Functional analysis of Dof transcription factors controlling heading date and PPDK gene expression in rice

Zhang, Y.

Citation

Zhang, Y. (2015, December 22). *Functional analysis of Dof transcription factors controlling heading date and PPDK gene expression in rice*. Retrieved from https://hdl.handle.net/1887/37134

Author: Zhang, Yu
Title: Functional analysis of Dof transcription factors controlling heading date and PPDK gene expression in rice
Issue Date: 2015-12-22

Chapter 1

General Introduction

Y. Zhang[1, 2, 3], M. Wang[1,4], Z. Zhu[2,] and P.B.F. Ouwerkerk[1]

[1] Department of Molecular and Developmental Genetics, Institute of Biology (IBL), Leiden University, Sylvius Laboratory, Sylviusweg 72, P.O. Box 9505, 2300 RA Leiden, The Netherlands

[2] State Key Laboratory of Plant Genomics and National Center for Plant Gene Research, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, No.1 West Beichen Road, Chaoyang District, Beijing 100101, China

[3] Graduate School of the Chinese Academy of Sciences, 100049 Beijing, China

[4] SU BioMedicine/TNO Quality of Life, Zernikedreef 9, P.O. Box 2215, 2301 CE Leiden, The Netherlands

Introduction

Four millennia ago, people completed the first steps in the domestication of all major cereal crops including rice, barley, wheat and maize (Doebley *et al.* 2006). Rice amongst cereal grasses like maize, millet, barley, sorghum and wheat is the key food for more than half of mankind. The goal of modern rice breeding is to improve cultivars for yield and yield stability under adverse conditions and to improve resistance against biotic stresses. Rice yield is determined by several factors such as the number of tillers per plant, the number of grains per panicle, characteristics of grain filling and grain size. Since the 1960s, the productivity of rice has been largely improved by development of inbred cultivars, which was called the Green Revolution. In the 1970s, Longping Yuan developed the Chinese super-hybrid rice, which increased yield by 30% compared to the parental lines. This development is sometimes called the Second Green Revolution. Heterosis, or hybrid vigor, refers to the improved yield and performance of a hybrid offspring. The molecular genetics and biology behind this biological phenomenon needs to be further investigated in order to reveal the responsible genes.

Rice is an excellent system for plant molecular research as it represents a modest size genome of 430 Mb, containing about 50,000 genes (Goff *et al.* 2002; Tyagi *et al.* 2004). Many rice genomics studies have been initiated in the last decade, some of which took place as international projects like the rice genome research programme (RGP). The rice genome has been completely sequenced (Sasaki *et al.* 2005) for both the japonica (Goff *et al.* 2002) and indica (Yu *et al*. 2002) subtypes and recently low-coverage sequencing of a collection of 3,000 cultivars went public (Li *et al.* 2014). This is excellent material for allele mining and genome wide association studies. Also a large number of T-DNA insertion and transposon-tagged mutants have been produced (Miyao *et al.* 2007), and global gene expression profiles have been obtained using SAGE (Serial Analysis of Gene Expression) or microarray (Bao *et al.* 2005; Li *et al.* 2006). All this will provide useful information and act as a resource platform for further studies on the functional genomics level. However, for the majority of rice genes no functions have yet been demonstrated (Zhang *et al.* 2006). Several genetics studies especially in rice and maize revealed important roles for transcription factors (TFs) and also other regulatory proteins in QTLs determining plant architecture and yield, which were the bases for crop domestication in the past millenia. This chapter will briefly review the recent advances in understanding of the molecular mechanism and roles that TFs have in crop domestication such as apical dominance, seed shattering, tillering, grain size and flowering time.

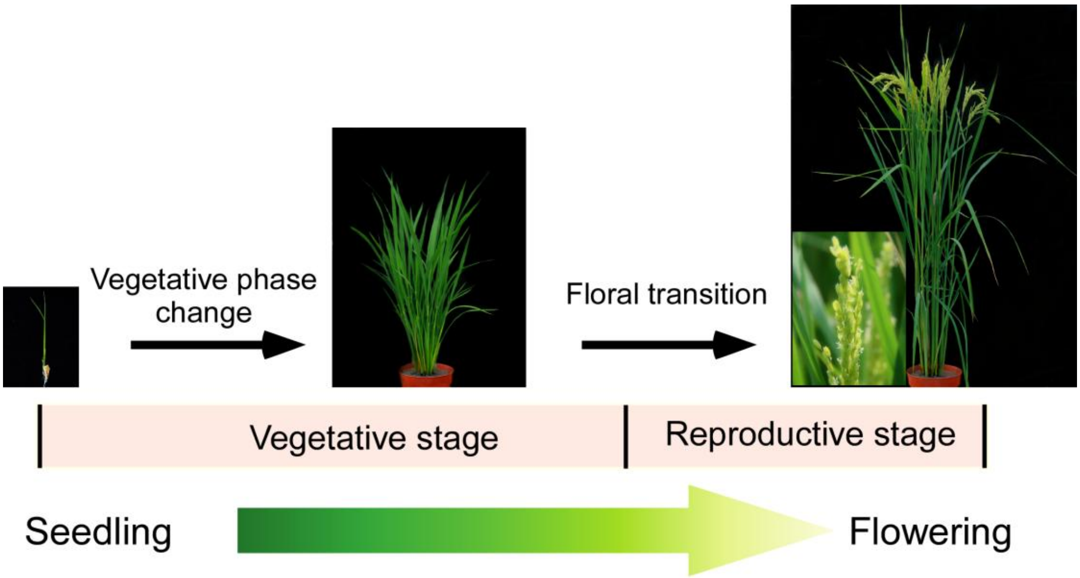

Figure 1. Rice growth and development till flowering.
Flowering is the transition from vegetative stage to reproductive stage, which is important during the rice life cycle. Both environmental signals and endogenous signals affected the transition. Transcription factors play important roles during the life cycle.

Flowering time is the transition from vegetative to reproductive development; it represents one of the major phase changes during the life cycle of a crop such as rice (Figure 1). This transition is initiated by both endogenous and environmental signals. In rice, Heading date genes play roles as endogenous factors controlling the flowering time.

