An in silico comparative genomic report on transcription factors in three Arabidopsis species

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Abstract

Transcription factors (TF) are the elements, which regulate gene expression. Regulatory function of TFs play an important role in plant biological processes and mechanisms. They may interconnect with other transcription factors or functional genes to modulate their expression in response to an internal/external factor like life cycle stage, growth, development and stress. Arabidopsis is the well-known and the most used model organism. Transcription factors of three Arabidopsis species including A. halleri, A. lyrata and A. thaliana, were compared. basic/helix-loop-helix (bHLH) with 220 TFs was the most abundant family among three Arabidopsis species while MYB and MYB-related families considering as a whole group were more than bHLH with 308 TFs. No STERILE APETALA (SAP) TF homolog was found for A.halleri. The common transcription factors among three species were 4,172 grouped in 1,212 clusters. The species-specific clustered TFs were 12, 30 and 58 for A. halleri, A. lyrata and A. thaliana respectively. Eight hundred ninety two singletons were not clustered and are unique among three species. For clustered TF belonging to each species, GO terms and SwissProt hits showed that A. halleri has two species-specific TFs involved in heavy metal response including Zinc finger protein AZF2 and two-component response regulator ARR11 while for A. lyrata specific TFs are involved in stress response and plant development. A. thaliana specific clustered TFs work on plant flower development and acclimation.

Keywords: Arabidopsis, species, bHLH, ZF2, ARR11.

Palabras clave: Arabidopsis, especies, bHLH, ZF2, ARR11.
Introduction

Transcription factors are regulators, which modulate genes whose expression is activated or suppressed regarding to time, space and condition. They possess normally a DNA-binding region, an oligomerization site, a transcription-regulation domain, and a nuclear localization signal. However, there are exceptions for this typical structure (Liu et al., 1999). The DNA-binding regions are normally found in cis-regulatory elements; i.e. specific sequences in the promoters of their target genes (Franco-Zorrilla et al., 2014). They can switch on and off genes and link genes in downstream and upstream of a biological pathway acting to regulate desired reactions. In *A. thaliana*, 6-10% of all genes encode TFs while in other organism is less as seen only 3% in Drosophila melanogaster and 5% in humans. In *A. lyrata* and *A. halleri* TFs form around 5-6% of all genes. The importance of TFs has been disclosed via studying mutants affected in spatiotemporal transcription regulation (Pireyre and Burow, 2015). As plants are sessile, this relatively high amount of TFs may allow them to react to their changing environment and adapt to undesirable condition rapidly via regulation of gene expression, RNA transcription and protein translation. The TF involvement in various biological processes and mechanisms in plants and their regulatory function make it mandatory to study them to disclose their interaction with other TFs and genes.

There are various plant TF databases. Plant TFs are distributed in 58 families according to PlantTFDB (Jin et al., 2017) (http://planttfdb.cbi.pku.edu.cn/) or 63 families according to PnTFDB (Pérez-Rodriguez et al., 2010) (http://pntfdb.bio.uni-potsdam.de/v3.0/). In other database they are listed in 70 groups (http://itak.feilab.net/) (Zheng et al., 2016). The basic helix-loop-helix (bHLH) family is the biggest and SPOROCYTELESS/NOZZLE (NZZ/SPL) is the smallest TF in terms of the number of family members. *Arabidopsis* is the well-known and mostly ever used plant model, particularly *A. thaliana*. *A. thaliana* has highly contributed in providing the information and data for almost all of genomes even human and animals, as it is the first ever-published living organism and the most annotated among plants. Its genome has restructured biology in terms of Omics, mainly genomics and transcriptomics and revealed many mechanisms those had not previously been discovered. *Arabidopsis* has 11 accepted species names (http://www.theplantlist.org/browse/A/Brassicaceae/Arabidopsis/) with different chromosome number as five (*A. thaliana*), eight (*A. lyrata* and *A. halleri*), thirteen (*A. suecica*) and sixteen (*A. arenosa*). The chromosome number has changed during evolutionary events by duplication, deletion and insertion among the different species starting around 13 MYA from a common ancestor (Beilstein et al., 2010). It seems that *A. thaliana* is separated from the other species of *Arabidopsis* and each species has acquired somewhat characters differing from the others like heavy metal tolerance adaptation seen in *A. halleri* (Bomblies and Weigel, 2010). Among *Arabidopsis* species, only three genomes including *A. thaliana*, *A. lyrata* and *A. halleri* have been sequenced.

