Journal of Life and Social Sciences
eISSN: 3006-2675
www.bbasrjlifess.com
J. Life Soc. Sci, 2026; Volume, 5: 74
https://doi.org/10.64013/bbasrjlifess.v2026i1.74

Original Research Article *Open Access*

IDENTIFICATION OF PLANT-SPECIFIC YABBY TRANSCRIPTION FACTOR GENE FAMILY IN FALSE FLAX (*CAMELINA SATIVA* L.) AND IN SILICO EXPRESSION PROFILING

TAHIR K[1*], YASEEN E[1], NADEEM M [1], SHAFIQ M[2], TAHIR S[3], WASIM M[4], KHAN T[5]

[1]*Department of Plant Breeding and Genetics, Faculty of Agricultural Sciences, University of the Punjab, Lahore, Pakistan*
[2]*Department of Horticulture, Faculty of Agricultural Sciences, University of the Punjab, Lahore, Pakistan*
[3]*Department of Plant Pathology, Faculty of Agricultural Sciences, University of the Punjab, Lahore, Pakistan*
[4]*Department of Agronomy, Faculty of Agricultural Sciences, University of the Punjab, Lahore, Pakistan*
[5]*School of Life Sciences, University of Warwick, Coventry, CV47AL, United Kingdom*
Correspondence Author Email Address: kanzatahir85@gmail.com

(Received, 15th February 2026 Accepted 24th October 2026, Published 7th November 2026)

Abstract *Camelina sativa is a hexaploid oilseed crop with remarkable agronomic resilience and industrial value; however, the YABBY transcription factor gene family remains insufficiently characterized. In this study, we conducted a comprehensive genome-wide identification and in silico characterization of the YABBY gene family in C. sativa, providing insights into its evolutionary relationships, structural organization, and potential regulatory functions. Seventeen YABBY genes (CsYABBYs) were identified through conserved-domain-based screening and systematically characterized for physicochemical features, evolutionary relationships, exon–intron architecture, conserved motifs, chromosomal locations, cis-regulatory elements, and evolutionary selection pressure. Comparative phylogenetic analysis with Arabidopsis thaliana and Theobroma cacao separated the CsYABBY proteins into five clusters (FIL/YAB3, YAB2, YAB5, CRC, and INO), indicating strong evolutionary conservation and functional similarity in each subfamily. Gene structure analysis showed that exon–intron organization was highly conserved in every clade. In contrast, MEME-based motif analysis identified ten conserved motifs, including the characteristic C2C2 zinc-finger and YABBY domains. Promoter analysis uncovered abundant cis-regulatory elements associated with various regulatory functions, suggesting extensive involvement of CsYABBY genes in integrating environmental signals. The Ka/Ks analysis also supports purifying selection, as K_a/K_s values are below 1. Collectively, these findings establish an integrated genomic framework for the YABBY transcription factor family in C. sativa and serve as a valuable reference for YABBY gene function or for cloning individual YABBY genes*.

[Citation: Tahir, K., Yaseen, E., Nadeem, M., Shafiq, M., Tahir, S., Wasim, M., Khan, T. (2026). Identification of plant-specific yabby transcription factor gene family in false flax (*Camelina sativa* L.) and in silico expression profiling. *J. Life Soc. Sci, 5: 74. https://doi.org/10.64013/bbasrjlifess.v2026i1.74]*
Keywords: *YABBY transcription factors; genome-wide analysis; abiotic stress tolerance*; *Camelina sativa*

Introduction

The oilseed crop *Camelina sativa* (L.), sometimes known as gold-of-pleasure, fake flax, or linseed dodder, belongs to the Camelineae tribe of the mustard family (*Brassicaceae*) (Berti et al., 2016; Vollmann et al., 2007; Zubr, 1997). Its oil is regarded as a premium-quality edible oil(Orczewska-Dudek et al., 2020). *Camelina* propagates by seed and is predominantly self-pollinating (Francis and Warwick, 2009; Manish Sainger et al., 2017; Sainger et al., 2017). Reports describe the discovery of a region of high genetic diversity in Ukraine and Russia. The name "false flax" comes from the fact that *Camelina*, which is native to Europe and Southwest Asia, was unintentionally brought to America and Canada as flax (Ghamkhar et al., 2010). *C. sativa* was one of the earliest agricultural plants cultivated; archaeological findings indicate that agriculture began in southeast Europe during the Neolithic era. It was widely grown all over Europe during the Iron Age. In the Roman Empire, *Camelina* oil was primarily used as lamp fuel, for cosmetics, and for medicinal purposes. In the Rhine valleys, *Camelina* grew in isolation as a monoculture around 600 BC. It was still grown until 1940 in all of France, Belgium, and Russia, where its oil was also employed for fuel. The proportion of this crop has decreased significantly since 1950 and has been replaced by more economically viable crops (Eynck and Falk, 2013; Larsson, 2013; Vollmann et al., 2007). *Camelina* has garnered renewed interest as a viable crop in recent years, especially in the US, Canada, and Europe. Because of their potential use in bio-lubricants, oilseed crops like Camelina, hemp,

flax, crambe, and castor bean—plants that produce highly unsaturated oils—are receiving more attention (Hergert et al., 2016; Matteo et al., 2020; Vollmann et al., 2007).

Camelina is a "low-input and environment-friendly" crop with higher oil content (36–47%)(Moser, 2012) and has emerged as a popular oil crop worldwide because of its low input and environmental requirements. Up to 90% of C. sativa seed oil is made up of unsaturated fatty acids (UFAs), including 40% of the health-promoting ω-linolenic acids (ω-3 fatty acids)(Kiczorowska et al., 2019; Moser, 2012). Feeding the ecologically sustainable food production, feed, biofuels (including aviation fuel and biodiesel), and several valuable industrial raw materials on a large scale, commercially. In addition, it has outstanding agronomic characteristics like a short growing period, abiotic stress resilience, and tolerance to primary pests and diseases when compared with traditional oil crops, such as soybean and oilseed rape(Bansal and Durrett, 2016). Because of the seed's oil potential and the plant's remarkable stress resilience, research has focused on the regulatory processes governing oil biosynthesis and stress sensitivity in C. sativa. Camelina needs less water, nutrients, and pesticides to grow.(Kagale et al., 2014; Manca et al., 2013) and is resilient against pests (Séguin-Swartz et al., 2009). Although it has potential, C. sativa has received relatively little attention; breeding and the establishment of breeding lines have been conducted with very few approved cultivars, and few modern breeding lines have been identified to date because of the limited genetic variability recognized within small sets of discovered genetic material (Berti et al., 2016). Genetic studies of camelina suggest that it is a hexaploid (genome of 750 Mbp having 2n = 40 chromosomes) (Manish Sainger et al., 2017; Sainger et al., 2017).

Previous work has illustrated that YABBYs are crucial in various biological mechanisms (Bowman, 2000; Zhao et al., 2020). Additionally, *YABBYs* can regulate seed development (Finet et al., 2016; Li et al., 2022). growth of leaves (Bowman, 2000; Bowman and Smyth, 1999; Siegfried et al., 1999; Toriba et al., 2007) and floral organs (Ha et al., 2010; Yamada et al., 2011). YABBY proteins are members of the zinc finger protein superfamily. They are identified by a C-terminal helix–loop–helix motif (also known as the YABBY domain) and a C2C2 zinc finger domain at their N-terminus. While the remaining YABBY proteins show minimal sequence conservation, the C2C2 and YABBY domains are distinguished by two highly conserved regions. (Bowman and Eshed, 2000; Bowman and Smyth, 1999; Golz et al., 2004; Kanaya et al., 2002; Sieber et al., 2004). The angiosperm YABBY family was divided into five different subfamilies by phylogenetic analysis: FILAMENTOUS FLOWER (FIL)/YABBY3 (YAB3), CRABS CLAW (CRC), YABBY2 (YAB2), INNER NO OUTER (INO), and YABBY5 (YAB5) (Bowman, 2000). While INO and CRC are expressed in developing floral organs (ovules and carpels, respectively), which are evolutionarily derived from leaves, FIL, YAB2, YAB3, and YAB5 are collectively referred to as "vegetative" and are all preferentially expressed in leaves and leaf-derived lateral organs (cotyledons, sepals, petals, stamens, and carpels) (Bowman and Smyth, 1999; Eshed et al., 2004; Sarojam et al., 2010; Sawa et al., 1999a; Sawa et al., 1999b; Siegfried et al., 1999; Villanueva et al., 1999). INO plays an essential part in the formation of the integument (Villanueva et al., 1999), while CRC was the first gene shown to play part in Nectary bud formation in Arabidopsis flowers at the base of stamen filaments (Bowman and Smyth, 1999; Lee et al., 2005). Several plant species have been shown to have different numbers of YABBY genes. The absence of YABBY members in terrestrial plants, bryophytes, and stone pine (Pinus pinea) suggests that this gene family is exclusive to seed plants (Finet et al., 2016). We carried out genome-wide isolation, classification, and evolutionary analysis of YABBY genes in C. sativa (including the model species A. *thaliana*). A detailed analysis was then performed to investigate their physicochemical characteristics, conserved motifs, gene distribution and duplication on their chromosomes, and their intron-exon architecture. We then analysed the phylogenetic relationships among YABBY genes in camelina, Arabidopsis, and Theobroma cacao. Our study offers useful information to gain insight to the function of CsYABBY in biology, particularly in plant to resist various stresses.

