



# Systematic analysis of the *OFP* genes in six Rosaceae genomes and their roles in stress response in Chinese pear (*Pyrus bretschneideri*)

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**Abstract** OVATE family proteins (OFPs) are the plant-specific transcription factors, and have significant functions in regulating plant growth, development and resistance. The *OFP* genes have been investigated in several plants, but they still lack a systematic analysis of *OFP* genes in Chinese pear and some other five Rosaceae genomes. Here, 28 *PbrOFPs* were identified within Chinese pear and compared them with those of other five Rosaceae genomes. Evolutionary tree revealed that all *OFP* genes from six Rosaceae genomes were divided into eight groups. Seventeen conserved microsynteny regions were detected in Chinese pear genome, suggested that these *PbrOFP* genes might be considered to have originated from the large-scale duplication events., indicating these *PbrOFP* genes might contain specialized regulatory mechanisms in these tissues, such as flower, ovary and fruit. Remarkably, two *PbrOFP* genes (*PbrO10426.1* and *PbrO10427.1*) were up-regulated under *Venturia nashicola* treatment, and five *PbrOFP* genes were up-regulated under PEG treatment, suggesting that these genes might play crucial roles in defence to environmental stresses. Our data presented a systematic analysis and might aid in the selection of appropriate *PbrOFPs* for further functional studies in Chinese pear, especially in response to the mechanism of biotic and abiotic stresses.

**Keywords** OFPs · Chinese pear · Expression · Microsynteny

## Introduction

OVATE family protein (OFP), a novel plant-specific transcription factor, belongs to plant growth inhibitory protein and plays important roles in regulating plant growth and development due to a conserved OVATE domain (also known as DUF623) in its C-terminal (Liu et al. 2002; Wang et al. 2007; Wang et al. 2011). OVATE was identified for the first time as a quantitative trait locus, which mainly controls the shape of tomato fruit, and it can also negatively regulate the growth and development of tomato leaves flowers (Liu et al. 2002; Wang et al. 2007; Wang et al. 2011). Recently, many *OFPs* have been cloned and identified in Arabidopsis, rice and tomato, etc. A total of 18, 31 and 31 of the *OFP* family members exists in the genomes of Arabidopsis, rice and tomato, respectively, which exert vital effects on plant growth and development (Huang et al. 2013; Yu et al. 2015). Among them, most *AtOFPs* play a transcriptional inhibitory role in Arabidopsis transient protoplast expression system (Wang et al. 2011). Besides, 31 *OsOFPs* have different spatial expression profiles, and mainly are expressed at the seed development stage, suggesting that *OsOFPs* may participate in multiple processes of rice growth and development, especially the seed development (Yu et al. 2015). Three amino acid loop extension (TALE) protein family is a typical ring structure composed of three amino acids, which can specifically interact with other protein molecules. The Yeast Two-Hybrid System showed that nine *AtOFPs* could interact with TALE homologous domain proteins (Hackbusch et al. 2005). *AtOFP1* and *AtOFP5*

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could jointly regulate the subcellular localization of BEL1 like homedomain (BLH1), which is the TALE homologous domain protein. When AtOFP1 and AtOFP5 were co-expressed in the tobacco leaves, BLH1 was relocated from the nucleus to the cytoplasm (Hackbusch et al. 2005). The accumulation of gibberellin can restore the character of shorter shoot tissue length to a certain extent. However, overexpression of *AtOFP1* can inhibit the expression of *AtGA20ox1* (a gibberellin synthesis gene), leading to the irrecoverable trait (Hackbusch et al. 2005; Wang et al. 2007). *AtOFP1* also interacts with *AtKu*, a DNA double-strand break repair-related gene, to jointly participate in the regulation of DNA double-strand break repair process (Wang et al. 2010). AtOFP5, as a negative regulator of BLH1-KNAT3, plays a role in the early stage of embryo sac development, and they coordinate to regulate embryo sac development (Pagnussat et al. 2007). AtOFP4 is involved in the plant secondary cell wall formation via the interaction with KNAT7 (Li et al. 2011). AtOFP1 and AtOFP4 can mutually regulate the BLH6-KNAT7 multi-protein complex, which is required for the formation of the secondary cell wall (Liu and Douglas 2015). In contrast to OVATEs in tomato, the deletion of *AtOFP1*, *AtOFP4*, *AtOFP8*, *AtOFP10*, *AtOFP15* and *AtOFP16* alone showed no growth defects in the mutant Arabidopsis, suggesting that the above genes have functional redundancy (Wang et al. 2011). These studies suggest that *OFP* may regulate plant growth and development by directly or indirectly affecting the transcriptional regulation of target genes.

The Rosaceae genomes, including Chinese pear (*Pyrus bretschneideri*), European pear (*Pyrus communis*), peach (*Prunus persica*), strawberry (*Fragaria vesca*), Chinese plum (*Prunus mume*), and apple (*Malus domestica*) have been published and released to date (Chagné et al. 2014; Daccord et al. 2017; Shulaev et al. 2011; Verde et al. 2013; Wu et al. 2013). These data lay a foundation for performing a systematic analysis of the *OFP* genes in these Rosaceae genomes. Here, we identified the *OPF* family members in Chinese pear and other five Rosaceae genomes, and then analyzed their phylogeny relationships, microsynteny, gene duplication events, and expression patterns. Finally, we found several *PbrOFP* genes might be associated with *Venturia nashicola* and drought resistance. These data provide valuable information and insights into the evolution of *OFPs* in Rosaceae genomes and will contribute to the future functional studies of *OFPs* in Chinese pear.

