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JOURNAL OF AGRICULTURAL PRODUCTION

ISSN: 2757-6620

https://prensip.gen.tr

RESEARCH ARTICLE

Genome-Wide Analysis and Characterization of *FBA* (Fructose 1,6-bisphosphate aldolase) Gene Family of *Phaseolus vulgaris* L

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ARTICLE INFO

Article History
Received: 06.02.2024
Accepted: 01.03.2024
First Published: 28.03.2024

Keywords
Fructose-bisphosphate aldolase
Gene duplication
Gene expression
In silico analysis
Phaseolus vulgaris L

ABSTRACT

Fructose-1,6-biphosphate aldolase (*FBA*) genes have important roles in plant stress responses. At the same time, these genes positively affect growth and development in plants. FBA is involved in gluconeogenesis, glycolysis, and the Calvin-Benson cycle, and it is an enzyme that plays an important role in signal transduction of these stages. This study aims to determine and characterize the *FBA* gene family in the bean genome. As a result of the study, 7 *Pvul-FBA* genes were determined in the bean (*Phaseolus vulgaris* L.) genome. The highest amino acid number of Pvul-FBA proteins was determined in the *Pvul-FBA-1* gene (1374), and the highest molecular weight (43.03 kDa) was determined in the *Pvul-FBA-7* gene. Again, the highest isoelectric point (8.03) was determined in the Pvul-FBA-3 gene. It has been determined that the *Pvul-FBA-6*/*Pvul-FBA-7* genes are segmental duplicated genes. The main four groups were obtained according to the phylogenetic analysis consisting of FBA proteins of three plants (*P. vulgaris*, *Glycine max*, and *Arabidopsis thaliana*). As a result of interproscan analysis, Motif-1, 2, 3, 4 and 5 were found to contain the fructose-bisphosphate aldolase domain. According to in silico gene expression analysis, it was determined that the expression rates of *Pvul-FBA* genes increased or decreased under salt and drought stress conditions. Synteny analyses of *FBA* genes in common bean and *A. thaliana* plants showed that these three plants have a relationship in terms of *FBA* genes. The results of this research will allow a better designation of the molecular structure of the *FBA* gene family in common bean.

Please cite this paper as follows:

Uçar, S., Alım, Ş., Kasapoğlu, A. G., Yiğider, E., İlhan, E., Turan, M., Polat, A., Dikbaş, N., & Aydın, M. (2024). Genome-wide analysis and characterization of *FBA* (fructose 1,6-bisphosphate aldolase) gene family of *Phaseolus vulgaris* L. *Journal of Agricultural Production*, *5*(1), 30-40. https://doi.org/10.56430/japro.1432135

1. Introduction

The common bean (*Phaseolus vulgaris* L.) is a species of plant belonging to the Fabaceae/ Leguminosae family (730 genera and 19400 species) (Broughton et al., 2003). Meanwhile, the most diverse vegetable crop among the legumes. Common bean is rich in protein, carbohydrates, fiber, and minerals and is a potential food source in the diet of the world's population (Blair et al., 2003; Schmutz et al., 2014; Cichy et al., 2015). Unfortunately, bean production is limited by abiotic and biotic stress factors (Fujita et al., 2006; Carvalho et al., 2011). Abiotic stresses such as salinity, drought, heavy metals, and cold are the main factors that negatively affect product productivity, quality, and sustainability (Sharma et al., 2019; Waqas et al., 2019). Because the bean is a glycophyte plant, it is not tolerant of high salt concentrations. Especially salinity and drought affect cell metabolism significantly (Taïbi et al., 2016).

