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Genome-wide analysis of the AP2/ERF gene family in *Populus trichocarpa*

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ABSTRACT

Populus is a model system for investigating the wood development, crown formation, and disease resistance in perennial plants. AP2/ERF is a large family of transcription factors in plant, encoding transcriptional regulators with a variety of functions involved in the developmental and physiological processes. Here, starting from database of *Populus* genome, we identified 200 AP2/ERF genes by *in silico* cloning method using the AP2/ERF conserved domain amino acid sequence of *Arabidopsis thaliana* as probe. Based on the number of AP2/ERF domains and the function of the genes, those AP2/ERF genes from *Populus* were classified into four subfamilies named the AP2, DREB, ERF, RAV, and a soloist. Among these genes, the number genes of total AP2/ERF family genes, DREB subfamily, and ERF subfamily from *Populus trichocarpa* were about 1.4–1.6-fold than those from *A. thaliana*. The rates were very similar for the putative homologs between *Populus* and *Arabidopsis*.

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The genus *Populus*, such as poplar, aspen, and cottonwoods, all of which are found in the Northern hemisphere, makes it a valuable forest resource and an important ecological species [1,2]. *Populus* have been used all over the world to produce a large variety of paper-making and timber products. It is an indispensable component of paper, plywood, and many other wood products. This wood species is also a suitable model for plant biology, such as using as a model to study wood formation [3]. The advantages of using *Populus* as a model species were its rapid growth process, simple propagation method, and easy genetic transformation.

Plant growth and productivity are greatly affected by environmental stresses such as drought, high salinity, and low temperature, which have an adverse effect on the growth of plants and the productivity of crops. Expression of a variety of genes is induced by these stresses in various plants. The products of these genes function not only in stress tolerance but also in the regulation of gene expression and signal transduction in stress responses [4]. Genome-wide analyses have identified thousands of genes encoding transcription factors that are induced or repressed by a range of environmental stresses. Various transcription factors and *cis*-acting elements in the stress-responsive promoters function for plant adaptation to environmental stresses. It is estimated

that the *Arabidopsis* and rice genomes each contains about 1300–1600 genes that encode transcription factors [5]. As a result of computational prediction and manual curation, a total of 2576 putative transcription factors were identified and classified into 64 families from *Populus* [6].

Many transcription factors involved in these stress-resistance pathways have been identified, among which the AP2/ERF are one of the most important factors. AP2/ERF genes act as nodes of regulatory network in plant response to many stresses, which are conserved in many plants [7]. Nanjo and colleagues found 13 candidate clones that contained the AP2/ERF domain from the poplar ESTs [8]. They further analyzed cDNAs encoding an AP2/ERF-domain transcription factor which is specific in poplar and plays an important role under stress [9]. Two other DREB-like genes from *Populus* were isolated by yeast one-hybrid system [10]. To determine whether the C-repeat binding factor (CBF) family of transcription factors contributing to this process in annual herbaceous species also functions in woody perennials, the changes in phenotype and transcript profile of transgenic *Populus* constitutively expressing CBF1 from *Arabidopsis* (AtCBF1) were investigated [11]. Two ERF-related transcription factors were expressed during the transition to dormancy in apical and axillary buds [12].

In this research, the establishment of an extensive picture of the AP2/ERF gene family in *Populus* was attempted. First, we finely describe the poplar AP2/ERF gene family. The data obtained revealed 200 distinct AP2/ERF gene sequences in *Populus trichocarpa*. Secondly, we completed the inventory of the *Populus* AP2/ERF gene

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family. Sequence analyses and phylogenetic studies revealed the structural diversity in *Populus* AP2/ERF proteins. We named the genes coding for AP2/ERF domain proteins by following a nomenclature stemming from the phylogenetic analysis. The resulting classification of groups and identification of putative functional motifs will be useful in studies on the biological functions of each gene in the *Populus* AP2/ERF families.

Materials and methods

Source of *P. trichocarpa* and *Arabidopsis thaliana* database. The *P. trichocarpa* genome DNA Database was downloaded from DOE Joint Genome Institute web site (<http://genome.jgi-psf.org/Poptr1/Poptr1.download.html>) [2]. Database of *A. thaliana* AP2/ERF family was downloaded from DATF web site (<http://datf.cbi.pku.edu.cn/>) [6].

Database search. Searching of *P. trichocarpa* genome database was performed for finding all members of the AP2/ERF family. The strategy to obtain every gene of the AP2/ERF family in a genome is the following. The amino acid sequence of the AP2/ERF domain from tobacco (*Nicotiana tabacum*) ERF2 was used as queries to search against the JGI (US Department Of Energy, Joint Genome Institute) (<http://genome.jgi-psf.org/Poptr1/Poptr1.download.html>) databases using the BLASTP program at the e-value of $1e^{-3}$ to avoid false positives. To increase the extent of the database search results, we also performed the position-specific iterated BLAST search against the *P. trichocarpa* genome database on the NCBI web site. We also performed the database searches using amino acid sequences of the AP2/ERF domain of some members of the *Arabidopsis* AP2/ERF family as a query sequence to confirm completion of the collection, such as using the soloist At4g13040 sequence.