2. Materials and methods

2.1 Screening and Sequence Identification

The Pfam database (https://pfam.xfam.org/family/PF04690) was used to obtain amino acid (AA) sequences containing the YABBY domain. The *YABBY* domain PF04690 was identified in these sequences (Mistry et al., 2021). This domain was used to identify CsYAB genes and to search for genes in the Camelina genome using the BLAST tool. The BLAST tool is a protein local alignment search tool available through the Phytozome database (**https://phytozome-next.jgi.doe.gov**). The NCBI CDD (Conserved Domain Database) (http://www.ncbi.nlm.nih.gov/Structure/cdd/wrpsb.cgi) and Motif Finder database were used to analyse and confirm the amino acid sequences of the YABBY domain using default settings(Sami et al., 2024). Proteins without a true YABBY domain (PF04690) in their sequences were removed. The genome, CDS, peptide, and promoter data were also searched and downloaded from Phytozome.

2.2 Physicochemical Characterization of YABBY Proteins

ProtParam (https://web.expasy.org/protparam/) and Phytozome were used to retrieve data on 12 HaYABBY proteins. Phytozome was used to

determine chromosome number and location, strand orientation (sense or antisense), mRNA length (CDS), and peptide length. ProtParam provided details such as isoelectric point (pI) and molecular weight. The WoLF PSORT database (https://wolfpsort.hgc.jp/) was used to obtain the localization of the YABBY gene(Akram et al., 2023), and then TBtool was used for the visualization of data in the form of a heatmap (Amjad et al., 2024).

2.3 Construction of Comparative Phylogenetic Tree

To investigate evolutionary relationships, phylogenetic analysis was done with MEGA (Molecular Evolutionary Genetics Analysis) software (Wen et al., 2016). The amino acid sequences of YABBY proteins were aligned with the ClustalW alignment algorithm from *Camelina sativa, Arabidopsis thaliana, and Theobroma cacao.* A phylogenetic tree was generated employing the Neighbour-Joining (NJ) algorithm with 1000 bootstrap replications to assess the evolutionary divergence within the YABBY gene family. For enhanced graphical interpretation, the phylogenetic tree was displayed and annotated with Interactive Tree of Life (iTOL) (https://itol.embl.de/upload.cgi)(Rehman et al., 2022)

2.4 Analysis of Gene Structure

We obtained DNA and coding sequences (CDS) for every identified CsYABBY protein from Phytozome. This was done to examine how introns and exons are arranged in CsYABBY. Gene Structure Display Server (GSDS) software(http://gsds.gao-lab.org/) was employed to analyze all of the identified YABBY gene structures(Hu et al., 2015).

2.5 Motif Analysis

The MEME Suite (version 4.11.3) (http://meme-suite.org/tools/meme) was employed to anticipate the conserved motifs among 12YABBY protein(Bailey et al., 2009)

2.6 Cis-Regulatory Analysis

The 1000 bp upstream promoter sequences of all *CsYABBY* genes were retrieved from the *Camelina sativa* genome, and the PlantCARE database(http://bioinformatics.psb.ugent.be/webtools/plantcare/html/) was employed to isolate cis-regulatory elements related to hormone, stress, light, and developmental responses(Buttar et al., 2020).

2.7 Analysis of Selection Pressure

Selection pressure on protein-coding genes is determined by comparing synonymous and non-synonymous mutations. Ka/Ks is calculated using Tbtools (https://bio.tools/tbtools)(Chen et al., 2020). Default parameters were used. Typically, a Ka/Ks ratio < 1 is indicative of purifying selection. Ka/Ks = 1 (neutral selection), Ka/Ks > 1 (positive selection).

3. RESULTS

3.1Identification and Physicochemical Characterization of Camelina YABBY Gene Family Members

Seventeen CsYABBY domains were found in Camelina. The length of the protein encoded by CsYAB genes ranges from86AA(CsYAB6) to 236AA(CsYAB17), and the molecular weight ranges from 18394(CsYAB14) to 9444.28D(CsYAB6). The pI value of proteins varies from 5.77(CsYAB2) to 9.69(HaYAB1).

Table 1. Physicochemical characterization of 17 non-redundant YABBY proteins in camelina

Gene ID/Accession	YABBY gene	Scaffold	Locations		Direction	mRNA(CDS)length	ProteinAA	MW	PI
No	Name		Start	End				(D)	
>Csa17g011910| Csa17g011910.1	CsYABBY1	Chr17	3423660	3425469	Forward	525	176	19616.24	9.69
>Csa17g030590| Csa17g030590.1	CsYABBY2	Chr17	11457020	11457020	Forward	699	232	25970.28	5.77
>Csa02g001230| Csa02g001230.1	CsYABBY3	Chr02	138074	141002	Reverse	612	203	22369.52	9.46
>Csa16g050800| Csa16g050800.1	CsYABBY4	Chr16	26033324	26036667	Reverse	495	164	18452.1	9.57
>Csa16g030480| Csa16g030480.1	CsYABBY5	Chr17	16142240	16143947	Reverse	543	180	19570.26	9.54
>Csa07g060160| Csa07g060160.1	CsYABBY6	Chr07	30429662	30433248	Reverse	495	86	9444.28	9.56
>Csa04g063090| Csa04g063090.1	CsYABBY7	Chr04	28568636	28571180	Reverse	903	300	34104.04	8.97
>Csa13g057240| Csa13g057240.1	CsYABBY8	Chr13	23939073	23942932	Forward	708	235	25672.16	8.66
>Csa03g027340| Csa03g027340.1	CsYABBY9	Chr03	10834342	10836287	Forward	699	232	25815.19	5.99
>Csa03g011910| Csa03g011910.1	CsYABBY10	Chr03	3545405	3550025	Forward	567	188	21055.94	9.37
>Csa14g030690| Csa14g030690.1	CsYABBY11	Chr14	11740180	11740180	Forward	699	232	25944.25	5.86
>Csa14g009930| Csa14g009930.1	CsYABBY12	Chr14	3614205	3619264	Forward	567	188	21043.93	9.37
>Csa05g004070| Csa05g004070.1	CsYABBY13	Chr05	1475650	1478640	Forward	918	305	34816.85	8.96
>Csa05g044630| Csa05g044630.1	CsYABBY14	Chr05	16972761	16976732	Forward	495	164	18394.01	9.6
>Csa05g085860| Csa05g085860.1	CsYABBY15	Chr05	30871641	30871641	Reverse	540	179	19497.21	9.54
>Csa06g051580| Csa06g051580.1	CsYABBY16	Chr06	24884440	24886998	Reverse	684	227	25524.14	6.78
>Csa08g001240| Csa08g001240.1	CsYABBY17	Chr03	120569	123456	Reverse	711	236	25849.37	8.65

3.2 Subcellular Localization

To investigate the features of CsYABBY proteins, we carried out subcellular localization analysis. Using the WoLF PSORT web server, subcellular localization of proteins was predicted based on the analysis of several sequence features such as sorting signals, amino acid composition, and localization-related motifs (e.g., nuclear localization signals or transit peptides).

