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GENOME-WIDE ANALYSIS OF THE *YABBY* TRANSCRIPTION FACTOR FAMILY IN OLIVE (*OLEA EUROPAEA* L.): STRUCTURAL DIVERSITY, MULTI-LAYERED REGULATION, AND FUNCTIONAL IMPLICATIONS IN ABIOTIC STRESS AND FRUIT DEVELOPMENT

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Abstract *In higher plants, YABBY transcription factors are critical for the development of lateral organs, polarity determination, and the response to environmental stress. Although the olive tree, Olea europaea L., is a valuable crop species in terms of ecology and economics, the YABBY gene family has received little attention. The current work discovered five unique OeuYAB genes from the five known subfamilies of the YABBY gene family: FIL/YAB3, YAB2, YAB5, CRC, and INO. Chromosomal mapping revealed that the distribution of these genes is not consistent throughout five genomic areas, denoted as SC_2771, SC_528, C_9, C_3, and C_1. Oeu055459.1 is placed at the distal end of C_1, while Oeu033104.1 and Oeu048822.1 are found in the higher sections of SC_2771 and SC_528, respectively. The clustering of Oeu055459.1, Oeu055459.2, and Oeu055459.3 in genomic regions C_9 and C_3 indicates the presence of genomic hotspots that could have resulted from the original gene's duplication. The physicochemical characterization of the genes revealed that OeuYAB proteins are compact (170-211 amino acids), hydrophilic, and unstable. The structural and motif analysis revealed that the genes contain the N-terminal C2C2 Zinc Finger and C-terminal YABBY domains. The Ka/Ks ratio is less than one, indicating strong purifying selection pressure on these genes. Furthermore, the presence of a complex regulatory system in the genes' promoters revealed that they are high in light responsiveness, phytohormones, and abiotic stress adaptation. To investigate post-transcriptional regulation, a miRNA target analysis revealed a specialized mode of regulation in which the OeuYAB1 and OeuYAB4 genes are regulated by two distinct miRNA clusters, Oeu-miRN1154 and Oeu-miRN2138, for translational inhibition and transcript cleavage, respectively. The OeuYAB genes were profiled using RNA-seq expression profiling in six anatomical tissues, revealing a high level of functional divergence; for example, OeuYAB3 of the CRC subfamily was found to have the highest expression level (1081.066 RPKM) in the fruit tissue, establishing its role as a key candidate for olive drupe development.*

Keywords*:* *YABBY transcription factors; Olea europaea; OeuYAB genes; phytohormones; abiotic stress*

1. Introduction

Olive (*Olea europaea* L.) is an economically valuable, perennially cultivated tree crop that is predominantly symbolic of peace, health, and longevity in the Mediterranean, where it has been highly valued for its dense compactness of unsaturated fatty acids and antioxidant phenolics in the form of oil and fruit (Elhrech et al., 2024). Olive production has come to characterize non-traditional areas in the last two years: Pakistan, for instance, has initiated large-scale olive cultivation (more than 5.6 million trees until 2024) with the support of foreign funds, with a vision to promote rural economies and sustainability. These trends highlight olive's socio-economic position and the necessity to alter its cultivation on new terms. Climate change presents new threats to olive cultivation. Olive trees were used to warm and humid winters and hot and dry summers, but increased global warming and changed precipitation patterns were bringing these to an end. It is projected that, by the late 21st century, Mediterranean winters would warm by 1.7–2.5 °C under moderate warming (RCP4.5) and 3.5–5 °C under high emissions (RCP8.5)(Fraga et al., 2020). Milder winters diminish the accumulation of chilling hours required by olive flowers to break dormancy, and shortages of chilling have been shown directly by research to correlate with decreases in flowering and fruiting (Malik et al., 2005). Likewise, hotter, drier summers enhance water and heat stress for olive, threatening physiological damage to the crop and disruption of flowering. Usually, climatic stresses would inhibit olive's regular flowering and production unless measures are taken (Zucchini, 2024). This gives a fillip to research into olive's flowering and stress tolerance genealogy. Molecularly, the YABBY class of transcription factors was identified as an essential controller of plant organ development and environmental adaptation (Benny, 2021). Dicot-specific transcription factors YABBY proteins possess both an N-terminal C2C2 zinc-finger structure and a C-terminal "YABBY" domain. Five dicotic YABBY gene subfamilies (CRABS CLAW/CRC, FILAMENTOUS FLOWER/FIL-YABBY3, INNER NO OUTER/INO, YABBY2, YABBY5) exist, while most monocots do not have the YABBY5 group (Yang et al., 2018). The YABBY factors are responsible for abaxially specifying cell identity of lateral organs and leaf and floral organ polarity. In reality, all the reports demonstrate that YABBY genes play a role in carpel and leaf margin development, style length, and other related characters (Han et al., 2025). Aside from growth, YABBY proteins also influence metabolism and stress. For instance, secondary metabolites are modulated by them: MsYABBY5 in peppermint inhibits monoterpene synthesis, while Artemisia AaYABBY5 increases artemisinin and flavonoid biosynthesis(Wang et al., 2016). Even plant hormones are regulated by YABBY genes, i.e., rice YABBY1 was involved in gibberellin biosynthesis feedback control, connecting YABBYS to the growth signal (Dai et al., 2007). Therefore, YABBY transcription factors play a role in several organogenesis processes, metabolite biosynthesis, and stress acclimatization. Whereas YABBYs are central to model and crop plants, the olive YABBY family is uncharacterized (Zhang et al., 2020). Other systems' genome-wide screens illustrate the potency of such analysis in establishing gene family affiliation and activity. In carrot (*Daucus carota*), 11 were discovered heterogeneously distributed onto nine YABBY gene chromosomes and classified into the known Arabidopsis-based subfamilies (Hussain et al., 2024). These studies utilized bioinformatics tools in annotating YABBY gene structure, conserved motifs, and expression patterns. Transcriptome analysis in *Osmanthus fragrans* and other plants also established that YABBY genes were extremely abundant in leaves and flowers and identified some YABBYs with flower scent and leaf shape traits (Shi et al., 2024). In this paper, we conduct the first genome-wide analysis of YABBY transcription factor family in olive, here. We use the genome sequence of olive europaea and public data, wherein we select putative YABBY genes, compare their gene structure and chromosomal positions, and derive evolutionary relationships (phylogeny, duplications, etc.) by comparison with other plant YABBYs (Xia et al., 2021). We focus on the olive ortholog of YABBY1, especially because YABBY1 was reported to be involved in the regulation of plant hormones. Our in silico strategy employs well-known methods (hidden Markov models for domain identification, sequence alignment, motif search, and phylogenies), like in other research on plant TFs (Romanova et al., 2021). Through the description of the olive YABBY gene family and the focus on YABBY1, we hope to leave an open door to ongoing functional and breeding research on olive development and stress reaction (Zhang et al., 2023).