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Plants respond to the stresses they are exposed to at molecular, biochemical, and physiological levels. This response varies according to species, genotype, organ, and cell type (Barnabás et al., 2008; Basu et al., 2016). Fructose-1,6-biphosphate aldolase (*FBA*) genes, one of these genes, have an important role in biotic and abiotic (high salt, drought, heavy metal, and low temperature, etc.) stress answer and regulate growth in plants (Michelis & Gebstein, 2000; Sarry et al., 2006; Khanna et al., 2014; Murad et al., 2014; Shu et al., 2014). FBA is involved in gluconeogenesis, glycolysis, and the Calvin-Benson cycle, and it is an enzyme that plays an important role in signal transduction of these stages (Anderson et al., 2005; Cho & Yoo, 2011; Cai et al., 2018). The translatable aldol division of fructose-1,6-biphosphate (FBP) into glyceraldehyde-3-phosphate (GAP) and dihydroxyacetone phosphate (DHAP) is catalyzed by the *FBA* gene, a metabolic enzyme. There are two classes of FBAs: class I and class II (Rutter, 1964; Cai et al., 2016). While class I FBAs are generally found in plants, animals, and protists, class II FBAs are found only in fungi (Rutter, 1964; Marsh & Lebherz, 1992; Lv et al., 2017). In addition, there are two isoforms (chloroplast /plastid FBA (CpFBA) and cytosolic FBA (cFBA) of FBA in plants (Lu et al., 2012). Chloroplast FBA is involved in starch biosynthesis, while cytosolic FBA is involved in the production of FBP, and sucrose. Inhibition of cytosolic FBA results in decreased sucrose synthesis (Fan et al., 2009; Strand et al., 2000). Some studies have determined that overexpression of the *FBA* gene in tobacco supports growth (Yamada et al., 2000). The decline in the expression of the *FBA* gene showed that the biomass of the tomato decreased (Cai et al., 2018). Diverse insider of the *FBA* gene family have been defined and characterized in spinach (Pelzer-Reith et al., 1993), rice (Kagaya et al., 1995), corn (Dennis et al., 1988), tobacco (Yamada et al., 2000), *Sesuvium portulacastrum* (Fan et al., 2009), Arabidopsis (Lu et al., 2012), tomato (Cai et al., 2016), *Triticum aestivum L*. (Lv et al., 2017), *Brassica napus* (Zhao et al., 2019), and cotton (Li et al., 2021). As a result of the research, no study was found related to the genome-wide analysis of the *FBA* gene members in the common bean plant.

Determining and describing the members of the *FBA* gene family in silico at the genome-wide level in beans is the primary goal of this work. Once more, the goal of this research is to determine the ortholog-paralogous link between *A. thaliana, G. max, and P. vulgaris L.* and the differences in *FBA* gene expression under salt stress and drought.

2. Materials and Methods

2.1. Identification of *Pvul-FBA* Genes

Using the Pfam database, Pfam accession numbers (class I: PF00274, class II: PF01116) in the bean genome were obtained. The protein, transcript, genomic, and CDS sequences in the genomes of *P. vulgaris* [7], *A. thaliana* [9], and *G.max* [15] of the *Pvul-FBA* gene family with accession numbers PF00274 and PF01116 were obtained using Phytozome database v13 (https://phytozome-next.jgi.doe.gov/). The blastp of the Phytozome database v13 and the Hidden Markov Model (HMM) (http://www.ebi.ac.uk) were used to identify FBA proteins present in the genomes of the three plants used. On the other hand, the presence of the *Pvul-FBA* domain was investigated with the HMMER (http://www.ebi.ac.uk) database. The instability index, amino acid number, and molecular weight, theoretical isoelectric point (pI), of the FBA proteins in the common bean were defined by the "ProtParam tool" (https://web.expasy.org/protparam/). In addition, intracellular localizations were estimated with the help of the WoLF SPORT database (Horton et al., 2007).

2.2. Identification of Gene Duplication, Physical Locations, Structure, and Conserved Motifs of *Pvul-FBA* Genes

Intron and exon regions of Pvul-FBA proteins in *A. thaliana, P. vulgaris*, and *G. max* were detected by the GSDS (Gene Structure Display Server v2.0) database (Guo et al., 2007). Using genomic sequences and CDS, the *Pvul-FBA* genes structure was discovered. Using by Phytozome v13, the chromosomal locations/sizes of the *Pvul-FBA* genes were ascertained. The MapChart tool was utilized to mark and depict the locations of *Pvul-FBA* genes on *P. vulgaris* chromosomes (Voorrips, 2002). *FBA* gene duplications between *P. vulgaris*, *G. max*, and *A. thaliana* were determined by MCScanX (Wang et al., 2012). Nonsynonymous ratios (Ka), synonymous ratios (Ks) and evolutionary strains (Ka/Ks) between binary pairs of *Pvul-FBA* genes were calculated using the PAML (Yang, 2007) with the help of PAL2NAL (Suyama et al., 2006). Conserved motifs of *Pvul-FBA* genes were detected with the tool "MEME Suite" (Bailey et al., 2006). The width of the motifs was recorded as minimum 6 and maximum 50 and the maximum number of motifs as 10. Possible domains were found by scanning the acquired motifs through the InterProScan database (Quevillon et al., 2005).

2.3. Phylogenetic Analysis

Phylogenetic and molecular evolutionary analyzes were realized by using the MEGA v11 (Tamura et al., 2021). Multiple sequence alignment of Pvul-FBA proteins was performed using ClustalW. To create phylogenetic trees, the bootstrap value of 1000 was repeated and the Neighbor-joining method was applied and the phylogenetic tree was designed (Thompson et al., 1997). Then, the obtained phylogenetic tree was shaped with the help of the iTOL (Letunic & Bork, 2011).

