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Original Paper

Genome-wide analysis and expression profile of bZIPs transcription factor gene family in Ethiopian lowland bamboo (*Oxytenanthera abyssinica*) in response to osmotic and salt stress

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Abstract

The basic leucine-region zipper (bZIP) transcription factors (TFs) are one of the largest TFs with significant roles in plant biological and developmental processes, and stress tolerance. Despite the important role of bZIPs in plants, genome-wide analysis and expression profiling under abiotic stress remain elusive in *Oxytenanthera abyssinica*. In this study, a total of 162 bZIP *O. abyssinica* TFs having the bZIP DNA binding domain (PF00170) were identified through genome-wide analysis. For the identified bZIPs, functional annotation, phylogenetic relationship and expression under osmotic and salt stress were investigated. The expression profile of the bZIP TFs revealed that the majority were highly responsive to osmotic and salt stress, as 99 of the 162 bZIP TFs were up-regulated. Metabolic pathway analysis revealed that environmental information processing and genetic information processing categories were the only represented pathways that revealed close association of bZIPs TFs with stress response. The study provided valuable information about the expression profile of bZIPs TFs associated with osmotic and salt stress, which could be used as a basis for further studies.

Key words: abiotic stress, bZIP transcription factors, *Oxytenanthera abyssinica*, RNA-Seq.
Abbreviations: bZIP, basic leucine-region zipper; FPKM, fragment per kilobases per million reads; Leu, leucine; RNA-Seq, RNA sequencing; RT-qPCR, real time quantitative PCR; TF, transcription factor.

Introduction

Plant growth and development are hampered by many environmental factors. The sessile nature of plants makes them unable to distance themselves from unfavorable conditions, and survival in harsh conditions requires adaptive mechanisms like synthesis of proteins with different functions (Hu et al. 2013; Llorca et al. 2014). Transcription factors (TFs) consist of one or more sequence-specific DNA binding domains that regulate gene expression through binding to the promoter and/or enhancer regions of target genes. Specific TFs are responsible for the expression of proteins with diverse functions. The basic leucine zipper (bZIP) transcription factor family is one of the largest and most conserved plants TFs. bZIP TFs are 60 to 80 amino acids in length and are comprised of a leucine (Leu) zipper and a basic region. These two parts are both functionally and structurally distinct. The Leu zipper is a less conserved dimerization motif and is comprised of heptad repeats of Leu or other bulky hydrophobic amino acids located nine amino acids towards the C-terminus. This region mediates homo- and/or hetero-dimerization of bZIP proteins. The basic region is composed of about 16 amino acid residues with the highly conserved invariant motif N-x7-R/K-x9 that is responsible for nuclear localization and DNA binding (Ptashne, Gann 1997).

Genes encoding bZIP transcription factor have been identified in many plants, including Arabidopsis (Jakoby et al. 2002), maize (Wei et al. 2012), rice (Nijhawan et al. 2008), sorghum (Wang et al. 2011), cucumber (Baloglu 2014), grapevine (Liu et al. 2014) and barley (Pourabed et al. 2015). Like other prominent TFs, bZIP are involved in various plant physiological and developmental processes as well as biotic/abiotic stress responses. Therefore, bZIP TFs play a significant role in assisting plants to withstand unfavorable environmental conditions (Wang et al. 2011;

Wang et al. 2017).

bZIP TFs have a crucial role as active regulators to various abiotic/biotic stresses like high salinity, osmotic, cold stress and disease resistance, which has been confirmed in many plant species, including maize (Kusano et al. 1995), Arabidopsis (Weltmeier et al. 2009; Yang et al. 2009), barley (Xue et al. 2004), rice (Shimizu et al. 2005; Mukherjee et al. 2006; Xiang et al. 2008), wheat (Kobayashi et al. 2008), *Chlamydomonas reinhardtii* (Ji et al. 2018), and cassava (Li et al.2017). The study of bZIP TFs in evolution of green plants has suggested that their ancestor possessed four bZIP genes functionally involved in oxidative stress, unfolded protein response and light-dependent regulations (Corrêa et al. 2008). Four transcript factors including bZIP were found to have a positive influence in cadmium tolerance in creeping bentgrass (Yuan et al. 2018).