General features of plant transcription factors

Transcription factors (TFs) are proteins or are part of protein complexes, which regulate transcription by binding to specific *cis*-elements in the promoters of target genes and affect the initiation of gene transcription (Ramirez and Basu 2009) and thereby control biological processes. A typical plant TF contains a DNA-binding domain, a transcription-regulation domain and a nuclear localization signal, while some of them also have domains enabling protein-protein interactions (Liu *et al.* 1999). TFs interact with DNA bases in *cis*-acting elements through their DNA binding domain, which in many cases has a basic character because of their amino acid content. Based on the DNA binding domain, the TFs can be divided into different families. For example, there are 57 TF families identified in sorghum and 58 in maize (Perez-Rodriguez *et al.* 2010) and 58 in Arabidopsis (Jin *et al*. 2014). TFs not only can bind to DNA but also regulate gene expression on the transcriptional level. Some TFs have a transcription repression domain by which they can repress target gene expression, whereas others have a transcription activation domain by which they can activate target gene expression. Another aspect of TF functionality is their intracellular localization. Translation of a TF-coding mRNA occurs in the cytoplasm, but transcription occurs in the nucleus, so the TFs have to enter the nucleus in order to be able to regulate the transcription of target genes. For entering the nucleus, TFs usually contain an NLS (Nuclear Localization Signal) which is characterized by a core peptide enriched in arginine and lysine (Boulikas 1994).

Many plant TFs form heterodimers or homodimers and as a consequence of the dimer interaction show more specificity in DNA recognition and functionality (Lu *et al.* 2002). Some TFs have oligomerization domains which are normally adjacent to or overlap with the DNA binding domain (Katagiri *et al.* 1992). The oligomerization domains and DNA binding domains display a tertiary structure which determines critical aspects of TF activity (Guiltinan and Miller 1994). The variations in oligomerization increase the versatility of the transcription machinery and of modulation of gene expression. Hence, studies of plant TFs are important not only for expanding our knowledge of plants but also for future challenges of generating genetically modified crops with superior characters.

Transcription factors play important roles in crop domestication

Over the past decade, several TFs have been identified, which control some of the important morphological changes associated with crop domestication. For instance, one of the biggest differences between maize and its progenitor, teosinte, is the difference in apical dominance (Doebley *et al.* 1997; Doebley 2004). Modern maize cultivars have a single stalk and one ear on the top of the plant, but wild type non-domesticated teosinte has multiple stalks and long branches. TEOSINTE BRANCHED1 (Tb1), a member of the TCP TF family, largely controls these differences between maize and teosinte. Tb1 can repress the outgrowth of the axillary meristems and branch elongation via a negative effect on the cell cycle (Dorweiler and Doebley 1997; Clark 2005; Camus-Kulandaivelu *et al.* 2008; Tsiantis 2011). Another well-described example of the role of a TF in crop domestication is Tga1. This is a member of the squamosa-promoter binding protein (SBP) TF family and was identified as a TF that played an important role in maize domestication (Wang *et al.* 2005). Tga1 might sit at the top of a cascade of transcription regulators, because some of the members of this family can regulate the expression of *MADS* TFs (Cardon *et al.* 1999). As major regulator of other TFs, the *Tga1* gene affects diverse traits such as cell lignification, three dimensional organ growth, and organ size and silica deposition (Dorweiler and Doebley 1997). Other *SBP* genes with important roles in QTLs for yield components in rice are *OsSPL14* and *OsSPL16* which respectively control grain number and tiller formation

(Miura *et al.* 2010; Liang *et al.* 2014; Wang *et al.* 2012). Likely these genes were also important for crop domestication.

Another important trait in cereal domestication is shattering of seeds. Normally seeds shatter easily from the rice panicle or the wheat spike but for agricultural purposes it is required that they stay attached during harvest. A number of QTLs controlling this process have been identified. *Sh4* and *qSH1* are two key genes required for reduced seed shattering during rice domestication. *Sh4* encodes a protein with homology to Myb3, which is a TF from the MYB domain family and controls whether the seed fall off the plant as in wild rice or adhere to the plant like in cultivated types. Transgenic experiments showed that a single amino acid change converts rice from shattering to non-shattering types. The decrease in expression of the cultivated allele compared to the wild type allele is also important in the domestication (Li *et al.* 2006). *qSH1* is a BEL1-type homeobox gene (Zhou *et al.* 2012). The single nucleotide change in cultivated rice interferes with a *cis*-regulatory element in the promoter required for the expression of *qSH1* in the abscission layer at the base of the rice grain, which is needed for the grain to break away from the axis of the panicle (Konishi *et al.* 2006; Zhou *et al.* 2012). In wheat, *Q* affects a range of traits including the tendency of the spike to shatter, the tenacity of the chaff surrounding the grain, and whether the spike is elongated as in wild wheat or compact like the cultivated forms after wheat domestication (Simons *et al.* 2006)

Tillering is also an important agronomic trait for determining rice yield, because it greatly affects the panicle number which is a key component of rice production and is one of three main yield components (Sakamoto and Matsuoka 2008; Xing and Zhang 2010). *MOC1* (*MONOCULM1*) was identified as important gene in the control of rice tillering. The *moc1* mutant has only one main culm without any other tillers because of a defect in the formation of tiller buds. *MOC1* does not code for a TF but encodes a putative GRAS family protein and is expressed mainly in the axillary buds and functions to initiate axillary buds and to promote their outgrowth (Li *et al.* 2003). *DLT* (*DWARF AND LOW-TILLERING*) also encodes a GRAS family protein and the knockdown mutant showed a reduction in tiller numbers associated with altered expression of several brassinosteroid signalling genes (Li *et al.* 2010; Tong *et al.* 2012). Recently, it was found that OsMADS57 interacts with OsTB1 (TEOSINTE BRANCHED1) and targets D14 (Dwarf14) to control tillering (Guo *et al.* 2013).

In addition, grain size is important for rice yield potential, and grain size has been an important target in rice breeding (Takeda and Matsuoka 2008). Gene *OsSPL1*6 controls grain size and shape in rice, which can improve grain quantity and yield (Wang *et al.* 2012). The over-expression of *PGL1* (*POSITIVE REGULATOR OF GRAIN LENGTH*), which is a TF of the bHLH family, increases grain length and weight due to increased cell length of lemma and palea. Moreover, *APG* (*ANTAGONIST OF PGL*) encodes a typical DNA-binding basic helix-loop-helix protein, which acts as an interaction partner of PGL1. Knock down of *APG* led to increased grain length, which suggested that APG was a negative regulator of grain length and weight, and PGL1 was an inhibitor of APG (Heang and Sassa 2012). Other genes involved in determining grain size are *GS3* (Mao *et al.* 2010), *OsPPKL1* (Zhang *et al.* 2012) and *GS6* (Sun et al. 2013).