2.4. Promoter Analysis of the bean *FBA* Gene Family

First, of Phytozome database v13, the first 2000 bp upstream areas of the *Pvul-FBA* genes were obtained. The PlantCARE database was then utilized to identify cis-acting

elements. Phenogram was then generated with TBtools (Lescot et al., 2002; Chen et al., 2020).

2.5. Synteny Analysis

The orthologous protein sequence information of *G. max, P. vulgaris, and A. thaliana* was retrieved using Phytozome v13. Synteny map was then drawn with the help of "TBtools" (Chen et al., 2020).

2.6. Homology Modeling of Pvul-FBA Proteins

The 3-dimensional structures of the Pvul-FBA protein sequences were determined with the help of the Phyre[2] (Kelley et al., 2015).

2.7. Pvul-FBA protein-protein interactions (PPI)

Help was taken from the STRING database (https://string-db.org/) to determine functional and physical aspects of protein-protein interactions. The software Cytoscape (Shannon et al., 2003) was utilized to categorize and present the collected data.

2.8. Gene Expression Analysis (In-silico)

Illumina RNA-seq data were acquired from the Sequence Reading Archive (SRA) data bank of the NCBI database in order to investigate the *Pvul-FBA* genes. Relevant RNA-seq data SRR957668 (salt stress treatment decontaminated leaf), SRR958469 (leaf salt control) (Hiz et al., 2014), and SRR8284480 (leaf drought control), SRR8284481 (drought stress treated leaf) accession numbers used and in silico expression profiles RPKM (Reads per kilobase: Transcripts per kilobase, expression of transcript normalized form) (Mortazavi et al., 2008) values log2 transform was calculated and CIMMiner (http://discover.nci.-nih.gov/cimminer) algorithm with heat graph (heatmap) was obtained.

3. Results

FBA gene family members were scaned in the common bean genome available in the Phytozome v13 with the PFAM accession number (class I: PF00274, class II: PF01116). As a result, were detected 7 genes in the common bean genome. Chromosome locations (Figure 1), molecular weights, theoretical isoelectric points and amino acid numbers of *Pvul-FBA* genes obtained from the common bean genome were determined and shown in Table 1. The amino acid numbers of *Pvul-FBAs* between 129 to 1374. The highest amino acid number was determined in the Pvul-FBA-1 protein (1374), while the lowest amino acid number was determined in the *Pvul-FBA-6* gene (129). Again, when the molecular weights of *Pvul-FBAs* were evaluated within themselves, the lowest molecular weight was determined by *Pvul-FBA-6* with a value of 14.15 kDa, while the highest molecular weight was detected in *Pvul-FBA-7* with a value of 43.03 kDa. In addition, the theoretical isoelectric points vary between 5.56 and 8.02, and the highest isoelectric point *Pvul-FBA-3* was obtained.

Table 1. Information on PvNPR-like proteins found in the common bean genome.

Gene Name	Phytozome ID	Chr No	Chromosome Location	aa length	MW (kDa)	pI	Instability index	Stability
Pvul-FBA-1	Phvul.004G150100	Chr04	45186912-45212757(+)*	1374	14.80	5,56	31.27	Stable
Pvul-FBA-2	Phvul.007G033800	Chr07	2745002-2747868(+)	382	41.82	7,6	44.69	Unstable
Pvul-FBA-3	Phvul.007G222900	Chr07	34634308-34636200(-)*	357	38.34	8,02	35.51	Stable
Pvul-FBA-4	Phvul.008G189200	Chr08	52718648-52721317(-)	358	38.60	6,73	31.47	Stable
Pvul-FBA-5	Phvul.008G282000	Chr08	62278473-62281022(+)	357	38.55	5,77	32.81	Stable
Pvul-FBA-6	Phvul.009G003100	Chr09	574960-575965(-)	129	14.15	6,73	41.19	Unstable
Pvul-FBA-7	Phvul.011G039100	Chr11	3560197-35630828(-)	398	43.03	7,62	35.35	Stable

