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SHORT COMMUNICATION

Vascular plant one zinc-finger (VOZ) transcription factors: novel regulators of abiotic stress tolerance in rice (*Oryza sativa* L.)

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Abstract The vascular plant one zinc-finger (VOZ) transcription factors have been found to be associated with several important traits in Arabidopsis (*Arabidopsis thaliana* (L.) Heynh.), including regulation of stress signaling, flowering and photoperiodic pathways. The VOZ2 protein has particularly been revealed to regulate the expression of the target genes. However, the role of *VOZ* gene family in the elucidation of stress responses and other aspects of growth and development remains uncharacterized in the other plant species. This article therefore attempts to get a preliminary idea about the possible involvement of *VOZ* gene family in rice (*Oryza sativa* L.) abiotic stress tolerance. Digital expression of this rice gene family has revealed its high responsiveness to various abiotic stress conditions, including drought, salinity, cold, heat, submergence and phosphorus stresses. The highest expression of *OsVOZ2* in submergence tolerant M202 (*Sub1*) rice genotype under submergence stress prompted us to analyze the promoters of three highly submergence-responsive genes of rice for the presence of different VOZ-binding sites. Interestingly, VOZ-binding sites were found in all these genes with *Sub1A* promoter having the maximum number of them. Lastly, the alleles of *OsVOZ* genes were mined from the wild species of rice which could serve as beneficial genomic resources for the improvement of rice abiotic stress tolerance. Taken together, *VOZ* genes can be postulated to have an immense promise for rice improvement under abiotic stresses. The different ideas generated by this article will stimulate the researchers to explore the potential of *VOZ* genes in the abiotic stress tolerance of rice and other plant species.

Keywords Abiotic stress · Microarray · *Oryza sativa* L. · Submergence · VOZ · Wild rice

Introduction

Because plants cannot escape from the various environmental stresses, they have developed complex regulatory mechanisms in response to the effects of

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these stresses. Transcriptional regulation is very crucial for controlling of gene expression specific to different abiotic stresses. Transcription factors (TFs) are extremely important for breeding abiotic stress tolerant crops because they control the reprogramming of expression of wide-ranging stress-related genes, and therefore regulate several stress-related molecular pathways and cellular activities (Ahammed et al. 2020; Zhang et al. 2017). These regulatory elements play a decisive role and serve in diverse molecular processes related to abiotic stress tolerance of rice (*Oryza sativa* L.) (Ganie et al. 2019; Jin et al. 2018; Joshi et al. 2016; Tang et al. 2019; Yokotani et al. 2008). Due to their regulatory roles, genetic manipulation of TF genes has been preferred over the individual functional genes for improving abiotic stress tolerance in rice (Wang et al. 2016a).

Among the different plant-specific TFs that have remained conserved during the evolution of land plants, vascular plant one zinc-finger (VOZ) TFs serve pivotal roles in the development and stress response (Koguchi et al. 2017). These TFs, possessing two conserved regions namely Domain-A and Domain-B, were first time isolated from Arabidopsis (*Arabidopsis thaliana* (L.) Heynh.), and only *AtVOZ2* was found to regulate the expression of a vacuolar proton-pump *AVP1* by binding to GCGTN*x*7ACGC palindromic sequence through its Domain-B (Mitsuda et al. 2004). *AVP1*, a V-PPase, has been found responsive to various environmental conditions (Gaxiola et al. 2001; Schilling et al. 2017).

