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Genome-Wide Identification and Characterization of the *Dof* Transcription Factor Gene Family in *Phaseolus vulgaris* L.

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Abstract

The Dof (DNA-binding with one finger) proteins are a class of plant-specific transcription factors that can trigger several processes involved in plant growth and development, as well as in stress responses. Here, we performed a systematic bioinformatics analysis to characterize all Dof genes in common bean, which included analysis of the genome sequence, conserved protein domains, chromosomal locations, subcellular locations, phylogenetic relationships, gene duplications, and gene expression profiles in different tissues. Bioinformatics analysis revealed 36 putative genes related to *PvDof* that were classified into seven subfamilies (A, B1, B2, C1, C2, D1, and, D2) by comparative phylogenetic analysis. Based on our genome duplication analysis, a total of 36 genes were found to be distributed on all 11 chromosomes, and they expanded through gene duplication in tandem, suggesting the involvement of segmental duplication events in the evolutionary process. Synteny events and phylogenetic comparisons of the Dof proteins of common bean with those of *A. thaliana*, *O. sativa*, and *G. max* L. led to the identification of several orthologous and paralogous genes, which provided further insight into the diversity of the evolutionary characteristics of genes of this family in other plant species. Expression profiles revealed that most of the *PvDof* genes were expressed in different tissues, indicating that *PvDof* genes may be involved in various physiological functions during plant development. The results of this study provide additional information and potential biotechnological resources for further understanding the molecular basis of this gene family and conse-

quently improvement of common bean crops.

Keywords

Common Bean, DNA-Binding with One Finger (Dof), Domain Proteins, Transcription Factor

1. Introduction

Transcriptional and post-transcriptional regulation of gene expression influences and controls many important biological processes in bothmonocots and dicots, such as cellular morphogenesis, signal transduction, and environmental stress responses [1] [2]. Transcription factors (TFs) are responsible for regulating the expression of genes involved in plant-specific cis-regulatory elements in the promoter regions [3]. Yanagisawa and Schmidt [4] were the first to isolate the TF in maize, with an array of Dof TF genes subsequently isolated and functionally characterized in many plants, including *Arabidopsis thaliana* and *Orizasativa* [5] [6], *Sorghum bicolor* (L.) Moench [7], *Brachypodium distachyon* [8], *Solanum lycopersicum* [9], *Ricinus communis* L. [10], *Cajanus cajan* [11], *Phyllostachys heterocycla* [12], *Chrysanthemum morifolium* [13], *Capsicum annuum* [14] and *Populus trichocarpa* [15].

The Dof (DNA-binding with one finger) is a plant-specific TF that contains 200 - 400 amino acids and a single C2C2-type (CX2CX21CX2C-type) zinc-finger-like motif composed of 52 amino acid residues at the N-terminal, which specifically binds to a 5′-(A/T)AAAG-3′element [16] [17]. Dof TFs are involved in several important functions [18], such as root light signaling [19], germination [20], regulation of stomatal development [21], development of the vascular system [22], and responses to biotic [23] and abiotic [24] [25] stress. As such, identification and classification of the Dof family in common beans is useful for future research on plant gene expression, as to date no study has been performed on identifying members of the Dof family in common bean.

Common bean (*Phaseolus vulgaris* L.) is one of the most important legume crops for human consumption, and is an exceptional source of protein, carbohydrates, and other nutrients [26] [27]. Despite being the world's largest producer of common bean, with an average annual production of 3.5 million tons [28], common bean productivity in Brazil is still considered to be low due to several factors, such as the adverse effects of climatic conditions, and the occurrence of pests and diseases [29]. Therefore, considering the importance of Dof TFs and the lack of information about this gene family in *P. vulgaris*, weidentified and characterized this gene family in *P. vulgaris* L. using a computational approach. We identified Dof-coding sequences and characterized them at both phylogenetic and structural levels in order to gain a better understanding of the genetic determinants of tolerance to abiotic and biotic stresses in this

crop.

2. Material and Methods

2.1. Identification and Annotation of Dof Genes in the Genome of *P. vulgaris*

Initially, we identified all members of the Dof proteins in sequences of the *A. thaliana* genome obtained from the TAIR database (http://www.arabidopsis.org/), whereas those for *O. sativa*, *G. max*, and *P. vulgaris* were downloaded from the databases TIGR (http://rice.plantbiology.msu.edu/) and Phytozome v12 (http://www.phytozome.net). To confirm the identity of the Dof genes, the sequences were compared to those in the GenBank database using BLASTP and BLASTX searches (National Center for Biotechnology Information [NCBI]: http://www.ncbi.nlm.nih.gov) [30]. Protein sequences were aligned using Clustal Omega v. 2.0.3 [31]. The physical and chemical characteristics of Dof proteins in common bean were described using the ProtParam tool (http://web.expasy.org/protparam/), including the number of amino acids, the theoretical isoelectric point (PI), and the molecular weight (kDa). All sequences of predicted Dofproteins were analyzed in silico regarding their subcellular location via the use of WoLF PSORT algorithms (http://wolfpsort.org/).

2.2. Protein Alignment and Phylogenetic Analysis

Multiple sequence alignment of the full-length deduced amino acid sequences of Dof proteins was performed with Clustal Omega v. 2.0.3 set to Hidden Markov Model (HMM) parameters [31]. Phylogenetic and molecular evolutionary analyses were conducted using MEGA v. 6.06 [32] and Maximum Likelihood (ML) using complete deletion. The reliability of the resulting tree was tested via bootstrapping with 1000 replicates.

2.3. Identification of Conserved Motifs

The conserved motifs of the Dof protein sequences were identified using the Multiple Expectation Maximization for Motif Elucidation (MEME; http://meme-suite.org/) [33], as the basis for the following parameters: motif length set to 6 ~ 100, motif sites set to 2 ~ 120, and maximum number of motifs set to 25. The resulting motifs were checked against NCBI (http://www.ncbi.nlm.nih.gov/gorf/gorf.html) and PROSITE (http://www.expasy.org) to verify their significance.

2.4. Genomic Structure

We used the online Gene Structure Display Server program tool (GSDS; http://gsds.cbi.pku.edu.cn/) [34] to predict the exon/intron organization of the Dofgenes. Complete sequences of the corresponding genomic DNA and full-length transcripts of each gene were used.

2.5. Chromosomal Location and Calculation of the Duplication Events

A local blast search of the P. vulgaris genome sequence was performed to map the physical location of the 36 genes. The locations of the genes on the 11 chromosomes of common bean were mapped with Mapchart 2.2 software [35]. The Plant Genome Duplication Database (http://chibba.agtec.uga.edu/duplication/) was used to estimate the synonymous (Ks; non-synonymous substitution (Ka) rates were calculated following the procedures described by [36], as well as the evolutionary constraints (Ka/Ks) between the duplicated pairs of PvDofs. The approximate dates of the duplication events were calculated by the equation ($T = Ks/2\lambda$), assuming an average value for the synonymous substitution rate (λ) of 8.46×10^{-9} [37].

2.6. Synteny Analysis

Plant Genome Duplication Database (PGDD; http://chibba.agtec.uga.edu/duplication/) [38] was used to search for orthologous genes in *P. vulgaris* and *A. thaliana*; *P. vulgaris* and *O. sativa*; and *P. vulgaris* and *G. max*. The resulting synteny map was constructed using Circos software (http://circos.ca/) [39].

2.7. Gene Expression Analysis *in Silico*

Illumina RNA-seq datasets were downloaded from Phytozome Database (http://phytozome.jgi.doe.gov/pz/portal.html#!info?alias=Org_Pvulgaris). The expression profiles of *PvDof* genes were analyzed in specific tissue libraries of plants at differentstages of development, consisting of young pods, stem_10, stem_19, flower buds, flowers, root_10, nodules, root_19, green mature buds, leaves, and young triloliates. The expression profile *in silico* were calculated by Cufflinks in FPKM units (expected number of fragments per kilobase of transcript sequence per millions base pairs sequenced). FPKM values were log2 transformed and the heatmap was generated with the algorithm CIMMiner (http://discover.nci.nih.gov/cimminer).

3. Results

3.1. Identification and Classification of *PvDof* Genes

Sequence homology analysis identified a total of 36 *PvDof* genes in the *P. vulgaris* genome (Table 1). When we compared the number of genes with other species, *A. thaliana* also had 36 *PvDOF* genes, whereas *O. sativa* had 30, *G. max* had 78, and *S. lycopersicum* had 34 (Table 1). All genes identified encoded proteins containing the Dof domain, and were designated as *PvDof*01 to *PvDof*36 based on their location on the chromosome. The names of the *PvDof* genes, Dof gene accession numbers, gene location, length of the coding sequences, and characteristics of the *PvDof* proteins are shown in Table 2. The full length coding sequences of the *PvDof* genes ranged from 612 bp (*PvDof*33) to 1086 bp (*PvDof*26),

Table 1. Comparison of the number of Dof genes of each classamong *P. vulgaris*, *A. thaliana*, *O. sativa*, *G. max*, and *S. lycopersicum*.

Species	*P. vulgaris*	*A. thaliana*[a]	*O. sativa*[a]	*G. max*[b]	*S. lycopersicum*[c]
Class	N	N	N	N	N
A	8	3	4	15	5
B	10	8	6	18	8
C	13	15	6	24	12
D	5	10	14	21	9
Total	36	36	30	78	34
Genome size (Mb)	650	115	420	1,115	950

[a][5], [b][40], [c][9].

Table 2. General physical and chemical characteristics of the 36 *PvDof* genes identified in *P. vulgaris*.