The vital role of bZIP TFs in developmental processes has been demonstrated in cell elongation (Fukazawa et al. 2000), organ and tissue differentiation (Silveira et al. 2007; Shen et al. 2007), somatic embryogenesis (Guan et al. 2007) seed storage protein regulation (Lara et al. 2003), carbon / nitrogen and energy metabolism (Weltmeier et al. 2006; Baena-Gonzalez et al. 2007), unfolded protein response (Liu et al. 2007), and ripening (Hu et al. 2016).

Some of the transcription factors like No Apical Meristem (NAM/NAC) are found only in plants. However, bZIP TFs are found in many eukaryotic genomes including humans. Numerous bZIP TFs have been investigated and characterized in many eukaryotic genomes. A total of 15, 498 bZIP TFs have been identified from various genomes (Jin et al. 2017). The number of identified bZIP TFs ranges from 17 in *Saccharomyces cerevisiae* (Fassler et al. 2002) to 131 in soya (Liao et al. 2008), including 49 in castor bean (Jin et al. 2014), 55 in grapevine (Liu et al. 2014), 56 in human (Vinson et al. 2002), 75 in Arabidopsis (Jakoby et al. 2002), 89 in rice (Nijhawan et al. 2008), 92 in sorghum (Vanitha, Ramachandran 2011), and 125 in maize (Wei et al. 2012).

Genome-wide survey, identification, and characterization of bZIP TFs have been conducted for many plant species. However, no such analysis is available about the genome-wide analysis of bZIPs TFs in *Oxytenanthera abyssinica*. We performed genome-wide identification and characterization of bZIP TFs based on whole transcriptome analysis. bZIP TFs annotation, phylogenetic relationship, and expression under osmotic and salt stress were investigated. This is the first comprehensive study of one of the largest gene families in *O. abyssinica* and it offers helpful information for further research into the function of the bZIP gene family.

Materials and methods

Gene ontology annotation and functional classification

Protein sequences of bZIP genes were loaded into CELLO2GO http://cello.life.nctu.edu.tw/cello2go (Yu et al. 2014) to obtain GO annotation against the Eukaryote database. Genes were also categorized as per the GO biological process, molecular function and cellular component according to CELLO2GO GO functional classification. The metabolic pathway analysis was conducted using the BlastKOALA tool (Kanehisa et al. 2015).

Expression analysis of the bZIP gene family

Using previously developed RNA-Seq data (Adem et al. 2019), expression patterns of *O. abyssinica* bZIP genes in response to osmotic and salt stress were investigated. For expression analysis, the unigene sequence file as a reference gene file, RSEM v1.2.6 (Li, Dewey 2011) was employed to estimate gene and isoform expression levels from the pair-end clean data. Fragment per kilobases per million reads (FPKM) was calculated and employed to quantify the expression abundance of transcripts in each sample. For differential expression analysis, the DESeq2 v1.6.3 (Anders, Huber 2012) R program, a model based on the negative binomial distribution, was used for determining differential expression from digital gene expression data. To control the false discovery rate, the *P*-value was adjusted by the Benjamini and Yekutieli (2001) approach. Genes with $|\log2 \text{ Fold\_change}| > 1$ and adjusted $P\text{-value} < 0.05$ were treated as differentially expressed.

Phylogenetic analysis

Phylogenetic analysis was performed on 162 bZIP proteins. The ClustalX program was used to perform multiple sequences alignment of protein sequences. Maximum parsimony which is considered a more reliable method was used to construct an un-rooted phylogenetic tree by using MEGA X (Kumar et al. 2018).Maximum parsimony tree was obtained using the Subtree-Pruning-Regrafting (SPR) algorithm.