2. Materials and methods

2.1 Identification of YABBY genes in Olea europea

The Arabidopsis thaliana YABBY protein sequence with Gene ID: O22152 was downloaded from UniProt (https://www.uniprot.org/) and stored in FASTA format. MotifFinder analysis was performed to determine conserved motifs and verify the existence of the YABBY signature domain based on Pfam annotation (Mazhar et al., 2023).This Arabidopsis sequence was then used as a query for a BLAST search against the *Olea europaea* genome in Phytozome (https://phytozome-next.jgi.doe.gov/) (Hai et al., 2024). The resulting olive protein sequences were then scanned in MotifFinder (https://www.genome.jp/tools/motif/)to identify conserved YABBY motifs and confirm the existence of the YABBY domain by Pfam annotation, and the genuineness of each candidate sequence was authenticated.

2.2 Physicochemical properties of YABBY genes in *O. europea*

Each olive YABBY protein sequence was separately downloaded and scanned in the Phytozome database to acquire exhaustive gene data, including the related Phytozome gene ID, chromosomal position, and other genomic details of interest (Rong et al., 2020). Furthermore, the physicochemical properties of every YABBY protein were computed with the ProtParam (https://web.expasy.org/protparam/), including the amino acid count, theoretical isoelectric point (pI), molecular weight, instability index, aliphatic index, and grand average of hydropathicity (GRAVY) (Jeba et al., 2025). All the gathered data were compiled and arranged in a Microsoft Excel spreadsheet systematically for further analysis.

2.3 Subcellular localization of YABBY genes in *O. europea*

Subcellular localization of *Olea europaea* YABBY proteins was predicted via WoLF PSORT (https://wolfpsort.hgc.jp/) (Bettaieb et al., 2020). Output data were tabulated in Microsoft Excel, and proteins were classified on the basis of predicted cellular localization. Processed data were then visualized using Heatmap Illustrator from TBtools to create a heatmap illustration of subcellular localization patterns, where visualization parameters are optimized for clarity and presentation quality (Köhler, 2024).

2.4 Phylogenetic analysis of *O. europea*

YABBY protein sequences from *Arabidopsis thaliana*, *Carica papaya*, *Olea europaea*, and *Solanum tuberosum* were compared based on the MUSCLE algorithm incorporated in MEGA 12 https://www.megasoftware.net/ . A phylogenetic tree was built using the maximum likelihood method with 1,000 bootstrap replicates to determine branch reliability. The phylogenetic tree obtained was then optimized and visualized through the iTOL (https://itol.embl.de/) platform to improve clarity and correctly illustrate the classification and evolutionary patterns of the YABBY gene family (Huang et al., 2013).

2.5 Cis regulatory element analysis of YABBY in Olive

Genomic sequences of each *Olea europaea* YABBY gene were downloaded individually from Phytozome (https://phytozome-next.jgi.doe.gov/) using the "G" option, with the upstream region set to 1,000 bp. The sequences preceding the designated regions were extracted and compiled into a single file named "promoter sequence" (Lv et al., 2025). This file was submitted to the PlantCARE database (https://bioinformatics.psb.ugent.be/webtools/plantcare/html/) for cis-regulatory element prediction, and the resulting data were visualized in TBtools using the "Gene Structure View (Advanced)" function to analyze the distribution of cis-regulatory elements (Wu et al., 2024).

2.6 Motif and Domain analysis of olive YABBY

Conserved domain (Hit) data were obtained in FASTA format from the NCBI CDD database (https://www.ncbi.nlm.nih.gov/), and motif data were retrieved in XML format from the MEME Suite https://meme-suite.org/meme/(Farooqi et al., 2023). In TBtools, the "Genomic Structure" function under the Graphics section was used by uploading the Newick tree file, MEME XML file, Hit data, and the renamed crop file. The analysis was executed to generate the final visualization of conserved domains and motif distribution (Guo et al., 2024).

2.7 Intron and exon analysis

Coding sequence (CDS) and genomic sequences of *Olea europaea* YABBY genes were retrieved from the Phytozome database and submitted to the Gene Structure Display Server (GSDS) (https://gsds.gao-lab.org/) for gene structure analysis (Gamas et al., 2025).

2.8 Ks Ka and Divergence time calculation of YABBY genes in olive

The Ka and Ks substitution rates were calculated using the Ka/Ks calculator in TBtools by uploading the CDS file of *Olea europaea* YABBY genes(Parvez et al., 2025). The obtained Ka and Ks values were imported into Microsoft Excel, where divergence time for each gene pair was estimated using the formula $T = Ks / (2 \times \lambda)$, with a substitution rate ($\lambda = 1.8 \times 10^{-9}$) for olive (Wang et al., 2011). The corresponding divergence times in million years ago (MYA) were also computed (Arnason et al., 1996). The resulting data were then visualized in TBtools using the heatmap function to display Ka/Ks ratios and divergence time values among YABBY genes (Zheng et al., 2023).

2.9 miRNA analysis

The YABBY gene family of Oeu was utilized to locate target locations using the available genomic data .miRNA of our yabby genes were obtained from Plant miRNA Encyclopedia (PmiREN) database (https://www.pmiren.com/), and this was further compared with the CDS sequence of our concerned yabby genes using the default parameters of the psRNATarget web server tool(https://www.zhaolab.org/psRNATarget/analysis?function=3) (Panwar et al., 2024). The relationships between the predicted miRNAs and the targeted genes were analyzed to determine the site of action and the type of regulatory inhibition (Gennarino et al., 2012).

