IMAM KHOMEINI INTERNATIONAL UNIVERSITY
IJGPB
Iranian Journal of Genetics and Plant Breeding
Print ISSN : 2251-9610
Online ISSN : 2676-346X

Bioinformatic analysis of *FAE1-A* and *FAD2-A* genes in *Camelina sativa*

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ABSTRACT INFO

Research Paper

Received: 04 Jun 2023

Accepted: 09 Mar 2024

ABSTRACT

Camelina (*Camelina sativa*), an oilseed plant in the *Brassicaceae* family, is recognized as a significant crop both biologically and industrially, with recent attention shifting towards its potential as a biofuel source. The close genetic resemblance between *Arabidopsis thaliana* and *C. sativa* has sparked interest among researchers in manipulating oleic acid levels through microRNAs and the gene sequences *FAE1-A* and *FAD2-A*. A recent bioinformatics study focused on these genes in *camelina* revealed that the *FAE1-A* protein is hydrophobic, while *FAD2-A* is hydrophilic. Structural analysis indicated GMQE values of 0.88% for *FAE1-A* and 0.93% for *FAD2-A*. The *FAE1-A* protein's secondary structure comprises 49% helix, 11% beta-sheet, 41% coil, and 9% membrane content with a confidence level of 79.2%. Similarly, the secondary structure of the *FAD2-A* consists of 43% helix, 12% beta-sheet, 45% coil, and 30% membrane content with a confidence level of 79.8%. Codon preference patterns were explored using the Sequence Manipulation Suite database to understand the relationship between codons and gene performance. Furthermore, analysis of *FAE1-A* and *FAD2-A* gene expression showed peak expression levels in developing seeds approximately 20 days after pollination. Further investigation into these structures promises to enhance our understanding of fat biosynthesis, thereby improving oil quality in *C. sativa*.

Key words: Bioinformatics analysis, *Camelina sativa*, Oilseed, *FAE1-A*, *FAD2-A*.

How to cite this article:
Bashiri H., Kahrizi D., Salmanian A. H., Rahnama H., and Azadi P. (2023). Bioinformatic analysis of *FAE1-A* and *FAD2-A* genes in *Camelina sativa*. *Iranian Journal of Genetics and Plant Breeding,* 12(2): 49-59.
DOI: 10.30479/IJGPB.2024.18866.1344

INTRODUCTION

Camelina sativa (*C. sativa*) is an important oilseed plant of both biological and industrial significance, originating from the Mediterranean regions of Europe and Asia. It is an allohexaploid species (2n=6x=40), with a genome size of 785 Mb, approximately six times larger than that of *Arabidopsis* (135 Mb) (Ghorbani *et al*., 2020; Soorni *et al*., 2021; Purnamasari, 2021). The small yellow flowers of Camelina grow at the apex of its stem branches. Its fruit is pear-shaped, housing tiny yellowish-brown or reddish seeds (Pratap and Gupta, 2009; Kumar *et al*., 2012) (Figure 1). *C. sativa* has a short growing season, making it suitable for breeding and gene manipulation. It exhibits strong resistance to drought and cold, especially spring cold, and is also resistant to common pests in oilseeds such as pollinating beetles (Borzoo *et al*., 2021; Borzoo *et al*., 2021; Soorni *et al*., 2022).

Since the oil from this plant contains high amounts of unsaturated fatty acids, such as linoleic acid, it plays a crucial role in human nutrition and health (Raziei *et al*., 2018; Rahimi *et al*., 2021; Mirmoeini *et al*., 2021; Piravi-Vanek *et al*., 2022; Rokni *et al*., 2022; Rokni *et al*., 2022). The plant's medicinal properties include treating burns, wounds, eye inflammation, and stomach ulcers, as well as aiding in cancer and obesity prevention (Zanetti *et al*., 2021).

The body requires unsaturated fats for proper functioning. These fats play a vital role in muscle movement and blood clotting. These fats are not produced by the body and must be obtained through diet (Kapoor *et al*., 2021). One of the most important groups of unsaturated fats is omega-3. As an important fatty acid, omega-3 is composed of three main precursors, which are alpha-linolenic acid (ALA), eicosapentaenoic acid (EPA), and docosahexaenoic acid (DHA). Vegetable and edible oils such as flaxseed oil, soybean oil, and canola oil are potentially good sources of ALA, EPA, and DHA (Simopoulos, 2002; Hixson *et al*., 2015).

FAE1-A facilitates the elongation of fatty acids, particularly very long chain fatty acids (VLCFA) biosynthesis, and aids in its storage in developing seeds, making it a crucial gene in erucic acid biosynthesis (Ma *et al*., 2021). For this reason, in breeding and genetic programs, the main focus is on restricting and suppressing this gene (Li *et al*., 2019; Ma *et al*., 2021). The function of *FAD2* also increases the dienoic fatty acids content, enhancing resistance to cold and salt stress. *FAD2* serves as the pivotal enzyme in the biosynthesis of unsaturated fats in non-photosynthetic tissues such as roots and seeds (Miquel and Browse, 1992; Zhang *et al*., 2012).

