Front. Agric. China 2010, 4(3): 272–279
DOI 10.1007/s11703-010-1009-7

RESEARCH ARTICLE

**Xihuan LI, Junyi GAI, Wensuo CHANG, Caiying ZHANG**

# Identification of phosphorus starvation tolerant soybean (*Glycine max*) germplasms



**Abstract** In the present study, 156 soybean genotypes mainly from the Hebei growing-area were identified for their low phosphorus starvation tolerance. The results showed that the relative values (value of dry wt. in zero soil P/value of dry wt. in adequate soil P) of shoot dry weight and root dry weight of all soybean varieties, at the phosphorus concentration of 0 mmol·$L^{-1}$ and 1.0 mmol·$L^{-1}$ in supplied solution, offered a quick and reliable method to identify and classify genotypes for phosphorus starvation tolerance. We describe three classes: tolerant, moderate and sensitive P starvation groups which had 29, 59, and 68 cultivars, respectively. Eight varieties, Ji-dou11, Lü75, Hei-da-li, Zhong-huang15, Zhe98-14, Da-mao-jiao, Da-huang-dou and Zha-lai-te-qi were screened out for their high tolerance to phosphorus deficiency under zero soil phosphorus conditions. In addition, the relationships between soybean phosphorus starvation tolerance and seed phosphorus content, root morphology, rhizosphere acidification are also discussed.

**Keywords** soybean germplasms, phosphorus deficiency, screening characters, variety identification

## 1 Introduction

Phosphorus (P) is one of the major nutrient elements required by plants, but it is also one of the most immobile, inaccessible, and unavailable nutrients found in soils (Holford, 1997). Many soils are deficient in inorganic phosphate (Pi), and even in fertile soils, available Pi seldom exceeds 10 μmol·$L^{-1}$ (Raghothama, 1999; Smith et al., 2003). In fact, the concentration of available Pi (about 2 μmol·$L^{-1}$) in most soils is several orders of magnitude lower than that in plant tissues (5–20 mmol·$L^{-1}$). Thus, P deficiency is a major abiotic stress that limits crop growth and productivity throughout the world.

The low concentration of available Pi in the soils and a high demand for P in cells poses a problem unique to plants. In response to this persistently low level of available Pi in the rhizosphere, plants have developed several highly specialized morphological, physiologic, biochemical and molecular mechanisms to acquire and utilize P from the environment (Hammond et al., 2004). More and more evidences show that low P tolerance varies widely among species, even among varieties. Some species, such as white lupine (*Lupinus albus*), pigeonpea (*Cajanus cajan*), radish (*Raphanus sativus*), buckwheat (*Fagopyrum* Mill.), are well-known for their tolerance to low P, while sunflower (*Helianthus annuus*), barley (*Hordeum vulgare*) for their low tolerance, or sensitivity, to low soil P (Yan and Zhang, 1997).

In recent years, more and more crop varieties have been characterized for their tolerance to low soil P. Many tolerant varieties have been screened out from different crop species, such as wheat (Li et al., 1995), rice (Yi et al., 2005), soybean (Xu et al., 2003), *Arabidopsis thaliana* (Narang et al., 2000) and others. Moreover, some phosphorus starvation tolerant cultivars have been developed through a combination of physiologic and genetic approaches based on identified tolerant varieties, such as the wheat breeding cultivar Xiao-yan 54 (Davies et al., 2002). Developing improved crop germplasms that are better adapted to low P conditions and have more efficient uptake and utilization of P fertilizers is a promising new approach to solve the P starvation problem. Therefore, it is necessary to screen more genotypes for phosphorus starvation tolerance from large quantities of germplasms.

In this study, an effective procedure was established for

Received March 10, 2010; accepted March 22, 2010

Xihuan LI, Wensuo CHANG, Caiying ZHANG (✉)
North China Key Laboratory for Crop Germplasm Resources of Education Ministry, Agricultural University of Hebei, Baoding 071001, China
E-mail: zhangcaiying@hebau.edu.cn

Junyi GAI
Soybean Research Institute of Nanjing Agricultural University, National Center for Soybean Improvement, National Key Laboratory for Crop Genetics and Germplasm Enhancement, Nanjing 210095, China

evaluating soybean tolerance to phosphorus deficiency. One hundred and fifty-six varieties, mainly from the Hebei growing-area, were screened for their P starvation tolerance. We expected seedlings grown without soil P would grow poorly but we sought to determine which of the 156 genotypes would grow relatively better than others under the zero P treatment. To identify these genotypes we used the 'relative value' of the shoot and root dry weights. We found the relative value by dividing the zero P dry weight from the adequate P dry weight for each genotype. From these results we sorted the 156 genotypes into three classes: highly tolerant, moderately tolerant and poorly tolerant to phosphorus deficiency.

