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A Study on Phosphorus Use Efficiency of Wheat

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Abstract Wheat is one of the most important grain crops in China with great demand. It plays an important role to use phosphorus fertilizer for improving wheat yield. Therefore, application and foundation studies on wheat phosphorus use efficiency are so vital nowadays. Here, we have a simple review on definition of phosphorus use efficiency, response to phosphate starvation in plant, relevant genes cloning, impact factors, screening high phosphorus efficiency genotype and QTL analysis of phosphorus utilization efficiency in wheat.

Key words Wheat (*Triticum aestivum* L.), Phosphorus use efficiency, QTL (Quantitative Trait Locus)

1 Introduction

Phosphorus is one of 17 kinds of mineral elements necessary for plant growth, and it plays an important role in energy metabolism, sugar metabolism, enzymatic reaction and photosynthesis. Phosphorus is also a component of nucleic acid, plant hormone and lecithin, and it determines the yield and quality of crops to a large extent[1-2]. The usable phosphorus mainly exists in the form of phosphate, and phosphate can be readily combined with some metal ions in soil such as Ca^{2+}, Fe^{3+} and Mn^{2+} to precipitate, resulting in scant available phosphorus in soil to meet the needs of the plant[3-4]. Even if the phosphorus fertilizer is applied, more than 80% of the phosphorus will be fixed in soil, and can not be used by crops[5-6]. The phosphorus, which is not absorbed and utilized by crops, will flow into rivers and lakes with the rain or irrigation water, causing eutrophication[7]. In addition, the phosphate ore, as the main source of phosphorus fertilizer, is a non-renewable resource. Experts predict that global phosphate reserves will be exhausted at the end of this century[8-12]. Wheat is China's major grain crop, and the average annual consumption of phosphorus fertilizer for wheat is 10^3 kg · ha, higher than that of rice (88 kg · ha) and maize (83 kg · ha)[13]. However, the utilization rate of phosphorus fertilizer is only 10% for wheat, lower than that of rice (14%) and maize (18%)[14]. Therefore, it is very necessary to improve the ability of wheat to absorb and utilize phosphorus, tap the genetic potential of wheat for efficiently using soil phosphorus, improve the genetic characteristics of phosphorus nutrition, and cultivate new varieties of high phosphorus efficiency, which is an effective way to solve the above problems, and of great significance to achieving sustainable development of agriculture[15-16].

2 Definition of phosphorus use efficiency

Phosphorus use efficiency is the biological yield or economic yield or fixed amount of CO_2 (g or mg) per unit of crop phosphorus concentration (%), namely plant phosphorus use efficiency = dry weight/phosphorus concentration. The plant phosphorus concentration is the ratio of phosphorus accumulation to dry weight, namely plant phosphorus concentration = phosphorus accumulation/dry weight. Therefore, the plant phosphorus use efficiency can be denoted by the amount of dry matter supported by per unit of phosphorus in crop, namely plant phosphorus use efficiency = dry weight of whole plant/phosphorus accumulation of whole plant[17-18]. High phosphorus use efficiency means that cells need low amount of biochemical phosphorus for various life activities, and phosphorus is transported rapidly in the plant, with high recycling efficiency, thus having particular importance to high efficiency phosphorus breeding[19]. How to improve phosphorus use efficiency while achieving increased crop yield, is a bottleneck on improving modern crop's phosphorus use efficiency[20]. In addition, the phosphorus harvest index can be viewed as additional indicator to evaluate phosphorus use efficiency, in order to select the genotype with high yield and phosphorus use efficiency[21-22].

3 Mechanism of plant's adaptation to low phosphorus stress

In the long process of evolution, plants have a series of strategies that adapt to low phosphorus environment, and they can be summarized as two simple mechanisms. One is the mechanism of improving root's soil phosphorus absorption efficiency, and the other is the mechanism of rationally using phosphorus in plants and improving phosphorus use efficiency[23-24]. Root is the main organ of plants to absorb nutrients, and under low phosphorus stress, the phosphorus absorption and use efficiency can be improved to adapt to low phosphorus stress through a series of changes in morphology, such as changing metabolic pathways and secreting acidic substances[25-27]. Athikkattuvalasu *et al.*[28] use active tag T-DNA insertion method to obtain the mutant *lpsi of Arabidopsis thaliana*, and this mutant can be used to detect the inhibiting effect on root growth and promoting effect on root hair differentiation under low phosphorus conditions. Through the study, Zhang Enhe *et al.*[29] find that under phosphorus deficiency conditions, the activity of

