

Genome-wide characterization of the PLATZ transcription factor family in chickpea reveals evolutionary diversification and genotype-dependent responses to drought and salinity

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Introduction

Chickpea (*Cicer arietinum* L.) is an important pulse crop and a major source of dietary protein, vitamins, minerals, and other nutritionally important compounds (Jha et al. 2024; Zhang et al. 2024). It also contributes to agroecosystem sustainability through symbiotic nitrogen fixation, which can increase soil nitrogen availability and reduce dependence on synthetic nitrogen fertilizers (Mahto et al. 2025). It is predominantly cultivated under rainfed and small-marginal lands where drought and soil salinity constrain growth and yield (Deokaret al. 2011; Garg et al. 2016; Singh et al. 2023). Improving resilience to these stresses requires elucidation of the molecular regulatory networks governing stress perception, signal transduction, and adaptive responses. Abiotic-stress responses in chickpea involve coordinated changes in osmotic adjustment, ion homeostasis, reactive oxygen species metabolism, hormone signaling, and transcriptional regulation (Garg et al. 2016; Singh et al. 2023). Transcription factors contribute to these responses by binding cis-regulatory elements and modulating downstream stress-responsive genes (Singh et al. 2013; Sinha et al. 2019).

PLATZ (Plant A/T-rich sequence- and zinc-binding) proteins constitute a plant-specific family of zinc-dependent DNA-binding transcription factors characterized by two conserved cysteine/histidine-rich zinc-binding motifs and preferential binding to A/T-rich DNA sequences (Nagano et al. 2001; Zhang et al. 2025; Zeng et al. 2025). Compared with extensively characterized transcription factor families such as WRKY, MYB, NAC, and bZIP, the molecular mechanisms controlled by PLATZ proteins remain less resolved. Functional studies show that PLATZ proteins regulate seed and grain development, meristem activity, leaf growth and senescence, phytohormone responses, and abiotic-stress responses (Baucher et al. 2024).

Genome-wide analyses reveal substantial variation in PLATZ family size, gene structure, duplication, and expression across plant species. Maize contains 17 *ZmPLATZ* genes, several of which interact with RNA polymerase III components (Wang et al. 2018). Eleven *GbPLATZ* genes were identified in *Ginkgo biloba*, with differential expression during seed development (Han et al. 2022), while 55 *MsPLATZ* genes were reported in alfalfa (Li et al. 2023). Recent studies in tomato, *Dendrobium huoshanense*, rice, soybean, and rapeseed further demonstrate variation in gene structure, duplication, developmental expression, and abiotic-stress responsiveness (Fan et al. 2025; Gu et al. 2024; Yang et al. 2025; Wang et al. 2025; Basharat et al. 2026).

Functional studies have identified distinct developmental and stress-responsive roles of individual PLATZ proteins. In soybean, *GmPLATZ1* transcription is induced by drought, salinity, and ABA, and *GmPLATZ1* overexpression in *Arabidopsis* delays germination under mannitol treatment and cotyledon development under ABA treatment (So et al. 2015). In *Arabidopsis*, *ORE15* controls leaf growth and senescence and root-meristem size through auxin- and cytokinin-related pathways (Kim et al.

25 2018; Timilsina et al. 2022), whereas *AIN1* regulates ABA-induced inhibition of primary-root elongation by modulating reactive oxygen species homeostasis (Dong et
26 al. 2021). *PLATZ2* directly represses *CBL4/SOS3* and *CBL10/SCaBP8* and reduces salt tolerance, whereas *PLATZ4* represses the aquaporin gene *PIP2;8* and enhances
27 drought tolerance (Liu et al. 2020; Liu et al. 2023).

28 In chickpea, however, the genomic organization, duplication history, promoter architecture, developmental expression, and genotype-dependent transcriptional
29 responses of the *PLATZ* family remain insufficiently characterized, limiting systematic prioritization of *CaPLATZ* genes for functional analysis. The present study
30 therefore identified and characterized the chickpea *PLATZ* gene family through integrated analyses of chromosomal distribution, gene and protein structure, conserved
31 motifs, phylogenetic relationships, gene duplication and synteny, promoter cis-regulatory elements, and tissue-specific expression. Independent drought- and salinity-
32 responsive RNA-seq datasets were analyzed together with RT-qPCR validation in contrasting chickpea genotypes to identify *CaPLATZ* genes with genotype- and
33 stress-dependent transcriptional responses. This integrated framework was used to prioritize *CaPLATZ* candidates for subsequent functional characterization under
34 abiotic stress.

35 **Materials and methods**

36 **Genome-wide identification of *PLATZ* genes in chickpea**

37 Members of the *PLATZ* family were identified in chickpea (*Cicer arietinum* L. cv. CDC Frontier) using keyword retrieval, BLASTP homology searching, and HMMER
38 conserved-domain screening. The chickpea genome and proteome were queried in Phytozome (<https://phytozome-next.jgi.doe.gov/>) using “Plant A/T-rich sequence-
39 and zinc-binding (*PLATZ*)” (Goodstein et al. 2012). Reference *PLATZ* proteins from *Arabidopsis thaliana* and *Oryza sativa* were retrieved from TAIR
40 (<https://www.arabidopsis.org/>) (Reiser et al. 2024) and NCBI Protein (<https://www.ncbi.nlm.nih.gov/protein/>) (Sayers et al. 2026) and searched against *C. arietinum*
41 using BLASTP (Altschul et al. 1997), with E-value $\leq 1 \times 10^{-5}$, identity $\geq 50\%$, and query coverage $\geq 50\%$. The *PLATZ* HMM profile (Pfam PF04640) was additionally
42 used to screen the chickpea proteome with HMMER (<https://www.ebi.ac.uk/Tools/hmmer/>) (Rajković et al. 2026). Candidate sequences were merged, duplicates
43 removed, and domain architecture verified using InterPro (Blum et al. 2025), Pfam (Paysan-Lafosse et al. 2025), and SMART v10 (Letunic and Bork 2026). Ten non-
44 redundant members were retained and designated *CaPLATZ1–CaPLATZ10*.

45 **Physicochemical properties and predicted subcellular localization of *CaPLATZ* proteins**

46 Physicochemical properties of the predicted *CaPLATZ* proteins were calculated using ExPASyProtParam (<https://web.expasy.org/protparam/>) (Gasteiger et al. 2005).
47 Protein length, molecular mass, theoretical isoelectric point (pI), instability index, aliphatic index, numbers of positively and negatively charged residues, and grand

average of hydropathicity (GRAVY) were determined for each protein. Subcellular localization was predicted independently using Plant-mPLOC (<https://www.csbio.sjtu.edu.cn/bioinf/plant-multi/>) and CELLO v2.5 (<http://cello.life.nctu.edu.tw/>) (Chou and Shen 2010; Yu et al. 2006).

Gene structure, conserved motifs, domain organization, and chromosomal distribution

Exon–intron organization was examined by comparing genomic and coding sequences of individual *CaPLATZ* genes using GSDS 2.0 (<https://gsds.gao-lab.org/>) (Hu et al. 2015). Conserved protein motifs were identified using MEME Suite v5.1.0 (<https://meme-suite.org/meme/tools/meme>) (Bailey et al. 2015). Protein domains were annotated using InterPro (<https://www.ebi.ac.uk/interpro/>) (Blum et al. 2025) and SMART v10 (<https://smart.embl.de/>) (Letunic and Bork 2026). Chromosomal coordinates were obtained from the chickpea genome annotation and used to map *CaPLATZ* genes across the eight chickpea chromosomes.

Phylogenetic, gene duplication, selection pressure, and comparative synteny analysis of *CaPLATZ* genes

Phylogenetic relationships were inferred using the neighbor-joining method (Saitou and Nei 1987) implemented in PHYLIP (Felsenstein 1989), and branch support was evaluated using 1,000 bootstrap replicates (Felsenstein 1985). Phylogenetic trees were visualized and annotated using MEGA11 (<https://www.megasoftware.net/>) (Tamura et al. 2021). Separate analyses were performed for the chickpea *PLATZ* family and the multispecies *PLATZ* dataset.

Gene duplication and collinearity among *CaPLATZ* genes were examined using an all-against-all BLASTP search ($E\text{-value} \leq 1 \times 10^{-5}$; top five hits retained), followed by MCScanX analysis (Wang et al. 2012). MCScanX was used to identify collinear gene pairs and distinguish tandem and segmental duplication events. For duplicated *CaPLATZ* pairs, nonsynonymous (K_a) and synonymous (K_s) substitution rates and K_a/K_s ratios were calculated using MEGA11 (Tamura et al. 2021). Only collinear gene pairs showing >90% sequence similarity and $K_s \leq 2.0$ were retained for evolutionary analysis. K_a/K_s ratios <1, =1, and >1 were interpreted as being consistent with purifying, neutral, and positive selection, respectively. Divergence time was estimated as $T = K_s/(2\lambda) \times 10^{-6}$, where T represents divergence time in million years ago (Mya) and λ was set to 6.05×10^{-9} substitutions per synonymous site per year, following previous chickpea gene-family analyses (Singh et al. 2017; Yadav et al. 2022). Comparative synteny between *Cicer arietinum* and *Oryza sativa*, *Medicago sativa*, and *Glycine max* was examined using MCScanX. Cross-species *PLATZ* sequence-similarity relationships were additionally visualized using Circoletto (<https://bat.infspire.org/circoletto/>) with an E -value threshold of $\leq 1 \times 10^{-10}$ (Darzentas 2010).

Cis-regulatory element analysis, transcription factor-binding site prediction, and miRNA target prediction

For each *CaPLATZ* gene, the 2-kb genomic sequence immediately upstream of the annotated gene start was retrieved and analyzed for cis-regulatory elements using PlantCARE (<https://bioinformatics.psb.ugent.be/webtools/plantcare/html/>) (Lescot et al. 2002). Elements were grouped into hormone-, stress-, and light-responsive categories, and their gene-wise distributions were visualized using TBtools-II (Chen et al. 2023). Putative transcription factor (TF)-binding sites were predicted using PlantRegMap (<https://plantregmap.gao-lab.org/>) at $P \leq 1 \times 10^{-6}$ (Tian et al. 2020), and predicted TF-binding-site links to *CaPLATZ* promoters were visualized in Cytoscape (<https://cytoscape.org/>) (Shannon et al. 2003). Potential miRNA–*CaPLATZ* target pairs were predicted using psRNATarget

74 (<https://www.zhaolab.org/psRNATarget/>) with an expectation score ≤ 3.0 (Dai et al. 2018). Plant miRNA sequences used for target screening were obtained from
75 PmiREN2.0 (<https://pmiren.com/>) (Guo et al. 2022), and predicted miRNA–target links were visualized using Cytoscape.

76 **Multiple sequence alignment, protein-association network prediction, structural modeling, and Gene Ontology enrichment analysis of CaPLATZ proteins**

77 Deduced *CaPLATZ* proteins were aligned using ClustalW (<https://www.genome.jp/tools-bin/clustalw>) (Larkin et al. 2007) to examine sequence conservation; the same
78 procedure was used for proteins included in the multispecies phylogeny. STRING v12.0 (<https://string-db.org/>) was used to generate predicted association networks at a
79 high-confidence score ≥ 0.7 (Szkłarczyk et al. 2023), with edges interpreted as predicted functional associations rather than evidence of direct physical interaction.
80 Networks were visualized in Cytoscape (Shannon et al. 2003). Three-dimensional protein structures were predicted using Phyre2.2 (Powell et al. 2025). Promoter
81 sequences were aligned to examine nucleotide conservation, and conserved nucleotide positions were visualized as a sequence logo. GO Biological Process enrichment
82 analysis was performed using ShinyGO v0.85 (Ge et al. 2020), with *Cicer arietinum* selected as the reference organism and the default genome-wide background.
83 Statistical significance was evaluated using the hypergeometric test followed by Benjamini–Hochberg false-discovery-rate correction, and terms with FDR-adjusted $P <$
84 0.05 were considered significantly enriched.

85 **Tissue, developmental-stage and stress-responsive transcriptome profiling of CaPLATZ genes**

86 Tissue- and developmental-stage-specific expression was examined using two independent public chickpea transcriptome resources. The first dataset comprised 32
87 tissues and organs spanning germination, vegetative growth, floral development, reproductive tissues, seed development, and nodulation (Jain et al. 2022) and was
88 accessed through the NCBI Gene Expression Omnibus (GEO) (Clough et al. 2024) under accession GSE147831. The second dataset comprised 27 tissue and
89 developmental samples reported by Kudapa et al. (2018) and deposited under NCBI BioProject PRJNA413872. Processed FPKM values corresponding to CaPLATZ
90 genes were retrieved from each resource and transformed as $\log_2(\text{FPKM} + 1)$ for heatmap visualization.

91 Stress-responsive expression was evaluated using independent RNA-seq datasets deposited in NCBI GEO. Drought-responsive data for the drought-tolerant genotype
92 ICC4958 and drought-sensitive genotype ICC1882 were obtained from GSE193077 (Singh et al. 2023), whereas salinity-responsive data for the salt-tolerant genotype
93 JG62 and salt-sensitive genotype ICCV2 were obtained from GSE204727 (Gupta and Garg 2023). Processed FPKM matrices were used directly; raw sequencing reads
94 were not reprocessed in the present study. FPKM values for all ten *CaPLATZ* genes were transformed as $\log_2(\text{FPKM} + 1)$ and visualized as heatmaps using TBtools-II
95 (Chen et al. 2023). The heatmaps were interpreted descriptively within each dataset, and the drought and salinity datasets were analyzed independently because they
96 originated from separate experiments.

97 **Validation of CaPLATZ expression under drought and salinity stress**

98 **Plant material and growth conditions**

99 Experiments were conducted at the ICAR–National Institute for Plant Biotechnology (NIPB), New Delhi, India. The drought experiment used ICC4958 (drought
100 tolerant) and ICC1882 (drought sensitive), whereas the salinity experiment used JG62 (salt tolerant) and ICCV2 (salt sensitive). Seeds were surface-sterilized with 3%
101 sodium hypochlorite for 3 min, rinsed thoroughly with double-distilled water, and sown in 25-cm pots containing soil:sand:farmyard manure (2:1:1, v/v). Five seeds
102 were sown per pot and thinned to three uniform seedlings after emergence. Plants were maintained in a completely randomized design with three biological replicates
103 under day/night temperatures of 25 ± 2 °C/ 18 ± 2 °C, a 12-h light/12-h dark photoperiod, photosynthetically active radiation of $400\text{--}500 \mu\text{mol m}^{-2} \text{s}^{-1}$, and 65% relative
104 humidity. Before stress imposition, pots were maintained at approximately 80–85% field capacity and supplied with full-strength Hoagland nutrient solution.