2.10 Synteny Analysis

Olea europaea genome was analyzed by creating three datasets: a file with chromosome lengths, a file with gene locations, and a file showing the paralogous relationships between genes. To find these relationships, we did a BLASTP search to identify pairs of genes with similar sequences (Ozdemir Ozgenturk et al., 2010). We then used the Advanced Circos module of TBtools to put these data and visualize how the collinear blocks are spread across the genome (Chen et al., 2022). The map we got gave us a look at the genome's internal structure, showing us the regions that are conserved and where the chromosomes have been rearranged.

2.11 Chromosomal localization

Chromosomal localization of the identified genes in *Olea europaea* was carried out using gene position and chromosome length data sets (Barghini et al., 2017). The gene position data set contained gene identifiers, chromosome numbers, and genomic start and end positions, whereas the chromosome length data set contained the total size of each pseudo-chromosome (Harrison et al., 2002). The data sets were analyzed using the MG2C website (http://mg2c.iask.in/mg2c_v2.1/) to produce chromosomal distribution maps. The gene loci were depicted on the maps based on their physical positions to determine the distribution patterns of the genes in the genome (Cao et al., 2016).

2.12 Expression profiling analysis

To evaluate organ-specific expression patterns of olive YABBY genes, RNA-seq data from mature olive tree fruit, flower, leaf, meristematic tissue, root, and stem tissues were employed under natural settings (Rurek, 2025). The YABBY gene sequences were obtained from the Olive Genome Database (https://genomaolivar.dipujaen.es/db/run_blast.php) which was further processed, and normalized expression data (RPKM) were collected from the Gene Expression Omnibus database, accession GSE140648 (Zirak et al., 2024). To perform expression profiling, RPKM values were log2-transformed. TBtools was used for hierarchical clustering and creating heatmaps.

3. Results

3.1 Identification of Yabby genes in Olea europea

A genome-wide search of the *Olea europaea* genome led to the identification of five putative YABBY genes. The existence of the C2C2 zinc finger domain in the N-terminal region and the YABBY domain in the C-terminal region was verified using the domain verification method (Liu et al., 2020). The YABBY genes were named OeuYAB1, OeuYAB2, OeuYAB3, OeuYAB4, and OeuYAB5 based on their sequence similarity and chromosomal location. The YABBY genes were further investigated for physicochemical properties, gene structure, and expression (Kong et al., 2023).

3.2 Physicochemical properties

The physicochemical properties of the OeYAB proteins are shown in Table 1. The lengths of the amino acid chains varied between 170 (OeYAB3) and 211 (OeYAB1 and OeYAB4) residues, while the molecular weights varied between 19.38 kDa and 23.59 kDa. The theoretical isoelectric points (pI) varied from 6.23 to 8.80, which means that the majority of the OeYAB proteins are weakly basic. Instability index values (47.7–63.09) suggested that all the OeYAB proteins are unstable in vitro. GRAVY values were negative for all the proteins (−0.383 to −0.745), showing they are hydrophilic (Islam et al., 2017). These findings suggest OeYAB proteins as being hydrophilic, small-sized, and possibly unstable under normal conditions, as would be expected of transcription factors **(**Deeba et al., 2017**).**

Table 01: Physicochemical Properties of OeuYAB Genes. Summary of Genomic and Biochemical Features. The pI values for the proteins range from 6.23 to 8.8, indicating that they are basic. The hydrophilic character is indicated by a negative GRAVY and instability index values greater than 40. The amino acid lengths vary between scaffolds and chromosomes 1, 3, and 9, ranging from 170 to 211.

Gene ID	***Phytozome ID***	**Chromosome position**		**Direction**	**No. of amino acids**	**Theoratical pi**	**Molecular weight**	**Instability index**	**Gravy**	**Chromosome number**
		Start	**end**							
OeuYAB1	Oeu033104.1	52332	54840	Reverse	211	7.68	23591.94	51.24	-0.383	scaffold2771
OeuYAB2	Oeu048822.1	210708	216336	Forward	184	8.8	20666.58	47.7	-0.482	scaffold528
OeuYAB3	Oeu031003.1	1013483	1016606	Reverse	170	8.71	19384.12	50.89	-0.428	chr9
OeuYAB4	Oeu005814.1	4302348	4304756	Forward	211	7.69	23588.98	53.78	-0.352	chr3
OeuYAB5	Oeu055459.1	33880595	33882167	Forward	190	6.23	21711.46	63.09	-0.745	chr1

3.3 Subcellular localization

Subcellular localization study revealed that OeYAB3 and OeYAB5 were primarily found in the nucleus, with the highest prediction scores (10 and 14, respectively), confirming nuclear transcription factor roles(Zuckerman and Ulitsky, 2019). OeYAB1, OeYAB2, and OeYAB4 displayed lower and more distributed localization signals, primarily found in the chloroplast, cytoplasm, and vacuole. These findings indicate that OeYAB3 and OeYAB5 are most likely nuclear proteins, but the other OeYAB members may have more complex subcellular localizations (Harding et al., 2005).

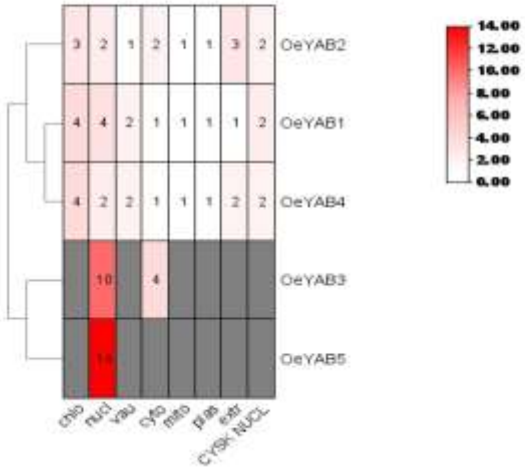

Figure 1: The subcellular localization prediction study of the OeYABBY proteins revealed that they are present in the nucleus, chloroplast, and vacuole.

The study found that the greatest number of proteins had the colour red, indicating subcellular localization.

3.4 Phylogenetic analysis

To better comprehend the YABBY family's evolutionary links, an unrooted tree was built from olive, potato, papaya, and Arabidopsis species (Figure 2). This tree categorized the YABBY family into five separate groups: FIL/YAB3, YAB2, YAB5, CRC, and INO, as previously defined. For example, the olive OeuFIL1/2 formed a different group with AtFIL and StYABB3, which were classified as FIL/YAB3 members, whereas OeuYAB2 created a distinct group with AtYAB2 and StYABB8 (Liu et al., 2022). This study demonstrated that the olive YABBY family has evolved into separate subgroups that are expected to have functional roles comparable to those of other dicot species (Finet et al., 2016).