Since their first isolation from Arabidopsis by Mitsuda et al. (2004), VOZ TFs have been extensively characterized for their involvement in flowering and abiotic stress signaling pathways only in Arabidopsis. Different mechanisms have been proposed for the VOZ proteins to regulate flowering in Arabidopsis. These proteins redundantly promote the flowering in Arabidopsis by mediating the initial steps of phytochrome B signal transduction pathway (Yasui et al. 2012). This role of VOZ TFs was studied further in Arabidopsis and it was proposed that they promote the flowering time by repressing the *FLOWERING LOCUS C* (*FLC*) clade members (Yasui and Kohchi 2014). Recently, a separate research group reported that VOZ proteins regulate flowering primarily by modulating CONSTANS function and that this process does not require *FLC* (Kumar et al. 2018). It is evident from these studies that VOZs regulate different molecular processes, and the actual mechanism by which the VOZs regulate flowering is not completely understood yet. Besides, *VOZ* genes have also been studied for their role in abiotic stress tolerance of Arabidopsis. The first studies about the role of *VOZ* genes in biotic and abiotic stress tolerance were published in 2013, where it was reported that these genes act as positive regulators of plant responses to biotic and heat stresses, and as negative regulators of cold and drought stresses (Nakai et al. 2013a, b). Later, the same group reported that VOZ2 protein is found in cytoplasmic stress granules under heat stress, and negatively regulates the responses to heat stress by repressing the transcription of *DREB2A* in Arabidopsis (Koguchi et al. 2017). VOZ1 has also been found to act as a negative regulator of heat stress by repressing heat stress-responsive *DREB2C* (Song et al. 2018). Regarding salt tolerance, VOZ proteins reportedly act as positive regulators of salt tolerance in Arabidopsis by increasing the expression of several salt-inducible genes (Prasad et al. 2018). All these studies indicate that VOZ TF family is actively involved in plant development and stress responses possibly by regulating the expression of different types of genes engaged in various molecular processes and signaling pathways. Although this gene family has been considerably studied in Arabidopsis, the identification of authentic direct target genes of these TFs remains to be determined. It would be interesting to know if there is any cross-talk among the different molecular processes directly or indirectly modulated by VOZ TFs for conferring stress tolerance. This gene family is quite novel and exploring its involvement in the stress responses of different agronomically important crops would be very exciting.

Rice is the most important model crop that is consumed worldwide, and the increased production of rice is highly essential to sustain the growing human population (Wang et al. 2017; Xu et al. 2018). However, due to its sensitive nature to abiotic stresses, its productivity is severely limited (Grover and Minhas 2000; Kou et al. 2017; Song et al. 2012). Like Arabidopsis, *VOZ* gene family in rice is comprised of only two members viz. *OsVOZ1* (LOC_Os01g54930) and *OsVOZ2* (LOC_Os05g43950) (Mitsuda et al. 2004). Like other crop plants, the VOZ TFs have not been studied for their involvement in any aspect of development or stress signaling in rice. Considering the important roles of VOZ TFs in plant abiotic stress tolerance, it is worthwhile determining the potential functions of VOZ TF family in abiotic stress tolerance of rice. We strongly believe that working on the VOZ TFs for their involvement in rice abiotic stress tolerance will broaden our understanding about the responses of rice to abiotic stresses, which will eventually lead to the enhanced abiotic stress tolerance and hence increased yield of rice. Taking all these factors into account, this article has made endeavors to associate the OsVOZ TFs with the abiotic stress tolerance of rice by determining the expression profiles of *OsVOZs* under different abiotic stress conditions. As a case study for the involvement of OsVOZs in submergence tolerance of rice, promoter sequences of three highly submergence-responsive genes of rice were analyzed for the enrichment of VOZ-binding sites. It also presents the allelic forms of *OsVOZs* from different wild species of rice as potential genomic resources for the improvement of abiotic stress tolerance of rice.

Digital expression of *OsVOZ* genes under different abiotic stresses

In order to get an opening idea about the responsiveness of *OsVOZ* genes to abiotic stresses, we determined the microarray-based expression potential of *OsVOZ* gene family members under drought, salinity, cold, heat, submergence and phosphorus (P) stresses with respective experimental IDs as OS-00041, OS-00023, OS-00103, OS-00235, OS-00042 and OS-00091. For each abiotic stress (except P stress), only that experiment was selected which had the expression data for rice genotype tolerant to that particular stress. This was done with the aim of understanding how the abundance of *OsVOZs* is altered in tolerant rice genotype under a particular abiotic stress, because tolerant plant species tend to protect themselves against the damaging effects of abiotic stresses by activating multiple genes associated with different stress-related molecular processes (Apel and Hirt 2004; Ganie et al. 2016; Hasan et al. 2019; Hasanuzzaman et al. 2013; Su et al. 2017; Wang et al. 2018). The different selected experiments had the expression data for DK151, FL478, LTH, N22 and M202 (*Sub1*) rice genotypes tolerant to drought, salinity, cold, heat and submergence, respectively. It is evident that *OsVOZs* were highly expressed in DK151 (drought), LTH (cold) and M202 (*Sub1*) (submergence) with *OsVOZ1* showing the highest expression under cold stress, whereas *OsVOZ2* exhibited the highest expression under submergence stress (Fig. 1; Table S1a). Under salinity and phosphorus stress, *OsVOZs* exhibited moderate expression, while as under heat stress, expression of *OsVOZs* was found to be highly downregulated. The downregulation of *OsVOZs* under heat stress is logical from the perspective of their high expression under cold stress suggesting that heat and cold stresses exert opposite effects on the molecular processes which involve the *OsVOZ* genes. Similar trend in the expression of other genes under cold and heat stress has been found in rice and other plants (Blair et al. 2019; Huang et al. 2016; Tripathi et al. 2015; Wang et al. 2016b). In comparison to Arabidopsis *VOZ* genes, *OsVOZ* genes were found to show opposite expression patterns under all abiotic stresses studied (except salt stress, where *VOZ* genes of rice show upregulation similar to those of Arabidopsis). The differential expression of orthologs of a particular gene in different plant species under a given abiotic stress has been reported in many studies (Ganie et al. 2017; Liu et al. 2017; Mustafiz et al. 2011; Wei et al. 2017). The opposite roles of *VOZ* genes of Arabidopsis and rice in abiotic stress responses might be due to their different gene targets in these plant species. The very high expression of *OsVOZ* genes under drought, cold and submergence indicates that these genes might be highly responsive to such stresses and might be contributing to the tolerant