## Materials and methods

### Database search for Chinese pear and other five Rosaceae genomes

The Chinese pear genome with protein, CDS and GFF files were obtained from the GigaDB database (<http://gigadb.org/>) (Wu et al. 2013). The European pear, apple, strawberry and peach with proteins, CDS and GFF files were downloaded from GDR database (<https://www.rosaceae.org/>) (Chagné et al. 2014; Daccord et al. 2017; Shulaev et al. 2011; Verde et al. 2013). The Chinese plum with protein, CDS and GFF files obtained from the GitHub (<https://github.com/lileiting/prunusmumegenome>) (Zhang et al. 2018a, b). The *A. thaliana* *AtOFP* genes were obtained and downloaded from TAIR (<https://www.arabidopsis.org/>). The HMM profile of *OFP* domain (PF04844) was downloaded from the Pfam database and then used the HMMER 3.1 software to determine *OFP* genes in Chinese pear and other five Rosaceae genomes (e-value  $\leq 1e^{-3}$ ) (Finn et al. 2011). Finally, these *OFPs* encoded proteins were discarded manually if they lacked a complete or core *OFP* domain (PF04844) which confirmed by Pfam (Punta et al. 2011), SMART (Letunic et al. 2011), and InterPro (Jones et al. 2014).

### Phylogenetic analyses

The multiple alignment of *OFP* proteins from Chinese pear and other five Rosaceae genomes were executed by MAFFT software (Katoh and Standley 2013). The neighbour-joining (NJ) tree was constructed by MEGA version 5.1 software with the following parameters: Poisson correction, pairwise deletion and a bootstrap test for 1000 replicate (Tamura et al. 2011).

### Microsynteny analysis

The MicroSyn software was used to detect microsynteny of *OFP* genes in Chinese pear and other five Rosaceae genome with a threshold e-value of  $< 1e^{-5}$  (Cai et al. 2011). In this study, we determined a syntenic block which this region including three or more conserved homolog genes were distributed within 15 genes upstream and downstream of *OFP* genes, as described by Cao et al. (2019b, 2020).

### RNA-seq expression analysis

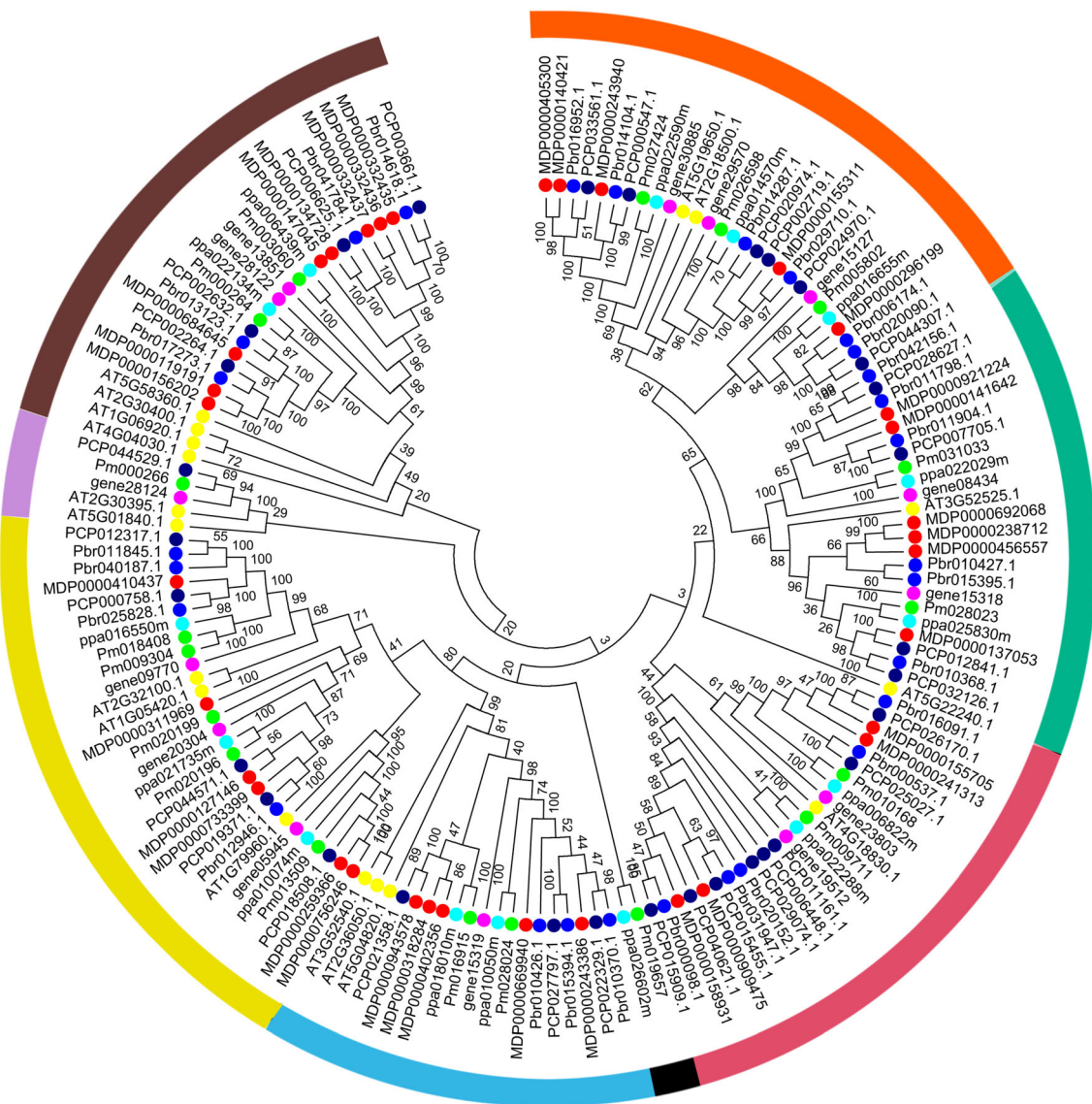
The RNA-seq reads, including ovary, petal, flower, leaves, sepal, bud, stem, and seven pear fruit development stages, were obtained from NCBI (PRJNA49877 and PRJNA309745) (Cao et al. 2019a). The HISAT2 was used

