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# Regulation of *StTCP15* gene expression and tuber dormancy characteristics of potato by gibberellic acid, abscisic acid, and low temperature

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## Abstract

Potato (*Solanum tuberosum* L.) cv. Eshu 10 was used to investigate the effects of exogenous gibberellic acid ($GA_3$), abscisic acid (ABA), and low-temperature stress on changes of hormone content, expression patterns of *StTCP15* gene, and tuber dormancy characteristics. Under $GA_3$ treatment and low-temperature stress, tuber dormancy was broken in about one week sooner compared with the control group, but ABA treatment did not significantly promote the breaking of tuber dormancy. The results of hormone determination using liquid chromatography-mass spectrometry (LC-MS/MS) showed that the content of ABA in tubers treated with $GA_3$ or low-temperature stress was lower than in the control group, and it was higher than in the control group under ABA treatment. The $GA_3$ content of tubers was higher than in the control group under $GA_3$ treatment and lower under low-temperature stress. During dormancy, the ABA content continued to increase and $GA_3$ content fluctuated, ABA content rapidly decreased and $GA_3$ content rapidly increased when the dormancy was breaking, and both ABA content and $GA_3$ content increased during germination. The results from the assay of real-time quantitative PCR showed that the expression of the *StTCP15* gene was continuously increased during the dormant period in all groups, and the expression of the *StTCP15* gene was the highest at the time of dormancy release. The expression of the *StTCP15* gene was increased about 15 times on the 7$^{th}$ d under low-temperature stress and was restored at room temperature. Thus, the *StTCP15* gene can respond to $GA_3$, ABA, and low-temperature stress and may be involved in the release of potato tuber dormancy.

*Keywords*: abscisic acid, gibberellin, low temperature, potato, *Solanum tuberosum*, *StTCP15* gene, tuber dormancy.

## Introduction

Potato (*Solanum tuberosum* L.), one of the most important crops, has been grown for more than 6 000 years. Potato tubers contain a lot of nutrients, but improper storage after harvest can lead to serious waste (Alamar *et al*. 2014). The dormancy length and breaking time of potato tuber has great economic significance for potato planting. The excessive dormancy period has certain effects on the seeding period, emergence, and yield (Sonnewald and Sonnewald 2014).

Common methods of breaking potato tuber dormancy can be roughly divided into two types: chemical method and physical method. Among them, the chemical method mainly includes the exogenous hormones, and the physical method is mainly the alternating temperatures. Some researchers found that 10 mg dm$^{-3}$ of gibberellic acid ($GA_3$) had the best effect on breaking dormancy of virus-eliminating potato (Ye *et al*. 2000). Temperature-changing treatment can effectively shorten the dormancy

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*Abbreviations*: ABA - abscisic acid; $GA_3$ - gibberellic acid.
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range of potato with an average decrease of 20.2 d (Yang *et al*. 2003). Zhong *et al*. (2017) found that abscisic acid (ABA) treatment effectively prolonged potato dormancy. Therefore, it is a need to elucidate the effects of $GA_3$ and ABA for regulating potato tuber dormancy for the planting of potatoes suitable for markets.