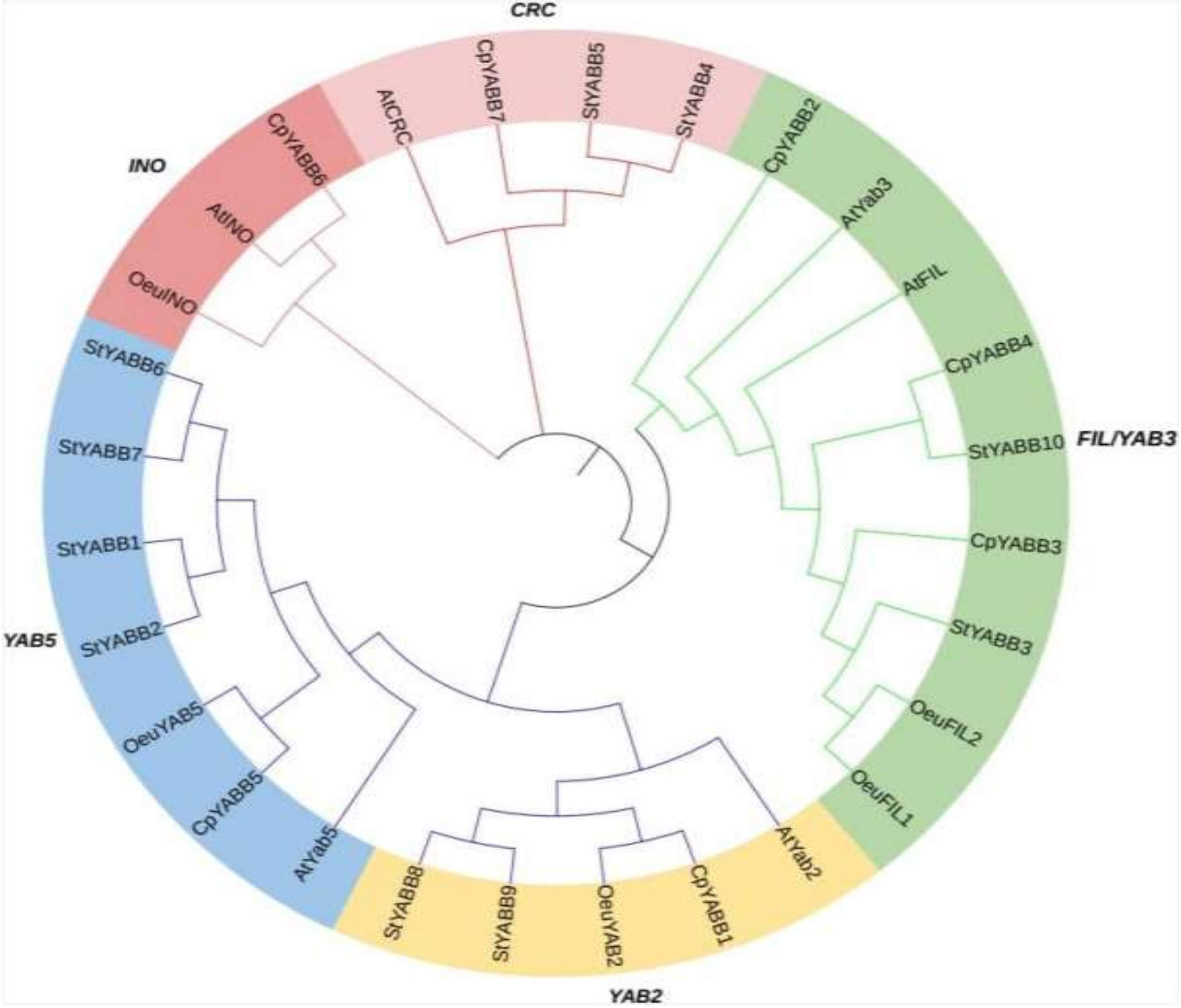

Figure 2: Phylogenetic relationships among YABBY proteins from *Olea europaea*, *Arabidopsis thaliana*, *Solanum tuberosum*, and *Carica papaya*. The phylogenetic relationship between the YABBY proteins of the aforementioned plants was built by the MEGA 11 software package using the neighbor-joining method after 1000 replicates with bootstrap support and the phylogenetic tree.

3.5 Gene structure (Exon –intron)

The examination of the genomic organization of the YABBY genes in the olive plant revealed moderate heterogeneity in their structural makeup (Julca, 2018). As illustrated in the figure above, the bulk of the OeuYAB genes contained multiple exons separated by introns. Specifically, the YABBY genes OeuYAB1, 2, and 4 included numerous exons. On the other hand, the YABBY genes OeuYAB3 and 5 have shorter exons (Buttar et al., 2020). Furthermore, the picture above showed that the YABBY gene OeuYAB3 had a specific region upstream or downstream of it, as indicated by the blue blocks. All YABBY genes contained several exons. Furthermore, the variety in the composition of the YABBY genes suggests that their functional control may vary (Wang et al., 2024).