**Table 1** The genome information for six Rosaceae genomes

Species	Genome genes	Chromosomes	<i>OPF</i> genes	Gene name
Chinese pear ( <i>Pyrus bretschneideri</i> )	42,341	34	28	<i>PbrOPFs</i>
European pear ( <i>Pyrus communis</i> )	43,419	34	30	<i>PcOPFs</i>
Apple ( <i>Malus domestica</i> )	63,541	34	34	<i>MdOPFs</i>
Chinese plum ( <i>Prunus mume</i> )	31,390	16	17	<i>PmOPFs</i>
Peach ( <i>Prunus persica</i> )	27,864	16	15	<i>PpOPFs</i>
Strawberry ( <i>Fragaria vesca</i> )	32,831	14	9	<i>FvOPFs</i>

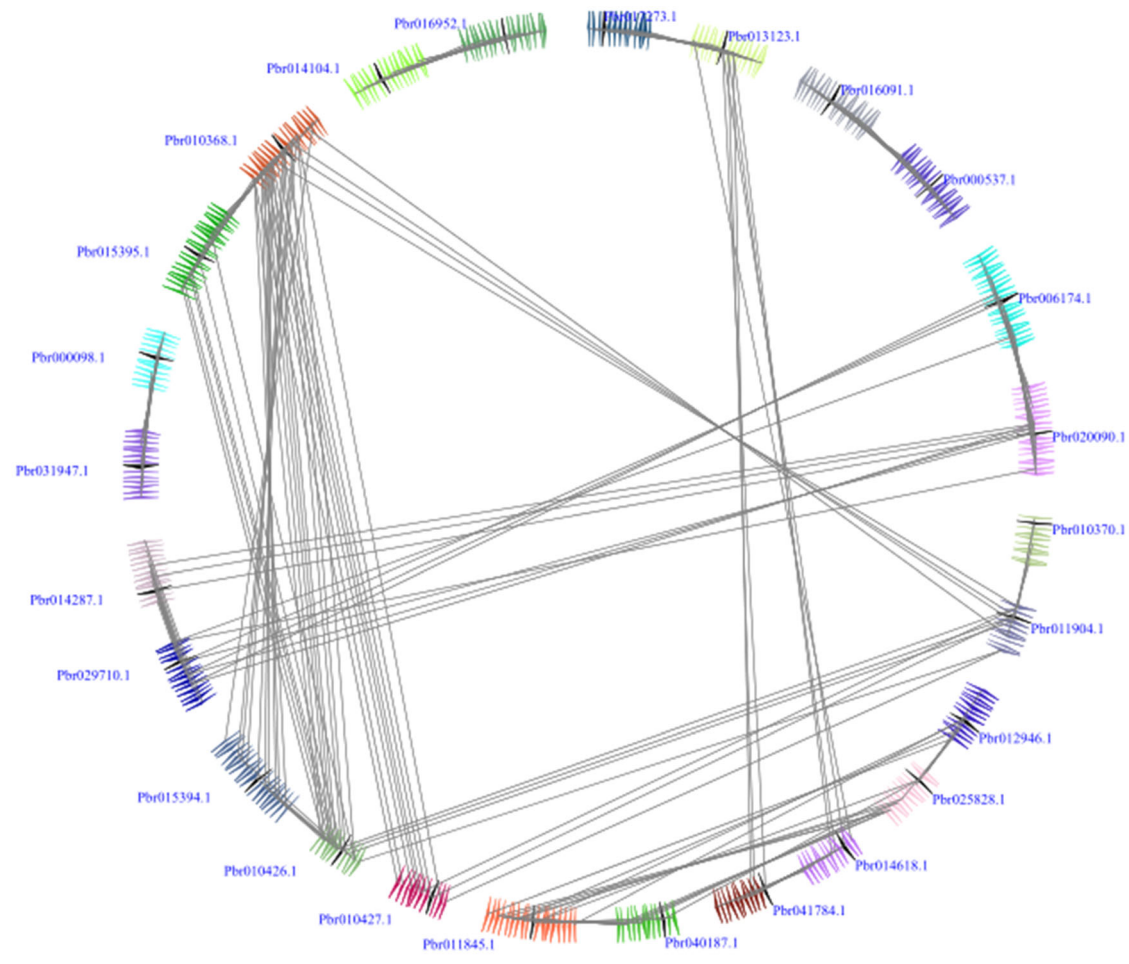
to map the paired reads to the Chinese pear genome with defaults parameters (Kim et al. 2015). The StringTie was used to calculate the FPKM (fragments per kilobase of

exon model per million reads mapped) values of differently expressed genes (Pertea et al. 2016).