The name of TCP (Teosinte branched 1, Cycloidea, Proliferating cell factor) transcription factor derived from the initials of functionally identified members: TB1 (Teosinte Branched 1) of *Zea mays* (Doebley *et al*. 1997), *CYC* (Cycloidea) of *Antirhimum majus* (Luo *et al*. 1996), and *PCF1/2* (Proliferating cell factor 1/2) of *Oryza sativa* (Kosugi *et al*. 1997). According to the homology of TCP domains, TCPs can be classified into two categories: one is PCF1/PCF2 and the second is CYC and TB1 (Martín-Trillo *et al*. 2010, Navaud *et al*. 2007). At present, the *TCP* gene family has been identified in a variety of plants, including 24 in *Arabidopsis thaliana* (Riechmann *et al*. 2000), 96 in *Nicotiana tabacum* (Chen *et al*. 2016), 28 in *Triticum aestivum* (Ding *et al*. 2018), 29 in *Oryza sativa* (Navaud *et al*. 2007, Xiong *et al*. 2005, Yao *et al*. 2007), 31 in *Solanum tuberosum* (Wang *et al*. 2018) and so on. TCP transcription factors play important roles in plant development, hormonal responses, and responses to abiotic stresses. In *Arabidopsis*, AtTCP3 interacts with R2R3-MYBs to regulate flavonoid synthesis (Li and Zachgo 2013); AtTCP13 was involved in the cytokinin signalling pathway, which affects cell division (Suzuki *et al*. 2001); DELLA protein binds to AtTCP14 and inhibits plant growth and germination (Davière *et al.* 2014, Resentini *et al*. 2015). In rice, overexpression of the *OsTCP19* gene dependent on miR319 increases drought and salt tolerance in plants (Zhou *et al*. 2014).

In *Arabidopsis*, *AtTCP14* and *AtTCP15* genes can promote the development of germplasm through the gibberellin signalling pathway to relieve early dormancy of seeds (Resentini *et al*. 2015). There is higher homology between StTCP15 and StTCP23 in potato with AtTCP14 and AtTCP15 in *Arabidopsis* (Wang *et al*. 2018). Our previous study has found that seven potato *StTCP* genes including *StTCP4*, *StTCP11*, *StTCP14*, *StTCP15*, *StTCP22*, *StTCP23* and *StTCP29* changed significantly in different tubers dormancy stages (dormancy, dormancy release, and sprouting), where *StTCP15* gene expression was significantly upregulated. Combining with *Gene Ontology* (*GO*) annotation, it was found that the *StTCP15* gene contains abscisic acid and gibberellin response elements, indicating that the gene may play a role in potato tuber dormancy release.

In this study, to elucidate the effect of exogenous $GA_3$, ABA, and low-temperature stress on *StTCP15* gene expression and potato tuber dormancy, the content of the hormones was determined by liquid chromatography-mass spectrometry (LC-MS/MS), and the relative expression of *StTCP15* gene was determined by RT-qPCR analysis. The results could lay a foundation for further study on potato tuber dormancy and sprouting mechanism.

## Materials and methods

**Plants and treatments:** Potato (*Solanum tuberosum* L. cv. Eshu 10) tubers with uniform size, similar shape, and no obvious scar were selected as experimental materials, which were randomly divided into four groups: *1*) soaked in 10 mg $dm^{-3}$ $GA_3$ solution for 15 min, *2*) soaked in 10 mg $dm^{-3}$ ABA solution for 15 min, *3*) stored at 4 °C for one week, and *4*) control group without any treatment. All groups were stored separately in a dark and at room temperature of about 25 - 28 °C. All groups were repeated three times. Samples were taken every 7 d, placed into liquid nitrogen, and stored in a refrigerator at -80 °C for further use.

The tuber sprouting rate was calculated when the first bud length of the tuber was 2 mm (Zhong *et al*. 2017). Sprouting rate [%] = number of germinated tubers/total tubers × 100.

**Extraction and determination of $GA_3$ and ABA content in potato tubers:** The hormones were extracted from potato tubers according to the method of Ding *et al*. (1979). Sampling was performed using an 8 mm aperture punch for sampling, removing the tissues at both ends and after obtaining the samples (1 g) and addition of liquid nitrogen it was ground to powder. Then 8 $cm^3$ of 80 % (v/v) methanol (precooled at 4 °C) was added and extracted at 4 °C overnight. After centrifugation at 6 297 *g* and 4 °C, the residue was extracted again. A total of 16 $cm^3$ of supernatant was obtained. A rotary evaporator was used to remove the alcohol phase and retain the water phase, adjust the pH to 8.0 with 0.4 M $NaHPO_4$ and extracted twice with an equal volume of petroleum ether to retain the aqueous phase. The excess petroleum ether was removed on a rotary evaporator, and then the pH was adjusted to 2.8 with 0.4 M citric acid and extracted three times with the same volume of ethyl acetate, and the aqueous phase was discarded to leave the ether phase. Then it was evaporated to dryness on a rotary evaporator, dissolved the residue with methanol and passed through 0.22 μm organic filter membrane (*Biosharp*, Hefen, Anhui Province), to be tested.

