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RESEARCH ARTICLE

Genome-wide identification and characterization of the *Dof* gene family in moso bamboo (*Phyllostachys heterocycla* var. pubescens)

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Abstract The Dof (DNA binding with One Finger) family of single zinc finger proteins is a family of plant-specific transcription factors. These transcription factors have a variety of important functions in different biological processes in plants. In the current study, we identified 26 Dof family genes in moso bamboo (*Phyllostachys heterocycla* var. pubescens). A complete overview of *PhDof* genes in moso bamboo is presented, including the gene structures, phylogeny, protein motifs and expression patterns. Phylogenetic analysis of the 26 PhDof proteins identified four classes constituting seven clusters (A, B1, C1, C2, D1, D2 and D3). In addition, a comparative analysis between the *Dof* genes in moso bamboo, *Arabidopsis* (*Arabidopsis thaliana* L.) and rice (*Oryza sativa* L.) was also performed, and several putative paralogous and orthologous genes were identified. The exon numbers in *Dof* genes ranged from one to three in many plants; however, the exon number in *PhDofs* ranged from one to four. The *PhDof* genes displayed differential expression in different parts of the shoot and at different flower development stages. This study represents the first step towards a genome-wide analysis of the *Dof* genes in moso bamboo. Our study provides a useful reference for cloning and functional analysis of members of the *Dof* gene family in moso bamboo and other species.

Keywords Genome-wide analysis · *Dof* gene · *Phyllostachys heterocycla* var. pubescens · Transcription factor

Introduction

In plants, the transcriptional and post-transcriptional regulation of gene expression influences and controls many important biological processes, such as cellular morphogenesis, signal transduction and environmental stress responses (Riechmann et al. 2000).

Transcription factors (TFs) are important regulating proteins that bind specific DNA sequences in gene promoters to initiate a program of increased or decreased gene transcription (Latchman 1997). Therefore, the identification and functional characterization of TFs is essential for building predictive models of transcriptional regulatory networks. In the plant TF database, PlantTFDB v3.0, 129,288 TFs (~60 families) from 83 species have been identified systematically, based on bioinformatics analysis, of which 67 species have genome sequences, covering the main lineages of green plants (Jin et al. 2014a). Thus, PlantTFDB provides a resource for functional and evolutionary studies of plant TFs. The *Arabidopsis* genome encodes at least 1533 TFs, which account for about 5.9 % of its estimated total number of genes (Riechmann et al. 2000). For moso bamboo (*Phyllostachys heterocycla* var. pubescens), ~5.53 % of the 31,987 protein-coding genes (Peng et al. 2013) have been

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identified to encode 1768 putative TFs, which could be classified into 54 families (Jin et al. 2014a).

The Dof (DNA-binding with one finger) proteins belong to the zinc finger superfamily, and contain a highly conserved DNA-binding C2C2-type-zinc-like motif named the Dof domain, which comprises 52 amino acid residues (Yanagisawa 1995). Dofs play critical roles as transcriptional regulators in plant growth and development. In 1993, the first two Dof proteins were identified from maize by Yanagisawa and Izui. Subsequently, numerous *Dof* genes were cloned or predicted from genome databases in plants, such as single-celled green algae (*Chlamydomonas reinhardtii*), moss (*Physcomitrella patens*), fern (*Selaginella moellendorffii*) and gymnosperms (*Pinus taeda*) to higher angiosperms, including 37, 30, 41, 26, 78, 31, 18, 28, 27, 34, 1, 8, 19 and 8, *Dof* genes in *Arabidopsis* (Lijavetzky et al. 2003), rice (Lijavetzky et al. 2003), poplar (Yang et al. 2006a, b), barley (Moreno-Risueno et al. 2007b), soybean (Guo and Qiu 2013), bread wheat (Shaw et al. 2009), maize (Jiang et al. 2012), sorghum (Kushwaha et al. 2011), *Brachypodium distachyon* (Hernando-Amado et al. 2012), tomato (Cai et al. 2013), algae, fern, moss (Shigyo et al. 2007) and gymnosperms (Moreno-Risueno et al. 2007b), respectively. As the development of genomic sequencing and bioinformatics technology expands rapidly, more and more Dof family members will be identified, emphasizing their critical role in plant development.

Dof protein binding elements have been discovered in many plant-specific promoter sequences. It has been suggested that the Dof proteins have diverse roles in the regulation of specific biological processes unique to plant development, such as carbon–nitrogen metabolism in maize (Yanagisawa 2000), pea (*Pisum sativum*) (Tanaka et al. 2009), wheat (Kumar et al. 2009), *P. taeda* (Rueda-Lopez et al. 2008) and *P. patens* (Park et al. 2003; Imaizumi et al. 2005; Ward et al. 2005; Sawa et al. 2007; Fornara et al. 2009); photoresponse and photoperiodic control of flowering in *Arabidopsis* (Rueda-Lopez et al. 2008), rice (Iwamoto et al. 2009; Li et al. 2009) and *Jatropha curcas* (Yang et al. 2010, 2011); floral organ and pollen development *Arabidopsis* (Wei et al. 2010) and maize (Chen et al. 2012); seed development and germination in *Arabidopsis* (Papi et al. 2000; Gualberti et al. 2002; Gabriele et al. 2010; Rizza et al. 2011; Rueda-Romero et al. 2012), soybean (Wang et al. 2007), maize (Vicente-Carbajosa et al. 1997, Marzabal et al. 2008), barley (Mena et al. 1998; Diaz et al. 2002; Mena et al. 2002; Moreno-Risueno et al. 2007b), wheat (Dong et al. 2007), rice (Washio 2003; Kawakatsu and Takaiwa 2010; Gaur et al. 2011); synthesis of secondary metabolites in *Arabidopsis* (Skirycz et al. 2006, 2007); guard cell-specific gene regulation in *Arabidopsis* (Cominelli et al. 2011) and potato (Plesch et al. 2001); vascular development in *Arabidopsis* (Konishi and Yanagisawa 2007; Guo et al. 2009; Gardiner et al. 2010); defensive reaction in *Arabidopsis* (Kang and Singh 2000; Kang et al. 2003), and auxin-response regulation in *Cucurbita moschata* (Kisu et al. 1998; Baumann et al. 1999).