Results

Identification of the bZIP TFs gene family in O. abyssinica *genome*

Previously, we conducted osmotic and salt stress-induced genome-wide transcriptome analysis of *O. abyssinica* (Adem et al. 2019). As a result of the experiment 406 181 *de novo* assembled unigenes of *O. abyssinica* were obtained and served as a source for the identification of bZIP unigenes used in this study. To identify bZIP genes, deduced protein sequences of *O. abyssinica* were submitted to the plant transcription factor database, http://itak.feilab.net/cgi-bin/itak/online_itak.cgi (Zheng et al. 2016), resulting in the identification of 182 putative bZIP proteins. To confirm the presence of the conserved bZIP domain (PF00170), the resulting protein sequences from the iTAK database were further subjected to Pfam analysis (https://pfam.xfam.

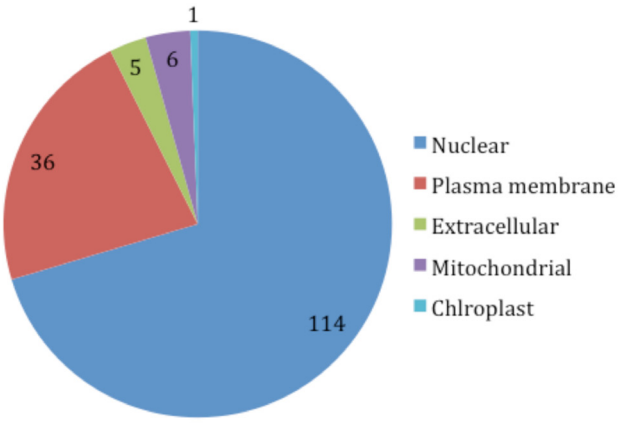

Fig. 1. Sub-cellular localization of 162 unigenes of bZIP transcription factor family.

org/), and then 162 proteins were confirmed to be under the bZIP binding domain.

The *O. abyssinica* bZIP (*OabZIP*) genes encoded proteins varied in size and sequences. Length of proteins of OabZIPs ranged from 77 to 1840 amino acids. The molecular weights of OabZIPs were determined using the ExPASy database (http://expasy.org/). The molecular weight of OabZIPs proteins ranged from 75.07 kD for glycine to 204.23 kD for tryptophan.

Gene ontology and KEGG analysis

Using CELLO sub-cellular localization predictor analysis, the bZIP unigenes were classified into five cellular components. The majority of the bZIP unigenes (114) were found in the nuclear compartment, followed by 36 localized to the plasma membrane. The remaining subcellular components were associated with a small number of bZIPs (Fig. 1).

Gene ontology enables us to identify genes involved in biological processes, those enabling molecular function and those that are cellular components. CELLO2GO gene ontology analysis showed that out of 162 unigenes 140 (86.41%) were cellular components, 141 (87.03%) had molecular function, and 137 (84.56%) were involved in biological processes.

Organelle, intracellular, cell, and nucleus were represented by a similar number of unigenes (Fig. 2). Ontologies with a significant role in molecular function included DNA binding and nucleic acid binding transcription factor activity. When compared to cellular components (nine ontologies) and molecular function (six ontologies), several ontologies with diverse functions were involved in biological process (16 ontologies). The most represented ontologies in the biological processes were cellular nitrogen, biosynthetic processes and signal transduction. Most importantly, about 16 unigenes were