105 **Seedling-stage drought treatment**

106 For the seedling-stage drought experiment, plants were maintained under well-watered conditions until 15 days after sowing (DAS). During establishment, all pots
107 received equal volumes of water to minimize initial variation in soil moisture. At 15 DAS, irrigation was withheld from the drought-treatment group for 15 consecutive
108 days, whereas control plants remained adequately irrigated throughout the treatment period. The drought-treatment framework was adapted from Singh et al. (2023).

109 **Salinity treatment**

110 For salinity treatment, JG62 and ICCV2 seedlings were established under controlled conditions. Beginning 12 days after germination, stress-treated plants received 80
111 mM NaCl at alternate-day intervals for 6 days, whereas control plants received reverse-osmosis water without NaCl, following Gupta and Garg (2023).
112 Root tissues from control and stress-treated plants were harvested at the end of each experiment, immediately frozen in liquid nitrogen, and stored at -80 °C until RNA
113 isolation.

114 **RNA isolation, cDNA synthesis, RT-qPCR, and statistical analysis**

115 Total RNA was isolated from root tissues using TRIzol Reagent (Invitrogen, Thermo Fisher Scientific, Waltham, MA, USA) according to the manufacturer's
116 instructions. RNA integrity was assessed by agarose-gel electrophoresis, and RNA concentration and purity were determined spectrophotometrically. Residual genomic
117 DNA was removed using RNase-free DNase (Promega Corporation, Madison, WI, USA), and first-strand cDNA was synthesized from 1 μg of total RNA using the
118 SuperScript III First-Strand Synthesis System (Invitrogen, Thermo Fisher Scientific, Waltham, MA, USA). RT-qPCR was performed using a CFX96 Real-Time PCR
119 Detection System (Bio-Rad Laboratories, Inc., Hercules, CA, USA) with a SYBR Green-based qPCR master mix (Takara Bio Inc., Shiga, Japan) in a final reaction
120 volume of 10 μL according to the manufacturer's instructions. Gene-specific primers for *CaPLATZ1*–*CaPLATZ10* are provided in Supplementary Table S2. *CaGAPDH*

121 and *CaEF1a* were used as reference genes, and the mean Ct value of the two reference genes was used for normalization. Relative expression was calculated using the
122 $2^{-\Delta\Delta Ct}$ method (Livak and Schmittgen 2001), with the corresponding genotype-specific control used as the calibrator. For graphical presentation, relative expression
123 values were transformed as $\log_2 (2^{-\Delta\Delta Ct})$. Values are presented as mean $\pm$ SE of three independent biological replicates, with three technical replicates per biological
124 replicate. Statistical analysis was performed on biological-replicate ΔCt values using two-way analysis of variance followed by Tukey's multiple-comparison test.
125 Differences were considered significant at $P < 0.05$ and are denoted as * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, and **** $P < 0.0001$; ns denotes a non-significant
126 difference.

127 **In silico nuclear localization signal prediction and transient subcellular localization of CaPLATZ1**

128 **Prediction of nuclear localization signals**

129 The *CaPLATZ1* protein sequence was analyzed for classical nuclear localization signals (NLSs) using cNLS Mapper ([https://nls-mapper.iab.keio.ac.jp/cgi-](https://nls-mapper.iab.keio.ac.jp/cgi-bin/NLS_Mapper_form.cgi)
130 [bin/NLS_Mapper_form.cgi](https://nls-mapper.iab.keio.ac.jp/cgi-bin/NLS_Mapper_form.cgi)) (Kosugi et al. 2009). The same protein sequence was independently analyzed using LOCALIZER (<https://localizer.csiro.au/>)
131 (Sperschneider et al. 2017), which predicts nuclear localization and potential chloroplast transit peptides and mitochondrial targeting peptides. cNLS Mapper was used to
132 identify monopartite and bipartite NLSs and estimate their NLS scores. Concordant predictions from cNLS Mapper and LOCALIZER were interpreted as computational
133 evidence for nuclear targeting of *CaPLATZ1*.

134 **Transient GFP-based localization assay**

135 To examine *CaPLATZ1* subcellular distribution, its coding sequence without the stop codon was cloned in-frame with GFP in pCambia1304 using *NcoI* and *SpeI*
136 (Supplementary Table S2). The 35S::*CaPLATZ1*-GFP construct and a 35S::GFP control were sequence-verified and introduced into *Agrobacterium tumefaciens*
137 GV3101. Agrobacterial cultures were resuspended in 10 mM MES (pH 5.6), 10 mM MgCl₂, and 100 μ M acetosyringone, adjusted to OD₆₀₀ = 0.5, incubated for 3 h, and
138 infiltrated into the abaxial surface of fully expanded *Nicotiana benthamiana* leaves. At 48 h after infiltration, leaf discs were examined using a Leica TCS SP5 confocal
139 laser-scanning microscope. GFP was excited at 488 nm and fluorescence was detected using the standard GFP detection settings of the Leica TCS SP5. GFP, bright-
140 field, and merged images were acquired under comparable settings for the 35S::GFP control and 35S::CaPLATZ1-GFP fusion construct.

141 **Results**

142 **Genome-wide identification, physicochemical properties, and predicted subcellular localization of CaPLATZ proteins**

143 The combined keyword, BLASTP, and HMMER searches identified a set of candidate PLATZ proteins in the chickpea genome. After removal of redundant sequences
144 and independent domain verification, ten non-redundant PLATZ-family members were retained and designated *CaPLATZ1*–*CaPLATZ10*. Domain analysis confirmed

the canonical PLATZ domain in *CaPLATZ1–CaPLATZ9*, whereas *CaPLATZ10* exhibited a more divergent PLATZ-superfamily domain architecture. These ten members were subsequently studied for structural, evolutionary, regulatory, and expression analyses. The ten CaPLATZ proteins ranged from 166 amino acids in *CaPLATZ3* and *CaPLATZ5* to 246 amino acids in *CaPLATZ8* and *CaPLATZ9*, with predicted molecular masses ranging from 18.57 kDa for *CaPLATZ5* to 28.42 kDa for *CaPLATZ9* (Table 1). Theoretical pI values ranged from 8.52 to 9.99, indicating that all CaPLATZ proteins were basic. GRAVY values were negative for all members, ranging from –0.875 to –0.345, indicating hydrophilic character. Instability-index values ranged from 48.38 to 69.66 and were >40 for all ten proteins. Aliphatic-index values ranged from 18.70 to 26.57. Subcellular-localization prediction revealed *CaPLATZ1*, *CaPLATZ2*, *CaPLATZ4*, *CaPLATZ6*, *CaPLATZ8*, *CaPLATZ9*, and *CaPLATZ10* in the nucleus, *CaPLATZ5* and *CaPLATZ7* in the chloroplast, and *CaPLATZ3* at the plasma membrane.

152 **Gene structure, conserved motifs, domain organization, and chromosomal distribution of CaPLATZ genes**

Exon–intron organization varied among the CaPLATZ genes (Fig. 1A). Most members contained three exons, whereas *CaPLATZ3* contained two exons, *CaPLATZ2* contained four, and *CaPLATZ10* contained six. Conserved-motif analysis identified three recurrent motifs (Fig. 1B). *CaPLATZ1*, *CaPLATZ2*, *CaPLATZ4*, *CaPLATZ6*, *CaPLATZ7*, and *CaPLATZ8* contained all three motifs; *CaPLATZ3* and *CaPLATZ5* lacked motif 2; *CaPLATZ9* lacked motif 3; and *CaPLATZ10* retained only one motif. Domain analysis had shown the canonical PLATZ domain in *CaPLATZ1–CaPLATZ9*, within the central region of each protein (Fig. 1C), whereas *CaPLATZ10* contained a more divergent PLATZ-superfamily domain closer to the N terminus. *CaPLATZ7* additionally contained an N-terminal zinc-finger B-box domain. The ten CaPLATZ genes were unevenly distributed across six of the eight chickpea chromosomes (Fig. 1D), with no CaPLATZ genes detected on chromosomes 1 and 5. Three genes, *CaPLATZ3*, *CaPLATZ4*, and *CaPLATZ9*, were located on chromosome 6. *CaPLATZ1* and *CaPLATZ8* mapped to chromosome 7, whereas *CaPLATZ2* and *CaPLATZ5* mapped to chromosome 8. *CaPLATZ10*, *CaPLATZ6*, and *CaPLATZ7* were individually located on chromosomes 2, 3, and 4, respectively.

161 **Evolutionary relationships, gene duplication, selection pressure, and comparative synteny of the CaPLATZ family**

The chickpea-specific phylogeny classified the ten CaPLATZ proteins into four groups (Fig. 2A). Group I comprised *CaPLATZ1*, *CaPLATZ2*, *CaPLATZ5*, and *CaPLATZ6*, forming two sister pairs with bootstrap support of 99 and 90, respectively. Group II included *CaPLATZ3*, *CaPLATZ4*, *CaPLATZ7*, and *CaPLATZ8*, with sister-pair support of 99 and 98. *CaPLATZ9* formed Group III, whereas *CaPLATZ10* occupied the basal position as Group IV, with no bootstrap value shown for its terminal branch. A multispecies phylogenetic tree constructed from full-length PLATZ protein sequences of chickpea (*Cicer arietinum*), *Arabidopsis thaliana*, rice (*Oryza sativa*), and soybean (*Glycine max*) resolved the proteins into four major clades (Fig. 2B). Nine chickpea PLATZ proteins, *CaPLATZ1–CaPLATZ9*, grouped within Clade IV together with PLATZ homologs from *A. thaliana*, *O. sativa*, and *G. max*, showing extensive interspecific clustering within this clade. In contrast, *CaPLATZ10* was assigned to Clade II and clustered with GmPLATZ5. OsPLATZ8 and AtPLATZ9 were assigned to Clades III and I, respectively. The distribution of CaPLATZ proteins across the phylogeny indicates differential evolutionary relationships among chickpea PLATZ family members and their homologs in the examined species. Three segmentally duplicated CaPLATZ gene pairs were identified: *CaPLATZ1/CaPLATZ2*, *CaPLATZ4/CaPLATZ5*, and *CaPLATZ6/CaPLATZ7* (Fig. 2C; Table 2). No tandem duplication event was detected. Ka/Ks ratios ranged from 0.172 to 0.371 and were <1 for all three duplicated pairs, consistent with purifying

172 selection. The estimated divergence times were 44.63 Mya for *CaPLATZ1/CaPLATZ2*, 28.10 Mya for *CaPLATZ4/CaPLATZ5*, and 42.98 Mya for
173 *CaPLATZ6/CaPLATZ7*. Comparative synteny analysis revealed conserved PLATZ-associated collinear relationships between *Cicer arietinum* and *Oryza sativa*,
174 *Medicago sativa*, and *Glycine max* (Fig. 2D). More syntenic relationships were detected between *C. arietinum* and the legume species *M. sativa* and *G. max* than
175 between *C. arietinum* and *O. sativa*, with the greatest number observed between *C. arietinum* and *G. max*. The highlighted PLATZ-associated syntenic links were
176 concentrated mainly on *C. arietinum* chromosomes Ca6–Ca8. Circoletto analysis further visualized cross-species sequence-similarity relationships among PLATZ
177 proteins (Fig. S1).

178 **Promoter cis-regulatory architecture and predicted transcriptional and post-transcriptional regulation of CaPLATZ genes**

179 Promoter analysis identified diverse predicted cis-regulatory elements across the *CaPLATZ* genes (Fig. 3A). These included stress- and hormone-responsive motifs such
180 as ABRE, GARE-motif, P-box, TATC-box, CGTCA- and TGACG-motifs, MBS, MYB- and MYC-related elements, LTR, TC-rich repeats, W-box, and WRE, together
181 with light-responsive elements including G-box, Box 4, Box 5, ACE, and AT-rich elements. The distribution and frequency of these motifs varied among the *CaPLATZ*
182 promoters. PlantRegMap analysis predicted associations of 27 transcription-factor families with the ten *CaPLATZ* promoters (Fig. 3B). The bHLH family showed the
183 highest predicted association counts, reaching 51 for both *CaPLATZ2* and *CaPLATZ9* and 48 for *CaPLATZ1*. Other prominent promoter-specific associations included
184 CAMTA in *CaPLATZ3* (30), E2F in *CaPLATZ2* (27), bZIP in *CaPLATZ7* (20), YABBY in *CaPLATZ7* (16), and HD-ZIP in *CaPLATZ9* (15). The TF–*CaPLATZ*
185 network further showed recurrent predicted associations of bHLH, MYB, NAC, bZIP, C2H2, HD-ZIP, and WRKY families with multiple *CaPLATZ* promoters (Fig.
186 3C). The predicted miRNA–*CaPLATZ* regulatory network showed considerable variation in the number and distribution of miRNA target sites among family members
187 (Fig. 3D). Cross-species prediction identified *CaPLATZ2* as having the highest number of putative miRNA interactions, with several members of the miR437 family,
188 whereas *CaPLATZ9* was predominantly associated with miR172-family members. Comparatively fewer miRNA interactions were predicted for *CaPLATZ1*,
189 *CaPLATZ3–CaPLATZ7*, and *CaPLATZ10*. Because these miRNA sequences were derived from multiple plant species, these interactions represent computationally
190 predicted cross-species associations. To complement the cross-species predictions, chickpea-derived miRNAs were independently screened against the *CaPLATZ* genes.
191 This analysis identified a putative target site for Car-miR11010 in *CaPLATZ5* at approximately 228–248 bp and a predicted binding site for nov-miR101a in *CaPLATZ3*
192 at positions 1–24 bp. Mapping of these sites onto the corresponding gene structures indicated distinct target-site locations among the *CaPLATZ* family members,
193 suggesting gene-specific potential for post-transcriptional regulation by chickpea miRNAs.