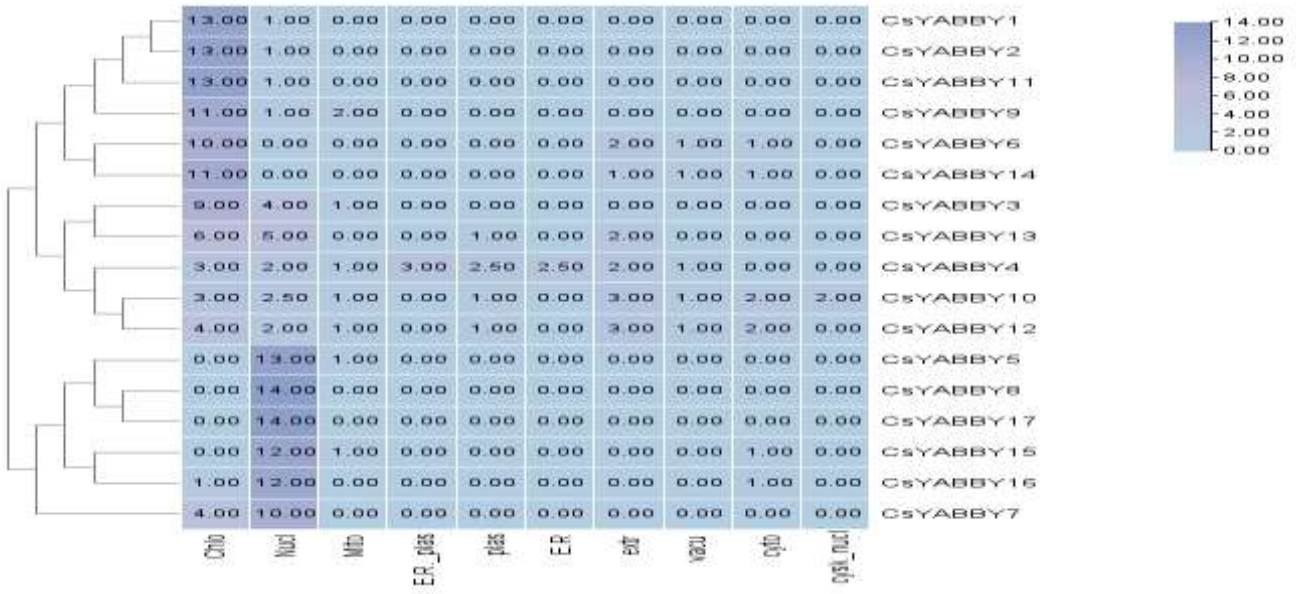


Figure 1 Subcellular localization anticipation of CsYABBY proteins in Camelina sativa, putative distribution across different cellular compartments and phylogenetic relationships among different proteins.

3.2 Phylogenetic Analysis

The maximum likelihood phylogenetic tree construction showed the phylogenetic relationships of YABBY proteins from *Arabidopsis*, *Theobroma cacao* and *Camelina*. The phylogenetic tree illustrated that the CsYABBY genes in Arabidopsis have five subgroups, namely INO, CRC, YAB5, YAB3 and YAB2. YAB3 is the largest subgroup among them with 10 genes, followed by YAB5 with 6 genes, and INO and YAB2 with 5 genes, and CRC is the fourth largest with 4 genes**.**

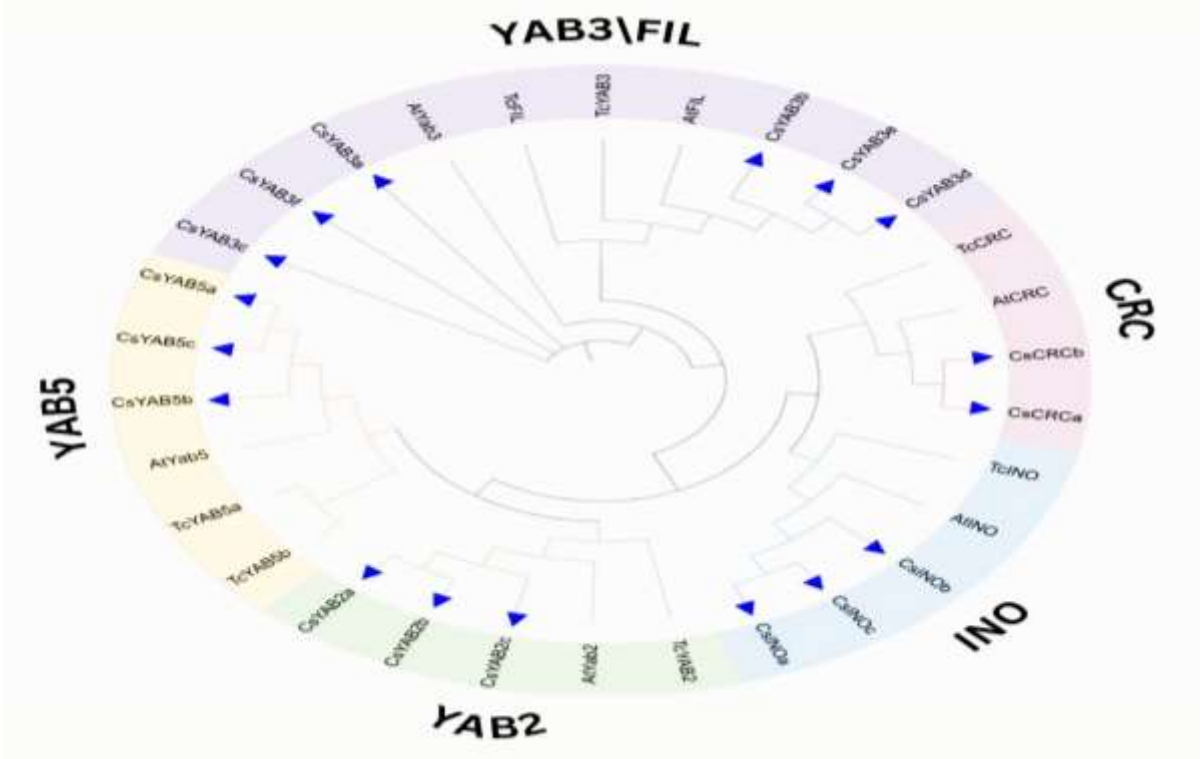


Figure 1. Phylogenetic and evolutionary linkage amongYABBY gene of Camelina, Arabidopsis and Theobroma cacao. Blue arrow show proteins which are CsYABBY proteins

3.3 Structure of CsYABBY genes

Prediction of gene structure revealed that 10 out of 17 CsYAB genes have seven exons and six introns, one gene (CsYAB 2a) contains 5 exons and 4 introns, and six genes contain 6 exons and 5 introns.

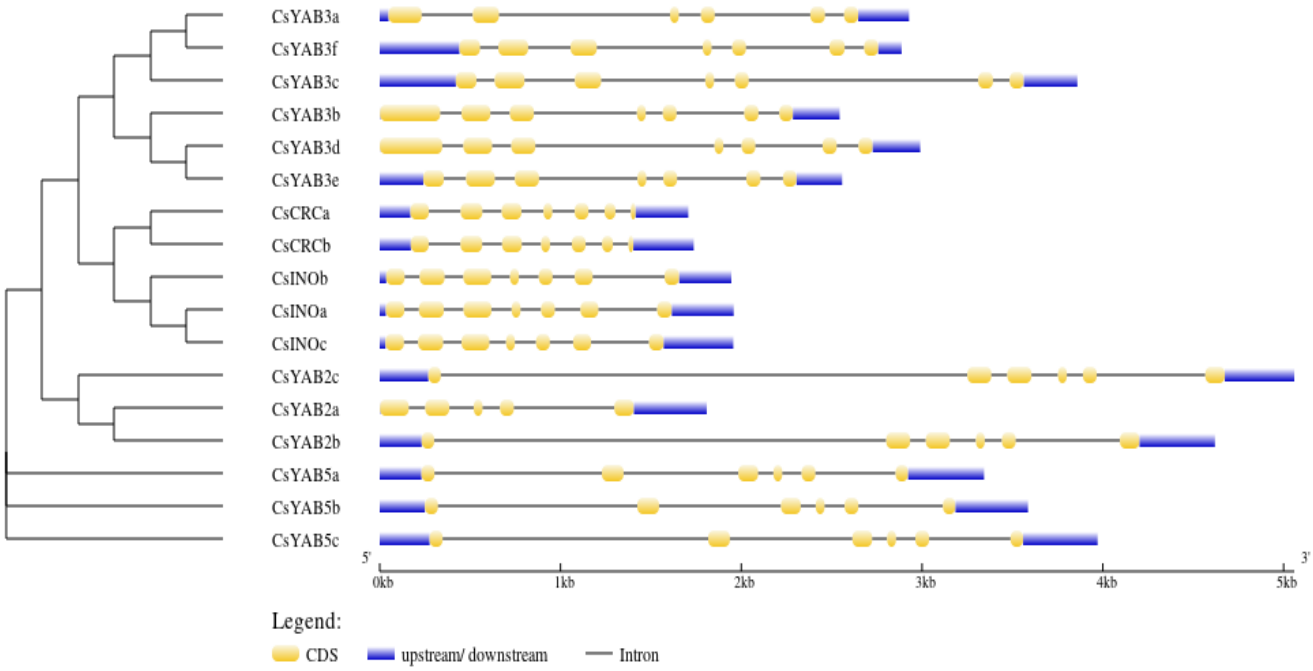


Figure 2Phylogenetic relationships and gene framework of YABBY genes. Yellow colour indicates exons, grey represents introns and blue indicates upstream/downstream

3.4 Conserved Motif Analysis

Ten conserved motifs were found in CsYABBY proteins, and each one had 3-7 motifs. Motifs 1 and 2 were found in almost all members and represent the conserved YABBY domain and zinc finger-like domain, respectively; both are mainly located towards the C-terminal region. The motif numbers were observed to vary between the groups, with the CsYAB3 group having relatively higher numbers of motifs. In addition, selected proteins contained HMG-box-like motifs showing small differences in structure among the family members, with the conserved domains being identical.

