



International Journal of Agriculture Innovations and Cutting-Edge Research



Genome-Wide Identification, Structural Characterization and Phylogenetic Analysis of Dof (DNA-Binding with one finger) Transcription Factor in Lima Bean (*Phaseolus lunatus L.*)

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Abstract

Dofs are plant-specific transcription factors involved in diverse functions, including growth, development, hormonal and Abiotic stress response regulation. Although genome-wide analysis of Dof genes has been performed in many species, these genes have yet to be analyzed in lima bean. The current study was aimed at exploring and characterizing the Dof gene family across the genome of the lima bean. Forty PlDof genes in the genome of lima bean were detected during the present study, and named as PlDof1-PlDof40 based on their location on the chromosome in the ascending order. PlDof12 was recorded as the largest gene with 1560 bp CDS, 519 amino acid protein length (PL) and 57.126 kDa protein molecular weight (PMW), while PlDof-23 was found as the smallest one with only 522 CDS, 173 PI and 19.75 kDa PMW, respectively. Nucleus was predicted as a major residence for all 40 PlDof proteins. Isoelectric points and GRAVY were found in the range of 5.35 to 8.91 and -0.269 to -0.746, respectively. The varying number of exons reveals that deletions/additions have occurred during evolution, resulting in variation in motif number. Motif1was conserved in all PlDof genes. The phylogenetic tree reveals that paralogs contributed 33% to the PlDof gene family expansion. Ka/Ks ratios of paralogs reveal that they were all under purifying selection. The promoter region has environmental, developmental, light and hormone-responsive elements that might contribute to the diverse function of PlDof. This study provides a basis for the functional validity of PlDof genes.

Keywords: Lima bean, Dof, genome-wide analysis, evolutionary analysis, transcription factor

DOI:	https://zenodo.org/records/15656357
Journal Link:	https://iai.bwo-researches.com/index.php/jwr/index
Paper Link:	https://iai.bwo-researches.com/index.php/jwr/article/view/117
Publication Process	Received: 30 Mar 2025 / Revised: 15 Jul 2025 / Accepted: 23 Jul 2025 / Published: 27 Jul 2025
ISSN:	Online [3007-0929], Print [3007-0910]
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Indexing:	     
Publisher:	BWO Research International (15162394 Canada Inc.) https://www.bwo-researches.com

Introduction

Dof genes encode 200-400 amino acid-long transcription factors with 2 distinct ends. The N-terminal end with 52 52-amino-acid conserved domain and a variable domain occupying the C-terminal end (Yang *et al.*, 2017). Specific cis-acting element (AAAG or CTTT) in upstream regions of target genes is recognized by the highly conserved N-terminal domain (Plesch *et al.*, 2001; Yanagisawa, 2004). The C-terminal domain is less conserved and mainly concerned with the regulation of diverse genes at the transcriptional level (Gupta *et al.*, 2015). Thus, the cross-talk of DNA binding N-terminal and variable C-terminal ends with cis-acting elements and other proteins helps in regulating the genes of interest (Noguero *et al.*, 2013).

The Dof gene family has been explored in diverse plant species with a vital role in plant growth (Fornara *et al.*, 2009), stresses (Cai *et al.*, 2016) and light signal transduction (Kondhare *et al.*, 2019). The AtDofs help in the healing of mechanical injury and promote callogenesis in *Arabidopsis thaliana* by enhancing the growth (Zhang *et al.*, 2022). The inhibition of SIDof1, via RNAi approach, delayed the production of lycopene, resulting in late maturity of *Solanum lycopersicum* (Wang *et al.*, 2021). Similarly, PavDof6 and PavDof2/15 are involved in switching on and off of cell wall modifying genes, respectively, eventually leading to early maturity and delayed softening of cherry fruit (Zhai *et al.*, 2022). AdDof3 bind to cis-acting elements and activates the AdBAM3L gene and hence promoting kiwifruit maturity (Zhang *et al.*, 2018). Likewise, the role of AdDof4 in inhibiting fatty acid desaturase gene (AdFAD1) was unlocked while evaluating the response of ethylene(to volatile compounds) in kiwifruit (Zhang *et al.*, 2020). Hardness provides a barrier for the protection of

