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Quantitative Trait Locus Locating Analysis of Bud Set time in an F_1 Hybrid Population of *Populus deltoides* and *Populus simonii*

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Abstract Growth and dormancy are the two most important biological processes in the life cycle of perennial plants. Studying dormancy-related traits is of great significance for understanding the adaptability of forest growth and improving the efficiency of plant molecular breeding. In order to reveal the genetic mechanism of poplar bud set, we performed quantitative trait locus (QTL) locating analysis of the trait with the KW method in the software MapQTL, based on the F_1 hybrid population derived from a cross of *Populus deltoides* and *Populus simonii* and the two parental linkage maps. As a result, 15 QTLs controlling bud set were identified distributing on 7 linkage groups, among which 12 QTLs were located in linkage groups LG-1, LG-7, LG-9, LG-11 and LG-15 on the maternal *P. deltoides* map, whereas the other 3 QTLs were distributed in linkage groups LG-9 and LG-12 on the paternal *P. simonii* map. According to the location of the QTLs on the *P. trichocarpa* genome, a total of 45 candidate genes for bud set were identified. Furthermore, GO and KEGG enrichment analyses revealed that 71% of the candidate genes possessed potential functions in light and hormone signal transduction pathways. The research results provide a valuable resource for exploring the genes involved with bud set in poplar and for the application in molecular marker-assisted breeding.

Keywords Poplar; Bud set; QTL mapping; Candidate genes

Introduction

Growth and dormancy are the two most important biological processes in the life cycle of perennial plants, comprehensively representing their adaptation to various environments. Most of the plants live in an obvious seasonal environment where the four seasons are defined by distinct temperature and light (Leith, 1975; Vitasse et al., 2014). In forest trees, many growth traits such as bud set and bud flush are greatly affected by local climate. If there is no self-protection or defensive mechanism, the growth and development process of plants will be blocked or die. As a defense mechanism that make plants resistant to freezing injury and dehydration stress, vegetative dormancy is defined as a phenomenon in which a slow-growth or temporary suspension growth of the whole or parts of plants can be observed (Vegis, 2003). When perennial plants undergo an unfavorable environment, the onset of bud set is marked by the cessation of stem elongation and the formation of terminal bud with protected scale, so as to keep out of the low temperature or dehydration environment. When the temperature rises in the next year, bud flush or new leaves occurs when the outermost bud scales fade.

As a key process for perennial plants to go through the dry and cold weather, the bud set time plays a vital role during the vegetative growth and development in forest trees (Benvenuti et al., 2001; Way and Montgomery 2015). In agriculture and forestry production, if set bud is too late in the fall, the trees will be damaged; likewise, if bud set occurs too early in the fall, the trees will have a shortened growing season, reduced biomass and low germination. An improper timing of bud set will reduce tree competitive capacity and growth potential, even reducing the wood yield and quality (Larson and Isebrands, 1972). Thus, a full understanding of the rhythm and genetic mechanism of bud dormancy would allow us to improve the efficiency of forest tree breeding and select superior genotypes in tree improvement programs (Chen et al., 2002).

As a model system in forest trees, the poplar has several advantages for QTL (quantitative trait locus) mapping (Zhou et al., 2015), including small genome size, rapid growth, facile vegetative propagation, and easy genetic transformation (Navarro et al., 2014; Sabatti et al., 2014). A large number of F_1 progeny could be produced as a mapping population by crossing two individual trees between or within species (Stettler et al., 1980; Bradshaw et al. 1994). Moreover, with the continuous development of global warming, bud growth may be affected by climatic change, which will increase the risk of frost damage. Although various models for predicting tree bud dormancy were used to predict the effects of global warming (Hänninen, 1990; Kramer, 1995; Chuine and Rousseau, 1999), very little is known about the genetic mechanism of bud set trait in poplar. Bradshaw and Stettler (1995) and Frewen et al. (2000) successively identified 4 QTLs controlling bud set in *P. trichocarpa* and *P. deltoides*. Subsequently, QTLs for bud set in four different poplar pedigrees were recurrently detected in six regions by Rohde et al. (2011). Due to the small number of molecular markers available and the sparse linkage maps constructed in the previous studies, it is limited to know the number and accurate effects of QTLs for bud set in poplar.