Liquid Chromatograph-Mass Spectrometer (LC-MS; *Agilent 1290-6460*, Santa Claram, California) with a resolution of 0.4 amu (atomic mass units), scanning range 5 - 3 000 m/z, for separation and determination of trace target compounds in a complex matrix. Chromatographic conditions: *Agilent ZORBAX Eclipse Plus* C18, rapid resolution HD 2.1 × 150 mm, 1.8-Micro, (P.N. 959759-902), its surface area is 160 $m^2 g^{-1}$, a pore diameter of 95 Å. Column temperature: 35 °C, injection volume: 3 $mm^3$, mobile phase A: 0.1 % methanoic acid water, mobile phase B: methanol, flow rate 0.3 $cm^3 min^{-1}$; gradient elution (Table 1 Suppl.). Mass spectroscopic parameters: in MRM mode, with ESI negative ion mode, a capillary voltage 4 kV, dryer flow 11 $dm^3 min^{-1}$, dryer temperature 350 °C and a materialized pressure 15 psi (pound per square inch), MS parameters (Table 2 Suppl.).

Standard solution preparation: 0.01 g of $GA_3$ and ABA standards, made up to 100 $cm^3$ of methanol, and the

concentration of the single standard mother liquor was 100 mg $dm^{-3}$. The mixed standard solution was diluted to 1 000 µg $dm^{-3}$ with methanol and was gradually diluted with methanol, and the final working standards were 200, 100, 50, 20, 10, and 2 µg $dm^{-3}$ standard working solutions.

***StTCP15* gene expression by real-time quantitative PCR detection:** Total RNA was extracted using *RNA Simple Total RNA* kit (*Tiangen Biotech*, Beijing, China) from potato tubers. *FastKing gDNA Dispelling RT SuperMix* (*Tiangen*) was used for cDNA first-strand synthesis. The specific primers were designed based on *StTCP15* gene sequence as forward primer 5′-TCCACCAAAGACCGCCATAC-3′ and reverse primer 5′-GGTTCCTGTAGCGGCGATTA-3′. *EF1α* gene was as the internal reference gene (Tang *et al.* 2017), and its specific primers were: forward primer 5′-GATGGTCAGACCCGTGAACA-3′ and reverse primer 5′-CCTTGGAGTACTTCGGGGTG-3′. All primers were synthesized by *Suzhou Jinweizhi Biotechnology Co.* (Suzhou, Jiangsu Province) To calculate the relative expression of the *StTCP15* gene the $2^{-\Delta\Delta CT}$ method was used (Livak and Schmittgen 2001).

**Statistical analysis:** *Microsoft Excel 2010* was used for data processing, and *Origin 8.6* was used for mapping. Duncan's multiple range test was used to determine significant differences at the 5 % probability level.

## Results

The sprouting rate of tubers under different treatments was shown in Fig. 1 Suppl. The tuber dormancy was broken earlier under $GA_3$ treatment and low-temperature stress than under ABA treatment and in the control group. Also, the sprouting rate under $GA_3$ treatment and low-temperature stress was higher than that under ABA treatment and in the control group in the same period. These results showed that $GA_3$ and low temperature can effectively promote the breaking of tuber dormancy. ABA treatment did not show a significant effect on tuber sprouting, and the sprouting rate was only slightly lower than in the control group.

In the control group, the content of $GA_3$ decreased after a slight increase on the 7th day and maintained low to the 28th day, and began to increase rapidly on the 35th day (Fig. 1). The content of $GA_3$ in tubers was significantly higher than that in the control group under $GA_3$ treatment and was about 5 times that of the control group on the 1st day. The $GA_3$ content decreased on the 7th day under the $GA_3$ treatment, and the content of source $GA_3$ fluctuated within 7 - 35 d and the peak of $GA_3$ content was on the 14th and 28th d under $GA_3$ treatment, respectively.