MATERIALS AND METHODS

First, the protein sequences of *FAE1-A* (GU929420.1) and *FAD2-A* (GU929417.1) from *C. sativa* were retrieved from the NCBI website. The proteins were 505 and 384 amino acids in length, respectively. The sequences were aligned using Vector-NTI software. Protein domains in the amino acid sequences were identified using the InterPro database. Secondary and three-dimensional structures were determined using the SOPMA and MBC databases. The ProtScale database was utilized for hydropathicity analysis, molecular weight determination, and isoelectric point evaluation.

Figure 1. A: *Camelina sativa* flowers, **B:** *Camelina sativa* seeds.

Additionally, codon preference investigation was conducted using the Sequence Manipulation Suite (SMS) database (Alhashimi *et al.,* 2021; Alsaedy *et al*., 2022; Mirzaei and Shakoory-Moghadam, 2022; Mirzaei and Fazeli, 2022; Kanwal *et al*., 2023; Al-Zaidi *et al*., 2023).

During the evaluation of FAE1-A and FAD2-A gene expression, *C. sativa* plants were cultivated under controlled conditions at 24 °C with a photoperiod of 8 to 16 hours. Flowers were tagged, and the embryos were collected at specified intervals. The expression of *FAE1-A* and *FAD2-A* genes was analyzed in growing seeds at 10, 20, 30, and 40 days post-anthesis (DPA) and in 2-week-old seedlings. RNA was extracted utilizing the column RNA isolation kit of DENAZist company. cDNA synthesis was performed with a Fermentas cDNA synthesis kit and oligo dT primer. Subsequently, real-time PCR reactions were conducted using a Bioer device from China and Takara's SYBR Premix Ex Taq II kit. Gene expression was normalized using the formula $2^{-\Delta\Delta Ct}$.

RESULTS

FAE1-A gene

The *FAE1-A* gene, with accession number GU929420.1, is located on chromosome 11 of the *C. sativa* plant. It consists of 5288 bp nucleotides, encoding a protein with 505 amino acids. The molecular weight of the protein is 55844.73 Daltons, and its isoelectric point is 9.34. Its molecular weight is 55844.73 Daltons and its isoelectric point is 9.34. Additionally, it includes an exon, as indicated in Table 1.

FAD2-A gene

The *FAD2-A* gene, bearing accession number GU929417.1, is located on chromosome 1 of the *C. sativa* plant. It comprises 2791 bp nucleotides and encodes a protein with 384 amino acids. The molecular weight of this protein is 44045.76 Daltons and its isoelectric point is 8.39. Furthermore, it contains three exons, as shown in Table 1.

Three-dimensional structure of *FAE1-A* and *FAD2-A* proteins

Molecular homology modeling using the SWISS-MODEL server on Expasy resulted in the 3D structure of *FAE1-A* and *FAD2-A* proteins. GMQE values of 0.88 for *FAE1-A* and 0.93 for *FAD2-A* indicated high accuracy in the structural estimation of these genes. These results were consistent with previous findings of genomic similarity of these proteins (Figure 2) (Kang *et al*., 2011; Liang *et al*., 2013).

Secondary structure analysis and protein domains in *FAE1-A* and *FAD2-A* genes

Protein domain analysis was performed using the InterPro database at https://www.ebi.ac.uk/interpro. Results revealed the presence of a PLN02932 protein domain in the *FAE1-A* sequence. This PLN02932 protein domain is the sole member of the large cl30445 family with an E-value=0e+00 and is highly conserved within the *FAE1* family. This protein domain extends from amino acid 10 to amino acid 490 (Figure 3). Analysis of the InterPro database for the *FAD2-A* gene indicated the absence of a protein domain. The *FAE1-A* protein's secondary structure consists of 49% helix, 11% beta-sheet, 41% coil, and 9% membrane content with 79.2% confidence (Figure 4), whereas the

Table 1. Genes sequence results of *FAE1-A*, and *FAD2-A*.

Name	*FAE1-A*	*FAD2-A*
ORGANISM	Camelina sativa	Camelina sativa
Accession number nucleotide	GU929420.1	GU929417.1
Accession number protein	ADN10812.1	ADN10824.1
Gene ID	104721342	104776214
Gene symbol	LOC104721342	LOC104776214
Gene description	3-ketoacyl-CoA synthase 18-like	omega-6 fatty acid desaturase, endoplasmic reticulum
Chromosome	11	1
Chromosome location bp	3110775-3112479	4948902-4952339
Nucleotide length	5288 bp	2791bp
Protein length	505aa	384aa
Molecular weight (Da)	55844.73	44045.76
Isoelectric point	9.34	8.39
Total Exon	1	3

