

Insights into structural and functional diversity of Dof (DNA binding with one finger) transcription factor

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Abstract

Main conclusion The structural, functional and in-silico studies of Dof transcription factor attempted so far reveals immense opportunity to analyze the plant genomes in terms of number of Dof genes and discuss in light of the evolution. The multiple functions of Dof genes needs to explored for crop improvement.

Transcription factors play a very vital role in gene regulation at transcriptional level and are being extensively studied across phylas. In recent years, sequencing of plant genomes has led to genome-wide identification and characterizations of diverse types of plant-specific transcription factor gene family providing key insights into their structural and functional diversity. The DNA binding with one finger (Dof), a class belonging to C2H2-type zinc finger

family proteins, is a plant-specific transcription factor having multiple roles such as seed maturation and germination, phytohormone and light-mediated regulation and plant responses to biotic and abiotic stresses. Dof proteins are present across plant lineage, from green algae to higher angiosperm, and represent a unique class of transcription factor having bifunctional binding activities, with both DNA and proteins, to regulate the complex transcriptional machinery in plant cells. The structural and functional diversity of the Dof transcription factor family along with the bioinformatics analysis highlighting the phylogeny of Dof families is reviewed in light of its importance in plant biotechnology for crop improvement.

Keywords Transcription factor · Dof · Zinc finger · Gene regulation · In silico

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Introduction

Transcription factors (TFs) recognize specific DNA sequence elements within promoter and are responsible for activating or repressing the activity of RNA polymerase vis-a-vis controlling the temporal and spatial expression of a target gene. TFs manifest their function through direct or indirect (through co-activators) interactions with the basal apparatus that lead to changes in the properties of RNA polymerase. A typical plant transcription factor contains a DNA-binding domain, an oligomerization site, a transcription regulation domain and a nuclear localization signal. Most of the transcription factors have only one type of DNA-binding region and oligomerization region although some lack transcription regulation domain or a specific DNA-binding region. The DNA-binding domain of a TF interacts with DNA at the *cis*-sequence elements owing to the

presence of basic amino acid and thus determines the specificity of the transcription factor. The spatial arrangement of these amino acid residues in DNA-binding domain seems to affect their affinity and selectivity. The oligomerization region is responsible for determining protein–protein interactions, as most transcription factors can form hetero and/or homodimers, which ultimately affects sequence element specificity, trans-activation efficiency or DNA-binding affinity and nuclear localization (Kono et al. 2012). It is estimated that approximately 5 % of eukaryotic genes encode TFs (Riechmann et al. 2000; Riechmann and Ratcliffe 2000). To date, more than 100 different DNA-binding domains have been recognized (Kummerfeld and Teichmann 2006). Based on their DNA-binding domains, TFs are classified into different families, some of which are found in all eukaryotes (e.g. MYB or bHLH) whilst others are kingdom specific (DOF, DREB, WRKY, NAC). A list of plant-specific transcription factors, their structural features, DNA-binding Domain, biological roles and a representative of 3D structure with their PDB entry is summarized in supplementary table 1.

DNA binding with one finger (Dof) transcription factors

The Dof family is one of the well-characterized plant-specific transcription factor having diverse roles in plant growth and development. In recent years, the sequencing of plant genomes has led to the identification of multiple *Dof* genes from different plant species. Dof transcription factors play key role in a variety of biological processes like photosynthetic carbon assimilation, light-regulated gene expression, accumulation of seed storage proteins, germination, dormancy, response to phytohormones, flowering time, guard cell-specific gene expression and many more that are considered to be unique to plants. Dof genes are widely distributed in plant kingdom ranging from green unicellular algae to vascular plants and are characterized by the presence of two major domains namely an N-terminal conserved DNA-binding domain and a C-terminal transcriptional regulation domain. Dof proteins generally comprise 200–400 amino acids having a highly conserved domain (Dof domain) of 50–52 amino acids including a C2C2-type zinc finger

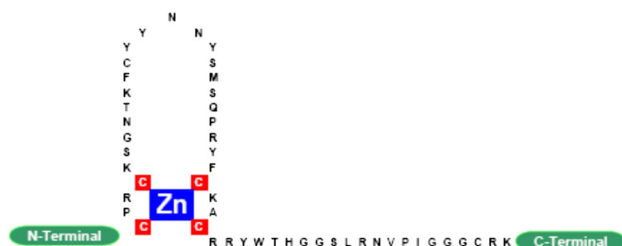


Fig. 1 Structure of Dof domain of *E. coracana* and its amino acid sequence (Kushwaha et al. 2008)

motif at N-terminal end. Transcriptional regulation domain having diverse amino acid sequences reflects the expected varied functions of the Dof proteins. The typical structure of Dof domain as elucidated from sequence clone of *Elusine coracana* (EU760631) is shown in Fig. 1 (Kushwaha et al. 2008). The serine stretches that are frequently located immediately downstream of the Dof domains might be the molecular hinges linking the two domains. The strong similarity among Dof DNA-binding domains suggested that all Dof proteins display similar DNA-binding specificity. Indeed, an AAAG sequence or its reversibly oriented sequence, CTTT, is always found in the binding sequence of individual Dof proteins.

DNA-binding domain consists of CX₂CX₂₁CX₂C motif that has been predicted to have the ability to form a single zinc finger and hence named Dof (DNA binding with one finger) domain proteins (Yanagisawa 2002). The typical feature of Dof families of proteins is the presence of four cysteine residues in the conserved Dof domain region, as shown in Fig. 2. The sequence-specific DNA binding of the Dof domain proteins has been established by many in vitro and in vivo experiments. All Dof proteins analysed so far, except for protein of pumpkin, recognized an AAAG motif as the essential sequence element in DNA-binding assays in vitro (Yanagisawa 2002). Therefore, the conserved Dof domain alone was able to confer its sequence-specific DNA binding (Kisu et al. 1998; Yanagisawa 1995) and the regions outside the Dof domain do not appear to play a major role in interaction with DNA (Yanagisawa and Schmidt 1999). A study revealed that maize Dof1 can bind an AAAG motif in the surface of the nucleosome reconstructed in vitro as well as the motif on naked DNA, although the binding was dependent on the position of the AAAG motif in nucleosome (Cavalari et al. 2003).