In addition, some highly tolerant varieties were screened out and the relationship between P tolerance and morphologic or physiologic characteristics was also investigated. We hope to develop new cultivars that are adapted to P starvation based on these soybean screening results. We also seek to identify P starvation tolerance related genes from these selected P tolerant genotypes and use genetic engineering techniques to help solve the problems.

## 2 Materials and methods

### 2.1 Plant materials

One hundred and fifty-six soybean genotypes mainly from Hebei, China were used in this study. They were provided by Hebei Crop Germplasm Resources Center, Hebei Academy of Agricultural and Forestry Sciences and Agricultural University of Hebei.

### 2.2 Seeding culture and treatment in pot with vermiculite

Soybean seeds were surface washed and sterilized, then were treated for germination at 26°C for 2 d. After germination, seedlings were transplanted into flowerpots filled with moist vermiculite. The plants grew up in a clear plastic awning. Two phosphate treatments ($0\ \mathrm{mmol \cdot L^{-1}}$ or $1.0\ \mathrm{mmol \cdot L^{-1}}$) were randomly applied in the soil solution ten days after being transplanted. There were eight seedlings in four flowerpots for each treatment of one genotype. The plants were harvested after flowering (about 45 days after being transplanted). The relative values ($0\ \mathrm{mmol \cdot L^{-1}} / 1.0\ \mathrm{mmol \cdot L^{-1}}$) of plants including root fresh and dry-weight, shoot fresh and dry-weight, shoot and root P content, and ratio of root to shoot dry-weight were investigated.

### 2.3 Seedling culture and treatment in hydroponic culture system

Twenty-four selected varieties differing in their P starvation tolerance were used to study the mechanisms of P deficiency tolerance in soybean, including eight sensitive (which have the lowest relative values of shoot and root dry weight in P sensitivity group), eight tolerant (which have the highest relative values of shoot and root dry weight in P tolerance group) and eight moderate (which have the moderate relative values of shoot and root dry weight in P medium group) genotypes based on the identification results of this research.

The seedlings were grown in a tank with a nutrient solution under the two phosphorus treatments as stated above ($0\ \mathrm{mmol \cdot L^{-1}}$, $1.0\ \mathrm{mmol \cdot L^{-1}}$). The solution was well aerated and the pH was maintained between 5.8 and 6.0 with daily additions of $1.0\ \mathrm{mol \cdot L^{-1}}$ KOH or HCl. The soybean plants were grown in a hydroponic culture for 20 days and the root rhizosphere acidification was monitored by application of agar sheets containing bromocresol purple as a pH indicator, for legumes (including soybean) are more efficient than other species in producing and excreting organic acids to the rhizosphere to enhance P solubilization under phosphorus deficiency (Raghothama, 1999; Neumann et al., 2000).

### 2.4 Seed phosphorus content determination of different type soybean germplasms

The seed total and inorganic phosphorus content of the twenty-four selected varieties as stated above (eight sensitive, eight tolerant and eight moderate genotypes) were determined to investigate the relationship between phosphorus tolerance and seed phosphorus content. Seed total phosphorus content was determined with five replications by a modification of the vanado-molybdenum spectro-photometric method, and inorganic phosphorus content was determined with five replications by a modification of the molybdenum blue spectro-photometric method (Li et al., 2008).

## 3 Results

### 3.1 Soybean plant performance under P starvation

Seedling soybeans grown under the two phosphorus treatments showed great differences in growth after 45 days. The zero P treatment plants were shorter and with smaller leaves than the adequate P group (Fig. 1). Moreover, the appearance of soybean leaves, stems and roots were also severely affected by phosphorus deficiency. The leaves became necrotic and discolored, the stems purple, and the roots brown under the zero P treatment. However, those plants grown in the P sufficient environment appeared to have normal green leaves, green stems and yellow roots (Fig. 2).


**Fig. 1** Photos of seedlings and 45 d bean plants under zero and adequate soil P
Note: A represents Bean seedlings of the same genotype prior to treatments. B represents Comparison of same genotype plants grown in zero and adequate P after 45 d. C represents photos of all genotype bean plants under zero and adequate soil P.

