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# Identification of COR413 Gene Family in Peach and Its Expression in Low Temperature and LTC Treatment at Postharvest

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**Abstract** Peach were susceptible to chilling injury during low temperature (0°C) storage at postharvest, and LTC (Low temperature conditioning) treatment could reduce chilling injury such as of $H_2O_2$ production and fruit browning. In order to study the function of peach *COR413* in the regulation of postharvest chilling injury in peach 'Beijing No. 9', four COR413 gene family members were identified based on the peach genome database, namely *PpCOR1~PpCOR4*. Phylogenetic analysis showed that the four *PpCORs* could be clustered into two subfamilies. *PpCOR1~PpCOR3* belonged to the first subfamily, and most of the members in this subfamily were located in plasma membrane. *PpCOR4* belongs to the second subfamily, and its members are mainly located in thylakoid membrane. The cis-acting elements analysis of *PpCORs* promoter showed that *PpCOR3* contained abundant abiotic stress responsive and hormone responsive elements such as jasmonate and abscisic acid. The results of gene expression showed that *PpCOR3* was induced by low temperature while LTC treatment could repress the induction of *PpCOR3* by low temperature. Interestingly, the expression of *PpCOR3* was positively correlated with the change of $H_2O_2$ content in peach, which indicated that *PpCOR*3 was involved in the regulation of postharvest chilling injury in peach fruit. This result provides a theoretical basis for the study of postharvest storage and quality maintenance of peach fruit as well as the breeding of cold resistant peach varieties.

**Keywords** Peach; Low-temperature; COR413; Expression analysis

Low temperature can prolong the storage period of fruits and slow down the decay rate, which is the main way of fruit storage after harvest. However, nearly half of the fruits sold in China are sensitive to chilling injury, which is easy to occur in the process of postharvest cryogenic storage, leading to quality deterioration such as fruit browning (Lurie and Crisosto, 2005; Zhang and Xie, 2016). Peach (*Prunus persica* L.) is a respiratory climacteric fruit. Harvested during the high temperature and rainy season, it enters the senescence and post-ripening stage after harvest, and there is an obvious peak of respiration and ethylene release, leading to the decline of fruit quality and storage tolerance. Low temperature storage can effectively inhibit ethylene release, prolong storage period and inhibit fruit mildew (Li et al., 2014). However, peach, as a sensitive fruit of chilling injury, is prone to chilling injury in fruits stored at low temperature after harvest, which is manifested as browning of flesh, flocculation, weakening of flavor or even loss (Wang et al., 2017b).

Previous studies on chilling injury mainly focused on crops, and there were relatively few studies on fruits and vegetables. Plant chilling stress involves cooperative regulation of multiple transcription factors. Currently, *ICE-CBF-COR* signal transduction pathway has been widely studied and plays a crucial role in the regulation of plant chilling injury (Tang et al., 2020). The COR413 gene family was first identified when the model plant *Arabidopsis thaliana* was subjected to low temperature stress (Breton et al., 2003). The COR413 gene family can be divided into two groups: plasma membrane proteins (*COR413-PM*) and thylakoid membrane proteins (*COR413-TM*), which target the plasma membrane and thylakoid membrane, respectively (Breton et al., 2003). In recent years, more and more studies have shown that it plays an important role in the regulation of low temperature stress. In *Arabidopsis thaliana*, *Phlox subulata PsCOR413im1* was overexpressed, and transgenic plants showed higher germination and survival rates under low temperature and freezing stress (Zhou et al., 2018; Wang et al., 2020). The transgenic tobacco (*Nicotiana tabacum*) overexpressing *SikCOR413PM1* of *Saussurea involucrata* is more resistant to cold and drought stress than the wild type tobacco (Guo et al., 2019). Båga et al. (2022) conducted a genome-wide association analysis of 96 rye (*Secale cereal* L.) with different cold resistance, and identified 10 of the most important SNPs related to winter field survival, including *COR413-PM1* and *ICE1*. However, the function of peach *COR413* in the regulation of chilling injury at postharvest cryogenic storage is still unclear and has not been systematically studied.