Transcription factors representing same family might have diverse activity owing to the presence of transcriptional regulation domain, which may act as repressor or activator, depending on whether they inhibit or stimulate the transcription of target genes. Repression of gene expression may occur via exclusion of activators from target promoters by competitive binding between transcription factors for the same *cis*-acting element. It may also be due to masking of regulation domains by dimerization of transcription factors, as well as interaction of repression domains with transcription factors. A barley Dof protein (BPBF) is reported to activate the transcription from a putative target promoter, but BPBF with a mutation on the cysteine residue results in its inactivation (Mena et al. 1998).

Dof domain shows bifunctional binding activities

The Dof domain earlier identified as a DNA-binding domain is now regarded as a bifunctional domain showing

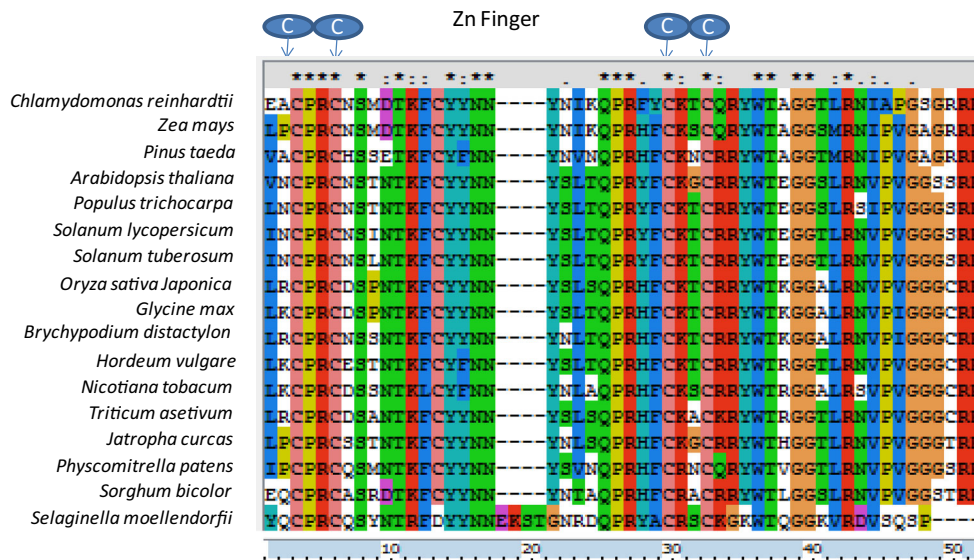


Fig. 2 Typical feature of Dof proteins showing four cysteine residues associated with the zinc finger structure

both DNA-binding and protein–protein interaction activities. The first protein–protein interaction was observed with an *Arabidopsis* Dof domain protein (OBP1), which was identified as a protein interacting with bZIP proteins associated with stress responses. OBP1 specifically increased the binding of the OBF proteins to ‘ocs’ element sequences (Zhang et al. 1995). The Dof2 transcription factor of maize interacts with five different maize High Mobility Group (HMGB) proteins and is stimulated by them for its DNA target site with different efficiencies (Krohn et al. 2002). OsDof3 of rice regulates the gibberellin response with interaction of a GAMYB as studied in a yeast two-hybrid assay (Washio 2003). In another report from Diaz et al. 2002, HvGAMYB and BPBF in barley are part of a regulatory complex wherein (1) both factors display physical interactions in vivo in the yeast two-hybrid system; and (2) for the interaction to occur in the developing endosperm, both TFs were expressed at the same time in this tissue, as documented both by Northern blotting and by in situ hybridization analyses. Another Dof protein from barley, SAD that activates transcription of endosperm-specific genes interacts with R2R3MYB protein (GAMYB) that was studied via bimolecular fluorescent complex (BiFC) approach (Diaz et al. 2005).

PBFs (P-box binding factor) can bind to Dof box in the promoter of storage protein gene and also interact with other transcription factors which bind to the same promoter in the adjacent region such as PBF with O2 in maize (Vicente-Carbajosa et al. 1997) and RPBF with RISBZ in rice (Kawakatsu et al. 2009). WPBF, a wheat PBF Dof, interacts with a protein TaQM, identified from a wheat root cDNA library and activates transcription of an alpha-

gliadin gene during wheat seed development (Dong et al. 2007). The BPBF has also been reported to form a ternary complex with two other seed transcription factors, BLZ2 and HvMYBS3 (a R1MYB) from barley in the yeast three-hybrid system. HvMYBS3 is also an activator of gene expression during endosperm development (Rubio-Somoza et al. 2006).

Regulation of a MYB32b in barley under GA signaling is mediated through modulation by two protein complexes, one for activation includes SAD and HvGAMYB while the other WRKY38 and BPBF for repression (Zou et al. 2008). AtDOF4.7 which is involved in regulation of floral organ abscission interacts with another abscission-related transcription factor, *Arabidopsis* ZINC FINGER PROTEIN2 (Wei et al. 2010). AtDof3.2 which acts as a negative regulator of seed germination was reported to interact in a yeast two-hybrid system and in planta with TCP14, a positive regulator of seed germination and opposes TCP14 function in the regulation of a specific set of ABA-related genes (Rueda-Romero et al. 2012). A list of key Dof interacting proteins reported till date from different plant species along with their functions is summarized in Table 1.