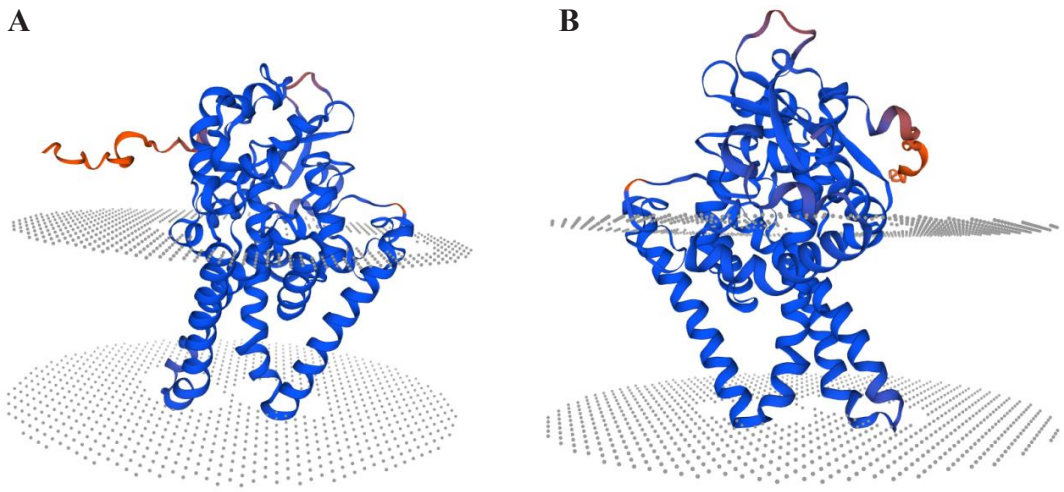


Figure 2. A: Three-dimensional structure of *FAE1-A* protein, **B:** Three-dimensional structure of *FAD2-A* protein.

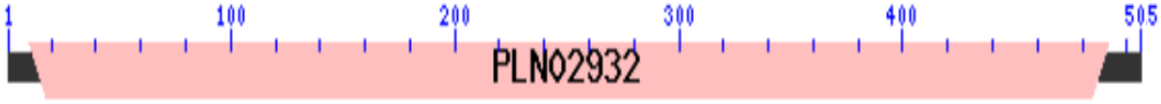


Figure 3. PLN02932 protein domain in *FAE1*-A sequence.

FAD2-A protein comprises 43% helix, 12% beta-sheet, 45% coil, and 30% membrane content with 79.8% confidence (Figure 5).

Hydropathicity analysis of *FAE1-A* and *FAD2-A* proteins

Hydropathicity analysis of proteins was performed using the ProtScale database. The results showed that *FAE1-A* exhibits hydrophobic characteristics attributed to the abundance of hydrophobic amino acids (with positive hydrophilicity) in its structure (Figure 6). The average hydropathicity of the amino acids sequence was +0.02251713 (with a maximum hydropathicity of 3.167, and a minimum hydropathicity of -3.067). In contrast, it was found that *FAD2-A* is a hydrophilic protein due to the prevalence of hydrophilic amino acids (with negative hydrophilicity) in its structure. It has been well known that hydrophilic proteins play a crucial role in enhancing tolerance to abiotic stress. The average hydrophilicity of the *FAD2-A* amino acid sequence was determined to be -0.63303191 (with a maximum hydrophilicity of 2.9 and a minimum hydrophilicity of -3.144) (Figure 7).

