

Article

Genome-Wide Identification of the PLATZ Gene Family and Its Roles in Stress Responses in Flax (*Linum usitatissimum* L.) Based on the Telomere-to-Telomere Genome

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Abstract

The *PLATZ* gene family influences plant growth, development, and responses to both biotic and abiotic stresses. Flax (*Linum usitatissimum* L.), an important oilseed and fiber crop, has not been extensively studied for its *PLATZ* genes. In this study, 27 *LuPLATZ* genes were identified in the recently assembled T2T (Telomere-to-Telomere) flax genome through bioinformatics analyses. Phylogenetic analysis grouped these genes into five subfamilies. Examination of gene structure and motifs showed conserved exon–intron arrangements and similar motif compositions within the same clade. Promoter analysis revealed that most cis-elements are associated with plant hormone responses (such as MeJA and ABA) and abiotic stresses, including anaerobic induction, drought, and low temperature. Duplication analysis identified 33 segmental duplication events, and miRNA target prediction indicated that *lus-miR167* is the primary regulator of *LuPLATZ* genes. Expression profiling based on RNA-seq data showed high expression levels of most *LuPLATZ* genes in leaves and roots, and qRT-PCR confirmed their stress-responsive expression under cold, drought, and salt conditions, with *LuPLATZ14* and *LuPLATZ21* significantly upregulated in all treatments. Furthermore, overexpression of these two genes enhanced drought tolerance in yeast transformants.

Keywords: flax; *PLATZ* genes; phylogeny analysis; subcellular localization; drought stress



Academic Editor: Ainong Shi

Received: 20 August 2025

Revised: 13 September 2025

Accepted: 19 September 2025

Published: 22 September 2025

Citation: Lu, J.; Wu, H.; Wang, H.; Li, J.; Zang, Z.; Wu, G.; Zhang, J. Genome-Wide Identification of the *PLATZ* Gene Family and Its Roles in Stress Responses in Flax (*Linum usitatissimum* L.) Based on the Telomere-to-Telomere Genome. *Agronomy* **2025**, *15*, 2233. <https://doi.org/10.3390/agronomy15092233>

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1. Introduction

PLATZ proteins are plant-specific DNA-binding factors belonging to the zinc finger transcription factor superfamily, which comprises about 15% of all plant transcription factors [1]. Zinc finger proteins are categorized into nine structural types—C2H2, C8, C6, C2HC, C3HC4, C2HC5, C4, C4HC3, and CCCH—according to the number and arrangement of cysteine (Cys) and histidine (His) residues that coordinate zinc ions in their secondary structures [2]. According to their functional characteristics, zinc finger proteins are further divided into several subfamilies, including *TFIII*, *GATA*, *WRKY*, *RING*, *DOF*, *PHD*, and *PLATZ* [3]. The first *PLATZ* protein, *PLATZ1*, was identified in pea (*Pisum sativum* L.) in 2001. As a zinc-dependent DNA-binding protein, *PLATZ1* binds non-specifically to A/T-rich sequences and acts as a transcriptional repressor. Sequence comparisons revealed

that *PLATZ1* contains two discontinuous zinc finger motifs: C-x₂-H-x₁₁-C-x₂-C-x₍₄₋₅₎-C-x₂-C-x₍₃₋₇₎-H-x₂-H and C-x₂-C-x₍₁₀₋₁₁₎-C-x₃-C. These distinct motifs differ from previously described zinc-binding domains, defining *PLATZ* proteins as a unique class of plant-specific zinc finger transcription factors [4].

In recent years, research on the *PLATZ* gene family has increased substantially, and members of this family have been identified and analyzed in a range of plant species, including barley [5], tartary buckwheat [6], soybean [7], rice [8], cucumber [9], tomato [10], and *Solanum lycopersicum* L. [11]. Studies have shown that *PLATZ* proteins play important roles in plant growth and development by regulating meristem activity, leaf development, and seed development. For example, the *PLATZ* transcription factor ORESARA15 (ORE15) in *Arabidopsis* is expressed in leaves, where it promotes the rate and duration of cell proliferation, thereby regulating leaf growth and senescence [12]. Repression of *PtaPLATZ18* in poplar increased internode length, xylem thickness, and lignin content, accompanied by upregulation of lignin biosynthesis genes, highlighting their role in growth and secondary cell wall development [13]. A mutation of the conserved histidine in the *PLATZ* domain to asparagine produces a semi-dominant *fl3* mutant that severely disrupts maize endosperm development, likely by reducing tRNA and 5S rRNA transcription and consequently impairing nutrient accumulation [14]. The rice *PLATZ* transcription factor GL6 interacts with two key components of RNA polymerase III, RPC53 (RNA polymerase III subunit C53) and the class C1 transcription factor (TFC1), to participate in RNA Pol III-mediated transcription, thereby regulating grain length and spikelet number in rice [15].

The *PLATZ* gene family plays a role not only in regulating plant growth and development but also in mediating responses to abiotic stress [7]. Studies showed that *Arabidopsis PLATZ1* and *PLATZ2* regulated dehydration tolerance in vegetative tissues and played a key role in seed drought resistance [16]. The *Arabidopsis PLATZ* family member A1N1 participated in the abscisic acid (ABA) signaling pathway by regulating reactive oxygen species (ROS) homeostasis, thereby affecting root elongation and inhibition in response to drought and salt stress [17]. Heterologous expression of *GhPLATZ1* from cotton (*Gossypium hirsutum* L.) in transgenic *Arabidopsis* enhanced osmotic tolerance under salt stress and mannitol-induced osmotic stress, and resulted in faster seed germination and higher seedling establishment rates [18]. *Arabidopsis AtPLATZ2* suppressed plant salt tolerance by repressing the transcription of CBL4/SOS3 and CBL10/SCaBP8 [19].

The continuous advancement of high-throughput sequencing technologies has driven the in-depth development of genomics, making it possible to assemble complete, gapless telomere-to-telomere (T2T) genomes [20]. A T2T genome not only contains the full genetic information of a species and is regarded as the ultimate form of genome assembly, but also effectively avoids assembly errors, improves the accuracy of variant detection, and facilitates the identification of missing genes as well as the evolutionary study of complex structures such as telomeres and centromeres [21]. In flax research, the most widely used reference genomes were previously derived from the oilseed cultivars CDC Bethune and Longya10, both assembled based on the Illumina platform [22,23]. However, these versions showed significant deficiencies in continuity and completeness. Recently, by integrating PacBio HiFi, Hi-C, and Illumina sequencing technologies, researchers assembled a 482.51 Mb T2T reference genome of fiber flax, with 46,634 genes predicted. This genome achieved an N50 of 33.03 Mb, representing ~17-fold increases compared with Longya10 (1.94 Mb) and CDC Bethune (0.023 Mb) [24]. This genome assembly represents a milestone achievement, laying a solid foundation for further studies in flax genomics.

Flax, an ancient crop species, is cultivated globally, particularly in temperate regions [25]. Based on its usage, flax can be categorized into three agronomic types: linseed (oil-flax), fiber flax, and dual-purpose flax [26,27]. Flaxseeds are packed with nutrients,

including lignans and dietary fiber. Notably, alpha-linolenic acid (ALA) is an essential omega-3 fatty acid vital for human health [28]. While *PLATZ* genes have been well-studied in various model plants, the functions of this gene family in flax, a key fiber crop, remain poorly understood. In this study, we systematically analyzed flax *PLATZ* genes using bioinformatics approaches, investigating their phylogeny, chromosomal distribution, physicochemical properties, conserved motifs, collinearity, cis-regulatory elements in promoters, subcellular localization, and expression patterns based on RNA-seq data, as well as their responses to cold, salt, and drought stresses. Additionally, we preliminarily confirmed that *LuPLATZ14* and *LuPLATZ21* could enhance drought tolerance in yeast transformants. This work provides a foundation for further functional characterization of *PLATZ* genes in flax and represents the first comprehensive survey of the organization and stress-responsive regulation of this gene family in the species.

2. Materials and Methods

2.1. Plant Material

Experiments were performed using the fiber-type flax cultivar “Gaosi,” obtained from the College of Agriculture, Jilin Agricultural University [24]. Seeds were surface-sterilized with 75% ethanol for 10 min, thoroughly rinsed with sterile water, and sown in soil. Plants were grown in a controlled growth chamber under a 16 h light/8 h dark photoperiod at 26/18 °C, with a relative humidity maintained at approximately 60%. Three-week-old seedlings were used for all experiments. Stress treatments were imposed once seedlings reached 6–7 cm in height. For drought and salt stress treatments, plants were gently removed from soil, washed with distilled water, and transferred to conical flasks containing 10% polyethylene glycol (PEG) or 100 mM NaCl, respectively, as these concentrations have been commonly used in previous studies to simulate drought and salt stress in flax and were shown to induce clear physiological responses [29,30]. Control plants were maintained in distilled water, while low-temperature treatment plants were transferred to a 4 °C chamber. Leaf samples were harvested simultaneously from all groups at 0, 3, 6, 12, and 24 h, with three biological replicates per time point, to avoid time-of-day effects. All collected samples were immediately frozen in liquid nitrogen and then stored at −80 °C to preserve RNA integrity for subsequent analyses.