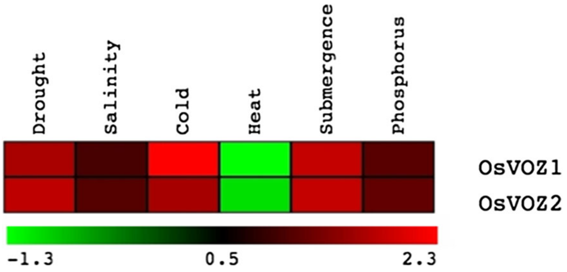

Fig. 1 Digital expression profile of *OsVOZ* genes in rice under different abiotic stress conditions. Publicly available microarray data (retrieved from Genevestigator) and MeV software package were used to generate heat map showing the expression potential of *VOZ* genes under drought, salinity, cold, heat, submergence and phosphorous stresses in rice genotypes tolerant to corresponding stresses. The color bar below the heat map represents relative expression values with green and red colors representing the downregulation and upregulation, respectively

nature of the corresponding rice genotypes—functionally validating which is a future task. Since, the submergence tolerance of M202 (*Sub1*) is due to the introgressed *Sub1* locus, it implicates that there might a connection between *Sub1* and *OsVOZ2* for imparting submergence tolerance to rice. Further, the downregulation of *OsVOZs* under heat stress (in heat tolerant N22) suggests that these genes might be acting as negative regulators of heat tolerance in rice. Therefore, it is prudent to functionally characterize their corresponding miRNAs (osa-miR1870 for *OsVOZ1*, osa-miR166 for *OsVOZ2*; predicted from psRNATarget), the overexpression of which should confer heat tolerance to rice. In fact, these miRNAs have been found to be highly expressed in the root and shoot tissues of N22 under heat stress (Mangrauthia et al. 2017), which provides a further indication about the involvement of *OsVOZs* in the abiotic stress responses of rice.

Potential VOZ binding sites in the promoters of submergence tolerance genes—a case study

To further augment our perspective about the involvement of OsVOZ TFs in abiotic stress responses of rice, we were intrigued to analyze the promoters of abiotic stress-responsive genes of rice for the presence of VOZ-binding sites. VOZ TFs of Arabidopsis have been found to bind canonical motifs such as $GCGTN_{x7}ACGC$, $GCGTN_{x7}ACGT$, $GCGTN_{x8}ACGC$, $GCGTN_{x7}AAGC$, $GCTTN_{x7}ACGC$ and $ACGTN_{x7}ACGC$ (Kumar et al. 2018; Mitsuda et al. 2004). In addition to these binding sites, some other *cis*-elements have been reported to be the consensus VOZ-binding motifs which include *CGT[GA]*, *ACGTG* and *ACGT* (Prasad et al. 2018).