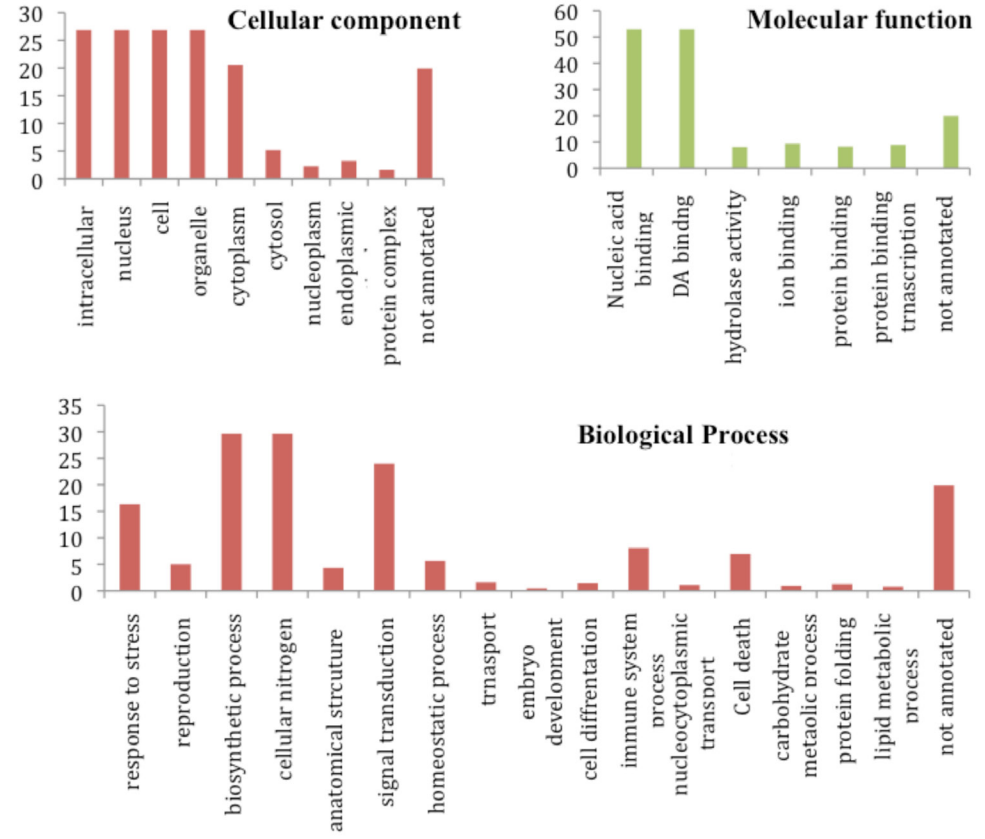

Fig. 2. Gene ontology classification of bZIP transcript factors.

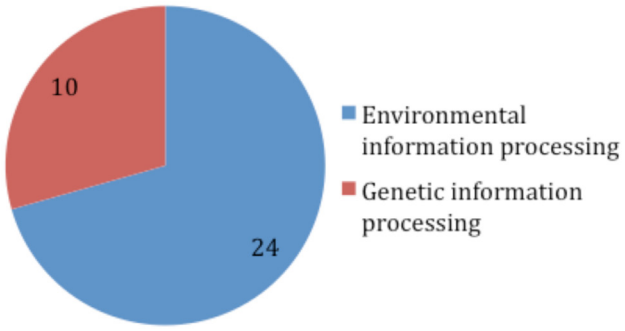

Fig. 3. KEGG analysis using the Blast KOALA tool.

involved in response to stress.

As shown in Fig. 3, among the162 unigenes of bZIPs, only 34 (21%) were annotated. Metabolic pathway analysis revealed that environmental information processing and genetic information processing categories were the only represented pathways. This indicates that the bZIPs transcript factor family is actively involved in stress regulation. Although bZIPs transcript factor activity is limited to two pathway categories, these two categories are highly associated with stress response and regulation, which implies that bZIPs might be highly associated with stress response.