In this study, we reported a QTL mapping study of bud set in an F_1 hybrid population derived by crossing *P. deltoides* and *P. simonii.* The female parent *P. deltoides* has the characteristics of rapid growth and resistance to *Marssonina* leaf spot disease, but it shows poor abilities in adapting, rooting, and resisting to alkali-salt, cold and drought (Zhang et al., 2009). The male parent *P. simonii* has excellent capacities of cold and drought resistance, tolerance in alkali-salt soils, and extensive self-adaption as well as the strong rooting system, but it grows slowly and has a lower economic value (Wei et al., 2011). The two parental poplars produced a large number of progeny significantly segregating in most morphological and physiological traits. Based on the linkage maps constructed in the previous study (Yao et al., 2018), we explored genetic relationships between SNPs and bud set trait. The result revealed the genetic mechanism of bud set time, providing a valuable resource for the application in molecular marker-assisted breeding.

1 Results

1.1 Phenotypic data analysis

We collected the bud set time data of 297 progenies in the F_1 hybrid population of *P. deltoides* and *P. simonii*. The histogram showed that the data had a skewed distribution with a skewness of -0.60 and kurtosis of 1.41 (Figure 1). The earliest bud set occurred on September 20 (DOY=264) and the last on November 1 (DOY=306), lasting 43 days. The paternal *P. simonii* was the earliest in bud setting, while the maternal *P. deltoides* was the last. The bud set time for progeny was between the times of the paternal and maternal. From the frequency distribution, it can be seen that the bud set time data of the whole progeny displayed a significant variation and can be applied for locating QTLs underlying this trait.

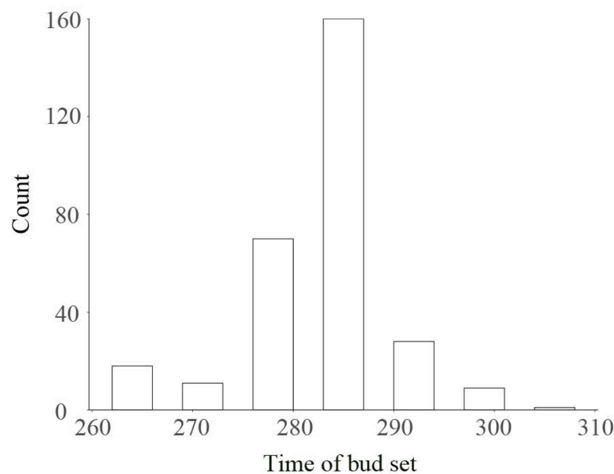

Figure 1 Histogram of the bud set time in the F_1 hybrid population of *P. deltoides* × *P. simonii*

1.2 The QTL analysis of bud set

Based on the high-density linkage maps of *P. deltoides* and *P. simonii*, the Kruskal-Wallis (KW) method in MapQTL6 software was used to detect QTL for bud set. According to the significance test, each SNP marker got its *P* value. The significant threshold of *P* value was determined to be 0.0017 ($-\log_{10}P$ =2.80) by the BH method (Benjamini and Hochberg, 1995). Figure 2 was the scatter plot of the negative logarithm of the *P* value against the position on the parental genetic maps. If there were many SNPs with *P* values exceeding the critical level within a region of 50 cM, we selected the highest peak as the QTL for bud set.

A total of 15 significant QTLs were detected affecting bud set time in poplar, among which 12 QTLs were located in linkage groups LG-1, LG-7, LG-9, LG-11 and LG-15 on the maternal *P. deltoides* map, and 3 QTLs were distributed in linkage groups LG-9 and LG-12 on the paternal *P. simonii* map. The detailed QTL information about linkage group, marker interval, genetic and physical distances were summarized in Table 1. The genetic distances of intervals that contained the significant QTLs ranged from 6.91 to 31.7cM, whereas the physical distances ranged from 203.93 to 2399.64 Kb, with an average physical distance of 853.18 Kb. Compared with the studies of Rohde et al. (2011) and Fabbrini et al. (2012) where the average interval distances of QTLs were 5 651.034 and 6 212.698 Kb, respectively, the intervals of QTLs identified in the current study were greatly shortened, which improved the accuracy of QTL mapping.

