Journal of Integrative Agriculture 2018, 17(2): 285–295

Available online at www.sciencedirect.com

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RESEARCH ARTICLE

A major quantitative trait locus controlling phosphorus utilization efficiency under different phytate-P conditions at vegetative stage in barley

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Abstract

Organic phosphorus (P) is an important component of the soil P pool, and it has been proven to be a potential source of P for plants. The phosphorus utilization efficiency (PUE) and PUE related traits (tiller number (TN), shoot dry weight (DW), and root dry weight) under different phytate-P conditions (low phytate-P, 0.05 mmol L^{-1} and normal phytate-P, 0.5 mmol L^{-1}) were investigated using a population consisting of 128 recombinant inbred lines (RILs) at the vegetative stage in barley. The population was derived from a cross between a P-inefficient genotype (Baudin) and a P-efficient genotype (CN4027, a *Hordeum spontaneum* accession). A major locus (designated *Qpue.sau-3H*) conferring PUE was detected in shoots and roots from the RIL population. The quantitative trait locus (QTL) was mapped on chromosome 3H and the allele from CN4027 confers high PUE. This locus explained up to 30.3 and 28.4% of the phenotypic variance in shoots under low and normal phytate-P conditions, respectively. It also explains 28.3 and 30.7% of the phenotypic variation in root under the low and normal phytate-P conditions, respectively. Results from this study also showed that TN was not correlated with PUE, and a QTL controlling TN was detected on chromosome 5H. However, dry weight (DW) was significantly and positively correlated with PUE, and a QTL controlling DW was detected near the *Qpue.sau-3H* locus. Based on a covariance analysis, existing data indicated that, although DW may affect PUE, different genes at this locus are likely involved in controlling these two traits.

Keywords: barley, phosphorus utilization efficiency, quantitative trait locus, recombinant inbred line, phytate-P

1. Introduction

Phosphorus (P) is an essential nutrient for plant growth and development. Globally, application of P fertilizer was greater than removal of P by harvested crops in 2000. In addition, deficits of P occurred in 30% of cropland areas around the globe (MacDonald *et al*. 2011). In soils, P has

Received 26 January, 2017 Accepted 17 May, 2017
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doi:10.1016/S2095-3119(17)61713-1

low mobility and a high rate of fixation (Schachtman *et al*. 1998; Tian *et al*. 2012). Because of these characteristics, P limits crop productivity around the world (Vance *et al*. 2003). At present, applying phosphate fertilizer is still an effective way to improve yield and quality of crops (Cordell *et al*. 2009). Statistics from the International Fertilizer Industry Association (IFA) (http://www.fertilizer.org/ifa/) in 2006 showed that the annual input of phosphate fertilizer (P_2O_5) was more than 30 million tons, with the average input into wheat crops being 20 kg or more P_2O_5 per ha (FAO 2006). However, the extensive application of phosphate fertilizer has fundamentally altered the global P cycle, and caused eutrophication and other environmental problems (Ma *et al*. 2012). Organic P constitutes 50–80% of total P in soils (Turner *et al*. 2002). Phytate-P is an important component of soil organic P, which can be absorbed and used by plants *via* acid phosphatase and phytase hydrolysis (Sharma *et al*. 2007; Starnes *et al*. 2008; Ye *et al*. 2015). Therefore, it is desirable to develop cultivars with enhanced efficiency of phytate-P use because they may offer a sustainable solution for managing P supplementation in crop production.