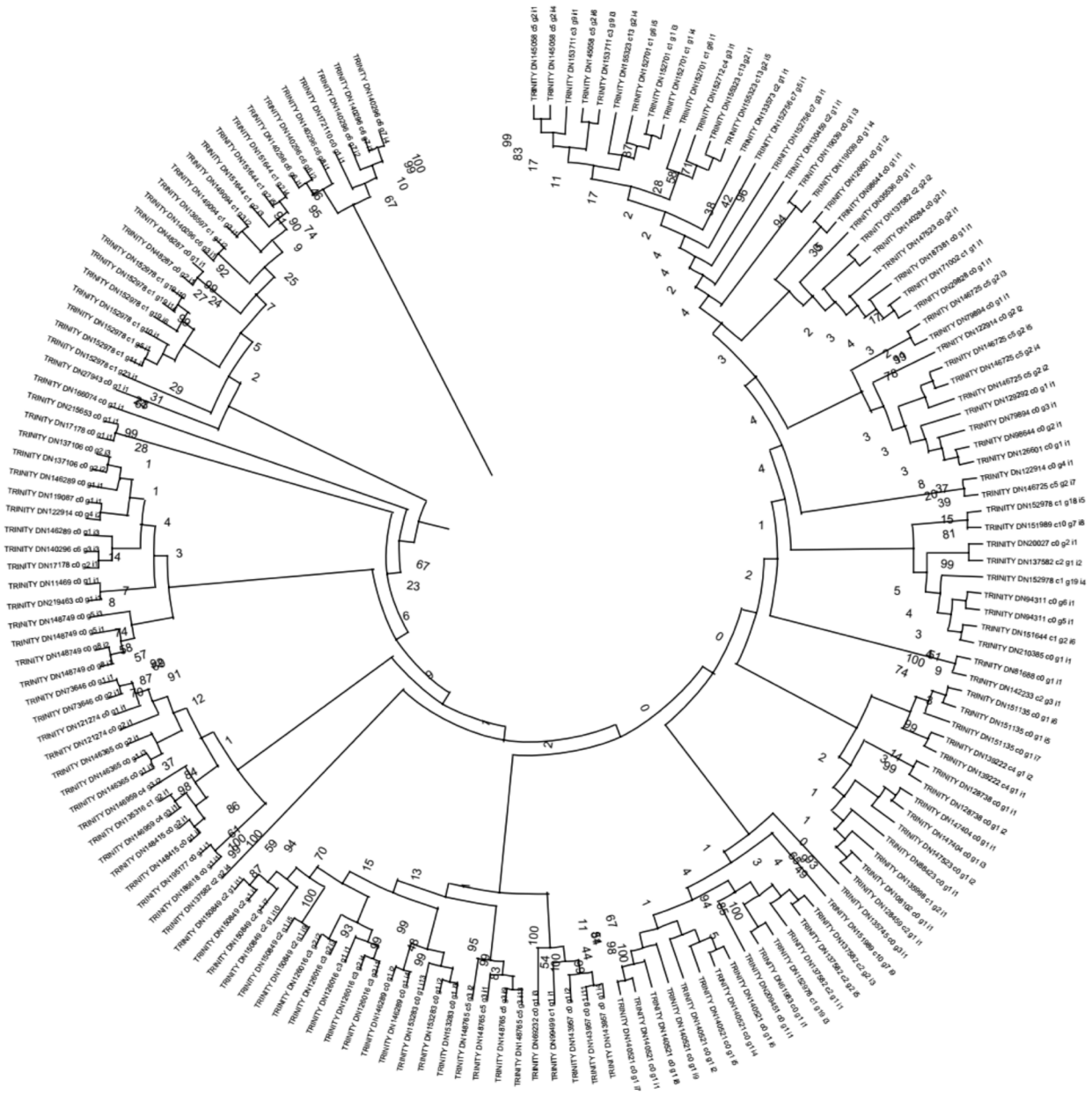

Fig. 4. Phylogenetic tree of 162 aligned bZIP subfamily proteins in *O. abyssinica*. The phylogenetic tree was constructed using MEGA X, employing maximum parsimony method and bootstrap values from 1000 replicates. Numbers on each branch represent the percentages of bootstrap.