Evolution and expansion of *Dof* gene family across plant lineage

The complete or nearly complete genome sequence information of rice, *Arabidopsis* and many other vascular and non-vascular plants provides an opportunity to identify *Dof* gene family through genome annotation and genome-wide comparative analysis. Using tools of bioinformatics and

Table 1 List of Dof interacting proteins and their function in plant growth and development

Dof gene	Interacting protein	Function	References
OBP1	OBF	Increase the binding of OBF to ocs element	Zhang et al. (1995)
PBF	O2	Regulate expression of endosperm-specific genes	Vicente-Carbajosa et al. (1997)
Dof 2	HMGB	Stimulate binding to target DNA site	Krohn et al. (2002)
BPBF	HvGAMYB	Regulate expression of endosperm-specific genes	Diaz et al. (2002)
OsDof 3	GAMYB	Regulate gibberellin response	Washio (2003)
SAD	GAMYB	Regulate expression of endosperm-specific genes, <i>Itr1</i> and <i>hor2</i>	Diaz et al. (2005)
BPBF	BLZ2/HvMYBS3	Ternary complex formation and regulate expression of endosperm-specific genes	Rubio-Somoza et al. (2006)
WPBF	TaQM	Activates transcription of an alpha-gliadin gene	Dong et al. (2007)
SAD	GAMYB	Activates the expression of α -amylase gene <i>Amy32b</i> in alurone layer synergistically	Zou et al. (2008)
BPBF	HvWRKY38	Inhibits the synergistic effect of SAD and HvGAMYB and stops expression of α -amylase gene <i>Amy32b</i> in alurone layer	Zou et al. (2008)
RPBF	RISBZ	Regulate expression of endosperm-specific genes	Kawakatsu et al. (2009)
AtDOF4.7	ZINC FINGER PROTEIN2	Regulates cell wall modification/loosening proteins during abscission.	Wei et al. (2010)
AtDof 3.2	TCP14	Controls early germination by inhibiting TCP14 function	Rueda-Romero et al. (2012)

Table 2 In silico prediction of *Dof* genes in different plant species

S. no.	Plants (scientific name)	Taxonomic group	Number of <i>Dof</i> genes	References
1.	<i>Chlamydomonas reinhardtii</i>	Algae	01	Moreno-Risueno et al. (2007b)
2.	<i>Physcomitrella patens</i>	Moss	09	Moreno-Risueno et al. (2007b)
3.	<i>Selaginella moellendorffii</i>	Fern	08	Moreno-Risueno et al. (2007b)
4.	<i>Pinus taeda</i>	Gymnosperm	08	Moreno-Risueno et al. (2007b)
5.	<i>Arabidopsis thaliana</i>	Angiosperm	36	Lijavetzky et al. (2003)
6.	<i>Oryza sativa</i>	Angiosperm	30	Lijavetzky et al. (2003)
7.	<i>Hordeum vulgare</i>	Angiosperm	24	Moreno-Risueno et al. (2007a)
8.	<i>Glycine max</i>	Angiosperm	78	Guo and Qiu (2013)
9.	<i>Populus trichocarpa</i>	Angiosperm	41	Yang et al. (2006)
10.	<i>Triticum aestivum</i>	Angiosperm	31	Shaw et al. (2009)
11.	<i>Sorghum bicolor</i>	Angiosperm	28	Kushwaha et al. (2011)
12.	<i>Zea mays</i>	Angiosperm	54	Jiang et al. (2012)
13.	<i>Brychypodium distactylon</i>	Angiosperm	27	Hernando-Amado et al. (2012)
14.	<i>Solanum lycopersicum</i>	Angiosperm	34	Cai et al. (2013)
15.	<i>Saccharum officinarum</i>	Angiosperm	25	Gupta et al. (2014)
16.	<i>Cajanus cajan</i> (L) Millsp.	Angiosperm	38	Malviya et al. (2014)

availability of genome sequence information, attempts have been made to predict the number of Dof genes in different crops (Table 2). There exists great diversity in terms of number of Dof genes in different crops, which possibly reveals their multiple and diverse gene functions across crops.

A genome-wide comparative phylogenetic analysis of the rice and *Arabidopsis* Dof gene families revealed the presence of at least 30 and 36 Dof genes, respectively.

Further analysis led to their classification into four major clusters of orthologous genes and showed gene loss and duplication events in *Arabidopsis* and rice that occurred before and after the last common ancestor of the two species (Lijavetzky et al. 2003). Similar types of phylogenetic analyses have been reported for other plant TF families such as the WRKY, R2R3-MYB, bZIP, MADS, GATA, and others (Eulgem et al. 2000; Jakoby et al. 2002; Martin and Paz-Ares 1997; Parenicova et al. 2003;

Reyes et al. 2004). A comparison of *Dof* gene family among poplar, *Arabidopsis* and rice has been made with emphasis on evolution of *Dof* genes (Yang et al. 2006). A total of 41 *Dof* genes were predicted in poplar and their analysis with *Arabidopsis* and rice based on ancestral paralogous sequences concluded that after a gene duplication event, the evolution of the duplicated genes is driven by purifying selection, Darwinian positive selection, local duplication, translocations and domain co-option (or domain shuffling) (Yang et al. 2006).

The origin and evolution of the *Dof* transcription factor family based on phylogenetic analysis of *Dof* sequences across the representative organisms belonging to green unicellular algae to vascular plants have also been reported. A total of 116 *Dof* genes representing green unicellular alga (*Chlamydomonas reinhardtii*), moss (*Physcomitrella patens*), fern (*Selaginella moellendorffii*), gymnosperm (*Pinus taeda*), dicotyledonous angiosperm (*Arabidopsis thaliana*) and monocot (*Oryza sativa* and *Hordeum*

vulgare) have been in silico characterized. The phylogenetic tree constructed (Fig. 3) revealed the existence of six major clusters of orthologous and paralogous genes that probably originated by gene duplication events from a paraphyletic basal grade (Moreno-Risueno et al. 2007b).

Attempts have also been made to use various bioinformatics tools for characterizing *Dof* gene family in cereals and millets. Sequence analysis of PCR-amplified 13 *Dof* domains of cereals (rice, wheat, sorghum, barley, oat, maize, barnyard millet, proso millet, little millet, kodo and foxtail millet) and five *Dof* genes (rice, wheat, barley, maize and finger millet) revealed its identity to *Dof*-like proteins. Further, in silico investigation of the cloned *Dof* genes of finger millet, barley, wheat and maize revealed its identity to PBF *Dof*, based on the presence of motifs related to regulation of endosperm-specific seed storage protein genes (Kushwaha et al. 2008).