*(-): reverse strand, (+): forward strand

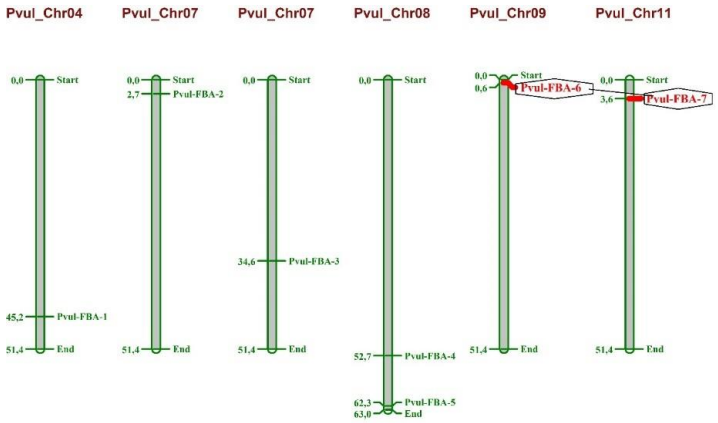

Figure 1. *Pvul-FBA* gene distribution in bean chromosomes (red indicates segmental duplicated genes).

Gene duplication events among *Pvul-FBA* genes were examined and the results are shown in Table 2. According to the analysis, while tandem duplication could not be detected in *Pvul-FBA* genes, segmental duplication was detected between *Pvul-FBA-6*/*Pvul-FBA-7* gene pairs. It was determined that the Ka/Ks ratio of genes showing segmental duplication was less than 1.

Table 2. Ka, Ks and Ka/Ks values of *Pvul-FBA* segmental duplicate genes.

Gene 1	Gene 2	Ka	Ks	Ka/Ks
Pvul-FBA-6	*Pvul-FBA-7*	0.4562	0.0695	0.1523

As a result of the information obtained from the WoLF PSORT database, it was identified that the *Pvul-FBA* genes are located in different intracellular regions such as the mitochondria, cytoplasm, and chloroplast, and are shown in Table 3. It has been determined that all *Pvul-FBA* genes in beans are located in the cytoplasm.

A phylogenetic tree was formed with the FBA protein sequences of *A. thaliana* and *G. max* plants and the relationship between Pvul-FBA proteins was determined. The phylogenetic tree was drawn utilizing the Neighbor-joining system, depending on the amino acid sequence of the FBA proteins, with a bootstrap value of 1000 repetitions. FBA proteins are clustered in 4 main groups as A, B, C, and D as shown in Figure 2.

Table 3. Intracellular localization of *Pvul-FBA* genes.

Gene	WoLF PSORT
Pvul-FBA-1	pero: 9, cyto: 3, nucl: 1, golg: 1
Pvul-FBA-2	chlo: 14
Pvul-FBA-3	cyto: 5, E.R.: 4.5, E.R._plas: 3.5, mito: 2, plas: 1.5, nucl: 1
Pvul-FBA-4	cyto: 11, chlo: 1, nucl: 1, E.R._vacu: 1
Pvul-FBA-5	chlo: 4, cyto: 5, pero: 2, nucl: 1, mito: 1, cysk: 1
Pvul-FBA-6	nucl_plas: 5.5, nucl: 7mito: 3, plas: 2, chlo: 1, cyto: 1
Pvul-FBA-7	hlo: 8, cyto: 2, mito: 2, nucl_plas: 2

*chr: chromosome, chlo: chloroplast, nucl: nucleus, mito: mitochondria.

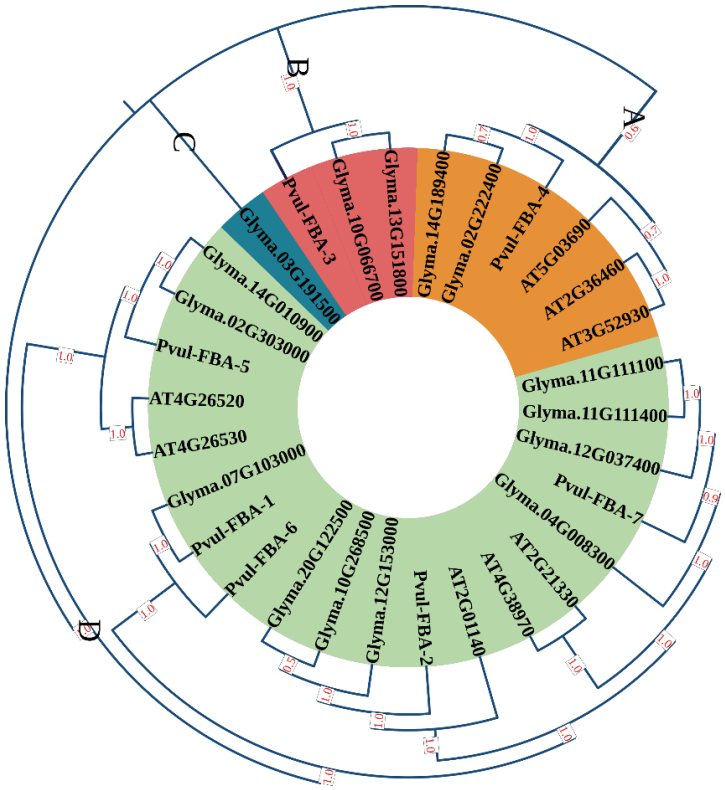

Figure 2. Phylogenetic tree constructed with Pvul-FBA proteins from *P. vulgaris*, *A. thaliana* and *G. max*.