Studies have shown that 1-methylcyclopropene (1-MCP), low temperature conditioning (LTC), salicylic acid (SA) and other treatments can delay the chilling injury caused by low temperature storage in different peach varieties. 1 mmoL/L SA treatment could maintain higher fruit hardness and lower chilling damage index and decay rate, thus alleviating chilling damage (Wang et al., 2006). Qian et al. (2021) found that 1-MCP (1.0 μL/L) treatment can increase the content of fruit proline and polyamine, and reduce the chilling damage of peach fruit. Studies have shown that LTC treatment can effectively delay the occurrence of chilling injury in peach fruit 'Hujing Milu' and reduce fruit browning index (Wang et al., 2017b). LTC treatment, in which fruits are stored at slightly above storage temperature for a period of time before being transferred to cryogenic storage. Due to the simple operation, low cost and no introduction of other exogenous reagents, the treatment has high application and research value.

In this study, the peach fruit of 'Beijing No. 9' was used as the research material, and the COR413 family members were identified based on peach genome database system. From the perspective of genetic evolution analysis and gene expression, the function of *PpCOR* in postharvest storage and LTC treatment alleviates the regulation of chilling injury in peach fruit was revealed. This study will provide theoretical basis for the study of post-harvest storage and preservation of peach fruit and breeding of cold-resistant varieties.

## 1 Results and Analysis

### 1.1 Identification and chromosome distribution of COR413 family members in peach

Based on the characteristics of COR413 (PF05562) protein conserved domain in peach genome database and Pfam database, four COR413 family members were identified. *PpCOR1* and *PpCOR2* are tandem repeats distributed on chromosome 7 (Figure 1). *PpCOR3* and *PpCOR4* were located on chromosomes 8 and 4, respectively. The protein molecular weights and amino acid sequence lengths of the four *PpCOR* showed little difference. *PpCOR4* was predicted to be distributed in the thylakoid membrane, while *PpCOR1*-*PpCOR3* was predicted to be distributed in the plasma membrane (Table 1).

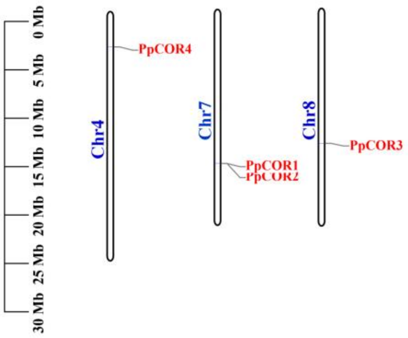

Figure 1 Chromosomal localization of COR413 gene family members in peach

### 1.2 Conserved domain and gene structure of COR413 gene family members in peach

Based on the peach genome database, the distribution of the intron and exon of *PpCOR* and its protein-conserved motif were determined. Plasma membrane types *PpCOR1*~*PpCOR3* contain at least 6 conserved motifs with similar intron and exon composition (Figure 2). Thylakoid membrane types of *PpCOR4* contain two conserved motifs, motif 2 and motif 5 (Figure 3), and the composition of intron and exon is significantly different from that of *PpCOR1*~*PpCOR3*.

Table 1 The basic physical and chemical properties of peach COR413 family members

| Gene name | Genbank | Amino acid | Isoelectric point | Molecular weight | Subcellular localization |
|---|---|---|---|---|---|
| *PpCOR1* | XM_007202530.2 | 203 | 9.20 | 22 839.11 | Plasma membrane |
| *PpCOR2* | XM_020568695.1 | 203 | 9.20 | 22 839.11 | Plasma membrane |
| *PpCOR3* | XM_007200475.2 | 202 | 9.30 | 22 309.61 | Plasma membrane |
| *PpCOR4* | XM_007211919.2 | 230 | 10.39 | 24 820.43 | Thylakoid membrane |