In another study, 31 *Dof* gene family members of wheat have been identified through extensive analysis of

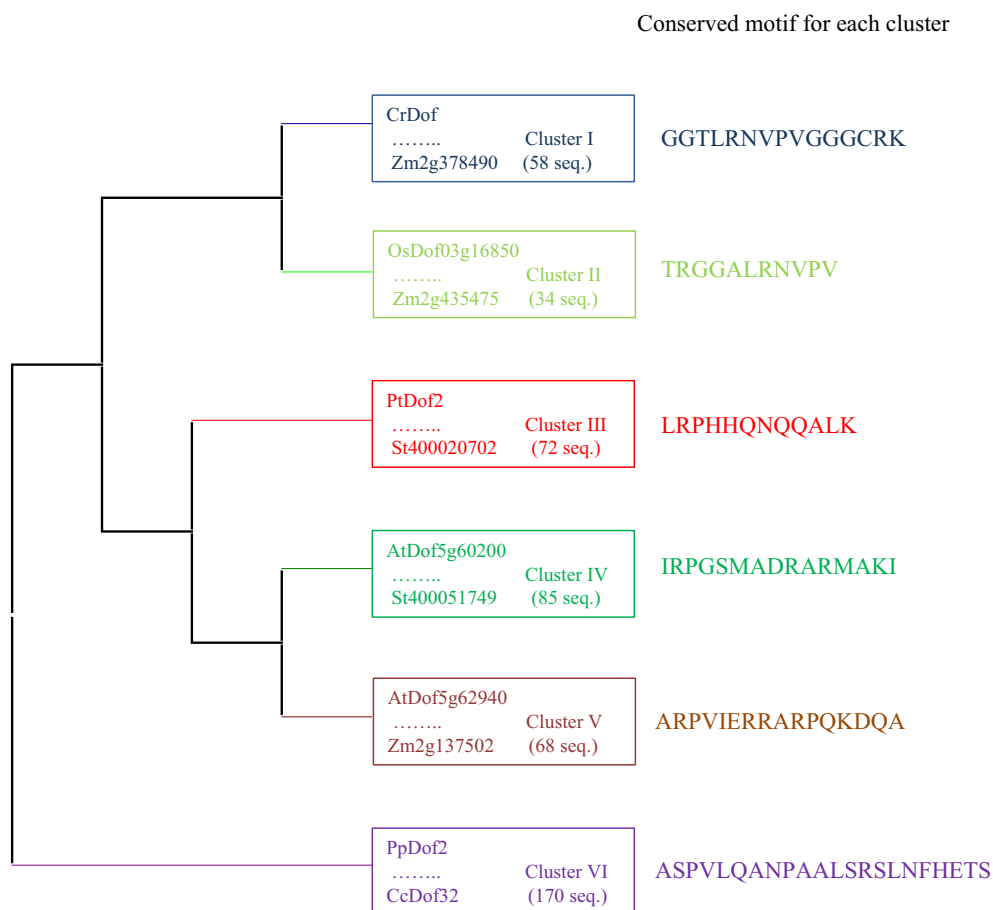


Fig. 3 Phylogenetic tree constructed using full-length *Dof* protein sequences from *Chlamydomonas reinhardtii* (1), *Selaginella moellendorffii* (10), *Physcomitrella patens* (5), *Pinus taeda* (7), *Arabidopsis thaliana* (36), *Oryza sativa Japonica* (30), *Sorghum bicolor* (28), *Glycine max* (78), *Hordeum vulgare* (21), *Nicotiana tobacum*

(17), *Populus trichocarpa* (43), *Triticum aestivum* (17), *Zea mays* (44), *Brychypodium distachyon* (25), *Solanum lycopersicum* (30), *Solanum tuberosum* (34), *Jatropha curcas* (23) and *Cajanus cajan* (38) using MEGA5.2.2 by NJ method. The full expanded figure has been provided as supplementary Fig. 1

nucleotide databases (Dong et al. 2007). Expression analysis of the TaDof family across all major organs using quantitative RT-PCR revealed that the majority of TaDof members were predominately expressed in vegetative organs. A large number of TaDof members were down-regulated by drought and/or were responsive to the light and dark cycle. Light-responsive *Dof* genes showed their involvement in photosynthesis or sucrose transport. TaDof family might have an important role in light-mediated gene regulation, including involvement in the photosynthetic process (Shaw et al. 2009).

Similarly, 28 *Dof* genes were identified and in silico characterized in *Sorghum bicolor* (L.) Moench (Kushwaha et al. 2011). Analysis of intron/exon organization revealed majority of the predicted *Dof* genes to be intronless as observed in case of rice and *Arabidopsis*. The *cis*-regulatory element analysis of the predicted *Dof* genes revealed the major putative functions as regulation of genes associated with seed storage proteins, abiotic and biotic stresses, photoperiod, growth hormone and meristem. The in silico prediction of two-dimensional and three-dimensional structures of *Dof* proteins of *Sorghum* has been generated by multiple threading and iterative structural assembly simulations (Kushwaha et al. 2013). Further, based on gene ontology (GO) terms in I-TASSER server, putative functions of modelled SbDof proteins have been predicted. Very recently, the genome-wide in silico characterization of 25 *Dof* genes of sugarcane along with comparative phylogenetic analysis with rice, *Arabidopsis* and sorghum has also been reported (Gupta et al. 2014).

Brachypodium distachyon, the first Pooideae grass sequenced, has been analysed for *Dof* family members (Hernando-Amado et al. 2012). A total of 27 *Dof* genes were identified in this grass and a phylogenetic comparison with *Oryza sativa* and *Hordeum vulgare* Dofs classified the DOF proteins into four Major Cluster of Orthologous Groups (MCOGs). Using qRT-PCR analysis, the expression profiles of the annotated *BdDof* genes across four organs (leaves, roots, spikes and seeds) was investigated, which further classified them into two distinct groups based on their expression patterns across the tested tissue types. In tomato, 34 *Dof* genes distributed on 11 chromosomes along with their gene structures, chromosomal locations, phylogeny, protein motifs and evolution pattern have been reported recently (Cai et al. 2013). The expression profiling of these *SlDof* genes displayed differential expression either in their transcript abundance or in their expression patterns under normal growth conditions (Cai et al. 2013). Recently, 78 putative *Dof* genes have been reported in soybean, which constitute the largest *Dof* gene family known from any plant species (Guo and Qiu 2013). These predicted *GmDof* genes are non-randomly distributed within and across 19 out of 20 chromosomes. The

expression pattern of some duplicate genes is partially redundant while others are showing functional diversity, suggesting the occurrence of sub-functionalization during subsequent evolution. These *Dof* proteins were phylogenetically clustered into nine distinct subgroups. The analysis of whole genome sequence of pigeonpea has identified 38 putative *Dof* genes (Malviya et al. 2014). Thus there exists a huge diversity of *Dof* gene members, and their phylogenetic clustering across plant species, which possibly suggest a high degree of functional diversity of *Dof* proteins in plants.