As a result of the conserved motif analysis performed on Pvul-FBA proteins with the MEME suite v5.4.1 program, 10 conserved motifs were established. The length of the obtained motifs was in the range of 14-50 amino acids (Table 4). While 10 motifs were specified in *Pvul-FBA-2*, *Pvul-FBA-3*, *Pvul-FBA-4*, *Pvul-FBA-5* and *Pvul-FBA-7* genes, 3 motifs were specified in *Pvul-FBA-6* gene (Figure 3). The best possible match sequences corresponding to the motifs are shown in Table 4. In addition, it was identified that Motif-1, 2, 3, 4, and 5 were fructose-bisphosphate aldolase domains.

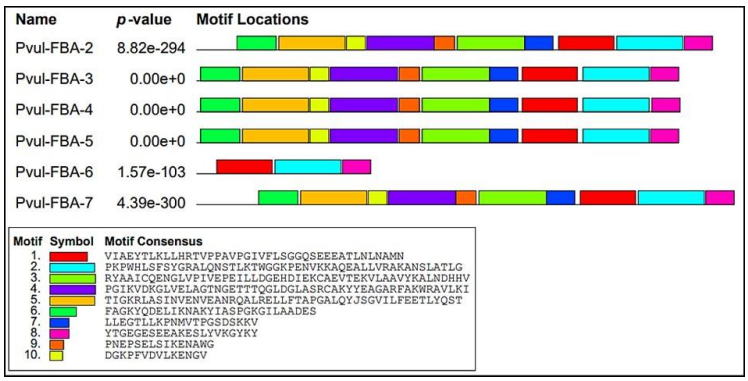

Figure 3. Conserved sequence regions of *Pvul-FBA* genes.

Table 4. Sequence information of possible motifs in Pvul-FBA proteins.

Motif id	WIDTH	Possible best match	Contains domain
1	41	VIADYTVRMLHRRVPPAVPGIMFLSGGQSEEEATLNLNAMN	Fructose-bisphosphate aldolase
2	49	PNPWHVSFSYGRALQQTTLKTWGGKPENVKKAQDALLFRCKANSEAQLG	Fructose-bisphosphate aldolase
3	50	RYAAICQENGLVPIVEPEILLDGDHDIHKCAEVTERVWAECYFYLNDHHV	Fructose-bisphosphate aldolase
4	50	PGIKVDKGTVPLAGTNGETWCQGLDGLAQRCAKYYEQGARFAKWRTVLKI	Fructose-bisphosphate aldolase
5	49	TCGKRLASINVENVEANRQAYRELLFTAPGCLQYLSGVILFEETLYQST	Fructose-bisphosphate aldolase
6	29	FKGKYQDELIKNAKYIASPGKGILAMDES	N/A
7	21	LFEGTLLKPNMVTPGSDSKKV	N/A
8	21	YTGEGESDEAKESMFVKGYKY	N/A
9	15	PNEPSELSIHENAWG	N/A
10	14	DGKPFVDVLKENNV	N/A

Exons and introns of *Pvul-FBA* genes were identified according to structural analysis with GSDS (Figure 4). According to the results, it was found that the exon numbers of *Pvul-FBA* genes varied between 2 and 42, and the intron numbers varied between 1-41. The highest number of exons was determined in *Pvul-FBA-1* (42) genes, while the lowest number of exons was determined in *Pvul-FBA-3* and *Pvul-FBA-6* (2) genes. On the other hand, while the highest intron number was designated in the *Pvul-FBA-1* gene, the lowest intron number was designated in the *Pvul-FBA-6* gene (Figure 4).

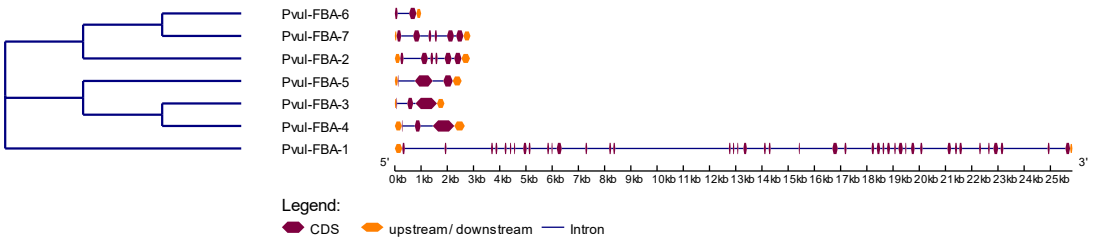

Figure 4. Number, position, and length of introns and exons in *Pvul-FBA* genes.