fruits against insects, which is attributed to the deposition of lignin and cellulose in the plant cell wall (Zhao and Dixon, 2011). Dof factors regulate these polymers by playing a vital role in carbon metabolism (Kasirajan *et al.*, 2018). VDof1 and VDof2 target different genes at various stages and facilitate differentiation of vascular tissues in *Arabidopsis thaliana* (Ramachandran *et al.*, 2020).

Recent research has demonstrated the role of Dof genes in combating the ill-effects of high/low temperature, salinity and drought stress. Over-expression of SLDOF25/26 in *Arabidopsis* elevates its resistance to water deficiency and salinity (Park *et al.*, 2003). Transforming upland cotton with DOF1 changes oil composition in seeds and enhances resistance to cold and salt stresses (Su *et al.*, 2017). SoDof15 and SoDof3 up-regulated against drought and heat stress, respectively (Yu *et al.*, 2021).

Among the bean crops, lima bean is the second largest one, both with respect to area under cultivation and consumption (López-Alcocer *et al.*, 2016). Lima bean originated from the USA, but over time its cultivation gained speed and has grown in many regions all across the globe (Baudoin *et al.*, 2006; Martínez-Castillo *et al.*, 2014). Lima bean is a rich source of proteins, fibres, vitamins and minerals (Jin *et al.*, 2014). The fat-free proteins make this crop superior to other legume crops (Adebo *et al.*, 2023). Lima bean has shown enhanced tolerance to abiotic stresses (Nascimento *et al.*, 2017) and exhibited vigorous growth to plant growth-promoting hormones (Sá *et al.*, 2023). Thus, the current study was carried out on the assumption of lima bean as a rich source of Dof genes.

Materials and Methods

Identification of Dof genes across the lima bean genome

DOF sequence of *Arabidopsis thaliana* (NP_201099.1) was isolated from NCBI (<https://www.ncbi.nlm.nih.gov/>) and inserted in Motif finder (<https://www.genome.jp/tools/motif/>) for detecting zf-Dof domain. AtDOF domain was blasted against Lima bean genome using Phytozome v.13 (<https://phytozome-next.jgi.doe.gov>) ([Goodstein et al., 2012](#)) for extracting PlDof transcripts. Short sequences, with no more use in the onward process, were deleted.

Physical characterization and predicting the location of PlDofs proteins

Molecular weight, protein length and CDS of PlDofs were taken from Phytozome. Similarly, other features of PlDof proteins, including PI and GRAVY, were obtained from Expasy Protparam (<https://web.expasy.org/protparam>, [Gasteiger et al., 2003](#)). PlDof protein sequences were inserted into Wolf Psort for predicting their sub-cellular location. Wolf Psort-based generated data was used for making a heatmap through TBtool.v1.09854

Conserved domain and interspecific phylogeny of PlDof Proteins

Two files, including renamed protein and hit data files, mandatory for finding conserved domains, were obtained from TBtool.v1.09854 ([Chen et al., 2018](#)) and conserved domain database ([Marchler-Bauer et al., 2015](#)), respectively. The files were subjected to TBtool v1.09854 for generating domain architecture ([Chen et al., 2018](#)). PlDof sequences were inserted in MEGA 11 ([Kumar et al., 2016](#)) for exploring phylogeny between lima bean and *Arabidopsis thaliana* based on maximum likelihood (ML, 1,000 bootstrap replicates). Two leaf (Dof) from the same plant and originating from the most recent common

ancestor (node) in the phylogenetic tree were termed as paralogs, while those belonging to different plants were named as orthologs.