2.2. Identification of *PLATZ* Gene in Flax

The T2T flax (Gsosi) genome assembly and annotation data, including genome, CDS, and protein sequences, were obtained from the China National Center for Bioinformation (PRJCA037526, <https://ngdc.cncb.ac.cn/>, accessed 3 April 2025). Twelve *Arabidopsis* *PLATZ* protein sequences were obtained from the TAIR database (<https://www.arabidopsis.org/>, accessed 3 April 2025) [31]. Candidate *PLATZ* genes in flax were initially identified via BLASTp (BLAST+ v2.15.0) against the complete flax proteome using an E-value threshold of 1×10^{-5} . In parallel, the Hidden Markov Model (HMM) for the *PLATZ* domain (PF04640) was downloaded from the Pfam database (<http://pfam.xfam.org/>, accessed 3 April 2025) and employed with HMMER3.0's *hmmsearch* program to further predict *PLATZ* genes [32]. To ensure accuracy, only sequences containing an intact and complete *PLATZ* domain (PF04640) were considered as true *PLATZ* genes. The presence of the domain was verified using both SMART (<https://smart.embl-heidelberg.de>, accessed 3 April 2025) and the NCBI Conserved Domain Database (CDD, <https://www.ncbi.nlm.nih.gov/cdd/>, accessed 3 April 2025). After removing redundant sequences, a total of 27 non-redundant *LuPLATZ* genes were identified. The genome and protein sequence files of maize and wheat were obtained from the publicly available Phytozome database (<https://phytozome-next.jgi.doe.gov/>, accessed on 25 April 2025). The identification of *PLATZ* gene family members

in these species was performed using the same approach as applied for flax. These genes were named with the prefix “Lu” and numbered according to their chromosomal locations. Physicochemical properties of the *LuPLATZ* proteins, including coding sequence length, amino acid number, molecular weight (MW), theoretical isoelectric point (pI), and grand average of hydropathicity (GRAVY), were calculated using ExPASy ProtParam (<https://web.expasy.org/protparam/>, accessed 3 April 2025). Subcellular localization predictions were obtained through the BUSCA web server (<https://busca.biocomp.unibo.it>, accessed 3 April 2025).

2.3. Phylogeny, Chromosome Location, Conserved Domain and Conserved Motif of *LuPLATZ* Gene

PLATZ amino acid sequences from rice, soybean, maize, *Arabidopsis*, and flax were aligned using ClustalW in MEGA version 11 with default parameters. A maximum likelihood (ML) phylogenetic tree was then constructed in MEGA 11 under default settings (neighbor-joining; bootstrap = 1000) and visualized using iTOL version 6 (<https://itol.embl.de/>, accessed 10 April 2025). The chromosomal positions of *LuPLATZ* genes were determined from the flax genome FASTA and GFF3 annotation files. Conserved domains were predicted using NCBI’s CD-Search tool (<https://www.ncbi.nlm.nih.gov/Structure/cdd/wrpsb.cgi>, accessed 10 April 2025), and motif analysis of *LuPLATZ* proteins was performed with MEME (<https://meme-suite.org/meme/tools/meme>, accessed 10 April 2025), with results visualized in TBtools (v2.069) [33].

2.4. Genome-Wide Replication and Collinear Analysis of *LuPLATZ* Gene

Genome sequences and annotation files for *Arabidopsis*, maize, and wheat were obtained from the public Phytozome database (<https://phytozome-next.jgi.doe.gov/>, accessed 25 April 2025) [34]. Collinearity analyses were performed using the MCScanX toolkit (version 1.0). *LuPLATZ* genes arising from whole-genome duplications (WGDs) were identified, while tandem duplicates were defined as two or more homologous genes on the same chromosome separated by ≤ 100 kb with no intervening genes. Segmental duplications were detected using nucleotide BLAST (BLAST+ v2.12.0) with an E-value cutoff of $<1 \times 10^{-5}$ within a 100 kb window surrounding the coding sequences (50 kb upstream and downstream). Duplicated genes were confirmed based on a minimum alignment length of 200 bp and sequence identity exceeding 85% [35].

2.5. MiRNA Prediction and Cis-Acting Element Analysis

Flax miRNA sequences were obtained from previous studies [36]. Potential targets of these miRNAs were predicted by comparing them against the 5′ and 3′ untranslated regions (UTRs) and coding sequences (CDS) of all *LuPLATZ* genes using the Plant MicroRNA Target Analysis Server (psRNATarget) with default settings (<https://www.zhaolab.org/psRNATarget/analysis?function=3>, accessed 25 April 2025). The 2000 bp upstream genomic sequences of *LuPLATZ* genes were extracted using TBtools. To explore their possible regulatory roles under environmental stress, cis-regulatory elements within the 2.0 kb promoter regions were identified via the PlantCARE database (<http://bioinformatics.psb.ugent.be/webtools/plantcare/html/>, accessed 25 April 2025) and visualized using TBtools.

2.6. Analysis of Expression Pattern of *LuPLATZ* Gene Family

In this study, we performed a hypothetical analysis of the expression patterns of the *LuPLATZ* gene family using publicly available RNA-seq data from five flax transcriptome datasets: (i) pistil, stamen, fruit, and apical stem tissues (PRJNA1002756; <https://www.ncbi.nlm.nih.gov/sra/?term=>, accessed 5 May 2025); (ii) floral tissues at 30, 20, 10, and 5 days after anthesis (PRJNA833557); (iii) embryo, anther, and seed tissues at different developmental stages (PRJNA663265); (iv) roots and leaves under salt stress (PR-

JNA977728); and (v) stems exposed to heat stress (PRJNA874329). Raw sequencing reads were processed with fastp v0.23.2, mapped to the T2T reference genome of the Gaosi flax variety, and gene expression levels were quantified using the R packages tidyverse v1.3.1 [37], Rsubread v2.10.5 [38] and limma v3.54.2 [39]. Log2-transformed FPKM values were then visualized as heatmaps using TBtools.

2.7. RNA Extraction and Fluorescence Quantitative PCR Analysis

The total RNA of flax leaves was extracted by Trizol method (Invitrogen, Carlsbad, USA). First-strand cDNA was synthesized from the total RNA using the M-MLV reverse transcription kit (Promega, Madison, WI, USA). Leaf samples were collected at 0, 3, 6, 9, 12, and 24 h after stress treatments for RNA extraction and subsequent cDNA synthesis. Oligo 7 was used to design upstream and downstream primers (Table S3), and TB Green[®] Premix ExTaqTMII (Takara Bio, Kyoto, Japan) was used for RT-PCR test. Each sample included three biological replicates and three technical replicates. The experimental results were statistically analyzed by $2^{-\Delta\Delta CT}$ method [40]. Using GAPDH as the internal control gene, each sample was repeated 3 times to calculate the CT value [41].

2.8. Subcellular Localization of LuPLATZ14 and LuPLATZ21 Genes

The full-length coding sequence of *LuPLATZ* was amplified by PCR (Table S3) using specific primers designed with Oligo 7 (Thermo Fisher Scientific, Waltham, MA, USA), and cloned into the pGM-T vector (Promega, Madison, MA, USA) before transformation into *Escherichia coli* (DH5 α , Thermo Fisher Scientific, Waltham, MA, USA). The target fragment was excised from pGM-T-*LuPLATZ14* and pGM-T-*LuPLATZ21* using XhoI and SalI restriction enzymes (New England Biolabs, Ipswich, MA, USA) and ligated into the similarly digested pCAMBIA1301 vector (Clontech, Mountain View, CA, USA) to generate pCAMBIA1301-*LuPLATZ14*-GFP and pCAMBIA1301-*LuPLATZ21*-GFP. Both the empty pCAMBIA1301 vector and recombinant plasmid were separately introduced into *Agrobacterium tumefaciens* GV3101 (strain, Agilent Technologies, Santa Clara, CA, USA) via the freeze–thaw method. The bacterial culture was resuspended in infiltration buffer (10 mM MES, pH 5.6, 10 mM MgCl₂, and 150 μ M acetosyringone, Sigma-Aldrich, St. Louis, MO, USA), and after 3 h of induction at 28 °C, the culture was injected into *Nicotiana benthamiana* leaves. After 3 days of dark incubation, GFP fluorescence signals were observed using a confocal microscope (Leica TCS SP8, Leica Microsystems, Wetzlar, Germany).

2.9. Heterologous Expression of LuPLATZ14 and LuPLATZ21 Genes in the *Saccharomyces cerevisiae* Strain INVSc1

Using a directional cloning approach with HindIII and BamHI restriction enzymes (Takara Bio, Kyoto, Japan), *LuPLATZ14* and *LuPLATZ21* were inserted into the multiple cloning site of the *Saccharomyces cerevisiae* expression vector pYES2 (Invitrogen, Carlsbad, CA, USA), producing the recombinant plasmids pYES2-*LuPLATZ14* and pYES2-*LuPLATZ21*. These plasmids were subsequently transformed into *S. cerevisiae* INVSc1 (Thermo Fisher Scientific, Waltham, MA, USA). The empty pYES2 vector served as a negative control. Recombinant plasmids pYES2-*LuPLATZ14*, pYES2-*LuPLATZ21*, and the empty vector were serially diluted 10^{-1} to 10^{-4} , and 2 μ L of each dilution was spotted onto SD-ura plates (BD Biosciences, Franklin Lakes, NJ, USA) and SD-ura plates containing 300 mM mannitol (Sigma-Aldrich, St. Louis, MO, USA), followed by observation of their phenotypic responses.

3. Results

3.1. Identification and Phylogenetic Analysis of PLATZ Gene Family in Flax

Based on the hidden Markov model (HMM) of the *PLATZ* structural domain (PF04640), a total of 27 *PLATZ* genes were identified in the flax T2T genome (Gaosi) and were named *LuPLATZ1* to *LuPLATZ27* according to their chromosomal locations (Table 1). Analysis of the physicochemical properties of the proteins encoded by the *LuPLATZ* gene family revealed that *LuPLATZ12* encodes the longest protein, containing 547 amino acids, whereas *LuPLATZ4* encodes the shortest protein, with only 124 amino acids. The molecular weights of *LuPLATZ* family proteins ranged from 13.19 kDa to 61.67 kDa, showing considerable variation. Isoelectric point (pI) analysis indicated that most proteins in this family are basic, with 81.5% having a pI greater than 8, suggesting enrichment in basic amino acids. The instability index ranged from 46.13 to 85.33, with all proteins exceeding 40, indicating that *LuPLATZ* family proteins are generally unstable. The aliphatic index varied from 49.01 to 75.99, suggesting relatively small differences in thermal stability and an overall moderate stability. GRAVY analysis showed that all *LuPLATZ* proteins had negative values (−0.002 to −1.045), indicating hydrophilicity, with *LuPLATZ12* being the most hydrophilic (−1.045). Subcellular localization prediction indicated that all *LuPLATZ* proteins are located in the nucleus, suggesting that they may function as transcription factors within the nucleus.