As the most contributing organism, there is a need for more details on their structure and genomic information on one of the most important gene groups, namely TFs. To our knowledge, no comparative report is available on *Arabidopsis* genus detailing TFs among three genome-published species. In this article, we compare the TF datasets of three genome-published *Arabidopsis* species to disclose similarities and differences among them. The common and differed TFs among three species are discussed.

Materials and methods

The TF protein sequences of three *Arabidopsis* species including *A. halleri*, *A. lyrata* and *A. thaliana* were downloaded from PlantTFDB (Jin et al., 2017) website (http://planttfdb.cbi.pku.edu.cn/), as it includes both TF number and loci while the other available databases do not. The OrthoVenn was used to compare and cluster three TF datasets. The pvalue ≤ 1e-03 was used to form the clusters related to GO terms. This program is a web platform that cluster orthologous gene datasets and generates Venn diagram and relevant annotation data outputting SwissProt hit and GO terms (Wang et al., 2015). MEME version 4.8.1 was employed for finding protein motif sequences (Bailey and Elkan, 1994) (http://meme-suite.org/). Blast+ were used to find homologs (Camacho et al., 2009).

Results and discussion

The info about TFs of the three species have been disclosed in terms of quantity and loci (Table 1) and the number of each TF family (Table 2). *A. thaliana* possesses more TFs than the other two species although it has a smaller genome size. Interestingly, *A. lyrata* has most TF loci because of its bigger genome while *A. thaliana* with the smallest genome size stands in the second place. Considering the same ancestor from whom *Arabidopsis* species diverged, the speciation events such as deletion and duplication have differed for *A. thaliana* whose loci possess various TFs from *A. lyrata* that each locus present one TF. Further study for each TF family related to loci is required to reveal how TFs are distributed on loci in *Arabidopsis* genus.
Three smallest families were LFY, NZZ/SPL and SAP. STERILE APETALA (SAP) has no TF in A. halleri while LFY and NZZ/SPL possess only one TF for each species. The same TF number for these three families were seen in other plant TF databases including iTAK and PlnTFDB (Pérez-Rodríguez et al., 2010; Zheng et al., 2016). SAP plays a role in female reproductive organs; inflorescence, flower and ovule development. It is required for flower recognition in a manner similar to APETALA1 and modulates processes and gene expression related to organ size by targeting the KIX-PPD repressor complex for degradation (Byzova et al., 1999). SAP functions in development of flower and its mutants have shown severe aberrations in such developmental process related to inflorescence, ovule and flower. SAP and APETALA2 (AP2) are involved in the initiation of female gametophyte development (Byzova et al., 1999). In addition, it can interact with AGAMOUS to maintain floral identity acting in a manner similar to APETALA1.

The plant-specific LEAFY (LFY) protein is also involved in switching vegetative stage to reproductive stage. It controls the process of flower production and development and is known as a meristem identity gene (William et al., 2004). It also interact with AGAMOUS and APETALA as floral homeotic genes in flower morphogenesis like what seen in SAP. Another rare TF family is the “floral organ-building” gene SPOROCYTELESS/NOZZLE (SPL/NZZ). It also plays a central role in male flower development regulating anther cell differentiation (Liu et al., 2009). Interestingly, it interact with AGAMOUS and AP2 involving in stamen identity. These TFs may work as a network sharing common interacting among various TFs in flower development. However, they exist in the least number in Arabidopsis and this makes them interesting to be studied further.

As seen generally in plants and reported in PlantTFDB, bHLH family with totally 522 TFs is the most abundant family in three Arabidopsis species (Table 2). Previously the MYB

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**Table 1. TF loci and gene numbers of three Arabidopsis species. The information compiled from PlantTFDB.**

| Species     | TFs | Loci |
|-------------|-----|------|
| A. thaliana | 2,296 | 1,717 |
| A. lyrata  | 1,759 | 1,759 |
| A. halleri | 1,586 | 1,446 |