It was discovered that the *Pvul-FBA* genes' promoter regions aid in plant growth, the molecular reaction to abiotic stressors, and environmental adaptation. As a result of the analyzes performed in the PlantCARE database, the cis-acting elements in the *Pvul-FBA* gene sequences were shown using the TBtools program (Figure 5). The information demonstrated that all *Pvul-FBA* genes had elements linked to photosensitive elements, including the CAT-box, W box, and AE Box.

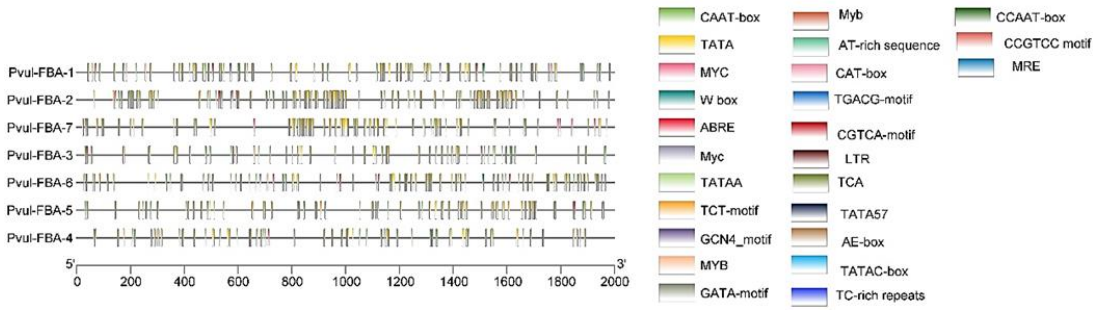

Figure 5. Promotor regions of *Pvul-FBA* genes.

Using FBA proteins from *P. vulgaris* and *A. thaliana* plants, a synteny map was produced. The synteny analysis revealed a connection between *P. vulgaris* and *A. thaliana* (Figure 6). Eight syntenic relationships were identified among *P. vulgaris* and *A. thaliana FBA* genes. Orthology was found between the *Pvul-FBA-1*/AT1G18270.3, *Pvul-FBA-2*/AT2G01140.1, *Pvul-FBA-3*/AT3G52930.1, *Pvul-FBA-3*/AT2G21330.1, *Pvul-FBA-6*/AT4G38970.1, *Pvul-FBA-6*/AT2G21330.1, *Pvul-FBA-7*/ AT4G38970.1 and *Pvul-FBA-7*/ AT2G21330.1 genes.

The structure and function of the proteins were predicted with the help of the EzMol database. Three-dimensional homology modeling of the identified Pvul-FBA proteins is shown in Figure 7. The Cytoscape tool was utilized to show the protein-protein interactions of the identified FBA proteins, as a consequence of the data obtained from the STRING database (Figure 8).

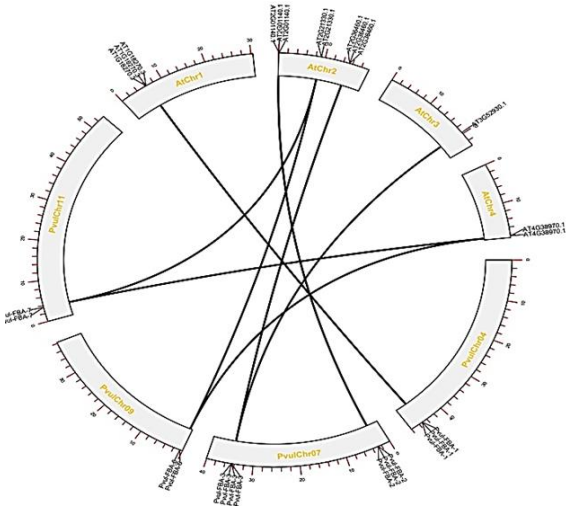

Figure 6. Syntenic relationship among *P. vulgaris* and *A. thaliana FBA* genes.