Table 1. Prediction and characterization of *PLATZ* Gene in Flax.

Gene	Gene ID in Genome	Number of Amino Acids	Molecular Weight (KDa)	PI	Instability Index	Aliphatic Index	Grand Average of Hydropathicity (GRAVY)	Subcellular Localization
LuPLATZ1	LusiChr1G187770.1	197	21.27	8.01	47.65	74.21	−0.145	Nuclear
LuPLATZ2	LusiChr1G194980.1	215	24.13	9.11	61.43	62.14	−0.502	Nuclear
LuPLATZ3	LusiChr1G203360.1	217	24.4	8.99	62.81	64.24	−0.499	Nuclear
LuPLATZ4	LusiChr1G209970.1	124	13.19	9.08	46.13	75.4	−0.002	Nuclear
LuPLATZ5	LusiChr2G076260.1	277	31.87	8.28	51.57	61.16	−0.711	Nuclear
LuPLATZ6	LusiChr2G088000.1	277	30.92	9.59	57.96	66.9	−0.416	Nuclear
LuPLATZ7	LusiChr3G370300.1	286	32.81	8.13	48.57	62.97	−0.714	Nuclear
LuPLATZ8	LusiChr4G319920.1	263	29.16	8.39	67.7	58.33	−0.501	Nuclear
LuPLATZ9	LusiChr5G385480.1	271	30.41	7.84	51.58	65.06	−0.543	Nuclear
LuPLATZ10	LusiChr6G235470.1	227	24.64	9.56	49.13	75.99	−0.204	Nuclear
LuPLATZ11	LusiChr7G269670.1	249	27.90	8.37	59.6	75.98	−0.25	Nuclear
LuPLATZ12	LusiChr7G276620.1	547	61.67	10.24	85.33	49.01	−1.045	Nuclear
LuPLATZ13	LusiChr8G043760.1	264	29.76	8.97	53.31	69.73	−0.418	Nuclear
LuPLATZ14	LusiChr8G058360.1	326	36.27	8.61	51.75	66.41	−0.601	Nuclear
LuPLATZ15	LusiChr9G100100.1	258	28.91	6.6	59.68	69.19	−0.489	Nuclear
LuPLATZ16	LusiChr9G112840.1	244	27.37	8.83	62.28	74.34	−0.273	Nuclear
LuPLATZ17	LusiChr10G125160.1	257	29.23	9.06	58.64	66.34	−0.651	Nuclear
LuPLATZ18	LusiChr10G134580.1	258	28.88	8.5	58.04	68.8	−0.495	Nuclear
LuPLATZ19	LusiChr11G290390.1	316	36.35	9.63	50.88	68.04	−0.553	Nuclear
LuPLATZ20	LusiChr12G460550.1	226	25.22	8.52	84.03	59.51	−0.7	Nuclear
LuPLATZ21	LusiChr13G417460.1	246	27.42	8.72	59.1	71.75	−0.393	Nuclear
LuPLATZ22	LusiChr13G419590.1	244	27.75	9.23	53.06	57.5	−0.746	Nuclear
LuPLATZ23	LusiChr13G431690.1	270	29.84	7.93	66.66	59.33	−0.494	Nuclear
LuPLATZ24	LusiChr14G023030.1	233	26.28	9.01	53.58	62.27	−0.597	Nuclear
LuPLATZ25	LusiChr15G164250.1	245	27.21	9.12	57.91	67.27	−0.456	Nuclear
LuPLATZ26	LusiChr15G166600.1	245	27.81	9.32	55.2	60.04	−0.753	Nuclear
LuPLATZ27	LusiChr15G184210.1	285	31.56	9.46	59.92	67.82	−0.381	Nuclear

To gain deeper insight into the phylogenetic relationships of the flax *PLATZ* gene family, we constructed a phylogenetic tree using the Maximum Likelihood (ML) method

with 1000 bootstrap replicates, incorporating *PLATZ* proteins from five species: *Arabidopsis*, *Oryza sativa*, *Zea mays*, *Glycine max*, and *Linum usitatissimum* (Figure 1) (Table S1). Bootstrap support values are shown at the nodes to assess the reliability of the clades. Based on the phylogenetic analysis, the 27 *LuPLATZ* proteins were classified into five major evolutionary groups (Group I–V). Group I contained the largest number of *LuPLATZ* members, totaling nine, followed by Group IV and Group V, which contained six and five *LuPLATZ* genes, respectively. Group II and Group III included four and three members, respectively. This distribution pattern suggests that the *LuPLATZ* family has undergone significant gene expansion during evolution. Several *LuPLATZ* genes clustered together with *PLATZ* proteins from different species, indicating strong conservation and suggesting that they may perform similar functions in plant growth, development, and environmental responses.

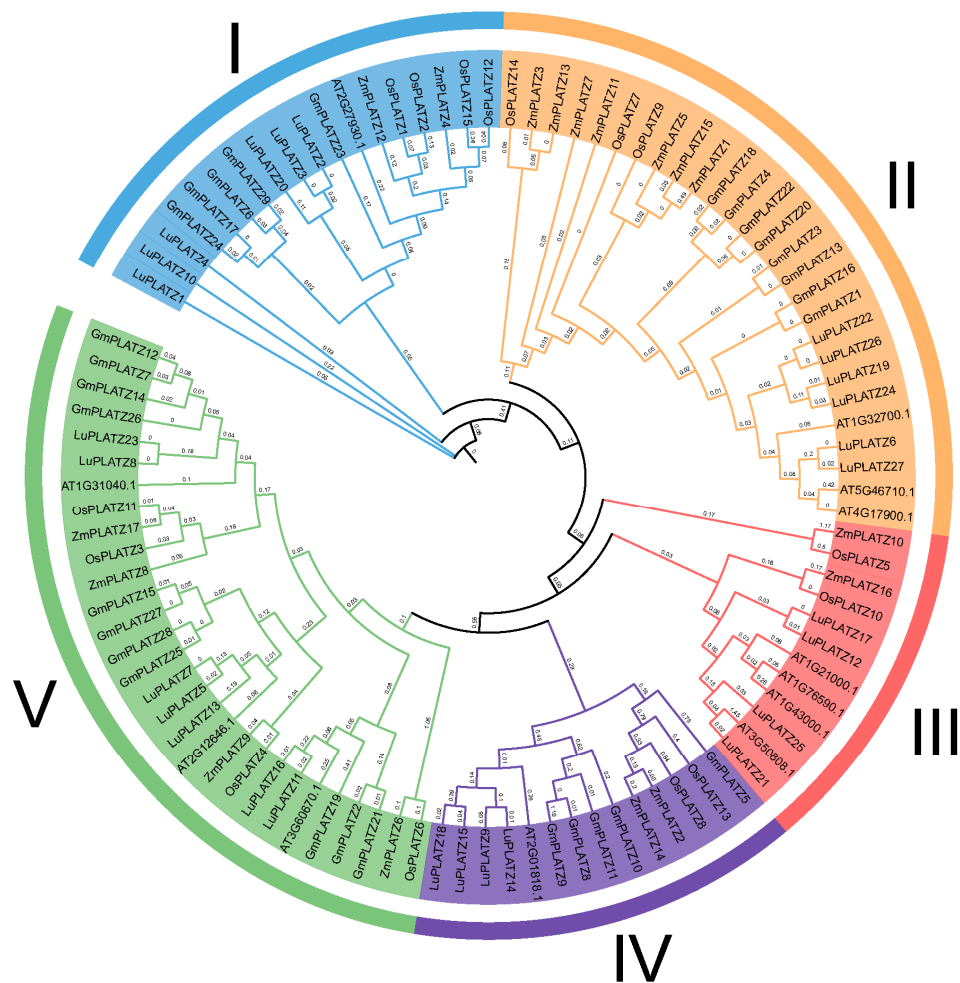


Figure 1. Phylogenetic tree of *PLATZ* proteins. The prefixes At, Lu, Gm, and Zm represent genes from *Arabidopsis*, flax, soybean, and maize, respectively. All *PLATZ* genes were classified into five subfamilies, which are indicated by different colors and letters.

3.2. Analysis of Gene Structure and Conservative Motif of *LuPLATZ*

To elucidate the domain composition of the *LuPLATZ* family proteins, we performed a systematic analysis of conserved motifs for all 27 *LuPLATZ* genes. The phylogenetic tree constructed based on multiple sequence alignment (Figure 2A) showed a clustering pattern consistent with that in Figure 1. Ten conserved motifs were predicted and named motif1 to motif10 (Figure 2B). All members contained motifs 1, 3, and 6; all members except *LuPLATZ4* contained motif8; all members except *LuPLATZ4* and *LuPLATZ10* contained motif4; and all members except *LuPLATZ4* and *LuPLATZ13* contained motif2. All members

except four genes (*LuPLATZ1* and *LuPLATZ4*) contained motif5. We further found that only *LuPLATZ12*, *LuPLATZ17*, *LuPLATZ21*, and *LuPLATZ25* contained motif7, which is a unique motif of the III subfamily. Overall, the types, numbers, and distribution patterns of motifs were comparable among *LuPLATZ* proteins within each branch. Exon–intron structure analysis of *LuPLATZ* genes showed that exon numbers varied from 2 to 11 and intron numbers from 1 to 10 (Figure 2C). *LuPLATZ11* possessed the most complex structure, with 11 exons and 10 introns, followed by *LuPLATZ19*, which contained 5 exons and 4 introns. *LuPLATZ25* had the fewest, with only 2 exons and 1 intron. Sixteen genes (59.26% of the total) contained three exons. We also observed that genes in the Group V branch all contained four exons, suggesting functional similarity among these genes.