Since, VOZ2 has already been found to regulate the target gene expression by binding as a dimer to *cis*-elements (Mitsuda et al. 2004), and since the expression of *OsVOZ2* was found to be the highest under submergence stress (Fig. 1), as a case study, we therefore analyzed the promoter sequences (~ 1 kb) of three highly submergence-responsive genes of rice, including *Sub1A*—the most submergence-responsive gene of rice (Xu et al. 2006), *SLR1* (Fukao and Bailey-Serres 2008) and *LGF1* (Kurokawa et al. 2018) for potential VOZ2-binding sites. Xu et al. (2006) have demonstrated that overexpression of *Sub1A* (more specifically its tolerant allele *Sub1A-1*) confers enhanced submergence tolerance to submergence-intolerant *O. sativa* ssp. *japonica* plants, indicating that *Sub1A* is the major determinant of submergence tolerance in rice. The authors also maintain that introgression of *Sub1* locus (harboring *Sub1A* gene) from a highly submergence tolerant *indica* cultivar (FR13A) results in the high yield and enhanced tolerance to submergence in a widely grown and *Sub1A*-lacking Indian rice variety. Since, *Sub1* locus of Nipponbare (*japonica*) does not possess *Sub1A* gene, we downloaded the promoter sequence of *Sub1A* gene of *indica* rice from gramene genome browser (http://ensembl.gramene.org/genome_browser/index.html). This *Sub1A* gene (Gene ID—BGIOSGA038325) is located on Supscaffold AAAA02037639. Two years after the *Sub1A* gene was reported to be highly submergence-responsive, Fukao and Bailey-Serres (2008) found that submergence tolerance in rice due to *Sub1A* is mediated by GA-signaling repressors Slender Rice-1 (SLR1) and SLR1 Like-1 (SLRL1), indicating GA-regulated processes affect negatively on submergence tolerance of rice. Moreover, it has been recently demonstrated that *Leaf Gas Film 1* (*LGF1*) gene is very essential for maintaining abundant epicuticular wax platelets, leaf hydrophobicity and gas films on submerged rice leaves—the traits very crucial for sustained underwater photosynthesis and hence submergence tolerance (Kurokawa et al. 2018).

Analysis of promoter sequences of these three genes resulted in the finding of different types and numbers of VOZ-binding sites (Table 1). Highest number of VOZ-binding canonical motifs (2) and other consensus *cis*-elements (13) were found in the promoter sequence of *Sub1A*. Among the three canonical sites, $GCGTN_{x6}ACGC$ was found downstream of the transcription start site (TSS) of *Sub1A*. Similarly, in case of *LGF1*, the only canonical binding site was also found downstream of the TSS. Although, these canonical sites are not present in promoter sequence, they might act as enhancers to increase the transcription of the genes concerned under submergence. Enhancers can be present upstream or downstream from the TSS, and even can be located within introns (Pennacchio et al. 2013). From the canonical motifs found in this work, it is evident that the sequences of binding sites (two binding halves for two monomers of VOZ2) have been conserved between

Table 1 VOZ-binding sites in the promoter (− 1000 bp) region of three submergence-responsive genes of rice and comparison of the canonical sites with the corresponding sites in Arabidopsis

Gene	Gene ID	# CGT[GA]	# ACGTG	# ACGT	Canonical binding sites	
					Rice	Arabidopsis
Sub1A	BGIOSGA038325	0	1	12	GCGTN$_{x10}$AAGC (1)	GCGTN$_{x7}$AAGC
					GCTTN$_{x18}$ACGC (1)	GCTTN$_{x7}$ACGC
					GCGTN$_{x6}$ACGC (1)	GCGTN$_{x7}$ACGC
SLR1	LOC_Os03g49990	1	1	2	GCTTN$_{x8}$ACG**G** (1)	GCTTN$_{x7}$ACGC
LGF1	LOC_Os11g30560	0	0	0	*ACGTN$_{x7}$ACGC* (1)	ACGTN$_{x7}$ACGC

VOZ-sites present downstream of transcription start site are in italics. Nucleotide in bold indicates substitution