**Table 2. TF families and their member number of three Arabidopsis species. The info compiled from PlantTFDB.**

| TF Family | A. thaliana | A. lyrata | A. halleri |
|-----------|-------------|-----------|------------|
| LBD       | 130         | 33        | 47         |
| LFY       | 3           | 1         | 1          |
| LSD       | 20          | 5         | 3          |
| MIKC MADS | 154         | 39        | 39         |
| M-type MADS | 161        | 51        | 40         |
| MYB       | 441         | 124       | 149        |
| MYB related | 233        | 72        | 64         |
| NAC       | 359         | 99        | 122        |
| NF-X1     | 8           | 3         | 3          |
| NF-YA     | 47          | 14        | 12         |
| NF-YB     | 58          | 15        | 16         |
| NF-YC     | 47          | 10        | 16         |
| Nn-like   | 53          | 20        | 16         |
| NZZ/SPL   | 3           | 1         | 1          |
| RAV       | 16          | 3         | 6          |
| S1Fa-like | 8           | 1         | 3          |
| SAP       | 2           | 0         | 1          |
| SBP       | 65          | 20        | 15         |
| SRS       | 35          | 9         | 10         |
| STAT      | 9           | 2         | 3          |
| TALE      | 75          | 21        | 21         |
| TCP       | 75          | 17        | 25         |
| Trihelix  | 88          | 24        | 30         |
| VOZ       | 9           | 3         | 3          |
| Whirly    | 11          | 3         | 4          |
| WOX       | 48          | 14        | 16         |
| WRKY      | 229         | 60        | 79         |
| YABBY     | 21          | 7         | 6          |
| ZF-HD     | 44          | 9         | 17         |

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Ciencia y Tecnología. 2018. 11(1): 1-9
TF family has been reported as the biggest TF family among plants and particularly Arabidopsis (Toledo-Ortiz et al., 2003). Reported by Pireyre and Burow, a large proportion of the TFs in Arabidopsis were MYB with 339 and bHLH with 162 members (Pireyre and Burow, 2015). However, considering two MYB and MYB-like families together with 674 TFs, they are bigger than bHLH family. These two TF families forms different MYB/bHLH complexes regulate distinct cellular processes such as cell wall synthesis, cell death, circadian clock, responses to abiotic and biotic stress, hormone signaling, and the biosynthesis of specialized metabolites (Lindemose et al., 2013; Pireyre and Burow, 2015; Seo and Mas, 2014; Stracke et al., 2007, 2001; Vailleau et al., 2002). In addition, bHLHs and MYB can physically interact with each other to success their function. In total 220 bHLH (Table 3) were common among three species while MYB and its related TFs were 308 (Supplementary File). bHLH35 and bHLH115 in A. thaliana and A. lyrata respectively were the species-specific bHLHs. bHLH115 is found among the three but they might be other isoforms found in A. lyrata as specific TFs. No specie-specific bHLH was found for A. halleri.

Table 3. The clustered bHLH genes among three Arabidopsis.

| ID        | # Proteins | Swiss-Prot Hit                  | ID        | # Proteins | Swiss-Prot Hit |
|-----------|------------|--------------------------------|-----------|------------|----------------|
| cluster15 | 7          | bHLH69                         | cluster704| 3          | bHLH115       |
| cluster47 | 6          | bHLH {ECO:0000313|EMBL:CAE09167.1} | cluster756| 3          | bHLH136       |
| cluster86 | 5          | bHLH76                         | cluster766| 3          | bHLH28        |
| cluster98 | 5          | bHLH13                         | cluster776| 3          | bHLH81        |
| cluster116| 4          | bHLH61                         | cluster799| 3          | bHLH30        |
| cluster152| 4          | bHLH23                         | cluster827| 3          | bHLH101       |
| cluster169| 4          | bHLH100                        | cluster831| 3          | bHLH18        |
| cluster172| 4          | bHLH112                        | cluster842| 3          | bHLH14        |
| cluster207| 4          | bHLH17                         | cluster857| 3          | bHLH62        |
| cluster213| 4          | bHLH155                        | cluster871| 3          | bHLH10        |
| cluster222| 4          | bHLH115 {ECO:0000313|EMBL:AEE32619.1} | cluster882| 3          | bHLH131       |
| cluster224| 4          | bHLH104                        | cluster887| 3          | bHLH84        |
| cluster235| 4          | bHLH137                        | cluster913| 3          | bHLH19        |
| cluster243| 4          | bHLH27                         | cluster932| 3          | bHLH27        |
| cluster263| 4          | bHLH129 {ECO:0000313|EMBL:AEC10214.1} | cluster943| 3          | bHLH131       |
| cluster266| 4          | bHLH148                        | cluster952| 3          | bHLH81        |
| cluster268| 4          | bHLH109                        | cluster963| 3          | bHLH27        |
| cluster298| 4          | bHLH18                         | cluster1005| 3         | bHLH10        |
| cluster304| 4          | bHLH89                         | cluster1016| 3         | bHLH101       |
| cluster312| 4          | bHLH144                        | cluster1042| 3         | bHLH13        |
| cluster318| 4          | bHLH119                        | cluster1054| 3         | bHLH23        |
| cluster556| 3          | bHLH114                        | cluster1062| 3         | bHLH137       |
| cluster559| 3          | bHLH85                         | cluster1065| 3         | bHLH119       |
| cluster616| 3          | bHLH30                         | cluster1092| 3         | bHLH23        |
| cluster617| 3          | bHLH92                         | cluster1093| 3         | bHLH60        |
| cluster618| 3          | bHLH10                         | cluster1097| 3         | bHLH118       |
| cluster641| 3          | bHLH131                        | cluster1098| 3         | bHLH80        |
| cluster648| 3          | bHLH139                        | cluster1100| 3         | bHLH82        |
| cluster670| 3          | bHLH28                         | cluster1114| 3         | Putative bHLH086 |
| cluster684| 3          | bHLH30                         | cluster1199| 3         | bHLH179       |
| cluster690| 3          | bHLH30                         | cluster1204| 3         | bHLH117       |
| cluster1277| 3        | Putative bHLH086               | cluster1273| 3         | bHLH137       |