194 **Multiple sequence alignment, STRING-predicted protein networks, structural modeling, promoter sequence conservation, and GO enrichment of CaPLATZ proteins**

195
196 Multiple sequence alignment identified a conserved region corresponding to the PLATZ domain, including conserved cysteine and histidine residues characteristic of its
197 zinc-binding motifs, whereas the N- and C-terminal regions showed greater sequence variability (Fig. 4A). *CaPLATZ7* was additionally distinguished by the B-box
198 region detected in the domain analysis. STRING analysis revealed distinct predicted protein-association networks among CaPLATZ proteins (Fig. 4B). All CaPLATZ

199 proteins except CaPLATZ8 showed associations with ethylene-responsive transcription factors, whereas Dof zinc-finger proteins were predicted for all members except
200 CaPLATZ7 and CaPLATZ8. Other recurrent partners included OHP1, photosystem reaction center subunit IV, ORANGE/ORANGE-like proteins, RAP2- and ABR1-
201 related factors, together with ACT-domain-containing proteins, LOW PHOSPHATE ACCUMULATION1, photosystem II 22-kDa protein, and growth-regulating
202 factors. The promoter sequence logo showed variable nucleotide conservation across the aligned sequences (Fig. 4C), while predicted three-dimensional models
203 revealed structural variation among CaPLATZ proteins (Fig. S2). GO biological-process enrichment analysis identified significant enrichment of terms related to
204 hormone response, regulation of reactive oxygen species metabolism, and developmental processes (Fig. 4D). Response to peptide hormone showed the strongest
205 enrichment, followed by regulation of reactive oxygen species metabolic process. Other enriched terms included stem cell population maintenance, maintenance of cell
206 number, response to organonitrogen compound, system development, multicellular organism development, anatomical structure development, maintenance of root
207 meristem identity, regulation of root development, tissue development, regulation of developmental process, and anatomical structure morphogenesis. Related GO terms
208 were further visualized by hierarchical clustering and functional-network analyses (Figs. S3–S4).

209 **Spatiotemporal and stress-responsive expression profiling of *CaPLATZ* genes**

210 **Tissue- and developmental stage-specific expression**

211 Expression of the *CaPLATZ* genes was examined using two independent transcriptome datasets representing multiple tissues and developmental stages. In the 32-tissue
212 atlas, the ten *CaPLATZ* genes showed marked differences in tissue- and stage-specific expression (Fig. 5A). *CaPLATZ1*, *CaPLATZ5*, *CaPLATZ6*, and *CaPLATZ10*
213 showed low expression across most tissues, whereas *CaPLATZ2* showed low-to-moderate expression. In contrast, *CaPLATZ3*, *CaPLATZ4*, *CaPLATZ7*, *CaPLATZ8*, and
214 *CaPLATZ9* showed higher expression in reproductive tissues and seed-development stages. *CaPLATZ8* and *CaPLATZ9* showed their highest expression during embryo,
215 endosperm, and late seed-development stages, while *CaPLATZ3* and *CaPLATZ4* showed higher expression during late reproductive development. Analysis of the
216 independent 27-sample developmental dataset revealed broader expression of *CaPLATZ1* and *CaPLATZ2* across germination, seedling, vegetative, reproductive, and
217 senescence stages (Fig. 5B). In contrast, *CaPLATZ10* showed low expression across nearly all developmental stages. The remaining *CaPLATZ* genes showed low
218 expression in most samples, with increased expression restricted to specific developmental stages. Across the two datasets, *CaPLATZ* genes therefore differed in both
219 the breadth and developmental timing of expression, with several members showing reproductive- and seed-associated expression patterns.

220 **RNA-seq expression under drought stress**

221 RNA-seq profiling revealed distinct *CaPLATZ* expression patterns between ICC4958 and ICC1882 under control and drought conditions (Fig. 5C). *CaPLATZ1* and
222 *CaPLATZ2* showed the strongest expression across both genotypes and treatments. In contrast, *CaPLATZ3*, *CaPLATZ6*, *CaPLATZ7*, and *CaPLATZ10* were weakly

expressed across the four control and stress conditions. *CaPLATZ8* showed the most pronounced drought-responsive expression, particularly in ICC1882, whereas *CaPLATZ4*, *CaPLATZ5*, and *CaPLATZ9* displayed moderate expression between genotypes and treatments.

RNA-seq expression under salinity stress

Salinity RNA-seq profiling also revealed gene- and genotype-specific variation in *CaPLATZ* expression (Fig. 5D). *CaPLATZ1* and *CaPLATZ2* showed the strongest expression in both JG62 and ICCV2 under control and salinity conditions. *CaPLATZ10* was weakly expressed across all samples, while *CaPLATZ4* and *CaPLATZ5* showed intermediate expression. *CaPLATZ3*, *CaPLATZ6*, *CaPLATZ7*, *CaPLATZ8*, and *CaPLATZ9* displayed comparatively weak to moderate expression in both genotypes under control and stress.

RT-qPCR validation of *CaPLATZ* expression under drought and salinity stress

RT-qPCR analysis revealed significant gene-, genotype-, and stress-specific expression patterns among the *CaPLATZ* genes (Fig. 6). *CaPLATZ1* (Fig. 6A) expression increased significantly in both ICC4958 and ICC1882 under drought and in both JG62 and ICCV2 under salinity, with greater induction in the drought-tolerant ICC4958 and salt-tolerant JG62, respectively. *CaPLATZ2* (Fig. 6B) showed contrasting responses under drought, with significant induction in ICC4958 and repression in ICC1882, whereas its expression increased significantly in both JG62 and ICCV2 under salinity. *CaPLATZ3* (Fig. 6C) was significantly repressed in both drought-treated genotypes and in salinity-treated JG62, while no significant change was detected in ICCV2. *CaPLATZ4* (Fig. 6D) was significantly induced under both stresses in all tested genotypes, with greater induction in ICC4958 under drought and in ICCV2 under salinity. In contrast, *CaPLATZ5* (Fig. 6E) was significantly repressed in both ICC4958 and ICC1882 under drought but induced in both JG62 and ICCV2 under salinity. *CaPLATZ6* (Fig. 6F) showed no significant change in ICC4958 but was significantly repressed in ICC1882 under drought; under salinity, it was significantly induced in both JG62 and ICCV2. *CaPLATZ7* (Fig. 6G) showed contrasting drought responses, with significant induction in ICC4958 and repression in ICC1882, whereas under salinity it was significantly induced in JG62 but showed no significant change in ICCV2. *CaPLATZ8* (Fig. 6H) was significantly induced in both genotypes under drought and significantly repressed in JG62 under salinity, while no significant change was detected in ICCV2. *CaPLATZ9* (Fig. 6I) was significantly induced in ICC4958 but showed no significant change in ICC1882 under drought; under salinity, it was significantly induced in both JG62 and ICCV2. *CaPLATZ10* (Fig. 6J) was significantly induced in ICC4958 but showed no significant change in ICC1882 under drought; under salinity, no significant change was detected in JG62, whereas significant repression was observed in ICCV2. The RT-qPCR-validated expression responses of the ten *CaPLATZ* genes under drought and salinity stress in contrasting chickpea genotypes are summarized in Table 3.

In silico prediction and transient GFP-based localization of CaPLATZ1

In silico analysis identified a strong basic C-terminal region in *CaPLATZ1* with multiple nuclear localization signals. cNLS Mapper identified two overlapping monopartite NLSs, YRTAKRRKGI and RTAKRRKGIP, beginning at amino-acid positions 193 and 194 with scores of 9.0 and 8.0, respectively. A bipartite NLS, RLKNIKVSFTPSTPPPTSVNYRTAKRRKGI, was predicted from position 172 with a score of 5.0. LOCALIZER v1.0.4 independently predicted nuclear targeting based on the RTAKRRK motif and detected neither a chloroplast transit peptide nor a mitochondrial targeting peptide. Thus, both algorithms predicted nuclear targeting of *CaPLATZ1*. In transient-expression assays, free GFP showed broad fluorescence in *Nicotiana benthamiana* leaf epidermal cells, whereas *CaPLATZ1*–GFP showed a more spatially restricted intracellular fluorescence pattern (Fig. 7). The fluorescence intensity of the fusion construct was comparatively weak under the imaging conditions. The observed distribution was consistent with the computational nuclear-targeting predictions; however, nuclear localization was not independently confirmed using a nuclear marker.

Discussion

PLATZ proteins are plant-specific, zinc-dependent DNA-binding transcription factors characterized by conserved cysteine/histidine-rich zinc-binding motifs and preferential binding to A/T-rich DNA sequences (Nagano et al. 2001; Baucher et al. 2024; Zhang et al. 2025; Zeng et al. 2025). Characterized PLATZ proteins regulate reproductive development, meristem activity, leaf growth and senescence, phytohormone responses, and abiotic-stress responses (Baucher et al. 2024; Yang et al. 2025; Zhang et al. 2025; Zeng et al. 2025). Genome-wide studies across diverse plants show substantial variation in PLATZ family size, gene structure, duplication, tissue-specific expression, and stress responsiveness. The ten *CaPLATZ* genes identified in chickpea comprise a compact family showing conserved PLATZ-family features together with variation in gene structure and expression.

Subcellular-localization predictions varied among *CaPLATZ* proteins, with seven members predicted to localize to the nucleus, two to the chloroplast, and one to the plasma membrane. Nuclear localization has been validated in characterized PLATZ proteins; maize PLATZ FL3 localizes to the nucleus and interacts with RNAPIII subunit RPC53 and TFIIC subunit TFC1, while rice PLATZ GL6 interacts with OsRPC53 and OsTFC1 in the nucleus (Li et al. 2017; Wang et al. 2019). In this study, cNLS Mapper and LOCALIZER predicted nuclear targeting of *CaPLATZ1*, and *CaPLATZ1*–GFP showed a more restricted intracellular fluorescence pattern than free GFP in *Nicotiana benthamiana*.

Variation in exon–intron organization and motif/domain composition among the *CaPLATZ* members further indicates structural diversification within the family. Notably, *CaPLATZ7* possessed an additional N-terminal zinc-finger B-box domain, whereas *CaPLATZ10* exhibited a comparatively divergent motif and domain architecture. Comparable structural heterogeneity has been reported for PLATZ families in tomato, soybean, rapeseed, and *Medicago truncatula* (Fan et al. 2025; Wang et al. 2025; Basharat et al. 2026; Zhou et al. 2026), suggesting that such variation is a recurrent feature of PLATZ-family evolution. These structural differences support differentiation in gene architecture within the family; however, their consequences for DNA binding, protein interactions, transcriptional activity, or other biochemical properties require experimental validation.

Three segmentally duplicated *CaPLATZ* gene pairs were identified, whereas tandem duplication was absent, indicating a predominant contribution of segmental duplication to PLATZ family expansion in chickpea. Similar duplication patterns have been reported in rapeseed and *Medicago truncatula* (Basharat et al. 2026; Zhou et al. 2026). Ka/Ks ratios <1 for all duplicated pairs indicate strong purifying selection, suggesting conservation of protein-coding function after duplication. However, differences in promoter architecture and stress-responsive expression among paralogs indicate subsequent divergence in transcriptional regulation.

Promoter, miRNA, and STRING analyses identified predicted regulatory and protein-association patterns among *CaPLATZ* family members. *CaPLATZ* promoters contained hormone-, stress-, and light-responsive cis-elements, and PlantRegMap predicted binding sites for multiple TF families, including AP2/ERF, NAC, WRKY, MYB, bHLH, and HD-ZIP. PLATZ proteins are known to regulate developmental and hormone-responsive processes. *ORE15* controls leaf growth and senescence and root-meristem activity through auxin–cytokinin-related pathways (Kim et al. 2018; Timilsina et al. 2022), whereas *AIN1* regulates ABA-mediated inhibition of root elongation through reactive oxygen species homeostasis (Dong et al. 2021). PLATZ proteins are also involved in protein complexes; maize FL3 interacts with RPC53/TFC1, whereas wheat TaPLATZ5 interacts with the histone acetyltransferase TaHAG1 to activate TaPAD4 during powdery-mildew resistance (Li et al. 2017; Song et al. 2022). Hence, the presence of hormone- and stress-responsive cis-regulatory elements within *CaPLATZ* promoters, together with predicted associations with stress-related regulatory proteins, suggests that these genes may participate in stress-responsive regulatory networks. Functional validation through promoter editing, cis-element mutagenesis, or deletion-mapping approaches will be required to determine the contribution of individual CaPLATZ proteins.

Developmental transcriptome profiling revealed marked spatiotemporal variation among *CaPLATZ* genes. *CaPLATZ2* showed broad expression, whereas *CaPLATZ3*, *CaPLATZ4*, *CaPLATZ7*, *CaPLATZ8*, and *CaPLATZ9* showed preferential expression in reproductive tissues and seed-development stages. These patterns are consistent with experimentally established PLATZ functions in reproductive development. In maize, FL3 is required for normal endosperm development through RNAPIII-dependent transcription, whereas *ZmPLATZ2* has been implicated in transcriptional regulation of starch synthesis (Li et al. 2017; Li et al. 2021). In rice, GL6 and SG6 regulate grain size, and OsPLATZ1 regulates caryopsis development and grain filling (Wang et al. 2019; Zhou and Xue 2020; Yang et al. 2025). Reproductive-stage-specific PLATZ expression has also been reported in *Ginkgo*, alfalfa, and apple (Han et al. 2022; Li et al. 2023; Sun et al. 2023). The two independent chickpea transcriptome atlases used in this study revealed developmental stage-specific expression patterns across the chickpea life cycle (Kudapa et al. 2018; Jain et al. 2022).