Arabidopsis and rice (except *SLR1* which has a ‘G’ substituted for ‘C’ in the second half); however, the sequence of spacer/linker between the binding halves shows variations in length ranging from 6 to 18 nucleotides in rice. The high conservation of binding sites in canonical motifs is reminiscent of the fact that Domain-B (VOZ domain) of VOZ2 protein has been highly conserved across different plant genomes (Mitsuda et al. 2004), which might have resulted in the conservation of its binding sites too. Regarding the variation in spacer lengths, it has been found that although spacer length has a dramatic effect on binding of transcription factors and therefore on the gene expression (Bilioni et al. 2005; Krawczyk et al. 2002), there are several studies reporting that the spacer length is less conserved in the binding elements of certain TFs. For example, spacing found in functional *activation sequence-1* (*as-1*)-like elements in pathogenesis related promoters of Arabidopsis and tobacco (*Nicotiana tabacum* L.) have been found to be considerably variable (Strompen et al. 1998; Zhang et al. 1999). Similarly, significant variations in spacer length between *ACGT cis*-elements across four plant species, such as, Arabidopsis (*A. thaliana* (L.) Heynh.), soybean (*Glycine max* (L.) Merr.), rice (*O. sativa* L.) and sorghum (*Sorghum bicolor* (L.) Moench) has been found (Mehrotra et al. 2013). Most importantly, mutations introduced in the spacer region of AtVOZ2 binding site (*GCGTN$_{x7}$ACGC*) in *AVP1* promoter have been demonstrated to not affect the ability of the AtVOZ2 to bind to DNA (Mitsuda et al. 2004), which indicates that VOZ TFs might have evolved as the DNA binding proteins which are more specific about the binding site rather than the spacer length. This evolutionary conservation of VOZ-binding sites in dicots and monocots indicates that such binding sequences might be involved in vital physiological processes related to stress tolerance. Taking all these factors into account, it is plausible to postulate that canonical binding sites along with the other consensus VOZ-binding elements found in the promoters of three submergence-responsive genes of rice are potential binding sites for OsVOZ2. In particular, the highest number of VOZ-binding sites in the *Sub1A* promoter is an indication of possible regulation of *Sub1A* gene expression by OsVOZ2 TF in rice. In parallel to this case study, it is more important to mention that expression of *OsVOZ2* was found to be the highest in submergence tolerant M202 (*Sub1*) under submergence stress (Fig. 1). Since, *Sub1* locus determines the submergence tolerance of this rice line, it is likely that OsVOZ2 TF enhances the expression of *Sub1A* gene under submergence stress in M202 (*Sub1*). Based on the reports about rice submergence tolerance as discussed above, the possible regulation of rice submergence tolerance genes, particularly *Sub1A*, by OsVOZ2 would mean that rice VOZ TFs are involved in as diverse processes as ethylene-, ABA-, and GA-mediated signaling, photosynthesis, respiration, programmed cell death, carbohydrate metabolism, and other metabolic pathways to confer abiotic stress tolerance to rice. This logical association of OsVOZ TFs with the submergence tolerance in rice is a pure indication of involvement of OsVOZ TF family in other abiotic stresses and ultimately with the yield. Nonetheless, the assumptions about the binding of OsVOZ TFs to the regulatory elements in submergence tolerance genes of rice need to be confirmed by functional studies, which keeps an exciting avenue open for the future research work on abiotic stress tolerance of rice. Based on our understanding of the rice submergence tolerance from the related literature as discussed in this case study, we proposed a hypothetical model for the involvement of OsVOZ TFs in rice submergence tolerance (Fig. 2).

Genomic resources of OsVOZ transcription factors from wild rice species

Since, rice production is severely affected by abiotic stresses, sincere efforts are necessary for the fast generation of new stress tolerant rice germplasm so as to keep up with the increasing human demands for rice. Such demands might not be completely met by current within-species rice diversity. Identification of new genomic resources, in the form of novel genes and QTLs, for prolonged tolerance to abiotic stresses is therefore essential for sustained rice production. The