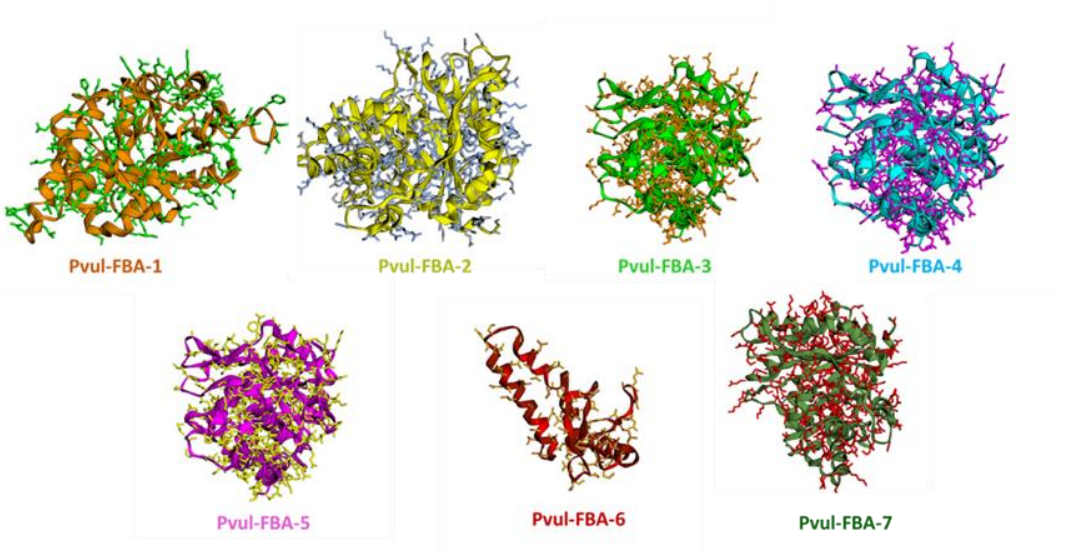

Figure 7. 3D structure modeling of Pvul-FBA proteins.

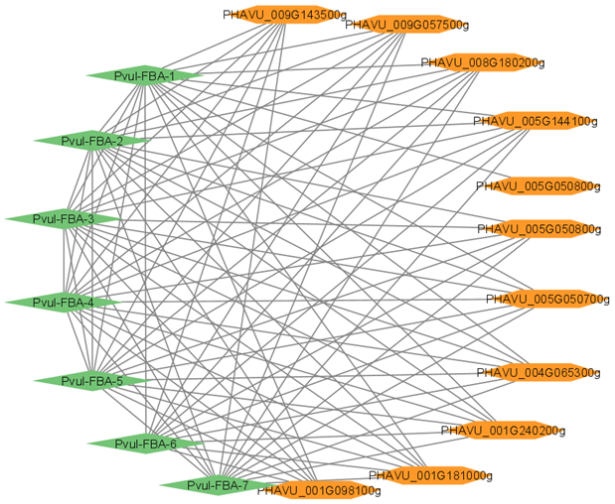

Figure 8. Protein-protein interactions (PPI) of the determined FBA proteins.

For the in silico evaluation of the expression of *Pvul-FBA* genes under drought and salt stress, RNAseq from the NCBI SRA database (Sequences Read Archive), SRR957668 (salt-stressed leaf), SRR958469 (leaf salt control), SRR8284480 (leaf drought control) data and SRR8284481 (drought stressed leaf) were used. The expression levels of the *Pvul-FBA* genes under drought and salt stresses were shown Figure 9 according to the heatmap constituted by the log2 transformation of the RPKM values based on the results obtained from the RNAseq data. Expression profiles of *Pvul-FBA* genes were identified in the shoot tissue of beans under drought and salt stress compared to the control (Figure 9). In salt application, the highest expression profile was determined in the *Pvul-FBA-7* gene, and it was determined that this increase was higher than the control group. The lowest expression profile was found in the *Pvul-FBA-6* gene in salt applications. On the other hand, when drought application was evaluated, the highest expression was detected in the *Pvul-FBA-7* gene.