RT-qPCR validation further revealed distinct gene-, genotype-, and stress-dependent expression patterns among CaPLATZ family members. *CaPLATZ1* and *CaPLATZ4* were consistently induced under both drought and salinity, indicating that these genes may participate in relatively broad abiotic-stress responses. In contrast, *CaPLATZ2* and *CaPLATZ7* exhibited contrasting drought-responsive expression, with induction in the tolerant ICC4958 genotype and repression in the sensitive ICC1882 genotype, suggesting possible genotype-dependent regulatory roles during drought adaptation. *CaPLATZ3* was predominantly repressed under stress, whereas *CaPLATZ5* displayed clear stress-dependent regulation, being repressed under drought but induced under salinity. Differential responses were also evident for *CaPLATZ6* and *CaPLATZ9*: *CaPLATZ6* expression remained unchanged in ICC4958 but was repressed in ICC1882 under drought, while *CaPLATZ9* expression was induced in ICC4958 but unchanged in ICC1882; both genes were induced in JG62 and ICCV2 under salinity. Notably, *CaPLATZ8* showed strong stress-specific

299 regulation, with induction in both genotypes under drought but repression only in JG62 under salinity, while *CaPLATZ10* was induced specifically in ICC4958 under
300 drought and repressed only in ICCV2 under salinity. Collectively, these contrasting transcriptional responses indicate that CaPLATZ members are unlikely to function
301 uniformly across abiotic stresses and instead may contribute through distinct stress- and genotype-specific regulatory mechanisms. Among them, *CaPLATZ1*,
302 *CaPLATZ2*, *CaPLATZ4*, *CaPLATZ8*, and *CaPLATZ9* emerge as potential candidates for further functional validation because of their genotype-dependent expression
303 pattern. Comparable stress-responsive expression of PLATZ genes has been reported in tomato, rapeseed, and *Medicago truncatula* (Fan et al. 2025; Basharat et al.
304 2026; Zhou et al. 2026).

305 Functional studies further show that PLATZ proteins act through distinct molecular targets. *Arabidopsis* PLATZ2 represses *CBL4/SOS3* and *CBL10/SCaBP8* and
306 thereby reduces salt tolerance, whereas PLATZ4 represses *PIP2;8* and enhances drought tolerance (Liu et al. 2020; Liu et al. 2023). Ectopic expression of cotton
307 *GhPLATZ1* in *Arabidopsis* alters ABA-, gibberellin-, and ethylene-dependent responses under osmotic and salt stress (Zhang et al. 2018), while *PhePLATZ1*
308 overexpression enhances drought resistance and promotes ABA-induced stomatal closure (Zhang et al. 2022). Heterologous overexpression of *GhPLATZ01* and
309 *GhPLATZ15* enhanced drought resistance in transgenic tomato, whereas overexpression of *SIPLATZ17* increased tolerance to drought and salinity (Liu et al. 2025; Jia et
310 al. 2025). To date, functional validation of *CaPLATZ* genes through genome editing or overexpression in chickpea has not been reported. Identification of key genes
311 would provide valuable resources for chickpea crop improvement strategies focused on developing climate-smart, sustainable agriculture. Given the constraints
312 associated with chickpea transformation and regeneration, functional validation in heterologous systems can substantially advance understanding of the roles of these
313 key genes in development and stress response.

314 Collectively, the chickpea PLATZ family retains the characteristic structural features of PLATZ transcription factors while exhibiting substantial variation in gene
315 organization, promoter architecture, developmental expression, predicted regulatory associations, and responses to drought and salinity. GO enrichment for hormone
316 response, regulation of reactive oxygen species metabolism, root development, and meristem maintenance is consistent with biological processes previously associated
317 with PLATZ proteins in other plant species. However, these functional associations cannot be assigned to individual *CaPLATZ* members without experimental
318 validation. The genotype- and stress-dependent expression patterns identified here provide a rational basis for prioritizing selected *CaPLATZ* genes for promoter-binding
319 assays, protein-interaction studies, and gain- and loss-of-function analyses under drought and salinity stress.

320 **Proposed working model of CaPLATZ-mediated drought and salinity responses in chickpea**

321

322 Integrating promoter architecture, GO enrichment, expression, and localization analyses, we propose a working model for *CaPLATZ*-mediated drought and salinity
323 responses in chickpea (Fig. 8). Drought- and salinity-induced changes in ABA, ROS, and Ca²⁺ signaling may activate stress-responsive TFs that could regulate
324 *CaPLATZ* transcription through corresponding promoter cis-elements. PLATZ proteins that localize to the nucleus may bind A/T-rich regulatory sequences and

325 modulate genes associated with osmotic adjustment, ROS detoxification, and root growth. Because these links are based largely on computational predictions and
326 expression data, direct DNA binding, interacting proteins, downstream targets, and physiological effects require experimental validation.

327 **Conclusion and future perspectives**

328 This study provides a genome-wide characterization of the PLATZ family in chickpea, integrating gene organization, evolutionary relationships, developmental
329 expression, and drought- and salinity-responsive expression. Ten *CaPLATZ* genes were identified, including three segmentally duplicated gene pairs with Ka/Ks ratios
330 <1, consistent with purifying selection. Gene structure, promoter architecture, developmental expression, and stress-responsive expression varied among family
331 members. Integration of independent RNA-seq datasets with RT-qPCR validation highlighted several candidates, particularly *CaPLATZ1*, *CaPLATZ2*, *CaPLATZ4*,
332 *CaPLATZ8*, and *CaPLATZ9*, for further functional analysis. cNLS Mapper and LOCALIZER predicted nuclear targeting of *CaPLATZ1*, while transient *CaPLATZ1*–
333 GFP expression showed a spatially restricted intracellular fluorescence pattern consistent with the computational predictions. Future studies should use gain- and loss-
334 of-function approaches to identify direct targets and protein-interaction partners and determine the physiological roles of individual *CaPLATZ* genes under drought and
335 salinity.

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485 **Table 1. Genomic and physicochemical characteristics of *CaPLATZ* genes identified in chickpea**

486 **Table 2. Ka/Ks ratio and divergence time among paralogous *CaPLATZ* gene pairs in chickpea**

487 **Table 3. Summary of RT-qPCR-validated *CaPLATZ* transcriptional responses to drought and salinity stress in contrasting chickpea genotypes.**

488 **Fig. 1** Genome-wide structural characterization and chromosomal distribution of *CaPLATZ* genes. (A) Exon–intron organization of the ten *CaPLATZ* genes. (B)
489 Distribution of conserved protein motifs identified by MEME. (C) Protein-domain organization showing the PLATZ domain and additional domains detected in
490 individual family members. (D) Chromosomal distribution of *CaPLATZ* genes across the chickpea genome.

491 **Fig. 2** Phylogenetic relationships among chickpea *CaPLATZ* proteins. Bootstrap support values are indicated at internal nodes, and branch colors distinguish major
492 phylogenetic groups. *CaPLATZ10* occupied the basal position, whereas the remaining members formed supported sister-group relationships. (A) Neighbor-joining
493 phylogeny of the chickpea *CaPLATZ* family. (B) Comparative phylogenetic analysis of PLATZ proteins from chickpea (*Cicer arietinum*), *Arabidopsis thaliana*, rice
494 (*Oryza sativa*), and soybean (*Glycine max*). (C) Segmental duplication relationships among *CaPLATZ* genes. (D) Comparative synteny of PLATZ loci between
495 chickpea and *Glycine max* (soybean), *Medicago sativa* (alfalfa), and *Oryza sativa* (rice).

496 **Fig. 3** Predicted regulatory architecture of *CaPLATZ* genes. (A) Distribution of hormone-, stress-, and light-responsive cis-regulatory elements within the 2-kb upstream
497 regions. (B) PlantRegMap-predicted transcription-factor-binding sites in *CaPLATZ* promoters. (C) Predicted TF–*CaPLATZ* regulatory network. (D) psRNATarget-
498 predicted miRNA–*CaPLATZ* network.

499 **Fig. 4** Sequence conservation, predicted protein networks, promoter sequence conservation, and Gene Ontology enrichment of *CaPLATZ* genes. (A) Multiple sequence
500 alignment of *CaPLATZ* proteins highlighting the conserved PLATZ region. (B) STRING-predicted functional-association networks for *CaPLATZ* proteins; STRING
501 edges do not by themselves demonstrate direct physical protein–protein interactions. (C) Sequence-logo representation of nucleotide conservation in the aligned
502 promoter set. (D) ShinyGO enrichment of Biological Process terms at FDR-adjusted $P < 0.05$.

503 **Fig. 5** Developmental and stress-responsive transcriptome profiles of *CaPLATZ* genes. (A) Expression across the 32-tissue chickpea atlas (GSE147831). (B) Expression
504 across the independent 27-sample developmental atlas (PRJNA413872). (C) Drought-responsive expression in ICC4958 and ICC1882 (GSE193077). (D) Salinity-
505 responsive expression in JG62 and ICCV2 (GSE204727). Processed FPKM values were transformed as $\log_2(\text{FPKM} + 1)$ for heatmap visualization; the independent
506 datasets were interpreted separately.

507 **Fig. 6** RT-qPCR validation of *CaPLATZ1–CaPLATZ10* transcription under drought and salinity stress in contrasting chickpea genotypes. Relative transcript abundance
508 was calculated using the $2^{-\Delta\Delta C_t}$ method with the corresponding genotype-specific control as the calibrator and is presented as $\log_2(2^{-\Delta\Delta C_t})$. Error bars represent SE of
509 three biological replicates. Statistical significance was evaluated using two-way ANOVA on biological-replicate ΔC_t values followed by Tukey's multiple-comparison
510 test; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$; ns, non-significant.

511 **Fig. 7** Subcellular localization analysis of CaPLATZ1 in *Nicotiana benthamiana* leaf epidermal cells. Schematic representation of the 35S::GFP control and
512 35S::CaPLATZ1–GFP fusion constructs, each driven by the cauliflower mosaic virus (CaMV) 35S promoter and terminated by the NOS terminator (NOS-ter). The
513 constructs were transiently expressed in *N. benthamiana* leaves through *Agrobacterium*-mediated infiltration and visualized using confocal microscopy. GFP
514 fluorescence images show the localization of free GFP or the CaPLATZ1–GFP fusion protein, bright-field images display leaf epidermal-cell morphology, and merged
515 images show the GFP signal overlaid on the corresponding bright-field image. Compared with the free GFP control, the CaPLATZ1–GFP fusion protein exhibited a
516 more spatially restricted intracellular fluorescence pattern than free GFP. Scale bars are indicated within the respective images.

517 **Fig. 8** Proposed working model of *CaPLATZ*-mediated drought and salinity responses in chickpea. Drought- and salinity-induced cellular signals, including reactive
518 oxygen species (ROS), Ca^{2+} signaling, and ABA biosynthesis through NCED, may activate ABA-dependent and ABA-independent transcriptional pathways involving
519 AREB/ABF, DREB, MYB, and NAC transcription factors. These regulators may act through stress-responsive cis-elements, while *CaPLATZ* proteins preferentially
520 bind A/T-rich DNA sequences and may modulate transcription through interactions with other regulatory proteins and chromatin-associated complexes. Downstream
521 responses may include osmotic adjustment through proline and LEA proteins, ROS detoxification by SOD, CAT, and APX, and modulation of root growth and
522 development. Arrows represent proposed regulatory relationships and do not indicate experimentally validated direct interactions.

523 **Fig. S1** Circoletto visualization of cross-species PLATZ sequence-similarity relationships.

524 **Fig. S2** Predicted three-dimensional structures of the ten CaPLATZ proteins generated using Phyre2.2.

525 **Fig. S3** Hierarchical clustering of significantly enriched Gene Ontology Biological Process terms associated with CaPLATZ genes.

526 **Fig. S4** Functional network of significantly enriched Gene Ontology Biological Process terms associated with CaPLATZ genes.

527 **Fig. S5. In silico prediction of nuclear localization signals in CaPLATZ1.**
528 (A) Nuclear localization signals (NLSs) in the CaPLATZ1 protein were predicted using cNLS Mapper. Two overlapping monopartite NLSs were identified near the C-terminal region:
529 **YRTAKRRKGI** beginning at amino acid position 193 with a score of **9.0**, and **RTAKRRKGIP** beginning at position 194 with a score of **8.0**. A bipartite NLS,
530 **RLKNIKVSFTPTSPPTSVNYRTAKRRKGI**, was additionally predicted beginning at amino acid position 172 with a score of **5.0**. (B) Independent analysis using LOCALIZER
531 v1.0.4 predicted nuclear localization of CaPLATZ1 based on the basic **RTAKRRK** motif. No chloroplast transit peptide or mitochondrial targeting peptide was detected. Together, the
532 two independent prediction approaches support a putative nuclear localization of *CaPLATZ1*.

533 **Supplementary table S1:** PLATZ proteins from *Arabidopsis thaliana* and *Oryza sativa* used for identification of chickpea PLATZ family members

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535 **Supplementary table S2:**Primer sequences used for *CaPLATZ*gene expression analysis and reference genes

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554 **Table 1. Genomic and physicochemical characteristics of *CaPLATZ* genes identified in chickpea**

Putative Name	Gene Id	Locus	Chromosome and location	Gene length (Kb)	CDS length (Bp)	Total Number of Amino Acids	Molecular Weight (kDa)	Aromaticity	Instability Index	Isoelectric Point	GRAVY	Aliphatic Index	Number of Negatively Charged Amino Acids	Number of Positively Charged Amino Acids	Subcellular localization
CaPLATZ1	Ca_12361	LOC101508712	Chr7 - 19831512:19833416	1.9	648	215	24.33	0.074	49.09	9.36	-0.563	21.86	19	32	Nucleus
CaPLATZ2	Ca_11505	LOC101498018	Chr8 - 8739018:8740782	1.8	717	238	27.04	0.067	51.74	9.37	-0.661	22.27	24	37	Nucleus
CaPLATZ3	Ca_17446	LOC101515457	Chr6 - 29403911:29406255	2.3	501	166	18.69	0.048	55.58	9.99	-0.530	26.51	14	29	Plasma membrane
CaPLATZ4	Ca_11235	LOC101510728	Chr6 - 22048835:22050246	1.4	642	213	24.03	0.066	54.31	9.49	-0.520	22.07	19	33	Nucleus
CaPLATZ5	Ca_11837	LOC101497682	Chr8 - 833196:834660	1.5	501	166	18.57	0.072	54.18	9.57	-0.433	22.29	12	25	Chloroplast
CaPLATZ6	Ca_00735	LOC101513580	Chr3 - 34634858:34636494	1.6	615	204	22.96	0.074	61.54	8.84	-0.436	24.02	22	28	Nucleus

Putative Name	Gene Id	Locus	Chromosome and location	Gene length (Kb)	CDS length (Bp)	Total Number of Amino Acids	Molecular Weight (kDa)	Aromaticity	Instability Index	Isoelectric Point	GRA VY	Aliphatic Index	Number of Negatively Charged Amino Acids	Number of Positively Charged Amino Acids	Subcellular localization
CaPLATZ7	Ca_19047	LOC101495331	Chr4 - 20950219:20951443	1.2	624	207	23.33	0.072	69.66	9.42	-0.345	26.57	18	29	Chloroplast
CaPLATZ8	Ca_06740	LOC101509020	Chr7 - 6166467:6168229	1.8	741	246	28.18	0.085	68.78	8.52	-0.440	21.14	26	32	Nucleus
CaPLATZ9	Ca_10399	LOC101513941	Chr6 - 2660689:2662497	1.8	741	246	28.42	0.069	48.38	9.14	-0.875	18.70	28	39	Nucleus
CaPLATZ10	Ca_14319	LOC101506814	Chr2 - 29206598:29208253	1.7	636	211	23.35	0.038	63.83	9.04	-0.608	24.17	22	28	Nucleus

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560 **Table 2. Ka/Ks ratio and divergence time among paralogous *CaPLATZ* gene pairs in chickpea**

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Gene pairs	Ka	Ks	Ka/Ks	Divergence time (Mya)	Duplication type	Type of selection
CaPLATZ1– CaPLATZ2	0.09	0.54	0.172	7.73	Segmental	Purifying (negative) selection
CaPLATZ4– CaPLATZ5	0.12	0.34	0.371	10.37	Segmental	Purifying (negative) selection
CaPLATZ6– CaPLATZ7	0.12	0.52	0.234	10.14	Segmental	Purifying (negative) selection

563 *Synonymous (Ks) and non-synonymous (Ka) substitution rates, Ka/Ks ratios, and estimated divergence times for duplicated *CaPLATZ* gene pairs in chickpea. The
564 Ka/Ks ratio was used to infer selection pressure, where values <1 indicate purifying selection, =1 indicate neutral evolution, and >1 indicate positive selection.