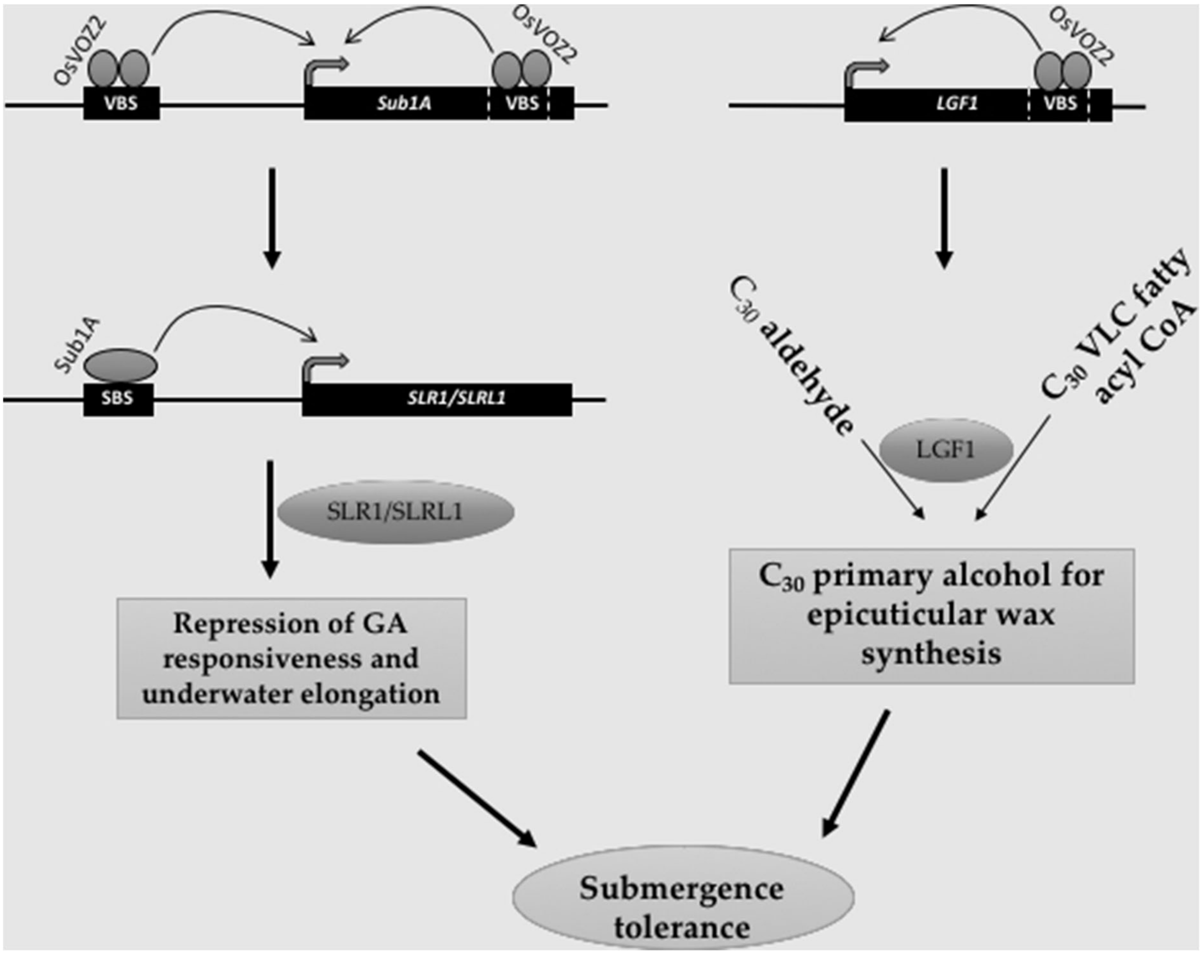

Fig. 2 Hypothetical model for the involvement of OsVOZ TFs in rice submergence tolerance (based on our opinion and the other information as described in this caption). OsVOZ2 binds as a dimer to the VOZ-binding site (VBS) upstream and downstream of the TSS to activate the expression of *Sub1A* gene. Sub1A transcription factor then increases the expression of GA-repressor genes (*SLR1* and *SLRL1*) the products of which cause the repression of GA responsiveness and underwater elongation (Fukao and Bailey-Serres 2008) resulting in the submergence tolerance. Also, OsVOZ2 binds VBS downstream of TSS to activate the expression of *LGF1* gene. LGF protein then results in the submergence tolerance by converting either C_{30} aldehydes or C_{30} very long chain (VLC) fatty acids into C_{30} primary alcohol which is important for epicuticular wax synthesis and efficient underwater photosynthesis (Kurokawa et al. 2018)