All TFs were 5,641 for three species and classified in 4,503 clusters (Table 4, Supplementary File). Singletons those are species unique genes and not clustered were 445 in total. 892 single-copy gene clusters including 2,676 TFs were generated, i.e. the clusters containing one TF from one species summing 3 TFs. A. thaliana showed most numbers of TFs and subsequently clusters and singletons followed by A. lyrata and A. halleri (Table 4). This might be due to well assembled genome and information availability on A. thaliana although it has less chromosome number and its variation is less than other species (Hu et al., 2011). However, the number of genes and GO distribution is well similarly distributed among the species.
As shown in Venn diagram (Figure 1) and Table 5, there were 1,212 clusters containing 4,172 genes (74%) those are common among three species. Four hundred eleven clusters containing 924 genes (16.38%) were pairwise interspecific TFs, i.e. common between two species. Common interspecific TFs between A. thaliana and A. lyrata are more than those of A. halleri and A. lyrata. This more similarity between A. thaliana and A. lyrata suggest that these species might be closer to each other than A. halleri in terms of TF families. Considering singletons and species-specific clustered TFs, A. thaliana showed more species-specific TFs as 2.53% of all its TFs while for A. lyrata and A. halleri it was 1.7 and 0.75% respectively. However, further comparative analyses are required to study each TF family to reveal the speciation and evolutionary relation between three Arabidopsis species.

### Table 4. The proteins, clusters and singletons for three Arabidopsis species.

| Species          | TF Proteins | Clusters | Singletons |
|------------------|-------------|----------|------------|
| A. halleri       | 1586        | 1350     | 102        |
| A. lyrata        | 1759        | 1556     | 117        |
| A. thaliana      | 2296        | 1597     | 226        |
| Total            | 5641        | 4503     | 445        |

### Table 5. The number of TF clusters and genes among three Arabidopsis

| Comparison         | No. of cluster | No. of gene |
|--------------------|----------------|-------------|
| Three species      | 1,212          | 4,172       |
| A. halleri vs A. lyrata | 54             | 111         |
| A. halleri vs A. thaliana | 79             | 197         |
| A. lyrata vs A. thaliana | 278            | 616         |
| A. halleri         | 5              | 12          |
| A. lyrata          | 12             | 30          |
| A. thaliana        | 28             | 58          |
Homeobox-leucine zipper protein HAT22/ATHB-15 is the first cluster with most proteins containing eighteen TFs distributed among three species with eight in A. halleri, seven in A. lyrata and nine in A. thaliana (Supplementary File). It is unique to plants and belongs to HD-Zip class II that has nine members in Arabidopsis (Ariel et al., 2007) or class III (Prigge et al., 2005). The TFs of the family are involved in light response, shade avoidance, auxin signaling, cellular redox status perception (Elhiti and Stasolla, 2009), lateral organ formation, formation or maintenance of vascular development in inflorescence stems (Prigge et al., 2005; Turchi et al., 2015). Its more highly conserved homeodomain motif is shown in Figure 2. It contains 41 sites from which 33 are constant in all three species. 5 sites show two alternatives for the site. Only 3 sites show substitution of 3 amino acids. Its regular expression is CPILSNIEPKQIKVWFQNRRCREKQRKEA[SAR][ATS][AT][VT][AV][NR][KL][TS]A.