PvDof	Phytozome ID	Chromosomal location	Nucleotide CDS (bp)	Length (aa)	pI	MW (kDa)	Sequence	Subcellular location
*PvDof*01	Phvul.001G062100.1	Chr01:7655746..7657228	810	269	8.20	29.99	full-length	nucleus
*PvDof*02	Phvul.001G080800.1	Chr01:13241653..13243692	1068	355	9.22	39.11	partial	-
*PvDof*03	Phvul.001G196100.1	Chr01:46235911..46236696	786	261	6.19	29.41	full-length	nucleus
*PvDof*04	Phvul.002G022000.1	Chr02:2381355..2382917	1020	339	8.92	35.87	full-length	nucleus
*PvDof*05	Phvul.002G144900.1	Chr02:28149833..28151588	1035	344	8.81	37.05	full-length	nucleus
*PvDof*06	Phvul.002G226100.1	Chr02:39099335..39101145	942	313	8.41	34.17	full-length	nucleus
*PvDof*07	Phvul.002G230100.1	Chr02:39579558..39580512	786	261	9.75	27.96	full-length	nucleus
*PvDof*08	Phvul.002G230200.1	Chr02:39587482..39589579	1044	347	9.06	37.11	full-length	nucleus
*PvDof*09	Phvul.002G238400.1	Chr02:40406454..40408578	552	183	7.71	20.98	full-length	nucleus
*PvDof*10	Phvul.003G182100.1	Chr03:39382825..39384177	864	287	6.52	30.94	full-length	nucleus
*PvDof*11	Phvul.003G200600.1	Chr03:41410491..41412765	987	328	6.82	35.85	full-length	nucleus
*PvDof*12	Phvul.003G247900.1	Chr03:47381617..47383283	1017	338	8.64	36.06	full-length	nucleus
*PvDof*13	Phvul.003G248500.1	Chr03:47458824..47459525	702	233	8.72	24.49	full-length	nucleus
*PvDof*14	Phvul.003G287600.1	Chr03:51349107..51350494	1038	345	8.89	37.12	full-length	nucleus
*PvDof*15	Phvul.005G137700.1	Chr05:36604141..36605891	864	287	8.08	31.55	full-length	nucleus
*PvDof*16	Phvul.005G143100.1	Chr05:37185922..37187662	918	305	9.58	33.38	full-length	nucleus
*PvDof*17	Phvul.005G161200.1	Chr05:38639927..38641622	618	205	9.02	22.04	full-length	nucleus
*PvDof*18	Phvul.006G114900.1	Chr06:23050676..23052519	765	254	8.66	27.74	full-length	nucleus
*PvDof*19	Phvul.006G176400.1	Chr06:28683988..28685016	546	181	9.45	20.76	full-length	nucleus
*PvDof*20	Phvul.006G184000.1	Chr06:29308624..29310821	1038	297	9.26	32.20	full-length	nucleus
*PvDof*21	Phvul.006G184100.1	Chr06:29322500..29324409	894	345	8.68	37.33	full-length	nucleus
*PvDof*22	Phvul.006G188300.1	Chr06:29645412..29647711	843	280	8.12	31.11	full-length	nucleus
*PvDof*23	Phvul.007G267600.1	Chr07:50584990..50585817	828	275	5.25	30.12	full-length	nucleus
*PvDof*24	Phvul.008G012500.1	Chr08:1111164..1112976	1053	350	9.31	37.82	full-length	nucleus
*PvDof*25	Phvul.008G012500.2	Chr08:1111666..1112976	933	310	9.33	33.49	full-length	nucleus
*PvDof*26	Phvul.008G099400.1	Chr08:10664656..10666281	1086	361	9.08	37.64	full-length	nucleus
*PvDof*27	Phvul.009G047500.1	Chr09:9121973..9124052	837	278	8.88	30.49	full-length	nucleus
*PvDof*28	Phvul.009G136400.1	Chr09:20017224..20018880	897	298	5.03	33.10	full-length	chlo:6, nucl.:4
*PvDof*29	Phvul.009G178300.1	Chr09:26082689..26084869	1011	336	6.58	36.77	full-length	nucleus
*PvDof*30	Phvul.009G204000.1	Chr09:30151578..30153734	957	318	6.49	34.50	full-length	nucleus
*PvDof*31	Phvul.010G013500.1	Chr10:2139058..2140753	1002	333	9.18	35.59	full-length	nucleus
*PvDof*32	Phvul.010G115600.1	Chr10:38220876..38223161	849	282	9.04	30.64	full-length	nucleus
*PvDof*33	Phvul.010G141400.1	Chr10:41333505..41336027	612	203	8.70	21.94	full-length	nucleus
*PvDof*34	Phvul.011G064800.2	Chr11:5628982..5631847	768	255	9.63	27.75	full-length	nucleus
*PvDof*35	Phvul.011G064800.1	Chr11:5629789..5631847	930	309	9.53	33.52	full-length	nucleus
*PvDof*36	Phvul.011G071900.1	Chr11:6441508..6443452	897	298	7.51	32.87	full-length	nucleus

CDS: coding sequence; bp: base pairs; aa: amino acids; MW: molecular weight (kDa); pI: isoelectric point.

and their putative proteins contained between 203 and 361 amino acid (aa) residues, with an average of ~294 aa. The theoretical pI ranged from 5.03 (*PvDof*28) to 9.75 (*PvDof*07), and molecular weights ranged from 20.76 kDa (*PvDof*19) to 39.11kDa (*PvDof*02). The majority of common bean *PvDof* proteins were found in the nucleus, indicating the specific nature of their transcription regulation.

Homologous sequences were analyzed through multiple alignment using the amino acid sequences containing Dof domains. All bean Dof domains had a typical DNA-binding domain of 55 residues spanning a single C2/C2 zinc finger (Figure 1). In general, the regions of the Dof domains had 55 basic residues located in the N-terminal region (Figure 1), with alignments of the other highly

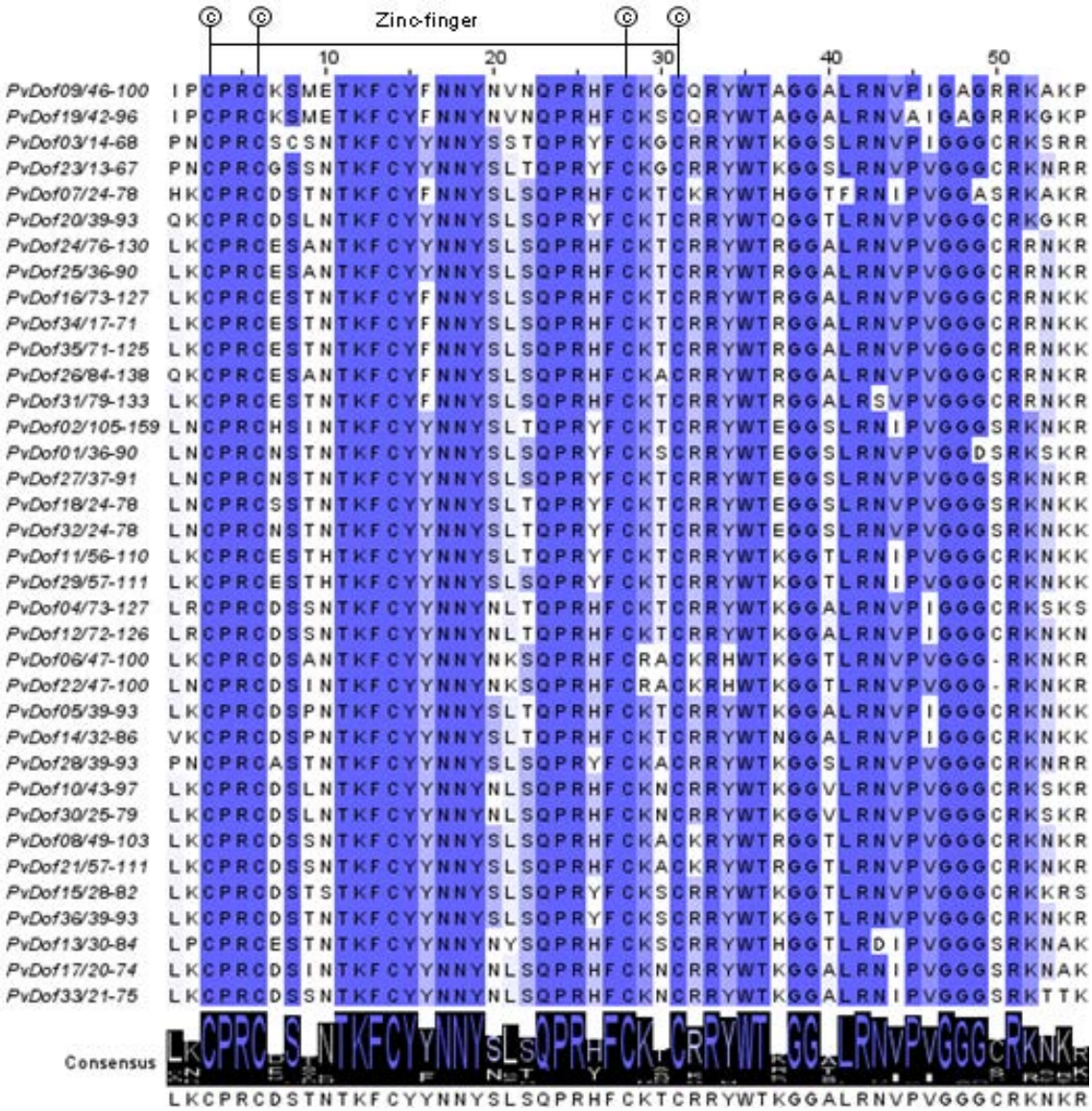


Figure 1. Multiple sequence alignment of Dof domain sequences from the proteins of *P. vulgaris*. The typical features of Dof proteins showing four cysteine residues are indicated. Below the alignment, the conserved residues of amino acids are represented in blue in the upper boxes.

conserved residues belonging to the Dof family identified in *P. vulgaris* consisting of Cys-3, Pro-4, Arg-5, Cys-6, Ser-8, Thr-11, Lys-12, Phe-13, Cys-14, Tyr-15, Asn-17,Asn-18, Tyr-19, Gln-23, Pro-24, Pro-25, Phe-27, Cys-28, Cys-31, Arg-33, Trp-35, Thr-36, Gly-38, Gly-39, Arg-42, Pro-45, Gly-47, and Arg-51 (Figure 1). In addition, we observed several partially conserved amino acid residues, consisting of Tyr-16, Ser-20, Ser-22, His-26, Lys-29, Tyr-34, Leu-41, Asn-43, Val-44, Val-46, Gly-48, Gly-49, and Lys-52 (Figure 1).