**Fig. 1** The phylogenetic relationships of *OPF* genes in Chinese pear and other five Rosaceae genomes. The Neighbor-Joining method was used to construct the phylogenetic tree using all *OPF* genes with 1000

bootstrap replicates. The numbers beside the branches suggest the values of bootstrap that support the adjacent node



**Fig. 2** Extensive microsynteny of *OFP* genes in Chinese pear. The gene's orientations and genomic fragments were represented by a series of triangles. The homologous genes on two fragments were connected by grey lines

## Results and discussion

### Identification of *OFP* genes in Chinese pear and other five Rosaceae genomes

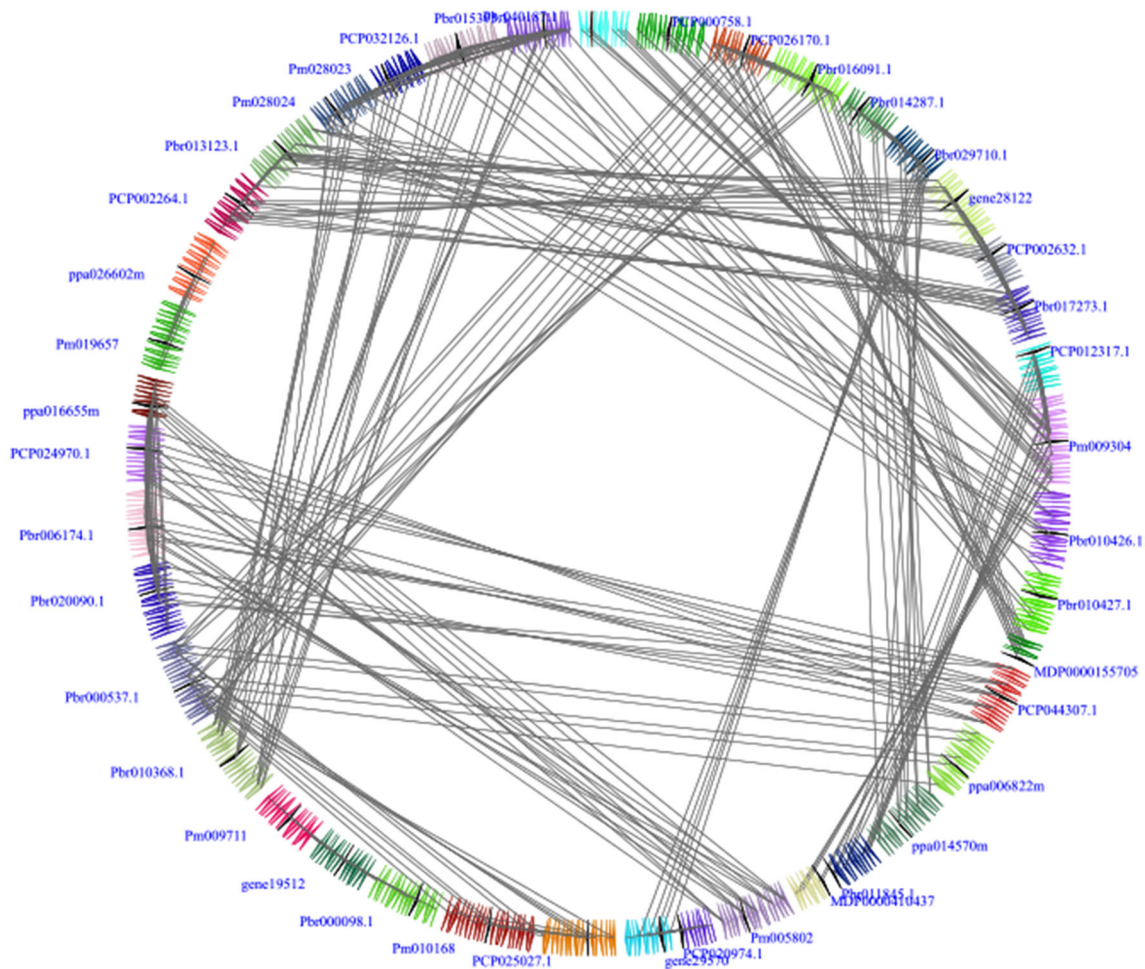
To determine the best candidates of *OFP* genes in six Rosaceae genomes, we downloaded all *AtOFP* sequences from TAIR database and then identified the *OFP* genes in local databases, as described by Cao et al. (2020). Finally, we identified 133 *OFP* genes in six Rosaceae genomes, including 28 *PbrOFPs* in Chinese pear, 30 *PcOFPs* in European pear, 34 *MdOFPs* in apple, 17 *PmOFPs* in Chinese plum, 15 *PpOFPs* in peach, and 9 *FvOFPs* in strawberry, respectively (Table 1 and Table S1). The numbers of *OFPs* in Chinese pear, European pear, and apple was more than that in Chinese plum, peach, and strawberry, thus revealing a greater expansion in the *OFP* genes of Chinese pear, European pear and apple (Table 1). As previously reported, the recent whole-genome duplication events (WGD) (~ 40 MYA) was shared by Chinese

pear, European pear and apple, but not appeared in Chinese plum, peach, and strawberry (Chagné et al. 2014; Daccord et al. 2017; Shulaev et al. 2011; Verde et al. 2013; Wu et al. 2013), indicating that the *OFP* gene family members might have undergone an expansion corresponding to the members of the WGD events.