Bamboo is one of the most important non-timber forest products in the world, with high ecological, economic, edible and cultural value (Peng et al. 2010, p. 1013). The moso bamboo, a large woody bamboo, has one of the highest growth speeds in the world. However, moso bamboo has a rather striking life history, characterized by a prolonged vegetative phase lasting decades before flowering, which has hindered its genetic improvement. A high-quality draft genome sequence of moso bamboo should be published soon and represents a comprehensive genome dataset that will accelerate research into gene functions in moso bamboo. Despite the crucial roles of Dof proteins in transcriptional regulation of plant growth and development, little is known about this family in moso bamboo. In this study, we identified 26 *Dof* genes in the moso bamboo genome, named as *PhDof* 1–26. We then constructed a phylogenetic tree to evaluate the evolutionary relationships of *Dof* genes in moso bamboo. We also analysed the gene structures and conserved motifs. To identify the putative functions and evolution of *PhDof* genes, we performed phylogenetic analyses of the moso bamboo, *Arabidopsis* and rice *Dof* gene families and determined their expression profiles in moso bamboo. Thus systematic analysis provides a foundation for further functional dissection of *PhDof* genes, and could help elucidate *Dof* gene functions in other species.

Materials and methods

Identification of Dof genes in moso bamboo

We identified the members of the Dof genes family in moso bamboo using two approaches. First, the Dof sequences of *Arabidopsis* and rice were downloaded from the *Arabidopsis* genome TAIR database (http://www.arabidopsis.org/) and the rice genome annotation database (http://rice.plantbiology.msu.edu/). The protein sequences of the Dof domains were used to search for potential Dof-domain homolog hits in the whole genome sequence of moso bamboo, using BLASP searches against the protein profile, which has been published in the moso bamboo genome database (http://www.ncgr.ac.cn/bamboo). Additionally, hidden Markov model (HMM) searches (Finn et al. 2011) were performed locally in the moso bamboo database, using the Dof domain family HMM profile (PF02701). We subjected all the obtained protein sequences to domain analysis using the InterProScan (http://www.

ebi.ac.uk/Tools/pfa/iprscan5/) and SMART (http://smart.embl-heidelberg.de/) tools, with the default parameters, to reveal the presence of Dof domains. Protein sequences lacking a Dof domain were rejected.

Multiple alignment and phylogenetic analysis

We performed alignments of Dof protein sequences using the Clustal X 2.1 program with its default settings (Larkin et al. 2007). Phylogenetic trees were constructed in the MEGA5.1 software using the Neighbor-Joining (NJ), Minimum Evolution (ME) and Maximum Likelihood (ML) methods (Tamura et al. 2011). We tested the reliability of the obtained trees using bootstrapping with 1000 replicates.

Genome structure and conserved motifs analysis

The GSDS (Gene Structure Display Server; http://gsds1.cbi.pku.edu.cn/) program was used to illustrate the exon/intron organization for individual Dof genes by comparing the coding sequences with their corresponding genomic DNA sequences from the moso bamboo genome database. The deduced amino-acid sequences of the PhDofs were analyzed using the online version of MEME 4.10.1 (http://meme-suite.org/tools/meme) for motif analysis. To identify conserved motifs in these sequences, selection of the maximum number of motifs was set to 25, with a minimum width of six and a maximum width of 120 amino acids, while other factors were set at default values.

mRNA sequencing and analysis

All the bamboo samples were taken from Baizhu Park, which is located at Yiyang city in Hunan province, China, on April 4, 2013. Samples from the tip of the shoot (ST), the middle part of shoot (SM), the base part of shoot (SB), and shoot sheaths (tip, middle, base of shoot sheaths mixtures, SS) were obtained from the wild *P. heterocycla* var. pubescens. Samples were collected from three plants whose heights were about 6.0 m. In all cases, samples were collected, immediately frozen in liquid nitrogen and stored at −80 °C until RNA extraction.

Total RNA was isolated from the plant tissues using an Easy-spin^{TM} kit (Aidlab, Beijing, China), following the manufacturer's instructions. Purified mRNA was chemically fragmented to 200–500 bp fragments. Next, we synthesized the fist- and second-strand cDNAs, followed by end repair and index adapter ligation. Finally, the resulting libraries were sequenced using an Illumina HiSeq^{TM} 2000 (Illumina, San Diego, CA, USA) to generate paired-end sequences.

We conducted a gene expression analysis using Illumina RNA-Seq technology. The sequencing and assembly were performed at the Shanghai Hanyu Biotech Co. Transcriptome sequencing (RNA-Seq) data were generated using the Illumina HiSeq^{TM} 2000 platform. Approximately 21957740, 20979560, 21704837 and 21759266 reads were generated from the four sample libraries (ST, SM, SB and SS), respectively. The adapters or low-quality reads, where the number of 'N' bases exceeded 5 %, were removed from the raw data. The reads were then mapped to genes and the genome of moso bamboo, allowing for a maximum of two mismatches. The gene expression values were normalized by the measure of reads per kilobase per million (RPKM). Finally, heat maps of gene expression from the four tissues were visualized using HemI 1.0 software (Deng et al. 2014).

Results

Dof gene family in moso bamboo

An HMM search with the Dof domain HMM profile (PF02701) and BLASTP using *Arabidopsis* and rice Dof protein as queries were used to identify moso bamboo Dof sequences. The obtained sequences were analyzed using InterProScan and SMART for the presence of the Dof domain. Twenty-six *PhDof* family genes were identified (Table 1), and all of them have a typical binding domain of 52 residues spanning a single C2/C2 zinc finger structure (DOF domain, Fig. S1). In the PlantTFDB (http://planttfdb.cbi.pku.edu.cn/), although 31 *PhDof* genes were identified, InterProScan and SMART analysis found that Dof domains were absent from five sequences (PH01000290G0170, PH01000789G0200, PH01000941G0150, PH01003477G0030, and PH01155840G0010). There was no standard annotation assigned to these newly identified genes; therefore, we named these *PhDof* genes *PhDof*-1 to *PhDof*-26, according to their location on the genome scaffolds. The names of the *PhDof* genes, the locus gene, the length, molecular weight (MW), isoelectric point (pI), and the grand average of hydropathicity (GRAVY) are shown in Table 1. The identified *PhDof* genes encode peptides ranging from 197 to 542 amino acids in length, with an average of 357.5.