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574 **Table 3. Summary of RT-qPCR-validated CaPLATZ transcriptional responses to drought and salinity stress in contrasting chickpea genotypes.**

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Gene	Drought–ICC4958 (Tol.)	Drought–ICC1882 (Sens.)	Salinity–JG62 (Tol.)	Salinity–ICCV2 (Sens.)
<i>CaPLATZ1</i>	↑	↑	↑	↑
<i>CaPLATZ2</i>	↑	↓	↑	↑
<i>CaPLATZ3</i>	↓	↓	↓	ns
<i>CaPLATZ4</i>	↑	↑	↑	↑
<i>CaPLATZ5</i>	↓	↓	↑	↑
<i>CaPLATZ6</i>	ns	↓	↑	↑
<i>CaPLATZ7</i>	↑	↓	ns	↓
<i>CaPLATZ8</i>	↑	↑	↓	↓
<i>CaPLATZ9</i>	ns	↓	↑	↑
<i>CaPLATZ10</i>	↑	↓	ns	↓

577 ↑, significant induction; ↓, significant repression; ns, no significant change (two-way ANOVA on biological-replicate Δ Ct values, Tukey's test, $P < 0.05$), relative to the
578 corresponding genotype-specific control. Summarized from Fig. 6 and the accompanying text

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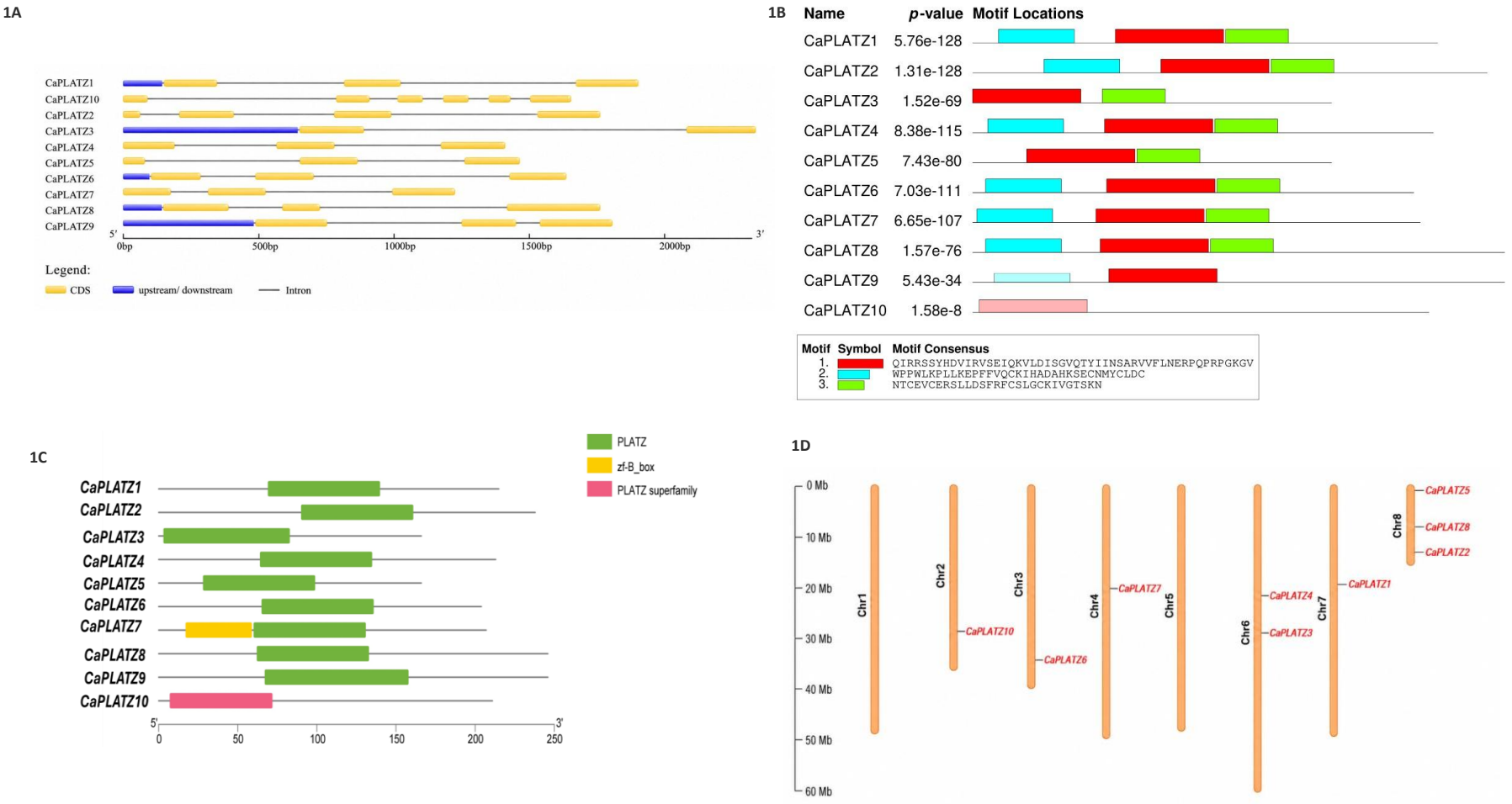


Fig. 1 Genome-wide identification and structural characterization of *CaPLATZ* genes. (A) Exon–intron structures of the 10 identified *CaPLATZ* genes in chickpea (*Cicer arietinum* L.). Yellow boxes represent coding sequences (CDS), blue boxes indicate upstream/downstream untranslated regions, and black lines represent introns. Gene models are drawn to scale, as indicated by the scale bar in base pairs (bp). (B) Distribution of conserved motifs in *CaPLATZ* proteins identified using MEME analysis. Three distinct motifs (Motifs 1–3) are represented by differently coloured boxes along each protein sequence, with their relative positions preserved to scale. The amino acid consensus sequence corresponding to each motif is provided in the accompanying table. (C) Predicted domain organization of *CaPLATZ* proteins.

590 Conserved PLATZ, zf-B_box and PLATZ-superfamily domains are represented by green, yellow and pink boxes, respectively, with their positions mapped along the
591 protein sequences. (D) Chromosomal distribution of *CaPLATZ* genes across the eight chickpea chromosomes (Chr1–Chr8). Orange bars represent the chromosomes,
592 while the physical positions and names of the genes are indicated in red. The vertical scale denotes chromosome length in megabases (Mb).

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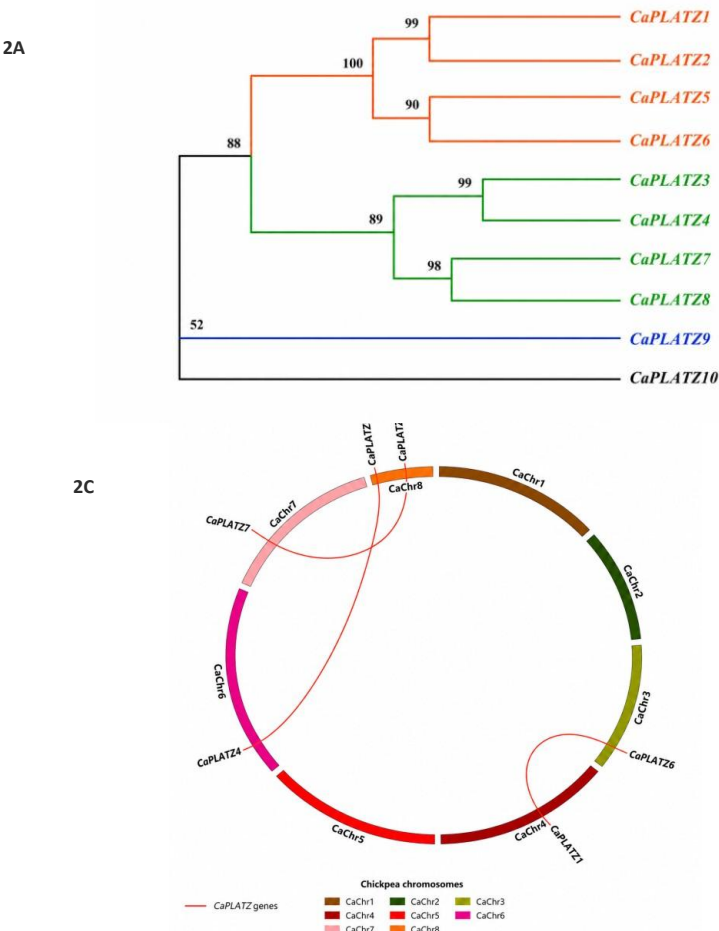
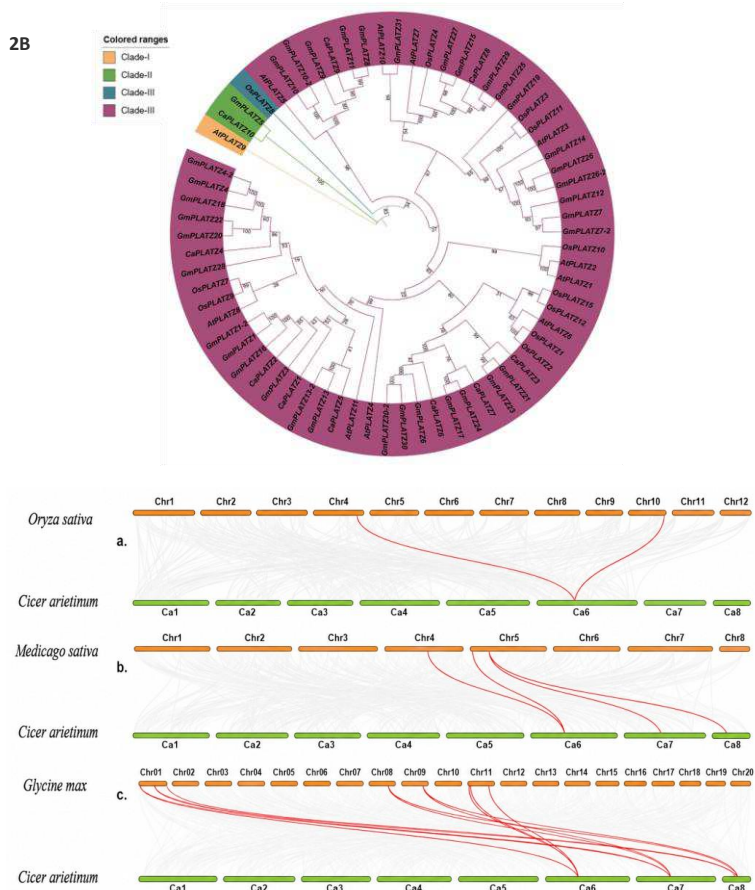
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614 **Fig. 2 Evolutionary relationships, gene duplication and comparative synteny analysis of *CaPLATZ* genes in chickpea.** (A) Phylogenetic relationships among
615 chickpea *CaPLATZ* proteins. Bootstrap support values are indicated at internal nodes, and branch colors distinguish major phylogenetic groups. *CaPLATZ*10 occupied
616 the basal position, whereas the remaining members formed supported sister-group relationships. (B) Comparative phylogenetic analysis of *PLATZ* proteins from
617 chickpea and other plant species, including *Arabidopsis thaliana*, *Glycine max*, *Oryza sativa* and *Solanum tuberosum*. The unrooted tree illustrates the evolutionary
618 relationships and clustering of *PLATZ*-family members across species. Different background colours represent the four major phylogenetic clades (Clades I–IV), while

619 numbers at the nodes indicate bootstrap support values. (C) Circos plot depicting segmental duplication events among *CaPLATZ* genes within the chickpea genome.
620 Coloured arcs on the outer ring represent chickpea chromosomes, and red connecting lines indicate duplicated *CaPLATZ* gene pairs. (D) Comparative synteny analysis
621 of PLATZ genes between chickpea and *Oryza sativa*, *Medicago sativa* and *Glycine max*. Orange and green bars represent the chromosomes of the respective
622 comparison species and chickpea, respectively. Red lines highlight syntenic PLATZ gene pairs, whereas grey lines represent other syntenic blocks shared between the
623 genomes.