The expression of *FAE1-A* and *FAD2-A*

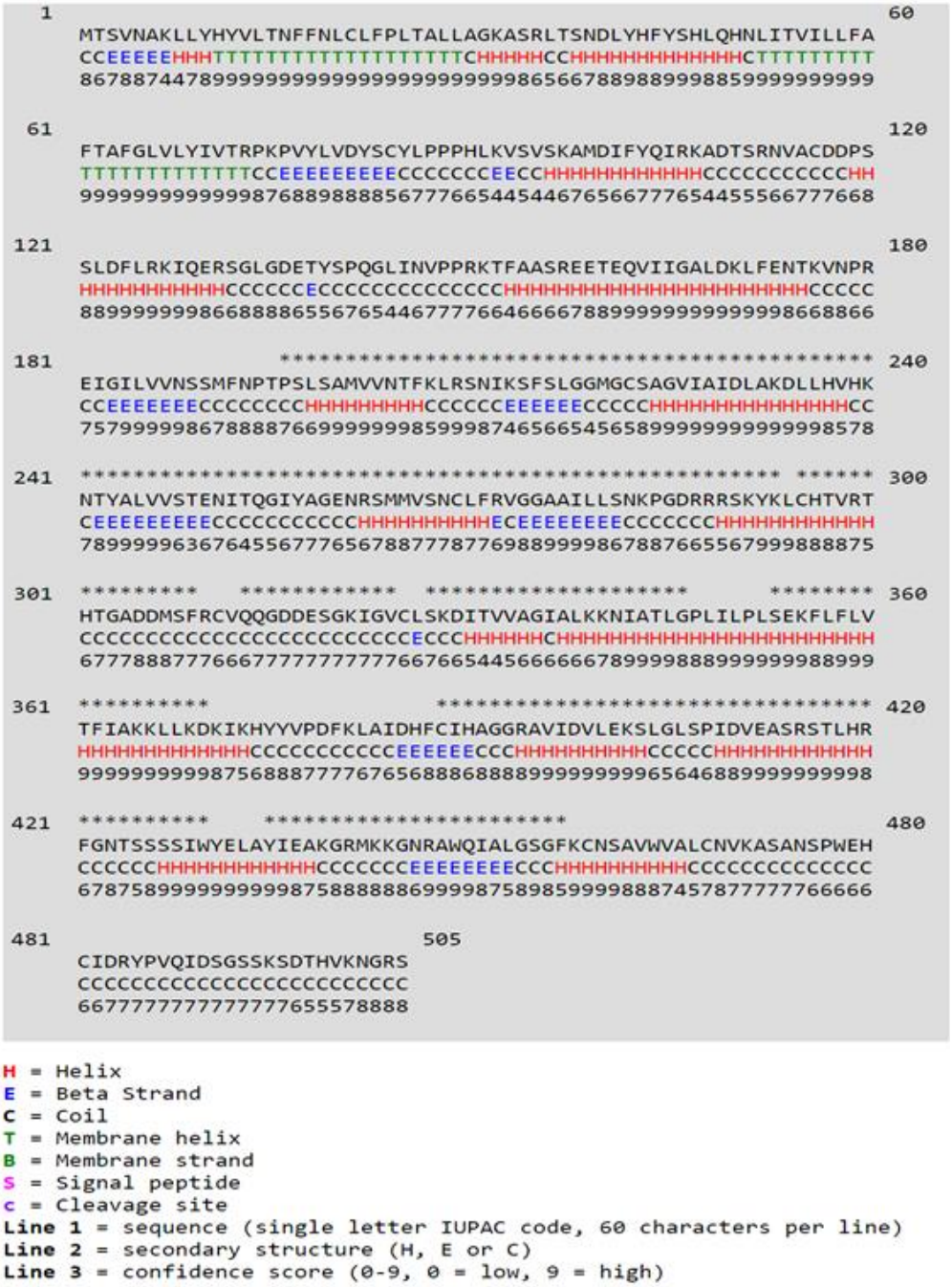
In both genes, the highest and lowest expressions were related to 20 DPA and 40 DPA, respectively (Figures 8 and 9).

Investigating the codon preference of the *FAE1-A* and *FAD2-A* genes

The codon preference of *FAE1-A* and *FAD2-A* genes was investigated using the Sequence Manipulation Suite (SMS) database. The results for *FAE1-A* and *FAD2-A* genes are shown in Tables 2 and 3. This data is valuable for further studies, including protein analysis and their transfer. Moreover, codon analysis may help identify specific and preferred sequences for synonymous codons.

DISCUSSION

The *FAE1-A* and *FAD2-A* genes are two key and important genes in the biosynthesis of unsaturated fatty acids in the *C. sativa* plant (Hutcheon *et al.*, 2010; Nguyen *et al.*, 2013). Genetic and biological analyses indicate three copies of the *FAD2* and *FAE1* genes, similar to that found in other species such as *Arabidopsis thaliana*. Comparative genomics reveals similarities between the *FAD2* gene's downstream and the *FAE1* gene's upstream regions with the Arabidopsis genome. Also, gene expression analyses demonstrate higher activity of these genes in developing seeds. On the other hand, flow cytometry reveals nearly triple the DNA content in Camelina compared to diploid relatives. Phylogenetic studies