To investigate the features of the homologous domain sequences, and the frequency of the most prevalent amino acids at each position within the moso bamboo Dof domain, multiple alignment analysis of the Dof domains from the 26 PhDofs was performed (Fig. 1). The Dof domain of moso bamboo was revealed to be a highly conserved sequence, and 25 out of 52 amino acids were 100 % conserved in all PhDof proteins, including four absolutely conserved cysteine residues that presumably coordinate the zinc ion. Other highly conserved residues in

Table 1 Dof genes in the *P. heterocycla* genome

Name	Gene ID	Length (aa)	MW (kDa)	pI	GRAVY	Intron number	Postion of Dof domain	*E* value
PeDof-1	PH01000000G4160	351	35,241.8	8.46	−0.440	0	66–117	6e−022
PeDof-2	PH01000004G1130	324	34,749.5	4.95	−0.372	0	34–85	6e−022
PeDof-3	PH01000087G0200	197	20,928.2	6.56	−0.445	1	45–96	7e−021
PeDof-4	PH01000113G0300	432	46,372.8	8.32	−0.675	1	103–154	3e−018
PeDof-5	PH01000188G0230	434	46,086.5	8.29	−0.591	1	105–156	2e−014
PeDof-6	PH01000200G0640	408	41,043.7	8.71	−0.323	2	118–169	7e−021
PeDof-7	PH01000209G1040	490	53,195.3	8.06	−0.514	1	110–161	1e−016
PeDof-8	PH01000211G0640	365	37,197.4	9.03	−0.408	0	74–125	3e−020
PeDof-9	PH01000219G0080	422	45,105.4	7.58	−0.583	1	92–143	4e−018
PeDof-10	PH01000226G1160	239	24,274.0	9.47	−0.454	1	79–130	6e−014
PeDof-11	PH01000266G0140	538	58,714.0	8.85	−0.431	2	172–223	2e−016
PeDof-12	PH01000309G0960	323	34,409.3	4.79	−0.316	0	34–85	3e−024
PeDof-13	PH01000323G0330	246	26,213.1	6.16	−0.635	0	54–105	3e−020
PeDof-14	PH01000664G0640	305	32,952.7	5.54	−0.426	0	35–86	4e−022
PeDof-15	PH01000901G0540	203	21,695.8	6.56	−0.618	1	51–102	3e−021
PeDof-16	PH01000949G0120	198	20,938.5	8.32	−0.538	3	78–129	7e−018
PeDof-17	PH01001038G0580	271	27,978.3	8.90	−0.367	2	104–155	2e−018
PeDof-18	PH01001117G0310	317	33,349.2	8.52	−0.391	2	78–129	8e−023
PeDof-19	PH01001184G0160	443	47,232.8	7.83	−0.580	0	70–121	8e−017
PeDof-20	PH01001264G0440	479	51,417.5	7.49	−0.560	2	149–200	2e−017
PeDof-21	PH01001385G0300	542	59,131.0	5.07	−0.765	1	164–215	3e−017
PeDof-22	PH01001983G0170	282	28,930.4	8.64	−0.221	0	36–87	5e−021
PeDof-23	PH01002384G0100	250	25,770.4	9.98	−0.147	0	67–118	4e−022
PeDof-24	PH01003147G0100	294	30,822.2	8.63	−0.163	2	59–110	8e−021
PeDof-25	PH01003628G0010	245	25,693.0	9.05	−0.280	1	62–113	2e−018
PeDof-26	PH01007575G0040	537	58,470.2	5.37	−0.796	1	163–214	6e−018

MW molecular weight, *pI* isoeletric point, *GRAVY* grand average of hydropathicity

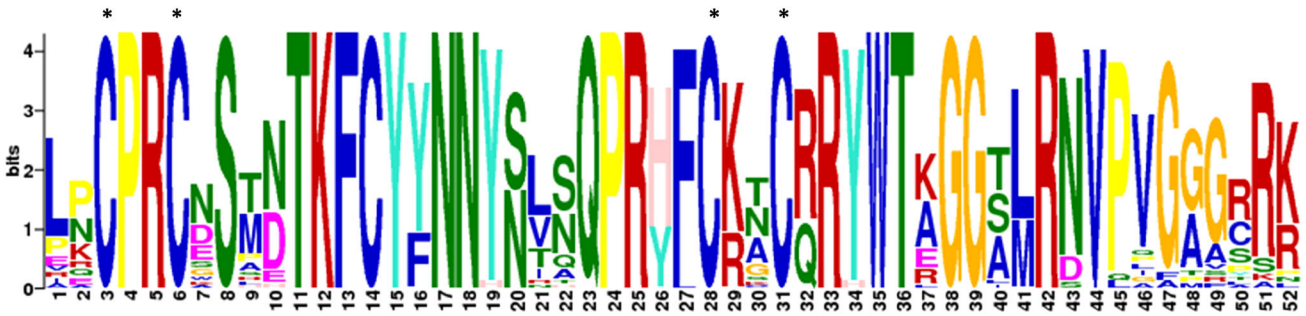

Fig. 1 Dof domains are highly conserved across all Dof proteins in moso bamboo. The sequence logos are based on aligments of all moso bamboo Dof domains. Multiple alignment analysis of 26 typical moso bamboo Dof domains was performed with ClustalW. The *bit score* indicates the information content for each position in the sequence. *Asterisks* indicate the conserved cysteine residues (Cys) in the Dof domain

the moso bamboo Dof domains were Pro-4, Arg-5, Ser-8, Thr-11, Lys-12, Phe-13, Cys-14, Tyr-15, Asn-17, Asn-18, Gln-23, Pro-24, Arg-25, Arg-33, Trp-35, Thr-36, Gly-38, Gly-39, and Arg-42. These highly conserved residues were also nearly identical to the Dof domain proteins of other plants, such as soybean (Guo and Qiu 2013), sorghum

(Kushwaha et al. 2011) and tomato (Cai et al. 2013). Moreover, eight other amino-acid residues showed variation in less than three sequences among all PhDofs.

We analysed 16 species that, according to publications, contained 432 Dof proteins (Table 2). After the comparative genomic analysis, the number of Dof transcription factors in moso bamboo (26) was equal to that of barley (26) and exceeded that of *Ricinus communis* (21), *Vitis vinifera* (25), maize (18), *P. patens* (19), *P. taeda* (8), *S. moellendorffii* (8). It was, however, less than that of soybean (78), *Arabidopsis* (37), *P. trichocarpa* (41), tomato (34), rice (30), wheat (31), sorghum (28) and *B. distachyon* (27). In general, angiosperms have more *Dof* genes than gymnosperms, mosses, ferns and green algae. The genome size of moso bamboo (2.1 Gb) was less than that of maize (2.3 Gb), barley (5.1 Gb), wheat (17 Gb), and *P. taeda* (23.2 Gb), but greater than that of other species examined. We found that the number and genome size of the *Dof* genes showed no pattern among angiosperms, gymnosperm, moss, fern and green alga, which was the same for dicotyledons and monocotyledons. Although the genome size of barley (5.1 Gb) is 2.4 times that of moso bamboo (2.1 Gb), the two had equal numbers of *Dof* genes; however, the genome size of moso bamboo was 8.08 times larger than that of *B. distachyon* (260 Mb), and the two had similar numbers of *Dof* genes.