Table 3. DEGs and functional analysis of selected bZIP transcript factors

Gene ID	|log2FoldChange|	Regulation	GO_ID	KO_Definition
TRINITY_DN145821_c6_g2_i2	3.070293243	Up	-	transcription factor TGA
TRINITY_DN150849_c2_g1_i9	2.332884004	Up	GO:0003677	plant G-box-binding factor
TRINITY_DN140653_c0_g1_i1	2.9684483	Up	-	ABA responsive
TRINITY_DN145058_c5_g2_i4	8.1826365	Up	GO:0006355	ABA responsive element binding -factor
TRINITY_DN152701_c1_g1_i1	7.4411664	Up	GO:0003700	ABA responsive element binding factor
TRINITY_DN153711_c3_g9_i3	7.4033188	Up	GO:0003700	ABA responsive element binding factor
TRINITY_DN150849_c2_g1_i10	6.7880783	Up	GO:0003677	plant G-box-binding factor
TRINITY_DN145821_c6_g2_i4	1.9251616	Up	-	transcription factor TGA
TRINITY_DN145821_c6_g2_i3	3.8560311	Up	GO:0005634	transcription factor TGA
TRINITY_DN143358_c12_g3_i3	3.26747	Up	GO:0005634	transcription factor HY5
TRINITY_DN153556_c2_g1_i6	1.2501836	Up	GO:0006355	plant G-box-binding factor
TRINITY_DN143358_c12_g3_i5	2.0792177	Up	GO:0005634	transcription factor HY5
TRINITY_DN126016_c3_g2_i1	3.15973622	Up	GO:0006355	salt-stress inducible bZIP protein

Expression analysis of bZIP genes under osmotic and salt stresses

Among the identified 162 expressed genes of bZIPs, 149 were differentially expressed genes (DEGs), 99 were up-regulated, 50 were down-regulated and 13 genes were not differentially expressed i.e. their level of expression was not affected by osmotic nor salt. Among the differentially expressed genes, 49 genes were functionally annotated while the functions of the remaining genes were not identified. The most represented functional annotations of bZIPs in response to osmotic and salt stress in *O. abyssinica* were salt-stress inducible bZIP protein and abscisic acid-insensitive protein (Table 1).

Phylogenetic analysis

Phylogenetic analysis was conducted to understand the evolutionary implication of bZIPs in *O. abyssinica*. A phylogenetic tree was constructed for 162 OabZIP proteins by employing the maximum parsimony method and bootstrap values from 1000 replicates. The phylogenetic analysis grouped bZIP proteins into 14 distinct groups: clusters I to XIV. The number of proteins in each cluster significantly varied: cluster III and cluster VII each with one protein and cluster XIV with 28 proteins (Fig. 4).

The phylogenetic tree was constructed using MEGA X, employing the maximum parsimony method and bootstrap values from 1000 replicates. The numbers on each branch represent the percentages of bootstrap.

Discussion

To date, there is no data about the molecular and genetics properties of *O. abyssinica*, except for publication of the whole genome transcriptome by the same authors (Adem et al. 2019). The lack of reference genomic data has significantly hampered research on the species. Transcriptome sequencing using the Illumina Seq platform enabled to create relatively comprehensive sequence data that could be utilized for further research, including gene cloning, expression analysis, and EST-SSR markers development.

Transcript factors as proteins regulating gene expression have received special attention from researchers engaged in plant whole-genomic sequencing and transcriptome sequencing. Osmotic and high salinity are key factors causing plant stress. Among the different transcription factors, previous studies have shown that bZIP transcription factors are highly associated to plant stress response (Wang et al. 2011; Wang et al. 2017). Molecular responses to abiotic stress include signal transduction, gene expression and ultimately metabolic changes in the plant thus confering stress tolerance (Agarwal et al. 2006).