1.3 Candidate Genes

To explore the candidate genes of bud set, we used the software Blast2go to re-annotate candidate genes within the physical regions near the detected QTLs. The number of candidate genes in the regions nearby each QTL was listed in Table 1. A total of 45 genes within 10 functions were found to be possibly related to the bud set by the annotation results. A detailed list of candidate genes ID and references were shown in Table 2. Among the dormancy-related studies in poplar, the abscisic acid (Rohde and Bhalerao, 2007), ethylene and gibberellin (Howe et al., 2015) were reported to play an important role in the process of cessation growth and dormancy in the hybrids of *P. tremula* and *P. alba* and the progeny of *P. trichocarpa*. Meanwhile, Baba et al. (2011) found that auxin involved in the dormancy in a hybrid population of *P. tremula* and *P. tremuloides*. We found 5 candidate genes related to abscisic acid, 7 to ethylene, 7 to gibberellin and 4 to auxin. In addition to the above genes, we also found 9 candidate genes related to light signal transduction and 7 related to cold regulation. These genes were also reported in *P. tremula* and *P. alba* (Ruttink et al., 2007), *P. nigra* (Fabbrini et al., 2012) and *P. trichocarpa* (Howe et al., 2015). Other candidate genes for bud set and the corresponding references were listed in Table 2.

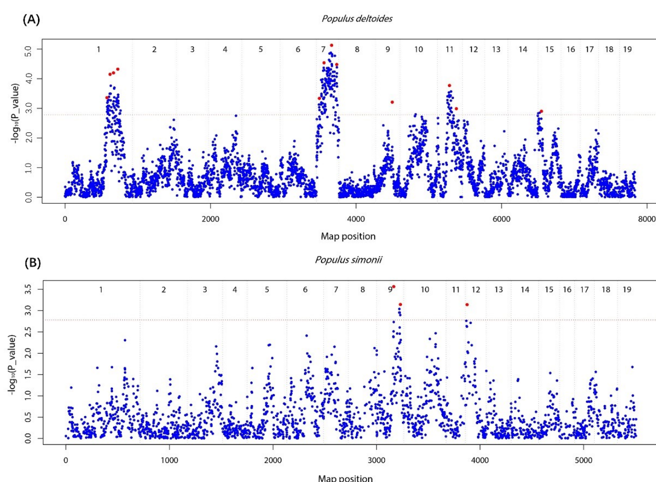

Figure 2 The scatter plot of negative logarithm of the *P* value against the position on the genetic maps of the (A) maternal *P. deltoides* and (B) paternal *P. simonii* for each SNP in the QTL analysis for bud set time in the F_1 hybrid population of *P. deltoides* × *P. simonii*

Note: The dotted red line represents the threshold of negative logarithm of *P* value and the red dot indicates significant QTL

Table 1 Summary of QTLs for bud set time in the F_1 hybrid population of *P. deltoides* × *P. simonii*

QTL	Marker interval	Genetic distance(cM)	Physical distance(Kb)	Candidate genes
qBS-D1-1	CLS140396_14-CLS169051_49	20.67	1016.944	5
qBS-D1-2	CLS57718_71-CLS176127_50	22.63	1296.908	6
qBS-D1-3	CLS89276_67-CLS61391_36	24.28	1090.792	2
qBS-D1-4	CLS84402_41-CLS72148_37	22.87	1677.225	5
qBS-D7-5	CLS116897_15-CLS27649_61	22.32	810.95	1
qBS-D7-6	CLS126145_32-CLS69450_15	21.35	1429.423	4
qBS-D7-7	CLS90539_29-CLS40707_236	22.42	918.45	2
qBS-D7-8	CLS68546_29-CLS67659_37	9.88	652.961	3
qBS-D9-9	CLS183135_23-CLS112630_61	9.99	659.704	1
qBS-D11-10	CLS58626_24-CLS96009_19	30.1	1952.335	2
qBS-D11-11	CLS210290_72-CLS160010_7	21.17	1395.347	3
qBS-D15-12	CLS6356_21-CLS220995_204	17.65	1035.015	5
qBS-S9-13	CLS111793_47-CLS113086_28	14.33	599.211	1
qBS-S9-14	CLS77757_40-CLS57808_22	12.88	676.183	2
qBS-S12-15	CLS148221_8-CLS59042_50	6.91	997.432	3