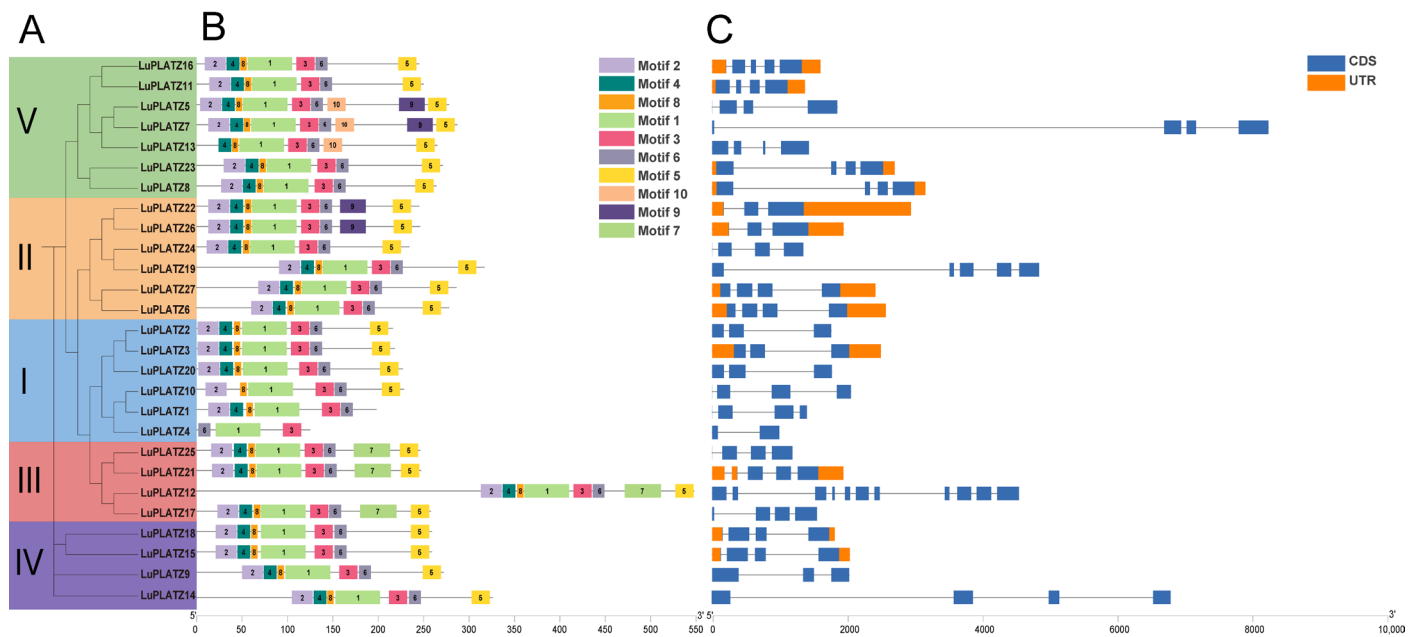


Figure 2. Gene structure, motif composition, and chromosomal distribution of *LuPLATZ* genes. (A) Phylogenetic relationships among *LuPLATZ* genes. (B) Motif composition of *LuPLATZ* genes. Gray lines indicate the full gene length, while distinct colors correspond to different conserved motifs. (C) Structural organization of *LuPLATZ* genes. Orange boxes denote UTR, dark blue boxes represent coding sequences (CDS), and black lines indicate introns.

3.3. Chromosome Mapping and Collinearity Analysis of *LuPLATZ* Gene

Using the flax reference genome, we determined the chromosomal distribution of *LuPLATZ* genes. The 27 genes were unevenly mapped to 15 chromosomes (Figure 3). Chromosome 1 harbored the most members (four, 14.81%), followed by chromosomes 13 and 15 with three each (11.11%), while chromosomes 3–6, 11–12, and 14 contained only one gene (3.7%).

We performed a gene duplication analysis of the *LuPLATZ* gene family using BLAST and MCScanX. No tandem duplication events were identified within the *LuPLATZ* family. To further investigate gene duplication, we constructed a Circos map (Figure 4A), which revealed 33 pairs of duplicated *LuPLATZ* genes in the flax genome, indicating a substantial expansion of this gene family. We also found that all collinear gene pairs of *LuPLATZ* have Ka/Ks ratios less than 1, indicating that they evolved under purifying selection (Table 2). To clarify the evolutionary relationships of flax, we analyzed its collinearity with three representative species—*Arabidopsis*, maize, and wheat (Figure 4B). The results showed 15, 3, and 1 collinear gene pairs, respectively. Among them, all five *Arabidopsis* chromosomes displayed collinearity with flax chromosomes; maize *PLATZ* collinear pairs

were located on flax chromosomes 2, 11, and 15; and the wheat *PLATZ* collinear pair was located on flax chromosome 13. Taken together, these results indicate that most *PLATZ* genes exhibit conserved collinearity among flax and the three representative species, while species-specific variations in gene pairs also exist, highlighting the important role of *LuPLATZ* genes in the evolutionary history of the family.

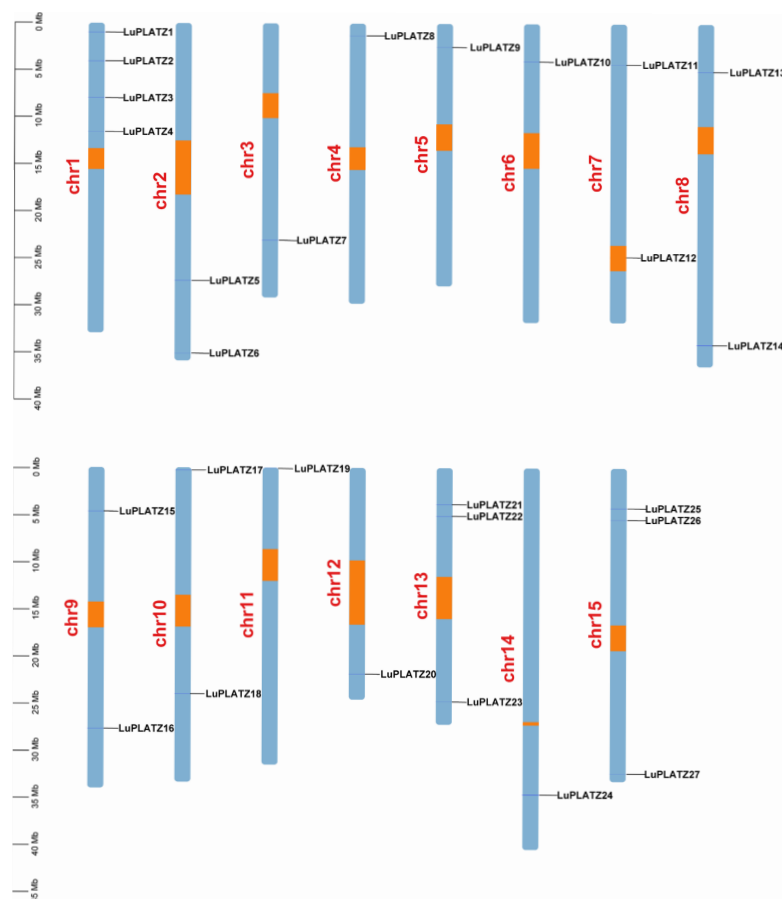


Figure 3. The chromosome distribution map of *LuPLATZ* genes. Orange represents the centromere region.

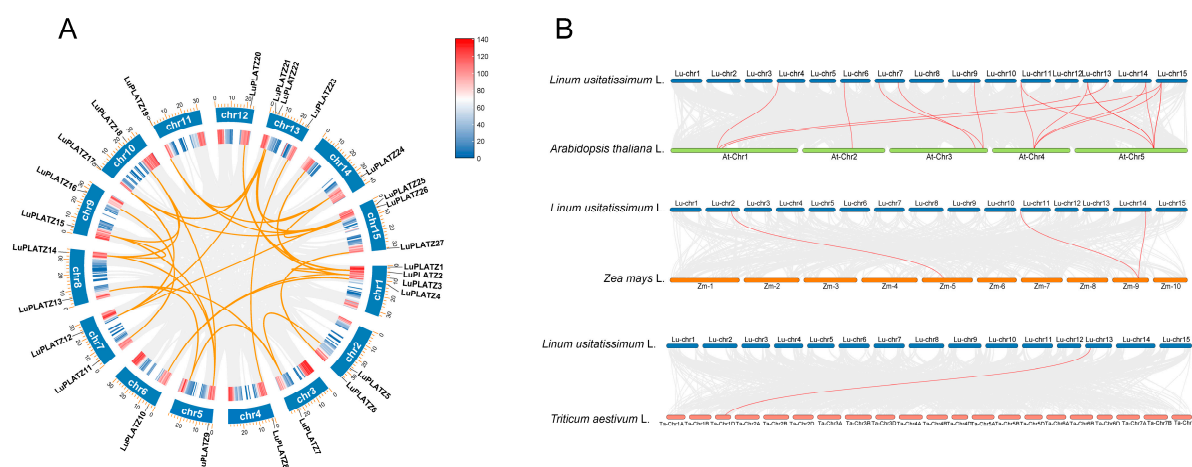


Figure 4. Synteny analysis of the *LuPLATZ* gene family. (A) Intra-species syntenic relationships among *LuPLATZ* members. (B) Cross-species synteny comparisons of *PLATZ* genes between flax and three representative species: *Arabidopsis*, maize and wheat. In both panels, gray connections indicate genome-wide collinear gene pairs, while orange linkages specifically highlight syntenic pairs involving *LuPLATZ* genes.