Sequences analysis and construction of the phylogenetic tree. Open reading frames (ORFs) were performed with ORF Finder (Open Reading Frame Finder) in NCBI (<http://www.ncbi.nlm.nih.gov/gorf/gorf.html>). A multiple alignment analysis was performed with ClustalW (<http://bioinformatics.ubc.ca/resources/tools/clustalx>) [13]. Phylogenetic trees were constructed using the neighbor-joining (NJ) method and the pictures of phylogenetic trees were drawn with program MEGA4 (<http://www.megasoftware.net/mega.html>) [14].

Bioinformatics analysis. Bioinformatics of AP2/ERF family transcriptional factors from *P. trichocarpa* and *A. thaliana*, such as gene and deduced amino acid sequence, composition, physical and chemical characterization, conserved domain sequences, and function domain, were analyzed using Expert Protein Analysis System (ExPASy) proteomics server of the Swiss Institute of Bioinformatics (SIB) (<http://cn.expasy.org/>) [15]. Recombinant proteins, solubility was predicted using the statistical model assuming the protein is being overexpressed in *Escherichia coli* at web site of University of Oklahoma (<http://biotech.ou.edu/>) [16]. The folding states of AP2/ERF family transcription factors from *P. trichocarpa* and *A. thaliana* were predicted by FoldIndex program (<http://bioportal.weizmann.ac.il/fldbin/findex>) [17].

The location of AP2/ERF Genes on *P. trichocarpa* chromosomes. Information on chromosomal location was gathered from the *Populus* genome browser (http://genome.jgi-psf.org/Poptr1_1/Poptr1_1.home.html). Chromosomal locations were determined according to chromosomal information from JGI.

Results

Identification of the AP2/ERF family transcription factors in *P. trichocarpa*

The completed genomes of *P. trichocarpa* and *A. thaliana* provide ideal systems for trans-genomic comparison of AP2/ERF among

these plant species. In order to carry out the cross-species comparison of the AP2/ERFs, a comprehensive list of AP2/ERF encoded in the two plant species has been obtained by sequence search as described under Materials and methods section. A total of 200 full length AP2/ERF family genes were identified as possibly encoding AP2/ERF domain (Table 1). The individual genes are listed in Supplementary Tables 1–5. This super-family included 5 putative genes in RAV family, which were identified as encoding one AP2/ERF domain together with one B3 domain. Twenty-six genes were predicted to encode protein containing two AP2/ERF domains, which were classified into AP2 family. One hundred sixty-eight genes were predicted to encode proteins containing a single AP2/ERF domain. Those 168 genes could be further classified into two families on the basis of similarity of the amino acid sequences. Seventy-seven genes were identified as possibly encoding DREB family, and 91 genes were predicted to encode ERF family. The remaining gene, eugene3.00002518, which was obtained using a soloist of AP2/ERF transcript factor from *A. thaliana* At4g13040 as query sequence, includes an AP2/ERF-like domain sequence, but its homology appears quite low in comparison with the other AP2/ERF genes. Therefore, this gene was also designated as a soloist.

Sakuma et al. reported 145 genes that are classified as members of the AP2/ERF super-family [18]. Of these genes, 121 were classified as part of the ERF subfamily and DREB subfamily, 17 were classified as part of the AP2 family, six were classified as part of the RAV family, and one remaining gene, At4g13040, was identical to the soloist gene. The number genes of total AP2/ERF family genes from *P. trichocarpa* (200) was 1.379-fold than those genes from *A. thaliana* (145). The number genes of DREB subfamily from *P. trichocarpa* (77) were 1.375-fold than those genes from *A. thaliana* (56). The number genes of ERF subfamily from *P. trichocarpa* (91) were 1.400-fold than those genes from *A. thaliana* (65). The number genes of AP2 subfamily from *P. trichocarpa* (26) were 1.529-fold than those genes from *A. thaliana* (17). The rates of total gene and same subfamily genes were similar between *P. trichocarpa* and *A. thaliana* (Fig. 1). Moreover, those rates were also similar with protein-coding genes of *Populus/Arabidopsis*. *Populus* has more protein-coding genes than *Arabidopsis*, ranging on average from 1.4 to 1.6 putative *Populus* homologs for each *Arabidopsis* gene [2].

Table 1
Summary of the AP2/ERF family between *P. trichocarpa* and *A. thaliana*

Plant	Group	<i>P. trichocarpa</i>		<i>A. thaliana</i>	
		Number	Percent	Number	Percent
DREB subfamily	A1	6	3.00	6	4.14
	A2	18	9.00	8	5.52
	A3	2	1.00	1	0.70
	A4	26	13.00	16	11.03
	A5	14	7.00	16	11.03
	A6	11	5.50	9	6.21
	Total	77	38.50	56	38.63
ERF subfamily	B1	19	9.50	15	10.34
	B2	6	3.00	5	3.44
	B3	35	17.5	18	12.41
	B4	7	3.50	7	4.83
	B5	8	4.00	8	5.52
	B6	16	8.00	12	8.28
	Total	91	45.50	65	44.82
Ap2 subfamily		26	13.00	17	11.71
RAV subfamily		5	2.50	6	4.14
Soloist		1	0.50	1	0.70
Total		200		145	

The number of AP2/ERF family from *A. thaliana* was according to Sakuma et al. [18].

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