Note: BS: bud set, D: *P. deltoids*; S: *P. simonii*

Table 2 The functional information of candidate genes

Gene function	ID for candidate genes	Reference
ethylene	Potri.001G280100; Potri.001G315300; Potri.001G313500; Potri.001G356100; Potri.007G043400; Potri.007G046500; Potri.015G023200	Ruttink et al., 2007; Howe et al., 2015
auxin	Potri.001G327500; Potri.001G358500; Potri.011G091900; Potri.012G023400	Baba et al., 2011
gibberellin	Potri.001G278200; Potri.001G315500; Potri.001G350600; Potri.007G103800; Potri.011G095600; Potri.011G134100; Potri.011G134000	Rohde and Bhalerao 2007; Baba et al., 2011
abscisic acid	Potri.001G356100; Potri.007G045800; Potri.007G044300; Potri.011G127800; Potri.015G020500	Rohde and Bhalerao 2007; Ruttink et al., 2007
dormancy	Potri.001G281200; Potri.001G317200; Potri.007G123900; Potri.007G128400; Potri.015G018700; Potri.015G022400; Potri.009G149400	Rohde and Bhalerao 2007
CO/FT	Potri.001G324600; Potri.001G281700; Potri.007G045800; Potri.007G131100	Ruttink et al., 2007; Hsu et al., 2011
light signaling pathway	Potri.001G281000; Potri.001G358400; Potri.007G044300; Potri.007G103800; Potri.011G095600; Potri.009G157600; Potri.012G022400	Ruttink et al., 2007; Fabbrini et al., 2012
ultraviolet-B receptor	Potri.007G100200; Potri.012G018600	Ruttink et al., 2007; Fabbrini et al., 2012
cold-regulated	Potri.001G318100; Potri.001G312700; Potri.001G353500; Potri.007G023100; Potri.009G109800; Potri.015G019800; Potri.009G109800	Howe et al., 2015

We further performed GO enrichment and KEGG enrichment analyses of the selected candidate genes. These genes significantly enriched in 73 GO terms, of which 65 belonged to the category of biological processes, 6 to the cell components, and 2 to the molecular functions. The bubble diagram showed that 20 significant enriched terms involved in bud set development (Figure 3), including light stimulus, temperature stimulus, response to cold, response to hormone, system development, plant organ development and so on. The results of GO enrichment analysis revealed that the bud set of poplar were inextricably bound up with stress responses and developmental processes. The KEGG database was employed to investigate the metabolic and signaling pathways in which the candidate genes were involved. We found that there were 19 candidate genes associated with 11 pathways, including three primary pathways of metabolism, genetic information processing and environmental information processing. The primary metabolic pathways were further subdivided into 5 subordinate metabolic pathways. The predicted pathways were shown in Figure 4, in which only the pathway of diterpenoid biosynthesis was significantly enriched. The results of KEGG enrichment analysis indicated that diterpenoid biosynthesis played an important role in the development of bud set.