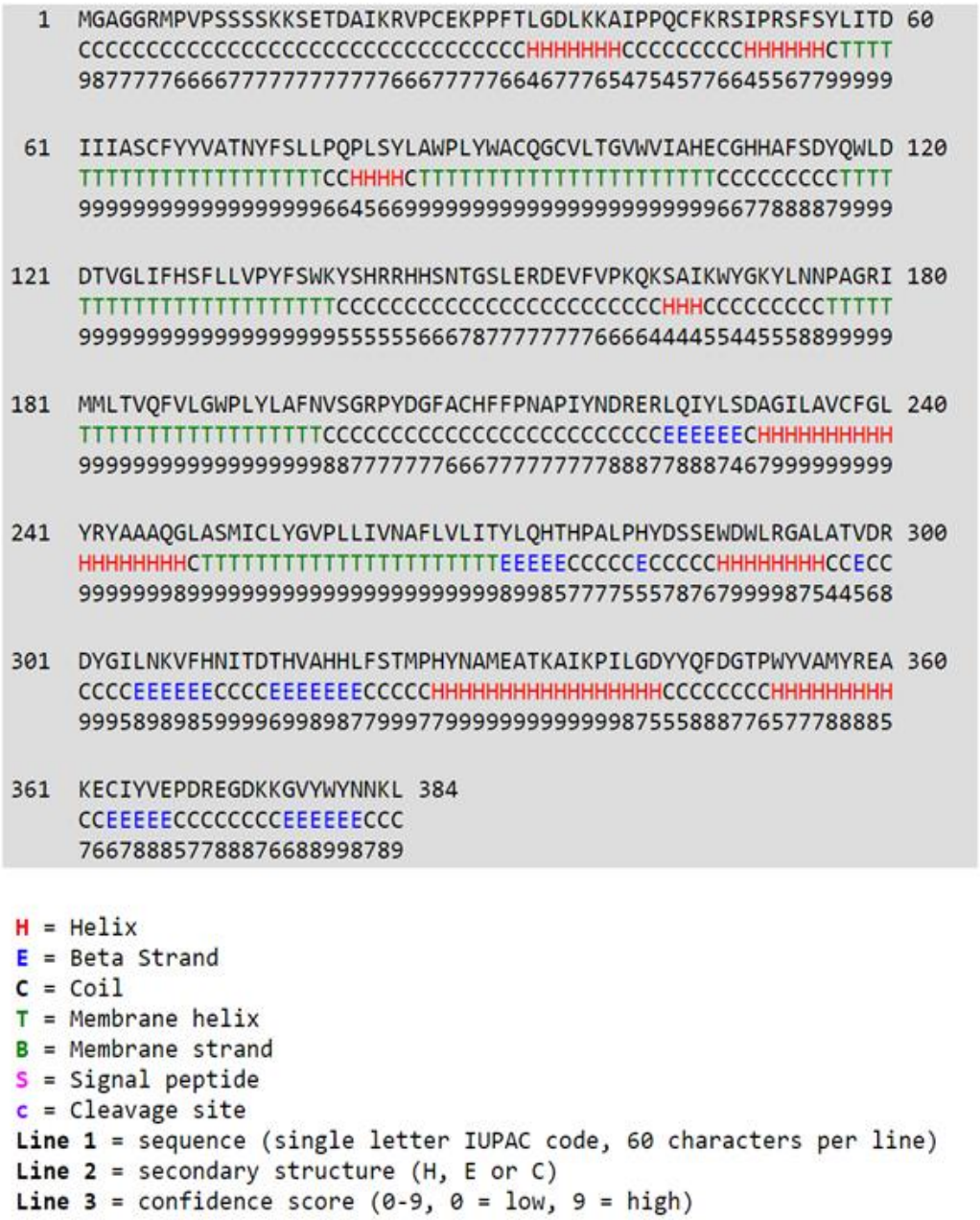
H = Helix
E = Beta Strand
C = Coil
T = Membrane helix
B = Membrane strand
S = Signal peptide
c = Cleavage site
Line 1 = sequence (single letter IUPAC code, 60 characters per line)
Line 2 = secondary structure (H, E or C)
Line 3 = confidence score (0-9, 0 = low, 9 = high)

Figure 4. Investigation of secondary structure in *FAE1-A* protein.

suggest a shared ancestry between *C. sativa* and *C. microcarpa* (Hutcheon *et al.,* 2010). Therefore, the detailed study of the structure and function of these key genes is an effective step for a deeper understanding of the regulatory pathways of fatty acids in this plant. Therefore, the present study focuses on evaluating nucleotide and protein sequences, secondary structures, three-dimensional structures, domains, hydrophilicity, and codon preference to identify similarities and differences between these genes. Understanding secondary and 3D structures and investigating the protein's local order is crucial for determining protein function. Our findings highlight differences in hydrophilicity (*FAD2-A*) and hydrophobicity (*FAE1-A*) between the proteins.

Analyzing codon preference is essential for studying codon-gene expression relationships, aiding in the investigation of gene expression variations across species.

Regarding gene expression, *FAE1-A* and *FAD2-A* genes exhibit increased expression levels up to 20



H = Helix
E = Beta Strand
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S = Signal peptide
c = Cleavage site
Line 1 = sequence (single letter IUPAC code, 60 characters per line)
Line 2 = secondary structure (H, E or C)
Line 3 = confidence score (0-9, 0 = low, 9 = high)

Figure 5. Investigation of secondary structure in *FAD2-A* protein.

days post-pollination, peaking at day 20, as depicted in Figures 1 and 2. Hutcheon *et al.* (2010) research supports these findings, indicating minimal *FAD2* gene expression in seedlings and undetectable *FAE1* gene expression. In general, the results show that *FAE1-A* and *FAD2-A* genes have common copies, SNPs, and polymorphisms that can inform future research. Finally, it can be said that the detailed study of these structures provides a broad insight into the biosynthesis of fats and a suitable model for genetic manipulations to improve oil quality in *C. sativa*.

ACKNOWLEDGEMENTS

We would like to express our sincere gratitude to all the individuals and organizations who have contributed to the publication of this research paper. Also, we sincerely thank Biotechnology Headquarters and the Razi University of Kermanshah for the financial support and support necessary to complete this project. We thank Dr. Fateme Forootan (Maya Milk, Inc., Delaware, USA), for her technical support.