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acid phosphatase in wheat Ganchun 20 increases by 41.6% and 101.9%, respectively, when compared with the treatments of moderate phosphorus supply and plentiful phosphorus supply, indicating that this genotype adapts to phosphorus-deficient environment through the release of phosphatase to rhizosphere. Yang Ruiji *et al*. and Wu Zhaohui *et al*.[30-31] also do a similar study and find that under phosphorus stress, Ganchun 20 has high sensitivity to phosphorus, high acid phosphatase activity, as well as great root dry weight, shoot dry weight and strong yield potential, so it is a high phosphorus efficiency genotype. Phosphorus is also a component of some important substances involved in a variety of biochemical reactions inside the cell such as ATP, NADPH, RNA and DNA. Therefore, under low phosphorus conditions, many of the genes with a variety of metabolic pathways may respond to low phosphorus environment, including phosphorus transport and recycling, etc., in order to maintain the balance of intracellular phosphorus concentration[24].

4 Cloning of genes related to phosphorus use efficiency

4.1 Plant phosphate transporter gene Inorganic phosphorus enters into the plants through the root membrane, which is regulated by a plurality of phosphorus transporter genes in the same or different family. People first cloned two phosphate transporter genes in *Arabidopsis thaliana*, and also cloned a number of new encoded phosphate transporter genes in other higher plants such as rice, tomatoes, wheat, and potatoes[32-34]. So far, the plant phosphate transporter genes obtained by researchers generally belong to Pht1 and Pht2 families, and people have also cloned a few phosphate transporter genes belonging to Pht3, Pho1 and Pho2 families[35].

4.2 Enzyme genes related to phosphorus use efficiency

Plant has adaptive response to low phosphorus stress, and the phosphorus deficiency inducing the secretion of acid phosphatase in roots is a universal mechanism for higher plants to adapt to low phosphorus stress. Purple acid phosphatase, as a special kind of acid phosphatase, is involved in the plant's use of soil organic phosphorus and reallocation of phosphorus in plants. The gene has been cloned in transgenic *Medicago truncatula*, *Arabidopsis thaliana*, *Aegilops searsii*, wild soybean and other plants[36-37]. Calcium-dependent protein kinase (CDPK) exists in the form of multi-gene family, and it is an important signal transmitter mediating abiotic stress signal transduction. In recent years, the CDPK genes have been cloned in *Arabidopsis thaliana*, rice, wheat and other plants[38].

4.3 Transcription factor gene related to phosphorus use efficiency The research of transcriptional regulatory mechanism under phosphorus starvation response is most detailed in yeast studies. The two transcription factors of yeast, namely PH02 and PH04, play an important regulatory function in the PHO system, and they belong to homeo and bHLH families, respectively. Currently, PTF1 gene in bHLH family has been cloned in rice, corn and other plants[39-40]. Some WRKY transcription factors in plant species play an important role in responding to and resisting low phosphorus abiotic stress, and some genes in this transcription factor family have been cloned in rice, *Arabidopsis thaliana* and wheat[41-42]. In addition, WER, a transcription factor controlling root hair initiation, has been cloned in *Arabidopsis thaliana*, rape, cabbage and other plants[43].