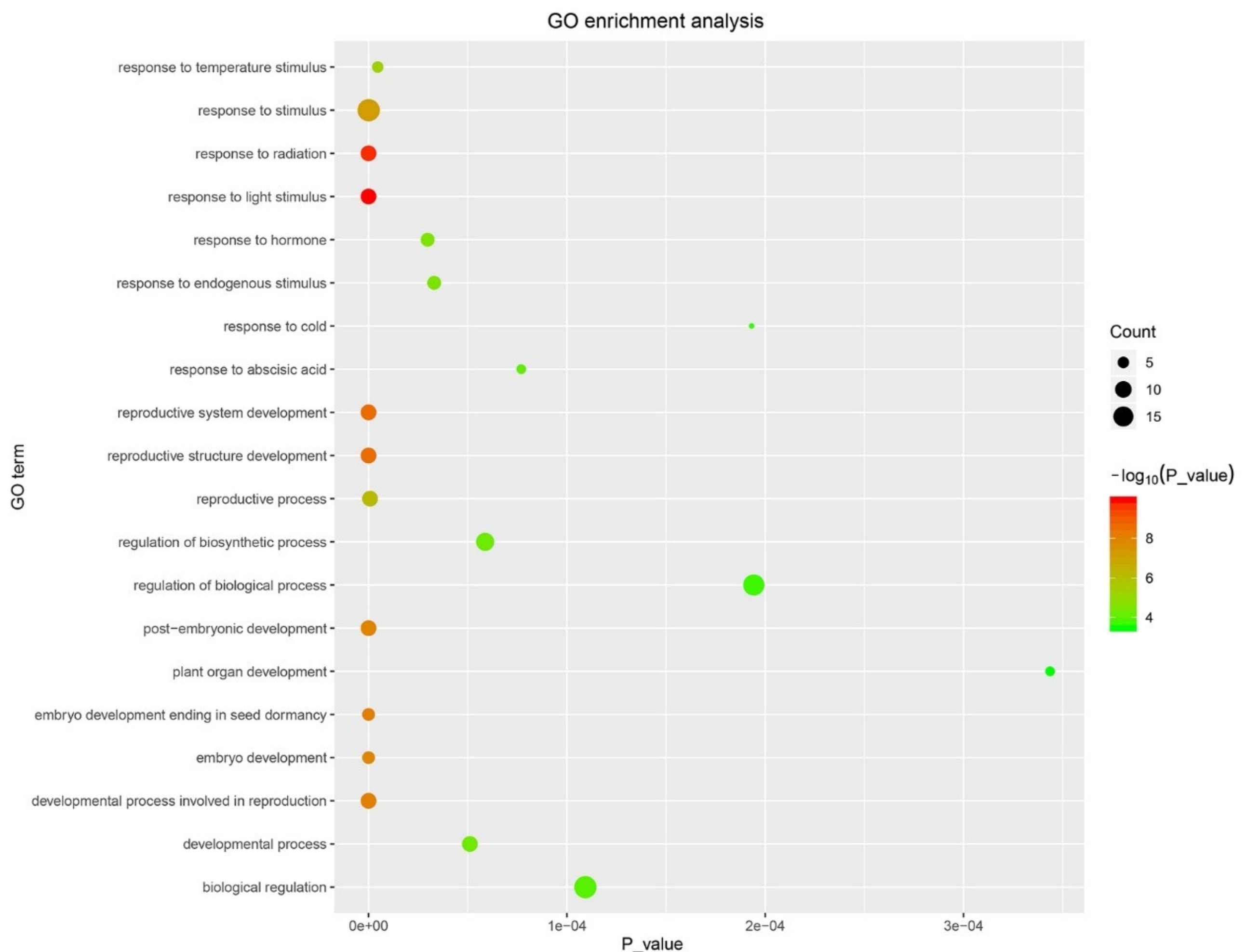

Figure 3 GO enrichment analysis of candidate genes

Note: The abscissa represents the *P* value of each GO term, the ordinate represents the contents of the GO term, and the circle size represents the number of genes searched in the GO database