### Phylogenetic analysis of *OFP* genes in Chinese pear and other five Rosaceae genomes

To determine the phylogenetic relationship among the *OFP* genes in Chinese pear and other five Rosaceae genomes, we constructed the neighbour-joining phylogenetic tree using the total length amino acid sequences of these proteins with 1000 bootstrap values. As shown in Fig. 1, all *OFP* genes were divided into eight groups, including group-I, group-II, group-III, group-IV, group-V, group-VI, group-VII, and group-VIII. Group-IV had the fewest *OFPs* (two), while group-VI contained the most *OFPs* (twenty-nine), followed by group-VIII (twenty-six). Each of these





**Fig. 3** Microsynteny related to *OFP* families in Chinese pear and other five Rosaceae genomes. The gene's orientations and genomic fragments were represented by a series of triangles. The homologous genes on two fragments were connected by grey lines

six Rosaceae species contributed at least one *OFP* to group-I, group-II, group-III, group-V, group-VI and group-VIII, but the members of the group-IV and group-VII included two or four Rosaceae species, indicating that there may be divergent evolutionary mechanisms in different Rosaceae species. Subsequently, we found that the members of *OFP* gene family from Chinese pear and European pear showed higher similarity according to the genetic distance, which was consistent with the previous reports showing the closer evolutionary relationships of Chinese pear and European pear (Cao et al. 2016). Also, thirty-nine *OFP* orthologous gene pairs were found among these six Rosaceae genomes, such as *Pbr016952.1* and *PCP000547.1*, and *Pm027424* and *ppa022590m*.

### Conserved microsynteny of *OFP* genes in Chinese pear and other five Rosaceae genomes

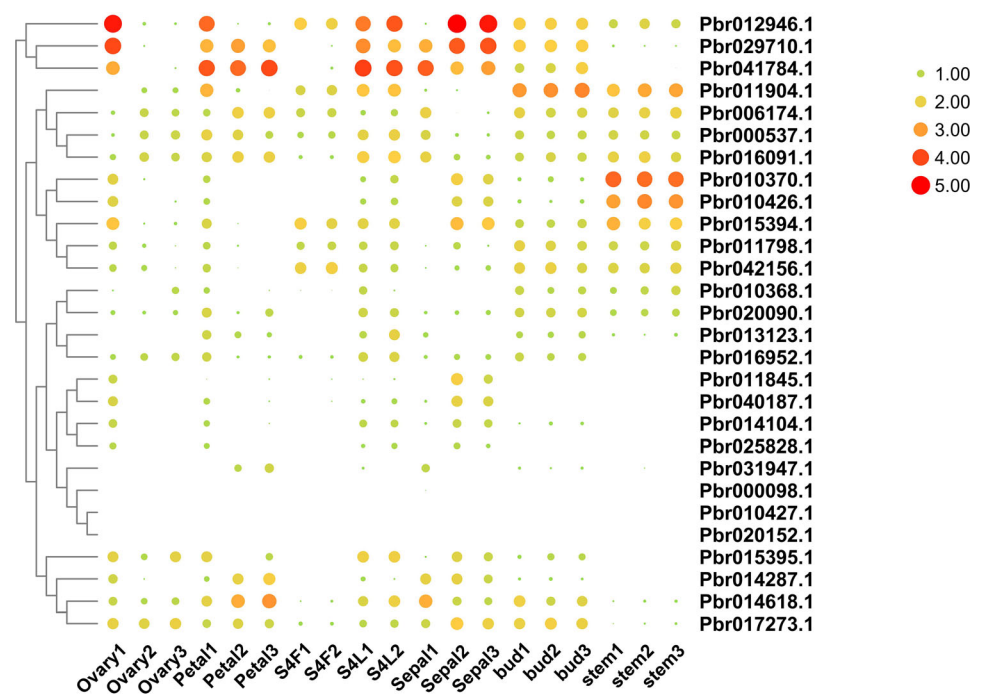
The genomes of Chinese pear, European pear, and apple had undergone two WGD, including a specific recent WGD

(about 30–45 MYA) and an ancient WGD (about 140 MYA) (Chagné et al. 2014; Daccord et al. 2017; Shulaev et al. 2011; Verde et al. 2013; Wu et al. 2013). However, the other Rosaceae genomes of Chinese plum, peach, and strawberry only experienced an ancient WGD (about 140 MYA) (Chagné et al. 2014; Daccord et al. 2017; Shulaev et al. 2011; Verde et al. 2013; Wu et al. 2013). To further understand the expansion and evolution of *OFP* genes, a performed microsynteny analysis of Chinese pear, European pear, apple, Chinese plum, peach, and strawberry was carried out by MicroSyn software (Cai et al. 2011). In the present study, we defined a WGD or large-scale duplication as these two regions which three or more of the 15 upstream, as well as downstream neighboring genes are homologous pairs.