Table 2. Ka, Ks and Ka/Ks of replication pairs of *PLATZ* gene family in flax.

Duplicated Gene Pairs	Non Synonymous (Ka)	Synonymous (Ks)	Ka/Ks
LuPLATZ1&LuPLATZ2	0.0103	0.104	0.099
LuPLATZ2&LuPLATZ3	0.027	0.067	0.408
LuPLATZ2&LuPLATZ20	0.148	0.941	0.158
LuPLATZ3&LuPLATZ20	0.189	0.913	0.207
LuPLATZ2&LusiChr14G009600.1	0.488	1.161	0.421
LuPLATZ3&LusiChr14G009600.1	0.432	0.980	0.441
LuPLATZ3&LuPLATZ10	0.394	3.448	0.114
LusiChr1G209960.1&LuPLATZ10	0.245	0.336	0.731
LuPLATZ17&LuPLATZ21	0.124	1.142	0.108
LuPLATZ17&LuPLATZ25	0.121	1.0738	0.112
LuPLATZ18&LuPLATZ9	0.301	1.248	0.241
LuPLATZ17&LuPLATZ12	0.0439	0.235	0.186
LuPLATZ18&LuPLATZ14	0.252	1.201	0.210
LuPLATZ18&LuPLATZ15	0.025	0.077	0.329
LuPLATZ19&LuPLATZ22	0.135	0.988	0.137
LuPLATZ19&LuPLATZ24	0.0281	0.113	0.248
LuPLATZ19&LuPLATZ26	0.151	0.901	0.167
LuPLATZ22&LuPLATZ24	0.142	1.056	0.134
LuPLATZ21&LuPLATZ25	0.034	0.174	0.196
LuPLATZ22&LuPLATZ26	0.014	0.158	0.089
LuPLATZ23&LuPLATZ8	0.016	0.188	0.087
LuPLATZ21&LuPLATZ12	0.125	1.102	0.113
LuPLATZ24&LuPLATZ26	0.162	0.934	0.173
LuPLATZ27&LuPLATZ6	0.014	0.118	0.125
LuPLATZ25&LuPLATZ12	0.119	1.025	0.116
LuPLATZ5&LuPLATZ7	0.022	0.205	0.110
LuPLATZ7&LusiChr5G398470.1	0.552	2.559	0.215
LuPLATZ7&LuPLATZ13	0.229	0.9002	0.255
LuPLATZ9&LuPLATZ14	0.069	0.255	0.270
LusiChr5G398470.1&LuPLATZ13	0.263	0.575	0.457
LuPLATZ9&LuPLATZ15	0.294	1.271	0.232
LuPLAT11&LuPLATZ16	0.025	0.124	0.202
LuPLAT14&LuPLATZ15	0.246	1.304	0.188

3.4. Analysis of Cis-Acting Elements and MiRNA Prediction

To investigate the regulatory roles of *LuPLATZ* genes under abiotic stress, we predicted and visualized cis-acting elements within the 2000 bp upstream promoter regions (Figure 5A). Excluding common motifs such as the TATA-box and CAAT-box, we identified 763 elements, which were classified into four categories: light-responsive, hormone-responsive, stress-related, and development-related (Figure 5B,C) (Table S2). Light-responsive elements were the most abundant, accounting for 355 elements (46.52%), and included G-box, Box 4, GT1-motif, and MRE. Hormone-responsive elements represented the second largest category, totaling 234 elements (30.67%), and included MeJA-responsive motifs (CGTCA- and TGACG-motifs), abscisic acid-responsive elements (ABRE), auxin-responsive motifs (TGA-element and AuxRR-core), gibberellin-responsive elements (GARE-motif and P-box), and salicylic acid-responsive motifs (TCA-element). Among these, MeJA- and ABA-related elements were the most abundant within *LuPLATZ* promoters. Stress-related elements accounted for 127 motifs (16.64%) and comprised anaerobic induction elements (ARE and GC-motif), low-temperature-responsive elements (LTR), MYBHv1 binding sites (CCAAT-box), drought-inducible MYB binding sites (MBS), defense- and stress-responsive elements (TC-rich repeats), and wound-responsive motifs (WUN-

motif). The smallest category was development-related elements, with 47 elements (6.16%), such as meristem expression elements (CAT-box), seed-specific regulatory elements (RY-element), zein metabolism regulatory elements (O2-site), cell cycle regulation elements (MSA-like), circadian-responsive elements (circadian), and endosperm expression elements (GCN4_motif).

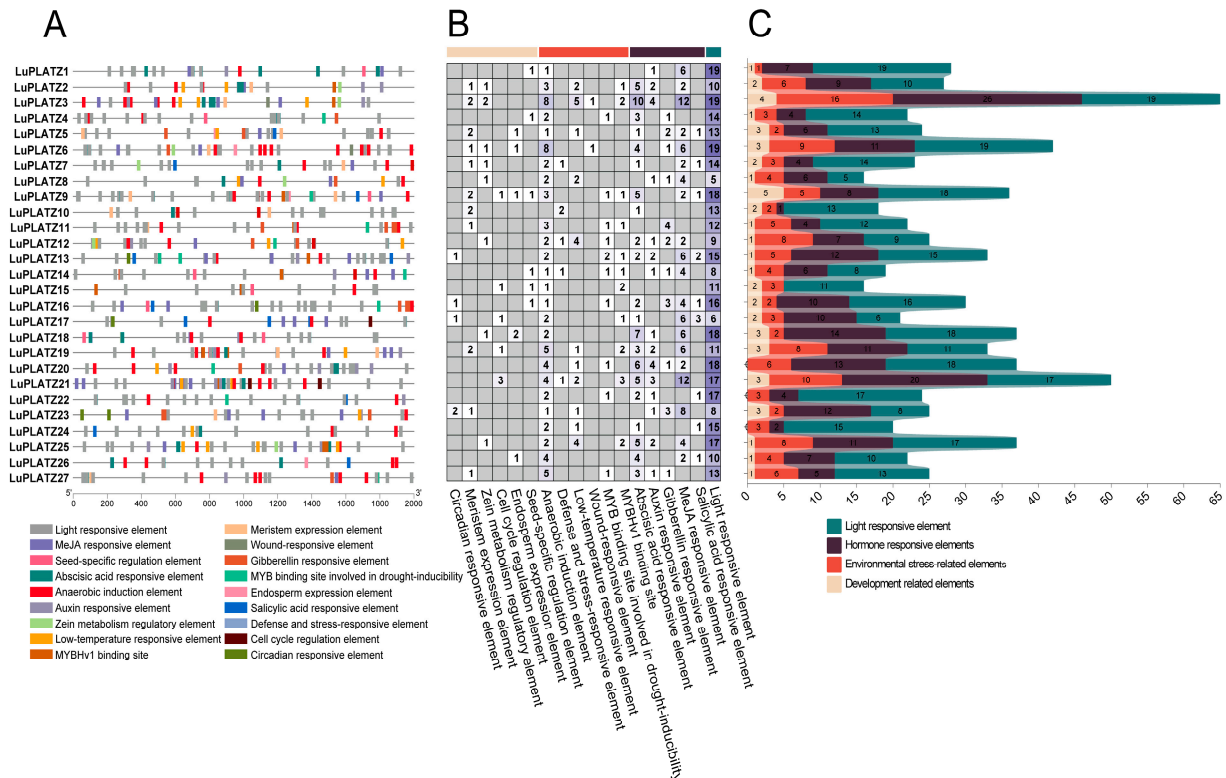


Figure 5. Prediction of cis-acting elements in *LuPLATZ* genes. (A) Distribution of cis-elements among the various *LuPLATZ* subfamilies. (B,C) Quantitative analysis of cis-element types in *LuPLATZ* genes. Light yellow indicates development-related elements, dark orange represents stress-related elements, dark purple corresponds to hormone-responsive elements, and dark green marks light-responsive elements.

MiRNA prediction analysis revealed that only 6 of the 27 *LuPLATZ* genes (22.22%) were targeted by 12 putative miRNAs (Table 3). Among them, *LuPLATZ1* and *LuPLATZ4* had the largest number of predicted miRNA targets, each with nine, including *lus-miR167a/b/c/d/e/f/g/h/i*. In contrast, *LuPLATZ9*, *LuPLATZ15*, and *LuPLATZ18* had the fewest, with only one predicted miRNA target each. We also observed that different *LuPLATZ* genes could be targeted by the same miRNA. For example, *lus-miR167* simultaneously targeted *LuPLATZ1* and *LuPLATZ4*, while *lus-miR408* targeted *LuPLATZ9*, *LuPLATZ15*, and *LuPLATZ18*. Taken together, these findings indicate that *lus-miR167* is the predominant miRNA regulator of the *LuPLATZ* gene family.

Table 3. Potential MiRNA targets of *LuPLATZ* gene.