Another very important trait in rice domestication is the diversification of flowering time (FT). Rice is a typical short day (SD) plant and it needs a suitable photoperiod for flowering in the correct time which is important to get seeds. In rice, OsGI-Hd1-Hd3a is the major pathway controlling flowering time (Yano *et al.* 2000; Hayama *et al.* 2002; Kojima *et al.* 2002). The genes orthologous to *CO* and *FT* in rice were identified as flowering-time QTLs and named *Hd1* and *Hd3a* accordingly. Under the SD condition, *Hd1* has functions downstream of *Hd3a* (Kojima *et al.* 2002; Takahashi and Shimamoto 2011), encoding a mobile flowering signal and promotes floral transition (Tamaki *et al.* 2007). *RFT1*, a gene homologous to *Hd3a*, is also essential for flowering in rice and it promotes flowering in the absence of Hd3a (Komiya *et al.* 2008). Both *RFT1* and *Hd3a* are floral activators under SD condition and they act up-steam of *OsMADS14* and *OsMADS15* (Komiya *et al.* 2008). *Early heading date 1* (*Ehd1*), a B-type regulator, promotes rice flowering under SD condition. No ortholog of *Ehd1* was found in the *Arabidopsis* genome (Doi *et al.* 2004). *Ehd2*, encoding a putative TF with zinc finger motifs, acts as a flowering promoter by up-regulating *Ehd1* under SD condition (Matsubara *et al.* 2008). *OsMADS51* is also a short day flowering promoter which functions upstream of *Ehd1*, *OsMADS14* and *Hd3a* (Kim *et al.* 2007). *OsMADS50*, which also belongs to the *MADS* TF family, also acts as an important flowering activator upstream of *OsMADS1*, *OsMADS14*, *OsMADS15*, *OsMADS18* and *Hd3a* (Lee *et al.* 2004). Yeast two hybrid screening and pull down experiments showed that one of the MADS-box genes controlling flowering development in rice, OsMADS1, interacted with OsMADS14 and OsMADS15 together (Lim *et al.* 2000).

Data from the Arabidopsis genome project indicated that more than 5% of the genes encode TFs (Riechmann *et al.* 2000), and in rice about 4% of the genes encode TFs (Tyagi *et al.* 2004). Since the number of non-TF genes is 20-25 larger than the number of TFs, the conclusion is that a single TF is able to regulate the expression of large sets of other genes. The utilization of TFs provides advantages in genetic engineering in that a set of genes can be manipulated at the same time. Plant TFs might act as a hub in the complicated net of gene expression and regulation. Research on TFs can reveal the molecular mechanism of gene expression and regulation, and the biological processes which are controlled by it. Furthermore, the study of transcription factors might lead us to meet future challenges in crop improvement.

In rice, in total 58 TF families are corresponding to 1,981 and 2,408 putative transcription factors in the *indica* and *japonica* subspecies respectively (Jin *et al.* 2014). One of these, the so-called Dof (DNA-binding with one finger), family is a plant specific group of zinc-finger TFs (Yanagisawa 1995). Although there are several reports about functions of Dof TFs in plants, the functions of most rice Dof genes is still far from clear, and they need to be further investigated and explored for their potential in plant breeding. The characteristics of this gene family and known functions are discussed in the next section of this chapter.

Dof transcription factor genes

The first protein identified with a Dof domain was MNB1a in maize which is identical to Dof1 and which can interact with the Cauliflower Mosaic Virus (CaMV) 35S promoter (Yanagisawa and Izui 1993; Yanagisawa 1995). Dof genes seem to be implicated in many different biological processes (Yanagisawa 1995, 1996, 1998). Dof domain proteins are TFs with a highly conserved DNA-binding domain, which presumably includes a single C_2-C_2 zinc finger (Figure 2). They form an important plant-specific transcription factor family (Yanagisawa 1998, 2002, 2004). In *Arabidopsis,* there are 36 annotated TFs belonging to the Dof family, whereas there are 30 Dof proteins in the rice genome (Lijavetzky *et al.* 2003; Noguero *et al*. 2013). Although mainly found in higher plants, Dof proteins have also been discovered in the unicellular alga *Chlamydomonas reinhardti,*mosses and gymnosperms. This indicates an ancient origin and the possibility of diversification throughout plant evolution. As we know, homologous sequences are paralogous if they were created by genome duplication, and they are orthologous if they are copies of a single gene in different species. Paralogs usually display different functions, while orthologs largely retain the same function (Tatusov *et al.* 1997). There is very little literature about rice Dof TFs, but a lot of data are available about Dof TFs in other species such as Arabidopsis and maize. Theinformation about the Dof transcription factors from these other species will be helpful to assay the homologous Dof gene in rice.

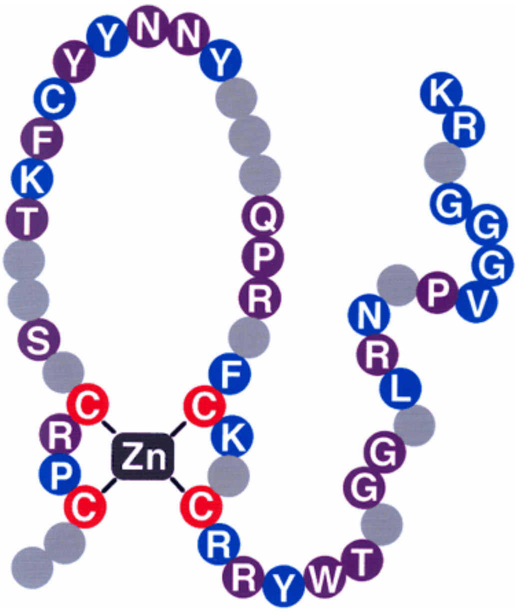

Figure 2. A proposal for the structure of the Dof domain (Yanagisawa, 2004). Absolutely conserved cysteine residues that presumably coordinate zinc and other amino acid residues conserved among all known Dof domain proteins are shown in red and purple, respectively. Well-conserved residues are shown in blue, and redundant residues are shown in gray.