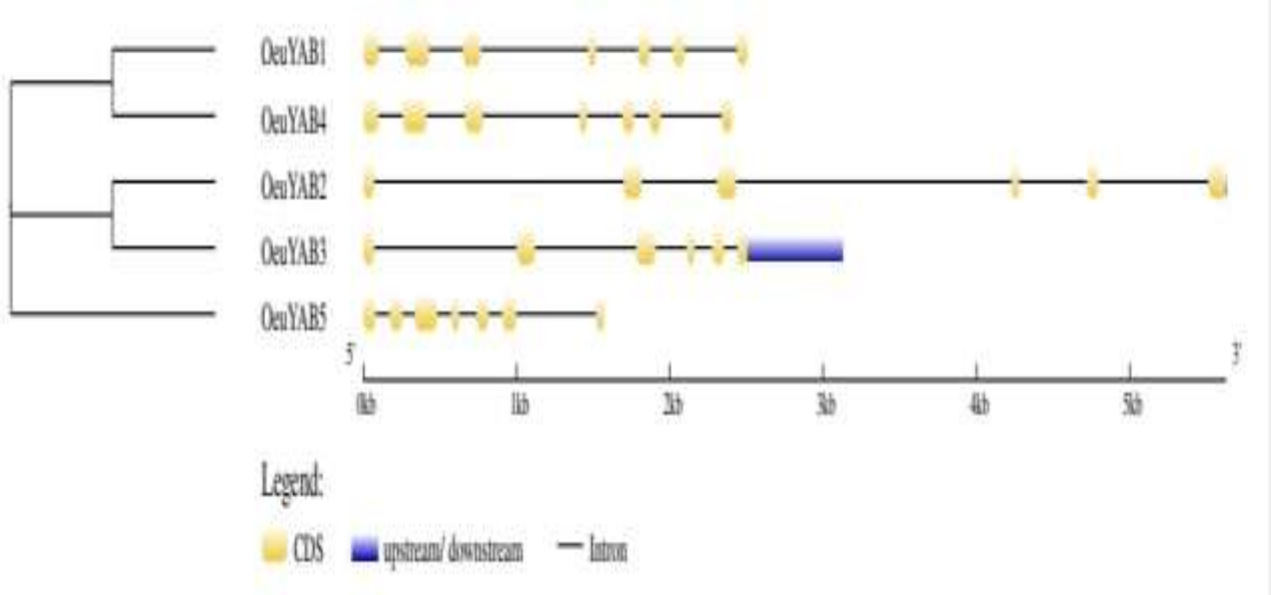

Figure 3: The olive YABBY genes have an exon-intron structure. Exons and introns are shown as yellow boxes and black lines, respectively. Gene models vary depending on the number of introns present in the various OeuYAB genes.

3.6 Motif and Domain analysis

OeuYAB gene motif analysis provides additional validation by identifying conserved motifs and domains within *Olea europaea*'s genome (Faize et al., 2020). It was discovered that the olive YABBY-like genes contained both the YABBY and YABBY superfamily domains. Numerically, motifs 5, 2, 4, 1, and 3 were found in OeuYAB1 and OeuYAB4, while motifs 7, 9, 8, 10, and 6 were found in OeuYAB2 and OeuYAB3.On the other side, OeuYAB5 has a less complex motif composition, consisting of only motifs 7 and 10 (Abou Assi et al., 2018). However, all of the motifs were conserved between the YABBY and YABBY superfamily domains, demonstrating the structures' stability and homology, as well as the protein's function (Shen et al., 2025).

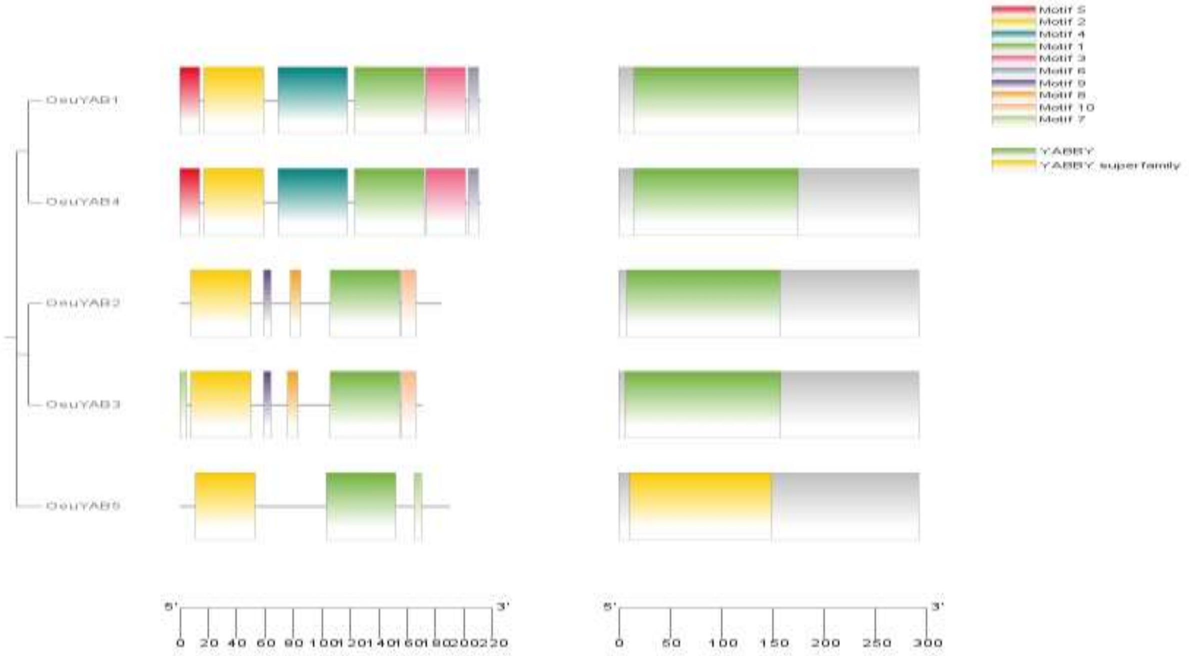

Figure 4:Structure of the conserved motif and domains found in olive YABBY proteins. Colored boxes symbolize different patterns and domains. All YABBY proteins share commonalities in motif and domain organization.

3.7 Promoter cis regulatory analysis

The 2000-bp promoter region of the olive YABBY genes (OeuYAB1-OeuYAB5) contains well-defined cis-regulatory features. Clustering is a strategy for grouping genes or components based on similarities in their promoter features. Because of their complex regulatory mechanisms, these results suggest that the olive YABBY genes are likely influenced by a variety of environmental and hormone stimuli(Luo et al., 2022).