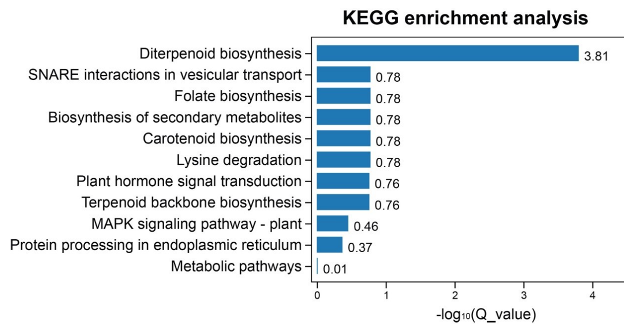

Figure 4 KEGG enrichment analysis of candidate genes

2 Discussion

The seasonal dormancy of trees has great significant practical effects for both agriculture and forestry (Chen et al., 2002). In order to better understand the characteristic of bud dormancy and explore its application in tree molecular breeding, it is worth studying the genetic mechanism of bud set. Bradshaw and Stettler (1995) revealed that the bud set in poplar was under strong genetic control and was affected by environmental factors. Frewen et al. (2000) observed the bud set time lasting 98 days in a hybrid population of *P. deltoides* and *P. trichocarpa*, while in the current study the time spanned much fewer days. The difference of bud set time may be attributed to the difference in geographical origins and climatic changes. Fabbrini et al. (2012) divided the process from growth cessation to the formation of bud set into 7 stages in the *P. nigra* family. They found that the genotype-environment interaction was weakest in the last stage, indicating that the bud set time was strongly controlled by genes but not knowing the accurate genetic mechanism. In this study, we reported a QTL mapping study of bud set with a distinct mapping pedigree and genetic background. In spite of the difference in genetic materials and backgrounds, it can still provide important information for QTL analysis of bud set.

Although Chen et al. (2002) detected some dormancy-related QTLs, but they cannot explain the majority of the phenotypic variations. The reason may be due to the fact that the genetic map contained 35 linkage groups which cannot match the number of chromosomes in *Populus*. On contrast, the genetic map used in this study perfectly matched the karyotype of *Populus*, which could greatly improve the accuracy of QTL analysis. Frewen et al. (2000) identified 4 QTLs controlling bud set in an F_2 hybrid population of *P. deltoides* and *P. trichocarpa*, which were located in linkage groups LG-3, LG-6 and LG-10. Rohde et al. (2011) detected 53 QTLs controlling bud set in four different poplar pedigrees, which were co-located in linkage groups LG-3, LG-5, LG-6, LG-8 and LG-13. Moreover, Fabbrini et al., (2012) detected 16 QTLs controlling bud set in *P. nigra* family, which were located in linkage groups LG-1, LG-3, LG-4, LG-6, LG-7, LG-10, LG-11, LG-13, LG-16, LG-17, LG-18 and LG-19. In this study, some QTLs for bud set were detected on the same linkage group of LG-7 and LG-11 as in the previous studies, which could be considered to be the most important regions underlying the bud set time. However, unlike in the previous studies, we did not detect QTLs on LG-3 and LG-6. There were three reasons for the different results. Firstly, the SNPs we used were not only larger in number but also stable in quality than the markers such as AFLP and SSR applied in the previous studies, which can provide more variation loci and complete genotype information. Secondly, different QTL mapping models were applied in different studies. Most previous studies used the interval mapping method for analysis, while in the current study we directly detected each marker using the KW method (Yan 2019). Since the BH method was used to reduce the probability of false positives in our study, it could greatly improve the efficiency of QTL detecting. Thirdly, different progeny sizes affected the results of QTL mapping to some extends. Without doubt, a large number of progeny could improve the power and accuracy of QTL mapping (Doerge, 2002). A total of 297 individuals were collected for QTL analysis in this study, which covered a large number of mutation loci and genetic information and provided more reliable locus information. Further research would be conducted by collecting multi-year phenotypic data for screening important genes that regulate poplar bud set to apply in tree breeding.

After identifying the QTLs on the genome, we performed re-annotation analysis according to the genes that near QTL. Chen et al. (2002) found that the bud set was affected by hormones, photoperiod, temperature, growth rate, branching rate, insect diseases and so on. Yet, 71% of candidate genes in this study were found to be involved in plant hormone and light signal transduction, while no genes were associated to photoperiod. The different results between the two studies may be caused by two reasons: on the one hand, the plant materials used were different in soil moisture content or improper management of vegetation practices under a natural surroundings; on the other hand, different QTL mapping methods could cause different results. It is most helpful to understand the molecular mechanism of regulating the bud set time by fine QTL mapping, for the development and utilization of poplar germplasm resources, and improving the molecular breeding of the adaptability of trees under the global warming.