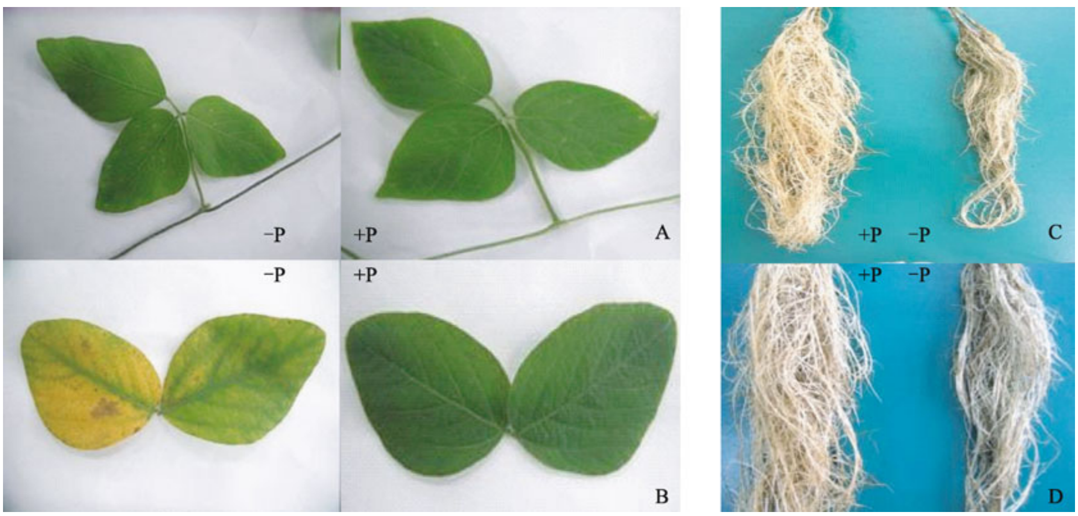


**Fig. 2** Photos of bean leaves and roots grown under two soil P treatments: zero and adequate
Note: A is purple stems on zero P treatment and normal green stems with adequate P. B is the yellowed and necrotic leaves under zero P treatment and normal leaves with adequate P. C and D are photos of roots grown under zero and adequate P with different size and color between groups.

### 3.2 Investigation of soybean genotypes to P starvation tolerance

The results of the screening experiment showed that all measured responses, root and shoot fresh and dry weights and root and shoot P content, differed significantly between treatments (Table 1). In all cases the zero P treatment plants were smaller and had less P in the tissues. Moreover, the relative values of P starvation tolerant varieties were higher than those P starvation sensitive varieties (Table 2). The screening results also suggest that the relative values of shoot dry-weight and root dry-weight, under similar treatments, could serve to screen characters. Such a test may quickly and reliably determine tolerant P starvation cultivars.

As determined by this screening system above, under the

**Table 1** Analysis of variance for soybean seedling dry-weight

| shoot dry-weight | | | root dry-weight | | |
|---|---|---|---|---|---|
| treatments | $1.0\ mmol \cdot L^{-1}$ | $0\ mmol \cdot L^{-1}$ | treatments | $1.0\ mmol \cdot L^{-1}$ | $0\ mmol \cdot L^{-1}$ |
| mean | 1.93±0.93 | 1.33±0.39 | mean | 0.52±0.05 | 0.46±0.04 |
| $P(t <= t)$ | $7.37 \times 10^{-41}$**($t$-test, $n$ = 156, two-tail) | | $P(t <= t)$ | $1.05 \times 10^{-22}$**($t$-test, $n$ = 156, two-tail) | |

**Table 2** The average relative values of shoot and root dry-weights in three groups

| group | variety number | relative shoot dry-weight | relative root dry-weight | tolerance to P starvation |
|---|---|---|---|---|
| I | 29 | 0.771 | 0.970 | tolerant |
| II | 59 | 0.664 | 0.857 | moderate |
| III | 68 | 0.584 | 0.731 | sensitive |
| average | | 0.649 | 0.823 | |

two phosphorus concentration treatments, the relative values ($0\ mmol \cdot L^{-1}/1.0\ mmol \cdot L^{-1}$) of shoot dry-weight of 156 genotypes ranged from 0.43 to 0.91 (2.12-fold variation), with the average of 0.65, and the relative values of root dry-weight ranged between 0.49 and 1.15 (2.35-fold variation), with the average of 0.82. It revealed that there exists great genetic variation among the tested genotypes. Based on these results we created three groups (Table 2), namely, P starvation tolerant (29 varieties), sensitive (68 varieties) and moderate (59 varieties) groups.