Expression and functional diversity of *Dof* proteins

Dof transcription factors are involved in the regulation of biological processes unique to plants such as photosynthetic carbon assimilation, phytochrome signaling, seed maturation and germination, the salicylic acid response, guard cell-specific gene expression, photoperiodic flowering, dormancy, response to phytohormones, accumulation of seed storage proteins, nitrogen assimilation, biosynthesis of glucosinolates and phenyl propanoid metabolism, regulation of oil content in seeds, regulation of glutamine synthetase (GS) gene expression, light-mediated gene regulation, regulation of interfascicular cambium formation and vascular tissue development and leaf axial patterning by promoting *revoluta* transcription. Recently, it has been reported that some *Dof* transcription factors also have motif for intercellular protein trafficking spanning highly conserved zinc finger motif (Chen et al. 2013). *Dof* transcription factor has also been reported to be involved in regulation of drought and salt stress in tomato (Corrales et al. 2014). The variable functions attributed to *Dof* transcription factor in different crops are summarized in Table 3.

Tissue-specific expression of *Dof* genes in plants

Regulation of gene expression is crucial for a variety of essential processes in plants such as growth, development, differentiation, metabolic regulation and adaptation to the environment. In maize, *Dof1* is a transcriptional activator which shows different activity in response to greening and etiolation of protoplast, whilst *Dof2* appears to be a repressor that can block trans-activation of *Dof1* (Yanagisawa and Sheen 1998). The *Dof* protein, PBF, binds to the prolamin box that is a strong candidate for a *cis*-element responsive for endosperm-specific gene expression (Vicente-Carbajosa et al. 1997). The DAG1 *Dof* gene in *Arabidopsis* is specifically expressed in the phloem of all organs of the plant but not in the seed or in the embryo at any stage of development (Papi et al. 2002). The binding of *Dof* proteins to diverse plant promoters suggests that *Dof*

Table 3 Summary of Dof proteins reported in different crops with specific functions and the regulated genes

S. no.	DOF protein	Crop	Functions	Regulated gene(s)	References
1.	ZmDOF1/ MNB1a	<i>Zea mays</i> (Maize)	Light response/nitrogen assimilation	PEPC gene	Yanagisawa and Sheen (1998), Yanagisawa (2004), Kurai et al. (2011)
2.	PBF	<i>Zea mays</i> (Maize)	Regulation of seed storage protein gene expression	Zein gene	Vicente-Carbajosa et al. (1997)
3.	DOF1	<i>Zea mays</i> (Maize)	Carbon metabolism	C4PEPC and CYPPDK gene	Yanagisawa (2000)
4.	DOF2	<i>Zea mays</i> (Maize)	Carbon metabolism	C4PEPC gene	Yanagisawa (2000)
5.	BPBF	<i>Hordeum vulgare</i> (Barley)	Orthologs of PBF	Hordein gene	Mena et al. (1998)
6.	SAD	<i>Hordeum vulgare</i> (Barley)	Regulation in aleurone layers upon seed germination	GA-induced protease (AI21) promoter	Isabel-Lamonedra et al. (2003)
7.	HvDOF19	<i>Hordeum vulgare</i> (Barley)	Hydrolase gene expression	Thiol protease gene (AI21)	Moreno-Risueno et al. (2007b)
8.	WPBF	<i>Triticum aestivum</i> (Wheat)	Orthologs of PBF	Prolamin gene	Dong et al. (2007)
9.	OBP1	<i>Arabidopsis</i>	Defence response	Increases the binding of OBF1 to octopine synthase (ocs) element	Zhang et al. (1995)
10.	OBP2	<i>Arabidopsis</i>	Glucosinolate biosynthesis	CYP83B1	Skirycz et al. (2006)
11.	OBP3	<i>Arabidopsis</i>	Phytochrome and cytochrome signaling	phyB gene Cry1 gene	Kang et al. (2003), Ward et al. (2005)
12.	DAG1	<i>Arabidopsis</i>	Seed germination	Seed coat integrity and GA biosynthetic gene AtGA3ox1	Papi et al. (2000, 2002); Gabriele et al. (2010)
13.	DAG2	<i>Arabidopsis</i>	Seed germination	Seed germination	Gualberti et al. (2002)
14.	COG1	<i>Arabidopsis</i>	Phytochrome signal	PhyA and phyB	Park et al. (2003)
15.	CDF1	<i>Arabidopsis</i>	Photoperiodic control of flowering	CONSTANS (CO) gene	Imaizumi et al. (2005)
16.	CDF2,3,5	<i>Arabidopsis</i>	Photoperiodic control of flowering	CONSTANS (CO) gene	Fornara et al. (2009)
17.	AtDof2.4	<i>Arabidopsis</i>	Regulate vascular development	AtDof2.4 promoter activity strong in the midvein Weak in secondary vein	Konishi and Yanagisawa (2007)
	AtDof5.8	<i>Arabidopsis</i>	Regulate vascular development	AtDof5.8 promoter activity strong in mid and secondary vein	Konishi and Yanagisawa (2007)
18.	AtDOF4;2	<i>Arabidopsis</i>	Phenylpropanoid metabolism	FLS, DFR, LDOX and TT19 PAL1-2, C4H, 4CL5	Skirycz et al. (2007)
19.	AtDof4.1	<i>Arabidopsis</i>	Involved in selective intercellular trafficking	Mediate selective intercellular trafficking	Chen et al. (2013)
20.	AtDOF4.2	<i>Arabidopsis</i>	Regulation of shoot branching and seed coat formation	Branching related gene, AtSTM, AtTFL1, AtCYP83B1 and cell wall loosening-related gene AtEXPA9	Zou et al. (2013)
21.	AtDOF4.7	<i>Arabidopsis</i>	Induces floral organ abscission deficiency	Abscission-related polygalacturonase gene (PGAZAT)	Wei et al. (2010)
22.	AtDof 5.1	<i>Arabidopsis</i>	Influences leaf axial patterning by promoting Revoluta transcription	REV gene	Kim et al. (2010)
23.	AtDof 5.6	<i>Arabidopsis</i>	Regulates interfascicular cambium formation and vascular tissue development	HCA2 gene	Guo et al. (2009)

