybean (*Glycine max*) ALDH genes is critical for uncovering the complex cross-talk between environmental stress signalling and developmental pathways. Therefore, this study aims to systematically analyse the *cis*-acting elements within the GmALDH promoters to elucidate their multifunctional roles and provide a theoretical basis for future genetic engineering efforts.

2. Materials and methods

2.1. Sequence retrieval and promoter extraction

To investigate the potential regulatory mechanisms governing the GmALDH family members, the upstream promoter sequences were retrieved for analysis. Specifically, the 1500 bp genomic sequences upstream from the translation start codon (ATG) of all identified GmALDH genes were obtained from the Phytozome v12.1 database (<https://phytozome.jgi.doe.gov/pz/portal.html>) (Goodstein *et al.*, 2012) [4]. This sequence length was selected as it typically encompasses the core promoter and the most critical proximal regulatory elements required for transcription factor binding.

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2.2. Cis-acting element analysis

The putative stress or hormone-responsive *cis*-acting regulatory elements within these 1500 bp promoter sequences were predicted using the PlantCARE online database (Lescot *et al.*, 2002) [5]. The raw data output was systematically filtered to exclude redundant structural elements (such as generic TATA and CAAT boxes), allowing the functional categorization to focus exclusively on motifs associated with biotic stress response, abiotic stress response and phytohormone responsiveness.

3. Results and discussion

3.1. Distribution and mapping of cis-acting elements

To understand the regulatory dynamics of the *GmALDH* genes, the 1500 bp promoter regions were mapped, revealing a dense and varied distribution of regulatory motifs dispersed across the sequences (Figure 1). This visual mapping demonstrates that multiple responsive elements frequently cluster together within the promoter regions of

individual *GmALDH* genes. Similar to findings in other stress-responsive gene families, such clustering indicates a sophisticated, multi-factor transcriptional control system, allowing a single gene to respond to diverse environmental stimuli simultaneously (Ali Q-u *et al.*, 2021) [6]. The presence of these varied *cis*-regulatory elements within the transcription factor binding sites reveals that the *GmALDH* genes likely have multiple intersecting roles in growth, metabolism, and stress-related pathways.

3.2. Functional categorization

The identified elements were systematically categorized into three primary functional groups: abiotic stress-responsive, biotic stress-responsive, and phytohormone-responsive. The identified *cis* acting elements were shown in figure 2. While core promoter elements such as the TATA-box and CAAT-box were excluded from functional categorization to focus on stimuli-specific responses, the remaining motifs provided significant insight into the environmental and hormonal regulation of the ALDH superfamily.