Under ABA treatment, the content of $GA_3$ in potato tubers fluctuated from 1st to 42nd day, peaked twice at 14th and 35th day, and increased significantly from 42 to 49 d (Fig. 2).

The content of $GA_3$ was significantly lower than that of the control group at 1 - 21 d under low-temperature stress (4 °C), especially it decreased to 1.48 ng $g^{-1}$(f.m.) on the 7th day (Fig. 3). However, the content of $GA_3$ began to increase obviously from 28 d. The content of $GA_3$ was not significantly different from that of the control group under the low-temperature treatment on the 42nd day and it is suspected to be a sampling error. On the 49th day, the $GA_3$ content in the low-temperature treatment was about twice higher than that in the control group.

On the first day, the content of ABA under $GA_3$ treatment was significantly lower than that in the control group and significantly increased to be even higher than that of the control group on the 7th day (Fig. 4). The

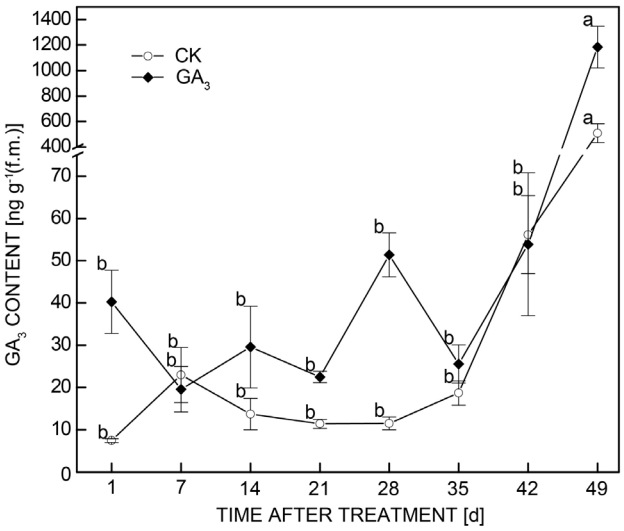


Fig. 1. Changes of $GA_3$ in tubers treated with exogenous $GA_3$. CK - control, $GA_3$ - $GA_3$ treatment. Means ± SEs, $n = 3$ biological replicates, different letters mark significantly different values in the same time (Duncan's multiple range test at $P < 0.05$).

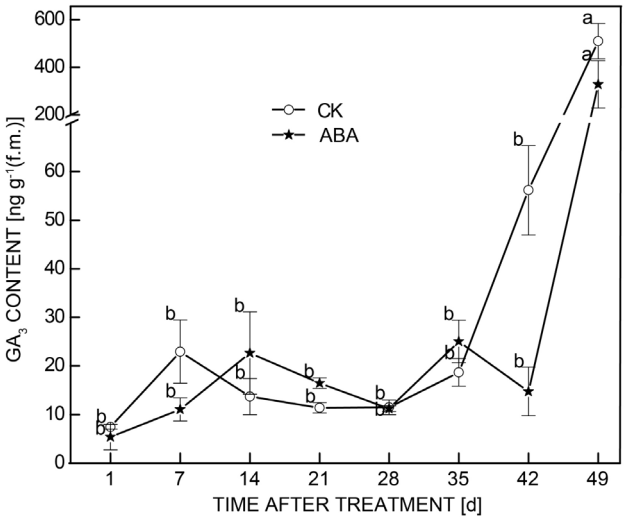


Fig. 2. Changes of $GA_3$ in tubers treated with ABA. CK - control, ABA - ABA treatment. Means ± SEs, $n = 3$ biological replicates, different letters mark significantly different values in the same time (Duncan's multiple range test at $P < 0.05$).