Phylogenetic, gene structure and conserved motif analysis of the *Dof* gene family in moso bamboo, *Arabidopsis* and rice

To investigate the molecular evolution and phylogenetic relationship among the Dof domain proteins in moso bamboo, *Arabidopsis* and rice, the 26 predicted PhDof proteins were subjected to multiple sequence alignment along with 36 *Arabidopsis* and 30 rice Dof proteins. Three unrooted phylogenetic trees were constructed using the NJ, ME and ML methods, based on the alignment of all the Dof amino-acid sequences. The tree topologies were similar, despite using different tree-building methods, except at the deep nodes (Fig. 2, Fig. S2). The NJ tree showed that all the Dof family proteins from the three higher plants were divided into four major clusters of orthologous groups and nine well-supported clades (A, B1, B2, C1, C2, C3 and D1, D2, D3; Fig. 2), similar to previous reports in *Arabidopsis* (Lijavetzky et al. 2003), soybean (Guo and Qiu 2013) and tomato (Cai et al. 2013). Among these, group D comprised the largest clade, containing 13 members and accounting for 50 % of the total Dof proteins. The other three groups contained two (Group A), three (Group B), and eight (Group D) members, respectively. Subgroup C3 comprised a species-specific group for *Arabidopsis* (monocotyledon), and subgroup D3 was specific for moso bamboo and rice

Table 2 Summary of the Dof transcription factors in 16 species

Classifiation	Species	Number of Dof	Genome size	References
Angiosperms				
Dicotyledons	*Ricinus communis*	21	350 Mb	Jin et al. (2014b)
	Vitis vinifera	25	490 Mb	Li et al. (2013)
	Solanum lycopersicum	34	900 Mb	Cai et al. (2013)
	Arabidopsis thaliana	37	135 Mb	Lijavetzky et al. (2003)
	Populus trichocarpa	41	480 Mb	Yang et al. (2006a)
	Glycine max	78	760 Mb	Guo and Qiu (2013)
Monocotyledons	*Zea mays*	18	2.3 Gb	Jiang et al. (2012)
	Hordeum vulgare	26	5.1 Gb	Moreno-Risueno et al. (2007b)
	Brachypodium distachyon	27	260 Mb	Hernando-Amado et al. (2012)
	Sorghum bicolor	28	730 Mb	Kushwaha et al. (2011)
	Oryza sativa	30	466 Mb	Lijavetzky et al. (2003)
	Triticum aestivum	31	17 Gb	Shaw et al. (2009)
Gymnosperm	*Pinus taeda*	8	23.2 Gb	Moreno-Risueno et al. (2007b)
Moss	*Physcomitrella patens*	19	480 Mb	Shigyo et al. (2007)
Fern	*Selaginella moellendorffii*	8	212 Mb	Moreno-Risueno et al. (2007b)
Green alga	*Chlamydomonas reinhardtii*	1	130 Mb	Shigyo et al. (2007)

MW molecular weight, *pI* isoeletric point, *GRAVY* grand average of hydropathicity

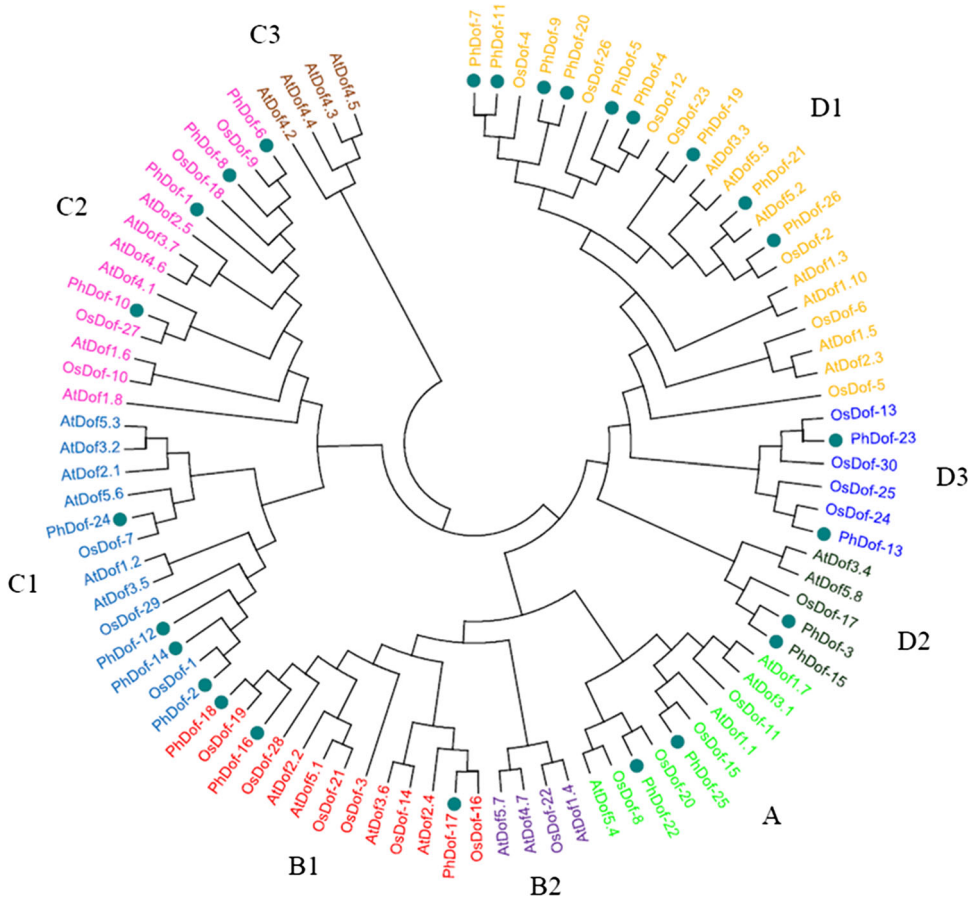

Fig. 2 Phylogenetic tree of all Dof domain-containing proteins from moso bamboo, *Arabidopsis* and rice. The deduced full-length amino-acid sequences of 26 moso bamboo, 36 *Arabidopsis* and 30 rice Dof genes were aligned by Clustal X 1.83 and the phylogenetic tree was constructed using MEGA 5.05 by the neighbor-joining method with 1000 bootstrap replicates. Each Dof subgroup is indicated by a specific *color*