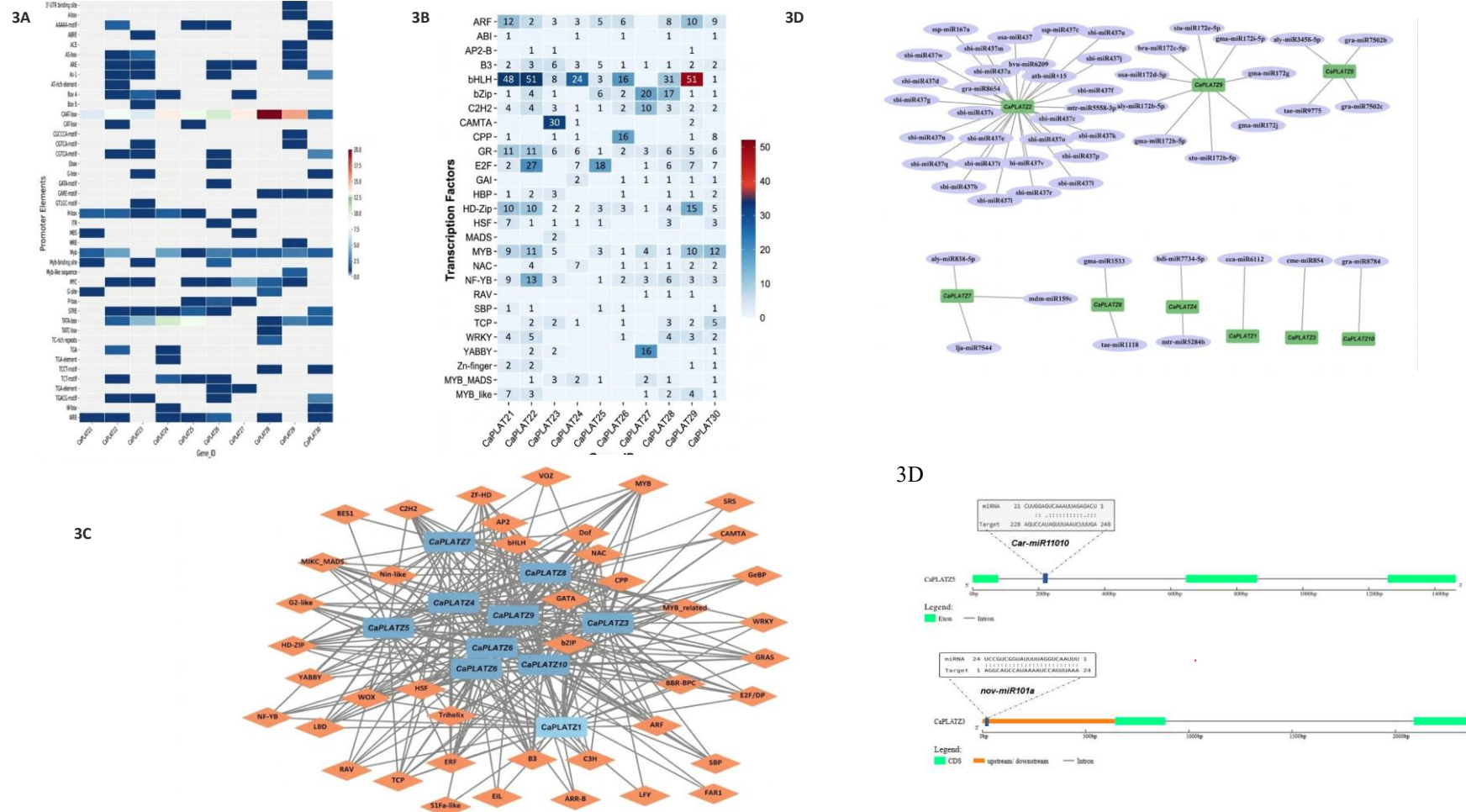
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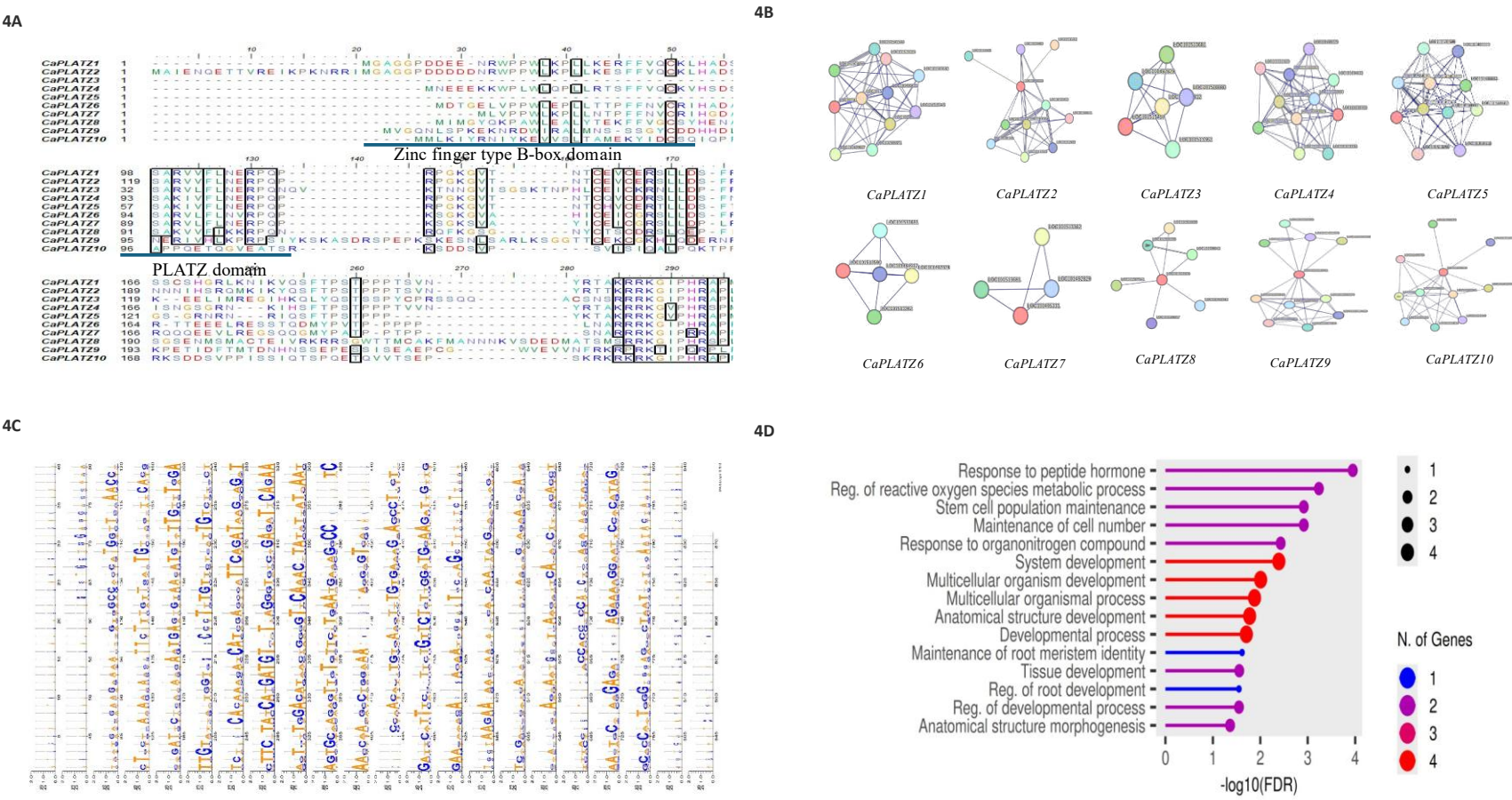
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630 **Fig. 3 Regulatory analyses of *CaPLATZ* genes.** (A) Heatmap displaying the distribution of predicted cis-regulatory elements in the promoter regions of *CaPLATZ*
631 genes. Rows represent individual cis-elements grouped into regulatory categories, including development-related, promoter/core, phytohormone-responsive and stress-
632 responsive elements, while columns represent individual *CaPLATZ* genes. Colour intensity indicates the copy number of each element, as shown in the accompanying
633 colour scale. (B) Heatmap showing predicted transcription factor (TF)-binding sites in the promoter regions of *CaPLATZ* genes. Rows represent different TF families,
634 and columns represent individual *CaPLATZ* genes. Colour intensity and numerical values within the cells indicate the predicted number of binding sites for each TF
635 family per gene, according to the accompanying colour scale. (C) Predicted regulatory interaction network between *CaPLATZ* genes and associated transcription factors.
636 Blue rectangular nodes represent *CaPLATZ* genes, orange diamond-shaped nodes represent TF families, and grey edges indicate predicted regulatory associations

637 between TFs and their corresponding *CaPLATZ* target genes. (D) Predicted miRNA–*CaPLATZ* regulatory network. Green rectangular nodes represent *CaPLATZ* genes,
638 purple oval nodes represent the corresponding miRNAs, and grey edges indicate predicted miRNA–target relationships.
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641 **Fig. 4 Functional annotation, interaction landscape and sequence architecture of *CaPLATZ* proteins.** (A) Multiple sequence alignment of the 10 *CaPLATZ*
642 proteins showing conserved and variable amino acid residues across the protein family. Coloured letters represent individual amino acid residues, while gaps indicate
643 sequence variation. Conserved residues within the zinc-finger-type B-box and PLATZ domains are highlighted by boxes. (B) Predicted protein–protein interaction (PPI)

644 networks for CaPLATZ proteins and their associated interactors, generated using STRING database analysis. Each subnetwork corresponds to an individual CaPLATZ
645 protein, with nodes representing proteins and connecting lines indicating predicted functional associations. Line thickness reflects the confidence of the predicted
646 interaction. (C) Promoter-sequence architecture of *CaPLATZ* genes represented through sequence-logo analysis. The relative height of each nucleotide indicates its
647 degree of conservation or contribution at the corresponding position within the promoter sequences. (D) Gene Ontology enrichment analysis of CaPLATZ proteins
648 showing significantly enriched biological-process terms. The horizontal axis represents statistical significance as $-\log_{10}(\text{FDR})$, while dot size and colour indicate the
649 number of genes associated with each enriched term, as shown in the accompanying scales.

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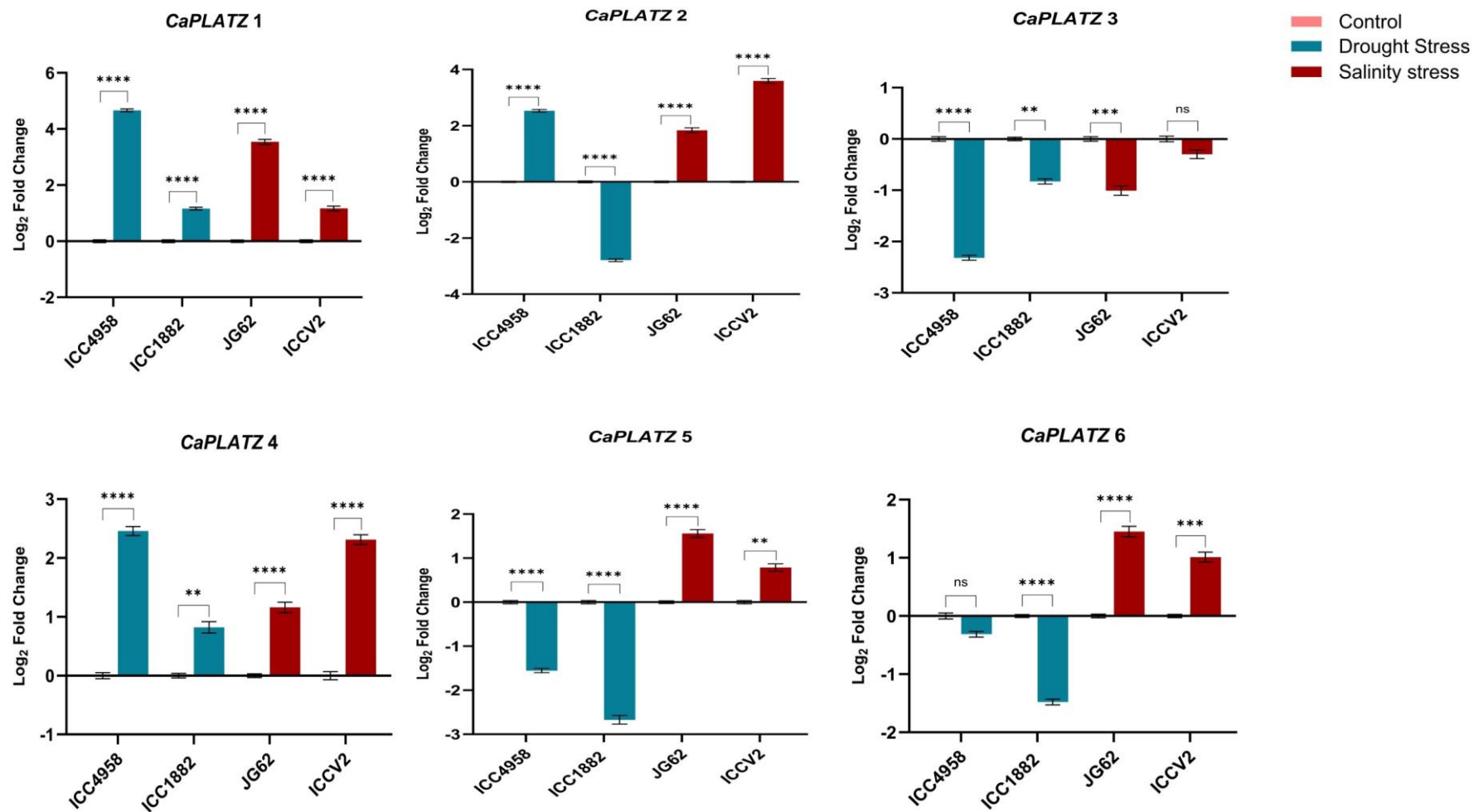
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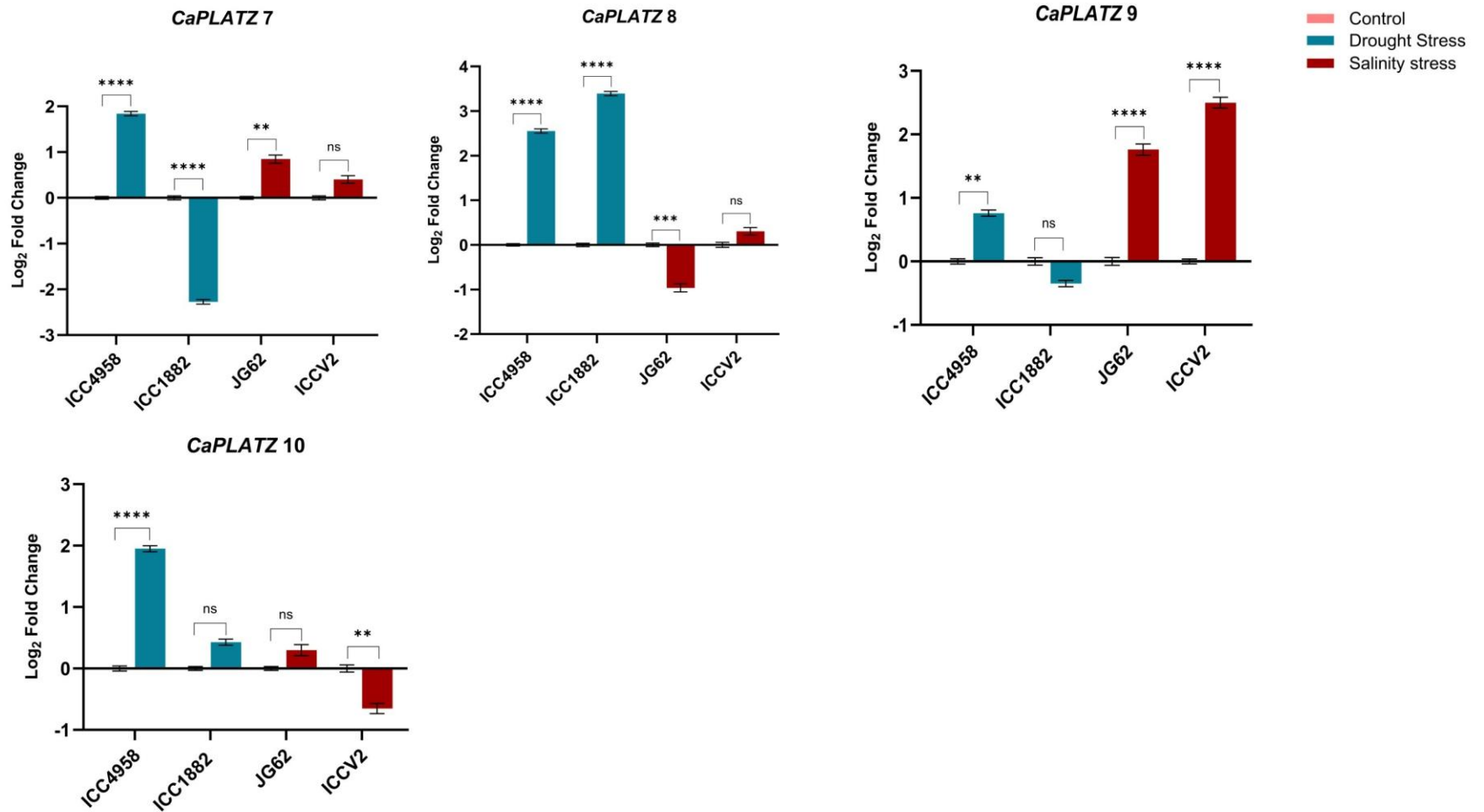
665 treatment combinations. Hierarchical clustering indicates similarities in gene-expression patterns, and colour intensity represents relative expression levels. (D) Heatmap
666 showing *CaPLATZ* gene expression under salinity stress in the salt-tolerant JG62 and salt-sensitive ICCV2 chickpea genotypes under control and stress conditions.
667 Rows represent *CaPLATZ* genes, and columns represent genotype–treatment combinations. Hierarchical clustering is shown by the dendrogram, while colour intensity
668 indicates relative expression levels.