The highly conserved Dof zinc finger domain, normally locates at the N-terminus, and the amino acid sequences outside the Dof domain are very diverse and show little homology (Yanagisawa 2002). The specific DNA sequences to which the Dof proteins bind have been verified by *in vitro* and *in vivo* experiments. All Dof proteins analyzed so far recognize an AAAG motif or its revise complementary sequence, CTTT, in the *in vitro* DNA binding assays (Yanagisawa 2002). The only exception is the pumpkin protein AOBP (Kisu *et al.* 1998), which takes AGTA repeats as DNA-binding motif. The Dof domain alone is able to confer the sequence specific DNA interaction (Yanagisawa 1995; Kisu *et al.* 1998), so the regions outside the Dof domain do not play a major role in the interaction with DNA. It has been reported that maize Dof1 can bind an AAAG motif in 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 (Cavalar *et al.* 2003). Moreover, the specific interaction of Dof proteins with the AAAG motif has been also verified *in vivo*. Dof proteins can bind and activate transcription from a synthetic promoter containing an AAAG motif or certain native promoters embracing an AAAG motif in protoplasts isolated from plants (Yanagisawa and Sheen 1998; Yanagisawa 2000). Furthermore, mutational assays showed the physiological significance of the AAAG sequences in the putative target promoters, such as the promoter of the maize *PEPC* gene and the maize *PPDK* gene

(Yanagisawa 2000). All Dof domains have four conserved cysteine residues, and metal chelators inhibit DNA-binding of maize Dof1 and some other Dof proteins *in vitro* (Yanagisawa 1995, 2002). Replacement of the conserved cysteine residues with alanine or serine completely abolished DNA-binding of the Dof proteins *in vitro* (Yanagisawa 1995) and *in vivo* (Mena *et al.* 1998). Although there are still no structural biological data, these results strongly indicate that the Dof domain is essential for DNA-binding.

The Dof domain was originally identified as a DNA-binding domain, but now it is regarded as a bifunctional domain for both DNA-binding and protein-protein interactions with other classes of transcription factors (basic domain-leucine zipper proteins, bZIP proteins) and non-histone nuclear proteins called high-mobility group (HMG) proteins. The first protein-protein interaction was found with an Arabidopsis Dof domain protein (OBP1), which was found interacting with bZIP proteins associated with stress responses (Zhang *et al.* 1995; Chen *et al.* 1996). Another example of a Dof-bZIP interaction was shown for a maize Dof domain protein (PBF) and a maize bZIP protein, Opaque2 (O2) which regulates endosperm-specific gene expression (Vicente-Carbajosa *et al.* 1997). The Dof domain also interacts with the conserved DNA-binding domain (the HMG-box) of HMG proteins, abundant non-histone nuclear proteins likely functioning in transcription and DNA replication. The binding of maize Dof1 and Dof2 to DNA was promoted by HMG protein (Yanagisawa 1997). Although protein-protein interactions mediated by the Dof domain were shown with only a few Dof proteins till now, all Dof domains might confer protein-protein interactions because the Dof domain is highly conserved.

As the amino acid sequences outside the Dof domain are divergent, the Dof domain proteins also play diverse roles in plants. These roles include responses to plant hormones such as gibberellin (Washio 2001; Mena *et al.* 2002) and auxin (DePaolis *et al.* 1996; Kisu *et al.* 1998), stress responses (Corrales *et al*. 2014), tissue specific expression (Yanagisawa 1998; Plesch *et al.* 2001) and photosynthesis (Yanagisawa and Sheen 1998; Yanagisawa 2000).

Maize Dof1 was associated with expression of multiple genes involved in carbon metabolism (Yanagisawa 2000). It can recognize the AAAG motif in the maize *C4PPDK* promoter and activates the expression of this gene (Yanagisawa 2000), whereas Dof2 acts as a tissue-specific repressor (Yanagisawa and Sheen 1998). Further *in vitro* experiments showed that the chromosomal high-mobility group (HMG) protein HMG5 can facilitate nucleosome binding of the transcription factor independent from the position of the recognition sites (Cavalar *et al.* 2003). Nowadays, *Dof* genes and functions have been described in many other plant species. Two soybean *Dof* genes, *GmDof4* and *GmDof11* can enhance the lipid contents in transgenic

Arabidopsis by up-regulating genes which are associated with the biosynthesis of fatty acids (Wang *et al.* 2007). *SRF1*, a Dof gene from sweet potato, modulates the carbohydrate metabolism in the storage roots by negative regulation of *Ibbfruct2*, a vacuolar invertase gene (Tanaka *et al.* 2009). In *Triticum aestivum* (wheat), members of the Dof transcription factor family are associated with light-mediated gene regulation, including involvement in photosynthesis (Shaw *et al.* 2009), and TaDof1 might be related to the up-regulation of C4 pathway-related genes functioning in heterosis (Chen *et al.* 2005). In Arabidopsis, *Dof* genes play important roles in different biological courses, for instance *OBP1* in the cell cycle regulation (Skirycz *et al.* 2008) and *COG1* and *OBP3* in regulating of phytochrome signaling (Ward *et al.* 2005), the *CDF1*, *CDF2* and *CDF3* genes in photoperiodic control of flowering (Fornara *et al.* 2009), the *DAG1* and *DAG2* genes in seed germination (Gualberti *et al.* 2002).

The Dof TFs in the rice genome (Lijavetzky *et al.* 2003; Noguero *et al.* 2013) have been classified into four major clusters, but thus far only OsDof3 and OsDof12 have been well described by functional analysis (Washio 2001; Engelmann *et al.* 2003; Li *et al.* 2009). OsDof3 plays an important role in the gibberellin-mediated expression of genes involved in seed germination (Washio 2001; Engelmann *et al.* 2003), is expressed in maturing endosperm and coordinately expressed with seed storage protein genes. OsDof3 was also found involved in the quantitative regulation of genes which are expressed in the endosperm in cooperation with this *RISBZ1* gene (Yamamoto *et al.* 2006). OsDof12 is a promoter of the rice heading date by up-regulating the genes *Hd3a* and *OsMADS14* under Long Day (LD) condition (Li *et al.* 2008; 2009). OsDof9 and OsDof18 were reported to be expressed in rice aleurone layer of grains (Washio 2001). Except for the few reported Dof genes, most of the Dof transcription factor genes have not been investigated in rice till now. Functions of most of the rice Dof transcription factors need to be researched and unraveled. In the thesis we studied two of the rice Dof genes, *OsDof24* and *OsDof25*, which are related to *OsC4PPDK* transcription and regulation, heading date and seeds storage proteins in rice.