(dicotyledons), similar to previous reports (Guo and Qiu 2013), indicating that there was a presumed gene loss event after the dicot–monocot split. Additionally, the B, C and D groups further clustered, forming a large clade, similar to previous reports for tomato and soybean, implying that they might have originated from a common ancestor by frequent gene duplication. Based on the phylogenetic tree, several putative paralogous (i.e. *PhDof-7*/*PhDof-11*, *PhDof-9*/*PhDof-20* or *PhDof-3*/*PhDof-15*) and orthologous (i.e. *AtDof5.6*/*PhDof-24*/*OsDof-7*, *AtDof2.4*/*PhDof-17*/*OsDof-16*, *AtDof1.1*/*PhDof-25*/*OsDof-15*, or *PhDof-13*/*OsDof-25*/*OsDof-24*, *PhDof-1*/*OsDof-2*, *AtDof5.2*/*PhDof-21*) genes were identified.

Gene structural diversity is a possible mechanism for the evolution of multigene families. To gain further insight into the structural diversity of *Dof* genes, we compared the exon/intron organization in the coding sequences of individual *PhDof* genes. A detailed illustration of the exon/intron structures is shown in Fig. 3. According to the predicted structures, most of the *Dof* genes have one or two exons in *Arabidopsis* (Lijavetzky et al. 2003), *B. distachyon* (Hernando-Amado et al. 2012), cater bean (Jin et al. 2014b), rice (Lijavetzky et al. 2003), sorghum (Kushwaha et al. 2011) and tomato (Cai et al. 2013). By contrast, *PhDofs* have one to four exons. Among these genes, nine have one exon, ten have two exons, six have three exons and one gene (*PhDof-16*) contains four exons.

To reveal the diversification of Dof genes in moso bamboo, putative motifs were predicted by the program MEME (Multiple Em for Motif Elicitation), and 25 motifs were found in the 26 Dof proteins (Fig. 4; Table S2). Motif 1 was present in all the Dof proteins and represents the conserved Dof domain. Moreover, a number of common motifs were found in all moso bamboo Dofs (Table S2). As expected, most of the closely related members in the phylogenetic tree had common motif compositions. For example, there were no conserved motifs outside the Dof domain in subgroup A, B1 and D3, while motifs 2, 3, 4, 5, 6, 7, 8, 10, 11, 14, 16, 19, 20, 22, 23 and 25 appeared in nearly all the members of subgroup D1. In other subgroups, motifs 9 and 17 were specific to subgroup C1; motifs 12, 18, 21 and 24 were specific to subgroup C2; and motifs 13 were specific to subgroup D2. Thus, the phylogenetic tree was further supported by the comparative motif analyses of the deduced amino acid sequences of the Dof family proteins.

Moreover, because most of the *Arabidopsis* and other plants *Dof* genes with similar functions tended to fall into one subgroup, moso bamboo *Dof* genes in the same

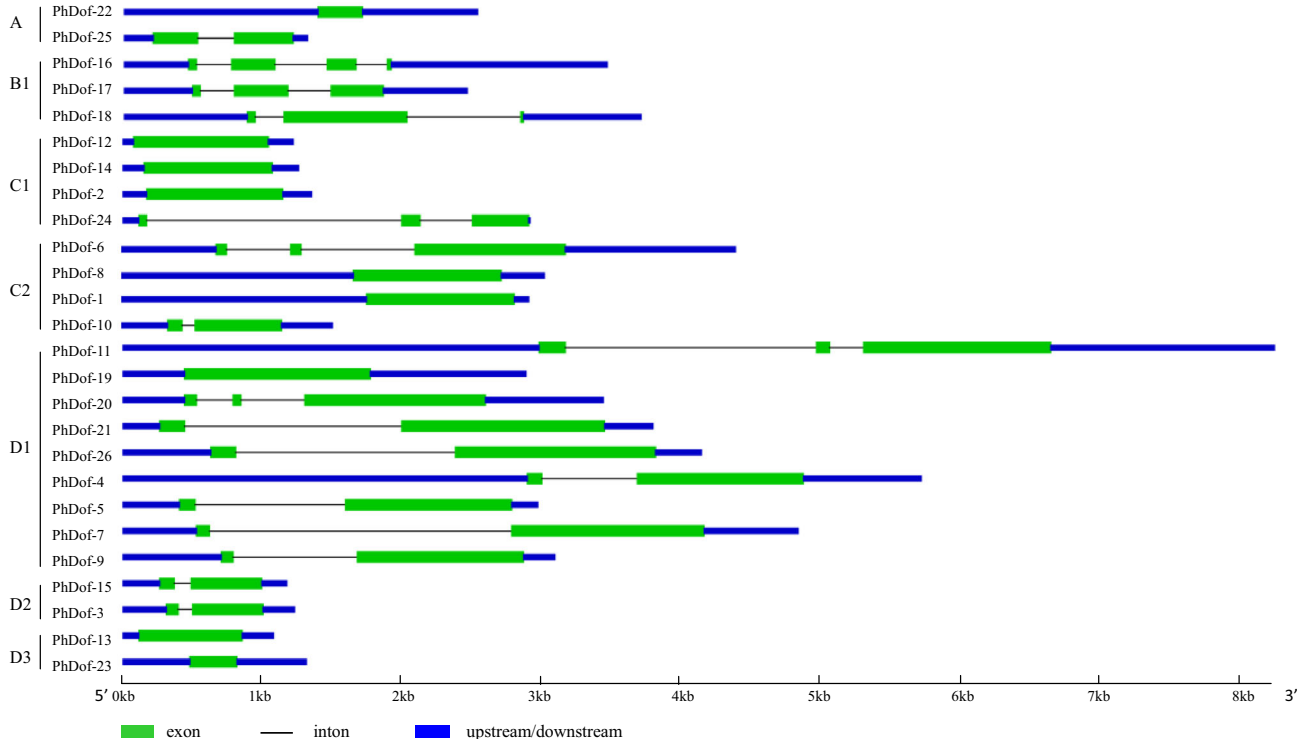

Fig. 3 Exon/intron structure of moso bamboo Dof genes. Exons are represented by *green boxes* and introns by *black lines*, and upstream/downstream by *blue boxes*. The size of exons, introns and upstream/downstreams can be estimated using the scale below