MiRNA	Target	Expectation	MiRNA Length	Target_Start	Target_End	Inhibition	Multiplicity
lus-miR408a	LuPLATZ18	4.5	1	21	325	345	Translation
lus-miR408a	LuPLATZ15	4.5	1	21	325	345	Translation
lus-miR167a/b/c/d/e/f/g/h/i	LuPLATZ1	5	1	21	386	406	Cleavage
lus-miR167a/b/c/d/e/f/g/h/i	LuPLATZ4	5	1	21	257	277	Translation
lus-miR408a	LuPLATZ9	5	1	21	406	426	Translation
lus-miR530a/b	LuPLATZ12	5	1	20	101	120	Cleavage

3.5. Analysis of LuPLATZ Gene Expression Pattern Based on RNA-Seq Data

To investigate the potential functions of *LuPLATZ* genes in abiotic stress responses, publicly available transcriptome data were analyzed under salt and heat stress (Figure 6A). No major transcriptional changes were observed under heat stress, except for *LuPLATZ15*, which was downregulated in stem tissue. In contrast, most *LuPLATZ* genes exhibited marked expression changes under salt stress in both leaves and roots. Compared with the control, six genes (*LuPLATZ4*, 15, 17, 18, 22, and 26) were upregulated in roots, with *LuPLATZ15* showing the strongest induction, while another six genes (*LuPLATZ2*, 3, 5, 7, 13, and 23) were downregulated. In leaves, eight genes (*LuPLATZ11*, 15, 16, 17, 20, 24, 25, and 27) were significantly upregulated, with *LuPLATZ16* displaying the highest induction.

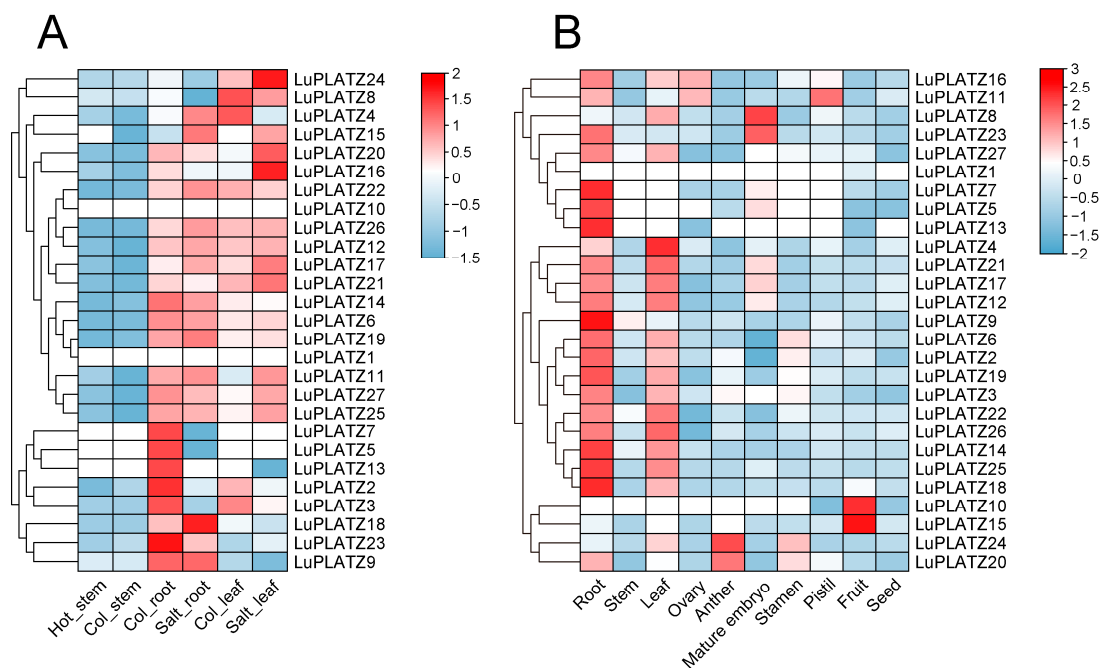


Figure 6. Expression patterns of the *LuPLATZ* gene family. (A) *LuPLATZ* gene expression under salt and heat treatments. (B) Expression of *LuPLATZ* genes across different flax tissues. FPKM values are log2-transformed, with colors representing relative expression levels from high (red) to low (blue).

To investigate their involvement in plant growth and development, RNA-seq data from 10 tissues were analyzed (Figure 6B). The results revealed clear tissue-specific expression patterns, with most *LuPLATZ* genes showing high expression in roots and leaves, but low levels in seeds. Specifically, all members except five (*LuPLATZ1*, 8, 10, 15, and 24) were strongly expressed in roots. *LuPLATZ11* and *LuPLATZ16* were predominantly expressed in the ovary, *LuPLATZ20* and *LuPLATZ24* in the anther and stamen, *LuPLATZ8* and *LuPLATZ23* in the mature embryo, *LuPLATZ11* in the pistil, and *LuPLATZ10* and *LuPLATZ15* in the fruit. Overall, these findings indicate that most *LuPLATZ* genes are preferentially expressed in roots and leaves, suggesting that these tissues serve as major sites for reactive oxygen species (ROS) regulation and represent the primary antioxidant defense system in flax. The *LuPLATZ* genes are therefore likely to play critical regulatory roles in stress adaptation and developmental processes.

3.6. qRT-PCR Analysis of *LuPLATZ* Gene Expression in Flax Under Abiotic Stress

To capture the diversity of the *LuPLATZ* gene family, ten genes were selected from five subfamilies, all exhibiting high homology with known *Arabidopsis* genes. The relative expression of these genes was evaluated by qRT-PCR under abiotic stresses in leaves sampled

at 0, 3, 6, 9, 12, and 24 h, with 0 h as the control (Figure 7). Under cold stress, all *LuPLATZ* genes responded significantly over time (Figure 7A). *LuPLATZ6* and *LuPLATZ13* peaked at 3 h, showing approximately 12.4- and 8.2-fold increases compared with the control, then rapidly declined. *LuPLATZ3*, *LuPLATZ14*, and *LuPLATZ25* peaked at 9 h, increasing by ~1.8-, 3.7-, and 6.2-fold, respectively. Five genes (*LuPLATZ9*, 11, 20, 21, and 27) were downregulated, with expression suppressed after 6 h. Under salt stress, significant changes were observed over time (Figure 7B). Seven genes (*LuPLATZ3*, 6, 11, 13, 14, 21, and 25) peaked at 3 h, with fold changes of 4.9-, 5.8-, 7.9-, 8.8-, 7.5-, 5.6-, and 7.3-fold, respectively, before declining. *LuPLATZ27* was upregulated at 12 h (~1.8-fold), while *LuPLATZ9* and *LuPLATZ20* were downregulated, reaching minima at 9 h and 3 h, respectively. Under drought stress, *LuPLATZ* genes also showed marked responses (Figure 7C). *LuPLATZ3* and *LuPLATZ25* peaked at 3 h (~3.3- and 5.2-fold). Six genes (*LuPLATZ6*, 9, 11, 14, 21, and 27) peaked at 12 h, with fold changes of 3.8-, 9.1-, 1.9-, 6.1-, 9.8-, and 5.2-fold, respectively. *LuPLATZ20* was significantly upregulated at 24 h (~9.5-fold). Overall, these results indicate that 6 h under salt stress and 12 h under drought stress may represent critical time points for *LuPLATZ* gene responses.

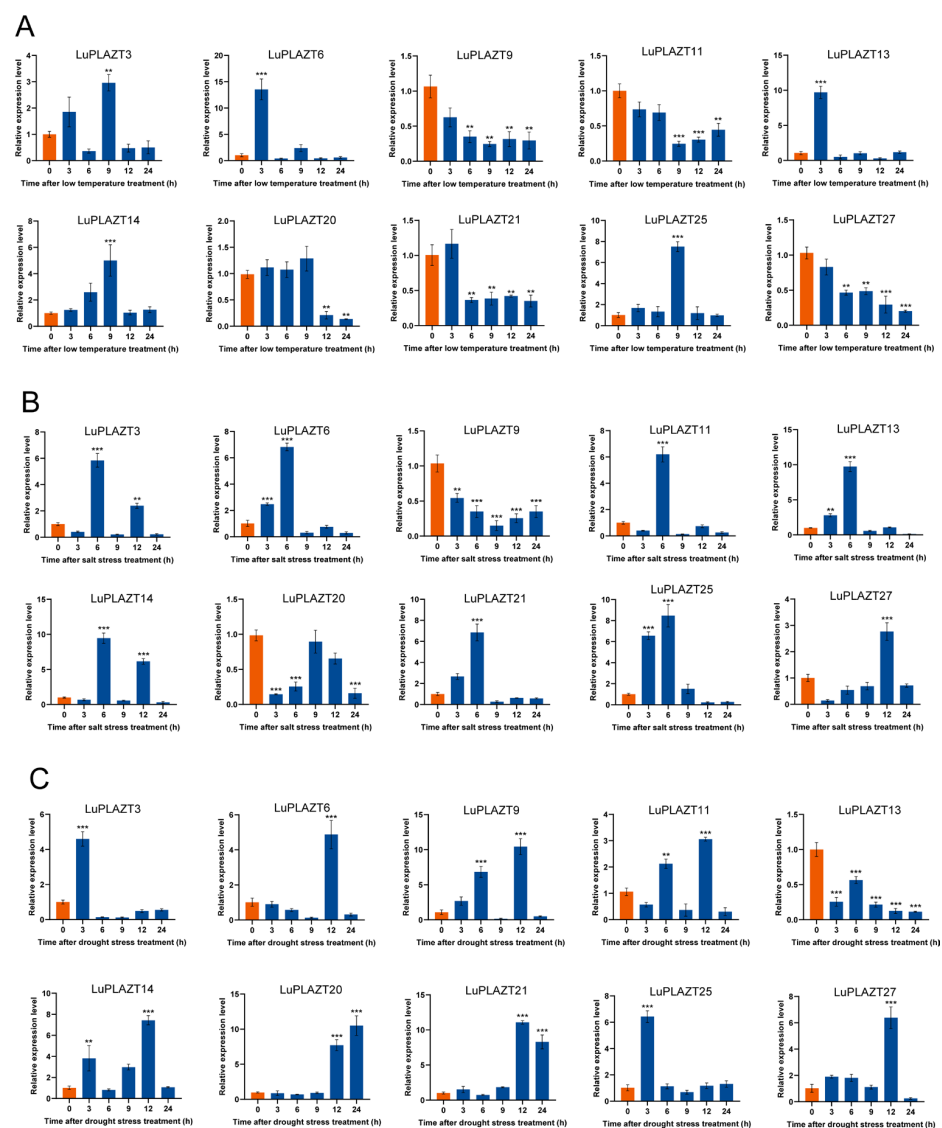


Figure 7. Expression profiles of *LuPLATZ* genes under abiotic stresses. (A) Cold stress. (B) Salt stress. (C) Drought stress. Control samples are shown in orange, and treated samples in blue. Statistical significance was determined by Student's *t*-test, with asterisks denoting * $p < 0.01$ and *** $p < 0.001$.