Conserved motif and structure of PlDof genes

Conserved motifs were visualized in PlDof proteins using Multiple Em for Motif Elicitation (<http://memesuite.org>). CDS and genomic sequences of *PlDof* genes were extracted from Phytozome and subjected to Gene Structure Display Server 2.0 (<http://gsds.gao-lab.org/>) ([Hu et al., 2015](#)) for visualizing the gene's structure.

Mapping and duplication of the PID of genes

The mandatory information required for locating PlDof genes, including chromosome number, position and length of PlDof genes, was extracted from Phytozome. The information was inserted in PhenoGram Plot for mapping PlDof on the chromosomes (<http://visualization.ritchielab.psu.edu/phenogram/s/plot>). The values of non-synonymous (Ka) and synonymous (Ks) substitutions, PlDof paralog pairs, were obtained from TBTool ([Chen et al., 2018](#)). The Ka/Ks ratio was analyzed to determine the pattern of duplicated PID of genes.

Promoter Region Analysis

A sequence of 1500bp upstream to the translation initiation site (ATG) was taken from Phytozome of each gene. PlantCARE (<https://bioinformatics.psb.ugent.be/web/tools/plantcare/html/>) was used for exploring *cis*-regulatory elements in PlDof genes ([Lescot et al., 2002](#)).

Statistical analysis

A factorial complete randomized design (CRD) with 3 replications was used to get valid estimates of treatment effect, having minimum experimental error. Statistical software was used for the analysis of data. ANOVA or the F test was used to determine the level of treatment

effect, while the least significant difference (LSD) test was applied to compare means after ANOVA.

Results

Detection of Dof genes across the lima bean genome and physico-chemical characterization of respective proteins

Forty *PlDof* genes across the genome of lima bean were detected during the present study, and named as *PlDof1*-*PlDof40* based on their location on the chromosome in the ascending order. *PlDof12* was recorded as the largest gene with 1560 bp CDS, 519 amino acids protein length (PL) and 57.126 kDa protein molecular weight (PMW), while *PlDof23* was found as the smallest one with only 522 CDS, 173 PI and 19.75 kDa PMW, respectively. Nucleus was predicted as a major residence for all *PlDof* proteins (Table 1). The predicted sub-cellular location of *PlDof* proteins has been visualized in Figure 1. Isoelectric points and GRAVY were found in the range of 5.35 to 8.91 and -0.269 to -0.746, respectively (Table 1)

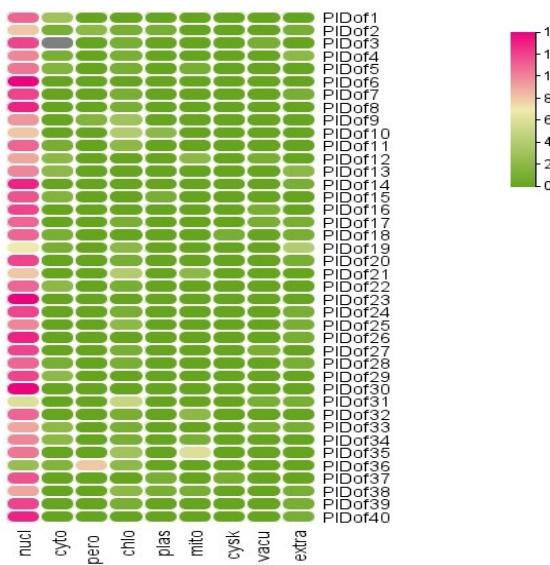


Figure 1. Wolf Psort-based sub-cellular localization of *PlDof* proteins. Quantitative heat map of the *PlDof* gene represents sub-cellular localization. The red bar represents a high quantity of

proteins, and the green bar represents a low quantity of proteins.