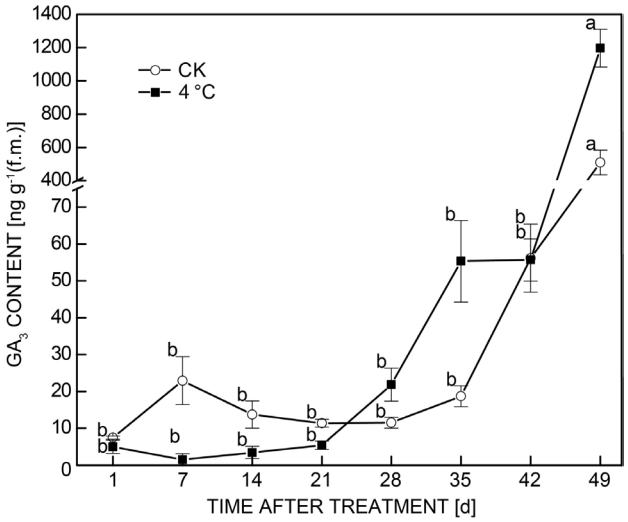


Fig. 3. Changes of $GA_3$ in potato tubers under low-temperature treatment. CK - control, 4 °C - low-temperature stress. Means ± SEs, $n = 3$ biological replicates, different letters mark significantly different values in the same time (Duncan's multiple range test at $P < 0.05$).

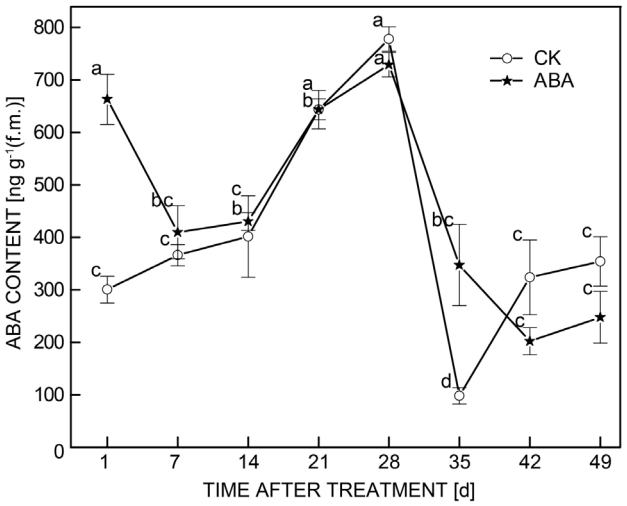


Fig. 5. Changes of ABA in tubers treated with exogenous ABA. CK - control, ABA - ABA treatment. Means ± SEs, $n = 3$ biological replicates, different letters mark significantly different values in the same time (Duncan's multiple range test at $P < 0.05$).

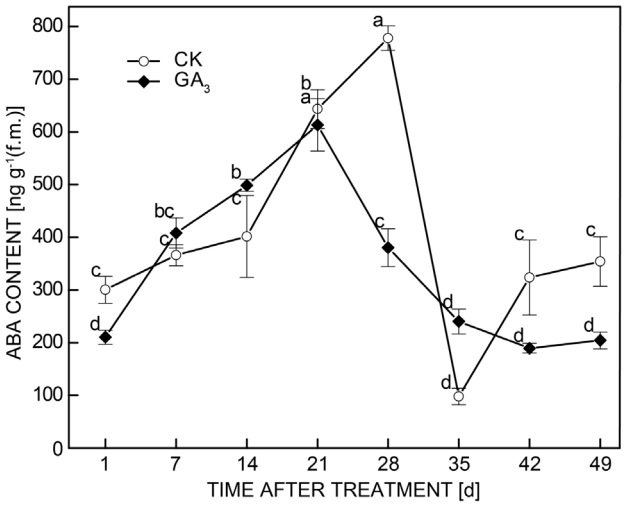


Fig. 4. Changes of ABA content in tubers treated with $GA_3$. CK - control, $GA_3$ - $GA_3$ treatment. Means ± SEs, $n = 3$ biological replicates, different letters mark significantly different values in the same time (Duncan's multiple range test at $P < 0.05$).