5 Factors influencing phosphorus use efficiency of wheat

Phosphorus use efficiency is closely related to soil moisture conditions. When the soil is dry, the absolute amount of phosphorus dissolved in soil solution will be low, far from meeting the needs of crops, thus leading to phosphorus deficiency symptoms[44]. Therefore, people have studied the relationship between the phosphorus use efficiency of wheat and water use efficiency. Peng Changlian *et al*.[45] find that under water stress, compared with the wheat varieties with low phosphorus efficiency, the varieties with high phosphorus efficiency have high photosynthetic rate in leaves, and high water use efficiency, showing strong drought resistance. The study of Liu Guodong *et al*.[44] indicates that under field conditions, some genotypes with high water use efficiency such as Ji87-4617, Luofulin 10, have strong ability to endure low phosphorus. Wang Yu *et al*.[19] find that in the case of water shortage, high yield and water use efficiency can be obtained by applying 180 kg · ha of phosphorus and using 60 mm of water to irrigate in the Hluanghuai wheat growth area. The difference in some soil nutrients such as nitrogen, phosphorus and potassium, or different sources of phosphorus, will also affect the phosphorus use efficiency of wheat. The study of Zan Yaling[46] shows that with the increasing application of nitrogen fertilizer to wheat, plants' phosphorus and potassium uptake, phosphorus partial productivity and phosphorus use efficiency will increase; likewise, wheat yield and plants' nitrogen, phosphorus and potassium uptake will also significantly increase with the increasing application of phosphorus. Wu Yipo *et al*.[47] find that compared with the wheat varieties with low phosphorus efficiency, the varieties with high phosphorus efficiency have stronger ability to absorb and use organic phosphorus, and under the same treatment, both the dry matter amount and phosphorus accumulation for the wheat varieties with high phosphorus efficiency are higher than for the varieties with low phosphorus efficiency; a certain concentration of inorganic phosphorus can promote assimilation substance to be allocated to the roots, improve root growth, and induce the secretion of acid phosphatase in roots, while organic phosphorus has no such effect. There are significant differences in phosphorus use efficiency between different wheat genotypes. Li Yan *et al*.[48] divide 133 parent materials into three categories according to different nitrogen and phosphorus use efficiency, and select seven parents with high nitrogen and phosphorus use efficiency. Song Qingjie *et al*.[49] use different concentration of phosphorus to treat four cultivars of wheat in Heilongjiang Province, and find that they have different response to phosphorus. Wang Shuliang *et al.*[21] there are highly significant differences in phosphorus use efficiency and harvest index between different wheat varieties, and the average phosphorus use efficiency and phosphorus harvest index for all varieties under high fertility are 10.22% and 2.61% lower than under low fertility, respectively. Yang Xianbin *et al.*[50] find that there are great differences in phosphorus use efficiency between wheat varieties at tillering, jointing, flowering and maturity stages. He Wenshou[51] finds that regardless of phosphorus application, there are obvious differences in phosphate yield rate and phosphorus use efficiency between wheat varieties, especially more apparent under low phosphorus conditions. These studies lay foundation for selecting high phosphorus efficiency wheat germplasm, carrying out basic research of high phosphorus efficiency wheat, and breeding high phosphorus efficiency wheat varieties.

6 Evaluation and selection of high phosphorus efficiency wheat genotype

Currently, hydroponics and potted soil culture are generally used to primarily choose high phosphorus efficiency wheat genotypes at seedling stage, and then re-select these genotypes in the field at adult plant stage[24]. Based on nutrient solution formula of Hoagland *et al.*, hydroponics uses 0.02mmol L^{-1} H_2PO^{4-} as the treatment standard for selecting high phosphorus efficiency wheat at seedling stage, but under other selection conditions, there is no additional phosphorus fertilizer to be added on the basis of original low phosphorus medium, and there are no specific low phosphorus treatment standards[52-53]. The screening indicators for high phosphorus efficiency are some traits significantly correlated with phosphorus efficiency, and the measuring method must be simple for these traits. Under low phosphorus, the phosphatase activity of wheat at the third-leaf stage is significantly correlated with phosphorus use efficiency ($R = 0.944$, $P < 0.1$), and it can be used as an indicator to select high phosphorus efficiency wheat genotype at seedling stage[54]. At adult stage of wheat, the higher the grain yield per unit of phosphorus or the lower the grain phosphorus content, the higher the phosphorus use efficiency of wheat, so it can be used as an indicator to select high phosphorus efficiency wheat genotype[55]. Under the same fertility conditions, spike number and grain number also can be used as indicators to select high phosphorus efficiency genotype[49]. In addition, Liu Guodong *et al.* use $Ca_3(PO_4)_2$ as the sole source of phosphorus, plus 0.75 mmol/L Ca^{2+}, to establish the phosphorus source liquid controlled release system as the phosphorus nutrient buffer solution to screen different wheat genotypes within 40 d[56]. During the selection of high phosphorus efficiency wheat genotype, it should be based on one or more traits supplemented by many reference traits for comprehensive evaluation.