Interspecific Phylogeny of *PlDof* Proteins

Seventy-six *PlDof* proteins across two different species, including *Phaseolus lunatus* and *Arabidopsis thaliana*, were clustered into 9 sub-groups (A, B1, B2, C1, C2.1, C2.2, C3, D1, and D2). Sub-group A comprise 7 genes, Sub-group B1 comprises 10 genes and Sub-group B2 on 10 genes. Sub-group C1 comprise 8 genes, C2.1 have 9 genes, C2.2 have 5 genes, and C3 have 6 genes. Sub-group D1 has 17 genes and D2 have 4 genes. A total of 23 paralogs were found, and out of 23, *P. lunatus* has the maximum (13) paralogs, while *A. thaliana* has 10. Two orthologs were reported in *Phaseolus lunatus* and *A. thaliana* (Figure 2).

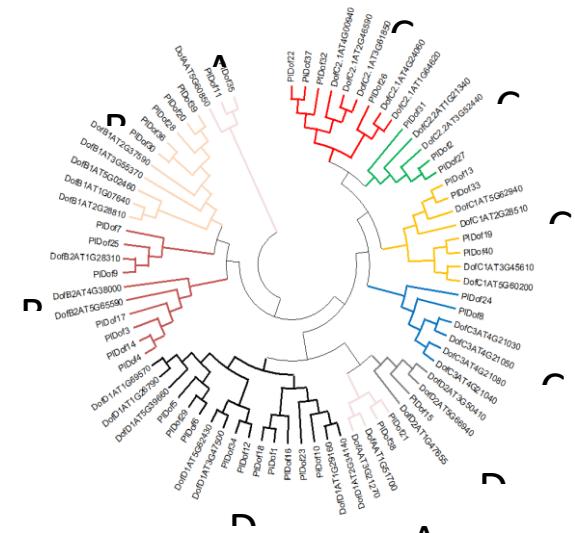


Figure 2. Comparative analysis of *PlDof* proteins across different plant species. A phylogenetic tree was constructed through MEGA 6.0 using the Maximum Likelihood (ML) method. Different subgroups are highlighted with different colours.

Chromosomal mapping and duplication of *PlDof* genes

Forty *PlDof* genes were unequally distributed on 11 chromosomes. Eight *PlDofs* (maximum) were placed on chromosome number 8, while only 1 *PlDof*

(minimum) was found on chromosome number 4 (Figure 3). Segmental duplication was witnessed in all the paralog pairs (Figure 3). The Ka/Ks ratio was less than 1 for 12 paralogs, so they were under purifying selection, while no result was shown for Pl01G0000238000-Pl04G0000060700 paralog (Table 2)

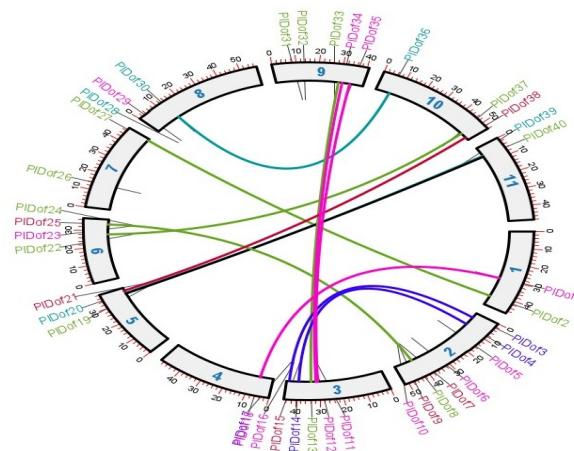


Figure 3. Chromosomal locations and duplication patterns of PIDof genes across the lima bean genome. The chromosome number is mentioned in each bar. Each line connects genes of a paralog pair. PID of genes, structural motifs, and configuration