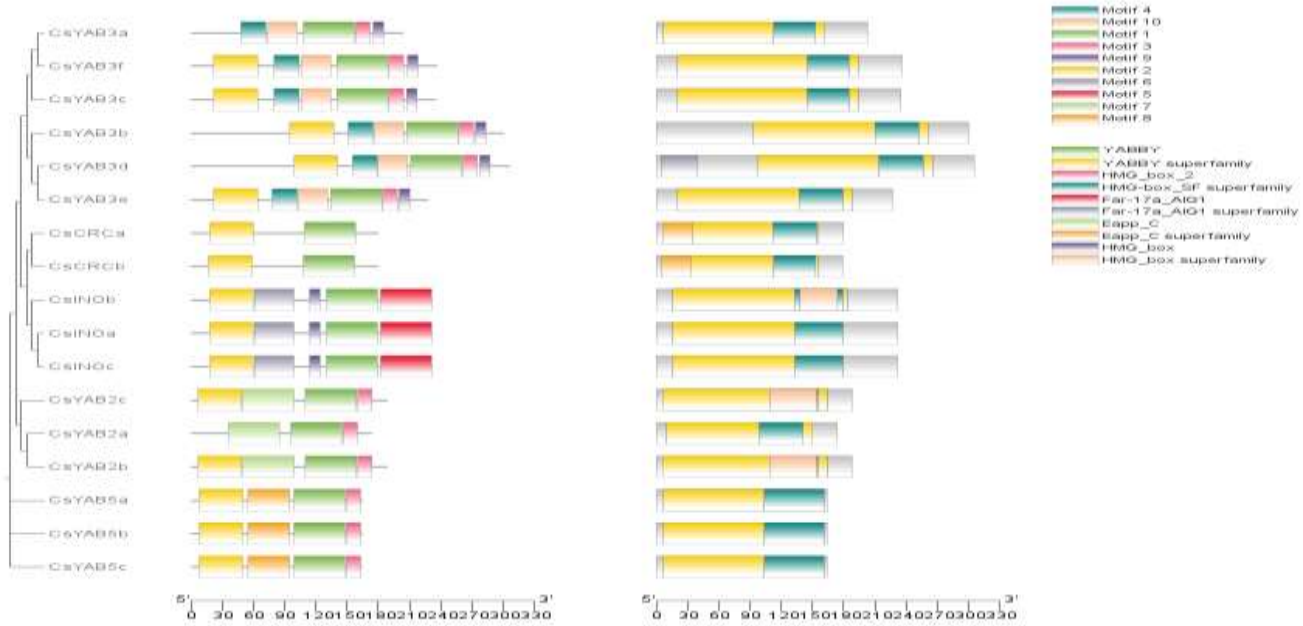


Figure 3. Distribution of conserved motifs, phylogenetic relationships and domains architecture among CsYABBY family members in Camelina sativa.

3.5 Cis-Regulatory Elements in CsYABBY Promoters

Promoter analysis of *CsYABBY* genes identified a wide range of cis-acting regulatory elements which play a role in light responsiveness, hormone signalling, stress sensitivity, and plant growth and development. Light-responsive motifs, including Box 4, G-box, GT1-motif, AT1-motif, ATC-motif, TCT-motif, AE-box, and ACE, were identified, indicating an important role of some CsYABBY genes in light-

mediated regulation. Some hormone-responsive elements include ABRE, CGTCA-motif, TGACG-motif, TGA-element, and GARE/P-box, indicating key involvement in abscisic acid, methyl jasmonate, auxin, and gibberellin signalling pathways. Stress-related motifs (MBS, LTR, and TC-rich repeats) were detected, indicating possible roles in abiotic stress tolerance. TATA-box and CAAT-box were heavily distributed among all *CsYABBY* genes.



Figure 4 Heat map showing the distribution of different Cs elements among the promoter regions of different CsYABBY proteins

3.6 Assessment of Ka/Ks ratio

All CsYAB gene pairs have Ka/Ks ratios below 1. Most pairs have very low ratios (close to 0–0.1). CsYAB2a–CsYAB2b and CsYAB3a–CsYAB3f show moderately higher ratios. CsYAB5a–CsYAB5b has the highest Ka/Ks ratio (0.91). Overall results show that the gene family is highly evolutionarily conserved.

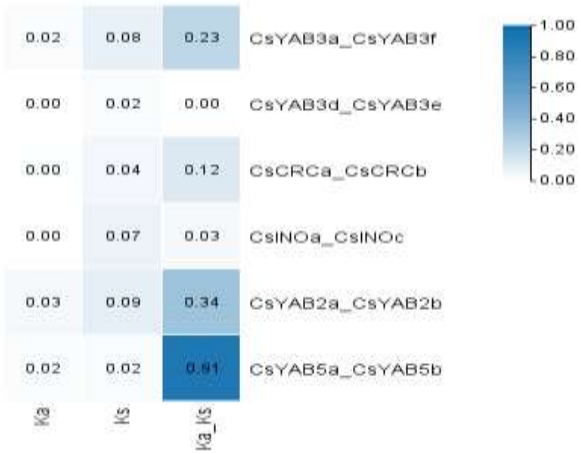


Figure 5 Ka and Ks values of CsYABBY proteins

4. Discussion

Plants are continuously exposed to environmental extremes throughout their life cycle, which can negatively affect development and productivity. Transcription factors (TFs) are key regulators of gene expression and regulatory networks. Isolating and functionally characterizing transcription factors provides essential insight into the molecular functions underlying plant growth and development in response to environmental changes. YABBY genes are associated with seed plants and play an essential part in plant life (Romanova et al., 2021; Zhang et al., 2020). They have been widely studied in A. thaliana, tomato, and rice (Bartholmes et al., 2012; Huang et al., 2013; Siegfried et al., 1999; Toriba et al., 2007). Camelina sativa is a major oilseed crop, known for its excellent nutritional profile and unique aroma. YABBY proteins are reported to play a critical role in establishing adaxial-abaxial polarity and developing side organs in a diverse range of species (Bowman, 2000; Siegfried et al., 1999; Tanaka et al., 2017; Yamaguchi et al., 2004; Yang, 2008). These findings offer very useful insights for future research and breeding programs to improve resistance and yield of C. sativa under changing climatic conditions (Aristya et al., 2024; Berhow et al., 2014). Therefore, studying YABBY function in C. sativa is highly significant, as it increases our understanding of plant adaptation to stress and development.

To this end, we conducted an in-depth survey of the C. sativa genome for YABBY proteins and identified 17 CsYABBY genes in the allohexaploid C. sativa. Physicochemical characterization of CsYABBY proteins indicated their distinct nature. Furthermore, we investigated the subcellular localization of CsYABBY genes using the online web server WoLF PSORT. According to it, chloroplasts and the nucleus are the major localization sites for YABBY genes. CsYABBY1, CsYABBY2, CsYABBY6,

CsYABBY9, CsYABBY11, and CsYABBY14 are predicted to localize to the chloroplast, suggesting a potential association with chloroplast-associated cellular processes, whereas CsYABBY5, CsYABBY8, and CsYABBY17 show strong nuclear localization scores, suggesting a role in gene regulation. Other proteins displayed lower prediction scores for mitochondria, endoplasmic reticulum/plasma membrane, cytoplasm, vacuole, extracellular space, and other cellular compartments (Horton et al., 2007).