7 QTL analysis of phosphorus use efficiency of wheat

The development of molecular marker technology and the establishment of high-density genetic linkage map, make it possible to test QTL of phosphorus use efficiency of wheat in genome. Using different groups, researchers have successively located some QTLs closely linked with the phosphorus use efficiency and related traits (Table 1). Under normal supply of phosphorus and phosphorus stress, Cao Weidong *et al.*[57] use RIL population to detect five QTLs related to phosphorus use efficiency of shoot and whole plant, respectively, and they are distributed in 5 and 4 chromosomes. In addition, under two phosphorus supply conditions, the fragment *Xfba*354 – *Xfba*69 in 7A chromosome can significantly affect phosphorus use efficiency of whole plant, and under normal supply of phosphorus, it interacts with other genes to affect phosphorus use efficiency of whole plant, and plays an important role in improving the phosphorus use efficiency of wheat. Under normal phosphorus, low phosphorus and phosphorus starvation conditions, Li Zhenxing *et al.*[58] also use RIL population to detect 30 (LOD >2.0) QTLs related to wheat root traits and phosphorus stress response, distributed in 14 chromosomes, and there are 5 QTLs with single locus contributing 10% to phenotype. Su *et al.*[59] use DH population to detect 20 QTLs under low phosphorus treatment and 19 QTLs under high phosphorus treatment, and these 39 QTLs are distributed in 21 chromosomes; there are 3 QTL clusters playing an important role in controlling low phosphorus tolerance, and two loci are closely linked with essential catalysis genes *VRN* – *A*1 (5A) and *VRN* – *D*1 (5D). Su *et al.*[60] use DH population to detect 7 QTLs controlling phosphorus uptake efficiency and 6 QTLs controlling phosphorus use efficiency, and detect 2 QTLs controlling both phosphorus use efficiency and phosphorus uptake efficiency under low phosphorus conditions, indicating that it is possible to improve phosphorus use efficiency and phosphorus uptake efficiency at the same time. They also detect many QTLs which control phosphorus uptake efficiency and tiller number at seedling stage, as well as spike number, biological yield and phosphorus uptake efficiency at adult plant stage. Peleg *et al.*[61] use RIL population to detect 82 QTLs related to 10 kinds of mineral elements, and 8 of these QTLs are related to grain phosphorus content and distributed in 7 chromosomes. Guo *et al.*[17] use RIL population to detect 171 QTLs linked with 12 wheat traits related to phosphorus use efficiency at seedling stage, 22 of which are linked with root phosphorus use efficiency, 9 of which are linked with shoot phosphorus use efficiency, and 13 of which are linked with whole plant phosphorus use efficiency.

Table 1 QTL analysis of phosphorus use efficiency and related traits of wheat

Varieties	Traits		QTL number	Chromosome	Contribution rate//%	References
W7984/Opata85 RIL: 150	Seedling stage	Phosphorus use efficiency of shoot^{a}	5	1B2D3B5A6D	6.55 – 14.2	Cao Weidong *et al.*, (2001)
		Whole plant phosphorus use efficiency^{b}	5	2B2D5A7A	7.80 – 18.01	
Nongda 3338/ Altgold RIL: 175	Seedling stage	Root dry weight	8	1A2A2B4D5A7B7D	5.44 – 9.65	Li Zhenxing *et al.*, (2007)
		Root length	12	1A2B5B6A7A7B7D	4.45 – 22.44	
		Root number	10	1B2A2B5D6B6D7B	6.04 – 16.77	
Luofulin 10/Zhongguochun DH: 92	Seedling stage	Shoot dry weight	5	5A5D7B	12.2 – 22.1	Su *et al.*, (2006)
		Tiller number	14	1A1B2D3A4B5D	5.7 – 34.6	
		Phosphorus content of shoot	11	2A4A4B5A5D6D7B	8.8 – 22.0	
		Phosphorus use efficiency of shoota	9	3B4B5A5D6A6B7A	11.2 – 22.9	
Hanxuan 10/Lumai 14 DH: 120	Seedling stage	Shoot dry weight	14	1D2D3B4D5A6A6B7A7B	5.7 – 21.3	Su *et al.*, (2009)
		Tiller number	22	1B2B2D3A3D4B5A6A7B7D	4.1 – 34	
		Phosphorus content of shoot	17	1A1B2B2D3B4B5A5B6A6B7A	4.4 – 38.8	
		Phosphorus use efficiency of shoot^{a}	10	2A2D3A5A5B6B7B	5.4 – 36	
	Adult plant stage	Shoot dry weight	17	1A2B2D3A3B3D4B5A6B7D	4.9 – 14.8	
		Spike number	22	1A1D2B3A3B5A5B5D6A7A	4.5 – 23.3	
		Grain number	22	1A1B2D4A4B4D5A6A6B7A7B	4.3 – 19.4	
		Grain weight	27	1B2A2D3A4A5B6A6B7A	4.4 – 17.5	
		Phosphorus content of shoot	16	1A2B2D3A3B4B5B7A7D	4.9 – 27.9	
		Phosphorus use efficiency of shoot^{a}	12	1A2A2B3A4A6B6D7A	6.4 – 26.6	
		Phosphorus use efficiency of grain	14	1A1B2B2D3A3B5A5B6D7A	6.2 – 18.4	
Chuan 35050/Shannong 483 RIL: 131	Seedling stage	Root number	13	1A1B1D4B5A5B5D7A		Guo *et al.*, (2012)
		The maximum root length	15	1A2A2B2D3A4A5B5D6B6D7B		
		Plant height	16	1B1D2B2D4B5B5D6A6B6D7A7D		
		Root dry weight	17	1A1B1D2D4A4B5D6A7A7B		
		Shoot dry weight	11	1A1B1D2B4B5D6B7A7B		
		Whole plant dry weight	11	1A1B1D2B5D6B7A7B		
		Phosphorus content of root				
	13	1B1D3B4A4B5A6A7A7B				
		Phosphorus content of shoot	16	1A1B1D2B3A4A4B5D6A6D7A7B7D		
		Phosphorus content of whole plant	15	1A1B1D2B3A4A4B5B5D7A7D		
		Phosphorus use efficiency of root$^{C'}$	22	1A1B1D2A2D3B4A5D6A6B7A7B		
		Phosphorus use efficiency of shoot$^{a'}$	9	1A1B1D3B4B5D6B7A		
		Whole plant phosphorus use efficiency$^{b'}$	13	1A1B1D3B4A4B5D6A6B7A7B		
Durum wheat/wild emmer RIL: 152	Adult plant stage	Phosphorus content of grain	8	1A2A4A4B5B6B7A	0.012 – 0.192	Peleg *et al.*, (2009)