3.7. Subcellular Localization of *LuPLATZ14* and *LuPLATZ21* Genes

The subcellular localization of *LuPLATZ14* and *LuPLATZ21* was determined by transiently expressing GFP-tagged fusion constructs, pCAMBIA1301-*LuPLATZ14*-GFP and pCAMBIA1301-*LuPLATZ21*-GFP, in young tobacco leaves using *Agrobacterium tumefaciens* GV3101. The empty vector control (pCAMBIA1301-GFP) showed GFP fluorescence throughout the cell, whereas the GFP signals of *LuPLATZ14* and *LuPLATZ21* were specifically localized to the nucleus (Figure 8), consistent with the predictions listed in Table 1.

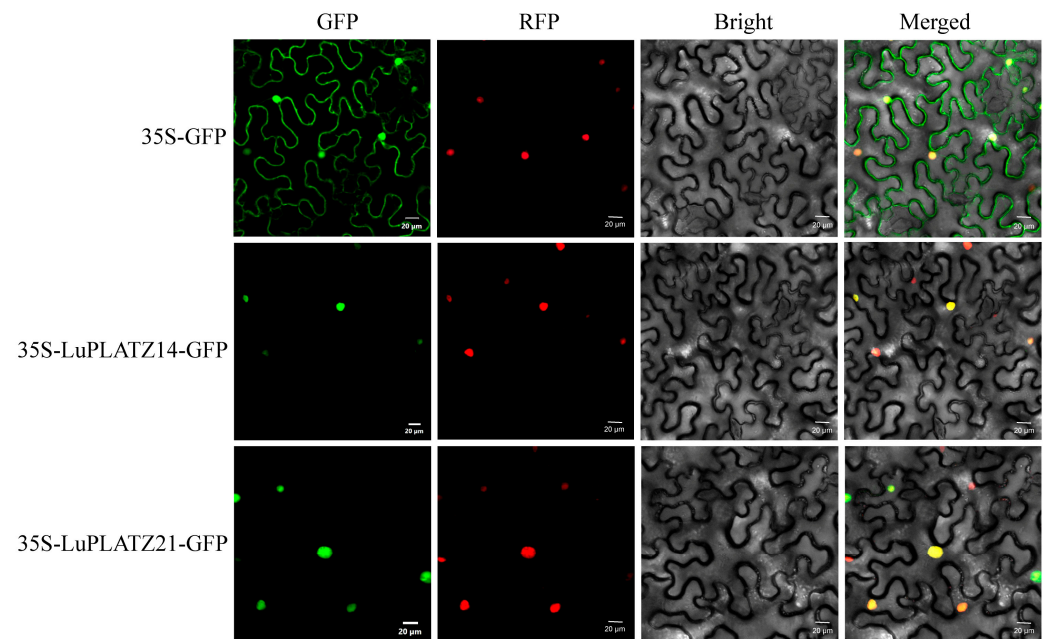


Figure 8. Subcellular localization analysis of *LuPLATZ14* and *LuPLATZ21* proteins in tobacco cells. RFP (red fluorescence protein) used as a marker for subcellular localization. Scale bar = 20 µm.

3.8. Drought Tolerance Assay of Yeast Transformants

Based on previous experiments, *LuPLATZ14* and *LuPLATZ21*, which exhibited the strongest drought tolerance, were selected as candidate genes for further study. To determine their effects on the survival of yeast recombinants under osmotic stress, yeast strains carrying pYES2-*LuPLATZ14*, pYES2-*LuPLATZ21*, or the empty vector (pYES2) were assessed for colony growth under 300 mM mannitol treatment (Figure 9). Under optimal growth conditions, no significant differences were observed between the transformants and control strains. Under 300 mM mannitol-induced drought stress, the transformants exhibited enhanced growth compared with the control. These results indicate that overexpression of *LuPLATZ14* and *LuPLATZ21* can improve drought tolerance in yeast transformants.

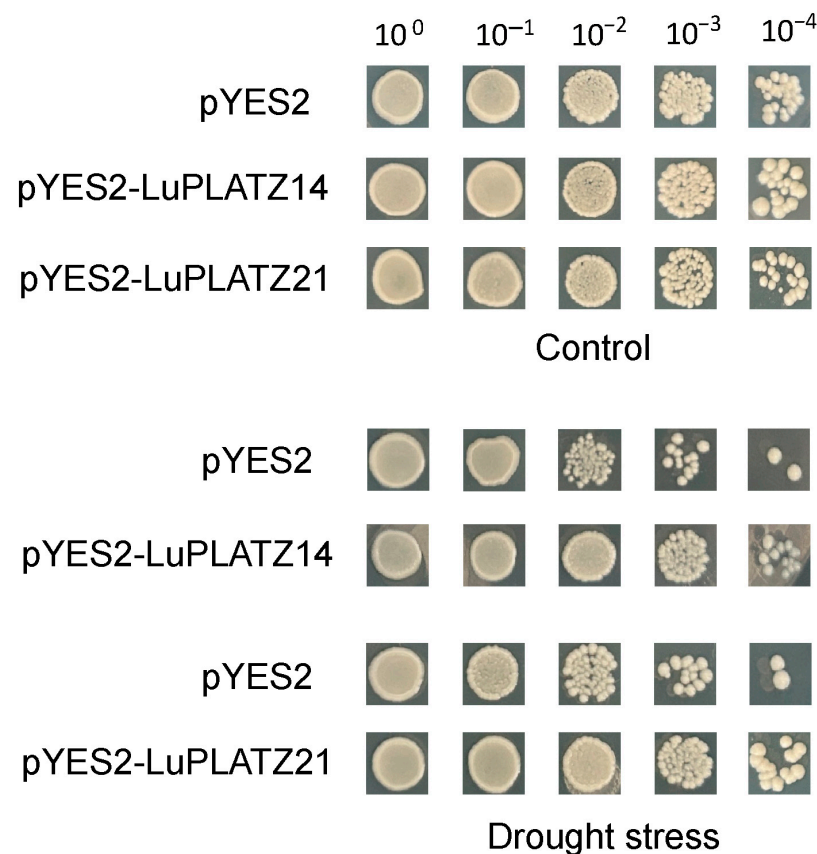


Figure 9. Overexpression of *LuPLATZ14* and *LuPLATZ21* enhanced drought tolerance in yeast transformants. Control yeast strains were grown at 30 °C for 48 h under normal conditions, while the treatment strains were cultured under the same temperature and duration in the presence of 300 mM mannitol to simulate osmotic stress.

4. Discussion

As plant-specific transcription factors with zinc-dependent DNA-binding ability, *PLATZ* proteins participate in regulating plant growth, developmental processes, and adaptation to environmental stresses by recognizing particular DNA motifs. [19]. Although *PLATZ* transcription factors have been reported in other plant species, information on *LuPLATZ* in flax remains limited. To date, no studies have comprehensively identified the *LuPLATZ* gene family using genomic approaches. In the present study, 27 *LuPLATZ* genes were identified in the flax T2T genome (Table 1). Our analysis showed that the number of *LuPLATZ* genes in flax (27) was slightly higher than that in *Arabidopsis* (12) [1], rice (15) [8], maize (17) [1], and cucumber (12) [9], but was comparable to that in soybean (29) [7] and tomato (24) [42]. Phylogenetic analysis further revealed that the *LuPLATZ* genes were classified into five subfamilies (Figure 1), which was largely consistent with previous studies [5].

Conserved motif analysis revealed that most *LuPLATZ* proteins share a similar motif arrangement (Figure 2B), consisting of motifs 2, 4, 8, 1, 3, 6, and 5, which is consistent with observations in tomato [42]. The exon–intron analysis of *LuPLATZ* genes revealed that exon numbers varied between 2 and 11, while intron counts ranged from 1 to 10 (Figure 2C), with most genes exhibiting structural variations. Such differences in *PLATZ* gene structures may result from exon/intron insertion or deletion events [43], may provide the genomic basis for alternative splicing under stress conditions, thereby contributing to functional diversification. Moreover, genes within the same *LuPLATZ* subfamily displayed similar exon–intron patterns and motif compositions, implying conserved functions in abiotic

stress responses, as also reported in pecan [44]. Compared with *Arabidopsis* and maize, flax is regarded as a temperate crop that is frequently exposed to abiotic stresses such as cold and drought, particularly during its vegetative growth stage. The adaptation of flax to these conditions may have been facilitated by the expansion and diversification of *LuPLATZ* genes, through which stress tolerance mechanisms could have been enhanced early in development. Moreover, conserved motif composition and exon–intron structures have been observed between *LuPLATZ* genes and their counterparts in tomato, another dicot species, suggesting that core regulatory functions may be retained by *PLATZ* genes across species while flax-specific roles associated with its growth habit and environmental resilience may also have been evolved [42].