Outline of this thesis

The aim of this thesis was to make a start with studying the molecular basis for heterosis in Chinese Super hybrid rice by focusing on the transcriptional regulation of *C4PPDK* which is an important gene in photosynthesis. Heterosis, hybrid vigor, or outbreeding enhancement, is the improved or increased function of any biological quality in a hybrid offspring. Chinese Super hybrid rice shows typical heterosis than the parental lines, which offer a good system for investigation of heterosis. Previous studies showed that several genes involved in C4 photosynthesis including *C4PPDK*, were upregulated in hybrid rice (Bao *et al.* 2005) compared to the parental lines. Based on the hypothesis that certain transcription factors may be responsible for these expression polymorphisms, we developed experiments where we finally identified two Dof proteins as regulatory factors of rice C4PPDK.

Chapter 1 presents a general introduction to the factors involved in crop domestication and the specific role of transcription factors in this process. **Chapter 2** describes the functional analysis of a Dof-type transcription factor, named *OsDof24,* from rice. Over-expressing *OsDof24* in rice resulted in plants with a reduced plant height and delayed flowering time, but down-regulation using an RNAi approach did not render any obvious phenotype. Detailed transcriptional profiling of heading date-related genes in *OsDof24*-overexpressing transgenic rice showed that OsDof24 can function in the delay of the heading date by down-regulating transcription of genes *Hd3a* and *RFT1*, which are two critical genes controlling this process. **Chapter 3** describes the role of *OsDof25* in the regulation of *OsC4PPDK.* Interactions between *OsDof25* and *OsC4PPDK* were confirmed in experiments involving EMSA, yeast one-hybrid analysis and transient expression in rice protoplasts. The regulatory role of *OsDof25* in *OsC4PPDK* expression was confirmed using *OsDof25* misexpression plants. The results suggested that OsDof25 is a trans-activator of the *OsC4PPDK* gene in rice. **Chapter 4** describes the effects of OsDof24 and OsDof25 on the content of rice seeds storage proteins. First the interaction between both OsDof24 and OsDof25 with the *GluB-1* promoter was investigated by a set of *in vitro* and *in vivo* experiments. Results showed that both OsDof24 and OsDof25 can affect seed storage protein content probably by activating the transcription of the *GluB-1* promoter. Finally, in **Chapter 5**, a general discussion of the results from Chapters 2, 3 and 4 is presented.

References

Bao, J.Y., Lee, S.G., Chen, C., Zhang, X.Q., Zhang, Y., Liu, S.Q., Clark, T., Wang, J., Cao, M.L., Yang, H.M., Wang, S.M. and Yu, J. (2005) Serial analysis of gene expression study of a hybrid rice strain (LYP9) and its parental cultivars. *Plant Phys*, **138**, 1216-1231.

Boulikas, T. (1994) Putative nuclear localization signals (NLS) in protein transcription factors. *J Cell Biochem*, **55**, 32-58.

Camus-Kulandaivelu, L., Chevin, L.M., Tollon-Cordet, C., Charcosset, A., Manicacci, D. and Tenaillon, M.I. (2008) Patterns of molecular evolution associated with two selective sweeps in the Tb1-Dwarf8 region in maize. *Genetics*, **180**, 1107-1121.

Cardon, G., Hohmann, S., Klein, J., Nettesheim, K., Saedler, H. and Huijser, P. (1999) Molecular characterisation of the Arabidopsis SBP-box genes. *Gene*, **237**, 91-104.

Cavalar, M., Moller, C., Offermann, S., Krohn, N.M., Grasser, K.D. and Peterhansel, C. (2003) The interaction of DOF transcription factors with nucleosomes depends on the positioning of the binding site and is facilitated by maize HMGB5. *Biochem*, **42**, 2149-2157.

Chen, R., Ni, Z., Qin, Y., Nie, X., Lin, Z., Dong, G. and Sun, Q. (2005) Isolation and characterization of TaDof1 transcription factor in wheat (Triticum aestivum. L). *DNA Seq*, **16**, 358-363.

Chen, W., Chao, G. and Singh, K.B. (1996) The promoter of a H2O2-inducible, Arabidopsis glutathione S-transferase gene contains closely linked OBF- and OBP1-binding sites. *Plant J*, **10**, 955-966.

Clark, R. (2005) Long-distance regulatory control of the tb1 gene and the evolution of plant architecture in maize. *Comp Biochem Phys A*, **141**, S261-S262.

Corrales, AR., Nebauer, SG., Carrillo, L., Fernandez-Nohales, P., Marques, J., Renau-Morata, B., Granell, A., Pollmann, S., Vicente-Carbajosa, J., Molina, RV. and Medina, J (2014) Characterization of tomato cycling Dof factors reveals conserved and new functions in the control of flowering time and abiotic stress responses. *J Exp Bot*, **65,** 995-1012

DePaolis, A., Sabatini, S., DePascalis, L., Costantino, P. and Capone, I. (1996) A rolB regulatory factor belongs to a new class of single zinc finger plant proteins. *Plant J*, **10**, 215-223.

Doebley, J. (2004) The genetics of maize evolution. *Ann Rev Genet*, **38**, 37-59.

Doebley, J. and Lukens, L. (1998) Transcriptional regulators and the evolution of plant form. *Plant Cell*, **10**, 1075-1082.

Doebley, J., Stec, A. and Hubbard, L. (1997) The evolution of apical dominance in maize. *Nature*, **386**, 485-488.

Doebley, J.F., Gaut, B.S. and Smith, B.D. (2006) The molecular genetics of crop domestication. *Cell*, **127**, 1309-1321.

Doi, K., Izawa, T., Fuse, T., Yamanouchi, U., Kubo, T., Shimatani, Z., Yano, M. and Yoshimura, A. (2004) Ehd1, a B-type response regulator in rice, confers short-day promotion of flowering and controls FT-like gene expression independently of Hd1. *Genes Dev*, **18**, 926-936.

Dorweiler, J. and Doebley, J. (1997) Developmental analysis of teosinte glume architecture1: A key locus in the evolution of maize (Poaceae). *Am J Bot*, **84**, 1313.

Engelmann, S., Blasing, O.E., Gowik, U., Svensson, P. and Westhoff, P. (2003) Molecular evolution of C4 phosphoenolpyruvate carboxylase in the genus Flaveria--a gradual increase from C3 to C4 characteristics. *Planta*, **217**, 717-725.

Favaro, R., Pinyopich, A., Battaglia, R., Kooiker, M., Borghi, L., Ditta, G., Yanofsky, M.F., Kater, M.M. and Colombo, L. (2003) MADS-box protein complexes control carpel and ovule development in Arabidopsis. *Plant Cell*, **15**, 2603-2611.