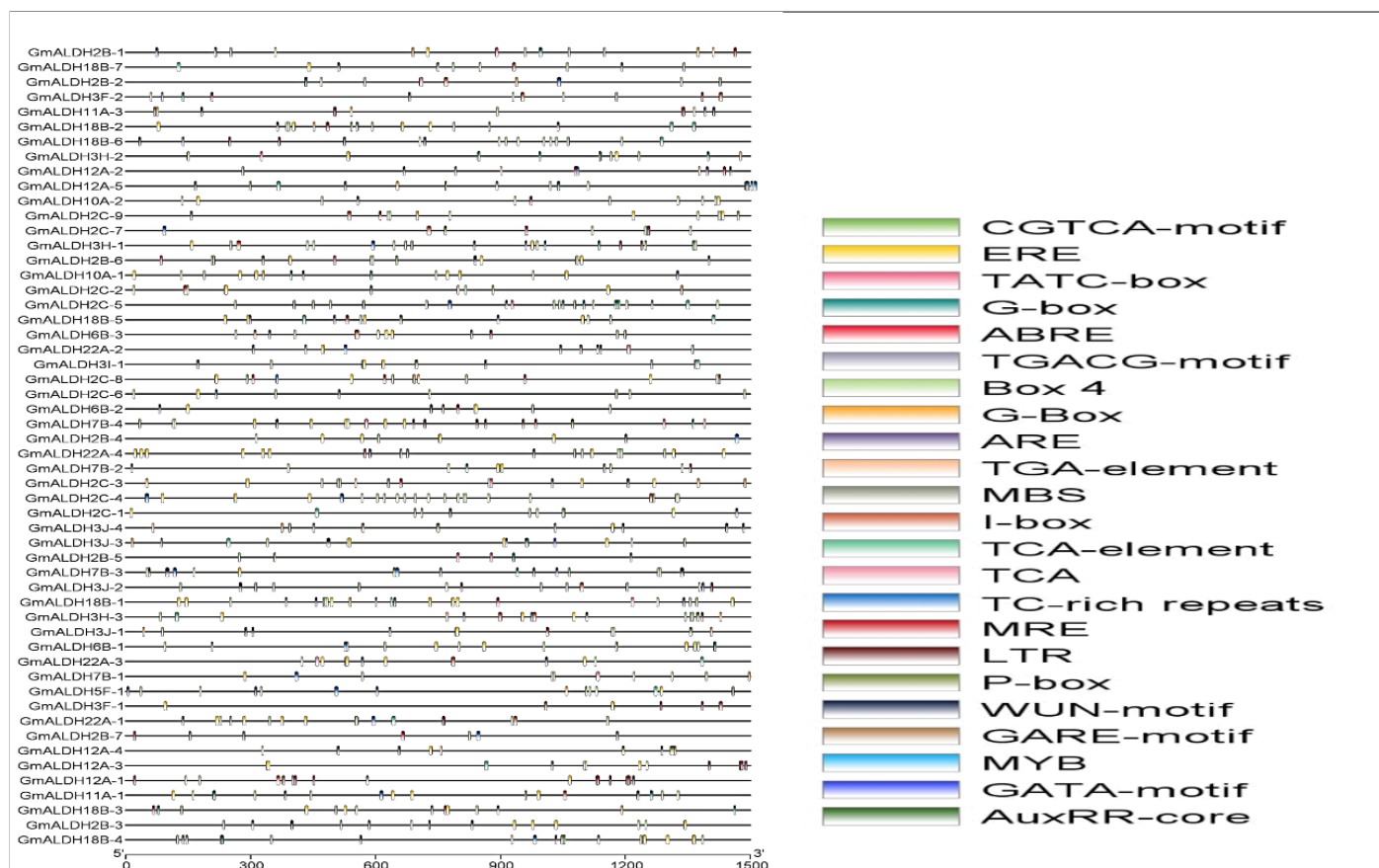


Figure 1. Cis-acting element analysis in the promoter regions (1500 bp upstream of the start codon) of ALDH gene family in *Glycine ma*