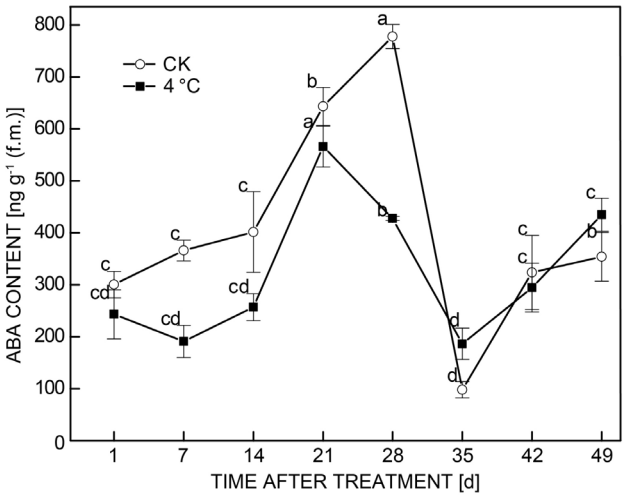


Fig. 6. Changes of ABA content in the tuber of potato under low-temperature stress. CK - control, 4 °C - low-temperature stress. Means ± SEs, $n = 3$ biological replicates, different letters mark significantly different values in the same time (Duncan's multiple range test at $P < 0.05$).

content of ABA under $GA_3$ treatment and in the control group decreased rapidly after reaching the maximum value on the 21st and 28th day, respectively. Under $GA_3$ treatment, the content of ABA was then stabilized at 180 - 240 ng $g^{-1}$(f.m.). The content of ABA in the control group dropped to the lowest value of 98 ng $g^{-1}$(f.m.) and then rose again.

On the first day of ABA treatment, the content of endogenous ABA was more than 2 times that of the control group (Fig. 5). The content of ABA decreased significantly on the 7th day and began to increase on the 14th day. After reaching the peak on the 28th day and after 42nd day it fell to the lowest value and then started to increase slightly.

Under low-temperature stress, the content of ABA was lower than that of the control group within 1 - 28 d (Fig. 6). The content of ABA started to increase on the 7th day and reached a peak after the 21st day, decreased to the minimum value on the 35th day and then increased to values similar to those in the control group.

The relative expression of the *StTCP15* gene showed that the whole expression trend in the control group and under the ABA treatment increased first and then decreased, and the relative expression of the *StTCP15* gene peaked