Fornara, F., Panigrahi, K.C., Gissot, L., Sauerbrunn, N., Ruhl, M., Jarillo, J.A. and Coupland, G. (2009) Arabidopsis DOF transcription factors act redundantly to reduce CONSTANS expression and are essential for a photoperiodic flowering response. *Dev Cell*, **17**, 75-86.

Goff, S.A., Ricke, D., Lan, T.H., Presting, G., Wang, R., Dunn, M., Glazebrook, J., Sessions, A., Oeller, P., Varma, H., *et al.* (2002) A draft sequence of the rice genome (Oryza sativa L. ssp. japonica). *Science*, **296**, 92-100.

Gualberti, G., Papi, M., Bellucci, L., Ricci, I., Bouchez, D., Camilleri, C., Costantino, P. and Vittorioso, P. (2002) Mutations in the Dof zinc finger genes DAG2 and DAG1 influence with opposite effects the germination of Arabidopsis seeds. *Plant Cell*, **14**, 1253-1263.

Guiltinan, M.J. and Miller, L. (1994) Molecular characterization of the DNA-binding and dimerization domains of the bZIP transcription factor, EmBP-1. *Plant Mol Biol*, **26**, 1041-1053.

Guo, S., Xu, Y., Liu, H., Mao, Z., Zhang, C., Ma, Y., Zhang, Q., Meng, Z. and Chong, K. (2013) The interaction between OsMADS57 and OsTB1 modulates rice tillering via DWARF14. *Nature Comm*, **4**, 1566.

Hayama, R., Izawa, T. and Shimamoto, K. (2002) Isolation of rice genes possibly involved in the photoperiodic control of flowering by a fluorescent differential display method. *Plant Cell Physiol*, **43**, 494-504.

Heang, D. and Sassa, H. (2012) Antagonistic actions of HLH/bHLH proteins are involved in grain length and weight in rice. *PloS One*, **7**, e31325.

Jin J.P., Zhang H., Kong L., Gao G. and Luo J.C. (2014) PlantTFDB 3.0: a portal for the functional and evolutionary study of plant transcription factors. *Nucl Acids Res*, **42**(D1), D1182-D1187.

Katagiri, F., Seipel, K. and Chua, N.H. (1992) Identification of a novel dimer stabilization region in a plant bZIP transcription activator. *Mol Cell Biol*, **12**, 4809-4816.

Kim, S.L., Lee, S., Kim, H.J., Nam, H.G. and An, G. (2007) OsMADS51 is a short-day flowering promoter that functions upstream of Ehd1, OsMADS14, and Hd3a. *Plant Physiol*, **145**, 1484-1494.

Kisu, Y., Ono, T., Shimofurutani, N., Suzuki, M. and Esaka, M. (1998) Characterization and expression of a new class of zinc finger protein that binds to silencer region of ascorbate oxidase gene. *Plant Cell Physiol*, **39**, 1054-1064.

Kojima, S., Takahashi, Y., Kobayashi, Y., Monna, L., Sasaki, T., Araki, T. and Yano, M. (2002) Hd3a, a rice ortholog of the Arabidopsis FT gene, promotes transition to flowering downstream of Hd1 under short-day conditions. *Plant Cell Physiol*, **43**, 1096-1105.

Komiya, R., Ikegami, A., Tamaki, S., Yokoi, S. and Shimamoto, K. (2008) Hd3a and RFT1 are essential for flowering in rice. *Development*, **135**, 767-774.

Komiya, R., Yokoi, S. and Shimamoto, K. (2009) A gene network for long-day flowering activates RFT1 encoding a mobile flowering signal in rice. *Development*,136, 443-50.

Konishi, S., Izawa, T., Lin, S.Y., Ebana, K., Fukuta, Y., Sasaki, T. and Yano, M. (2006) An SNP caused loss of seed shattering during rice domestication. *Science*, **312**, 1392-1396.

Lee, S., Kim, J., Han, J.J., Han, M.J. and An, G. (2004) Functional analyses of the flowering time gene OsMADS50, the putative SUPPRESSOR OF

OVEREXPRESSION OF CO 1/AGAMOUS-LIKE 20 (SOC1/AGL20) ortholog in rice. *Plant J*, **38**, 754-764.

Li, C., Zhou, A. and Sang, T. (2006a) Rice domestication by reducing shattering. *Science*, **311**, 1936-1939.

Li, D., Yang, C., Li, X., Gan, Q., Zhao, X. and Zhu, L. (2009) Functional characterization of rice OsDof12. *Planta*, **229**, 1159-1169.

Li, D., Yang, C., Li, X., Ji, G. and Zhu, L. (2008) Sense and antisense OsDof12 transcripts in rice. *BMC Mol Biol*, **9**, 80.

Li, J.Y., Wang, J. & Zeigler, R.S. (2014)The 3,000 rice genomes project: new opportunities and challenges for future rice research. *GigaScience*, **3**, 8.

Li, L., Wang, X.F., Stolc, V., Li, X.Y., Zhang, D.F., Su, N., Tongprasit, W., Li, S.G., Cheng, Z.K., Wang, J. and Deng, X.W. (2006b) Genome-wide transcription analyses in rice using tiling microarrays. *Nature Genet*, **38**, 124-129.

Li, W., Wu, J., Weng, S., Zhang, Y., Zhang, D. and Shi, C. (2010) Identification and characterization of dwarf 62, a loss-of-function mutation in DLT/OsGRAS-32 affecting gibberellin metabolism in rice. *Planta*, **232**, 1383-1396.

Li, X., Qian, Q., Fu, Z., Wang, Y., Xiong, G., Zeng, D., Wang, X., Liu, X., Teng, S., Hiroshi, F., Yuan, M., Luo, D., Han, B. and Li, J. (2003) Control of tillering in rice. *Nature*, **422**, 618-621.

Liang, W.H., Shang, F., Lin, Q.T., Lou, C. & Zhang, J. (2014) Tillering and panicle branching genes in rice. *Gene*, **537**, 1-5 .

Lijavetzky, D., Carbonero, P. and Vicente-Carbajosa, J. (2003) Genome-wide comparative phylogenetic analysis of the rice and Arabidopsis Dof gene families. *BMC Evol Biol*, **3**.

Lim, J., Moon, Y.H., An, G. and Jang, S.K. (2000) Two rice MADS domain proteins interact with OsMADS1. *Plant Mol Biol*, **44**, 513-527.

Liu, L., White, M.J. and MacRae, T.H. (1999) Transcription factors and their genes in higher plants functional domains, evolution and regulation. *Eur J Biochem*, **262**, 247-257.