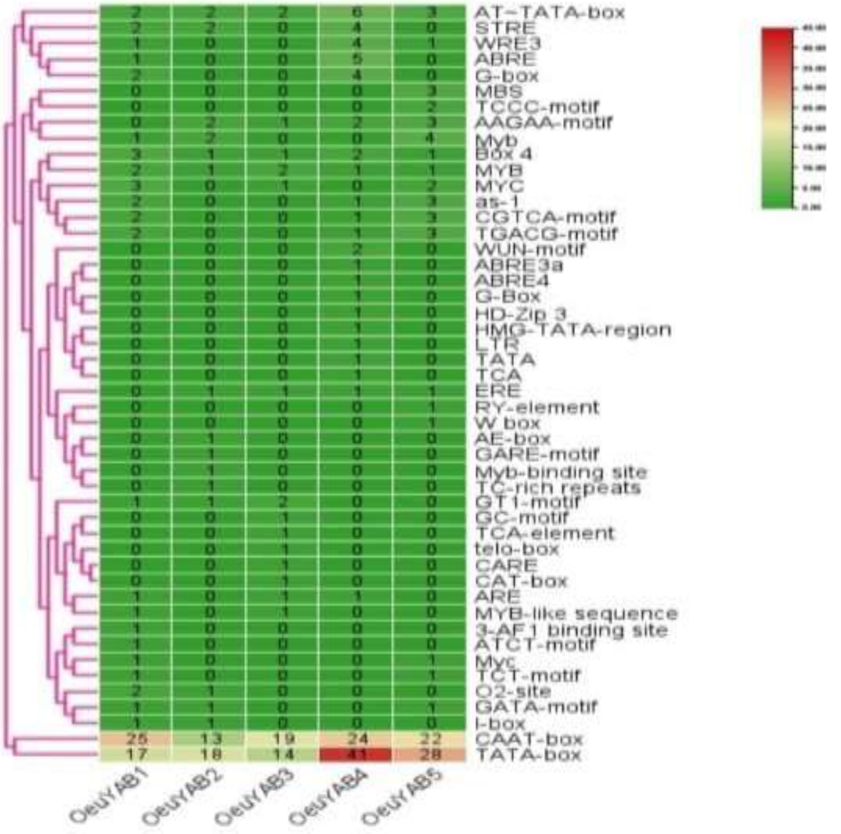

Figure 5: Cis-regulatory element study of olive YABBY genes. The heatmap depicts the number and distribution of putative cis-regulatory elements in the OeuYAB genes' promoter region. The colour scale depicts the changes in regulatory motif content among gene members.

3.8 Ka/Ks Analysis

Ka/Ks study of the *Olea europaea* YABBY gene family found that all duplicated gene pairs had Ka/Ks values < 1 (Figure 6) (Sami et al., 2023). This shows that the YABBY genes in olive plants have primarily been subjected to purifying selection pressure. This also implies that the YABBY genes have a high functional conservation potential following duplications (Smýkal et al., 2018). The diversity in Ks values between gene pairs indicates that YABBY gene duplication occurred at various stages of evolution. The heatmap visualisation also showed the evolutionary distance between the YABBY genes, indicating that the YABBY gene family evolved during the duplication event while maintaining conserved biological activity (Zhang et al., 2003).

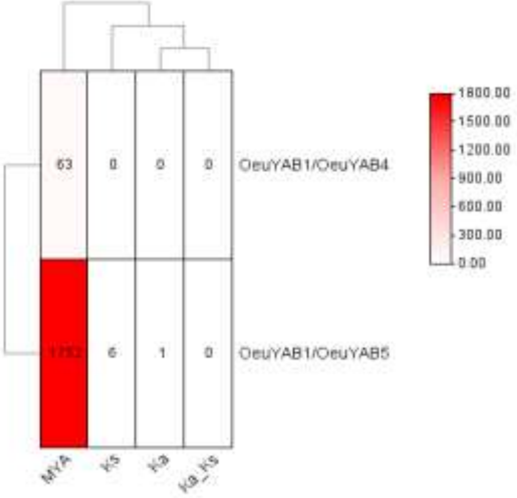

Figure 6: Heatmap of the duplicated YABBY gene pairs in *Olea europaea*, showing Ka, Ks, and Ka/Ks values. The YABBY gene family has undergone purifying selection during evolution, as indicated by low Ka/Ks values (<1).

3.9 miRNA analysis

Two microRNAs were targeting the OeuYAB1 and OeuYAB4 genes. These microRNAs belonged to two distinct families: Oeu-miRN1154 and Oeu-miRN2138. Both OeuYAB1 and OeuYAB4 have been identified as microRNA targets (Ye et al., 2019). The expectation score for each objective was 4.5. It is vital to understand that many microRNAs can target the same gene. MicroRNAs, in this situation, represent a distinct regulatory process (Riolo et al., 2020). It is also worth noting that Oeu-miRN2138 inhibits the expression of the OeuYAB1 and OeuYAB4 genes by cleavage, whilst the other microRNA, Oeu-miRN1154, inhibits their translation. These microRNAs regulate plants in a variety of ways. Cleavage inhibition is an example of mRNA degradation that happens quickly. These results contribute to the intricate network of YABBY gene regulation within the Oeu genome (Zhou and Luo, 2013).

3.10 Synteny Analysis

The *Olea europaea* genome was analyzed for intraspecific synteny. It showed a network of paralogous gene pairs, meaning there is a lot of genetic redundancy(Julca et al., 2023). The TBtools Advanced Circos module was used to plot the data at a resolution. The plot showed collinearity and segmental duplications as high-density ribbons between chromosomes (Danmaigona Clement, 2023).These findings show that the internal genomic organization is conserved. There have been large-scale chromosomal rearrangements. These rearrangements are likely the result of polyploidization events (Bento et al., 2008). The syntenic linkages were mapped to the pseudochromosomes giving insight into how the olive genome evolved. The duplicated regions that were identified are also very important (Mascagni et al., 2022).

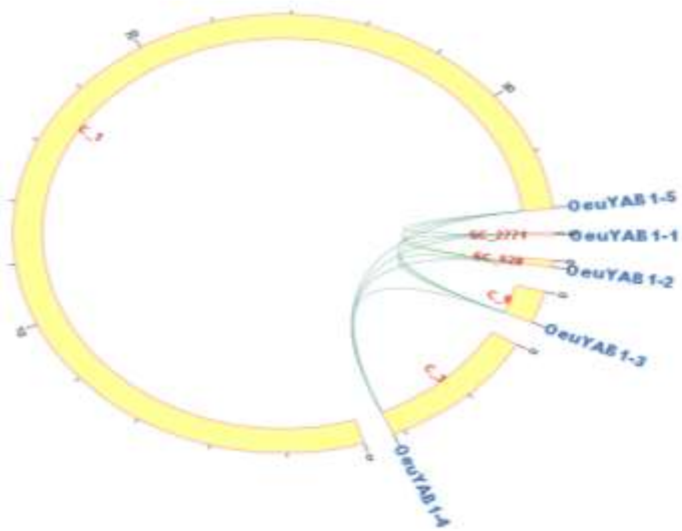

Figure 7: Synteny analysis showing collinearity among OeYABBY genes across olive chromosomes. Connecting lines indicate duplicated gene pairs resulting from segmental duplication events**.**