In addition, eight soybean varieties, see Table 3 for

**Table 3** The bean seed phosphorus content of different P starvation responsive types

| types | varieties | SSTP/mg | SSIP/mg |
|---|---|---|---|
| tolerant type | Ji-dou 11 | 1.653 | 0.041 |
| | Lü 75 | 2.443 | 0.070 |
| | Hei-da-li | 2.611 | 0.107 |
| | Zhong-huang 15 | 1.524 | 0.039 |
| | Zhe 98-14 | 2.072 | 0.061 |
| | Da-mao-jiao | 1.800 | 0.042 |
| | Da-huang-dou | 1.734 | 0.035 |
| | Zha-lai-te-qi | 1.516 | 0.047 |
| | **average** | **1.919** | **0.055** |
| moderate type | Ji-dou 7 | 1.373 | 0.036 |
| | Sui-nong 3 | 1.298 | 0.036 |
| | He-feng 35 | 1.038 | 0.041 |
| | Ri-ben-zao-mao-dou | 1.178 | 0.032 |
| | Nei-meng 440 | 1.178 | 0.038 |
| | Lu-dou 4 | 1.254 | 0.027 |
| | Shan-xi 8274 | 1.287 | 0.043 |
| | Huang-dou | 1.404 | 0.027 |
| | **average** | **1.251** | **0.035** |
| sensitive type | Ji-dou 3 | 1.059 | 0.033 |
| | Niu-mao-huang | 0.900 | 0.033 |
| | Fen-dou 53 | 1.097 | 0.030 |
| | Tian-zhuang-da-wu-dou | 1.059 | 0.032 |
| | Tian-e-dan | 1.192 | 0.036 |
| | Ping-ding-huang | 0.572 | 0.024 |
| | Nf-58 | 0.925 | 0.027 |
| | Zhong-dou 32 | 1.044 | 0.024 |
| | **average** | **0.981** | **0.030** |

Note: SSTP represents single seed total phosphorus content; SSIP represents single seed inorganic phosphorus content.

names, were selected for their high tolerance to P starvation under zero phosphorus conditions.

3.3 Characterization of morphological and physiologic attributes related to tolerance to P starvation

From the three groups in Table 2, we selected eight sensitive (which have the lowest relative values of shoot and root dry weight in group III), eight moderate (which have the moderate relative values of shoot and root dry weight in group II) and eight tolerant (which have the highest relative values of shoot and root dry weight in group I) genotypes to study various morphological and physiological characteristics of phosphate uptake and utilization. The results showed that soybean plants have developed many mechanisms to adapt to the P deficiency environment, such as seed phosphorus content (Table 3), the modification of root morphology (Fig. 3) and the acidification of root rhizosphere (Fig. 4).

The comparison of seed characteristics in Table 4 of the three different types showed that the tolerant varieties have much higher seed total phosphorus content (1.516–2.611 mg·seed$^{-1}$, with the average of 1.919 mg·seed$^{-1}$) and seed inorganic phosphorus content (0.035–0.107 mg·seed$^{-1}$, with the average of 0.055 mg·seed$^{-1}$). The P starvation sensitive varieties in contrast have lower seed total phosphorus content (0.572–1.192 mg·seed$^{-1}$, with the average of 0.981 mg·seed$^{-1}$) and seed inorganic phosphorus content (0.024–0.036 mg·seed$^{-1}$, with the average of 0.030 mg·seed$^{-1}$).

Therefore, the variation in seed total phosphorus content and seed inorganic phosphorus content could partially explain the difference in P starvation tolerance appearance observed for these varieties.