Lu, C.A., Ho, T.H., Ho, S.L. and Yu, S.M. (2002) Three novel MYB proteins with one DNA binding repeat mediate sugar and hormone regulation of alpha-amylase gene expression. *Plant Cell,* **14**, 1963-1980.

Mao, H., Sun, S., Yao, J., Wang, C., Yu, S., Xu, C., Li, X. and Zhang, Q. (2010) Linking differential domain functions of the GS3 protein to natural variation of grain size in rice. *PNAS*, **107**, 19579-19584.

Matsubara, K., Yamanouchi, U., Wang, Z.X., Minobe, Y., Izawa, T. and Yano, M. (2008) Ehd2, a rice ortholog of the maize INDETERMINATE1 gene, promotes flowering by up-regulating Ehd1. *Plant Physiol*, **148**, 1425-1435.

Mena, M., Cejudo, F.J., Isabel-Lamoneda, I. and Carbonero, P. (2002) A role for the DOF transcription factor BPBF in the regulation of gibberellin-responsive genes in barley aleurone. *Plant Physiol*, **130**, 111-119.

Mena, M., Vicente-Carbajosa, J., Schmidt, R.J. and Carbonero, P. (1998) An endosperm-specific DOF protein from barley, highly conserved in wheat, binds to and activates transcription from the prolamin-box of a native B-hordein promoter in barley endosperm. *Plant J*, **16**, 53-62.

Miyao, A., Iwasaki, Y., Kitano, H., Itoh, J., Maekawa, M., Murata, K., Yatou, O., Nagato, Y. and Hirochika, H. (2007) A large-scale collection of phenotypic data describing an insertional mutant population to facilitate functional analysis of rice genes. *Plant Mol Biol*, **63**, 625-635.

Miura, K., Sun, S., Yao, J., Wang, C., Yu, S., Xu, C., Li, X. and Zhang, Q. (2010) OsSPL14 promotes panicle branching and higher grain productivity in rice. *Nature Genet*, **42**, 545-549.

Nam, J., de Pamphilis, C.W., Ma, H. and Nei, M. (2003) Antiquity and evolution of the MADS-box gene family controlling flower development in plants. *Mol Biol Evol*, **20**, 1435-1447.

Noguero, M., Atif, RM., Ochatt, S. and Thompson, RD (2013) The role of the DNA-binding One Zinc Finger (DOF) transcription factor family in plants. *Plant Sci* **209**: 32-45

Perez-Rodriguez, P., Riano-Pachon, D.M., Correa, L.G., Rensing, S.A., Kersten, B. and Mueller-Roeber, B. (2010) PlnTFDB: updated content and new features of the plant transcription factor database. *Nucleic Acids Res*, **38**, D822-827.

Plesch, G., Ehrhardt, T. and Mueller-Roeber, B. (2001) Involvement of TAAAG elements suggests a role for Dof transcription factors in guard cell-specific gene expression. *Plant J*, **28**, 455-464.

Ramirez, S.R. and Basu, C. (2009) Comparative analyses of plant transcription factor databases. *Curr Genomics*, **10**, 10-17.

Riechmann, J.L., Heard, J., Martin, G., Reuber, L., Jiang, C., Keddie, J., Adam, L., Pineda, O., Ratcliffe, O.J., Samaha, R.R., Creelman, R., Pilgrim, M., Broun, P., Zhang, J.Z., Ghandehari, D., Sherman, B.K. and Yu, G. (2000) Arabidopsis transcription factors: genome-wide comparative analysis among eukaryotes. *Science*, **290**, 2105-2110.

Sakamoto, T. and Matsuoka, M. (2008) Identifying and exploiting grain yield genes in rice. *Curr Opin Plant Biol*, **11**, 209-214.

Sasaki, T., Matsumoto, T., Antonio, B.A. and Nagamura, Y. (2005) From mapping to sequencing, post-sequencing and beyond. *Plant Cell Physiol*, **46**, 3-13.

Shaw, L.M., McIntyre, C.L., Gresshoff, P.M. and Xue, G.P. (2009) Members of the Dof transcription factor family in Triticum aestivum are associated with light-mediated gene regulation. *Funct Integr Genomics*, **9**, 485-498.

Simons, K.J., Fellers, J.P., Trick, H.N., Zhang, Z., Tai, Y.S., Gill, B.S. and Faris, J.D. (2006) Molecular characterization of the major wheat domestication gene Q. *Genetics*, **172**, 547-555.

Skirycz, A., Radziejwoski, A., Busch, W., Hannah, M.A., Czeszejko, J., Kwasniewski, M., Zanor, M.I., Lohmann, J.U., De Veylder, L., Witt, I. and Mueller-Roeber, B. (2008) The DOF transcription factor OBP1 is involved in cell cycle regulation in Arabidopsis thaliana. *Plant J*, **56**, 779-792.

Sun, L., Li, X., Fu, Y., Zhu, Z., Tan, L., Liu, F., Sun, X. and Sun, C. (2013) GS6, a member of the GRAS gene family, negatively regulates grain size in rice. J *Integr Plant Biol*, *55*, 938-949.

Takahashi, Y. and Shimamoto, K. (2011) Heading date 1 (Hd1), an ortholog of Arabidopsis CONSTANS, is a possible target of human selection during domestication to diversify flowering times of cultivated rice. *Genes Genet Sys*, **86**, 175-182.

Takeda, S. and Matsuoka, M. (2008) Genetic approaches to crop improvement: responding to environmental and population changes. *Nature Reviews. Genetics*, **9**, 444-457.

Tamaki, S., Matsuo, S., Wong, H.L., Yokoi, S. and Shimamoto, K. (2007) Hd3a protein is a mobile flowering signal in rice. *Science*, **316**, 1033-1036.

Tanaka, M., Takahata, Y., Nakayama, H., Nakatani, M. and Tahara, M. (2009) Altered carbohydrate metabolism in the storage roots of sweetpotato plants overexpressing the SRF1 gene, which encodes a Dof zinc finger transcription factor. *Planta*, **230**, 737-746.

Tatusov, R.L., Koonin, E.V. and Lipman, D.J. (1997) A genomic perspective on protein families. *Science*, **278**, 631-637.

Tong, H.N., Liu, L.C., Jin, Y., Du, L., Yin, Y.H., Qian, Q., Zhu, L.H. and Chu, C.C. (2012) Dwarf and low-tillering acts as a direct downstream target of a GSK3/SHAGGY-Like Kinase to mediate brassinosteroid responses in rice. *Plant Cell*, **24**, 2562-2577.