3.2. Phylogenetic and Conserved Domain Analysis of Dof Proteins in *P. vulgaris*

A Maximum Likelihood tree was generated from the aligned amino acid sequences of theDof genes in order to assess evolutionary relationships. Our analysis revealed a distinct clustering of Dof proteins, and further analysis using phylogenetic tree topology allowed us to classify the *PvDof* gene family into four major classes (A, B, C, D) and seven orthologous subclasses (A, B1, B2, C1, C2, D1 and D2, which presented 8, 7, 6, 7, 5, 2, and 1 genes, respectively) (Figure 2). Phylogenetic relationships within multigenic families may provide additional information about the Dof genes evolution [9]. We present detailed information

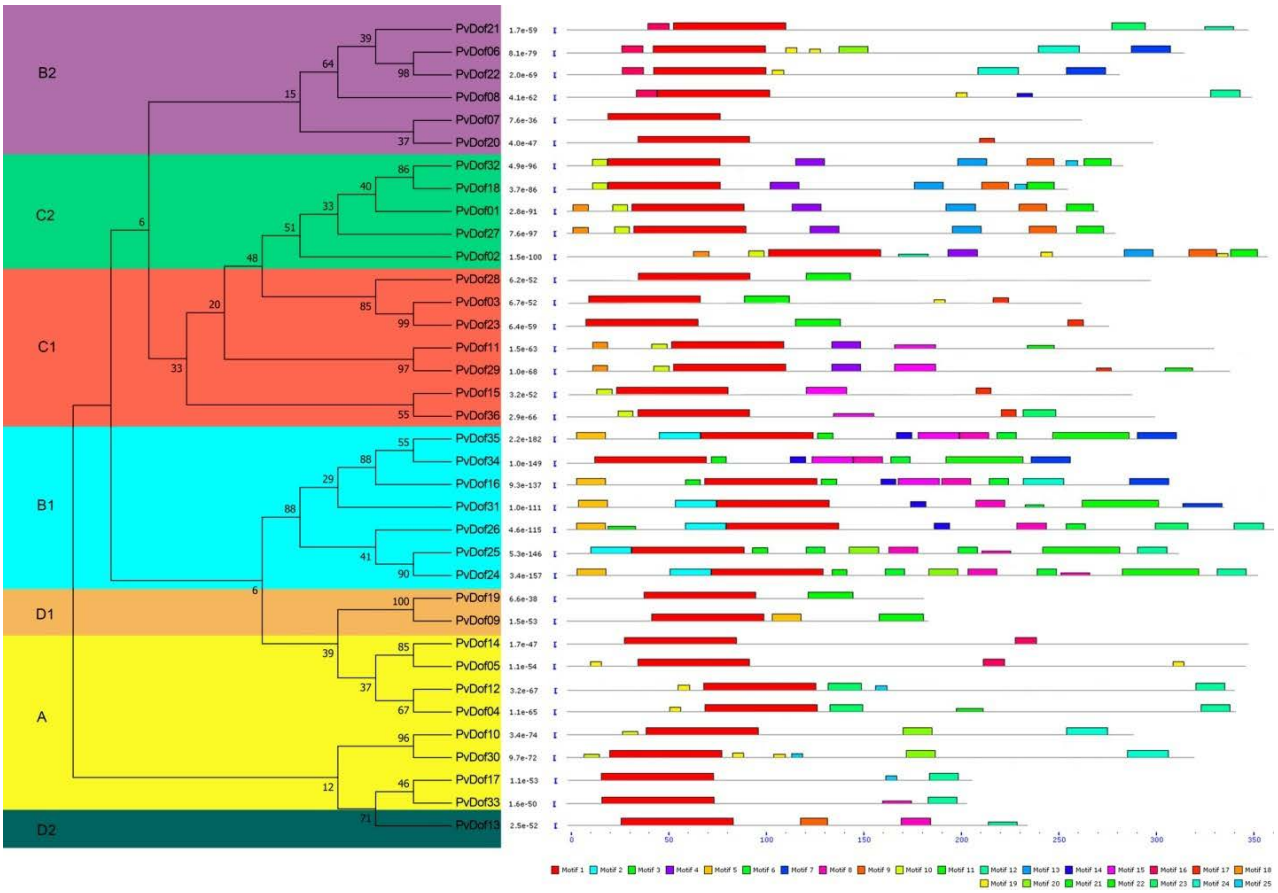


Figure 2. Phylogenetic relationships and organization of conserved motifs of *Dof*genes sequences in common bean. Phylogenetic tree of 36 *PvDof* proteins was constructed using MEGA; the motifs identified by MEME software are represented by colored boxes and their consensus sequences are shown in Table 3.

about the 25 putative motifs of the Dof gene sequences in *P. vulgaris*, including names, widths, and best possible matches, in Table 3. Identification of each of these motifs is also illustrated in Figure 2, in which motif 1 is represented by the Dof domain that is uniformly found in all bean protein sequences (Table 3). The motifs 12, 16, 19, 20, 23, 24, and 25 were observed in subclass A; motifs 2, 3, 5, 6, 7, 8, 12, 14, 15, 22, 23, and 24, were observed in subclass B1, which contained the highest number of motifs; motifs 7, 12, 16, 19, 20, 23, and 24 were observed in subclass B2; motifs 4, 10, 15, 17, 18, 21, and 23 were observed in subclass C1; motifs 4, 9, 10, 11, 13, 18, 19, and 25 were observed in subclass C2; and the subclasses D1 and D2 contained two motifs each, consisting of 5 and 21 and 8 and 9, respectively. From these results, it can be seen that the majority of the members

Table 3. The MEME motif sequences and lengths in *PvDof* proteins.

Motif	Conserved amino acid sequences	e-values	Sites	Width
1[1]	QALKCPRCDSTNTKFCYYNNYSLSQPRHFCKTCRRYWTKGGALRNVPVGGGCRKNKR	4.1e−1768	36	57
2	GSIRPGSMADRARMAKIPQPE	8.0e−043	5	21
3	EIPSKLDGIVATSGIMPQIPSVKMEESQALNLPKNLLMV	2.1e−026	5	39
4	KIHQGQDLNLAFPAV	3.0e−022	7	15
5	IPVYLDPPNWQQQQP	5.3e−018	6	15
6	QWRQQQFPFL	2.1e−018	8	10
7	HYWSWEDMDGLVSSDASHLW	4.9e−016	5	20
8	DMGFQIGGSGWGSAG	2.3e−009	8	15
9	GGRILFPFGDVKKQ	1.8e−009	6	14
10	LERKARPQ	3.1e−009	9	8
11	QRQQGDSTGYWTGM	8.2e−007	5	14
12	WGGTNAWSDLPIFTP	2.5e−004	8	15
13	YYTTGFPMQDFKPAL	1.8e−002	5	15
14	LPFMAPLQ	6.0e−002	5	8
15	LNRYAVGNMGIGLREIHAQND	8.0e−001	5	21
16	KPDLHWKQQQQ	7.6e−003	6	11
17	EMMIPYDQ	1.5e−001	5	8
18	DQWAQGII	3.3e+000	5	8
19	TTATTT	3.5e+000	10	6
20	GGIGSHIGAITTPIA	1.5e+000	5	15
21	HPIISDEPEIDIAQVYAAFLNVK	5.1e+001	5	23
22	RDRSKSPA	1.8e+002	6	8
23	VAKTAAVKMKDVKVELG	2.6e−001	5	17
24	AVYGYFDEPKTVEEPYWNHTH	1.2e+001	5	21
25	VEVEHN	1.7e+001	5	6

[1]Motif 1 represents the Dof domain.

of this gene family are closely related and share common motif compositions, indicating that the structures of the gene members are highly conserved within the same subclass.

3.3. Gene Structure, Chromosomal Location, and Gene Duplication Events of *PvDof* Genes

Structural diversity and characterizations of exon/intron structure were evaluated for each Dof gene (Figure 3). Genes in the subclasses A and D2 contained no introns, whereas genes in the subclasses B1, B2, C1, C2, and D1 all had one or two introns. The structural analyses of the *PvDof* genes were based on the results of the clades of the phylogenetic tree, suggesting that, as in other plants, members of the same subclass had similar structures and thus likely perform similar functions.

Genome chromosomal location analyses revealed that *PvDof* were randomly distributed in 10 out of 11 chromosomes (Figure 4), but the *PvDof* genes were unevenly distributed among chromosomes. The largest number of *PvDof* genes occurred on chromosome 2 (six *PvDof* genes), followed by five located on

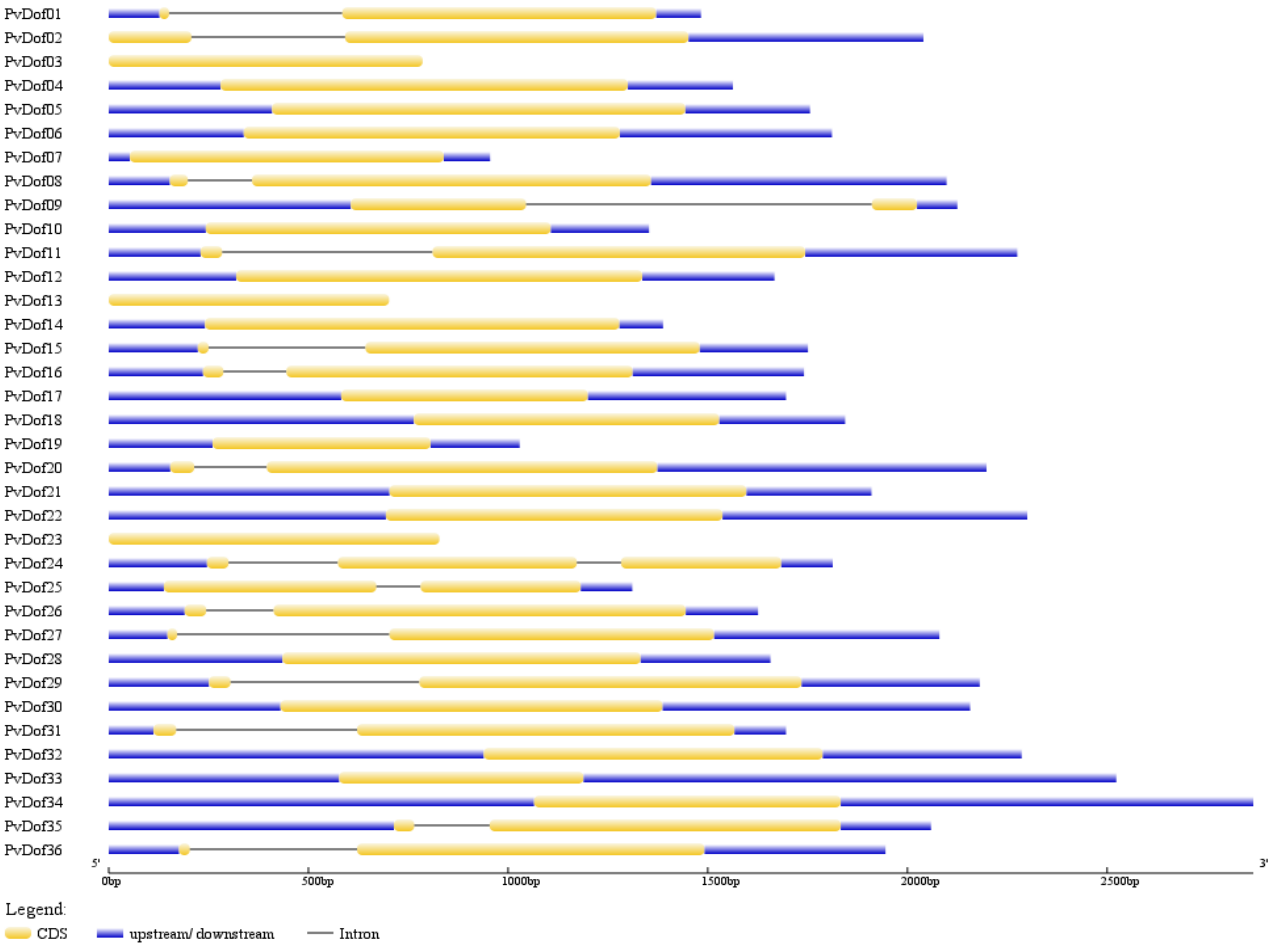


Figure 3. Schematic diagram of exon, intron, and untranslated region (UTR) organization, as indicated by yellow rectangles, gray lines, and blue rectangles, respectively.