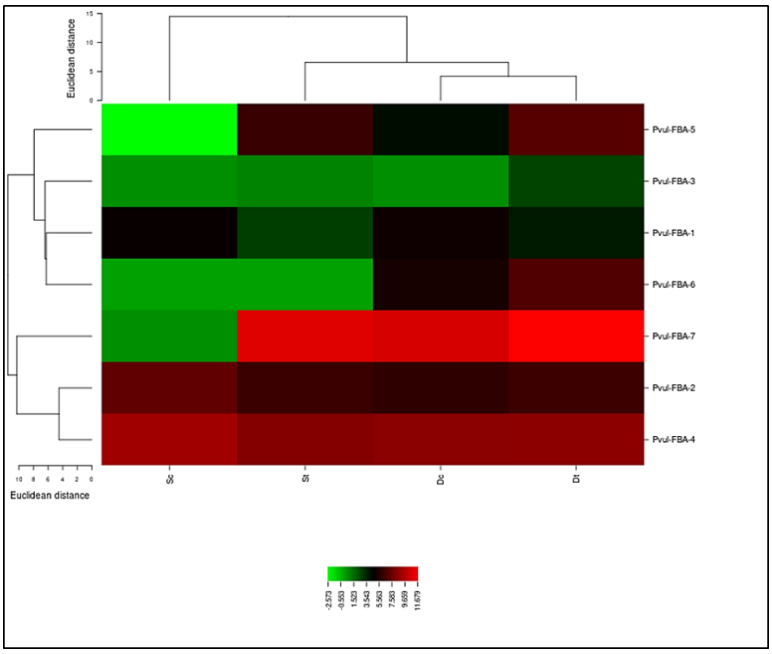

Figure 9. Heatmap of expression of *Pvul-FBA* genes in leaf tissue under drought and salt stress.

4. Discussion

Legumes are essential for human nutrition and the agricultural systems of poor nations since they are the primary source of protein and minerals and a fundamental component of agricultural production systems (Akibode & Maredia, 2012; Yeken et al., 2018). Common bean is the richest vegetable crop in terms of species diversity among legumes (Graham & Ranalli, 1997; Cichy et al., 2015). FBA is involved in gluconeogenesis, glycolysis, and the Calvin-Benson cycle and

is the enzyme that plays an essential role in signal transduction of these stages (Cai et al., 2018). *FBA* genes have essential roles in plant growth and have been determined in many plant species (Lv et al., 2017).

As a result of our study, *Pvul-FBA* genes carrying the FBA domain were determined in beans. Diverse *FBA* gene members have been found in *Spinach oleracea* (Pelzer-Reith et al., 1993), *Oryza sativa* (Kagaya et al., 1995), *Zea mays* (Dennis et al., 1988), *Nicotiana tabacum* (Yamada et al., 2000), *A. thaliana* (Lu et al., 2012), *S. portulacastrum* (Fan et al., 2009) *Solanum lycopersicum* (Cai et al., 2016), *Triticum aestivum* L. (Lv et al., 2017), *Brassica napus* (Zhao et al., 2019), and *Gossypium hirsitum* (Li et al., 2021). Whole Genome Folds or polyploidy is a common phenomenon in nature (Wendel, 2000). In this case, tandem and segmental gene duplications occur, which allow new members of existing gene families to arise. Gene duplication, including tandem and segmental duplications, is one of the essential driving strengths in the evolution of genomes (Kasapoğlu et al., 2022). When Ka/Ks<1, it indicates purifying selection, when Ka/Ks=1, it indicates natural selection, and when Ka/Ks>1, it indicates positive selection during the evolution of the gene sequence (İlhan, 2018; Aygören et al., 2022; Oner et al., 2022). As a result of our research, the Ka/Ks ratios of segmentally duplicated genes were found to be less than 1. This indicates that the evolutionary process of the bean has involved purifying selection. In our study, the relationship between the FBA proteins of *P. vulgaris*, *A. thaliana*, and *G. max* was determined by forming a phylogenetic tree and 4 main groups were obtained. In another study, they determined the phylogenetic relationship between FBA proteins tomato, *A. thaliana*, and rice (Cai et al., 2016). Salt and drought stress, which is one of the abiotic stresses, affects all the main processes in plants such as germination, photosynthetic pigments, growth, nutrient imbalance, water relationship, oxidative stress, and yield. Molecular responses of plants to salt stress are primarily mediated by transcriptional induction of specific genes (Carpici et al., 2009). *FBA* genes, one of these genes, have a vital role in biotic and abiotic (high salt, drought, heavy metal, and low temperature, etc.) stress responses and regulate growth and development in plants (Murad et al., 2014; Shu et al., 2014). As a result of our findings, it was determined that *FBA* genes generally increased more in salt and drought applications than the control. It has been reported that the *FBA* expression level increased under cold, salt, and drought stress in other studies (Abbasi & Komatsu, 2004).

5. Conclusion

This study supplied a thorough investigated of the *FBA* gene family in common beans (*P. vulgaris* L.). Therefore, 7 *Pvul-FBA* genes were obtained in the *P. vulgaris* genome as a result of our study. The gene structure, Ka/Ks findings, and motif suggest that *Pvul-FBA* were significantly protected. This suggests that the *FBA* gene family, has an essential role in the development stages of plants, was examined. This study mentions function of *FBA* genes in beans will be elucidated and will lay the groundwork for many future studies.

Conflict of Interest

The authors have no financial or non-financial interests that would influence the research in this study.

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