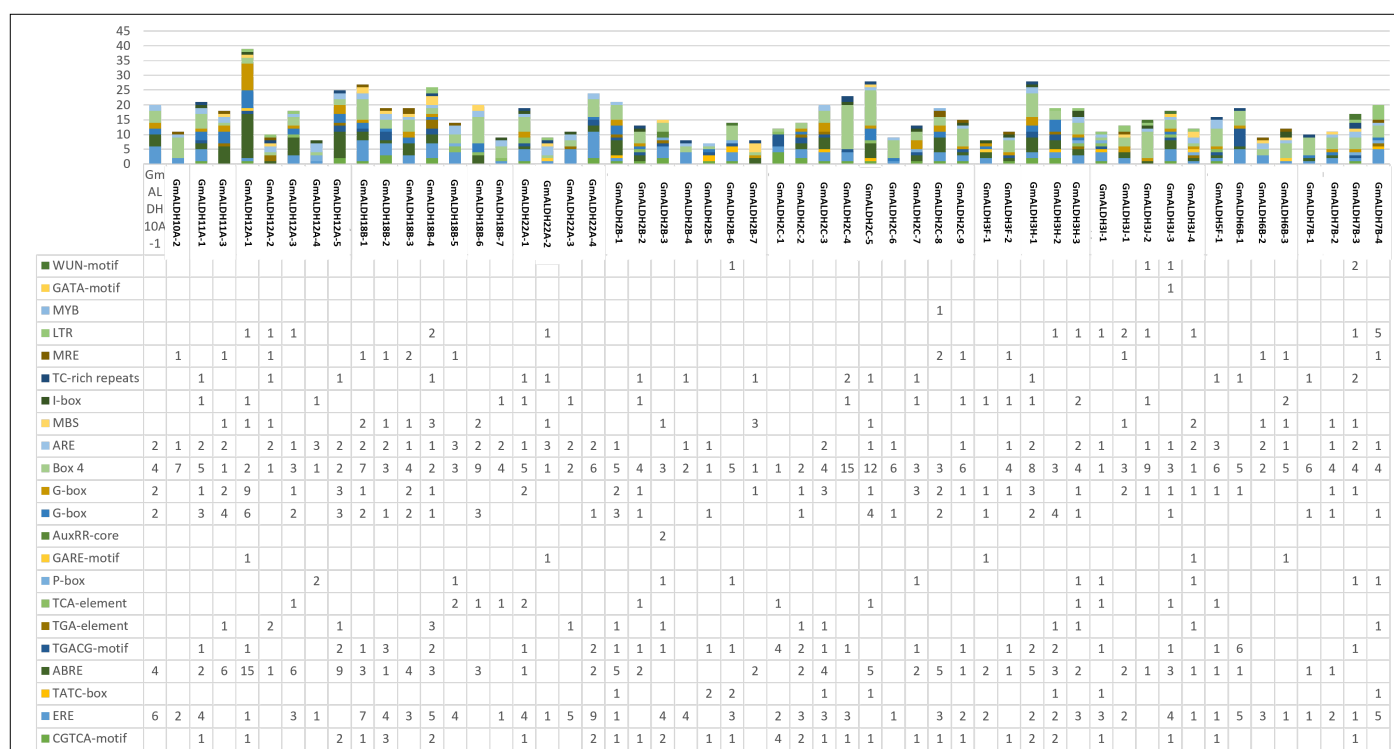
Abiotic and environmental stress-responsive cis-acting elements

This category exhibited the highest diversity of motifs, emphasizing the crucial role of the ALDH family in managing environmental fluctuations. Notable abiotic stress-responsive elements included the ARE (essential for anaerobic induction), LTR (low-temperature responsiveness), MBS (MYB binding site involved in drought inducibility), and TC-rich repeats (defense and stress responsiveness). Elements like MYB and ARE were particularly abundant across multiple *GmALDH* members. The MYB transcription factor binding sites are essential for the expression of drought-inducible genes, highlighting the sensitivity of these genes to dehydration and osmotic stress (Li *et al.*, 2015) [7]. The ARE motif serves as a critical regulatory element for anaerobic induction and is often associated with low oxygen and dehydration responses (Dolferus *et al.*, 2001) [8].

Furthermore, this category included several motifs known for their environmental and light-responsive roles, such as Box 4, G-Box, GATA-motif, I-box, and MRE. Motifs such as the G-box and Box 4 act as highly conserved molecular switches that are frequently regulated by environmental stresses, UV light, and injuries, suggesting their involvement in complex photoperiod and stress-signaling crosstalk (Shariatipour *et al.*, 2020) [9].

Biotic stress-responsive cis-acting elements

The defensive capabilities of the *GmALDH* genes against biological threats were highlighted by the presence of specific biotic stress-responsive elements. This response was primarily represented by the widespread presence of the WUN-motif. The WUN-motif is a wound-responsive element known to be rapidly activated upon the perception of mechanical wounding and pathogen invasion (Ali Q-u *et al.*, 2021) [6]. The existence of these elements in the promoter regions suggests that *GmALDH* genes are actively engaged in biotic stress response cascades and may play a vital role in defense signaling.



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