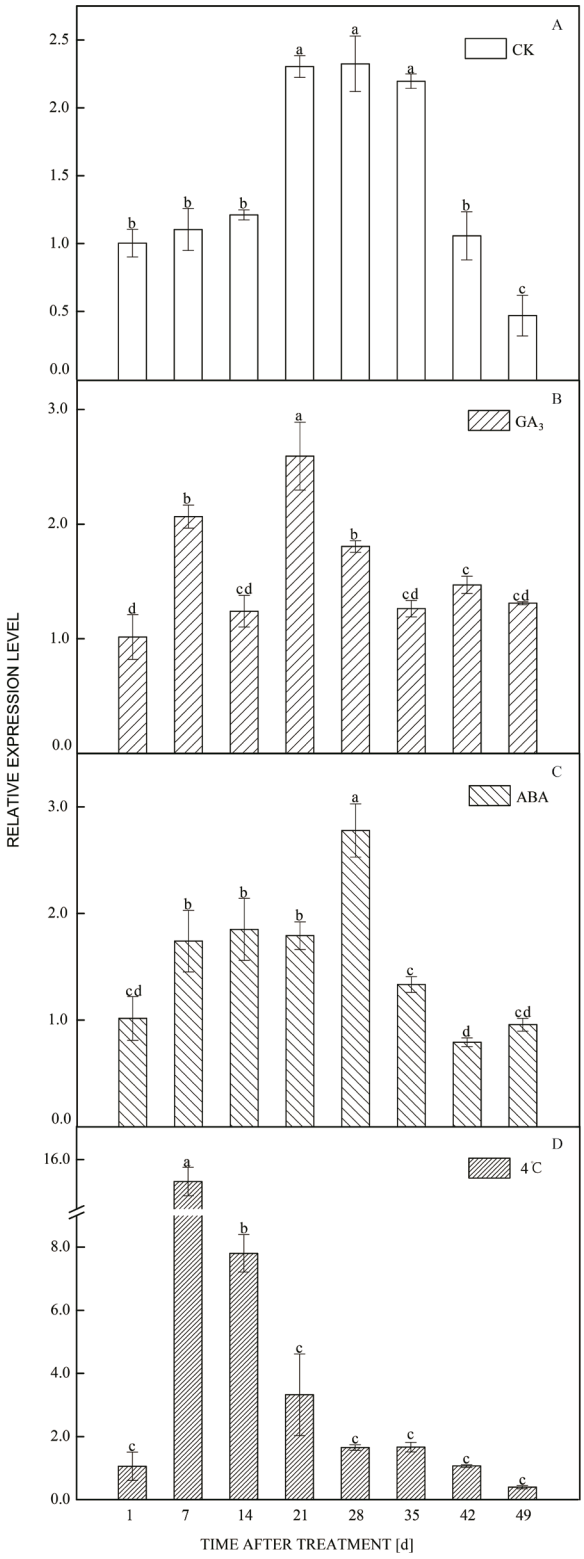


Fig. 7. Changes of relative expression of *StTCP15* gene under different treatments. *A*, *B*, *C*, and *D* indicate control group (CK), $GA_3$ treatment, ABA treatment and low-temperature stress, respectively. Means ± SEs, $n = 3$ biological replicates, different letters mark significantly different values in the same time (Duncan's multiple range test at $P < 0.05$).

on the 28th day (Fig. 7). The relative expression of the *StTCP15* gene was increased significantly on the 7th day under $GA_3$ treatment, slightly decreased on the 14th day, and fell back after peaking on the 21st day. The expression of the *StTCP15* gene decreased after a significant 15-fold increase on the 7th day under low-temperature stress (Fig. 7).

## Discussion

Tuber dormancy release was a complex process involving the regulation of hormones, nutrients, kinases, and the expression of genes associated with plant growth and development (Deng 2010). $GA_3$ and ABA play an important role in seed dormancy. $GA_3$ can promote seed germination by accelerating the metabolism of substances and the synthesis of related enzymes (Brady and McCourt 2003). ABA was considered a germination inhibitor (Footitt *et al.* 2011). In *Paeonia rockii* seeds, the content of $GA_3$ slowly increases during dormancy and it increases rapidly after breaking the dormancy (Li *et al.* 2019). The content of $GA_3$ needs to reach a certain level to release the dormancy (Liu *et al.* 2015). In this study, the content of $GA_3$ in potato tuber was stable during the dormancy stage, and increased rapidly and significantly during sprouting, indicating that the content of $GA_3$ increased and reached a certain value to break the dormancy. In the dormant period, the ABA content is high, and it decreases at the start of dormancy release (Coleman *et al.* 1984). In this study, it was found that the content of ABA increased continuously during dormancy and reached its maximum during dormancy release; the ABA content decreased rapidly and increased again during sprouting. Antagonism between $GA_3$ and ABA (Kang *et al.* 2007) is consistent with the results obtained during tuber dormancy in this study. However, during the sprouting, the content of $GA_3$ increased rapidly and the content of ABA also increased, indicating that $GA_3$ and ABA were not simply antagonistic but had more complex relationships in potato tubers.