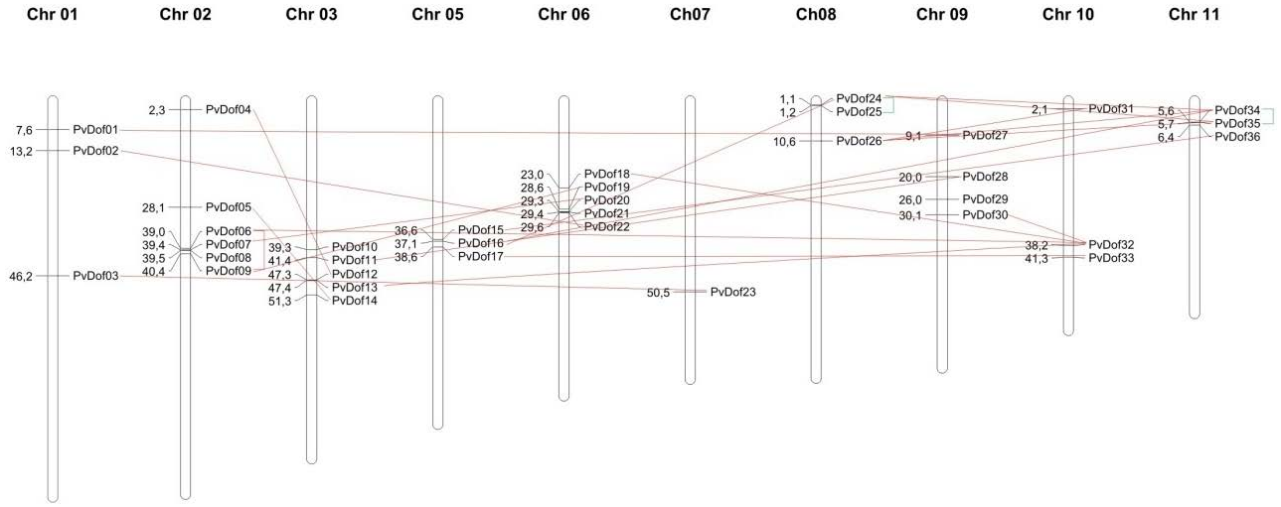


Figure 4. Physical map of *PvDof* genes showing their chromosomal locations. Vertical bars represent the chromosomes and numbers at the left indicate gene positions (the scale on the left is in megabases, Mb). The chromosome number is indicated on the top of each chromosome (vertical bar). Red and green lines reflect segmental and tandem duplications, respectively. Data extracted from **Table 4**.

chromosomes 3 and 6 (**Figure 4**). In addition, four genes were found on chromosome 9, chromosomes 1, 5, 10, and 11 each possessed three *PvDof* genes, and one gene was detected on chromosome 7 (**Figure 4**).

Expansion analysis of the Dof gene family in the *P. vulgaris* genome was examined. Based on their chromosomal distribution and the high rate of sequence similarity, we determined that 26 duplication pairs arose from segmental and tandem duplication events; the lines in **Figure 4** show the connections among these paralogs. Twenty-four of the paralog pairs were the result of putative segmental duplication events. Two pairs of paralogous genes occurred on the same chromosome, separated by only a short distance (<0.2 Kb), which suggests that the gene pairs *PvDof*24/*PvDof*25 and *PvDof*34/*PvDof*35 represent tandem duplication (**Figure 4** and **Table 4**). Our results indicate that segmental duplication predominated in the expansion of the *PvDof* gene family in common bean, but that tandem duplication was also involved.

We calculated Ka and Ks values, as well as the Ka/Ks ratio, in order to estimate the date of the duplication events (**Table 4**). Segmental duplication events of the Dof genes in common bean occurred from 2.13 mya (million years ago) (Ks = 0.04) to 26.06 mya (Ks = 0.44), with a mean of 11.54 mya. However, estimations of the date of tandem duplication events in the paralog genes were not possible because these gene pairs (*PvDOF*24/*PvDOF*25 and *PvDOF*34/*PvDOF*35) differed only in their intron sequences. The Ka/Ks ratio of all duplication events was >0.3, which implies that significant functional divergence could have occurred after duplication. The Ka/Ks ratios of six duplicate pairs were <1.0, indicating that the *PvDof* genes evolved under negative selection acting against protein-coding changes. These results suggest that segmental/tandem expansion of the Dof gene family in common bean could be dated to relatively recent duplication events.

Table 4. Date of duplication of the pairs of paralogous genes of the *PvDof* gene family. Ka represents the non-synonymous substitution number per non-synonymous site, Ks is the number of the synonymous substitution site; Ka/Ks represents the ratio of non-synonymous (Ka) to synonymous (Ks) substitutions.

Paralogous Pairs	Chromosomal location	Duplication event	Ka	Ks	Ka/Ks	Date (mya)
*PvDof*01/*PvDof*27	Chr01/Chr09	Segmental	0.20	0.07	2.74	4.31
*PvDof*03/*PvDof*23	Chr01/Chr07	Segmental	0.21	0.09	2.52	5.02
*PvDof*04/*PvDof*12	Chr02/Chr03	Segmental	0.17	0.13	1.24	7.92
*PvDof*06/*PvDof*09	Chr02/Chr06	Segmental	0.43	0.40	1.07	23.88
*PvDof*07/*PvDof*20	Chr02/Chr06	Segmental	0.44	0.33	1.35	19.27
*PvDof*09/*PvDof*19	Chr02/Chr06	Segmental	0.18	0.18	0.99	10.58
*PvDof*11/*PvDof*28	Chr03/Chr09	Segmental	0.41	0.28	1.48	16.25
*PvDof*14/*PvDof*05	Chr03/Chr02	Segmental	0.22	0.10	2.26	5.85
*PvDof*15/*PvDof*36	Chr05/Chr11	Segmental	0.09	0.04	2.58	2.13
*PvDof*16/*PvDof*24	Chr05/Chr08	Segmental	0.19	0.24	0.80	13.95
*PvDof*16/*PvDof*31	Chr05/Chr10	Segmental	0.24	0.18	1.32	10.58
*PvDof*16/*PvDof*35	Chr05/Chr11	Segmental	0.07	0.15	0.46	8.92
*PvDof*17/*PvDof*33	Chr05/Chr10	Segmental	0.21	0.22	0.94	13.00
*PvDof*18/*PvDof*32	Chr06/Chr10	Segmental	0.07	0.07	0.97	4.20
*PvDof*22/*PvDof*02	Chr06/Chr02	Segmental	0.36	0.28	1.31	16.43
*PvDof*24/*PvDof*25	Chr08/Chr08	Tandem	0.0	0.0	1	-
*PvDof*24/*PvDof*35	Chr08/Chr11	Segmental	0.25	0.11	2.29	6.38
*PvDof*26/*PvDof*31	Chr08/Chr10	Segmental	0.18	0.13	1.39	7.74
*PvDof*26/*PvDof*35	Chr08/Chr11	Segmental	0.32	0.18	1.75	10.70
*PvDof*30/*PvDof*32	Chr09/Chr10	Segmental	0.42	0.40	1.04	23.76
*PvDof*32/*PvDof*13	Chr10/Chr06	Segmental	0.44	0.44	1.00	26.06
*PvDof*32/*PvDof*06	Chr10/Chr09	Segmental	0.46	0.24	1.91	14.13
*PvDof*34/*PvDof*16	Chr11/Chr05	Segmental	0.07	0.15	0.46	8.92
*PvDof*34/*PvDof*24	Chr11/Chr08	Segmental	0.25	0.11	2.29	6.38
*PvDof*34/*PvDof*26	Chr11/Chr08	Segmental	0.32	0.18	1.75	10.70
*PvDof*34/*PvDof*35	Chr11/Chr11	Tandem	0.0	0.0	1	-

3.4. Comparative and Synteny Analyses of the Dof Gene Families in *P. vulgaris*, *A. thaliana*, *O. sativa*, and *G. max*

To evaluate the evolutionary relationship of the Dof gene family among different plants, a phylogenetic tree was generated from the amino acid sequences of *P. vulgaris*, *A. thaliana*, *O. sativa*, and *G. max*. Maximum Likelihood analysis revealed a distinct clustering pattern of Dof proteins, and phylogenetic tree topology allowed us to classify the Dof gene family into four major classes designated:

A, B, C, D and nine orthologous subclasses A, B1, B2, C1, C2, C3, D1, D2 and D3 (Figure 5). Of these, classes C and B were the largest, containing 63 and 41 orthologs and accounting for 36% and 23% of the total predicted number of Dof genes, respectively, whereas class A, the smallest class, contained only 35 members and accounted for 19% of predicted Dof genes. The number of clusters found here was similar to the results of previous research [5] [41]. Distribution among the subclasses was intervowen for the majority of the Dof members, indicating that Dof gene family expansion occurred prior to the divergence of common bean, *Arabidopsis*, soybean, and rice. The subclasses C3 and D3, which were species-specific to *Arabidopsis* and rice, respectively, may be the result of a gene loss event during dicot-monocot divergence [41] [42].