In our study, we detected 17 collinear gene pairs in Chinese pear (Fig. 2). Among them, *Pbr010368.1* was collinear with four genes, including *Pbr015394.1*, *Pbr010426.1*, *Pbr010427.1* and *Pbr011904.1*. *Pbr010426.1* was collinear with three genes, including

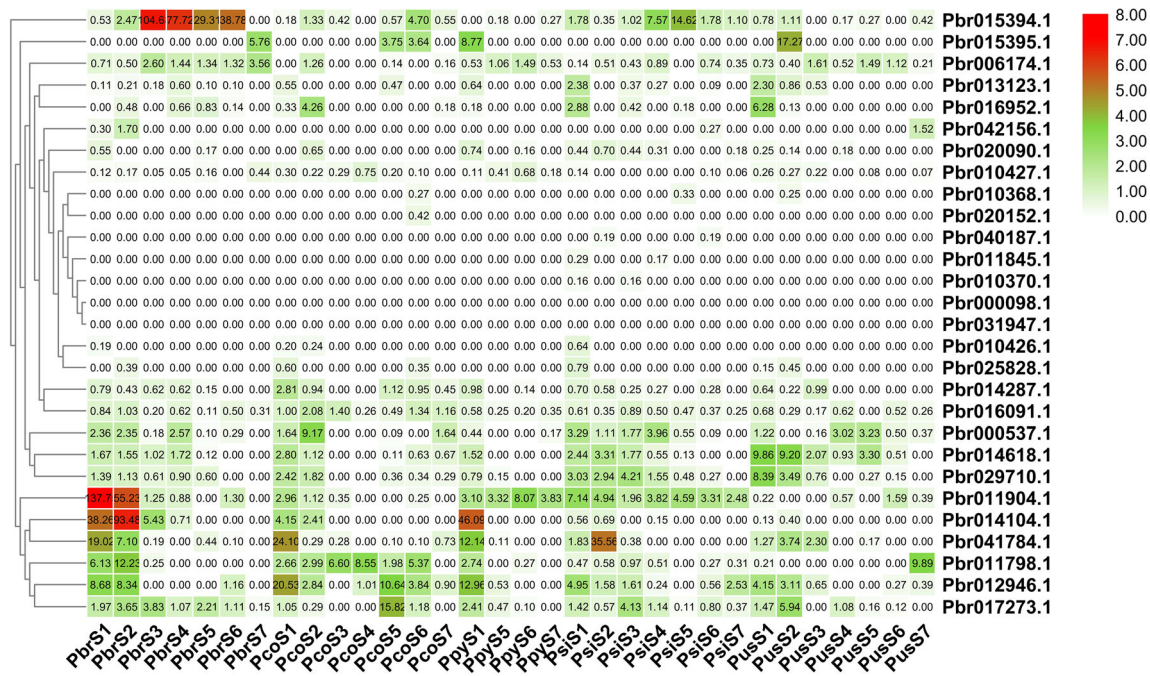
**Table 2** Ka/Ks ratios of OFP genes between Chinese pear and other five Rosaceae genomes

Gene_1	Gene_2	Ka	Ks	Ka/Ks
<i>Pbr017273.1</i>	<i>PCP002632.1</i>	0.062923687	0.154329561	0.407722844
<i>Pbr017273.1</i>	<i>gene28122</i>	0.235799225	0.702508661	0.335653121
<i>Pbr029710.1</i>	<i>Pbr014287.1</i>	0.036366602	0.207456604	0.175297395
<i>Pbr016091.1</i>	<i>PCP026170.1</i>	0.006452809	0.011897143	0.542383082
<i>Pbr040187.1</i>	<i>Pm009304</i>	0.142841862	0.600583384	0.237838518
<i>Pbr015395.1</i>	<i>PCP032126.1</i>	0.107262272	0.148685487	0.721403779
<i>Pbr015395.1</i>	<i>Pm028023</i>	0.089555799	0.823959217	0.108689601
<i>Pbr015395.1</i>	<i>Pm028024</i>	0.717059236	3.032288451	0.236474613
<i>Pbr013123.1</i>	<i>gene28122</i>	0.242829789	0.780391728	0.31116397
<i>Pbr013123.1</i>	<i>PCP002264.1</i>	0.064801076	0.165327892	0.391954892
<i>Pbr013123.1</i>	<i>Pbr017273.1</i>	0.066710615	0.159215945	0.418994558
<i>Pbr006174.1</i>	<i>Ppa016655m</i>	0.151979947	0.73500298	0.2067746
<i>Pbr020090.1</i>	<i>Ppa016655m</i>	0.141309608	0.634304716	0.222778744
<i>Pbr000537.1</i>	<i>Pbr016091.1</i>	0.104971588	0.27995433	0.374959688
<i>Pbr000537.1</i>	<i>PCP026170.1</i>	0.102081361	0.28466833	0.358597535
<i>Pbr006174.1</i>	<i>PCP024970.1</i>	0.021926044	0.020925507	1.047814207
<i>Pbr015395.1</i>	<i>Pbr010368.1</i>	0.026103777	0.069682579	0.374609799
<i>Pbr010368.1</i>	<i>PCP032126.1</i>	0.040311278	0.055865742	0.721574205
<i>Pbr000098.1</i>	<i>gene19512</i>	0.219017723	0.746997251	0.293197495
<i>Pbr000537.1</i>	<i>Pm010168</i>	0.152051512	0.520109183	0.292345371
<i>Pbr013123.1</i>	<i>PCP002632.1</i>	0.010050402	0.020479088	0.490764122
<i>Pbr013123.1</i>	<i>PCP002632.1</i>	0.010050402	0.020479088	0.490764122

**Fig. 4** Expression patterns of *PbrOFP* genes family in various tissues. The colour bar in each panel represents log<sub>2</sub> expression values. The colour scale for each value is present on the upper right corner