C. sativa developed through the hybridization of three ancestral genomes, leading to the extensive persistence of duplicated loci(Kagale et al., 2014). A phylogenetic analysis of YABBY proteins from Arabidopsis thaliana, Theobroma cacao, and Camelina sativa provides insight into these crops' evolutionary history. In the YABBY family, we found five YABBY subfamilies in cotton (YABBYs FIL/YAB3, YAB2, CRC, INO, and YAB5), but we identified no new YABBY subfamily in C. sativa. This classification of YABBY genes has been reported in angiosperms (Siegfried, Eshed et al. 1999; Bowman 2000). These five clades contain 6 YABBY genes from Arabidopsis and Theobroma. The FIL/YAB3 clade expanded more; it consists of six CsYAB genes, 2AtYAB, and one TcYAB gene. Lateral outgrowth of organs and lamina expansion in Arabidopsis are associated with this clade (Bowman, 2000; Siegfried et al., 1999). Six YABBY genes of Arabidopsis and Theobroma are distributed among these five clades. The FIL/YAB3 clade expanded more; it includes six CsYAB genes, 2AtYAB genes, and one TcYAB gene. This clade is associated with lateral organ outgrowth and lamina expansion in *Arabidopsis* (Sarojam et al., 2010; Siegfried et al., 1999). The YAB5 clade, the second-largest group, contains three CsYAB, two TcYAB, and one AtYAB gene. YAB2 and INO both contained 5 genes: three from C. sativa, one from A. Thaliana, and one from T. C*acao*. CRC is the smallest, containing two *C. sativa*, one *A. Thaliana*, and one *T. cacao*. CRC and INO proteins are involved in carpel formation, ovule integument differentiation, and nectary development (Bowman and Smyth, 1999; Villanueva et al., 1999). Gene structure and conserved motif analysis provided valuable insight into the conservation and diversification of YABBY genes in C. *sativa*. CsYABBYs in the same clade of the phylogenetic tree had similar structures and motif compositions. However, members of different subfamilies differed substantially. Structural conservation within subfamilies reflected shared evolutionary relationships and functional similarity among duplicated genes (Yang et al., 2018).

Analysis of gene structure suggested variation in intron-exon structure among CsYABBY genes, revealing differences in their genomic architecture. (Jing et al., 2022). Members of the same clade showed a similar number of exons and introns. In contrast, clades differed in exon and intron numbers (e.g., Arabidopsis, rice, and soybean), suggesting conservation of characteristic sequences among them.(Gu et al., 2013; Sami et al., 2023). Members of the CRC, YAB2, and YAB5 subfamilies showed a comparatively compact intron-exon structure. Proteins in the CRC and FIL/YAB3 clades contained seven exons and six introns, although intron length and exon arrangement varied among individual genes; CsYAB3a had six exons and five introns. Similarly, CsYAB2 and CsYAB5 clade members had six exons and five introns, except YAB2a, which had five exons and four introns. One missing intron and one missing exon can result from intron loss during evolution, mutation, or transposable element activity. CsYAB2 and CsYAB5 showed high structural conservation. Gene structure, together with phylogenetic relationships, showed clear evolutionary relationships among various YABBY gene families (Bondarenko and Gelfand, 2016; Haider et al., 2023).

Motif analysis identified highly conserved motifs present consistently among all CsYABBYs, indicating their strong functional importance across the family. Other motifs were confined to specific CsYABBY proteins, highlighting potential functional divergence within the gene family (Han et al., 2021). Motif2 is predominantly located in the N-terminal C2C2 zinc finger, which is associated with maintaining the characteristic zinc-coordinating structure of YABBY proteins. Motif 1,3,4 was consistently detected toward the C-terminal region corresponding to the YABBY domain. The predicted domain analysis further identified that the C-terminal YABBY domain possesses structural similarity to the HMG-box (HIGH MOBILITY GROUP) and is involved in DNA-binding(Meister et al., 2004; Santi et al., 2003; Wanke et al., 2011) and transcriptional regulatory functions. The sequence-level investigations revealed similarities among the proteins, leading to functional and structural interactions. Evolutionarily conserved domains can be reconfigured and organized while maintaining consistent functionality.

The cis-regulatory elements identified in CsYABBY promoters reveal insights into the regulation of their spatiotemporal expression. (Zhang et al., 2022) Cis-regulatory elements (CREs) are important in gene function prediction and control several pathways in the promoter region (Cahoon and Li-Beisson, 2020; Reich, 2017). These elements play a significant role in transcriptional regulation, controlling various functions during the life cycle (Wang et al., 2024; Zheng et al., 2023). CREs linked to light sensitivity were detected in almost all promoter regions from CsYABBY1 to CsYABBY17. Light-responsive elements can regulate genes involved in photosynthetic activity, photomorphogenesis, chloroplast development, and light signaling. ABRE and ABRE3a elements are associated with abscisic acid-mediated signaling, particularly during drought

(Simpson et al., 2003), salinity, seed maturation, dormancy, and gene expression regulation (Lee and Luan, 2012; Lee SungChul and Luan Sheng, 2012). ABREs especially control transcription in response to abscisic acid (Osakabe et al., 2014). AREs are anaerobic-inducible elements that mediate gene activation during waterlogging, flooding, or other hypoxic conditions and may be linked to metabolic adaptation under low oxygen. Meristem-specific proteins are present in plant meristematic tissues and are associated with organ development and cell differentiation. ABA- and (MeJA)-responsive elements regulate defense responses and other environmental stresses (Liu et al., 2022; Zhao et al., 2020). MeJA-responsive elements are extensively involved in fruit formation (Li et al., 2022). ERE influences fruit ripening, root development, and stress. The GCN4_motif is highly important for seed development and nutrient allocation. LTR and MBS *cis*-regulatory elements function cooperatively as upstream environmental sensors that co-regulate the plant's transcriptional defense network against harsh abiotic stresses (Rahman et al., 2024). MYB is one of the stress-responsive elements and plays a pivotal role in abiotic stress adaptation (Wai et al., 2022). MYB transcription factors play a pivotal part in abiotic stress adaptation (Wai et al., 2022). The MYB-like sequence is linked to gene expression at certain plant developmental stages and is related to cell-cycle progression, cell proliferation, and gibberellin levels. A few cis-regulatory elements were found to participate in endosperm expression. They control the expression of genes necessary for endosperm development and seed storage protein production and act as binding sites for transcription factors specifically active in the endosperm. This indicates that there is some involvement of YABBY gene in seed endosperm development. These components have been identified in camelina (CsYAB2a, CsYAB2b, and CsYAB2c). Further, other elements are circadian-, secondary metabolism-, and flavonoid-associated, suggesting the possibility of integration of temporal and specialized metabolic pathways. By analyzing the regulatory elements associated with the genes in silico, it is possible to anticipate the roles of the genes (Gudi et al., 2023).

Purifying selection and Ka/Ks analyses suggest that YABBY genes have evolved without losing some of their functions. Ka is the rate of nonsynonymous nucleotide substitutions per site, and Ks is the rate of synonymous nucleotide substitutions per site. The ratio of nonsynonymous to synonymous substitution rates (Ka/Ks) estimates selective pressure on a gene. Purifying selection of a gene pair means natural selection purges harmful mutations. Positive selection may help to maintain and diversify duplicated gene pairs. A Ka/Ks value less than one indicates purifying selection; a Ka/Ks value of one indicates neutral selection, and a Ka/Ks value greater than one signifies positive selection. Environmental and biological clock selection pressures contribute to genomic rearrangements and the emergence of novel traits (Morgan et al., 2010). Then, ratios of Ka to Ks in camelina YABBY genes were determined. All examined gene pairs showed ratios below 1, ranging from 0.00 to 0.91. The lowest ratios were observed for CsYAB3d_CsYAB3e (0.00) and CsCRCa_CsCRCb (0.12), indicating strong evolutionary conservation. CsYAB5a_CsYAB5b showed the highest K_a/K_s ratio (0.91), indicating comparatively relaxed selective constraint. CsYAB3a_CsYAB3f has a Ka/Ks ratio of 0.23, CsINOa_CsINOc has 0.03, and CsYAB2a_CsYAB2b has 0.34, these gene pairs support the predominance of negative selection and functional conservation.

Conclusion

This study provides a comprehensive overview of the YABBY gene family in C. sativa, including gene structures, phylogenetic relationships, purifying selection, evolutionary relationships, expression patterns, and other features. This study thoroughly characterised CsYABBY genes in the *Camelina* genome. The 11 CsYABBY proteins were divided into five groups, and then the structural and functional features of each CsYABBY protein were presented. Most of the genes were closely related to leaf and organ polarity. A full analysis of camelina YABBY proteins is a crucial first step to test the structural, functional, and evolutionary properties of YABBY genes in Camelina and, by comparison, in other crops. Functional interactions among YABBY proteins highlight their importance in transcriptional regulation. Similar numbers of YABBY genes, such as 33 in tomatoes, 34 in peppers, and 35 in potatoes, and comparatively larger numbers in other plants, such as 78 in soybeans and 51 in carrots, indicated significant genomic, structural, and functional diversification in YABBY genes.