Note: Phosphorus use efficiency of shoot ^{a} = shoot dry weight/phosphorus content of shoot; phosphorus use efficiency of shoot $^{a'}$ = shoot dry weight^{2}/phosphorus content of shoot; whole plant phosphorus use efficiency ^{b} = whole plant dry weight/phosphorus content of whole plant; whole plant phosphorus use efficiency $^{b'}$ = whole plant dry weight^{2}/phosphorus content of whole plant; phosphorus use efficiency of root $^{C'}$ = root dry weight^{2}/phosphorus content of root.

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Table 3 Economic benefits of different varieties of garlic under different treatments

Variety	Treatment	Economic benefits of garlic stems yuan/ha^{-1}	Economic benefits of garlic bulbs yuan/ha^{-1}	Economic benefits per ha yuan/ha^{-1}	Topdressing costs yuan/ha^{-1}	Income increase compared with T_1 // yuan/ha^{-1}
Early bolting garlic	T_1	61720.5	22596	84316.5	510	
	T_2	63901.5	23107.5	87009	574.5	2628
	T_3	68179.5	23580	91759.5	1263	6690
Cangshan garlic	T_1	25846.5	54568.5	80415	510	
	T_2	26341.5	57675	84016.5	574.5	3537
	T_3	28198.5	58129.5	86658	1263	5490

Note: For early bolting garlic, the price of garlic stems and garlic bulbs is 4.6 yuan/kg and 1.6 yuan/kg, respectively; for Cangshan garlic, the price of garlic stems and garlic bulbs is 3.4 yuan/kg and 2.4 yuan/kg, respectively; the price of urea, ammonium chloride and ammonium phosphor nitrate is 1700 yuan/t, 1000 yuan/t, and 2200 yuan/t, respectively.

4 Conclusions and discussions

With Cangshan garlic and early bolting garlic as experimental materials, this paper studies the effect of nitrogen topdressing on the garlic growth and yield of garlic stems and garlic bulbs. The results show that under the same amount of nitrogen, applying ammonium phosphor nitrate can better promote the growth of garlic than applying urea and ammonium chloride; both ammonium chloride and ammonium phosphor nitrate can effectively improve the yield of garlic stems and garlic bulbs, especially for ammonium phosphor nitrate; through economic benefit analysis, applying ammonium chloride and ammonium phosphor nitrate can produce greater economic benefits than applying urea, and especially ammonium phosphor nitrate increases the economic benefits of Cangshan garlic and early bolting garlic by 5490 yuan and 6690 yuan per ha, respectively. Thus, applying ammonium phosphor nitrate as topdressing for garlic can effectively increase yield and income. Different forms of nitrogen in the soil will be converted into each other, and then be absorbed by plants. Under suitable temperature, moisture and aeration conditions, due to the action of soil microbes and enzymes, urea is hydrolyzed into ammonium nitrogen, and ammonium nitrogen is oxidized into nitrate nitrogen. Nitrate and ammonium nitrogen can be directly absorbed by the plants, but plant absorption of nitrogen is mainly in the form of nitrate nitrogen, and excessive ammonium nitrogen may be toxic to plants. The fertilizers containing nitrate nitrogen can provide nitrogen for plants without conversion, while urea and ammonium nitrogen need to go through the conversion. And it is converted slowly in early spring and nitrogen supply is delayed, so ammonium phosphor nitrate has better effect than ammonium chloride and urea.

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