Table 3 continued

S. no.	DOF protein	Crop	Functions	Regulated gene(s)	References
25.	AtDOF6	<i>Arabidopsis</i>	Negatively affects germination in non-after-ripened seeds	ABA1 gene	Rueda-Romero et al. (2012)
26.	SCAP1	<i>Arabidopsis</i>	Regulation of expression of genes encoding key elements of stomatal functioning and morphogenesis	GORK and MYB60	Negi et al. (2013)
	AtDOF1	<i>Arabidopsis</i>	regulation of carbon skeleton production, nitrogen assimilation and reduction of glucose level	PEPC and PK gene	Yanagisawa (2004)
27.	OsDOF3	<i>Oryza sativa</i> (Rice)	Gibberlin-regulated expression of peptidase gene	CPD3 gene	Washio (2001), (2003)
28.	OsDof12	<i>Oryza sativa</i> (Rice)	Photoperiodic control of Flowering	Hd3a and OsMADS14 under long day conditions	Li et al. (2009)
29.	RPBF	<i>Oryza sativa</i> (Rice)	Regulation of seed storage protein gene expression	GluA1-3, GluB1, NRP33, Glb1 gene	Yamamoto et al. (2006)
30.	Rdd1	<i>Oryza sativa</i> (Rice)	Photoperiodic control of flowering time and grain size	CDF1 and phyA	Iwamoto et al. (2009)
31.	NtBBF1	<i>Nicotiana tabacum</i> (Tobacco)	Tissue-specific and auxin-inducible expression of oncogene	rolB gene	De Paolis et al. (1996), Baumann et al. (1999)
32.	AOBP	<i>Cucurbita maxima</i> (Pumpkin)	Regulation of ascorbate oxidase, which is involved in cell growth	Ascorbate oxidase gene	Kisu et al. (1998), Shimofurutani et al. (1998)
33.	StDOF1	<i>Solanum tuberosum</i> (Potato)	Guard cell specificity	KST1 gene	Plesch et al. (2001)
34.	GmDOF4	<i>Glycine max</i> (Soybean)	Lipid Biosynthesis	acetylCoA carboxylase gene	Wang et al. (2007)
	GmDOF11	<i>Glycine max</i> (Soybean)	Lipid Biosynthesis	Long-chain-acyl CoA synthetise gene	Wang et al. (2007)
35.	PpDof1	<i>Physcomitrella patens</i> (Moss)	Regulation of nutrient condition-dependent growth control of protonemal filaments	Repressor of vegetative growth of filament	Sugiyama et al. (2012)
36.	PpDOF5	<i>Pinus pinaster</i> (Pine)	Regulation of Glutamine synthetase gene expression	GS1a GS1b	Rueda-Lopez et al. (2008)
37.	PBF DOF	<i>Finger millet</i> (Ragi)	Seed storage protein expression	Kushwaha et al. (2008)
38.	JcDof1	<i>Jatropha curcas</i> (Arandi)	Respond to light signals	Red and blue light downregulated the JcDof1 expression	Yang et al. (2010)
39.	JcDof3	<i>Jatropha curcas</i> (Arandi)	Flowering time regulation	Circadian clock regulated gene	Yang et al. 2011
40.	SRF1	<i>Ipomoea batatas</i> (Sweet potato)	Regulation of carbohydrate metabolism	Vascularinvertase gene (Ibβfruct2)	Tanaka et al. (2009)
41.	PsDOF7	<i>Pisum sativum</i> (Sweet Pea)	Activates expression of the chloroplast thioredoxins f and m	TRX f and m	Barajas-lopez et al. (2012)
42.	SICDF1 and SICDF3	<i>Solanum lycopersicum</i> (tomato)	Drought and Salt tolerance	COR15, RD29A and RD10	Corrales et al. (2014)

The text in bold indicates up-regulation/positive regulation

The text in bold italics indicates down-regulation/negative regulation

proteins may be involved in a variety of signal-response and/or tissue-specific gene expressions in plants. Interestingly, all biological processes that are speculated to be mediated by Dof proteins are plant specific e.g. expression of a photosynthetic gene, seed-specific genes and a plant oncogene, and pathogen-responsive gene expression (Kuriakose et al. 2009).

Dof associated with biotic stress

The role of Dof transcription factors in biotic stress tolerance has been investigated in barley seeds based on their interaction with cystatin gene (Martinez et al. 2005). Cystatins are a group of cysteine proteinase inhibitors that have been identified in vertebrates, invertebrates and plants (Barrett 1987). The pathogen produces cysteine proteinases and peptidase which help them to colonize and proliferate into the host cells. The activities of all these degrading enzymes are influenced by the host cystatin proteins, which resist the pathogen proliferation by inhibiting these enzymes (Barrett 1981). Two Dof proteins, SAD and BPBF, interact specifically in vitro with oligonucleotides containing Dof binding sites derived from the cystatin gene promoter. The OBP1 protein from *Arabidopsis* that interacts with an OCS element-binding factor OBF4 is also shown to be involved in biotic stress (Singh et al. 2002; Zhang et al. 1995).