PIDof in phylogenetic tree were divided into nine sub-groups, including A, B1, B2, C1, C2.1, C2.2, C3, D1, and D2. The Sub-groups A, B1 and B2 have 4, 5 and 7 genes, respectively. Similarly, sub-groups C1, C2.1, C2.2 and C3 comprise 4, 4, 3 and 2 genes, respectively. Ten genes were allocated to sub-group D1 and only 1 gene to D2 (Figure 4A). Each member of subgroups A, C3 and D2 has only 1 exon. The number of exons in members of subgroups B1 and C2.1 range from 1-2, while genes associated with C1 have 2 exons. All genes belonging to B2 have 1 exon, except PIDof25, with 2 exons. Similarly, each gene of subgroup D1 has 2 exons, except PIDof12 with 1 exon. Subgroup C2.2 has the widest range with 1-3 exons (Figure 4B). Maximum motifs (7)

were detected in eight members of subgroup D1 with similar order and type, while only 1 motif (minimum) was found in each member of subgroups A, B2, C1, C2.1 and C3. All members belong to subgroup C2.2 have 1 motif except PIDof27, with 2 motifs (1 &10). Subgroup B1 revealed 3 motifs. A conserved motif1 was explored in all PIDofs (Figure 4C).

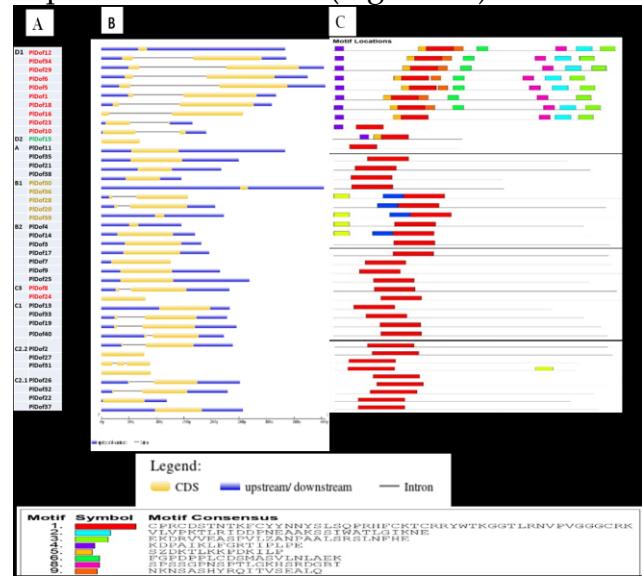


Figure 4. Phylogenetic (A), gene structure (B) and motif analysis (C) of PIDof in lima bean.

Promoter Analysis

From PlantCARE, a total of 838 cis-acting regulatory elements were explored 1500bp upstream region of 40 *PIDof* genes. Cis-regulatory elements were dominated by light-responsive elements(52%), followed by hormone-responsive elements (27%), environmental stress (11%), developmental (8%), and site binding elements (2%)(Figure 5). The detection of a large number of cis-regulatory elements indicates the involvement of *PIDof* genes in functions with a major emphasis on growth and response to environmental stresses.

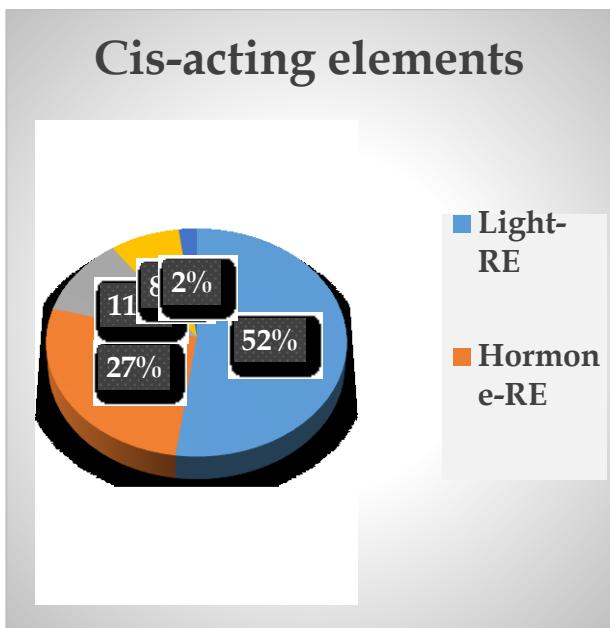


Figure 5: Different cis-regulatory elements (%) in the promoter region of PlDof genes