Moreover, the phenomenon of root growth modification and root rhizosphere acidification were also found in our study, just like the adaptation mechanisms to P starvation

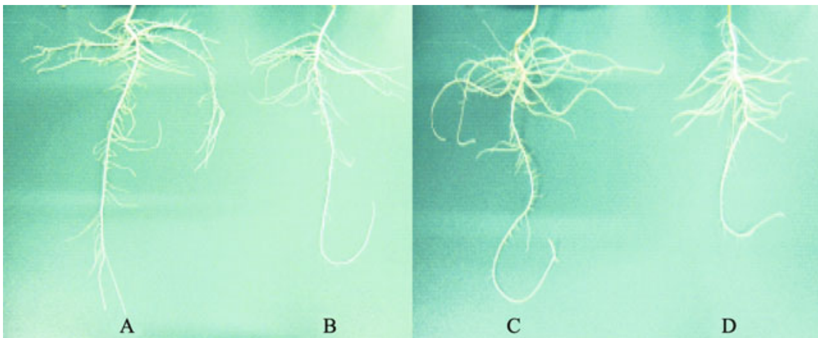


**Fig. 3** Differences of bean seedling roots between cultivars grown in zero P and adequate P
Note: A and C represent characteristic roots of P tolerant varieties. B and D represent characteristic roots of P sensitive varieties.

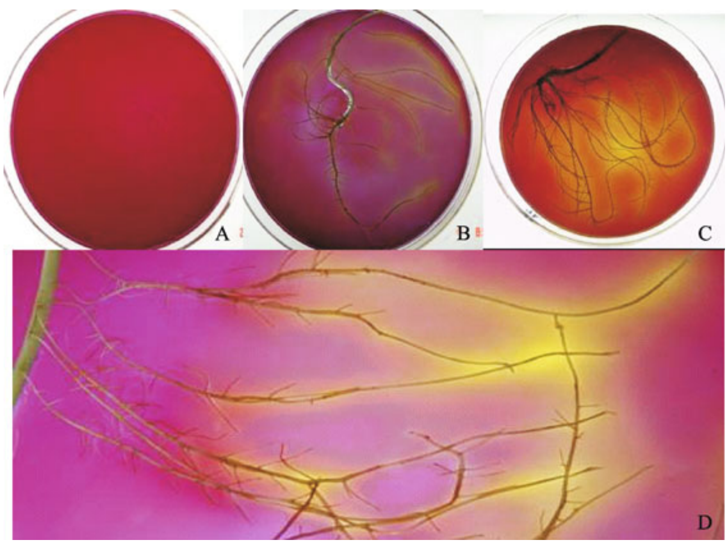


**Fig. 4** Rhizosphere acidification under P deficiency environment in soybean
Note: A–D represent control, soybean roots without P starvation, soybean roots under P deficiency environment and the acidification of different root positions under P deficiency environment, respectively (pH 6.5–7.0 = purple, pH 4.0–5.0 = yellow).

**Table 4** Multiple comparisons on seed phosphorus content of different P starvation responsive types

| type | SSTP mean | significance at 0.05 level | type | SSIP mean | significance at 0.05 level |
|---|---|---|---|---|---|
| tolerant | 1.919±0.414 | a | tolerant | 0.055±0.023 | a |
| moderate | 1.251±0.140 | b | moderate | 0.035±0.006 | b |
| sensitive | 0.981±0.185 | c | sensitive | 0.030±0.004 | b |

Note: Duncan multiple comparison, $n = 3$.

in many other crops (Neumann et al., 2000; Hammond et al., 2004). The P tolerant genotypes did produce a more proliferated root system in the dish than those P sensitive genotypes (Fig. 3). In addition, under the zero P conditions, soybean rhizosphere pH values were much lower (pH 4.0–5.0) than that in the P sufficient environment (pH 6.5–7.0) after transplanting to agar sheets (Fig. 4). This increase in root acid exudates under zero P conditions is known as the root rhizosphere acidification phenomenon. This rhizosphere acidification phenomenon was shown by the yellow discoloration of the agar around roots. In contrast, little decrease in pH variation occurred in the rhizosphere of the root zone of the plants grown in adequate P. This supports the conclusion that the root growth modification and rhizosphere acidification are important physiologic mechanisms by which soybean plants acquire and utilize P from the environments.

## 4 Discussion

Among the many inorganic nutrients required by plants, P is one of the most important elements that can significantly affect plant growth and metabolism. However, low availability of P is also one major constraint for crop production in many low-input systems of agriculture worldwide. Recently, one new approach, namely selecting or developing improved crop germplasms that are better adapted to low soil P conditions, with more efficient uptake and utilization of P fertilizers, has been put forward by many breeders and plant nutrition scientists (Yan et al., 2006).