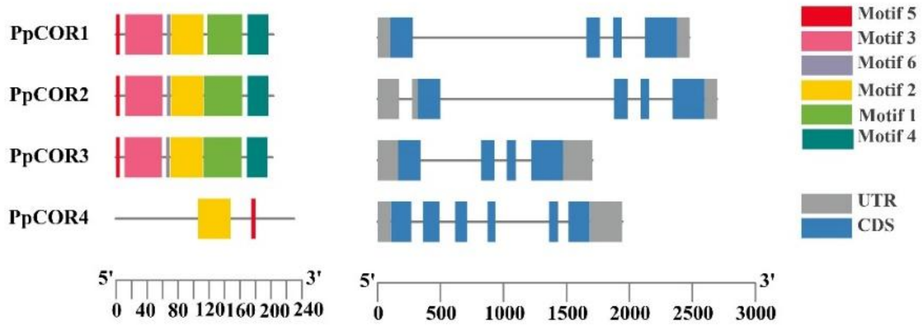

Figure 2 Conserved domain and gene structure of COR413 gene family members in peach

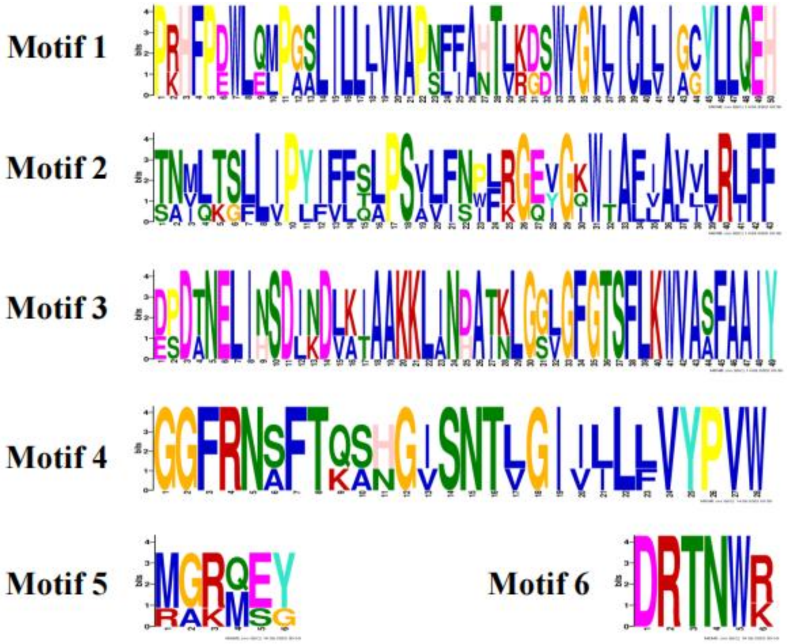

Figure 3 Conserved motifs of COR413 gene family members in peach

### 1.3 Collinearity of COR413 gene family members in peach with poplar and *Arabidopsis thaliana*

The collinearity analysis of COR413 family members in peach with poplar (*P. davidiana x P. bolleana*) and *Arabidopsis thaliana* showed (Figure 4) that peach and poplar *PpCOR* had 9 pairs of collinearity genes, mainly *PpCOR2* and *PpCOR3*. There are 5 pairs of collinear genes with *Arabidopsis thaliana PpCOR*, mainly *PpCOR2*. These results suggest that *PpCOR2* and *PpCOR3* are relatively conserved in genetic evolution and may play an important role in cold stress regulation.

### 1.4 Promoter cis-acting elements of a member of the peach COR413 gene family

The analysis of the cis-acting elements of the *PpCOR* promoter showed that the four *PpCOR* genes all contain a large number of hormone and stress response elements. For example, *PpCOR3* can be induced not only by abiotic stresses such as hypoxia, but also in response to jasmonic acid and abscisic acid (Figure 5).

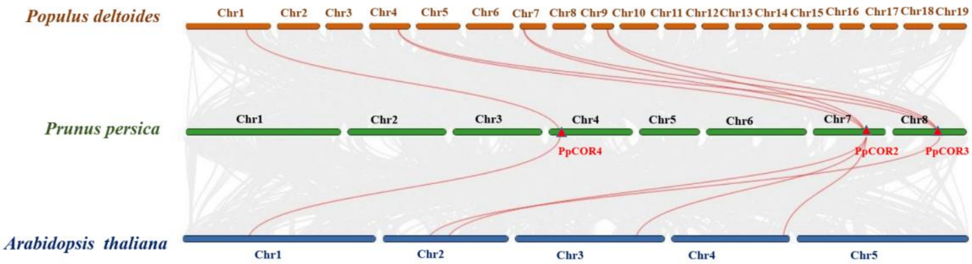

Figure 4 Collinearity analysis of COR413 gene family members in peach, poplar and *Arabidopsis*