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Fig. 6 Quantitative real-time PCR (qRT-PCR) validation of *CaPLATZ* gene expression under drought and salinity stress. Log 2 fold change expression levels of (A) *CaPLATZ1*, (B) *CaPLATZ2*, (C) *CaPLATZ3*, (D) *CaPLATZ4*, (E) *CaPLATZ5*, (F) *CaPLATZ6*, (G) *CaPLATZ7*, (H) *CaPLATZ8*, (I) *CaPLATZ9* and (J) *CaPLATZ10* were determined by qRT-PCR in chickpea genotypes subjected to drought stress (ICC4958 and ICC1882) and salinity stress (JG62 and ICCV2), relative to their respective untreated controls. Expression values were normalized against a housekeeping gene and are presented as mean $\pm$ standard error (SE) of three biological replicates. The y-axis represents log₂ fold change in relative gene expression. Bar colours indicate control (pink), drought stress (teal) and salinity stress (dark red), as shown in the legend. Asterisks indicate statistically significant differences relative to the corresponding control ($P < 0.05$, * $P < 0.01$, ** $P < 0.001$ and *** $P < 0.0001$), while ns indicates a non-significant difference.

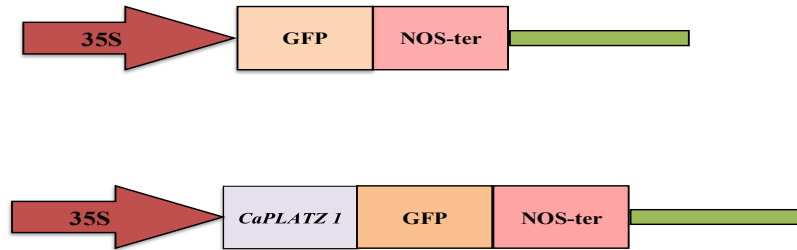
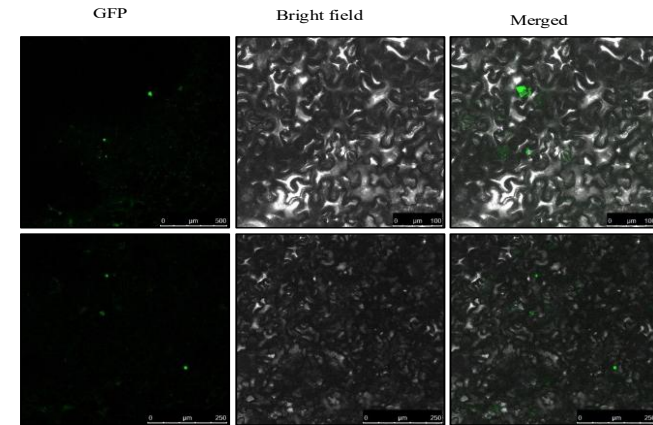


Fig.7 Subcellular localization analysis of CaPLATZ1 in *Nicotiana benthamiana* leaf epidermal cells. Schematic representation of the 35S::GFP control and 35S::CaPLATZ1–GFP fusion constructs, each driven by the cauliflower mosaic virus (CaMV) 35S promoter and terminated by the NOS terminator (NOS-ter). The constructs were transiently expressed in *N. benthamiana* leaves through *Agrobacterium*-mediated infiltration and visualized using confocal microscopy. GFP fluorescence images show the localization of free GFP or the CaPLATZ1–GFP fusion protein, bright-field images display leaf epidermal-cell morphology, and merged images show the GFP signal overlaid on the corresponding bright-field image. Compared with the free GFP control, the CaPLATZ1–GFP fusion protein exhibited concentrated intracellular fluorescence. Scale bars are indicated within the respective images.

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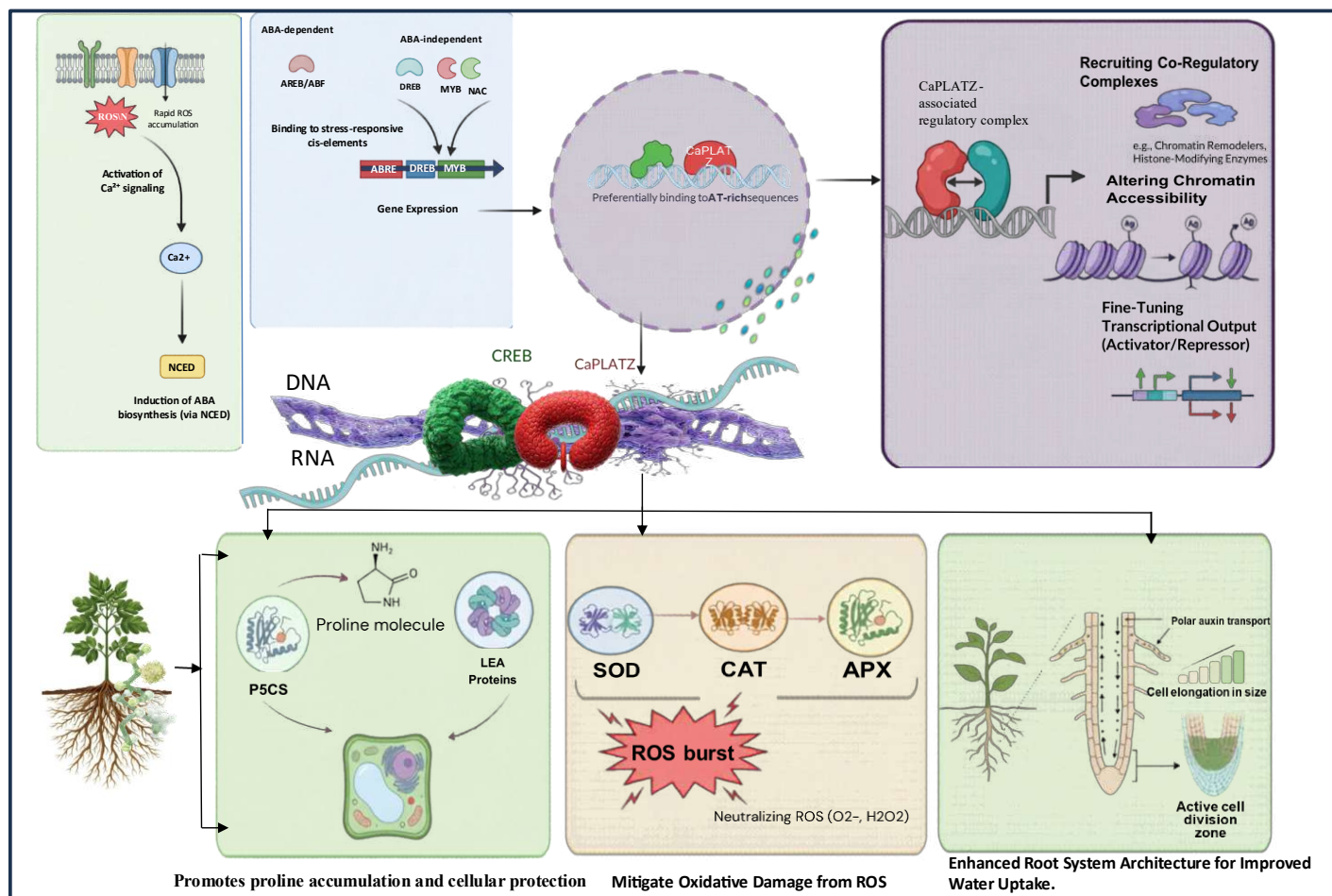


Figure. Proposed working model of CaPLATZ-mediated regulation of drought and salinity responses in chickpea.

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705 **Fig.8 Proposed working model of CaPLATZ-mediated drought and salinity responses in chickpea.**

706 Drought- and salinity-induced cellular signals, including reactive oxygen species (ROS), Ca²⁺ signaling, and ABA biosynthesis through NCED, activate ABA-dependent
707 and ABA-independent transcriptional pathways involving AREB/ABF, DREB, MYB, and NAC transcription factors. These regulators act through stress-responsive cis-
708 elements, while CaPLATZ proteins preferentially bind A/T-rich DNA sequences and may modulate transcription through interactions with other regulatory proteins and
709 chromatin-associated complexes. Downstream responses include osmotic adjustment through proline accumulation and LEA proteins, ROS detoxification by
710 antioxidant enzymes such as SOD, CAT, and APX, and modulation of root growth and development. Together, these interconnected processes illustrate a proposed role
711 for CaPLATZ proteins in coordinating transcriptional, hormonal, antioxidant, and developmental responses associated with drought and salinity adaptation in chickpea.
712 Arrows represent proposed regulatory relationships and do not necessarily indicate direct experimentally validated interactions.