In recent years, promising results have been found in the world toward selecting crop species or varieties for high tolerance to P starvation in wheat, rice, maize, sorghum, oilseed rape, soybean and other crops (Cao and Pan, 2000; Osborne and Rengel,2002b; Li et al.,2003; Gill et al., 2004; Ozturk et al., 2005). The selection results of soybean varieties in China are listed in Table 5. These cultivars are but a few of all the known genotypes and much more work needs to be done in order to develop and utilize such results in future breeding efforts. It is therefore necessary to select more soybean genotypes that have high tolerance to P starvation, either high P-uptake or P-utilization.

For screening of P tolerant genotypes, it is very important to determine the effective indexes reflecting P tolerance of soybean. Recently, for selecting the ideal parameters of P tolerance genotypes, 15 morphological

**Table 5** The selected soybean germplasms with high tolerance to P starvation in China

| types | genotypes | references |
|---|---|---|
| P starvation tolerant varieties | Chang-nong 4 | Li et al., 1995 |
| | Xi-dou 3, Lian-yuan-ni-dong-huang-dou, Xiang-chun 91-100, Zhe-chun 2 | Ding et al., 1999 |
| | Shuang-feng-hong-dou, Cheng-dou 4 | Ding et al., 1998 |
| | Ba-xi 10, Ba-xi 11 | Xu et al., 2003 |
| | Tie 7551, Tie 7555, Liao-dou 13, Jin-dou 33 | Li, 2004 |
| | Jin-dou 20, Tie-feng 30 | Ding et al., 2005 |
| | Shang-hai-da-qing-dou, Hui-min-tie-chu-gan, Qi-huang 1 | Liu, 2005 |
| | Ji-nong 21,Qi-huang 24, Jin-yi 15 | Ding et al., 2006 |
| | Jin-dou 33, Tie 7555, Da-huang-dou, Liao-dou 13 | Wang et al., 2007 |
| | Hei-he 27, Ken-jian 27, Sui-nong 4, Feng-shou 24, Ke-jiao 05-1397 | Wu et al., 2008 |
| | Genotype 12, 14, 17, 20, 67 (name not given) | Pan et al., 2008 |
| P starvation sensitive varieties | Chang-nong 5 | Li et al., 1995 |
| | Liao-dou 10, Hei-nong 37, Ji-lin 27 | Nian et al., 1998 |
| | E-dou 5 | Ding et al., 1998 |
| | Xiang-dou 3, Gui-yang-ao-quan-huang-dou | Ding et al., 1999 |
| | Feng-jiao 59-15, Liao-dou 11, Jin 8-14, Tie-feng 3, Liao 9111 | Li, 2004 |
| | Jin 8-14, Feng-jiao 59-15, Tie-feng 3, Liao-dou 11,Liao 9111 | Wang et al., 2007 |
| | Genotype 1, 9, 34, 43, 46 (name not given) | Pan et al., 2008 |

and physiologic parameters were involved in evaluating P tolerance of 96 soybean genotypes. The results of screening showed that the shoot dry weight under P deficiency and relative shoot dry weight were effective and simple indicators for screening P tolerance genotypes in soybean (Pan et al., 2008). In our study, bean seedlings grown under zero soil P were investigated to identify the P tolerance of soybean genotypes, and the results showed that the relative values of shoot and root dry-weights were most suitable as screening characters. With our method we quickly and reliably identified those bean cultivars which grew better under the zero soil P conditions.

Furthermore, in the present study, 156 soybean genotypes were sorted, based on the screening systems mentioned above, for their P starvation tolerance, and eight varieties, Ji-dou 11, Lü 75, Hei-da-li, Zhong-huang 15, Zhe 98-14, Da-mao-jiao, Da-huang-dou and Zha-lai-te-qi were selected for their high tolerance to P deficiency under P starvation conditions. These selected varieties not only can replenish the number of high tolerance to P deficiency soybean genotypes in China (Table 5), but also can provide more germplasm resources to isolate high tolerance P deficiency related genes, as has been done in the transcription factor gene *OsPTF1* (GenBank accession No. AY238991) cloned in the rice variety Kasalath (Yi et al., 2005), gene *GmPTF1* (GenBank accession No. FJ617239) cloned in soybean variety Zhong-huang 15 and gene *GmPHR1* cloned in soybean variety Ji-dou 11 (Li et al., 2009; Wang et al., 2010, Submitted to Acta Agronomica Sinica).

**Acknowledgements** This research was supported by the National Project (No. 2009ZX08004-004B) for Transgenic Research and Natural Science Foundation of Hebei Province (No. C2007000474).