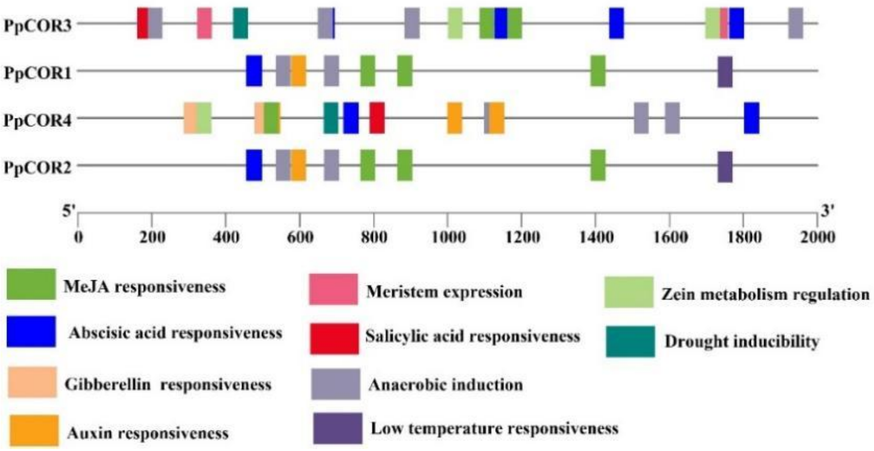

Figure 5 The cis-acting element of the COR413 promoters in peach

### 1.5 Genetic evolution of *COR413* in peach and other species

The phylogenetic tree of PpCOR protein amino acid sequence in peach and grape (*Vitis vinifera* L.), *Arabidopsis thaliana*, maize (*Zea mays* L.) and rice (*Oryza sativa* L.) was constructed. The results showed that COR413 family members could be divided into two subfamilies. *PpCOR1~PpCOR3* belong to the first subfamily, whose members are mainly distributed in the plasma membrane. *PpCOR4* belongs to the second subfamily and is mainly distributed in the thylakoid membrane (Figure 6). The classification results were consistent with the prediction results of subcellular localization. *PpCOR1* and *PpCOR2* cluster together with *AtCOR413-PM2* and *LeCOR413PM2*, *PpCOR3* cluster together with *ZmCOR413-PM1* and *PpCOR4* cluster together with *VvCOR413-IM1*.

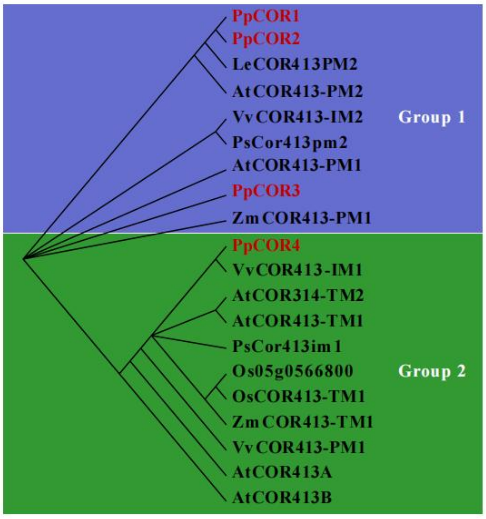

Figure 6 Phylogenetic analysis of the COR413 gene family members in peach and other species