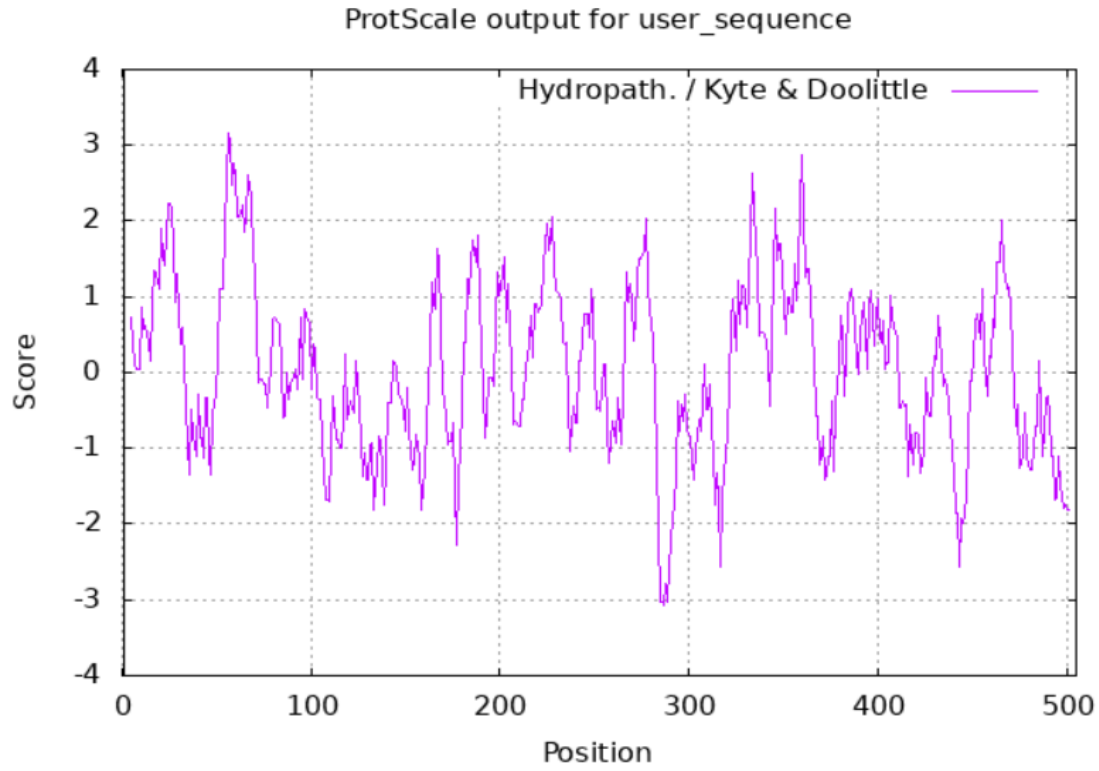

Figure 6. Hydropathicity diagram of *FAE1-A* protein.