References

Akram, J., Siddique, R., Shafiq, M., Tabassum, B., Manzoor, M. T., Javed, M. A., Anwar, S., Nisa, B. U., Saleem, M. H., and Javed, B. (2023). Genome-wide identification of CCO gene family in cucumber (Cucumis sativus) and its comparative analysis with A. thaliana. BMC Plant Biology **23**, 640. https://doi.org/10.1186/s12870-023-04648-5

Amjad, M., Wang, Y., Han, S., Haider, M. Z., Sami, A., Batool, A., Shafiq, M., Ali, Q., Dong, J., and Sabir, I. A. (2024). Genome-wide identification of phenylalanine ammonia-lyase (PAL) gene family in Cucumis sativus (cucumber) against abiotic stress. BMC Genomic Data **25**, 76. https://doi.org/10.1186/s12863-024-01258-w

Aristya, G. R., Nabillah, S. A. A., Kasiamdari, R. S., Damaiyani, J., and Prabowo, H. (2024). Phylogenetic and genetic variation of sugarcane (Saccharum spp.) from Island of Java, Indonesia based on trnK chloroplast gene. International

Journal of Agriculture and Biosciences **13**, 157-166. https://doi.org/10.46820/ijab.2024.13.157

Bailey, T. L., Boden, M., Buske, F. A., Frith, M., Grant, C. E., Clementi, L., Ren, J., Li, W. W., and Noble, W. S. (2009). MEME SUITE: tools for motif discovery and searching. Nucleic Acids Research **37**, W202-W208. https://doi.org/10.1093/nar/gkp335

Bansal, S., and Durrett, T. P. (2016). Camelina sativa: An ideal platform for the metabolic engineering and field production of industrial lipids. Biochimie **120**, 9-16. https://doi.org/10.1016/j.biochi.2015.06.009

Bartholmes, C., Hidalgo, O., and Gleissberg, S. (2012). Evolution of the YABBY gene family with emphasis on the basal eudicot Eschscholzia californica (Papaveraceae). Plant Biology **14**, 11-23. https://doi.org/10.1111/j.1438-8677.2011.00486.x

Berhow, M. A., Vaughn, S. F., Moser, B. R., Belenli, D., and Polat, U. (2014). Evaluating the phytochemical potential of Camelina: An emerging new crop of old world origin. In "Phytochemicals–Biosynthesis, Function and Application: Volume 44", pp. 129-148. Springer. https://doi.org/10.1007/978-3-319-04045-5_7

Berti, M., Gesch, R., Eynck, C., Anderson, J., and Cermak, S. (2016). Camelina uses, genetics, genomics, production, and management. Industrial Crops and Products **94**, 690-710. https://doi.org/10.1016/j.indcrop.2016.09.034

Bondarenko, V. S., and Gelfand, M. S. (2016). Evolution of the exon-intron structure in ciliate genomes. PLoS One **11**, e0161476. https://doi.org/10.1371/journal.pone.0161476

Bowman, J. L. (2000). The YABBY gene family and abaxial cell fate. Current Opinion in Plant Biology **3**, 17-22. https://doi.org/10.1016/S1369-5266(99)00035-7

Bowman, J. L., and Eshed, Y. (2000). Formation and maintenance of the shoot apical meristem. Trends in Plant Science **5**, 110-115. https://doi.org/10.1016/S1360-1385(00)01569-7

Bowman, J. L., and Smyth, D. R. (1999). CRABS CLAW, a gene that regulates carpel and nectary development in Arabidopsis, encodes a novel protein with zinc finger and helix-loop-helix domains. Development **126**, 2387-2396. https://doi.org/10.1242/dev.126.11.2387

Buttar, Z. A., Yang, Y., Sharif, R., Nan Wu, S., Xie, Y., and Wang, C. (2020). Genome wide identification, characterization, and expression analysis of YABBY-gene family in wheat (Triticum aestivum L.). Agronomy **10**, 1189. https://doi.org/10.3390/agronomy10081189

Cahoon, E. B., and Li-Beisson, Y. (2020). Plant unusual fatty acids: learning from the less common. Current Opinion in Plant Biology **55**, 66-73. https://doi.org/10.1016/j.pbi.2020.03.006

Chen, C., Chen, H., Zhang, Y., Thomas, H. R., Frank, M. H., He, Y., and Xia, R. (2020). TBtools: an integrative toolkit developed for interactive analyses of big biological data. Molecular Plant **13**, 1194-1202. https://doi.org/10.1016/j.molp.2020.06.009

Eshed, Y., Izhaki, A., Baum, S. F., Floyd, S. K., and Bowman, J. L. (2004). Asymmetric leaf development and blade expansion in Arabidopsis are mediated by KANADI and YABBY activities. Development **131**, 2997-3006. https://doi.org/10.1242/dev.01186

Eynck, C., and Falk, K. (2013). Camelina (Camelina sativa). In "Biofuel crops: production, physiology and genetics", pp. 369-391. CABI Wallingford UK. https://doi.org/10.1079/9781845938857.0369

Finet, C., Floyd, S. K., Conway, S. J., Zhong, B., Scutt, C. P., and Bowman, J. L. (2016). Evolution of the YABBY gene family in seed plants. Evolution & Development **18**, 116-126. https://doi.org/10.1111/ede.12173

Francis, A., and Warwick, S. (2009). The biology of Canadian weeds. 142. Camelina alyssum (Mill.) Thell.; C. microcarpa Andrz. ex DC.; C. sativa (L.) Crantz. Canadian Journal of Plant Science **89**, 791-810. https://doi.org/10.4141/CJPS08185

Ghamkhar, K., Croser, J., Aryamanesh, N., Campbell, M., Kon'kova, N., and Francis, C. (2010). Camelina (Camelina sativa (L.) Crantz) as an alternative oilseed: molecular and ecogeographic analyses. Genome **53**, 558-567. https://doi.org/10.1139/G10-034

Golz, J. F., Roccaro, M., Kuzoff, R., and Hudson, A. (2004). GRAMINIFOLIA promotes growth and polarity of Antirrhinum leaves. Development **131**, 3661-3670. https://doi.org/10.1242/dev.01246

Gu, X., Zou, Y., Su, Z., Huang, W., Zhou, Z., Arendsee, Z., and Zeng, Y. (2013). An update of DIVERGE software for functional divergence analysis of protein family. Molecular Biology and Evolution **30**, 1713-1719. https://doi.org/10.1093/molbev/mst069

Gudi, S., Saini, D. K., Halladakeri, P., Singh, G., Singh, S., Kaur, S., Goyal, P., Srivastava, P., Mavi, G., and Sharma, A. (2023). Genome-wide association study unravels genomic regions associated with chlorophyll fluorescence parameters in wheat (Triticum aestivum L.) under different sowing conditions. Plant Cell Reports **42**, 1453-1472. https://doi.org/10.1007/s00299-023-03040-0

Ha, C. M., Jun, J. H., and Fletcher, J. C. (2010). Control of Arabidopsis leaf morphogenesis through regulation of the YABBY and KNOX

families of transcription factors. Genetics **186**, 197-206. https://doi.org/10.1534/genetics.110.118935

Haider, M., Sami, A., Mazhar, H., Akram, J., NISA, B., Umar, M., and Meeran, M. (2023). Exploring morphological traits variation in Gomphrena globosa: A multivariate analysis. Biological and Agricultural Sciences Research Journal **2023**, 21-21. https://doi.org/10.59564/basrj/2023/21

Han, H., Xu, F., Li, Y., Yu, L., Fu, M., Liao, Y., Yang, X., Zhang, W., and Ye, J. (2021). Genome-wide characterization of bZIP gene family identifies potential members involved in flavonoids biosynthesis in Ginkgo biloba L. Scientific Reports **11**, 23420. https://doi.org/10.1038/s41598-021-02860-6

Hergert, G., Margheim, J., Pavlista, A., Martin, D., Supalla, R., and Isbell, T. (2016). Yield, irrigation response, and water productivity of deficit to fully irrigated spring canola. Agricultural Water Management **168**, 96-103. https://doi.org/10.1016/j.agwat.2016.02.003

Horton, P., Park, K.-J., Obayashi, T., Fujita, N., Harada, H., Adams-Collier, C., and Nakai, K. (2007). WoLF PSORT: protein localization predictor. Nucleic Acids Research **35**, W585-W587. https://doi.org/10.1093/nar/gkm259

Hu, B., Jin, J., Guo, A.-Y., Zhang, H., Luo, J., and Gao, G. (2015). GSDS 2.0: an upgraded gene feature visualization server. Bioinformatics **31**, 1296-1297. https://doi.org/10.1093/bioinformatics/btv005

