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# Additive and epistatic QTLs underlying the dormancy in a diploid potato population across seven environments

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ABSTRACT

Tuber dormancy is important for potato tuber quality and is a typical quantitative trait. Understanding the genetic basis of potato tuber dormancy is essential for controlling the potato tuber dormancy length. In order to analyze the quantitative trait, a diploid potato population EB with a genetic background derived from *S. tuberosum*, *S. berthaultii*, *S. phureja*, *S. vernei*, etc, was used for QTL analyses. With tubers of population EB harvested from seven environments, six QTLs with additive effects and four other QTLs involved in epistatic interactions were uncovered. These QTLs might partially demonstrate the gene regulatory network of tuber dormancy in potato. The fine mapping and map-based cloning of these QTLs, especially DorE4.6 and DorB5.3 with major additive effects across seven environments, will further the understanding of the genetic mechanism of potato tuber dormancy. The molecular markers linked to the stable QTLs, DorE4.6 and DorB5.3, provided good assistant marker candidates for pyramid breeding aiming at the potato cultivar with a desirable dormancy length.

## 1. Introduction

Tuber dormancy is one of the prominent and important features for potato (*Solanum tuberosum* L.) industry. During the postharvest storage, the breaking of dormancy and sprouting are detrimental to the nutritional and processing qualities of potatoes, accompanied by many physiological changes including the increases in reducing sugar content, respiration, water loss, and glycoalkaloid content (Suttle, 2004). Low temperature storage can prevent the breaking of dormancy and sprouting, but can also result in the conversion from starch to sugars and Maillard reaction, affecting the baking quality (Haase, 2007). On the contrary, a short dormancy period and early sprouting are needed for double cropping potato cultivars. Chemicals, including Rindite, are often used to induce early sprouting. However, the chemicals are under pressure of being abandoned because of public concern (Vreugdenhil, 2007). The genetic control aiming at desirable dormancy length is good alternative to avoid the disadvantages caused by low temperature and chemicals during storage. Understanding the genetic basis of potato tuber dormancy is essential for controlling the potato tuber dormancy length.

Transcriptomic and transgenic approaches have been used to reveal the genetic basis of dormancy of potato. The period of dormancy for the transgenic potato tubers expressing an inorganic pyrophosphatase gene derived from *Escherichia coli*, was reduced by six to seven weeks when compared to that of wild-type tubers (Farré et al., 2001). With RNA sequencing, Liu et al. (2015) identified 26,639 genes including 5912 (dormancy tuber vs dormancy release tuber) and 3885 (dormancy release tuber vs sprouting tuber) differentially expressed genes. Si et al. (2016) reported that the antisense *PPase* gene in transgenic potato plant delayed tuber sprouting time for two and three weeks, and the sense *PPase* gene shortened potato tuber sprouting time for approximately two weeks compared with that of the wild-type.

Dormancy, as a typical quantitative trait controlled by a large number of genes (Koornneef et al., 2002), is more amenable to QTL (quantitative trait locus) analysis. To date, more than twenty dormancy QTLs have been mapped on chromosome 1–5, 7–11 in diploid potato F1

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populations (Bisognin et al., 2018; Freyre et al., 1994; Naz et al., 2018; Sliwka et al., 2008; Simko et al., 1997; Van den Berg et al., 1996b). With population TRP133 planted in the field in 1989, Freyre et al. (1994) detected six QTLs controlling potato tuber dormancy. Van den Berg et al. (1996b) identified nine QTLs for tuber dormancy with population BCB and BCT grown in a polyethylene-covered greenhouse in 1990 and 1991. Sliwka et al. (2008) identified three dormancy QTLs with population 98-21 planted in the field in 2002 and 2003. Naz et al. (2018) mapped a dormancy QTL and a $GA_3$ QTL on the same position of chromosome 1 in a diploid potato population with potato microtubers harvested from in vitro plantlets in 2014 and 2015. Bisognin et al. (2018) identified eight QTLs underlying the number of days to dormancy release with population MSX902 in the greenhouse in 2013.

All the above-mentioned analyses of QTLs for potato tuber dormancy were conducted under one or two environments, in field, or in greenhouse, or in vitro alone. Potato tuber dormancy, however, is influenced by both genotype and the growth environments of the crop (Vreugdenhil, 2007). So far, no QTL for potato tuber dormancy was analyzed under more than two environments. With a diploid potato F1 population planted under seven environments, in both greenhouse and field, this study analyzed QTLs underlying tuber dormancy, especially the stable QTLs across environments, to increase genomic resources for potato breeding that aims at desirable length of tuber dormancy.

## 2. Materials and methods

### 2.1. Plant materials and genetic map

A diploid potato population named EB consisting of 178 individuals, which has been used for mapping QTLs conferring reducing sugar content in cold-stored tubers (Xiao et al., 2018), was used in this study for dormancy QTL analyses. The population EB has a genetic background derived from *S. tuberosum*, *S. berthaultii*, *S. phureja*, *S. vernei*, etc. The maternal parent ED25 (E) has a short dormancy phenotype while the paternal parent *S. berthaultii* acc. CW2-1 (B) has a long dormancy phenotype. A genetic map of maternal parent E with a total length of 1043.5 cM and a genetic map of paternal parent B with a total length of 1037.9 cM were constructed by Xiao et al. (2018) (https://www.frontiersin.org/articles/10.3389/fpls.2018.00315/full#supplementary-material, accessed 16 March 2018) with a two-way pseudo-testcross strategy (Grattapaglia and Sederoff, 1994).