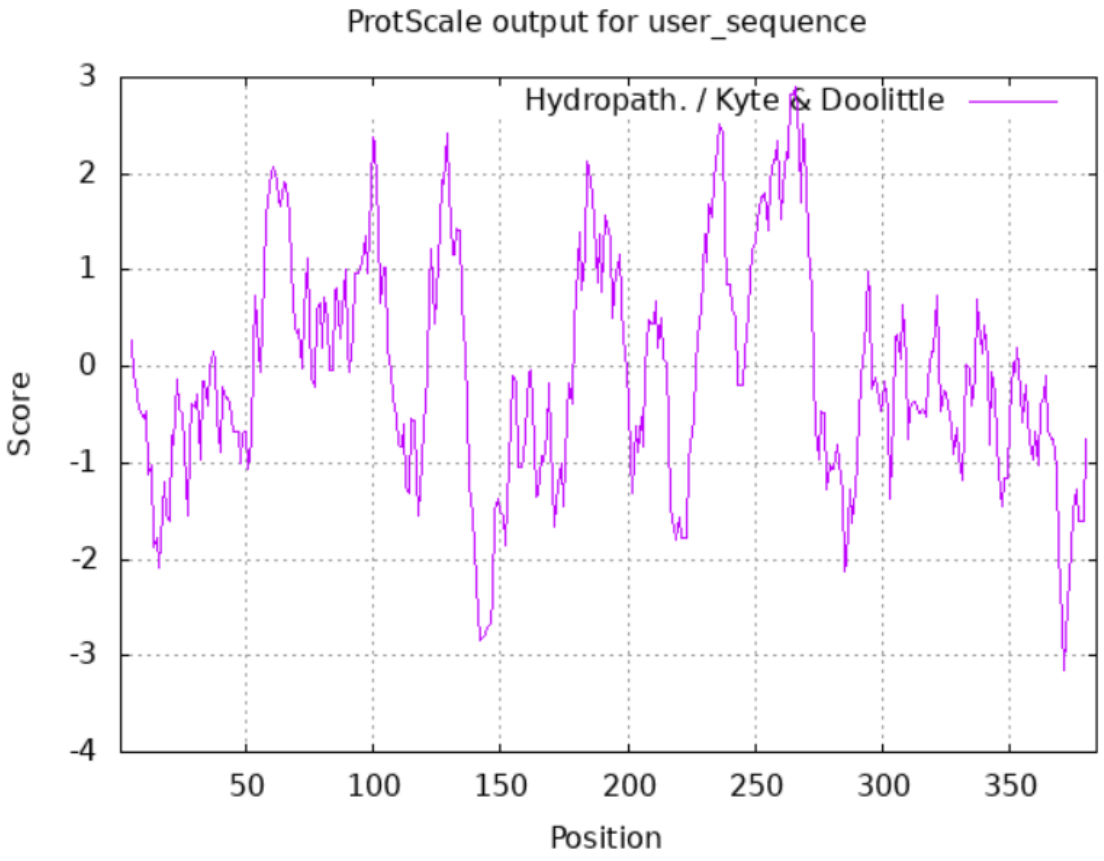

Figure 7. Hydropathicity diagram of *FAD2-A* protein.

Table 2. Codon Usage results. Results for 5288 residue sequence "*FAE1-A*" starting "GGTATGAATT".

AmAcid	Codon	Number	/1000	Fraction	AmAcid	Codon	Number	/1000	Fraction
Ala	GCG	9	5.11	0.23	Asn	AAT	56	31.78	0.63
Ala	GCA	19	10.78	0.47	Asn	AAC	33	18.73	0.37
Ala	GCT	11	6.24	0.28					
Ala	GCC	1	0.57	0.03	Pro	CCG	12	6.81	0.2
					Pro	CCA	21	11.92	0.35
Cys	TGT	33	18.73	0.73	Pro	CCT	17	9.65	0.28
Cys	TGC	12	6.81	0.27	Pro	CCC	10	5.68	0.17
Asp	GAT	34	19.3	0.72	Gln	CAG	17	9.65	0.3
Asp	GAC	13	7.38	0.28	Gln	CAA	40	22.7	0.7
Glu	GAG	21	11.92	0.4	Arg	AGG	10	5.68	0.09
Glu	GAA	31	17.59	0.6	Arg	AGA	41	23.27	0.38
					Arg	CGG	16	9.08	0.15
Phe	TTT	77	43.7	0.73	Arg	CGA	20	11.35	0.18
Phe	TTC	28	15.89	0.27	Arg	CGT	15	8.51	0.14
					Arg	CGC	7	3.97	0.06
Gly	GGG	6	3.41	0.13					
Gly	GGA	21	11.92	0.44	Ser	AGT	21	11.92	0.14
Gly	GGT	12	6.81	0.25	Ser	AGC	17	9.65	0.12
Gly	GGC	9	5.11	0.19	Ser	TCG	21	11.92	0.14
					Ser	TCA	44	24.97	0.3
His	CAT	24	13.62	0.59	Ser	TCT	24	13.62	0.17
His	CAC	17	9.65	0.41	Ser	TCC	18	10.22	0.12
Ile	ATA	66	37.46	0.46	Thr	ACG	20	11.35	0.19
Ile	ATT	49	27.81	0.35	Thr	ACA	44	24.97	0.41
Ile	ATC	27	15.32	0.19	Thr	ACT	23	13.05	0.21
					Thr	ACC	20	11.35	0.19
Lys	AAG	38	21.57	0.26					
Lys	AAA	111	63	0.74	Val	GTG	19	10.78	0.21
					Val	GTA	23	13.05	0.26
Leu	TTG	49	27.81	0.24	Val	GTT	31	17.59	0.35
Leu	TTA	61	34.62	0.3	Val	GTC	16	9.08	0.18
Leu	CTG	12	6.81	0.06					
Leu	CTA	20	11.35	0.1	Trp	TGG	23	13.05	1
Leu	CTT	37	21	0.18					
Leu	CTC	23	13.05	0.11	Tyr	TAT	44	24.97	0.72
					Tyr	TAC	17	9.65	0.28
Met	ATG	33	18.73	1					
					End	TGA	37	21	0.31
					End	TAG	19	10.78	0.16
					End	TAA	62	35.19	0.53

Table 3. Codon Usage results. Results for 2791 residue sequence "*FAD2-A*" starting "GCGGAGGAGC".