Huang, Z., Van Houten, J., Gonzalez, G., Xiao, H., and van der Knaap, E. (2013). Genome-wide identification, phylogeny and expression analysis of SUN, OFP and YABBY gene family in tomato. Molecular Genetics and Genomics **288**, 111-129. https://doi.org/10.1007/s00438-013-0733-0

Jing, Y., Yu, Y., Wang, H., Wu, Y., and Li, C. (2022). Genome-wide identification and expression analysis of the bZIP gene family in silver birch (Betula pendula Roth.). Journal of Forestry Research **33**, 1615-1636. https://doi.org/10.1007/s11676-021-01438-2

Kagale, S., Koh, C., Nixon, J., Bollina, V., Clarke, W. E., Tuteja, R., Spillane, C., Robinson, S. J., Links, M. G., and Clarke, C. (2014). The emerging biofuel crop Camelina sativa retains a highly undifferentiated hexaploid genome structure. Nature Communications **5**, 3706. https://doi.org/10.1038/ncomms4706

Kanaya, E., Nakajima, N., and Okada, K. (2002). Non-sequence-specific DNA binding by the FILAMENTOUS FLOWER protein from Arabidopsis thaliana is reduced by EDTA. Journal of Biological Chemistry **277**, 11957-11964. https://doi.org/10.1074/jbc.M111425200

Kiczorowska, B., Samolińska, W., Andrejko, D., Kiczorowski, P., Antoszkiewicz, Z., Zając, M., Winiarska-Mieczan, A., and Bąkowski, M. (2019). Comparative analysis of selected bioactive components (fatty acids, tocopherols, xanthophyll, lycopene, phenols) and basic nutrients in raw and thermally processed camelina, sunflower, and flax seeds (Camelina sativa L. Crantz, Helianthus L., and Linum L.). Journal of Food Science and Technology **56**, 4296-4310. https://doi.org/10.1007/s13197-019-03899-7

Larsson, M. (2013). Cultivation and processing of Linum usitatissimum and Camelina sativa in southern Scandinavia during the Roman Iron Age. Vegetation History and Archaeobotany **22**, 509-520. https://doi.org/10.1007/s00334-013-0395-5

Lee, J.-Y., Baum, S. F., Oh, S.-H., Jiang, C.-Z., Chen, J.-C., and Bowman, J. L. (2005). Recruitment of CRABS CLAW to promote nectary development within the eudicot clade. Development **132**, 5021-5032. https://doi.org/10.1242/dev.02067

Lee, S. C., and Luan, S. (2012). ABA signal transduction at the crossroad of biotic and abiotic stress responses. Plant, Cell & Environment **35**, 53-60. https://doi.org/10.1111/j.1365-3040.2011.02426.x

Li, C., Dong, N., Shen, L., Lu, M., Zhai, J., Zhao, Y., Chen, L., Wan, Z., Liu, Z., and Ren, H. (2022). Genome-wide identification and expression profile of YABBY genes in Averrhoa carambola. PeerJ **10**, e12558. https://doi.org/10.7717/peerj.12558

Liu, H., Ye, H., Wang, J., Chen, S., Li, M., Wang, G., Hou, N., and Zhao, P. (2022). Genome-wide identification and characterization of YABBY gene family in Juglans regia and Juglans mandshurica. Agronomy **12**, 1914. https://doi.org/10.3390/agronomy12081914

Manca, A., Pecchia, P., Mapelli, S., Masella, P., and Galasso, I. (2013). Evaluation of genetic diversity in a Camelina sativa (L.) Crantz collection using microsatellite markers and biochemical traits. Genetic Resources and Crop Evolution **60**, 1223-1236. https://doi.org/10.1007/s10722-012-9913-9

Matteo, R., D'Avino, L., Ramirez-Cando, L. J., Pagnotta, E., Angelini, L. G., Spugnoli, P., Tavarini, S., Ugolini, L., Foschi, L., and Lazzeri, L. (2020). Camelina (Camelina sativa L. Crantz) under low-input management systems in northern Italy: Yields, chemical characterization and environmental sustainability. Italian Journal of Agronomy **15**, 1519. https://doi.org/10.4081/ija.2020.1519

Meister, R. J., Williams, L. A., Monfared, M. M., Gallagher, T. L., Kraft, E. A., Nelson, C. G., and Gasser, C. S. (2004). Definition and interactions of a positive regulatory element of the

Arabidopsis INNER NO OUTER promoter. The Plant Journal **37**, 426-438. https://doi.org/10.1046/j.1365-313X.2003.01970.x

Mistry, J., Chuguransky, S., Williams, L., Qureshi, M., Salazar, G. A., Sonnhammer, E. L., Tosatto, S. C., Paladin, L., Raj, S., and Richardson, L. J. (2021). Pfam: The protein families database in 2021. Nucleic Acids Research **49**, D412-D419. https://doi.org/10.1093/nar/gkaa913

Morgan, C. C., Loughran, N. B., Walsh, T. A., Harrison, A. J., and O'Connell, M. J. (2010). Positive selection neighboring functionally essential sites and disease-implicated regions of mammalian reproductive proteins. BMC Evolutionary Biology **10**, 39. https://doi.org/10.1186/1471-2148-10-39

Moser, B. R. (2012). Biodiesel from alternative oilseed feedstocks: camelina and field pennycress. Biofuels **3**, 193-209. https://doi.org/10.4155/bfs.12.8

Orczewska-Dudek, S., Pietras, M., Puchała, M., and Nowak, J. (2020). Camelina sativa oil and camelina cake as sources of polyunsaturated fatty acids in the diets of laying hens: Effect on hen performance, fatty acid profile of yolk lipids, and egg sensory quality. Annals of Animal Science **20**, 1365-1377. https://doi.org/10.2478/aoas-2020-0043

Osakabe, Y., Yamaguchi-Shinozaki, K., Shinozaki, K., and Tran, L. S. P. (2014). ABA control of plant macroelement membrane transport systems in response to water deficit and high salinity. New Phytologist **202**, 35-49. https://doi.org/10.1111/nph.12613

Rahman, S., Ikram, A. R., AlHusnain, L., Fiaz, S., Rafique, M. U., Ali, M. A., AlKahtani, M. D., Attia, K. A., and Azeem, F. (2024). Genome-wide profiling of bZIP transcription factors in Camelina sativa: implications for development and stress response. BMC Genomic Data **25**, 88. https://doi.org/10.1186/s12863-024-01272-y

Rehman, O. U., Uzair, M., Chao, H., Fiaz, S., Khan, M. R., and Chen, M. (2022). Role of the type-B authentic response regulator gene family in fragrant rice under alkaline salt stress. Physiologia Plantarum **174**, e13696. https://doi.org/10.1111/ppl.13696

Reich, D. (2017). Ancestry-inspired genomic health. Nature Genetics **49**, 1287. https://doi.org/10.1038/ng.3941

Romanova, M. A., Maksimova, A. I., Pawlowski, K., and Voitsekhovskaja, O. V. (2021). YABBY genes in the development and evolution of land plants. International Journal of Molecular Sciences **22**, 4139. https://doi.org/10.3390/ijms22084139

Sainger, M., Jaiwal, A., Sainger, P. A., Chaudhary, D., Jaiwal, R., and Jaiwal, P. K. (2017). Advances in genetic improvement of Camelina sativa for biofuel and industrial bio-products. Renewable and Sustainable Energy Reviews **68**, 623-637. https://doi.org/10.1016/j.rser.2016.10.024

Sami, A., Haider, M., Imran, M., Abbas, A., and Javed, M. (2023). Synergizing food safety, quality and genetic improvement: the intersection of food microbiology and processing. Bulletin of Biological and Allied Sciences Research **2023**, 44-44. https://doi.org/10.54393/bbasr.v2i1.44

Sami, A., Haider, M. Z., Shafiq, M., Sadiq, S., and Ahmad, F. (2024). Genome-wide identification and in-silico expression analysis of CCO gene family in sunflower (Helianthus annuus) against abiotic stress. Plant Molecular Biology **114**, 34. https://doi.org/10.1007/s11103-024-01438-x

Santi, L., Wang, Y., Stile, M. R., Berendzen, K., Wanke, D., Roig, C., Pozzi, C., Müller, K., Müller, J., and Rohde, W. (2003). The GA octodinucleotide repeat binding factor BBR participates in the transcriptional regulation of the homeobox gene Bkn3. The Plant Journal **34**, 813-826. https://doi.org/10.1046/j.1365-313X.2003.01768.x

Sarojam, R., Sappl, P. G., Goldshmidt, A., Efroni, I., Floyd, S. K., Eshed, Y., and Bowman, J. L. (2010). Differentiating Arabidopsis shoots from leaves by combined YABBY activities. The Plant Cell **22**, 2113-2130. https://doi.org/10.1105/tpc.110.075853