### 1.6 Expression of COR413 gene family members in peach under postharvest low temperature and LTC treatment

Cryogenic storage of peach fruit after harvest is easy to cause chilling injury, accelerate the production of reactive oxygen species, and cause chilling injury symptoms such as fruit browning. Our results show that LTC treatment can slow down the chilling injury of ‘Beijing No.9’ peach fruit during post-harvest low-temperature storage, reduce the production of active oxygen $H_2O_2$, and slow down fruit browning (Figure 7A; Figure 7B). The gene expression results showed that *PpCOR1/2* and *PpCOR4* were down-regulated by low temperature. The expression of *PpCOR3* was up-regulated by low temperature treatment, which was positively correlated with $H_2O_2$ and browning index, indicating that *PpCOR3* may positively regulate chilling injury after harvest. The expression of *PpCOR3* was down-regulated after LTC treatment. It was speculated that LTC treatment reduced the chilling damage degree of fruit and thus reduced the induction of cold regulatory gene *PpCOR3* by low temperature. Interestingly, the expression pattern of *PpCOR3* at low temperature and LTC treatment was significantly positively correlated with the change of $H_2O_2$ content (Figure 7C). These results further indicated that *PpCOR3* was involved in the regulation of LTC treatment to slow down the chilling injury of postharvest peach fruit.

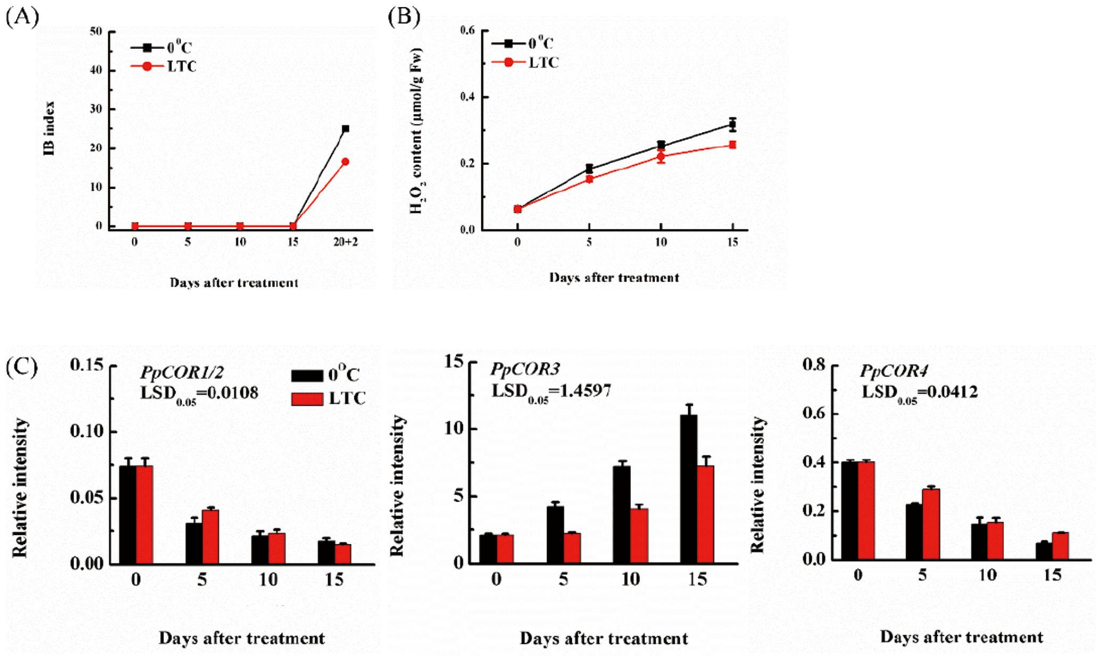

Figure 7 Gene expression of COR413 gene family members with 0°C and LTC treatment at postharvest

## 2 Discussion

LTC treatment can effectively reduce chilling injury caused by low temperature storage of peach (*Prunus persica* L.) (Wang et al., 2017b), mango (*Mangifera indica* L.) (Zhang et al., 2017), loquat (*Eriobotrya japonica* Lindl.) (Liu et al., 2019) and kiwifruit (*Actinidia deliciosa*) (Yang et al., 2013). However, the molecular mechanism remains unclear. Numerous studies have shown that the cold-regulating protein COR413 plays an important role in plant chilling injury regulation, suggesting that *COR413* may be involved in LTC treatment to slow down the regulation of postharvest chilling injury. The study on plant chilling injury has a key significance for the regulation network of *ICE-CBF-COR* in plant cold resistance (Wang et al., 2017a). Many COR413 gene family members are differentially expressed after abiotic stress (Ruibal et al., 2020). Results from *P. davidiana x P. bolleana* (Guo et al., 2009) and *Arabidopsis thaliana* (Su et al., 2018) suggest that *COR413* plays an important role in improving plant cold tolerance.