Gene duplication events play a critical role in the evolution of *PLATZ* genes, as duplicated genes can acquire new functions, thereby enhancing plant responses to environmental stresses [45]. In this study, chromosomal mapping revealed that the 27 *LuPLATZ* genes are unevenly distributed across 15 chromosomes, with no tandem duplications detected (Figure 3). However, collinearity analysis identified 33 pairs of segmentally duplicated genes (Figure 4A), indicating that segmental duplication is the main driver of *LuPLATZ* gene expansion [46]. Collinearity analysis is a powerful approach for investigating gene evolutionary trajectories [47]. Flax was an ancient diploid plant that underwent three whole-genome duplication (WGD) events approximately 11.5, 53.5, and 114 million years ago (MYA) [24]. WGD was likely one of the primary driving forces behind the expansion of the *LuPLATZ* gene family, providing a large number of redundant gene copies. Comparative analysis revealed 15, 3, and 1 collinear gene pairs between flax and *Arabidopsis*, maize, and wheat, respectively (Figure 4B), suggesting that these homologous gene pairs may have originated from a common ancestor prior to species divergence [48]. These findings demonstrate that *LuPLATZ* genes are highly conserved in flax, and their expansion is likely driven primarily by segmental duplication. The expansion of the *LuPLATZ* gene family may have contributed to flax's adaptation to temperate environments by enhancing its tolerance to abiotic stresses, such as cold and drought. Moreover, the functional diversification of duplicated genes might have facilitated the divergence between fiber and oilseed flax types by influencing traits related to growth, development, and stress responses.

Promoter cis-elements are key regulators of gene expression through their interactions with transcription factors [49]. Analysis of *LuPLATZ* promoters identified numerous elements involved in hormone signaling (MeJA and ABA) and abiotic stress responses, including anaerobic induction, drought, and cold (Figure 5). In detail, LTR elements were associated with cold response, ARE with anaerobic induction, and TC-rich repeats with drought and defense mechanisms [50]. The promoters also harbored ABA- and MeJA-responsive motifs (ABRE, TGACG-motif, CGTCA-motif) as well as MYB binding sites related to drought inducibility (MBS), indicating that these conserved cis-elements are likely pivotal for regulating both hormone-mediated and stress-related responses [51]. Notably, several drought-inducible genes (*LuPLATZ6*, 14, 21) contained MBSs, cold-responsive genes (*LuPLATZ3*, 25) carried LTR elements, and salt-induced genes (*LuPLATZ11*, 15) harbored ABRE motifs, suggesting that these cis-elements may underlie their stress-responsive expression.

MicroRNAs are key regulators that coordinate plant development and interactions with the environment [52]. In this study, *lus-miR167* was identified as the primary miRNA targeting the *LuPLATZ* gene family (Table 3). The conserved *miR167* has been shown to regulate plant growth and stress responses mainly through the targeting of auxin response factors (ARF6 and ARF8). In *Arabidopsis*, floral organ development was reported to be controlled by *miR167*, and misregulation of its expression was associated with defects in anther dehiscence and ovule formation [53]. In addition, *miR167* expression has been found to respond to multiple stresses, through which auxin signaling was fine-tuned to enhance

stress adaptation [54]. In *Tamarix chinensis*, the miR167/ARF6 module was observed to be negatively correlated under salt stress, suggesting that salt tolerance was promoted by this regulatory pathway [55]. In addition, *LuPLATZ1* and *LuPLATZ4* may be regulated by miR167, implying a potential post-transcriptional regulatory layer acting on these genes. Such regulation could contribute to fine-tuning their roles in growth and stress response pathways, adding further complexity to the regulatory network of the *LuPLATZ* gene family in flax. The regulatory mechanisms of *PLATZ* genes and the miR167–*PLATZ* module require further investigation.

Analysis of RNA-seq data revealed that *LuPLATZ* genes exhibit tissue-specific expression patterns. Most *LuPLATZ* genes were highly expressed in roots and leaves, whereas their expression levels were generally low in seed tissues (Figure 6). This pattern contrasts with observations in other species. For example, in *Arabidopsis*, *AtPLATZ1* and *AtPLATZ2* have been shown to contribute to seed desiccation tolerance, while *AtPLATZ2* negatively regulates salt tolerance [56]. In maize, Flury3 (*FL3*; *ZmPLATZ12*) interacts with the RNA polymerase III subunit *RPC53* and the transcription factor *TFC1*, playing a crucial role in the transcription of tRNAs and 5S rRNA in the endosperm, which is essential for proper seed development [14]. These observations suggested that *PLATZ* proteins have diversified functions across species. In flax, the predominant expression of *LuPLATZ* genes in vegetative tissues points to roles in growth and stress responses, while their low expression in seeds indicates limited involvement in reproduction. Overall, their tissue-specific expression highlights functional specialization in flax.

PLATZ transcription factors constitute a broadly conserved and versatile gene family in plants. Beyond their roles in growth and development, these genes are also key players in stress responses. In this study, several *LuPLATZ* genes showed marked transcriptional activation in both leaves and roots under salt stress, indicating their potential involvement in stress-responsive regulatory networks. Notably, the strong induction of *LuPLATZ15* in roots and *LuPLATZ16* in leaves suggests that specific members may play tissue-preferential roles in modulating stress responses (Figure 6). In this study, qRT-PCR analysis revealed dynamic and stress-specific expression profiles of several *LuPLATZ* genes. Under cold and salt stresses, many genes (*LuPLATZ6*, *LuPLATZ13*, *LuPLATZ14*, *LuPLATZ25*) responded rapidly with early expression peaks, whereas drought stress triggered a delayed but pronounced induction (*LuPLATZ6*, *LuPLATZ11*, *LuPLATZ21*, *LuPLATZ27*) (Figure 7). Phylogenetic analysis showed that several of these stress-inducible *LuPLATZ* genes are closely related to functionally validated orthologs in other crops. For example, *LuPLATZ14* and *LuPLATZ9* (cold/salt-responsive) clustered with *GmPLATZ11*, *LuPLATZ2* and *LuPLATZ3* (drought-responsive) grouped near *GmPLATZ17*, and *LuPLATZ22*, *LuPLATZ26*, *LuPLATZ8*, and *LuPLATZ23* were close to *OsPLATZ7/9/11* (stress- and hormone-responsive in rice). These relationships suggest that stress-related functions may be conserved between flax and other species. In rice, *OsPLATZ9* exhibited consistently high expression across diverse tissues, implying its multifaceted role in plant development, whereas *OsPLATZ7* and *OsPLATZ11* displayed variable expression under different abiotic stresses and hormone treatments, underscoring their significance in stress response and hormonal signaling [57]. Overexpression of *GhPLATZ1* in *Arabidopsis* enhanced seedling and seed tolerance to salt and osmotic stress and reduced sensitivity to ABA and GA/PAC treatments [18]. Functional validation of *SiPLATZ12* in foxtail millet indicated that it repressed salt-tolerance genes, thereby reducing salt resistance [58]. In *Arabidopsis*, *AtPLATZ2* was transcriptionally upregulated under salt stress, and overexpression increased salt sensitivity, whereas *AtPLATZ2/PLATZ7* double mutants exhibited markedly reduced salt tolerance [19]. Further yeast transformation assays in this study demonstrated that overexpression of *LuPLATZ14* and *LuPLATZ21* enhanced drought tolerance (Figure 9). Other studies supported similar mechanisms: *At-*

PLATZ4 improved drought tolerance by directly binding the A/T-rich promoter of *PIP2;8*, a plasma membrane aquaporin gene, repressing its expression to promote stomatal closure and reduce water loss [59]. In soybean, *GmPLATZ17* negatively regulated drought tolerance through interaction with *GmDREB5* [60]. Overexpression of bamboo *PhePLATZ1* in *Arabidopsis* enhanced drought resistance and improved physiological traits such as water retention and reduced oxidative damage, supporting a positive regulatory role via the ABA pathway [61]. Collectively, these findings provided strong evidence that *PLATZ* genes played crucial roles in abiotic stress responses, and characterization of the *LuPLATZ* gene family laid the foundation for further understanding their molecular functions in flax stress tolerance. However, as this study is primarily based on computational and expression analyses, the specific functions of *LuPLATZ* genes have not yet been experimentally validated, which represents a limitation that should be addressed in future work.

5. Conclusions

This study provides the first genome-wide characterization of the *PLATZ* gene family in flax, identifying 27 members based on the T2T gap-free genome. *LuPLATZ* genes are phylogenetically diverse and exhibit subfamily-specific responses to hormonal and abiotic stresses, with *LuPLATZ14* and *LuPLATZ21* conferring drought tolerance in yeast. These findings establish a molecular framework for understanding stress signaling in flax and highlight candidate genes for enhancing stress resilience, yield stability, and productivity in this dual-purpose oilseed and fiber crop. Future work should focus on functional validation of additional *LuPLATZ* genes and their incorporation into breeding strategies to improve flax performance under variable environments.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/agronomy15092233/s1>, Table S1. The *PLATZ* family genes in *Linum usitatissimum* L.; Table S2. Information of hormone- and stress-related cis-elements detected in the promoters regions of *LuPLATZs*; Table S3. The list primer was used for gene expression analysis.

Author Contributions: Conceptualization, J.L. (Jianyu Lu) and H.W. (Hanlu Wu); methodology, J.L. (Jianyu Lu) and H.W. (Hanlu Wu); validation, H.W. (Hang Wang); writing—original draft preparation, J.L. (Jianyu Lu), H.W. (Hanlu Wu), H.W. (Hang Wang), J.L. (Jinxi Li) and Z.Z.; writing—review and editing, J.L. (Jianyu Lu); visualization, Z.Z.; supervision, G.W. and J.Z.; project administration, G.W. and J.Z.; funding acquisition, G.W. and J.Z. All authors have read and agreed to the published version of the manuscript.

Funding: We acknowledge the Jilin Agricultural University high-level researcher grant JLAUHLRG20102006 and Jilin Provincial Department of Human Resources and Social Security Grant: No. 201020012.

Data Availability Statement: The original contributions presented in this study are included in the article/Supplementary Materials. Further inquiries can be directed to the corresponding authors.

Conflicts of Interest: The authors declare no conflicts of interest.

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