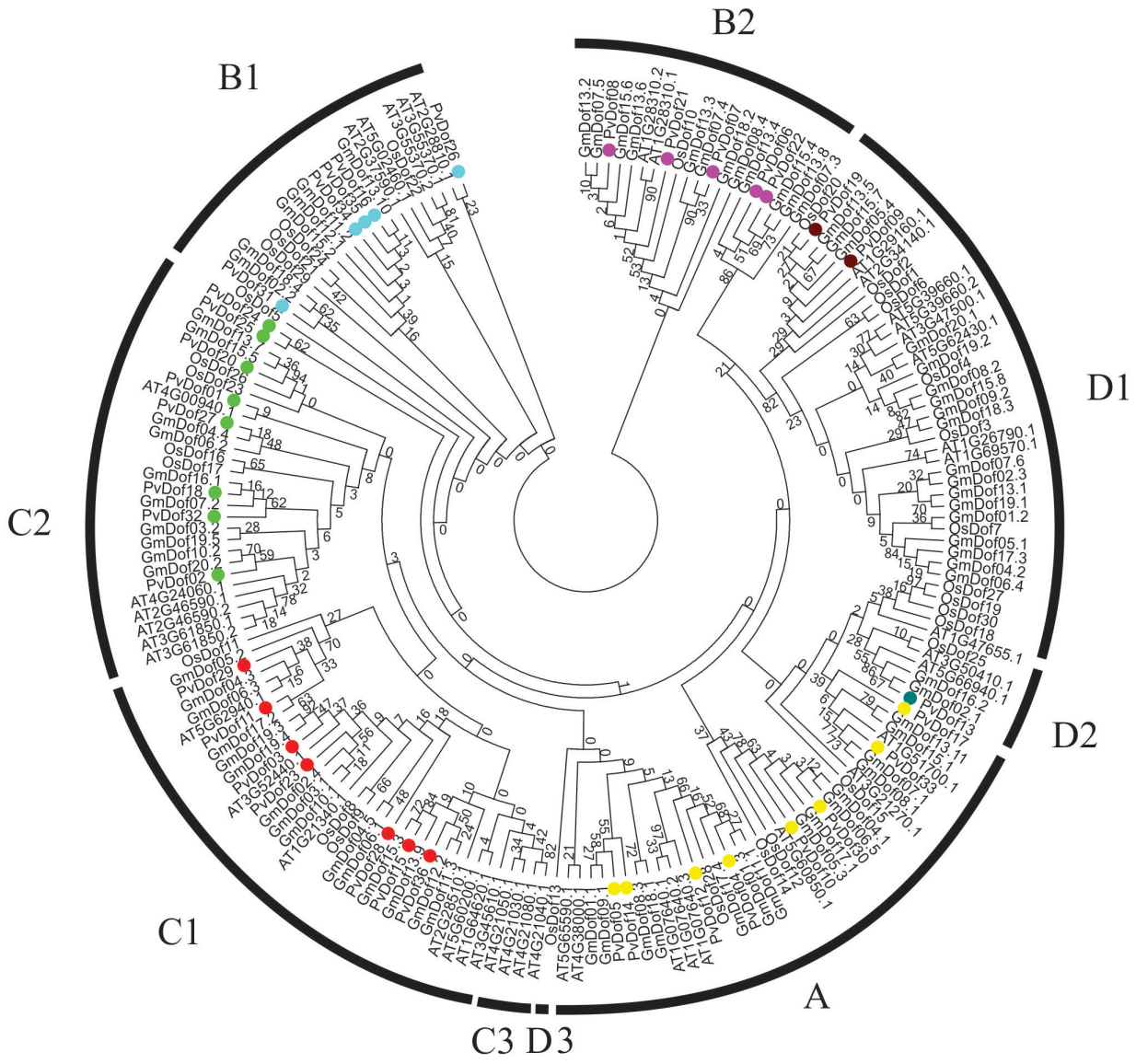
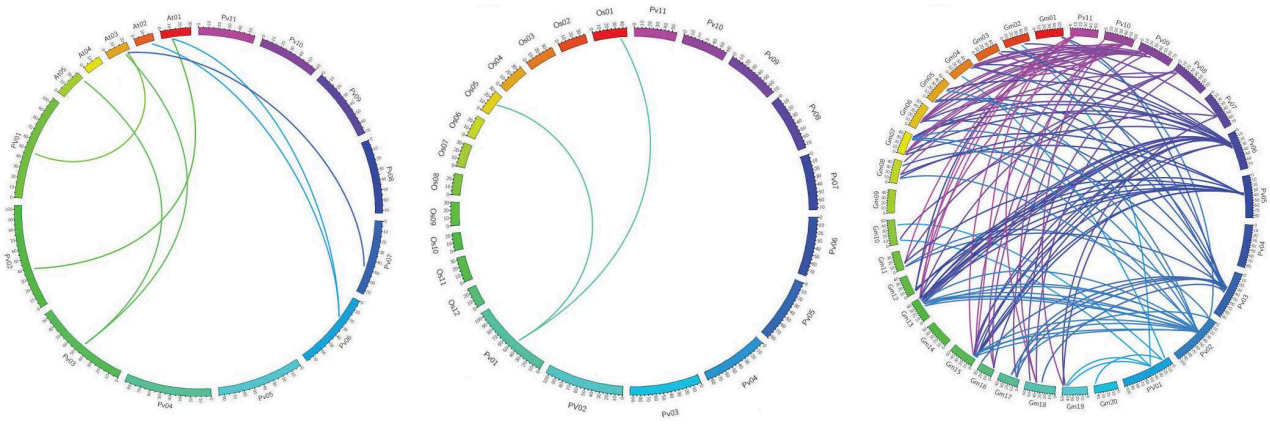


Figure 5. Phylogenetic tree of the amino acid sequences of Dof genes generated from 36 sequence of *P. vulgares*, 36 sequences of *A. thaliana*, 30 sequences of *O. sativa*, and 78 sequences of *G. max*, using 1000 bootstrap replicates. Individual *PvD of* subgroups are identified by the different colors on the tree.

A substantial number of Dof genes were systematically investigated, and synteny analysis was performed between *P. vulgaris* Dof genes and those of two other plants, one a dicot (*A. thaliana*) and the other a monocot (*O. sativa*). In addition, synteny analysis was performed on *G.max*, a legume closely related to *P. vulgaris* [37]. As such, three comparative synteny maps were constructed, consisting of *P. vulgaris* against *A. thaliana*, *O. sativa*, and *G. max* (Figure 6). A total of 123 pairs of orthologous genes with synteny relationships were identified. Seven pairs of Dof genes were found with synteny relationships, including five *AtDof* genes and five *PvDof* genes in *Arabidopsis* and common bean, respectively (Supplementary Table S1). Only two pairs of matching *Dof* synteny genes were common to bean and rice, including two *OsDof* genes and one *PvDof* gene (Supplementary Table S2). A total of 114 pairs of synteny relationships were found between soybean and common bean, of which 62 *GmDof* genes and 33 *PvDof* genes were detected (Supplementary Table S3). However, no synteny was observed for the *PvDof*03, *PvDof*31, and *PvDof*35 genes, suggesting that these orthologous genes were formed following the divergence of *P. vulgaris* and *G. max*. It would appear that the Dof genes in *P. vulgaris* share an origin with those in *A. thaliana*, *O. sativa*, and *G. max*, but that subsequent expansion of the *PvDof* genes occurred following the monocot/dicot divergence. In addition, we observed clear losses and/or duplications of several of the Dof genes in the genomes of these plants.

3.5. Transcription Profiling of *PvDof* Genes in Different Tissues

We analyzed the transcriptional profiles of all 36 *PvDof* genes in 11 different plant tissues (young pods, stem_10, stem_19, flower buds, flowers, root_10, nodules, root_19, green mature buds, leaves, and young triloliates) (Figure 7). The expression patterns indicated that the *PvDof*10, *PvDof*30, *PvDof*36, *PvDof*12, and *PvDof*27 genes were classified into classes A and C, and were preferentially expressed in young pod and stem tissues. We then examined the response of the



(a) (b) (c)

Figure 6. Genome-wide synteny analysis of Dof genes. (a) Comparative map between *P. vulgaris* and *A. thaliana*. (b) Comparative map between *P. vulgaris* and *O. sativa*. (c) Comparative map between *P. vulgaris* and *G. max*.