3.11 Chromosomal Distribution

The genes were found to be distributed in an unbalanced manner in the *Olea europaea* genome and were restricted to five different regions of the genome: SC_2771, SC_528, C_9, C_3, and C_1. Chromosome C_1 contained a single gene (Oeu055459.1), which was localized to the distal end, while SC_2771 and SC_528 contained a single gene (Oeu033104.1 and Oeu048822.1) localized to the upper part of each chromosome (Chee et al., 1995). The distribution of these genes suggests the presence of "hotspots" in the genome, particularly in C_9 and C_3, which could be an indication of gene family amplification in these regions or could be the result of tandem gene duplication events in the distant past (Chen et al., 2020).

Figure 8: Chromosomal distribution and localization of target genes across the *Olea europaea* genome. Labels indicate the physical positions of specific gene loci mapped onto pseudochromosomes and scaffolds using MG2C v2.1. The vertical scale on the left represents chromosomal length in Megabases (Mb).

3.12 Expression analysis

The differential expression of olive YABBY genes was also investigated using existing RNA-seq data from mature cultivated olive trees grown in field conditions and containing six anatomical tissues: fruit, flower, leaf, meristem, root, and stem tissues, which were represented by a heatmap (Fig. 9)(Lagiotis et al., 2024). Only five YABBY genes (Oeu033104.1, Oeu048822.1, Oeu031003.1, Oeu005814.1, and Oeu055459.1) showed detectable expression in the transcriptome, which could be attributed to the fact that the transcriptomic data were acquired from mature tissue (Manthey et al., 2004).Tissue-specific differences in expression levels were evident. Based on the expression patterns, it is obvious that Oeu033104.1 and Oeu005814.1 belong to the same cluster, as both genes had higher expression in meristem tissue and lower expression in root tissue (Livramento et al., 2022; Rasheed et al., 2026). On the other hand, Oeu031003.1 and Oeu055459.1 showed higher expression in fruit tissue, with Oeu031003.1 showing exceptionally higher expression levels in fruit tissue than in other tissues and Oeu055459.1 showing dominant expression in fruit tissue, albeit at a moderate level, implying that both genes may be involved in fruit development or reproduction (Janssen et al., 2008). However, Oeu048822.1 showed a rather uniform expression pattern in all tissues, with just small changes, showing that the genes may be involved in the regulation of YABBY genes throughout the family (Yin et al., 2022). The heatmap analysis revealed unique organ-preferential transcription patterns among the olive YABBY genes, indicating functional diversity within the family (Xia et al., 2022).

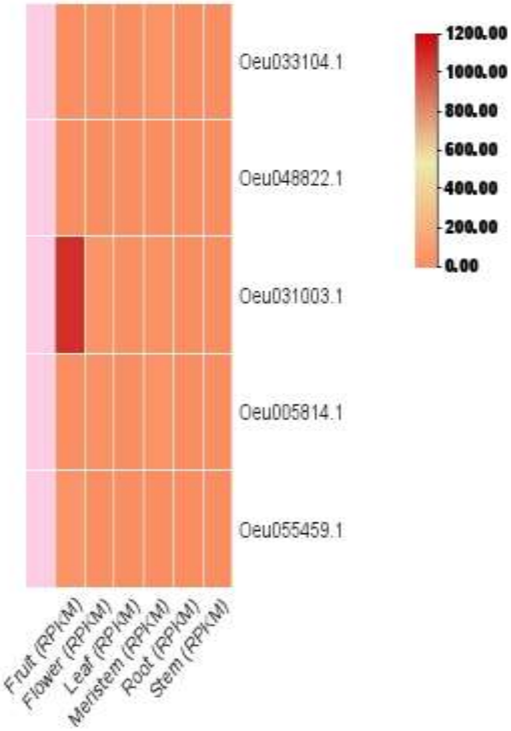

Figure 9: Heatmap of OeYABBY Expression shows Visual representation of gene activity across tissues. The intense red for Oeu031003.1 indicates high fruit specificity, while synchronized row patterns reflect collinearity from segmental duplication.

Table 2: Expression Profile of OeYABBY Genes. Quantitative RPKM values showing tissue-specific activity. Identical values for Oeu033104.1 and Oeu005814.1 highlight a duplicated gene pair with conserved expression patterns

Phytozome ID	Fruit (RPKM)	Flower (RPKM)	Leaf (RPKM)	Meristem (RPKM)	Root (RPKM)	Stem (RPKM)
Oeu033104.1	12.816	31.783	0.152	38.033	0.007	0.751
Oeu048822.1	1.793	2.774	2.204	3.246	2.173	3.529
Oeu031003.1	1081.066	41.646	7.842	31.1	0.272	1.345
Oeu005814.1	12.816	31.783	0.152	38.033	0.007	0.751
Oeu055459.1	43.88	6.351	3.398	4.211	0.005	0.397