Four hundred forty five singletons were found those were not classified into clusters (Table 4, Supplementary File). These genes will be analyzed in a further study. The specific clustered TFs of each species were subject to analyze using their GO and the SwissProt hit provided for each cluster. GO terms related to transcription were not considered and only those with unique functionality were kept and mined. Thus, the specific TFs of each species were shortlisted having unique SwissProt and GO terms. As there were similar TFs those might belong to the subfamilies or isoforms of TFs, we limited the unique TFs those particularly found in each species. A. halleri species-specific TFs were BEL1-like homeodomain protein 2, zinc finger protein AZF2 and two-component response regulator ARR11 (Supplementary File). BEL1-like homeodomain protein 2 under GO:0009965 “leaf morphogenesis” contributes in leaf shape by repressing growth in specific subdomains of the leaf. It is a negative regulator of knox homeobox gene KNAT1/BP expression that functions in shoot apical meristem (SAM) and carpel development (Scofield et al., 2008). Zinc finger protein AZF2 as a specific TF in A. halleri is classified under GO:0042538 hyperosmotic salinity response, GO:0009737 response to abscisic acid GO:0010200 response to chitin and GO:0009414 response to water deprivation. Intriguingly, it shows 80% similarity to ZAT6 that positively regulate cadmium tolerance (Chen et al., 2016). Taking into account this high similarity between ZAT6 and ZF2, it may be involved in heavy metal tolerance as well as in tolerance to other abiotic stresses such as drought, salinity and cold (Kodaira et al., 2011). Two-component response regulator ARR11 has been identified as DNA motif AGAT(T/C) containing TF that play role in cytokinin related processes (D’Agostino et al., 2000). The extended DNA motif (AAGAT[T/C]TT) has been reported as well (Raines et al., 2016). Interestingly, cytokinin can enhance
An in silico comparative genomic report on transcription factors of three Arabidopsis species

plant tolerance to heavy metals and in response to heavy metal (Gangwar et al., 2010). This TF is involved in His-to-Asp phosphorelay signal transduction with the ability to acquire a phosphoryl group from a histidine-containing phosphotransfer intermediate (AHP) improving cytokinin related process (Imamura et al., 2003). On the other hand, RR in bacteria regulate heavy metal response and expression of the Cu(I)/Ag(I) efflux system to extrude them (Fung et al., 2016). There might exist a similar process of responding to heavy metals and resisting them by interaction between cytokinin and two-component response regulator ARR family in A. halleri as it is a metal hyperaccumulator and pseudometalphyte (Sarret et al., 2009) and can tolerate excess of heavy metals. These two TFs might be involved in A. halleri resistance to heavy metals. The 4 genes of these two TF clusters are Araha.3286s0004.2.p and Araha.3286s0004.4.p belonging to two-component response regulator ARR11 and Araha.9992s0007.1.p and Araha.9992s0008.1.p belonging to Zinc finger protein AZF2. A. lyrata species-specific TFs (Supplementary File) were heat shock protein 90-2 functioning in ATPase activity, defense response to bacterium and protein folding; DnaJ protein homolog involved in protein folding; heat stress transcription factor A-4a, ethylene-responsive transcription factor ERF026 and ERF043 those participate in response to chitin and heat. The other A. lyrata specific TFs were scarecrow-like protein 23 engaging in leaf development and nuclear transcription factor Y subunit B-9 involved in positive regulation of fatty acid biosynthetic process. These TFs function mostly in different stress responses like heat for ERF026 and ERF043 and are as known stress responsive TF and development processes. For A. thaliana, according to their GO, mainly they are involved in plant development as flower development, negative regulation of vernalization response, double fertilization forming a zygote and endosperm and regulation of photoperiodism, for Agamous-like, MADS-box, bZIP, MADS affecting flowering5 respectively. In addition, MYB48 and dehydration-responsive element-binding protein 1B function in response to salicylic acid and cold acclimation. Zinc finger CCCH domain-containing protein 24 has RNA methyltransferase activity (Supplementary File). These specific TFs of A. thaliana participate in develop processes and stress responses

Conclusions

The importance of TFs make their study necessary in order to reveal how gene expression and function change in response to internal and external factors. Arabidopsis as the well-known model has revealed the function of TFs but it lacks more details of TF among its three genome-published species. This study was performed to compare TFs of these three Arabidopsis species in silico. Three Arabidopsis species showed 90.34% common TFs in all three or at least two species. There were 545 species-specific TFs for A. halleri, A. lyrata, and A. thaliana. A. halleri has a known metallophytic character and two specific TFs of this species are proposed to be involved in response to heavy metals, namely AZF2 and two-component response regulator ARR11. Our results revealed comparatively similarities and differences in genomic level among three Arabidopsis TF families and species-specific TFs those can be used in subsequent studies of this plant model to disclose more details on biological processes like that of heavy metal, stress response and plant development. However, as other TF databases are available, another study will be executed to disclose more details on the TFs of Arabidopsis genus.

The Supplementary File is accessible from https://doi.org/10.13140/RG.2.2.33662.08008.

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