The results showed that the decrease of ABA content under low-temperature stress played an important role in breaking the dormancy early (Xia *et al.* 2019). This study found that the content of ABA in potato tubers under low-temperature stress was significantly lower than that in the control group, and the content of ABA decreased to the lowest value within the 7th day of low-temperature stress, and the ABA content increased rapidly at room temperature. Therefore, it can be speculated that the low-temperature stress caused the decrease of ABA content in the potato tuber, which made potato tuber break dormancy quickly. It was found that $GA_3$ treatment increases the content of $GA_3$ in potato tubers and the nutrients in tubers are transformed to accelerate tuber sprouting, while ABA treatment increases the content of ABA to prolong dormancy and inhibits tuber sprouting for a short time (Li *et al.* 2019). Exogenous ABA and $GA_3$ changed the content of endogenous hormones in tubers, which indicated that their content might be affected by environmental factors and the change affects the dormancy and sprouting of

tubers.

Although exogenous $GA_3$ and low-temperature stress accelerated potato tubers to break dormancy about 7 d ahead of the control group, ABA treatment did not significantly inhibit tuber sprouting. The reason may be that the time of hormone treatment was not at the optimum time. Potato tubers were treated one week after harvest in the study, while Ye *et al*. (2000) thought that potato tubers should be stored for 15 d after harvest before treatment. It was also worth noting that ABA was found to have a negative regulatory effect on dormancy in the study of Zhang *et al*. (2003), but this effect can be reversed by $GA_3$, and to maintain its effectiveness, the ABA must be applied continuously or repeatedly.

TCPs are a class of plant-specific transcription factors and play an important role in plant development. Studies have shown that TCP transcription factors regulate plant morphology and structure and play a role in multiple pathways related to cell proliferation and hormone responses (Manassero *et al*. 2013). TCP transcription factors have been reported to participate in a variety of hormone signalling pathways, such as brassinosteroids (BRs) (Li *et al*. 2013), strigolactone (SL) (Davière *et al*. 2014), jasmonic acid (JA) (Resentini *et al*. 2015), cytokinin (CTK) (Lucero *et al*. 2015, Rueda-Romero *et al*. 2011), gibberellin (Guo *et al*. 2010), abscisic acid (Rueda-Romero *et al*. 2013), and other signal transduction pathways.

The *StTCP15* gene in potato was highly homologous to the *AtTCP14* gene in *Arabidopsis* (Wang *et al*. 2018). In *Arabidopsis*, AtTCP14 binds to the transcription factor DOF6, preventing DOF6 from activating ABA biosynthesis gene *ABADEFIENT1* (*ABA1*) and other ABA-related genes, inhibiting ABA signalling and promoting seed germination (Tatematsu *et al*. 2008, Lei *et al*. 2017). The results showed that the relative expression of the *StTCP15* gene in potato tubers treated with different hormones was consistent with the change of ABA content at room temperature, but not with the change of $GA_3$ content (Figs. 1-7). The *StTCP15* may be involved in the ABA signalling pathway and alter tuber dormancy by modulating hormone changes, especially under $GA_3$ and ABA treatments.

Davière *et al*. (2014) reported that the *AtTCP14* gene is involved in the $GA_3$ signalling pathway, and the circadian clock improves the stability of DELLA protein during the day and its sensitivity to $GA_3$ at night by transcriptionally regulating the expression of $GA_3$ receptor AtGID1. In this study, the relative gene expression of $GA_3$ treatment was significantly up-regulated on the 7$^{th}$ day and decreased on the 14$^{th}$ day. The content of ABA did not decrease and the expression of the *StTCP15* gene was significantly up-regulated on day 0 - 7 after $GA_3$ treatment, indicating that *StTCP15* may be involved in $GA_3$ signaling pathway to regulate tuber dormancy.

*MeTCP3a* and *MeTCP4* in cassava having altered expression under cold, drought, and salt stress indicated that *TCP* genes may play a role under abiotic stresses (Tatematsu *et al*. 2008). In this study, it was found that the relative expression of the *StTCP15* gene was significantly up-regulated under low-temperature stress (Fig. 7), it can be speculated that the *StTCP15* gene played a role in response to cold stress. The relative expression of the *StTCP15* gene was continuously up-regulated during the dormancy release of potato tubers, and the expression of the *StTCP15* gene peaked during the dormancy release. The *StTCP15* gene may have an important role in the release of tuber dormancy.

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