4. Discussions

Transcription factors are critical regulators of gene expression (Mitsis et al., 2020). They play a role in managing the complex regulatory systems that govern plant growth, development, and adaptation(Wolters and Jürgens, 2009). The YABBY transcription factor family has played a critical role in regulating plant lateral polarity and abaxial-adaxial identity, particularly in seed plants (Yusoff, 2017). In the current study, a genome-wide analysis of the olive genome database revealed the presence of five different *OeuYAB* gene sequences, implying the presence of a highly conserved evolutionary strategy in the case of the olive plant, in which the functional integrity of the YABBY family of transcription factors has been maintained as a distinct regulatory unit, despite the complex polyploid nature of the plant genome (Sherazi et al., 2026). The physicochemical characterization of the *OeuYAB* protein family using the ProtParam program (https://web.expasy.org/protparam/) revealed the proteins' compact nature, with molecular weights ranging from 19.38 to 23.59 kDa, sizes ranging from 170 to 211 amino acids, and theoretical pI ranging from 6.23 to 8.80 (Oyewusi et al., 2025). This suggests that proteins are mainly basic in nature. The negative GRAVY values range from -0.383 to -0.745, indicating that the protein is hydrophilic(Yoodee et al., 2024). Furthermore, the high instability index values greater than 40 for the whole family suggest that these transcription factors are intrinsically unstable *in vitro* (Gamage et al., 2019). This is because transcription factors are regulatory proteins that have a high turnover rate at specific developmental stages.MEGA12-based (https://www.megasoftware.net/) phylogenetic study of the five *OeuYAB* genes identified five conventional subfamilies: FIL/YAB3, YAB2, YAB5, CRC, and INO (Hao et al., 2022). The significant link between the subfamilies and the *OeuYAB* genes from *Arabidopsis*, potato, and papaya shows that these subfamilies have retained their functional specificity since the separation of these plant lines (Jue et al., 2017). Furthermore, gene structure insights into the structure of the *OeuYAB* genes using the Gene Structure Display Server (https://gsds.gao-lab.org/) and MEME tools (https://meme-suite.org/meme/) revealed that, while all of the genes contain the signature N-terminal C2C2-type zinc finger and C-terminal YABBY domains, differences in exon and intron distributions, as well as the presence of specific motifs, suggest functional specificity (Smith and Matthews, 2016). This is because, for example, whereas the motif patterns in *OeuYAB1* and *OeuYAB4* are similar, they diverge dramatically in *OeuYAB5* (Chowdhury et al., 2022). The family's evolutionary pattern is subject to rigorous purifying natural selection, as evidenced by the calculated Ka/Ks ratios of duplicated gene pairs being significantly lower than 1.0 (Zhao et al., 2022). This negative selection pressure ensures the conservation of the protein's functional domains by eliminating deleterious mutations, thereby maintaining the essential developmental roles of the YABBY family across evolutionary timescales (Soskine and Tawfik, 2010). Plant CARE (https://bioinformatics.psb.ugent.be/webtools/plantcare/html/) analysis of the regulatory regions, specifically the 1,000-bp upstream promoter regions, revealed a complex regulatory pattern rich in *cis*-regulatory elements involved in light responsiveness, hormone signalling pathways such as ABA and gibberellins, and abiotic stress adaptation (Komamytsky and Borisjuk). This has shifted the *OeuYAB* genes to the core of the regulatory axis, where external environmental inputs are incorporated into internal growth programs. To obtain insight into the post-transcriptional regulatory pattern, a miRNA target analysis was performed using the psRNA Target service (https://www.zhaolab.org/psRNATarget/analysis?function=3), which revealed a specialized regulatory pattern in which *OeuYAB1* and *OeuYAB4* are targeted by two distinct miRNA molecules, *Oeu-miRN1154* and *Oeu-miRN2138*. Analysis of these interactions with their respective target miRNAs yielded an expected score of 4.5 for both groups, indicating a high level of sequence complementarity. Notably, the inhibitory mechanisms of these interactions function in distinct ways depending on their coordinate positions (Chen et al., 2005). For example, *Oeu-miRN2138* was predicted to cause mRNA degradation by cleaving transcripts in the 65-85 bp area, whereas *Oeu-miRN1154* was predicted to influence gene expression by inhibiting translation in the 104-124 bp region. More crucially, RNA-seq expression analysis for six different anatomical areas revealed strong evidence of functional differences (Arraiano et al., 2010). Although *OeuYAB1* and *OeuYAB4* showed synchronized greater expression in meristematic tissues, as shown by their RPKM values of 38.033, Oeu031003.1, also known as *OeuYAB3*, belonging to the CRC subfamily, showed an extremely higher RPKM value of 1081.066 in fruit tissue(Sun et al., 2020). Such specialized regulation, which may include a complicated combination of *cis*-elements and miRNA-mediated control, strongly implies that *OeuYAB3* is an important regulator of olive drupe production or secondary metabolism in the oil-rich mesocarp (Tranbarger et al., 2011). As further validation of their unique nuclear localization, as indicated by their activity as active transcription factors, WoLF PSORT (https://wolfpsort.hgc.jp/) predictions of their subcellular localization revealed that these proteins are found in the nucleus (Deveshwar et al., 2020).

5. Conclusion

In this study, the OeuYAB transcription factor gene family in the olive genome was examined in a whole-genome. Five OeuYAB transcription factor genes were discovered, categorised into five subfamilies, and their structural and functional properties were studied. The genomic organization of the OeuYAB gene family revealed a moderate level of gene structural diversity, with many exons. Notably, the existence of a significant number of short exons in OeuYAB3 and OeuYAB5 indicates that the OeuYAB gene family is functionally diverse. The chromosomal mapping of the OeuYAB gene family revealed that the genes are unevenly distributed over five genomic regions. Notably, hotspots for the OeuYAB gene family can be discovered in C_9 and C_3, indicating that the YABBY gene family has been duplicated in the olive genome. The promoter study of the OeuYAB gene family indicated the presence of numerous stress response elements associated with heat, cold, and drought stress (HSE, LTR, and MBS). Notably, OeuYAB3 and OeuYAB5 were predicted to be nuclear-localized proteins, implying that they could act as transcriptional regulators during abiotic stress reactions. Additionally, miRNA interaction study revealed that Oeu-miRN1154 and Oeu-miRN2138 regulate OeuYAB1 and OeuYAB4 through translation inhibition and transcript cleavage mechanisms. Furthermore, the gene expression study revealed that OeuYAB3 is a strong candidate gene for reproductive development, with extraordinarily high levels of expression in fruit tissue (1081.066 RPKM). The findings from the study on olive YABBY proteins will be relevant for future functional analysis, gene cloning, and research into the regulatory connections of olive YABBY genes with other transcription factors. The study's findings will be important in the development of molecular breeding for olive trees to improve flowering, fruiting, and stress tolerance in response to changing climatic circumstances.

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Declaration

Data Availability statement

All authenticated data have been included in the manuscript.

Consent for publication

Not applicable

Declaration of Competing Interests

The authors declare that they have no conflict of interest.

Author Contribution Statement

All authors contributed to this work. AS, MH: Conceptualization, Investigation, Original Draft Writing. MS: Supervision, Validation, Reviewing and Final Editing. SM: Methodology, Data Curation, Visualization. SHUHS, and MS: Literature Support, Draft Improvement. AS: Reviewing and Editing.
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Ethical Statement

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