AmAcid	Codon	Number	/1000	Fraction	AmAcid	Codon	Number	/1000	Fraction
Ala	GCG	5	5.38	0.13	Asn	AAT	18	19.35	0.58
Ala	GCA	8	8.6	0.2	Asn	AAC	13	13.98	0.42
Ala	GCT	16	17.2	0.4					
Ala	GCC	11	11.83	0.28	Pro	CCG	5	5.38	0.12
					Pro	CCA	12	12.9	0.29
Cys	TGT	23	24.73	0.7	Pro	CCT	14	15.05	0.33
Cys	TGC	10	10.75	0.3	Pro	CCC	11	11.83	0.26
Asp	GAT	15	16.13	0.56	Gln	CAG	14	15.05	0.67
Asp	GAC	12	12.9	0.44	Gln	CAA	7	7.53	0.33
Glu	GAG	6	6.45	0.25	Arg	AGG	5	5.38	0.1
Glu	GAA	18	19.35	0.75	Arg	AGA	17	18.28	0.35
					Arg	CGG	1	1.08	0.02
Phe	TTT	53	56.99	0.6	Arg	CGA	5	5.38	0.1
Phe	TTC	36	38.71	0.4	Arg	CGT	12	12.9	0.24
					Arg	CGC	9	9.68	0.18
Gly	GGG	6	6.45	0.14					
Gly	GGA	14	15.05	0.33	Ser	AGT	7	7.53	0.1
Gly	GGT	16	17.2	0.38	Ser	AGC	1	1.08	0.01
Gly	GGC	6	6.45	0.14	Ser	TCG	7	7.53	0.1
					Ser	TCA	11	11.83	0.16
His	CAT	21	22.58	0.68	Ser	TCT	30	32.26	0.44
His	CAC	10	10.75	0.32	Ser	TCC	12	12.9	0.18
Ile	ATA	19	20.43	0.33	Thr	ACG	2	2.15	0.06
Ile	ATT	19	20.43	0.33	Thr	ACA	10	10.75	0.3
Ile	ATC	19	20.43	0.33	Thr	ACT	11	11.83	0.33
					Thr	ACC	10	10.75	0.3
Lys	AAG	18	19.35	0.43					
Lys	AAA	24	25.81	0.57	Val	GTG	13	13.98	0.19
					Val	GTA	10	10.75	0.14
Leu	TTG	27	29.03	0.25	Val	GTT	23	24.73	0.33
Leu	TTA	15	16.13	0.14	Val	GTC	24	25.81	0.34
Leu	CTG	11	11.83	0.1					
Leu	CTA	7	7.53	0.06	Trp	TGG	18	19.35	1
Leu	CTT	30	32.26	0.28					
Leu	CTC	19	20.43	0.17	Tyr	TAT	24	25.81	0.48
					Tyr	TAC	26	27.96	0.52
Met	ATG	24	25.81	1					
					End	TGA	13	13.98	0.43
					End	TAG	9	9.68	0.3
					End	TAA	8	8.6	0.27

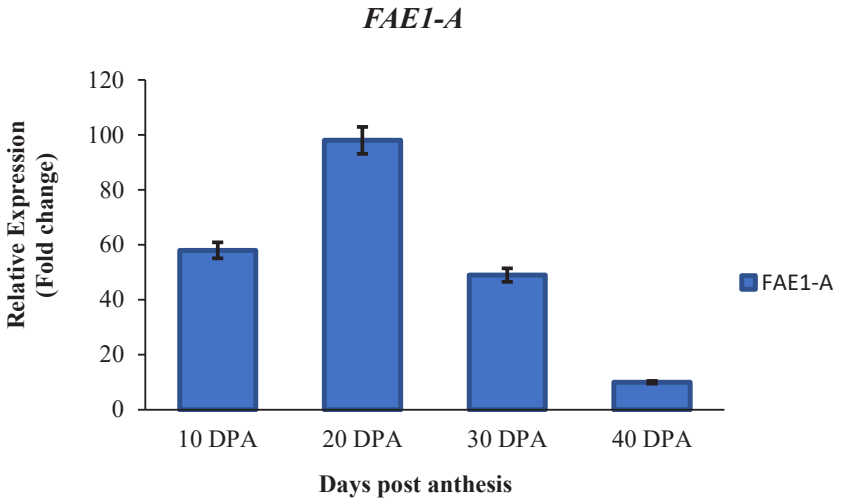

Figure 8. *FAE1-A* gene expression level.

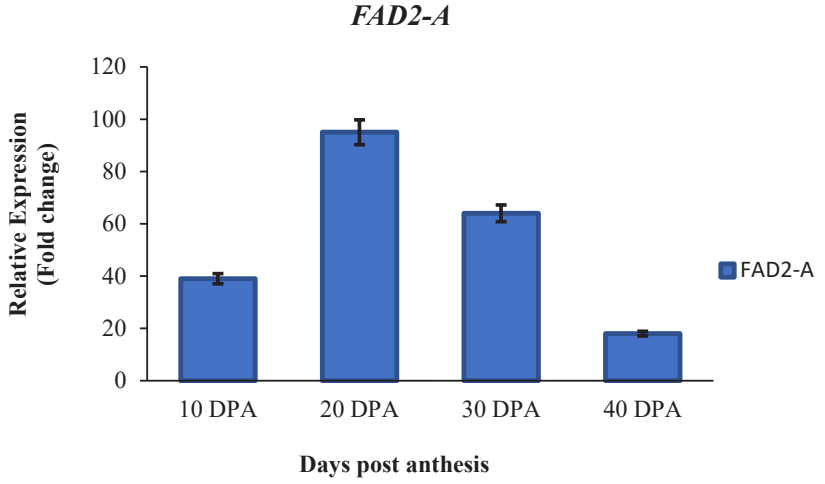

Figure 9. *FAD2-A* gene expression level.

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