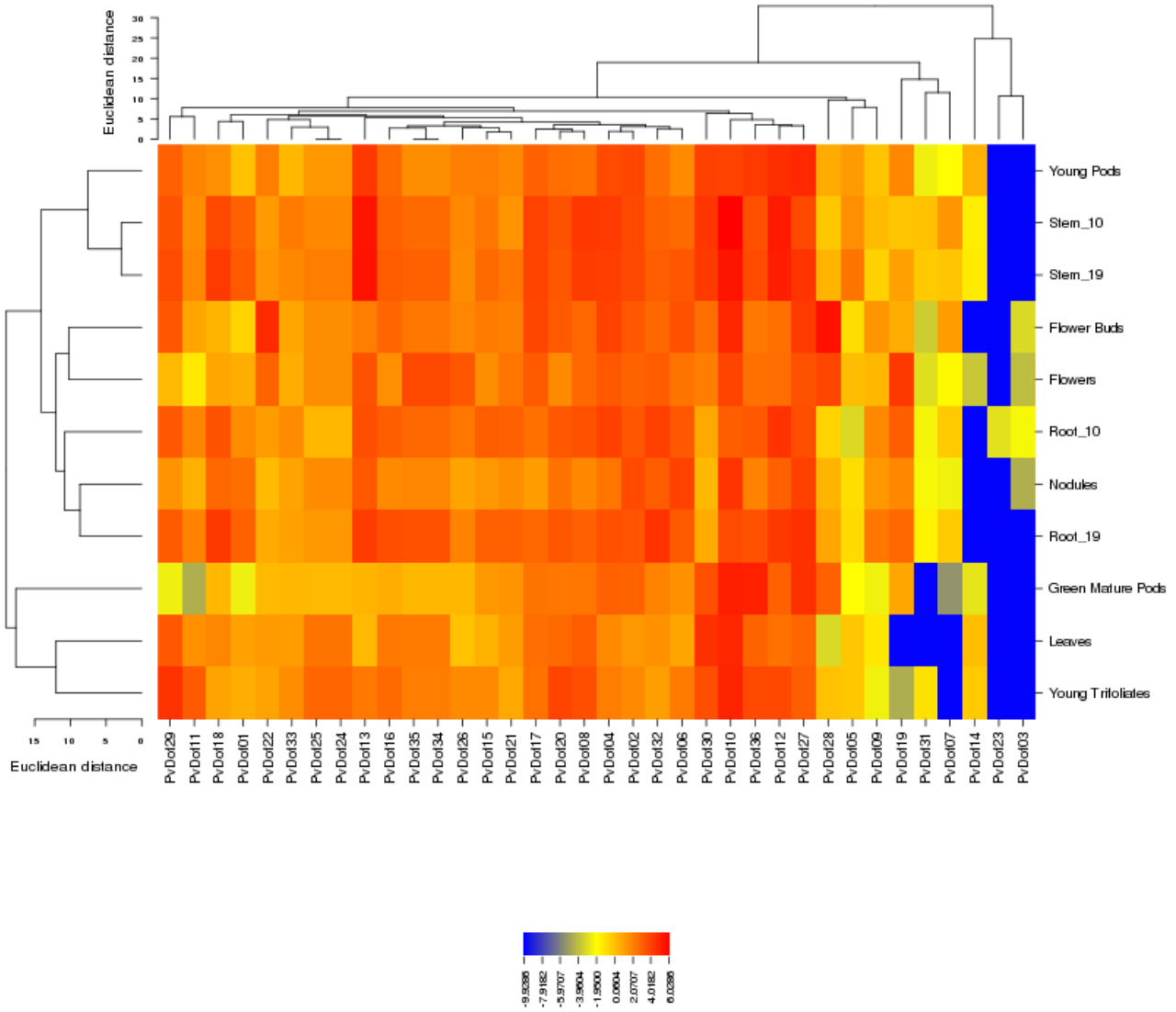


Figure 7. Heatmap showing the expression profiles of common bean *PvD of* genes across different tissues based on specific libraries. FPKM average values were used, and hierarchical clustering in the different tissues is represented by the color scale. Tissues included in the analysis consisted of young pods, stem_10, stem_19, flower buds, flowers, root_10, nodules, root_19, green mature buds, leaves, and young triloliates.

*PvDof*23 and *PvDof*03 genes in subclass C1, as these were expressed only at very low levels in almost all of the tissues and organs of common bean (**Figure 7**).

4. Discussion

The Dof gene family, which is found in many plant species, is responsible for numerous transcription regulation functions associated with various biotic and abiotic stress responses. This gene family is especially prominent in such plants as *Arabidopsis* spp. and *O. sativa* [5], *G. max* [40], *S. lycopersicum* [9], *S. officinarum* [43], and *P. heterocycla* [12]. In this study, we identified a total of 36 *PvDof* genes in *P. vulgaris* (**Table 1**). The number of *PvDof* homologs identified in this study was similar to that found previously in *Arabidopsis*, rice,

sorghum, and poplar [5] [7] [15]. Our results indicated that the Dof genes in *P. vulgaris* are highly similar to those in other species. Our results also revealed that the conserved C2C2-Dof domain was uniformly observed in all *PvDof* proteins. This domain is indicative to be considered a functional TF pertaining to the Dof gene family [40] [44]. Although the same number of Dof genes was found in *Arabidopsis* (36) and common bean (36), the common bean genome, at 650 Mb [45], is considerably larger than the *Arabidopsis* genome, at 145 Mb [46]. As shown in **Table 1**, Cai *et al.* [9] found 34 genes in tomato (with a genome size of 950 Mb), indicating that genome size is not proportional to the number of genes. Accurate classification was important for understanding the structures, functions, and evolution of the *PvDof* genes. In order to gain further insight into the evolutionary relationships between *PvDof* genes in common bean, we evaluated the exon/intron structural organization of all protein sequences. There were between zero and two introns in each gene, whereas most members of the same class/subclasses shared similar intron/exon organization (**Figure 3**). Our results corroborate those found in other species, such as *Arabidopsis* [5], *Cucumissativus* [47], and *S. lycopersicum* [9]. Divergence in the intron/exon structure can provide important information on evolutionary factors when processing the phylogenetic relationships of several multigenic families found in plants [48]. In addition, the MEME motif search tool was employed to identify and understand the diversity of the motifs in the *PvDof* genes, for which we identified 25 different conserved motifs that are present in each of the Dof protein sequences in *P. vulgaris.* The majority of *PvDof* genes within the same subclass shared similar motifs, suggesting that these conserved motifs are closely related and implying functional similarities between the proteins (**Figure 2**). Analysis of gene structure and conserved motif position provides additional information about the evolutionary relationships of this family in *P. vulgaris* [11].

Gene family expansion in plants is primarily the result of segmental/tandem duplication and transposition events. Gene duplication on different chromosomes is often due to segmental duplication events, whereas the presence of two or more genes on the same chromosome indicates a tandem duplication event [49]. Thus, we analyzed the chromosomal distributions of the *PvDof* genes, which are shown in **Table 4**. We identified 24 pairs of paralogous genes randomly scattered throughout the genome, which we considered to be evidence of segmental duplication, whereas two pairs of genes found on the same chromosome were considered to be evidence of a tandem duplication event. Gene duplication plays an important role in gene family expansion and functional diversification [50]. Comparing the ratio of non-synonymous (Ka) to synonymous (Ks) mutations provides a means of analyzing positive and negative selection of specific amino acid sites within the total length of Dof protein sequences between the different groups [11]. Analysis of the Ka/Ks ratio indicated that, despite differences between the Ka/Ks values, most were substantially less than or equal to one, which suggests that the sequences within each of the class are under strong

purification selection pressure and that positive selection may have acted.

Phylogenetic comparison and the construction of synteny maps of common bean Dof proteins showed that they were most similar to soybean Dof proteins, which reflects the similarity between the genomes of the two species. We found one extensive gene synteny between *P. vulgaris* and *G. max*, in which the total number of genes identified in common bean (91.66%, or 33 genes) were in synteny with Dof proteins in *G.max*. Previous studies have shown that *P. vulgaris* and *G. max* diverged from a common ancestor and shared a whole-genome duplication (WGD) event ~56.5 mya, and only diverged from one another ~19.2 mya [37] [51]. In addition, *G. max* experienced an independent WGD ~10 million years ago [37] [52]. This became evident when we compared the number of orthologous genes between these two species, in which 33 *PvDOF* syntenic genes from the common bean genome exhibited a 1:2 mapping to 62 *GmDof* syntenic ortholog genes in soybean. The *PvDof*05, *PvDof*25, and *PvDof*35 proteins appear to be unique to common bean, suggesting that these genes may have specific regulatory functions in this species, and may be involved in different physiological processes, although confirmation of this hypothesis requires further research.

Expression profiles were analyzed to determine the specificity of the Dof genes in common bean, which revealed that most of the *PvDof* genes were expressed in different tissues; moreover, detailed analysis of the expression patterns indicated that most genes pooled in the same subgroup had similar expression profiles. As shown in **Figure 7**, the expression levels of the *PvDof*10, *PvDof*30, *PvDof*36, *PvDof*12 and *PvDof*27 genes belonging to classes A and C were relatively higher in young pod and stem tissues, indicating that they may play important roles in the development of these tissues in bean. Wang *et al.* [14] reported that *CaDofs*28, *CaDofs*10, *CaDofs*14, and *CaDof*16 were primarily expressed in the stems of *Capsicum annuum*, which is perhaps unsurprising given that the stem contains abundant vascular tissue; Kim *et al.* [53] also observed, in *Arabidopsis*, that the *AtDof*5.1 gene was highly expressed in vascular tissues. These expression profiles suggest that *PvDof* genes may be involved in various physiological functions during plant development.

5. Conclusions

Here, we examined the genome sequence, classification, chromosomal locations, and conserved motifs of the 36 Dof genes in common beans via genome-wide analysis. The *PvDof*genes were distributed on 10 chromosomes, and the high degree of variation in their sequences provided potential evidence for diversifying functions. Multiple alignment of the *PvDoF* sequences revealed highly conserved cysteine residues, which are considered to be a unique feature of Dof TFs. In addition, extensive *in silico* characterization of these proteins will provide insight into the diversity of their genetic structures in terms of numbers and intron/exon positions, as well as in terms of their functional diversity. Finally,

phylogenetic comparisons of common bean Dof proteins with those found in *Arabidopsis*, rice, and soybean led to the identification of several orthologous and paralogous genes, which furthers our understanding of the evolutionary characteristics of this family of genes in *P. vulgaris* and other plant species. The results of this study provide additional information and potential biotechnological resources for further understanding the molecular basis of this gene family and consequently improvement of common bean crops.

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Conflict of Interests

The authors declare no conflict of interest.

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Supplementary

Table S1. Synteny between *Phaseolus vulgaris* and *Arabidopsis thaliana* Dof family genes.

Phaseolus vulgaris				*Arabidopsis thaliana*					
Pv gene	**ID Phytozome**	**Chromosome**	**Location in Chromosome**	**ID Phytozome**	**Chromosome**	**Location in Chromosome**	**Ka**	**Ks**	**Ka/ks**
PvDof03	Phvul.001G196100	PvChr01	46.14 - 46.34	AT3G52440	AtChr3	19.34 - 19.54	0	0	1
PvDof09	Phvul.002G238400	PvChr02	40.31 - 40.51	AT1G29160	AtChr1	10.08 - 10.28	0.32	1.76	0.181818
PvDof13	Phvul.003G248500	PvChr03	47.36 - 47.56	AT5G66940	AtChr5	26.63 - 26.83	0.53	1.62	0.32716
PvDof13	Phvul.003G248500	PvChr03	47.36 - 47.56	AT3G50410	AtChr3	18.61 - 18.81	0	0	1
PvDof19	Phvul.006G176400	PvChr06	28.58 - 28.78	AT2G34140	AtChr2	14.31 - 14.51	0.41	1.53	0.267974
PvDof19	Phvul.006G176400	PvChr06	28.58 - 28.78	AT1G29160	AtChr1	10.08 - 10.28	0.31	2.5	0.124
PvDof23	Phvul.007G267600	PvChr07	50.48 - 50.68	AT3G52440	AtChr3	19.34 - 19.54	0.57	4.63	0.12311

Table S2. Synteny between *Phaseolus vulgaris* and *Oryza sativa* Dof family genes.