In this study, members of the peach COR413 gene family were identified for the first time, providing a theoretical basis for the study on the function of the peach COR413 gene family. In this study, it was found that the peach COR413 gene family members encoded 202~230 amino acids with isoelectric points ranging from 9.20 to 10.39, all of which were basic proteins. The number of COR413 gene family members and the physicochemical properties of protein in peach also showed high similarity with Shanputao (*Vitis amurensis*) (Ding et al., 2017) and walnut (*Juglans regia* L.) (Liu et al., 2022).

Members of the peach COR413 gene family all contain conserved *WCOR413* conserved domain (PF05562). From the analysis of conserved structural domain, it can be seen that plasma membrane type *COR413* and thylakoid membrane type *COR413* have great differences in the number of motif, and the number and location of motif in plasma membrane type *PpCOR1~PpCOR3* are roughly the same. However, the conserved motif, intron and exon composition of thylakoid membrane type *PpCOR4* were significantly different from that of *PpCOR1~PpCOR3*, suggesting that there were some differences in gene function between the two *COR413* types.

The COR413 gene family can be divided into two subfamilies, among which *PpCOR1~PpCOR3* belong to the first subfamily, whose members are mainly distributed in the plasma membrane, and *PpCOR4* belong to the second subfamily, whose members are mainly distributed in the thylakoid membrane. This result is consistent with the classification result of COR413 gene family reported by Breton et al. (2003), that is, *COR413* can be divided into plasma membrane proteins (*COR413-PM*) and thylakoid membrane proteins (*COR413-TM*). *LeCOR413PM2* gene overexpression in tomato (*Solanum lycopersicum*) can reduce cell membrane damage, ROS accumulation. RNAi inhibition of *LeCOR413PM2* decreased cold tolerance of tomato plants (Zhang et al., 2021). *PpCOR1* and *PpCOR2* have strong homology with tomato *LeCOR413PM2*, suggesting that *PpCOR1* and *PpCOR2* may be involved in chilling injury regulation of other peach tissues and organs. *PpCOR3* and *PpCOR4* have strong homology with maize *ZmCOR413-PM1* and grape *VvCOR413-IM1*, respectively. However, the function of maize *ZmCOR413-PM1* and grape *VvCOR413-IM1* is still unclear. In addition, at present, there are relatively few reports on the functional differences between the two types of COR413 proteins (COR413-TM and COR413-PM) with different structures and classifications.

The results of this study indicated that LTC treatment could reduce chilling injury, $H_2O_2$ content and fruit browning index in the post-harvest cryogenic storage of 'Beijing No. 9' peach fruit. The occurrence of fruit browning is closely related to the activities of superoxide dismutase (SOD) and catalase (CAT), which scavenge active oxygen radicals, and the increase of malondialdehyde (MDA) and $H_2O_2$, the products of membrane lipid peroxidation (Zhang et al., 2010). The expression of *PpCOR3* in peach COR413 gene family was positively correlated with the change of $H_2O_2$ content, suggesting that *PpCOR3* may affect fruit browning by regulating the production of $H_2O_2$. In addition, analysis of cis-acting elements of promoters in peach COR413 gene family showed that *PpCOR3* could respond to MeJA in addition to a large number of abiotic stress response elements, suggesting the potential role of MeJA in the regulation of chilling injury. Relevant studies have confirmed that MeJA treatment can significantly inhibit the symptoms of post-harvest chilling injury in *Prunus persica* L. (Wei et al., 2017) and *Eriobotrya japonica* (Thunb.) Lindl. (Jin et al., 2012) fruits. Therefore, this study systematically identified COR413 family members and found that *PpCOR3* may play an important role in LTC treatment in alleviating the postharvest chilling injury of 'Beijing No.9' peach fruit. However, its specific regulatory mechanism remains to be clarified.