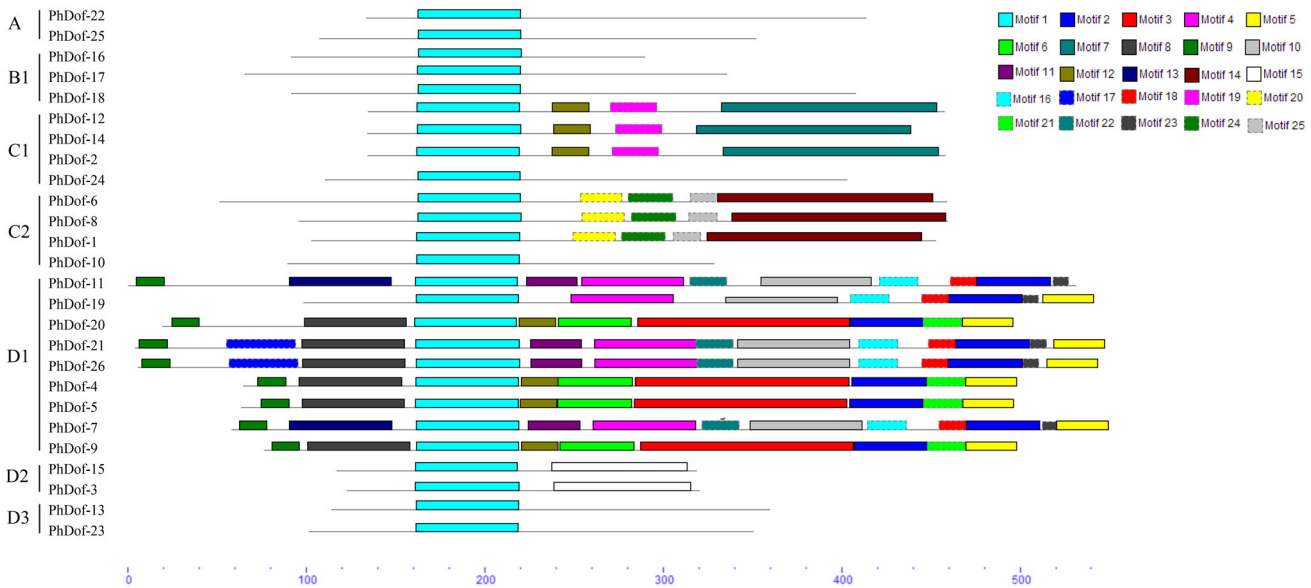

Fig. 4 Schematic distributions of the conserved motifs among the defined gene cluster. Motifs in the deduced amino-acid sequences of the 26 PhDofs were identified using MEME software. The relative position of each identified motif in all Dof proteins is shown. Each motif is represented by a *colored block* with a *number*. Multilevel consensus sequences for the MEME-defined motifs are listed in Table S2

subgroup may have similar functions. Therefore, another unrooted phylogenetic tree was constructed using the NJ method, based on the Dof amino-acid sequences for which the functions had been identified in many plants (Fig. S3).

In subgroup A, *PhDof-22* and *PhDof-25* clustered with *AtDof1.1* (*OBP2*), which is involved in regulating glucosinolate biosynthesis (Skirycz et al. 2006), laying the foundation for the study of moso bamboo secondary

metabolism. *PhDof-22* also is also closely related with *GmDof*, which plays important role in regulating the synthesis of lipids in soybean seeds (Wang et al. 2007) and *TaDof-1*, whose overexpression could improve the utilization rate of nitrogen in wheat (Kumar et al. 2009; Fig. S3).

In subgroup B1, three moso bamboo *Dof* genes (*PhDof-16, PhDof-17* and *PhDof-18*) clustered with *AtDof3.6 (OBP3)*, which modulates phytochrome and cryptochrome signaling in *Arabidopsis* (Ward et al. 2005), and *StDof1*, which controls guard cell-specific gene expression in tomato (Plesch et al. 2001). These data will add to the design of tailor-made guard cell promoters as a further tool in molecular engineering of guard cell function and, hence, the control of stomatal carbon dioxide (CO_2) uptake and water loss in crop plants.

In subgroup C1, four moso bamboo *Dof* genes (*PhDof-2, PhDof-12, PhDof-14* and *PhDof-24*) clustered with *AtDof5.6 (HCA2)*, which is expressed specifically in cells at an early stage of vascular tissue development (Guo et al. 2009).

In subgroup C2, four moso bamboo *Dof* genes (*PhDof-1, PhDof-6, PhDof-8* and *PhDof-10*) clustered with *AtDof3.7 (DAG1)*, *AtDof2.5 (DAG2)*, *OsDof-10 (RPBF)* and *HvSAD*, *PsDOF-7*, which are indirectly or directly involved in carbohydrate metabolism (sugar and thiol status, and seed storage protein accumulation) (Kawakatsu and Takaiwa 2010; de Dios Barajas-López et al. 2012) and seed development (Gualberti et al. 2002; Moreno-Risueno et al. 2007a).

In subgroup D1, nine moso bamboo *Dof* genes (*PhDof-4, PhDof-5, PhDof-7, PhDof-9, PhDof-1, PhDof19, PhDof-20*, *PhDof-21* and *PhDof-26*) clustered with *AtDof5.5 (CDF1)*, *AtDof5.2 (CDF2)*, *AtDof3.3 (CDF3)*, *AtDof1.5 (COG1)*, *AtDof1.10 (CDF5)*, *JcDof-1*, *JcDof-3*, and Os*Dof-12*, which are associated with the light-mediated circadian clock and regulation of flowering in *Arabidopsis* (Imaizumi et al. 2005; Sawa et al. 2007; Fornara et al. 2009; Song et al. 2012), *J. curcas* (Yang et al. 2010, 2011) and rice (Iwamoto et al. 2009; Li et al. 2009).

In subgroup D2, two moso bamboo *Dof* genes (*PhDof-3* and *PhDof-15*) clustered with *AtDof3.4 (OBP1)*, which specifically increases the binding of the OBF proteins to ocs element sequences, raising the possibility that interactions between these proteins are important for the activity of the 35 s promoter (Zhang et al. 1995), and *AtDof5.8*, which is the upstream regulator of *ANAC069* and is responsive to abiotic stress (He et al. 2015). In addition, the *AtDof5.8* promoter activity was specifically detected in the cells of prospective veins in leaf primordia of seedlings and cotyledons of developing embryos, and the vascular tissue of developing flower buds. The *AtDof5.8* promoter showed strong activity in advance of perceptible procambium formation. Thus, *AtDof5.8* might function in early, but different, processes in vascular development (Konishi and Yanagisawa 2007).