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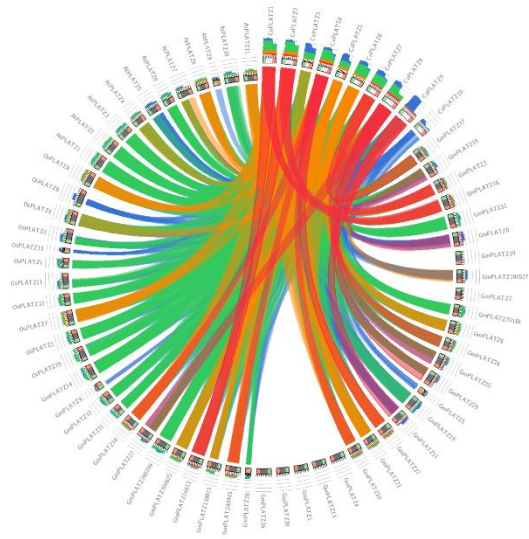


Fig. S1. Circos-based syntenic relationship plot

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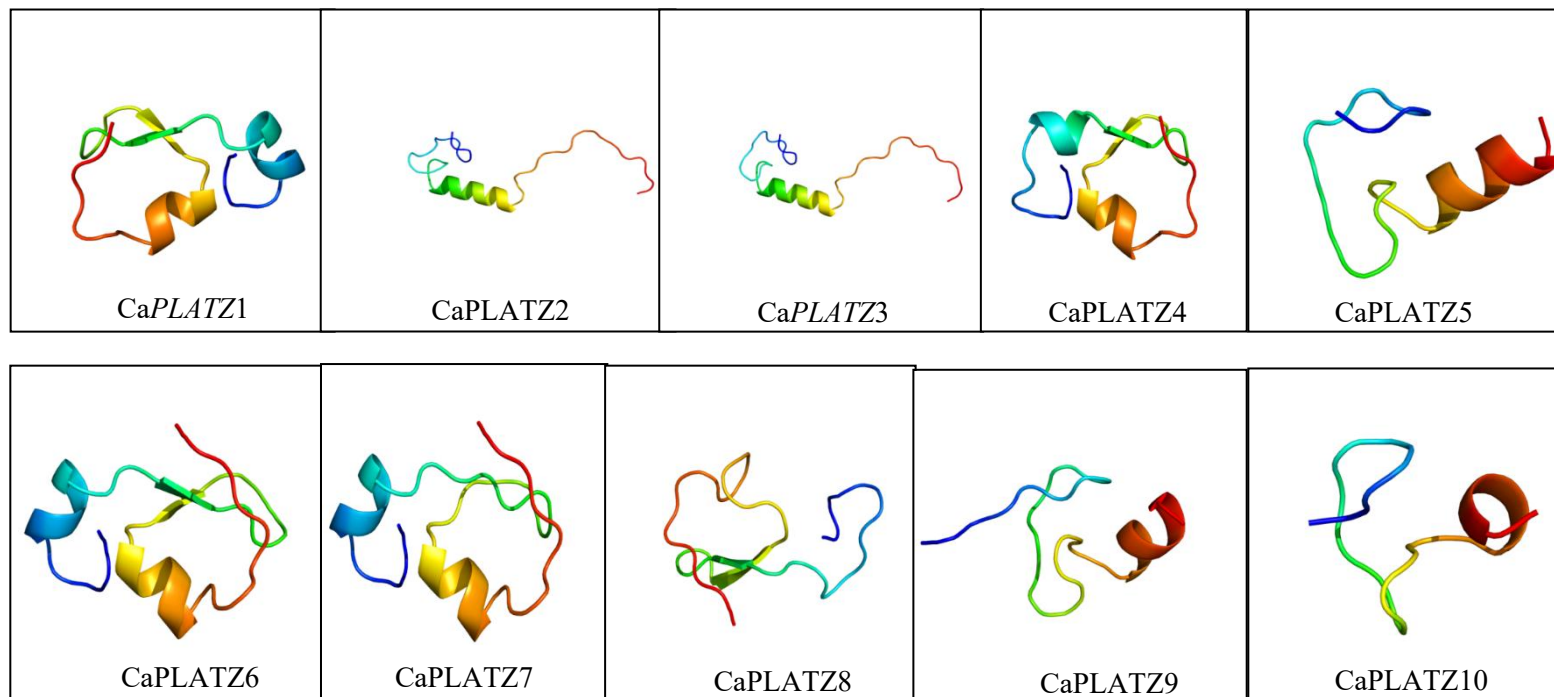


Fig. S2. Predicted 3D structures of CaPLATZ proteins

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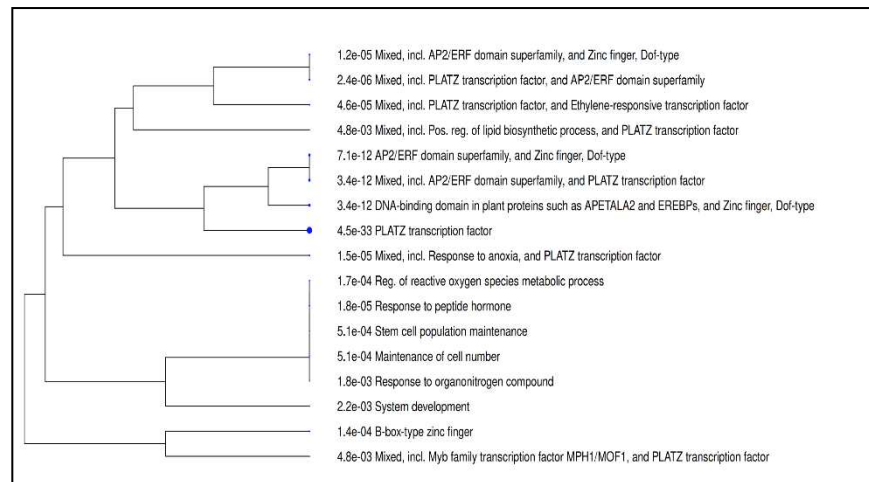
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Fig. S3. Hierarchical clustering tree of *CaPLATZ* gene

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Fig. S4. Functional interaction network of *CaPLATZ* and other Transcription factors

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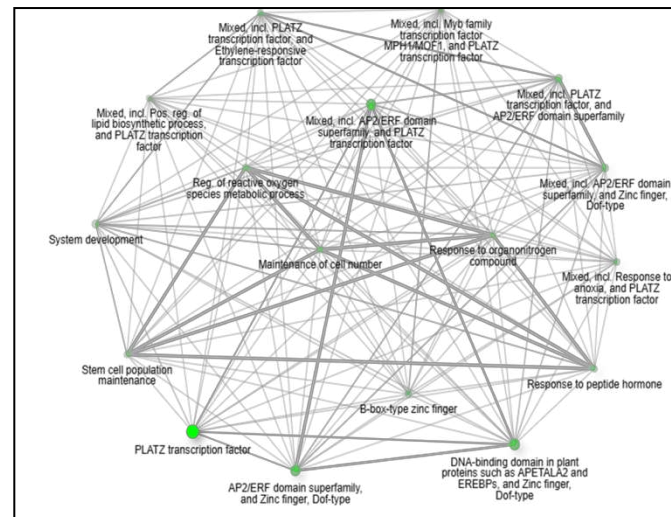
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cNLS Mapper Result

Predicted NLSs in query sequence

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MGAGGPDDEENRWPPWLKPLLKERFFVQCKLHADSHKSECNMYCLDCMNG 50
ALCSLCLNYHKDHRAIQIRSSYHDVIRVNEIQKVLDSGVQTYIINSAR 100
VWFLNERPQPRPGKGVNTCEVCERSLLDSFRFCSLGCKIVGTSKNFQKK 150
NKSTTMVSDSEDSYSSSCSHGRLKNIKVSFTPSTPPPTSVNYRTAKRRK 200
GIPHRAPMGGLVLQY 215
  
```

Predicted monopartite NLS

Pos.	Sequence	Score
193	YRTAKRRKGI	9
194	RTAKRRKGIP	8

Predicted bipartite NLS

Pos.	Sequence	Score
172	RLKNIKVSFTPSTPPPTSVNYRTAKRRKGI	5

Your results are here!

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# -----
# LOCALIZER 1.0.4 Predictions
# -----
Identifier Chloroplast      Mitochondria      Nucleus
default      -                -                Y (RTAKRRK)
  
```

Proteins analyzed: 1

```

# Number of proteins with cTP: 0 (0.0%)
# Number of proteins with cTP & possible mTP: 0 (0.0%)
# Number of proteins with cTP & NLS: 0 (0.0%)
# Number of proteins with cTP & possible mTP & NLS: 0 (0.0%)
# Number of proteins with mTP: 0 (0.0%)
# Number of proteins with mTP & possible cTP: 0 (0.0%)
# Number of proteins with mTP & NLS: 0 (0.0%)
# Number of proteins with mTP & possible cTP & NLS: 0 (0.0%)
# Number of proteins with NLS and no transit peptides: 1 (100.0%)
  
```

Summary statistics

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# Number of proteins with chloroplast localization (cTP, cTP & possible mTP, cTP & NLS, cTP & possible mTP & NLS): 0 (0.0%)
# Number of proteins with mitochondrial localization (mTP, mTP & possible cTP, mTP & NLS, mTP & possible cTP & NLS): 0 (0.0%)
# Number of proteins with nuclear localization and no transit peptides: 1 (100.0%)
# Number of proteins with nuclear localization and with transit peptides: 0 (0.0%)
  
```

Download proteins with predicted NLSs as FASTA file [here](#).

Fig S5. In silico prediction of nuclear localization signals in CaPLATZ1.

(A) Nuclear localization signals (NLSs) in the CaPLATZ1 protein were predicted using cNLS Mapper. Two overlapping monopartite NLSs were identified near the C-terminal region: **YRTAKRRKGI** beginning at amino acid position 193 with a score of **9.0**, and **RTAKRRKGIP** beginning at position 194 with a score of **8.0**. A bipartite NLS, **RLKNIKVSFTPSTPPPTSVNYRTAKRRKGI**, was additionally predicted beginning at amino acid position 172 with a score of **5.0**. (B) Independent analysis using LOCALIZER v1.0.4 predicted nuclear localization of CaPLATZ1 based on the basic **RTAKRRK** motif. No chloroplast transit peptide or mitochondrial targeting peptide was detected. Together, the two independent prediction approaches support a putative nuclear localization of CaPLATZ1.

No.	Species	PLATZ designation	Locus identifier	Reference source
1	<i>Arabidopsis thaliana</i>	<i>AtPLATZ1</i>	AT1G21000	Wang et al. (2018)
2	<i>Arabidopsis thaliana</i>	<i>AtPLATZ2</i>	AT1G76590	Wang et al. (2018)
3	<i>Arabidopsis thaliana</i>	<i>AtPLATZ3</i>	AT1G32700	Wang et al. (2018)
4	<i>Arabidopsis thaliana</i>	<i>AtPLATZ4</i>	AT1G43000	Wang et al. (2018)
5	<i>Arabidopsis thaliana</i>	<i>AtPLATZ5</i>	AT1G31040	Wang et al. (2018)
6	<i>Arabidopsis thaliana</i>	<i>AtPLATZ6</i>	AT2G01818	Wang et al. (2018)
7	<i>Arabidopsis thaliana</i>	<i>AtPLATZ7</i>	AT2G12646	Wang et al. (2018)
8	<i>Arabidopsis thaliana</i>	<i>AtPLATZ8</i>	AT2G27930	Wang et al. (2018)
9	<i>Arabidopsis thaliana</i>	<i>AtPLATZ9</i>	AT3G50808	Wang et al. (2018)
10	<i>Arabidopsis thaliana</i>	<i>AtPLATZ10</i>	AT3G60670	Wang et al. (2018)
11	<i>Arabidopsis thaliana</i>	<i>AtPLATZ11</i>	AT4G17900	Wang et al. (2018)
12	<i>Arabidopsis thaliana</i>	<i>AtPLATZ12</i>	AT5G46710	Wang et al. (2018)
13	<i>Oryza sativa</i>	<i>OsPLATZ</i>	LOC_Os01g33350	Wang et al. (2018)
14	<i>Oryza sativa</i>	<i>OsPLATZ</i>	LOC_Os01g33370	Wang et al. (2018)
15	<i>Oryza sativa</i>	<i>OsPLATZ</i>	LOC_Os02g07650	Wang et al. (2018)
16	<i>Oryza sativa</i>	<i>OsPLATZ</i>	LOC_Os02g09070	Wang et al. (2018)
17	<i>Oryza sativa</i>	<i>OsPLATZ</i>	LOC_Os02g10000	Wang et al. (2018)
18	<i>Oryza sativa</i>	<i>OsPLATZ</i>	LOC_Os02g44260	Wang et al. (2018)
19	<i>Oryza sativa</i>	<i>OsPLATZ</i>	LOC_Os02g46610	Wang et al. (2018)
20	<i>Oryza sativa</i>	<i>OsPLATZ</i>	LOC_Os03g12440	Wang et al. (2018)
21	<i>Oryza sativa</i>	<i>OsPLATZ</i>	LOC_Os04g50120	Wang et al. (2018)
22	<i>Oryza sativa</i>	<i>OsPLATZ</i>	LOC_Os06g41930	Wang et al. (2018)

23	<i>Oryza sativa</i>	<i>OsPLATZ</i>	LOC_Os06g45540	Wang et al. (2018)
24	<i>Oryza sativa</i>	<i>OsPLATZ</i>	LOC_Os08g44620	Wang et al. (2018)
25	<i>Oryza sativa</i>	<i>OsPLATZ</i>	LOC_Os09g02790	Wang et al. (2018)
26	<i>Oryza sativa</i>	<i>OsPLATZ</i>	LOC_Os10g42410	Wang et al. (2018)
27	<i>Oryza sativa</i>	<i>OsPLATZ</i>	LOC_Os11g24130	Wang et al. (2018)

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Gene	Primer Type	Sequence (5'–3')
<i>CaPLATZ1</i>	Forward	TGGTATCAGACTCAGAGGATTCA
	Reverse	GAAGTTGGTGGTGGTGTAGAA
<i>CaPLATZ2</i>	Forward	CAACATCCATAGCCGTCAGAT
	Reverse	GGCTCTATGTGGTATTCCCTTT
<i>CaPLATZ3</i>	Forward	CGCAAAGAAAGACGAGGAAATAG
	Reverse	TGAACGAGGACAATAAGGAGAAG
<i>CaPLATZ4</i>	Forward	TCCTTCAACTTCTGCTCTCTTG
	Reverse	ACCATCAGACCCATCTTTCTTAC
<i>CaPLATZ5</i>	Forward	TGTTCCCTTGGTTGTAAGATAGTT
	Reverse	TGTTTCTGCCACTTCCACTAC
<i>CaPLATZ6</i>	Forward	GGGTGTCAAGTAGAACAACAGA
	Reverse	GCATTTAAAGGAGGTGGAGGA
<i>CaPLATZ7</i>	Forward	CCCACTTCGTTTCTGTTCTTTG
	Reverse	CCCTCCTCAATTGTTGATACCT
<i>CaPLATZ8</i>	Forward	GCATGGTTGGAAGCTCTTTAC
	Reverse	GGCAAGCAATGAGGACAAATAC
<i>CaPLATZ9</i>	Forward	GATCGAAGCCCTGAACCTAAAT
	Reverse	CTTGCATGTAATGGAGCAGAAAC
<i>CaPLATZ10</i>	Forward	TCATTTCCATCCAGGCTCTTC
	Reverse	TGACGGAAGGAACTGAATCAATC
<i>CaEF1α</i>	Forward	ATCACCATGGTTCGTGCTGA

	Reverse	TATGACCACCGCCGATCAAG	836
<i>CaGAPDH</i>	Forward	ATGACCACCGTCCATTCCATCACTACT	837
	Reverse	GGAAGCACTTTGCCAACAGCCTTA	838
<i>CaPLATZ1</i> localization	Forward	TACGTCTAGAATGGGTGCTGGAGGACCTGAT	
	Reverse	TAGGGAGCTCGTATTGCAAGACTAGTCCTCC	

Table2 : Primer sequences used for *CaPLATZ* gene expression analysis and reference genes

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [PLATZsupplementaryfigures.pptx](#)
- [SupplementaryTableS1.docx](#)