Dof as regulator of plant hormone response

Phytohormone signaling pathways are quite complex and their regulation is achieved by binding and coordinated interactions of many transcription factors at *cis*-acting elements present in the promoter of phytohormone-responsive genes (Yanagisawa 1997). Dof proteins are regulators for plant hormone-responsive genes and have been shown to mediate the response of gibberellins (Washio 2003) and auxins (Baumann et al. 1999). Gibberellins are diterpenoid hormones that play crucial roles in plant growth and development including seed germination, leaf expansion, stem elongation, flower and fruit development (Hooley 1994). The analysis of the alpha-amylase promoters from barley, wheat and rice have identified a conserved *cis*-element required for GA induction, termed as GA-responsive element (GARE). Although this GARE may not always be tripartite, most often it includes three sequence motifs, the TAACAAA box or GA-responsive element (GARE), the pyrimidine box CCTTTT and the TATCCAC box (Gubler and Jacobsen 1992; Rogers and Rogers 1992; Skriver et al. 1991). The presence of CCTTTT pyrimidine box in GARE, the recognition core motif of Dof proteins, clearly indicates the role of Dof in gibberellins response. The pattern of expression of

NtBBF1, a Dof protein known to play a pivotal role in regulating the *rolB* expression, might provide the possible mechanism of auxin induction (Baumann et al. 1999). Ascorbate oxidases have been reported to be specifically expressed in the quiescent centre of maize root and are involved in organization of root meristems through auxin-independent expression (Kerk and Feldman 1995). Auxin-responsive *cis*-region of the pumpkin ascorbate oxidase gene has been identified using a transient assay method (Kisu et al. 1998) and it is likely to be involved in cell growth or division of higher plants.

Dof associated with seed storage protein accumulation

During cereal seed development, nitrogen and sulphur are stored in the starchy endosperm cells, mainly in the form of a complex group of proteins, the prolamines. The genes encoding prolamines are co-ordinately expressed in the developing endosperm where they are under spatial and temporal transcription control, involving *cis*-acting motifs in their promoters and trans-acting transcription factors. A PBF (Prolamin box)-DOF associated with regulation of endosperm-specific seed storage proteins has been studied in maize, barley, wheat, rice and finger millet (Noguero et al. 2013). The first PBF has been cloned from maize and identified as a transcriptional activator of zein gene, a seed storage protein of maize (Vicente-Carbajosa et al. 1997). A cDNA encoding a DNA-binding protein of the Dof class of transcription factor has been isolated from a barley endosperm library (Mena et al. 1998). Transient expression experiments in developing barley endosperms demonstrated that BPBF trans-activates transcription from the P-box element of a native *Hor2* (hordein) promoter. Similarly, rice PBF (RPBF), isolated from rice cDNA expressed sequence tag clones, is known to play important role as an activator for seed storage protein genes and involved in quantitative regulation by combinatorial interactions with RISBZ1 in determining endosperm-specific expression (Yamamoto et al. 2006). A transient expression experiment also demonstrated that the wheat prolamins-box binding factor (WPBF), isolated from wheat endosperm, could trans-activate transcription of native alpha-gliadin promoter by binding to the intact PB (Dong et al. 2007).

Dof associated with carbon and nitrogen metabolism

Dof proteins are found to be an activator for multiple genes associated with the organic acid metabolism, including expression of phosphoenolpyruvate carboxylase (PEPC) gene (Yanagisawa 2000). The maize Dof1 has been reported to be an activator of PEPC gene expression and enhances transcription from the promoters of orthophosphate dikinase and pyruvate kinase (Yanagisawa 2000), as

expression of Dof1-specific antisense RNA or the DNA-binding domain of Dof1 alone reduced the expression of these genes. Nitrogen assimilation is an essential process for the growth and development of plants, where inorganic nitrogen in the soil in the form of nitrate and ammonia is initially converted into glutamine and glutamate by two enzymes, glutamine synthase and glutamate synthase. Nitrogen assimilation requires not only inorganic nitrogen but also the carbon skeleton, 2-oxoglutarate. Because Dof1 appears to be a key regulator in the coordinated gene expression involved in carbon skeleton production and there is an intimate link between carbon and nitrogen metabolism, there is a speculation that Dof1 modulates nitrogen assimilation as well. Elementary analysis of Dof1 over-expression/knock-down transgenic *Arabidopsis* plants revealed increased nitrogen content in transgenic plants (30 %), indicating promotion of net nitrogen assimilation (Yanagisawa 2004). Most significantly, the Dof1 transgenic plants exhibit improved growth under low nitrogen conditions. Another Dof-type zinc finger transcription factor gene *SRF1* was isolated from sweet potato (*Ipomoea batatas*) preferentially expressing in storage roots and reported to modulate the carbohydrate metabolism in the storage roots through negative regulation of a vacuolar invertase gene (Tanaka et al. 2009).

Dof proteins involved in light responses

Plants can perceive subtle changes in light quality and quantity through a set of photoreceptors, including phytochromes and cryptochromes. Upon perception, these photoreceptors initiate signal transduction pathways leading to photomorphogenic changes in development. The Dof proteins are also involved in light responses to plants. OBP3, an *Arabidopsis* Dof protein, is a component in both phyB and cryptochrome 1 (*cry1*) signaling pathways, acting as a positive and negative regulator, respectively (Ward et al. 2005). Another *Arabidopsis* Dof protein, COG1 negatively regulates both phytochrome A and phytochrome B signaling pathway (Park et al. 2003). In *Arabidopsis*, several Dof transcription factors namely CDF1, CDF2, CDF3 and CDF5 are reported to be essential for photoperiodic control of flowering, and mutation in CDF is responsible for photoperiod-insensitive early flowering by increasing *CONSTANS* expression levels (Fornara et al. 2009; Imaizumi et al. 2005). Two of the rice *Dof* genes, *OsDof12* and *Rddl* are also phy-regulated genes. *OsDof12* regulates flowering in long-day condition and is inhibited by dark treatment (Li et al. 2009), while *Rddl* regulates grain size in rice and its expression differs in continuous dark and light conditions (Iwamoto et al. 2009). Dof transcription factor genes also exhibit circadian rhythms and play a crucial role in the control of flowering time by photoperiodic perception in

plants. Two full-length cDNA, *JcDof1* and *JcDof3* isolated from *Jatropha curcas* seedlings by yeast one-hybrid library reveal their expression under long day, short day and continuous light conditions and have been shown to interact with F-box proteins to regulate photoperiodic flowering (Yang et al. 2011). Recently, a full-length Dof1 of finger millet, associated with circadian cycle, has been reported (Kumar et al. 2014).