## 3 Materials and Methods

### 3.1 Plant materials and treatment

The plant material needed for this study is the main peach cultivar 'Beijing No.9' in Mengyin area, collected from Mengyin county, Linyi city, Shandong province. The fruits were collected at 80% ripening, and the fruits with no disease, no mechanical damage and even size were picked and transported to the laboratory for 0 °C and LTC treatment. LTC treatment: pre-storage at 10 °C for 5 days and then store at 0 °C.

### 3.2 Identification of COR413 gene family members

Peach genome was extracted from NCBI database (https://www.ncbi.nlm.nih.gov/genome/?term=peach) and the CDS sequence was extracted using TBtools software. The Simple HMM search plug-in of TBtool software was used to retrieve peach genome annotation protein files with conserved domain *WCOR413* (PF05562). The retrieved sequences were re-validated by the NCBI conserved domain database (http://www.ncbi.nlm.nih.gov/Structure/cdd/wrpsb.cgi/).

### 3.3 Analysis of basic physicochemical properties of gene family members

The basic physicochemical properties of protein sequences were analyzed using Expasy online website (http://web.expasy.org/protparam/), and subcellular localization prediction analysis was performed using PSORT website (http://psort1.hgc.jp/helpwww.html#id).

### 3.4 Chromosome localization and collinear analysis

The Gene Location From Gff module of TBtools software was used for visual analysis of chromosome location. Collinearity analysis was performed by MCscanX software, and the analysis results were visualized by TBtools software. MEME website was used for gene conserved motif analysis. The analysis results of gene structure and its conserved motifs were visualized using the Gene Structure View module of TBtools software.

### 3.5 Analysis of *COR413* genetic evolution

MEGAX software was used to analyze the genetic and evolutionary relationship between *Prunus persica* L. and *Arabidopsis thaliana*, *Vitis vinifera* L., *Oryza sativa* L. and *Zea mays* L. members of *COR413* family, and Muscle method was selected for multi-sequence clustering. The phylogenetic tree is constructed using the Neighbor-Jioning Tree mode. The parameters are as follows: Set the bootstrap method to 1 000, and use the Gaps/Missing Data Treatment to set the Partial deletion to 50%. The evolution tree visualization is visualized using the online software EVOLVIEW (https://evolgenius.info//evolview-v2/#mytrees).

### 3.6 Cis-acting element analysis of *COR413* promoter

The promoter sequence of 2 000 bp upstream of the start codon of *COR413* gene coding region in walnut genome was extracted. The online website PlantCARE (http://bioinformatics.psb.ugent.be/webtools/plantcare/html/) was used to analyze the promoter cis-acting elements, and the analysis results were visualized using TBtools software.

### 3.7 Gene expression

Peach RNA was extracted using Easy Plant (Polysaccharide and Polyphenols) RNA Extraction Kit (Easy-DO), cDNA synthesis was performed using TransScript® II Green One-Step qRT-PCR SuperMix (Transgene). *PpCOR* and internal reference (*EF2*) specific primers were designed using the Primer3 website (http://primer3.ut.ee/) and sent to Tsingke Biotechnology Co., Ltd. for synthesis (Table 2).

Table 2 Primer information for gene expression

| Gene | Forward primer (5′ to 3′) | Reverse primer (5′ to 3′) |
|---|---|---|
| *PpCOR1* | TTTCGCGCACACATTGAAGG | TTCTGAAGCCACCTGAAGCC |
| *PpCOR3* | GCGACTGGATTGGCGTTGTA | CCAAACAGGGTAGACGAACAGA |
| *PpCOR4* | GGGGAAGACAAGAAGGTGCT | GAGAAGGCCTGACACAGCA |
| *EF2* | AGCAGGCTCTTGGTGGTATCT | GATTCAATGACGGGGAGGTAG |

### 3.8 Data analysis

Significance test analysis was performed by Student's t-test, and the difference of minimum significance difference (LSD) at 5% was calculated. The calculation software was DPS 7.05.

### Authors' contributions

XM was the experimental designer and executor of this study. LSJ and ZWN completed the first draft of the paper. ZZG, ZYQ, LZN and DSJ participated in experimental design, analysis of experimental results and analysis of data results. XM was the proposer and leader of the project, directing experimental design, data analysis, paper writing and modification. All authors read and approved the final manuscript.

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