Sawa, S., Ito, T., Shimura, Y., and Okada, K. (1999a). FILAMENTOUS FLOWER controls the formation and development of Arabidopsis inflorescences and floral meristems. The Plant Cell **11**, 69-86. https://doi.org/10.1105/tpc.11.1.69

Sawa, S., Watanabe, K., Goto, K., Kanaya, E., Morita, E. H., and Okada, K. (1999b). FILAMENTOUS FLOWER, a meristem and organ identity gene of Arabidopsis, encodes a protein with a zinc finger and HMG-related domains. Genes & Development **13**, 1079-1088. https://doi.org/10.1101/gad.13.9.1079

Séguin-Swartz, G., Eynck, C., Gugel, R., Strelkov, S., Olivier, C., Li, J., Klein-Gebbinck, H., Borhan, H., Caldwell, C., and Falk, K. (2009). Diseases of Camelina sativa (false flax). Canadian Journal of Plant Pathology **31**, 375-386. https://doi.org/10.1080/07060660909507612

Sieber, P., Petrascheck, M., Barberis, A., and Schneitz, K. (2004). Organ polarity in Arabidopsis. NOZZLE physically interacts with members of the YABBY family. Plant Physiology **135**, 2172-2185. https://doi.org/10.1104/pp.104.040154

Siegfried, K. R., Eshed, Y., Baum, S. F., Otsuga, D., Drews, G. N., and Bowman, J. L. (1999). Members of the YABBY gene family specify abaxial cell fate in Arabidopsis. Development

126, 4117-4128. https://doi.org/10.1242/dev.126.18.4117

Simpson, S. D., Nakashima, K., Narusaka, Y., Seki, M., Shinozaki, K., and Yamaguchi-Shinozaki, K. (2003). Two different novel cis-acting elements of erd1, a clpA homologous Arabidopsis gene function in induction by dehydration stress and dark-induced senescence. The Plant Journal **33**, 259-270. https://doi.org/10.1046/j.1365-313X.2003.01624.x

Tanaka, W., Toriba, T., and Hirano, H. Y. (2017). Three TOB 1-related YABBY genes are required to maintain proper function of the spikelet and branch meristems in rice. New Phytologist **215**, 825-839. https://doi.org/10.1111/nph.14619

Toriba, T., Harada, K., Takamura, A., Nakamura, H., Ichikawa, H., Suzaki, T., and Hirano, H.-Y. (2007). Molecular characterization the YABBY gene family in Oryza sativa and expression analysis of OsYABBY1. Molecular Genetics and Genomics **277**, 457-468. https://doi.org/10.1007/s00438-006-0202-0

Villanueva, J. M., Broadhvest, J., Hauser, B. A., Meister, R. J., Schneitz, K., and Gasser, C. S. (1999). INNER NO OUTER regulates abaxial–adaxial patterning in Arabidopsis ovules. Genes & Development **13**, 3160-3169. https://doi.org/10.1101/gad.13.23.3160

Vollmann, J., Moritz, T., Kargl, C., Baumgartner, S., and Wagentristl, H. (2007). Agronomic evaluation of camelina genotypes selected for seed quality characteristics. Industrial Crops and Products **26**, 270-277. https://doi.org/10.1016/j.indcrop.2007.03.017

Wai, A. H., Rahman, M. M., Waseem, M., Cho, L.-H., Naing, A. H., Jeon, J.-S., Lee, D.-J., Kim, C.-K., and Chung, M.-Y. (2022). Comprehensive genome-wide analysis and expression pattern profiling of PLATZ gene family members in Solanum lycopersicum L. under multiple abiotic stresses. Plants **11**, 3112. https://doi.org/10.3390/plants11223112

Wang, W., Ma, J., Liu, H., Wang, Z., Nan, R., Zhong, T., Sun, M., Wang, S., Yao, Y., and Sun, F. (2024). Genome-wide analysis of the switchgrass YABBY family and functional characterization of PvYABBY14 in response to ABA and GA stress in Arabidopsis. BMC Plant Biology **24**, 114. https://doi.org/10.1186/s12870-024-04791-7

Wanke, D., Hohenstatt, M. L., Dynowski, M., Bloss, U., Hecker, A., Elgass, K., Hummel, S., Hahn, A., Caesar, K., and Schleifenbaum, F. (2011). Alanine zipper-like coiled-coil domains are necessary for homotypic dimerization of plant GAGA-factors in the nucleus and nucleolus. PLoS One **6**, e16070. https://doi.org/10.1371/journal.pone.0016070

Wen, C.-l., Cheng, Q., Zhao, L., Mao, A., Yang, J., Yu, S., Weng, Y., and Xu, Y. (2016). Identification and characterisation of Dof transcription factors in the cucumber genome. Scientific Reports **6**, 23072. https://doi.org/10.1038/srep23072

Yamada, T., Yokota, S. y., Hirayama, Y., Imaichi, R., Kato, M., and Gasser, C. S. (2011). Ancestral expression patterns and evolutionary diversification of YABBY genes in angiosperms. The Plant Journal **67**, 26-36. https://doi.org/10.1111/j.1365-313X.2011.04570.x

Yamaguchi, T., Nagasawa, N., Kawasaki, S., Matsuoka, M., Nagato, Y., and Hirano, H.-Y. (2004). The YABBY gene DROOPING LEAF regulates carpel specification and midrib development in Oryza sativa. The Plant Cell **16**, 500-509. https://doi.org/10.1105/tpc.018044

Yang, Z. (2008). Cell polarity signaling in Arabidopsis. Annual Review of Cell and Developmental Biology **24**, 551-575. https://doi.org/10.1146/annurev.cellbio.23.090506.123233

Yang, Z., Gong, Q., Wang, L., Jin, Y., Xi, J., Li, Z., Qin, W., Yang, Z., Lu, L., and Chen, Q. (2018). Genome-wide study of YABBY genes in upland cotton and their expression patterns under different stresses. Frontiers in Genetics **9**, 33. https://doi.org/10.3389/fgene.2018.00033

Zhang, T., Li, C., Li, D., Liu, Y., and Yang, X. (2020). Roles of YABBY transcription factors in the modulation of morphogenesis, development, and phytohormone and stress responses in plants. Journal of Plant Research **133**, 751-763. https://doi.org/10.1007/s10265-020-01211-1

Zhang, Z., Luo, S., Liu, Z., Wan, Z., Gao, X., Qiao, Y., Yu, J., and Zhang, G. (2022). Genome-wide identification and expression analysis of the cucumber PYL gene family. PeerJ **10**, e12786. https://doi.org/10.7717/peerj.12786

Zhao, Y., Liu, C., Ge, D., Yan, M., Ren, Y., Huang, X., and Yuan, Z. (2020). Genome-wide identification and expression of YABBY genes family during flower development in *Punica granatum* L. Gene **752**, 144784. https://doi.org/10.1016/j.gene.2020.144784

Zheng, Q., Zhao, X., Huang, Y., Zhang, M.-M., He, X., Ke, S., Li, Y., Zhang, C., Ahmad, S., and Lan, S. (2023). Genome-wide identification of the YABBY gene family in Dendrobium orchids and its expression patterns in Dendrobium chrysotoxum. International Journal of Molecular Sciences **24**, 10165. https://doi.org/10.3390/ijms241210165

Zubr, J. (1997). Oil-seed crop: *Camelina sativa*. Industrial Crops and Products **6**, 113-119. https://doi.org/10.1016/S0926-6690(96)00203-8

Statements and Declarations

Author Contributions

KT, EY, MN and MS contributed to the conception, development, and preparation of this research article. ST, MW, SHUHS and TK edited final version of article. All authors have read and approved the final version of the manuscript.

Funding

This review was conducted without external funding. The authors would like to clarify that no financial support or grants from any organization, institution, or individual were received for the completion of this review. The research was carried out as part of the authors' academic and professional responsibilities, and they did not rely on any external sources of funding for the design, execution, or publication of this work.

Acknowledgments

We would like to acknowledge that no individuals or organizations were involved in the development, funding, or support of this work. This research was solely conducted by the authors, and no external contributions, financial or otherwise, were received or utilized in the execution of this study.

Data Availability statement

All relevant data are within the manuscript file.

Acknowledgments

Not applicable

Ethical Statement

Not applicable

Conflict of interest

The investigation was undertaken without any financial conflicts of interest or any other commercial relationships that could be seen as such by any of the authors.

Declaration of Generative AI and AI-assisted Technologies in the Writing Process

During the preparation of this work, the author(s) have not used any ChatGPT (OpenAI) tool.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, Creative Commons Attribution-NonCommercial 4.0 International License, © The Author(s) 2026