wild species of rice are virtually unexploited genetic resources for the improvement of abiotic stress tolerance of rice. Due to their adaptation to wide-ranging biogeographical areas and their tremendous potential to tolerate many abiotic stresses, wild species of rice serve as an invaluable pool of important genomic resources for rice stress tolerance improvement. With this view, we mined the orthologous alleles of *OsVOZ1* and *OsVOZ2* from eight *Oryza* wild species with different genome types (Table S1b) from gramene. As already reported, VOZ TFs are highly conserved across plant species (Mitsuda et al. 2004), the OsVOZ orthologs were also found be overall conserved (Fig. S1). However, the sequences of *O. brachyantha*, *O. longistaminata* and *O. nivara* were found to be highly diverging. Moreover, all the orthologous sequences were highly conserved in Domain-B—the DNA binding domain of VOZ2 TF; whereas, the orthologous sequence region of Domain-A was considerably non-conserved—particularly from 90 to 105 amino-acid residues (amino-acid positions in the full-length protein sequences) where most of the wild *Oryza* species have inserted a short stretch of amino-acids which is absent in rice (Fig. 3). The high conservation of Domain-B can be understood from the fact that this domain has to bind the *cis*-elements (the binding sequence of which seems to be conserved between Arabidopsis and rice, as mentioned in the earlier section) in the promoters of target genes. Although, the Domain-A is not required for *cis*-element-binding, the nucleotide variations, accumulated in this region of wild rice species, can possibly alter the binding of Domain-B to the promoter elements, which makes *VOZ* genes of wild rice the potential genomic resources possibly for the stress tolerance improvement in rice. Therefore, the orthologous alleles of wild species of rice, particularly the highly divergent alleles from *O. brachyantha*, *O. longistaminata* and *O. nivara*, can prove as potential genomic resources for rice improvement. These three *Oryza* species have been already reported to harbor important genomic resources for the improvement of different biotic and abiotic stress responses (Atwell et al. 2014; Mammadov et al. 2018; Singh et al. 2015).

Conclusion

The VOZ TF family has been extensively studied for its involvement in flowering and abiotic stress signaling pathways only in Arabidopsis, and therefore the potential of this gene family has remained absolutely untapped in the stress signaling and other aspects of growth and development in other plant species including rice. VOZ TFs have been found to regulate the responses to different abiotic stresses in Arabidopsis. This article has therefore made endeavors to logically associate the VOZ TFs of rice with its abiotic stress tolerance. The results from the gene expression study and the promoter analysis of submergence tolerance genes has plausibly suggested a possible connection between *VOZ* genes and abiotic stress

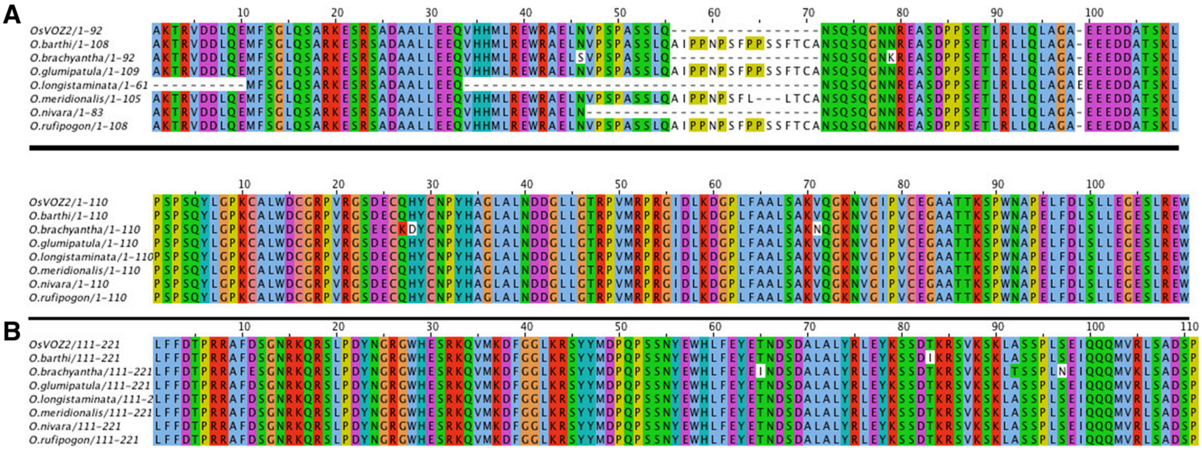

Fig. 3 Multiple sequence alignment of orthologs of Domain-A (**a**) and Domain-B (**b**) of OsVOZ2 from different *Oryza* species. Variations in the Domain-A indicate that it has more genomic resources in the form of nucleotide variations than Domain-B at genomic level. Alignment was generated using Jalview

tolerance of rice. Moreover, the discovery of different allelic forms of *OsVOZs* from wild *Oryza* species has hinted towards the potential of these sequence variants in rice improvement. Overall, this article has generated some exciting leads for the rice researchers to explore the involvement of OsVOZ TFs in rice abiotic stress tolerance and promises some advanced research work in future for improving abiotic stress tolerance of rice.

Compliance with ethical standards

Conflict of interest The authors declare that there is no conflict of interest.

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