Phaseolus vulgaris				*Oryza sativa*					
Pv gene	**ID Phytozome**	**Chromosome**	**Location in Chromosome**	**ID Phytozome**	**Chromosome**	**Location in Chromosome**	**Ka**	**Ks**	**Ka/ks**
PvDof03	Phvul.001G196100.1	Chr01	46.14 - 46.34	LOC_Os01g64590	OsChr1	37.37 - 37.57	0.00	0.00	1
PvDof03	Phvul.001G196100.1	Chr01	46.14 - 46.34	LOC_Os05g36900	OsChr5	21.46 - 21.66	0.00	0.00	1

Table S3. Synteny between *Phaseolus vulgaris* e *Glycine max* Dof family genes.

Phaseolus vulgaris				*Glycine max*					
Pv gene	**ID Phytozome**	**Chromosome**	**Location in Chromosome**	**ID Phytozome**	**Chromosome**	**Location in Chromosome**	**Ka**	**Ks**	**Ka/ks**
PvDOF01	Phvul.001G062100	PvChr01	7.56 - 7.76	Glyma.04G233300	GmChr04	19.92 - 2012	0.21	0.66	0.318181818
PvDOF02	Phvul.001G080800	PvChr01	13.14 - 13.34	Glyma.10G173700	GmChr10	40.65 - 40.85	0.12	0.33	0.363636364
PvDOF02	Phvul.001G080800	PvChr01	13.14 - 13.34	Glyma.20G216600	GmChr20	45.13 - 45.33	0.08	0.3	0.266666667
PvDof03	Phvul.001G196100	PvChr01	46.14 - 46.34	Glyma.02G195700	GmChr02	36.86 - 37.06	0.28	0.77	0.363636364
PvDof03	Phvul.001G196100	PvChr01	46.14 - 46.34	Glyma.10G082000	GmChr10	9.83 - 10.03	0.29	0.67	0.432835821
PvDof03	Phvul.001G196100	PvChr01	46.14 - 46.34	Glyma.19G200300	GmChr19	46.62 - 45.82	0.13	0.34	0.382352941
PvDof03	Phvul.001G196100	PvChr01	46.14 - 46.34	Glyma.19G199200	GmChr19	45.53 - 45.73	0.15	0.35	0.428571429
PvDof04	Phvul.002G022000	PvChr02	2.28 - 2.48	Glyma.01G183000	GmChr01	51.74 - 51.94	0.06	0.22	0.272727273
PvDof04	Phvul.002G022000	PvChr02	2.28 - 2.48	Glyma.11G059300	GmChr11	4.38 - 4.58	0.05	0.26	0.192307692
PvDof04	Phvul.002G022000	PvChr02	2.28 - 2.48	Glyma.11G059300	GmChr17	20.48 - 20.68	0.21	1.01	0.207920792
PvDof06	Phvul.002G226100	PvChr02	39.00 - 39.20	Glyma.07G193900	GmChr07	36.15 - 36.35	0.06	0.28	0.214285714
PvDof06	Phvul.002G226100	PvChr02	39.00 - 39.20	Glyma.13G241900	GmChr13	35.08 - 35.28	0.14	0.57	0.245614035
PvDof06	Phvul.002G226100	PvChr02	39.00 - 39.20	Glyma.13G182700	GmChr13	29.48 - 2968	0.07	0.32	0.21875
PvDof06	Phvul.002G226100	PvChr02	39.00 - 39.20	Glyma.15G071400	GmChr15	5.37 - 5.57	0.15	0.58	0.25862069
PvDof07	Phvul.002G230100	PvChr02	39.48 - 39.68	Glyma.07G198800	GmChr07	36.62 - 36.82	0.19	0.39	0.487179487

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PvDof07	Phvul.002G230100	PvChr02	39.48 - 39.68	Glyma.13G237600	GmChr13	34.70 - 34.90	0.45	1.32	0.340909091
PvDof07	Phvul.002G230100	PvChr02	39.48 - 39.68	Glyma.13G177600	GmChr13	29.07 - 29.27	0.25	0.51	0.490196078
PvDof07	Phvul.002G230100	PvChr02	39.48 - 39.68	Glyma.15G075800	GmChr15	5.72 - 5.92	0.45	1.5	0.3
PvDof08	Phvul.002G230200	PvChr02	39.49 - 39.69	Glyma.07G198900	GmChr07	36.63 - 36.83	0.1	0.26	0.384615385
PvDof08	Phvul.002G230200	PvChr02	39.49 - 39.69	Glyma.13G237500	GmChr13	34.68 - 34.88	0.35	0.73	0.479452055
PvDof08	Phvul.002G230200	PvChr02	39.49 - 39.69	Glyma.13G177500	GmChr13	29.06 - 29.26	0.11	0.26	0.423076923
PvDof08	Phvul.002G230200	PvChr02	39.49 - 39.69	Glyma.15G076000	GmChr15	5.74 - 5.94	0.41	0.87	0.471264368
PvDof09	Phvul.002G238400	PvChr02	40.31 - 40.51	Glyma.08G115900	GmChr08	8.79 - 8.99	0.1	0.42	0.238095238
PvDof09	Phvul.002G238400	PvChr02	40.31 - 40.51	Glyma.05G158200	GmChr05	34.93 - 35.13	0.13	0.48	0.270833333
PvDof09	Phvul.002G238400	PvChr02	40.31 - 40.51	Glyma.13G230200	GmChr13	34.12 - 32.32	0.24	1.11	0.216216216
PvDof09	Phvul.002G238400	PvChr02	40.31 - 40.51	Glyma.15G082400	GmChr15	6.18 - 6.38	0.24	1.33	0.180451128
PvDof10	Phvul.003G182100	PvChr03	38.28 - 39.48	Glyma.05G018100	GmChr05	1.51 - 1.71	0.08	0.4	0.2
PvDof10	Phvul.003G182100	PvChr03	38.28 - 39.48	Glyma.17G081800	GmChr17	6.25 - 6.45	0.07	0.49	0.142857143
PvDof11	Phvul.003G200600	PvChr03	41.31 - 41.51	Glyma.06G182200	GmChr06	15.50 - 15.70	0.19	0.74	0.256756757
PvDof11	Phvul.003G200600	PvChr03	41.31 - 41.51	Glyma.05G037800	GmChr05	3.26 - 3.46	0.06	0.22	0.272727273
PvDof11	Phvul.003G200600	PvChr03	41.31 - 41.51	Glyma.04G183700	GmChr04	45.09 - 45.29	0.19	0.89	0.213483146
PvDof11	Phvul.003G200600	PvChr03	41.31 - 41.51	Glyma.17G089300	GmChr17	6.84 - 7.04	0.08	0.23	0.347826087
PvDof12	Phvul.003G247900	PvChr03	47.28 - 47.48	Glyma.01G183000	GmChr01	51.74 - 51.90	0.19	0.9	0.211111111
PvDof12	Phvul.003G247900	PvChr03	47.28 - 47.48	Glyma.11G059300	GmChr11	4.38 - 4.58	0.18	0.85	0.211764706
PvDof12	Phvul.003G247900	PvChr03	47.28 - 47.48	Glyma.17G180600	GmChr17	20.48 - 20.68	0.05	0.49	0.102040816
PvDof13	Phvul.003G248500	PvChr03	47.36 - 47.56	Glyma.02G062700	GmChr02	5.55 - 5.75	0.08	0.56	0.142857143
PvDof13	Phvul.003G248500	PvChr03	47.36 - 47.56	Glyma.16G145000	GmChr16	30.46 - 30.66	0.11	0.39	0.282051282
PvDof14	Phvul.003G287600	PvChr03	51.25 - 51.45	Glyma.08G276300	GmChr08	36.76 - 36.96	0.28	0.98	0.285714286
PvDof14	Phvul.003G287600	PvChr03	51.25 - 51.45	Glyma.18G150800	GmChr18	27.95 - 28.15	0.22	0.79	0.278481013
PvDof15	Phvul.005G137700	PvChr05	36.50 - 36.70	Glyma.12G072400	GmChr12	5.23 - 5.43	0.21	0.92	0.22826087
PvDof15	Phvul.005G137700	PvChr05	36.50 - 36.70	Glyma.13G329000	GmChr13	42.25 - 42.45	0.1	0.25	0.4
PvDof15	Phvul.005G137700	PvChr05	36.50 - 36.70	Glyma.15G044800	GmChr15	3.49 - 3.69	0.12	0.21	0.571428571
PvDof15	Phvul.005G137700	PvChr05	36.50 - 36.70	Glyma.U021300	Gmscaf_21	3.35 - 3.55	0.19	0.75	0.253333333
PvDof16	Phvul.005G143100	PvChr05	37.09 - 37.29	Glyma.11G140200	GmChr11	10.59 - 10.79	0.26	0.79	0.329113924
PvDof16	Phvul.005G143100	PvChr05	37.09 - 37.29	Glyma.12G063800	GmChr12	4.58 - 4.78	0.18	0.7	0.257142857
PvDof16	Phvul.005G143100	PvChr05	37.09 - 37.29	Glyma.13G335200	GmChr13	42.77 - 42.97	0.19	0.4	0.475
PvDof16	Phvul.005G143100	PvChr05	37.09 - 37.29	Glyma.15G039300	GmChr15	3.00 - 3.20	0.08	0.25	0.32
PvDof17	Phvul.005G161200	PvChr05	38.54 - 38.74	Glyma.08G195300	GmChr08	15.65 - 15.85	0.19	0.98	0.193877551
PvDof17	Phvul.005G161200	PvChr05	38.54 - 38.74	Glyma.07G012100	GmChr07	0.84 - 1.04	0.18	0.89	0.202247191
PvDof17	Phvul.005G161200	PvChr05	38.54 - 38.74	Glyma.13G352000	GmChr13	44.00 - 44.20	0.1	0.41	0.243902439
PvDof17	Phvul.005G161200	PvChr05	38.54 - 38.74	Glyma.15G022800	GmChr15	1.68 - 1.88	0.08	0.45	0.177777778
PvDof18	Phvul.006G114900	PvChr06	22.95 - 23.15	Glyma.07G053900	GmChr07	4.60 - 4.80	0.22	0.57	0.385964912