Tsiantis, M. (2011) A transposon in tb1 drove maize domestication. *Nat Genet*, **43**, 1048-1050.

Tyagi, A.K., Khurana, J.P., Khurana, P., Raghuvanshi, S., Gaur, A., Kapur, A., Gupta, V., Kumar, D., Ravi, V., Vij, S., Khurana, P. and Sharma, S. (2004) Structural and functional analysis of rice genome. *J Genet*, **83**, 79-99.

Vicente-Carbajosa, J., Moose, S.P., Parsons, R.L. and Schmidt, R.J. (1997) A maize zinc-finger protein binds the prolamin box in zein gene promoters and interacts with the basic leucine zipper transcriptional activator Opaque2. *PNAS USA*, **94**, 7685-7690.

Wang, H., Nussbaum-Wagler, T., Li, B., Zhao, Q., Vigouroux, Y., Faller, M., Bomblies, K., Lukens, L. and Doebley, J.F. (2005) The origin of the naked grains of maize. *Nature*, **436**, 714-719.

Wang, H.W., Zhang, B., Hao, Y.J., Huang, J., Tian, A.G., Liao, Y., Zhang, J.S. and Chen, S.Y. (2007) The soybean Dof-type transcription factor genes, GmDof4 and GmDof11, enhance lipid content in the seeds of transgenic Arabidopsis plants. *Plant J*, **52**, 716-729.

Wang, S., Wu, K., Yuan, Q., Liu, X., Liu, Z., Lin, X., Zeng, R., Zhu, H., Dong, G., Qian, Q., Zhang, G. and Fu, X. (2012) Control of grain size, shape and quality by OsSPL16 in rice. *Nat Genet,* **44**, 950-954.

Ward, J.M., Cufr, C.A., Denzel, M.A. and Neff, M.M. (2005) The Dof transcription factor OBP3 modulates phytochrome and cryptochrome signaling in Arabidopsis. *Plant Cell*, **17**, 475-485.

Washio, K. (2001) Identification of Dof proteins with implication in the gibberellin-regulated expression of a peptidase gene following the germination of rice grains. *Biochim Biophy Acta*, **1520**, 54-62.

Xing, Y. and Zhang, Q. (2010) Genetic and molecular bases of rice yield. *Ann Rev Plant biol*, **61**, 421-442.

Yamamoto, M.P., Onodera, Y., Touno, S.M. and Takaiwa, F. (2006) Synergism between RPBF Dof and RISBZ1 bZIP activators in the regulation of rice seed expression genes. *Plant Physiol*, **141**, 1694-1707.

Yanagisawa, S. (1995) A Novel DNA-Binding Domain that may form a single zinc-finger motif. *Nucl Acids Res*, **23**, 3403-3410.

Yanagisawa, S. (1996) A novel multigene family that the gene for a maize DNA-binding protein, MNB1a belongs to: isolation of genomic clones from this family and some aspects of its molecular evolution. *Biochem Mol Biol Int*, **38**, 665-673.

Yanagisawa, S. (1997) Dof DNA-binding domains of plant transcription factors contribute to multiple protein-protein interactions. *Eur J Biochem*, **250**, 403-410.

Yanagisawa, S. (1998) Dof proteins: Involvement of transcription factors with a novel DNA-binding domain in tissue-specific and signal-responsive gene expression. *Seikagaku*, **70**, 280-285.

Yanagisawa, S. (2000) Dof1 and Dof2 transcription factors are associated with expression of multiple genes involved in carbon metabolism in maize. *Plant J*, **21**, 281-288.

Yanagisawa, S. (2002) The Dof family of plant transcription factors. *Trends Plant Sci*, **7**, 555-560.

Yanagisawa, S. (2004) Dof domain proteins: Plant-specific transcription factors associated with diverse phenomena unique to plants. *Plant Cell Physiol*, **45**, 386-391.

Yanagisawa, S. and Izui, K. (1993) Molecular-Cloning of 2 DNA-Binding Proteins of Maize That Are Structurally Different but Interact with the Same Sequence Motif. *J Biol Chem*, **268**, 16028-16036.

Yanagisawa, S. and Sheen, J. (1998) Involvement of maize Dof zinc finger proteins in tissue-specific and light-regulated gene expression. *Plant Cell*, **10**, 75-89.

Yang, Z.R., Wang, X.C., Li, X.M. and Yang, C.D. (2004) Transcription factors in higher plant.. *Yi Chuan*, **26**, 403-408.

Yano, M., Katayose, Y., Ashikari, M., Yamanouchi, U., Monna, L., Fuse, T., Baba, T., Yamamoto, K., Umehara, Y., Nagamura, Y. and Sasaki, T. (2000) Hd1, a major photoperiod sensitivity quantitative trait locus in rice, is closely related to the Arabidopsis flowering time gene CONSTANS. *Plant Cell*, **12**, 2473-2484.

Yu, J., Hu, S., Wang, J., Wong, G. K., Li, S., Liu, B., Deng, Y., Dai, L., Zhou, Y., Zhang, X. et al. (2002) A draft sequence of the rice genome (Oryza sativa L. ssp. indica). *Science*, **296**, 79-92

Zhang, B., Chen, W., Foley, R.C., Buttner, M. and Singh, K.B. (1995) Interactions between distinct types of DNA binding proteins enhance binding to ocs element promoter sequences. *Plant Cell,* **7**, 2241-2252

Zhang, J.W., Li, C.S., Wu, C.Y., Xiong, L.Z., Chen, G.X., Zhang, Q.F. and Wang, S.P. (2006) RMD: a rice mutant database for functional analysis of the rice genome. *Nucl Acids Res*, **34**, D745-D748.

Zhang, J.Z. (2003) Overexpression analysis of plant transcription factors. *Curr Opin Plant Biol*, **6**, 430-440.

Zhang, X., Wang, J., Huang, J., Lan, H., Wang, C., Yin, C., Wu, Y., Tang, H., Qian, Q., Li, J. and Zhang, H. (2012) Rare allele of OsPPKL1 associated with grain length causes extra-large grain and a significant yield increase in rice. *PNAS*, **109**, 21534-21539.

Zhou, Y., Lu, D., Li, C., Luo, J., Zhu, B.F., Zhu, J., Shangguan, Y., Wang, Z., Sang, T., Zhou, B. and Han, B. (2012) Genetic control of seed shattering in rice by the APETALA2 Transcription Factor SHATTERING ABORTION1. *Plant Cell*, **24**, 1034-1048.