3 Materials and Methods

3.1 Mapping population

The mapping material was a population of interspecific F_1 hybrids between *P. deltoides* and *P. simonii*. The female *P. deltoides* (clone I-69) were selected from Siyang Forest Farm, Siyang County, Jiangsu Province, China and the male *P. simonii* from Luoning, Luoyang, Henan Province, China. The crossing was successively performed in the early springs from 2009 to 2011. About 500 F_1 progeny were obtained and planted in Xiashu Forest Farm of Nanjing Forest University, Jurong County, Jiangsu Province, China (Tong et al., 2016).

3.2 Phenotypic data collection

The bud set time of each individual was recorded as described in Frewen et al. (2000). The number of days from December 31, 2011 to the date of bud set occurrence was regarded as the trait of DOY (Day of the year). Bud set date was recorded when all stems had no new leaf extension, all healthy apices on the tree had a terminal bud with scales and the buds became reddish brown.

3.3 QTL mapping for bud set

A total of 297 individuals were selected for QTL mapping from the F_1 hybrid population of *P. deltoides* and *P. simonii*. With the SNPs on the genetic linkage maps constructed in the previous study (Yao et al., 2018), QTL analyses were performed on the bud set time using the non-parametric Kruskal-Wallis (KW) rank sum test (Lehmann, 1975) in the MapQTL software (Van Ooijen, 2009). The linkage maps of *P. deltoides* and *P. simonii* consisted of 4018 and 2097 SNP markers, respectively (Yao et al., 2018). Because the bud set time data of the progeny deviated from a normal distribution, no assumptions were made for the probability distribution and the KW method was used to detect QTL (Jorge et al., 2005; Hanley et al., 2011; Dai et al., 2019). In order to explore the significant relationship between SNP markers and the bud set trait, the KW rank sum test first classified the individuals according to the marker genotypes, and then ranked the bud set data of the individuals in ascending. After that, the K value was obtained by calculating the sum of the squared ranks in each group and dividing by the total variance. The K value was approximately distributed as the chi-squared distribution with $k-1$ degrees of freedom. The *P* value of each SNP marker was calculated according to the chi-squared distribution, which represented the correlation level between the SNP marker and the phenotypic trait. This threshold was determined by the Benjamini–Hochberg (BH) correction method for multiple tests (Benjamini and Hochberg, 1995). The BH method first ranked the *P* values of all SNPs, and then calculated the Q value according to the formula: $Q=P*(m/k)$, where m is the number of tests (the number of SNP markers), and k is the rank of *P* values in the tests. When a former *Q* value of the SNP is greater than the next *Q* value of the SNP, then the former *Q* value should be revised. While the *Q* value of SNP was below the significant level of 0.05 (P=0.0017), it was considered that SNP was significantly correlated with the bud set.

The QTL naming was based on the method of McCouch et al. (1997). In brief, the QTL name consisted of the following parts: q + trait name + LG number + QTL number.

3.4 Candidate genes

In order to explore the candidate genes for bud set, we searched the encoding genes within the physical region of each QTL from the database of *P. trichocarpa* v4.1 at Phytozome (https://phytozome.jgi.doe.gov/). First, the position of SNP on *P. trichocarpa* genome was determined and then the coding sequences (CDS) of the genes within the region were extracted. Second, the Blast2go software (Conesa et al., 2005) was used to re-annotate these genes. The CDS were blasted in Non-Redundant Protein Sequence Database (Nr) and re-annotated. Finally, we carried out gene ontology (GO) (Ashburner et al., 2000) and Kyoto Encyclopedia of Genes and Genomes (KEGG) enrichment analyses (Ogata et al., 1999), so as to identify candidate genes for the bud set.

Authors' contributions

WZ participated in data interpretation and wrote the manuscript; WZ, HNW and HG analysed the phenotypic data and modified the manuscript; WZ, DYW, HXX, JJO and YW collected the phenotypic data and participated in the field management; CFT conceived and designed the study, contributed to phenotypic data analyses and writing. All authors read and approved the final manuscript.

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