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PvDof18	Phvul.006G114900	PvChr06	22.95 - 23.15	Glyma.06G131500	GmChr06	10.73 - 10.93	0.56	1.94	0.288659794
PvDof18	Phvul.006G114900	PvChr06	22.95 - 23.15	Glyma.04G233300	GmChr04	50.06 - 50.26	0.43	1.34	0.320895522
PvDof18	Phvul.006G114900	PvChr06	22.95 - 23.15	Glyma.03G258800	GmChr03	45.22 - 45.42	0.08	0.24	0.333333333
PvDof18	Phvul.006G114900	PvChr06	22.95 - 23.15	Glyma.16G022900	GmChr16	2.04 - 2.24	0.23	0.68	0.338235294
PvDof18	Phvul.006G114900	PvChr06	22.95 - 23.15	Glyma.19G257500	GmChr19	50.05 - 50.25	0.08	0.23	0.347826087
PvDof19	Phvul.006G176400	PvChr06	28.58 - 28.78	Glyma.05G158200	GmChr05	34.93 - 35.13	0.37	1.33	0.278195489
PvDof19	Phvul.006G176400	PvChr06	28.58 - 28.78	Glyma.08G115900	GmChr08	8.79 - 8.99	0.19	1.37	0.138686131
PvDof19	Phvul.006G176400	PvChr06	28.58 - 28.78	Glyma.13G230200	GmChr13	34.12 - 34.32	0.14	0.54	0.259259259
PvDof19	Phvul.006G176400	PvChr06	28.58 - 28.78	Glyma.15G082400	GmChr15	6.18 - 6.38	0.16	0.57	0.280701754
PvDof20	Phvul.006G184000	PvChr06	29.21 - 29.41	Glyma.07G198900	GmChr07	36.63 - 36.83	0.32	0.94	0.340425532
PvDof20	Phvul.006G184000	PvChr06	29.21 - 29.41	Glyma.13G237500	GmChr13	34.68 - 34.88	0.09	0.25	0.36
PvDof20	Phvul.006G184000	PvChr06	29.21 - 29.41	Glyma.13G177500	GmChr13	29.06 - 29.26	0.32	0.82	0.390243902
PvDof20	Phvul.006G184000	PvChr06	29.21 - 29.41	Glyma.15G076000	GmChr15	5.74 - 5.94	0.09	0.19	0.473684211
PvDof21	Phvul.006G184100	PvChr06	29.22 - 29.42	Glyma.07G198800	GmChr07	36.62 - 36.82	0.44	1.58	0.278481013
PvDof21	Phvul.006G184100	PvChr06	29.22 - 29.42	Glyma.13G237600	GmChr13	34.70 - 34.90	0.09	0.34	0.264705882
PvDof21	Phvul.006G184100	PvChr06	29.22 - 29.42	Glyma.13G177600	GmChr13	29.07 - 29.27	0.57	1.41	0.404255319
PvDof21	Phvul.006G184100	PvChr06	29.22 - 29.42	Glyma.15G075800	GmChr15	5.72 - 5.92	0.1	0.3	0.333333333
PvDof22	Phvul.006G188300	PvChr06	29.55 - 29.75	Glyma.07G193900	GmChr07	36.15 - 36.35	0.16	0.54	0.296296296
PvDof22	Phvul.006G188300	PvChr06	29.55 - 29.75	Glyma.13G241900	GmChr13	35.08 - 35.28	0.11	0.29	0.379310345
PvDof22	Phvul.006G188300	PvChr06	29.55 - 29.75	Glyma.13G182700	GmChr13	29.48 - 29.68	0.17	0.65	0.261538462
PvDof22	Phvul.006G188300	PvChr06	29.55 - 29.75	Glyma.15G071400	GmChr15	5.37 - 5.57	0.09	0.32	0.28125
PvDof23	Phvul.007G267600	PvChr07	50.48 - 50.68	Glyma.02G195700	GmChr02	36.86 - 37.06	0.07	0.25	0.28
PvDof23	Phvul.007G267600	PvChr07	50.48 - 50.68	Glyma.10G082000	GmChr10	9.83 - 10.03	0.08	0.22	0.363636364
PvDof23	Phvul.007G267600	PvChr07	50.48 - 50.68	Glyma.19G200300	GmChr19	45.62 - 45.82	0.28	0.67	0.417910448
PvDof26	Phvul.008G099400	PvChr08	10.56 - 10.76	Glyma.08G358100	GmChr08	46.92 - 47.12	0.05	0.28	0.178571429
PvDof26	Phvul.008G099400	PvChr08	10.56 - 10.76	Glyma.18G176300	GmChr18	41.94 - 42.14	0.05	0.27	0.185185185
PvDof24	Phvul.008G012500	PvChr08	1.01 - 1.21	Glyma.02G092700	GmChr02	8.11 - 8.31	0.07	0.35	0.2
PvDof24	Phvul.008G012500	PvChr08	1.01 - 1.21	Glyma.11G140200	GmChr11	10.59 - 10.79	0.56	1.72	0.325581395
PvDof24	Phvul.008G012500	PvChr08	1.01 - 1.21	Glyma.13G335200	GmChr13	42.77 - 42.97	0.51	3.63	0.140495868
PvDof24	Phvul.008G012500	PvChr08	1.01 - 1.21	Glyma.18G289700	GmChr18	56.81 - 57.01	0.12	0.4	0.3
PvDof27	Phvul.009G136400	PvChr09	19.92 - 20.12	Glyma.06G124300	GmChr06	10.01 - 10.21	0.18	0.56	0.321428571
PvDof27	Phvul.009G136400	PvChr09	19.92 - 20.12	Glyma.04G239500	GmChr04	51.70 - 50.90	0.18	0.49	0.367346939
PvDof28	Phvul.009G136400	PvChr09	19.92 - 20.12	Glyma.06G182200	GmChr06	15.50 - 15.70	0.05	0.26	0.192307692
PvDof28	Phvul.009G136400	PvChr09	19.92 - 20.12	Glyma.05G037800	GmChr05	3.26 - 3.46	0.16	0.62	0.258064516
PvDof28	Phvul.009G136400	PvChr09	19.92 - 20.12	Glyma.04G183700	GmChr04	45.09 - 45.29	0.05	0.26	0.192307692
PvDof28	Phvul.009G136400	PvChr09	19.92 - 20.12	Glyma.17G089300	GmChr17	6.84 - 7.04	0.16	0.63	0.253968254
PvDof29	Phvul.009G204000	PvChr09	30.05 - 30.25	Glyma.06G206400	GmChr06	19.68 - 19.88	0.15	0.54	0.277777778

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PvDof29	Phvul.009G204000	PvChr09	30.05 - 30.25	Glyma.04G158800	GmChr04	38.91 - 39.11	0.13	0.5	0.26
PvDof30	Phvul.009G047500	PvChr09	9.02 - 9.22	Glyma.07G053900	GmChr07	4.60 - 4.80	0.44	2.25	0.195555556
PvDof30	Phvul.009G047500	PvChr09	9.02 - 9.22	Glyma.06G131500	GmChr06	10.73 - 10.93	0.15	0.34	0.441176471
PvDof30	Phvul.009G047500	PvChr09	9.02 - 9.22	Glyma.04G233300	GmChr04	50.06 - 50.26	0.04	0.29	0.137931034
PvDof30	Phvul.009G047500	PvChr09	9.02 - 9.22	Glyma.16G022900	GmChr16	2.04 - 2.24	0.37	3.37	0.109792285
PvDof31	Phvul.010G013500	PvChr10	2.04 - 2.24	Glyma.18G176300	GmChr18	41.94 - 42.14	0.27	0.87	0.310344828
PvDof32	Phvul.010G115600	PvChr10	38.12 - 38.32	Glyma.07G053900	GmChr07	4.60 - 4.80	0.1	0.26	0.384615385
PvDof32	Phvul.010G115600	PvChr10	38.12 - 38.32	Glyma.06G131500	GmChr06	10.73 - 10.93	0.39	3.78	0.103174603
PvDof32	Phvul.010G115600	PvChr10	38.12 - 38.32	Glyma.04G233300	GmChr04	50.06 - 50.26	0.34	2.08	0.163461538
PvDof32	Phvul.010G115600	PvChr10	38.12 - 38.32	Glyma.03G258800	GmChr03	45.22 - 45.42	0.19	0.55	0.345454545
PvDof32	Phvul.010G115600	PvChr10	38.12 - 38.32	Glyma.16G022900	GmChr16	2.04 - 2.24	0.06	0.27	0.222222222
PvDof32	Phvul.010G115600	PvChr10	38.12 - 38.32	Glyma.19G257500	GmChr19	50.05 - 50.25	0.2	0.58	0.344827586
PvDof33	Phvul.010G141400	PvChr10	41.23 - 41.43	Glyma.07G012100	GmChr07	0.84 - 1.04	0.07	0.31	0.225806452
PvDof33	Phvul.010G141400	PvChr10	41.23 - 41.43	Glyma.08G195300	GmChr08	15.65 - 15.85	0.08	0.31	0.258064516
PvDof33	Phvul.010G141400	PvChr10	41.23 - 41.43	Glyma.13G352000	GmChr13	44.00 - 44.20	0.21	1	0.21
PvDof33	Phvul.010G141400	PvChr10	41.23 - 41.43	Glyma.15G022800	GmChr15	1.68 - 1.88	0.16	0.88	0.181818182
PvDof34	Phvul.011G064800	PvChr11	5.53 - 5.73	Glyma.11G140200	GmChr11	10.59 - 10.79	0.11	0.37	0.297297297
PvDof34	Phvul.011G064800	PvChr11	5.53 - 5.73	Glyma.12G063800	GmChr12	4.58 - 4.78	0.06	0.29	0.206896552
PvDof34	Phvul.011G064800	PvChr11	5.53 - 5.73	Glyma.13G335200	GmChr13	42.77 - 42.97	0.26	0.88	0.295454545
PvDof34	Phvul.011G064800	PvChr11	5.53 - 5.73	Glyma.15G039300	GmChr15	3.00 - 3.20	0.15	0.74	0.202702703
PvDof34	Phvul.011G064800	PvChr11	5.53 - 5.73	Glyma.18G176300	GmChr18	41.94 - 42.14	0.45	1.74	0.25862069
PvDof36	Phvul.011G071900	PvChr11	6.34 - 6.54	Glyma.12G072400	GmChr12	5.23 - 5.43	0.07	0.38	0.184210526
PvDof36	Phvul.011G071900	PvChr11	6.34 - 6.54	Glyma.13G329000	GmChr13	42.25 - 42.45	0.14	0.65	0.215384615
PvDof36	Phvul.011G071900	PvChr11	6.34 - 6.54	Glyma.15G044800	GmChr15	3.49 - 3.69	0.15	0.69	0.217391304
PvDof36	Phvul.011G071900	PvChr11	6.34 - 6.54	Glyma.U021300	Gmscaf_21	3.35 - 3.55	0.06	0.34	0.176470588