Dof influencing plant morphology

In *Arabidopsis*, Dof proteins related with plant morphological pattern have recently been reported. Guo et al. (2009) revealed the involvement of *AtDof5.6* in regulation of interfascicular cambium formation and vascular tissue development (Guo et al. 2009). Expression of three Dof proteins of *Arabidopsis* namely *Dof2.1*, *Dof4.6* and *Dof5.3* has been reported at preprocambial stage in leaves suggesting their role in preprocambial development (Gardiner et al. 2010). Promoter activation of *AtDof2.4* and *AtDof5.8* in procambial cells of leaf primordia, roots, embryo and prospective veins in leaf primordia of seedlings, cotyledons of developing embryo has also been reported (Konishi and Yanagisawa 2007). *AtDof5.1* has been reported to regulate leaf axial patterning (Kim et al. 2010). In a recent study, it was found that *AtDof4.2* regulates shoot branching and seed coat formation in *Arabidopsis*. Further, *AtDof4.2*-overexpressing plants exhibit an increased branching phenotype, and mutation of the T-M-D motif in *AtDof4.2* significantly reduces branching in transgenic plants. The seeds of an *AtDof4.2*-overexpressing plant showed a collapse-like morphology in the epidermal cells of the seed coat. The *Dof4.2* mutant did not exhibit changes in branching or its seed coat though there was substantial increase in the silique length and seed yield (Zou et al. 2013).

Dof involved in guard cell development

SCAP1, a Dof-type transcription factor isolated from *Arabidopsis* has been reported to express in maturing guard cell but not in guard mother cell. SCAP1 was reported to regulate expression of genes encoding key elements of stomatal functioning and morphogenesis, such as K^+ channel protein, MYB60 transcription factor and pectin methyl esterases (Negi et al. 2013). This clearly indicates that SCAP1 regulates essential processes of stomatal guard cell maturation and functions as a key transcription factor regulating the final stages of guard cell differentiation and ultimately influences the morphological development of plant. Dof transcription factor from potato, *StDof1*, has also been reported to control guard cell-specific gene expression (Plesch et al. 2001). Presence of Dof binding site in the

promoter of guard cell-specific genes has been reported in *Arabidopsis* (Galbiati et al. 2008). Requirement for a specific number of the Dof binding site in the promoter region for guard cell-specific expression has been demonstrated in *GAL-GFP* trap lines in *Arabidopsis* (Gardner et al. 2009). Dof binding sites also contribute to guard cell-specific expression of *AtMYB60* of *Arabidopsis* (Cominelli et al. 2011).

Dof associated with seed germination

Various reports in *Arabidopsis* have shown that Dof proteins are also involved in regulation of seed germination (Noguero et al. 2013). The *Arabidopsis* Dof gene, DAG1 (Dof Affecting Germination) is involved in the maternal control of seed germination. The DAG1 gene is expressed specifically in the vascular system of the mother plant but not in the embryo or anywhere else in the seed at any stage of development (Papi et al. 2000, 2002). Another member of the Dof gene family in *Arabidopsis*, DAG2, also showed its involvement in the control of seed germination. The DAG2 mutant seeds have germination properties opposite to those of seeds from the DAG1 knockout type, and the effect of the mutation of DAG2 is maternal. Moreover, seeds from plants that overexpressed DAG1 showed germination characteristics analogous to those of *dag2* mutant seeds, whereas seeds from double mutant *dag2dag1* plants behave like *dag1* seeds. Based on these studies, it was reported that DAG2 and DAG1 have opposite regulatory roles (Gualberti et al. 2002). Similarly, another Dof gene of *Arabidopsis*, Dof6 influencing seed germination has also been reported. The transcript levels of this gene accumulate in dry seeds and decay gradually after ripening and also upon seed imbibition. While constitutive over-expression of DOF6 produced aberrant growth and sterility in the plant, its over-expression induced upon seed imbibition triggered delayed germination, abscisic acid (ABA)-hypersensitive phenotypes and increased expression of the ABA biosynthetic gene ABA1 and ABA-related stress genes. Wild-type germination and gene expression were gradually restored during seed after ripening, despite DOF6-induced over-expression. These results indicate that DOF6 negatively affects seed germination (Rueda-Romero et al. 2012).

Conclusion

The gene regulation is a complex process involving repertoire of regulatory elements, the transcription factor being one of the most important elements influencing gene regulation at the level of transcription by modulating the *cis*-regulatory sequences of diverse genes. The significance

of transcription factors is being realized based on their quantitative and ubiquitous representation across the plant genomes and subsequently several plant-specific transcription factors have been deciphered. DNA binding with one finger (Dof) constitutes a large family of transcription factors that are associated with various biological processes unique to plants. The functional attributes of Dof have been elucidated in several crops, and the expansion of Dof gene family is being witnessed based on genome-wide analysis of crops whose genome sequences are available. The possible interactions with other transcription factors regulating diverse biological processes, functional characterization of in silico-identified Dof gene families of different crops, elucidating downstream genes being regulated by Dof transcription factors are some of the key issues to be addressed. Further, there is a need to understand developmental and evolutionary dynamics of regulatory networks formed by Dof domain across the phyla and identify Dof genes associated with newer functions like abiotic stresses. The structural diversification of Dof mediated by gene duplication might be closely associated with the development of complex regulatory network during plant evolution but still the epigenetic role associated with the evolution of duplicated Dof genes needs to be investigated. This review highlights the structural, functional and bioinformatics aspect of Dof transcription factor reported till date and tries to identify the gaps for further study.

Author contribution DY conceived, framed and wrote the final review. SG, NM, HK composed the structural and functional aspects of Dof transcription factor. VKS, NM and JN framed the bioinformatics aspects of Dof. NM composed the supplementary table comprising of description about different plant specific transcription factors and also finalized the phylogenetic tree. NCB revised the initial draft and reframed by finalizing the sub-headings with the required content. All authors coordinated to draft, read and approve the final manuscript.

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