In subgroup D3, two moso bamboo *Dof* genes (*PhDof-13* and *PhDof-23*) clustered with *ZmDof-1* and *ZmDof-2*. Transgenic expression of the maize *ZmDof-1* gene in rice enhanced carbon and nitrogen assimilation under low-nitrogen conditions (Kurai et al. 2011). Moreover, *ZmDof-1* is involved in light-regulated gene expression and has distinct activities in greening and the etiolated protoplast. Both *ZmDof-1* and *ZmDof-2* specifically interact with the promoter of the phosphoenolpyruvate carboxylase gene to enhance or repress its promoter activity, respectively (Yanagisawa and Sheen 1998; Yanagisawa 2000).

Expression profiles of *Dof* genes in bamboo shoots and flowers

The growth of the moso bamboo shoot is rapid and steady, and in suitable spring conditions, at the peak of its growth, the shoot can grow by as much as 100 cm within 24 h. Moreover, bamboo shoots are a traditional vegetable and natural health food in China (Peng et al. 2010, 2013). The expression analysis of *Dof* genes in bamboo shoots has important implications for moso bamboo genetic studies during the fast growth of shoots and provides potential gene candidates for further research.

High-throughput sequencing and gene expression analyses were performed on four moso bamboo shoot tissues, and the RNA-seq data generated is a useful resource for studying gene expression profiles. Based on the RPKM transcriptomic data of *Dof* genes in four moso bamboo samples (Table S4), the expression patterns of the 26 moso bamboo *Dof* genes were analyzed (Fig. 5). Two genes (*PhDof-5* and *PhDof-23*) had very low expression in all four tissues. This might be because these genes have some other functions during the bamboo development process. Only four genes, *PhDof-6*, *PhDof-8, PhDof-13* and *PhDof-15*, showed high expression levels (RPKM $>$ 100) among the four tissues. Half of the *PhDof* genes showed a certain degree of tissue specificity, with five genes being abundantly expressed in the shoot tops, seven genes being abundantly expressed in the bottom shoots and 1 gene being abundantly expressed in the shoot sheaths. No *Dof* genes showed abundant expression levels in the middle shoots.

Moso bamboo is an arborescent, perennial plant characterized by woody stems and a rather striking life history, such as flowering synchronously and dying collectively after flowering (Lin et al. 2010). Gao et al. (2014) characterized the floral transcriptome of moso bamboo at four

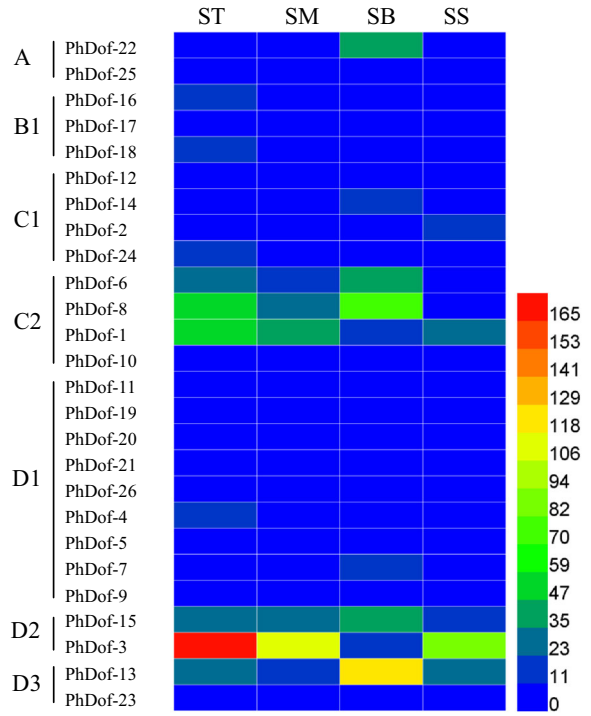

Fig. 5 Expression profiles of moso bamboo Dof genes in four samples. Transcriptome sequencing (next-generation RNA-seq) was employed to investigate expression patterns of Dof genes. The *color scale* is shown on the right, with *blue* indicating low expression levels while *red* indicates high levels. *ST* shoot tip, *SM* the middle part of the shoot, *SB* the base part of the shoot, and *SS* shoot sheaths (*tip*, *middle*, *base* of shoot sheaths mixtures)

flowering developmental stages (floral bud formation, inflorescence development, anthesis and flower withered stages) by transcriptome sequencing and RNA-seq analysis. The significance of differential transcript abundance of the 26 Dof family genes from Gao et al. (2014) data during the different flower developmental stages is shown in Table S5. All 26 *PhDofs* were significantly differentially expressed in the early stage of flowering, suggesting that *PhDofs* play important roles in the early stage of flower development. Most of them showed upregulated expression; nevertheless, four genes (*PhDof-4*, *PhDof-5*, *PhDof-20* and *PhDof-22*) were downregulated, and showed period-specific expression in the floral bud formation stage. *PhDof-2* and *PhDof-25* showed the most differential expressions (fold-change values of approximately 6.93 and 6.29) followed by *PhDof-3* (fold-change value approximately 5.12). They were all upregulated at the floral bud formation stage, although *PhDof-3* and *PhDof-25* had the opposite expression patterns at the inflorescence development stage. *PhDof-3*, *PhDof-15*, *PhDof-19* and *PhDof-25* were differentially expressed in the floral bud formation and inflorescence development stages, moreover, *PhDof-3* and *PhDof-15* showed similar expression trends, with upregulated expression at the floral bud formation stage and then downregulated expression at the inflorescence development stage. *PhDof-5* and *PhDof-12* were differentially expressed in the floral bud formation and the flower withered stages, and they were both downregulated during the stage representing the flower withering process. The only difference was that the expression of *PhDof-5* decreased significantly during the floral bud formation process, while *PhDof-12* was increased significantly at this stage. Only *PhDof-10* was increased significantly during the first three phases (floral bud formation, inflorescence development and anthesis stage), with significant differential expression during the last flower withered stage. Nine *PhDof* genes (*PhDof-6*, *PhDof-7*, *PhDof-9, PhDof-11, PhDof-14*, *PhDof-17*, *PhDof-21, PhDof-23* and *PhDof-26)* were all dramatically differentially expressed at the four flowering development stages, but showed different expression patterns.