*Pbr015395.1*, *Pbr010368.1* and *Pbr011904.1*, followed by *Pbr029710.1* was collinear with *Pbr006174.1* and *Pbr020090.1*, *Pbr011845.1* was collinear with *Pbr025828.1* and *Pbr0012946.1*, *Pbr013123.1* was

collinear with *Pbr041784.1* and *Pbr014618.1*, *Pbr020090.1* was collinear with *Pbr014287.1* and *Pbr029710.1*, and *Pbr011904.1* was collinear with *Pbr010426.1* and *Pbr010368.1* (Table S2). These series of



**Fig. 5** Gene expression pattern for five different pear cultivars (i.e. ‘Yali’, ‘Starkrimson’, ‘Hosui’, ‘Kuerlexiangli’, ‘Nanguoli’). Pbr, Pco, Ppy, Psi, Pus indicates ‘Yali’, ‘Starkrimson’, ‘Hosui’, ‘Kuerlexiangli’,

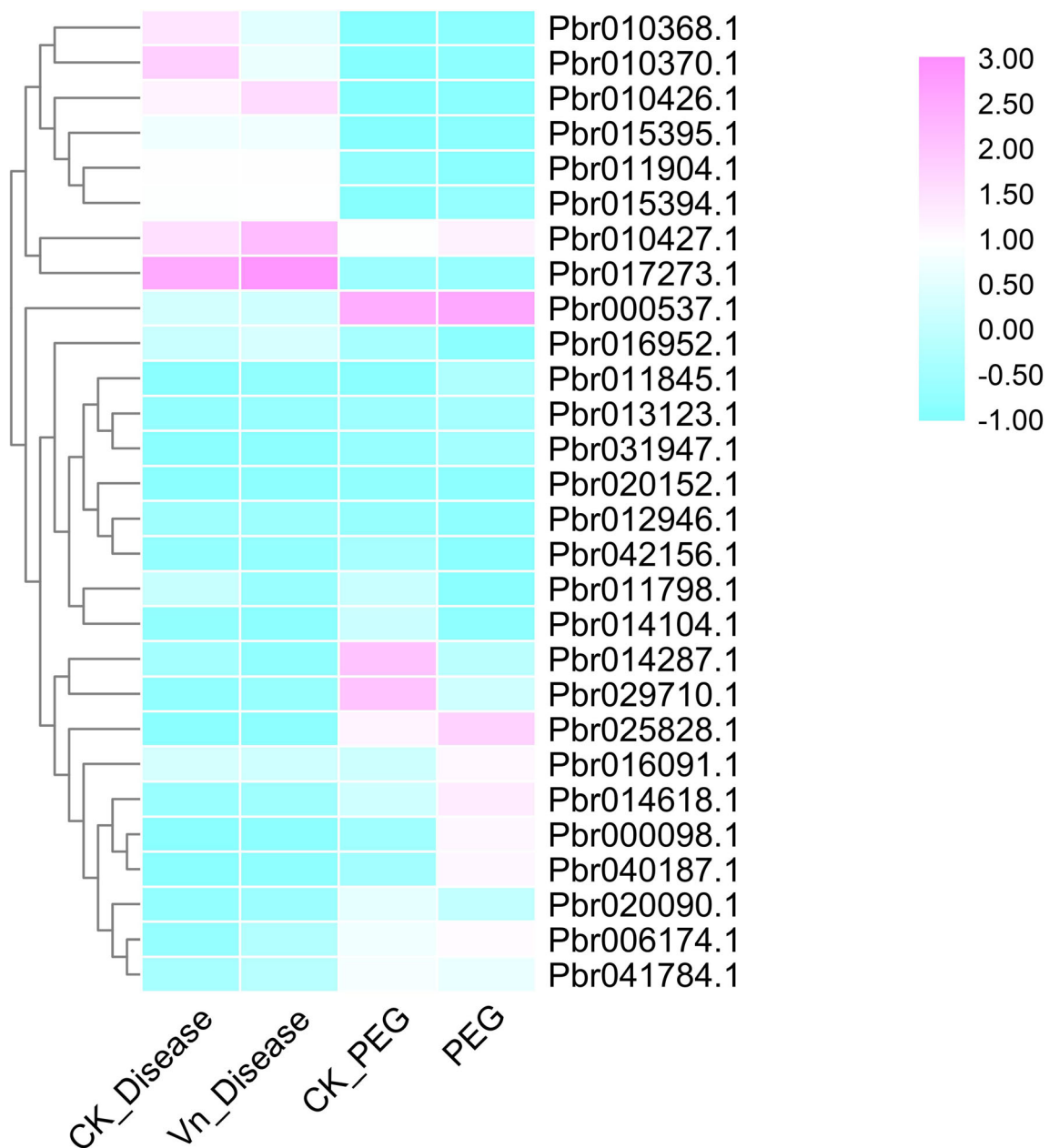
‘Nanguoli’, respectively. The colour bar in each panel represents log2 expression values. The color scale for each value is present on the upper right corner

several-for-one collinear relationships indicated that they play key roles in the expansion of the *OFP* gene family. Interestingly, all these collinear gene pairs contained more than three pairs of conserved flanking genes, indicating that these gene pairs evolved from the large-scale duplication events. Subsequently, we analyzed the interspecies microsynteny between the Chinese pear and European pear, apple, Chinese plum, peach, as well as strawberry (Fig. 3). Among these *OFP* genes, we scanned 31 conserved syntenic regions, including 13 orthologous gene pairs in the Chinese pear and European pear, 9 gene pairs in Chinese pear and Chinese plum, 4 pairs in Chinese pear and peach, 4 gene pairs in Chinese pear and strawberry, and only one gene pair in Chinese pear and apple (Table S2), which was consistent with the previous papers that showed closer evolutionary relationships of Chinese pear and European pear, versus the Chinese pear and apple/Chinese plum/peach/strawberry (Cao et al. 2016; Wu et al. 2013). The Ka/Ks ratios of *OFP* genes were calculated between Chinese pear and other five Rosaceae genomes, and these data suggested that these *OFP* genes were evolving under purifying selection during evolution (Table 2). These data might provide a novel material for studying the *OFP* genes evolution in different genomes.