### 2.2. Tuber dormancy evaluation

Tubers harvested from seven environments at two locations, Wuhan (30.5 °N, 114.4 °E) in 2012–2015 and Harbin (45.7 °N, 126.6 °E) in 2014, were used for dormancy evaluation. Each of the seven environments is designated a Roman numeral listed in Table 1. The progeny individuals as well as the parental clones were planted in the plastic greenhouse (Wuhan) or in the open field (Harbin) using a randomized complete block design with three repetitions of single row plots of ten plants each. The cultivation management was conducted according to local practices to ensure normal crop growth.

After plant maturity, fifteen healthy tubers for each plot from the each of the seven environments were harvested and kept in the room with a temperature of 25 °C for seven days until the tuber skins were dry, then were stored in the dark at a constant temperature of 20 ± 1 °C. The sprouting tubers among the fifteen tubers were counted at intervals of 4 days until all of the tubers sprouted with a sprout length of at least 1 mm instead of the common 2 mm (Van Ittersum et al., 1992) because of the shallow bud eyes of the tubers from population EB. The dormancy trait value was recorded as days after harvest to the observation of 80% sprouting tubers (12 out of each set of the fifteen tubers). The statistical analyses, including Pearson correlations of the dormancy traits between environments, were conducted by SPSS 22.0.

### 2.3. QTL mapping for dormancy

QTL mapping was conducted by MapQTL®6 based on the multiple-QTL models (MQM) (Van Ooijen, 2009) and by QTLNetwork 2.0 with the mixed-model based composite interval mapping (MCIM) method (Yang et al., 2008), respectively.

On one hand, with the map of population EB constructed by Xiao et al. (2018) and the dormancy trait values of tubers harvested from the seven environments, the QTL analysis was done by MapQTL®6 based on MQM (Van Ooijen, 2009). After 1000 permutations, the genome wide threshold ($p = 0.05$) was identified and the highest LOD (logarithm of the odds) threshold (LOD = 2.9) for the seven traits (one for each of the seven environments) was chosen as the threshold to declare significant QTL. *Regression algorithm* was selected, *mapping step size* was 1.0, *maximum number of neighbouring markers* was 5, and *maximum number of iterations* was 200.

On the other hand, the same data set, namely the genetic map and the dormancy trait values mentioned above in this section, was input into QTLNetwork and analyzed based on MCIM (Yang et al., 2008). The dormancy traits were treated as one trait in multiple environments by QTLNetwork. Significance levels for *candidate interval and interval pairs*, *putative QTL and epistatic QTL detection*, and *QTL effects* were 0.1, 0.05 and 0.05, respectively. *Testing window*, *walk speed* and *filtration window* were 5, 1 and 10 cM, respectively. The effects of QTLs and interactions were estimated by the Markov Chain Monte Carlo method.

If the two-LOD support intervals of two QTLs overlapped each other, the QTLs were considered as the same one. The linkage map and the positions of QTLs were drawn by MapChart 2.2 (Voorrips, 2002).

## 3. Results

### 3.1. Phenotypic data of dormancy

The dormancy trait values were evaluated with stored tubers harvested from seven environments. All of the dormancy trait values in seven environments displayed almost normal distributions with skewness ranging from −0.473 to 0.574 and kurtosis from −0.937 to 0.441.

**Table 1**
The mean values and standard deviations of dormancy in seven environments.

| Environment | Location | Planting date | Harvest date | First sprouting date | Mean[a] | SD[b] | Variance | Skewness | Kurtosis |
|---|---|---|---|---|---|---|---|---|---|
| I | Wuhan | Sep 20, 2012 | Dec 29, 2012 | Feb 1, 2013 | 67.51 | 12.09 | 145.28 | 0.338 | 0.055 |
| II | Wuhan | Sep 13, 2013 | Dec 21, 2013 | Jan 27, 2014 | 51.80 | 11.11 | 130.05 | 0.574 | 0.441 |
| III | Wuhan | Jan 7, 2014 | May 11, 2014 | Jul 1, 2014 | 77.92 | 27.72 | 763.21 | 0.133 | −0.316 |
| IV | Wuhan | Sep 10, 2014 | Dec 20, 2014 | Jan 11, 2015 | 56.15 | 18.45 | 336.71 | 0.222 | −0.937 |
| V | Wuhan | Jan 21, 2015 | May 1, 2015 | Jun 26, 2015 | 74.23 | 25.98 | 669.98 | −0.335 | −0.243 |
| VI | Wuhan | Jul 16, 2015 | Nov 4, 2015 | Dec 24, 2015 | 87.85 | 21.67 | 465.86 | 0.095 | 0.06 |
| VII | Harbin | Apr 21, 2014 | Sep 4, 2014 | Oct 11, 2014 | 117.93 | 31.38 | 976.54 | −0.473 | −0.255 |

[a] Average days after harvest to the observation of 80% sprouting tubers.
[b] Standard deviation in each environment.