We found that 15.44% of genes involved in the biological process, 22.97% in molecular function and 13.59% in the cellular component were not annotated in the GO database. This implies that there are no homologous sequences for the un-annotated genes in the GO database (Berardini et al. 2004).

This study identified 162 bZIPs under osmotic and salt stress transcriptome profiling, while other abiotic stress-induced transcriptome analysis identified 64 in *Syntrichia caninervis* (Gao et al. 2014), 17 in *Chlamydomonas reinhardtii* (Ji et al. 2018), 50 in *Fragaria vesca* (Wang et al. 2017), 64 in *Cucumis sativus* (Baloglu et al. 2014) and 200 in hexaploid hulless oat (Wu et al. 2017). One of the possible reasons for such differences might be the type and concentration of treatment and ploidy level variation, as oat generated more bZIPs.

Among the annotated bZIP genes of *O. abyssinica,* gene ontology analysis revealed a biological role of 15 genes in stress response. Metabolic pathway analysis of *O. abyssinica* bZIP genes generated only two pathway categories, environmental information processing and genetic information processing, which likely have a strong association with plant response to abiotic stress and adaptation. This indicates that bZIPs genes are active

participants in plant stress responses. Transgenic studies focusing on the role of bZIPs in plant stress responses have confirmed this. The significant role of plant bZIPs transcription factors in abiotic stress tolerances and adaptation has been confirmed in transgenic Arabidopsis and rice. *ABF2* confers osmotic tolerance in Arabidopsis (Kim et al. 2004), *GmbZIP78, GmbZIP44*, and *GmbZIP62* enable salinity tolerance in Arabidopsis (Liao et al. 2008a), and *OsABI5* promotes salt tolerance in rice (Zou et al. 2008). A novel *MHTGA2* bZIP gene from *Malus hupehensis* increase salt tolerances in transgenic tobacco (Zhang et al. 2012). Rice group A bZIP proteins, such as OsbZIP23 and OsbZIP46, also play crucial roles in ABA signaling and act as positive regulators under osmotic stress (Tang et al. 2012). Over-expression of exogenous and endogenous AREB/ABF orthologs in cotton substantially increase osmotic tolerance through stomatal regulation (Kerr et al. 2017). The cis-elements and expression pattern analysis of *SibZIP* genes indicates that they are widely involved in responses to abiotic stresses (Wang et al. 2018).

Differential expression analysis also revealed that, among the total 162 identified genes of bZIPs, 149 are differentially expressed (99 up-regulated while 50 are down-regulated). As much as 61% of the identified genes were observed to be stress-responsive, since their expression increased due to osmotic and salt stress. This supports the hypothesis that the bZIP gene family is highly linked to stress response. Most importantly, bZIPs have the highest number of both differentially expressed as well as the functionally annotated number of genes than any other explored gene families of *O. abyssinica* (Adem et al. 2019). As plant stress tolerances are regulated by a combined effect of many genes, further studies are needed to identify the complex regulatory networks of the bZIP genes in *O. abyssinica*. Phylogenetic analysis revealed that bZIPs of *O. abyssinica* have more cluster groups, compared to six in cucumber (Baloglu et al. 2014), seven in sorghum (Wang et al. 2011), and 10 in Arabidopsis (Jakoby et al. 2002). Hexaploidy and continuous flowering throughout the life of the plant might explain the higher number of clusters.

Conclusions

In conclusion, the first genome-wide-scale analysis of bZIP transcription factors in *O. abyssinica* was conducted and identified a total of 162 OabZIP proteins. The study has presented valuable information about role of the bZIP gene family in *O. abyssinica*. Both gene ontology and metabolic pathway analysis identified the stress responsiveness of bZIP genes, as the level of expression of 99 genes was increased in response to osmotic and salt stress. Those bZIP genes with the highest level of expression could serve as the foundation for further functional characterization, elucidating their specific regulatory mechanisms and eventually could be applied for genetic improvement programmes aiming to promote plant growth and development in the face of abiotic stress.

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