Discussion

In this study, 26 *PhDof* genes were identified in moso bamboo. This number is similar to the *Dof* genes present in barley (26; Moreno-Risueno et al. 2007b), grape (25; Li et al. 2013), *B. distachyon* (27; Hernando-Amado et al. 2012), sorghum (28; Kushwaha et al. 2011); but it is much less than that in soybean (78; Guo and Qiu 2013), which currently has the largest number of identified *Dof* genes. *Glycine max* is an ancient polyploid (palaeopolyploid), whose whole genome duplications (WGD) occurred at approximately 59 and 13 million years ago, resulting in a highly duplicated genome with nearly 75 % of the genes present in multiple copies (Schmutz et al. 2010). These facts suggested that the WGDs of soybean facilitated the expansion of the *Dof* gene family.

Among rice, *Arabidopsis*, tomato, *B. distachyon,* cater bean and sorghum Dof genes, the organizations of the exon/intron structures are conserved: the number of introns in the *Dof* genes ranged from 0 to 2 (Lijavetzky et al. 2003; Kushwaha et al. 2011; Hernando-Amado et al. 2012; Cai et al. 2013; Jin et al. 2014b). However, in moso bamboo, the intron number in *PhDofs* ranged from 0 to 3 (*PhDof-16* contained 3 introns. In *Arabidopsis* (Lijavetzky et al. 2003), rice (Lijavetzky et al. 2003), soybean (Guo and Qiu 2013), tomato (Cai et al. 2013), and many other plants, the most closely related *Dof* gene members in the same subgroup generally show the same exon/intron pattern, with the position and length of the introns being almost completely conserved within most subgroups. By contrast, the gene structure appeared to be more variable for the D2 and

D3 *PhDofs* subgroups (Fig. 3), suggesting that there might be larger evolutionary variation among moso bamboo *Dofs*.

Our results also revealed that certain *Dof* genes might have specific functions during moso bamboo shoot development and flower development process. For example, *PhDof-5* and *PhDof-23* had very low expressions, with an RPKM < 1, in the four moso bamboo shoot tissues (Table S4), suggesting that they might do not participate in regulating the growth of bamboo shoots. However, they showed significant differential expression patterns during the flower development processes (Table S5). *PhDof-5* showed downregulated expression at the floral bud formation stage, and might specificity negatively regulate the plant transition from the vegetative to the reproductive stage. *PhDof-5* was clustered with *PhDof-4* and *OsDof12*. Previous studies showed that a moso bamboo *Dof* (a homolog of *OsDof12*) might be active in the drought-*Dof-MADS14*-flowering pathway during bamboo flowering process under drought stress in Southern China (Peng et al. 2013); *PhDof-4* was also downregulated at the floral bud formation stage; therefore, *PhDof-4* or *PhDof-5* might participate in the drought-*Dof-MADS14*-flowering pathway in moso bamboo. *PhDof-23* might not participate in regulating the growth of bamboo shoots: it was obviously differentially expressed in the whole process of bamboo flower development, showed upregulated expression at the floral bud formation and inflorescence development stages, was specifically downregulated at the anthesis stage, and was then upregulated expression again at the withered stage. This expression pattern suggested that it might a key positive regulator for the early stages of floral development and withering, and negative regulator for flower opening.

Bamboo shoot shell extracts contain many kinds of biologically active substances that show significant antioxidative activity (Gao 2011). The expression of *PhDof-15* was abundant in the shoot sheaths. Phylogenetic analysis showed that it was closely related to *AtOBP1*, which was identified as responsive to abiotic stress. Thus, *PhDof-15* might be involved in producing antioxidants in shoot sheaths resist abiotic stress. Moreover, *PhDof-15* was dramatically differentially expressed during the floral bud formation and inflorescence development processes. This result agreed with those of previous studies, which also showed that a drought-responsive *PeDof* gene was highly expressed in the floral tissues, especially in the early stage of flowering (Gao et al. 2014; Peng et al. 2013).

In this study, *PhDof-1, PhDof-6,* and *PhDof-8* showed different site-specific middle–to–high expression levels in bamboo shoots (Table S4). Moreover, *PhDof-6* was differentially expressed at four flower development stages, and *PhDof-1* and *PhDof-8* were period-specifically differentially expressed at the floral bud formation stage (Table S5). In addition, they clustered with *DAG1*, *DAG2*, *RPBF*, *HvSAD* and *PsDOF-7*, which are indirectly or directly involved in carbohydrate metabolism (Kawakatsu and Takaiwa 2010; de Dios Barajas-López et al. 2012). *PhDof-1*, *PhDof-6* and *PhDof-8* might be site-specifically or period-specifically involve in carbohydrate metabolism for rapid bamboo shoots growth and flower development process, respectively. During the flower development process, *PhDof-2, PhDof-3* and *PhDof-25* showed the largest differential expressions at the early stage, suggesting that they all positively regulated floral bud formation. The phylogenetics analysis results showed that *PhDof-25* clustered with *AtDof1.1* (*OBP2*), *PhDof-2* clustered with *AtDof5.6* (*HCA2*), and *PhDof-3* clustered with *AtDof5.8*, which has been reported to involved in regulating glucosinolate biosynthesis (Skirycz et al. 2006). *AtDof5.8* is expressed specifically in cells at an early stage of vascular tissue development (Guo et al. 2009; Konishi and Yanagisawa 2007), and is responsive to abiotic stress (He et al. 2015), respectively. These results will help build a foundation for the study of moso bamboo secondary metabolism, vascular tissue development and abiotic stress responses.

Genes in the same group, with similar expression patterns, might have conserved functions. *PhDof-7* and *PhDof-11* had similar expression patterns in bamboo shoots but showed different patterns in flower development stages. However, some Dof members in the same subgroups had totally different expression patterns. For example, in the D3 subgroup, *PhDof-13* showed specific expression in the base of the shoots, while *PhDof-23* showed very low expression in all four shoot samples; even some paralogous genes with highly identical amino acid sequences had totally opposite expression patterns. For example, for the *PhDof-3*/*PhDof-15* paralogous gene pair, *PhDof-3* was mainly expressed in the base part of the shoots, while *PhDof-15* was rarely expressed there, suggesting that they might participate in the same process through different ways. This phenomenon was also observed in an expression analysis of the soybean *Dof* family genes (Guo and Qiu 2013). The results revealed that the Dof family genes show functional and regulative diversity, even among the paralogous genes, despite having highly similar amino acid sequences.

Conclusions

In this study, we conducted a detailed analysis of the *Dof* gene family in moso bamboo, including genome-wide identification, phylogeny, gene structure, protein motifs and expression pattern analyses. These results will form the basis for future gene-cloning and functional analysis to unravel the role of *Dof* genes in the fast growth and floral development of moso bamboo.

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Compliance with ethical standards

Conflict of interest We declare that no competing interests exist.

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