**The expression pattern of *PbrOFP* genes in various tissues**

Previously published work suggested that the *OFP* genes play significant roles in plant growth, development and stress response activities (Huang et al. 2013; Liu et al. 2015; Ma et al. 2017; Schmitz et al. 2015; Wang et al. 2016). Thus, differential expression analysis of *PbrOFPs* in Chinese pear is helpful for us to find out specialized functions of these genes in plant growth and development and stress response activities from the practical application point of view (Wang et al. 2016). In the present study, we only considered a *PbrOFP* was expressed if the value of Fragments Per Kilobase per Million (FPKM) was  $\geq 1$  in an expression atlas according to the previously published work. The results revealed that three *PbrOFP* genes were not expressed in any tissue, indicating that these *PbrOFPs* are pseudogenes or these *PbrOFPs* may be inducible genes (Fig. 4). In general, most of the *PbrOFP* genes were expressed in ovary, petal, flower, and sepal, which suggested that these genes contained a direct involvement with these tissues in Chinese pear. Interestingly, *Pbr010370.1* and *Pbr010426.1* were specifically expressed in the stem, and remaining *PbrOFPs* were diversely expressed in





**Fig. 6** Expression of *PbrOFP* genes family in response to disease and drought stresses. The colour bar in each panel represents log<sub>2</sub> expression values. The colour scale for each value is present on the upper right corner

several tissues, suggesting that these *PbrOFPs* might contribute to these tested tissues of Chinese pear.

Subsequently, we further investigated the expression pattern of *PbrOFPs* in five different pear cultivars (i.e. ‘Yali’, ‘Starkrimson’, ‘Hosui’, ‘Kuerlexiangli’, ‘Nanguoli’) during fruit development. Among them, some *PbrOFP* genes were expressed in different developmental stages of these five pear cultivars. The number of *PbrOFP* genes expressed in ‘Yali’ pear was the largest (15), followed by ‘Starkrimson’ pear (14) and ‘Nanguoli’ pear (14) (Fig. 5).

These data suggested that the *PbrOFP* gene family members contained diverse functions in different pear cultivars. Noteworthy, we found that most of *PbrOFP* genes were highly expressed in the early stages of fruit development (DAF15 and DAF30), such as *Pbr01904.1* and *Pbr01401.1*, indicating that these *PbrOFP* genes play important roles in the early stages of fruit development. Additionally, some genes, such as *Pbr0161798.1*, *Pbr016952.1*, *Pbr015395.1*, *Pbr014614.1* and *Pbr029710.1*, were also found to be highly expressed in ‘Nanguoli’ with small fruit shape



index, suggesting that these genes might affect the size of fruit during pear fruit development.

### The expression pattern of *PbrOFP* genes in response to biotic and abiotic stresses

Environmental stresses, including biotic and abiotic stresses, can affect the regulation of important genes, and finally, influence the health and growth of plants (Ghorbani et al. 2020; Li et al. 2019; Shafiei-Koij et al. 2020). Many stress-related genes can be induced under adverse conditions to help plants cope with stresses (Fan et al. 2018; Kavas et al. 2019). For example, the *OFP29* from *Oryza sativa* reached a peak of expression after 24 h in the ABA treatment (Kavas et al. 2019). The *OFP11*, *OFP14* and *OFP20* from apple were upregulated under the NaCl treatment, and *OFP6* and *OFP14* were upregulated under the mannitol treatment (Li et al. 2019). Drought and *V. nashicola* is an important factor affecting pear fruit quality and yield. Firstly, we investigated the expressed characteristics of *PbrOFPs* in pear showing resistance to *V. nashicola* (Fig. 6). Subsequently, we found that the only two *PbrOFP* genes (*Pbr010426.1* and *Pbr010427.1*) were up-regulated, and the remaining *PbrOFP* genes were almost unchanged under *V. nashicola* treatment. At the same time, we also surveyed the expression pattern of *PbrOFPs* in pear under drought treatment. Here, the expression levels of five *PbrOFPs* were higher compared with the control, while two *PbrOFPs* were down-regulated than that of the control under PEG treatment. Our results suggested that these *PbrOFP* genes might play key roles in response to biotic and abiotic stresses, and also could increase the understanding of *PbrOFP* genes resistance to stresses and molecular breeding in Chinese pear.

### Conclusion

Our study provided the first comprehensive analysis of *OFP* in Chinese white pear and compared them with those of other five Rosaceae species, including European pear, apple, Chinese plum, peach and strawberry. We observed the large-scale duplication events in Chinese pear and other five Rosaceae species *OFP* genes. Transcriptome data analysis of *PbrOFP* genes exhibited different expression pattern and revealed that these genes might play key roles during pear fruit development. Our data provided the first integrative analysis about these *OFP* genes and opened up new perspectives for studying the function of these genes in different processes, including different tissues and fruit development in the economical fruit crops (Chinese pear).

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### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no competing interests.

**Consent for publication** Not applicable.

**Ethical approval** This article did not include any experiments with human participants or animals performed by all the authors.

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