Phosphorus utilization efficiency (PUE) is mainly controlled by complex polygenic regulation, and significant differences in regulation exist between crop varieties and genotypes (Su *et al*. 2009; Wang *et al*. 2010). Previous studies have shown that plant tolerance to low P is regulated by multiple genes (Su *et al*. 2006; Oono *et al*. 2013). Tolerance to low P and quantitative trait locus (QTL) analysis of related traits has been conducted in rice (Wissuwa *et al*. 1998), corn (Zhu *et al*. 2005), rapeseed (Yang *et al*. 2011), common bean (Liao *et al*. 2004), and soybean (Li *et al*. 2005). In a rapeseed recombinant inbred line (RIL), Yang *et al*. (2011) conducted a QTL analysis and assessed six phenotypic traits at the vegetative stage under high P and low P conditions. They detected a total of 71 QTLs on 13 linkage groups, including 28 in low P conditions, 22 in high P conditions and 21 for relative traits. King *et al*. (2013) analyzed QTL for P accumulation in soybean, and identified three candidate genes on chromosomes 7, 12 and 17. In common bean, 19 related root morphology and P uptake traits were detected in eight linkage groups (Yan *et al*. 2004). Most of the phenotypic variance explained by these QTLs are low, and the identified markers could be difficult to use in breeding. A low P tolerance gene named as *PSTOL1* was detected in rice using a population of RILs under P deficiency (Wissuwa *et al*. 1998). Expression analysis in low P soil showed that this gene significantly enhanced grain yield. Further analysis showed that the gene significantly enhanced seedling root length and improved ability of P uptake (Gamuyao *et al*. 2012).

The genotypic differences of PUE in wheat under P deficiency have been confirmed (Batten 1992). Hayes *et al*. (2004) showed that the P-efficient wheat accumulated 32% more P at a similar dry weight than P-inefficient wheat under low P conditions. At present, a variety of methods have been used in studying resistance to low P in wheat. These methods include the use of Chinese Spring nullisomics and substitution lines for a given chromosome and as well as QTL mapping (Li *et al*. 1999a, b; Su *et al*. 2006, 2009). In Chinese Spring nullisomic-tetrasomic lines, genes conferring resistance to low P stress have been found on chromosomes 1A, 4A, 7A, 3B, 5B, and 7D. In addition, suppressor genes were also detected on chromosomes 1B, 4B, 7B, 3A, and 6D (Li *et al*. 1999a, b). QTL analysis using hybrids of Chinese Spring and the low P tolerant variety Lovrin 10 indicated that the main effect QTL controlling P efficiency was found on chromosomes 3B, 4B, and 5A (Su *et al*. 2006). A further study found seven QTLs for P absorption and six QTLs controlled PUE (Su *et al*. 2009).

Barley is one of the most important cereal crops and is grown all over the world; it is widely used in feed and in the food industry, and is the main raw material for brewing beer (Feuillet and Muehlbauer 2009). It has a planting area of about 560 000 km^2 worldwide, with a total output of about 120 000 million kg (FAO, http://www.fao.org). Widely used in feed and food industry, barley is the main raw material for brewing beer (Feuillet and Muehlbauer 2009). Genotype differences also exist in PUE in barley (Asmar *et al*. 1995; George *et al*. 2011). There are few studies on QTL mapping and genetic analysis of genes associated with PUE in barley, however, three QTLs for PUE have been identified on chromosomes 2H and 5H under different P conditions (Gong *et al*. 2016). Górny and Ratajczak (2008) successfully imported an exogenous gene to improve P uptake and utilization efficiency in barley and thus showed that improvement of PUE in barley is feasible. In this study, a RIL population derived from the cultivated barley variety Baudin and wild barley CN4027 was used to map QTLs for PUE, and to analyze the correlation of QTLs for PUE and P efficiency related traits at the vegetative stage under normal organic P (+P, 0.5 mmol L^{-1}) and low organic P (–P, 0.05 mmol L^{-1}) conditions using phytate-P as an organic P source.

2. Materials and methods

2.1. Plant materials

A population of RILs were generated using the embryo culture procedure described in previous studies (Chen *et al*. 2013; Zheng *et al*. 2013). The RIL population contained 128 lines derived from a hybrid between a P-efficient wild barley (*Hordeum spontaneum*) genotype CN4027 and a P-inefficient cultivated barley (*H. vulgare*) variety Baudin.