Discussion

Experimental evidence has unlocked the important role of Dof factors in regulating the expression of various genes under major stresses; however, this family has remained unexplored in lima bean. In this study, 40 Dof genes were detected across the genome of lima bean, which is in line with reports of [Cao et al. \(2020\)](#) in *Medicago sativa*. However, the number of Dof detected in the current study is more than 28 reported in *Eugenia uniflora* ([Waschburger et al., 2022](#)), 22 in spinach ([Yu et al., 2021](#)) and 16 in tea ([Yu et al., 2020](#)), 36 each in watermelon ([Zhou et al., 2020](#)) and *Areca catechu* ([Li et al., 2022a](#)), and 20 in *Chrysanthemum morifolium* ([Song et al., 2016](#)). Similarly, the number of Dof explored in the current study is less than 45, as detected in pear ([Liu et al., 2020](#)), and 103 in *Camellia sativa* ([Luo et al., 2022](#)). The high number of Dof genes can partially be attributed to the large genome size under study.

The division of the Dof family into nine sub-groups based on their phylogeny with AtDofs was found in agreement with

studies of [Zhou et al. \(2020\)](#) and [Li et al. \(2022\)](#) conducted in Tartary buckwheat and watermelon, respectively. These results reflect the conservation of PlDof genes.

Lima bean exhibited some closeness with *A. thaliana* on account of showing 2 orthologs. The higher number of paralog detected in lima bean (13) than *A. thaliana* (10) reveal wider expansion of the PlDof family.

Less than 1 of the Ka/Ks ratio, for PlDof paralogs, pointing towards a segmental pattern of duplication. The negative GRAVY value of PlDofs (-0.269 to -0.746) shows its hydrophilic nature and its solubility in water. The results about the Ka/Ks ratio and GRAVY are in agreement with [Brian et al. \(2021\)](#) and [Chen et al. \(2023\)](#), respectively. The pI range of PlDofs (5.11-9.77) in the present study strengthened earlier reports of [Cai et al. \(2024\)](#) in PsDofs.

The existence of highly conserved Dof domains in PlDof factor, as reflected in the present study, highlights the conservation of Dof transcription factors in plants during the course of evolution. Though a differential distribution of 10 motifs among PlDofs was witnessed, motif 1 was present across all members of the PlDof family. The results about the number of introns in PlDof genes (0-2) were found in agreement with [Wu et al. \(2016\)](#), and [Kushwaha et al. \(2011\)](#) reported in pepper (0-2) and sorghum (0-2), respectively. These results indicate a relatively stable structure of PlDof genes.

Cis-acting elements associated with hormonal response, plant growth and development, abiotic stresses, particularly light, drought, high and low temperatures, were found abundantly in promoters of PlDof genes. The study of these elements is crucial for understanding the pattern of gene expression in response to the

respective stresses or growth attributes. Closely resembling the cis-acting elements have been reported by Liu *et al.* (2020) and Cao *et al.* (2022) in wheat and lotus, respectively.

Conclusions and recommendations

The in silico analysis revealed 40 PIDof genes in lima bean. The protein length, pI, molecular mass, Gene structure and subcellular localization of PIDof protein synchronized with previous reported Dofs.

1. The gene duplication events contributed 33% to the expansion of the PIDof gene family.
2. The ka/ks ratio was less than 1 for all the paralogs, revealing a segmental pattern of duplication.
3. The detection of many cis-acting elements in the upstream region of PIDof uncovered its association with diverse functions.

Functional validity of all PIDof genes, explored in the current study, is recommended.

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