## References

Cao L M, Pan X H (2000). Screening and identification of rice (*Oryza sativa* L.) genotypes on the tolerance to low phosphorus environment. Journal of Jiangxi Agricultural University, 22: 162–168 (in Chinese)

Davies T G E, Ying J, Xu Q, Li Z S, Li J, Gordon-Weeks R (2002). Expression analysis of putative high-affinity phosphate transporters in Chinese winter wheats. Plant Cell Environ, 25(10): 1325–1339

Ding H, Cai G X, Jiang X Y, Li S X (1999). Tolerance changes of soybean cultivars with different low phosphorus tolerance on two types of soil. Chinese Journal of Oil Crop Science, 21(3): 56–60 (in Chinese)

Ding H, Guo Q Y, Li Z Y (1998). Effect of phosphorus on grain yield and quality in soybean cultivars. Chinese Journal of Oil Crop Science, 20(2): 66–70 (in Chinese)

Ding Y C, Chen M C, Cheng B, Li L J, Li D Y (2005). Phosphorous uptakes and use s of different soybean varieties. Acta Botanica Boreali-Occidentalia Sinica, 25(9): 1791–1797 (in Chinese)

Ding Y C, Chen M C, Cheng B, Li L J, Zhang H S (2006). The selection of spring soybean genotypes with high phosphorus efficiency in Northern China. Plant Nutrition and Fertilizer Science, 12(4): 597–600 (in Chinese)

Gill H S, Singh A, Sethi S K, Behl R K (2004). Phosphorus uptake and use efficiency in different varieties of bread wheat (*Triticum aestivum* L). Arch Agron Soil Sci, 50(6): 563–572

Hammond J P, Broadley M R, White P J (2004). Genetic responses to phosphorus deficiency. Ann Bot (Lond), 94(3): 323–332

Holford I C R (1997). Soil phosphorus: its measurement and its uptake by plants. Aust J Soil Res, 35(2): 227–240

Li J Y, Li Z S, Liu X D, Zhou W, Sun J H, Tong Y P (1995). Technique of wheat breeding for efficiency utilizing soil nutrient elements. Science China Chemistry (Series B), 38: 1313–1320

Li S C, Gong J, Wang J (2003). Screening maize inbred lines seedling for tolerance to low phosphate stress. Journal of Maize Sciences, 11: 85–89 (in Chinese)

Li X H, Chang W S, Liu Y, Wang J H, Zhang C Y (2008). Genetic variability for phosphorus content in seeds of soybean varieties. Journal of Plant Genetic Resources, 9(3): 381–384 (in Chinese)

Li Z G (2004). Screening of Soybeans with High Phosphorus Absorption Efficiency and Their Responses to Different Phosphorus Levels. Dissertation for the Doctoral Degree. Shenyang: Shenyang Agricultural University, 36–37(in Chinese)

Li Z H, Chen D, Cao G J, Wang J (1995). P stress response in the growth and the kinetics of P uptake on difference genotype soybean roots. Journal of Jilin Agricultural University, 17(2): 54–57 (in Chinese)

Liu Y (2005). Identification of Tolerance to Rhizosperical Stresses and Inheretance and OTL Locating of Related Root Traits in Soybean. Dissertation for the Doctoral Degree. Nanjing: Nanjing Agricultural University, 67–68 (in Chinese)

Narang R A, Bruene A, Altmann T (2000). Analysis of phosphate acquisition efficiency in different Arabidopsis accessions. Plant Physiol, 124(4): 1786–1799

Neumann G, Massonneau A, Langlade N, Dinkelaker B, Hengeler C, Romheld V, Martinoia E (2000). Physiological aspects of cluster root function and development in phosphorus deficient white Lupin (*Lupinus albus* L.). Ann Bot (Lond), 85(6): 909–919

Nian H, Guo Z H, Yu R C, Lu Y G, Huang H (1998). Evaluations for low-P tolerance of soybean cultivars from different geographical origins. Soybean Science, 17(2): 108–114 (in Chinese)

Osborne L D, Rengel Z (2002b). Genotypic differences in wheat for uptake and utilization of P from iron phosphate. Aust J Agric Res, 53: 837–844

Ozturk L, Eker S, Torun B, Cakmak I (2005). Variation in phosphorus efficiency among 73 bread and durum wheat genotypes grown in a phosphorus-deficient calcareous soil. Plant Soil, 269: 69–80

Pan X W, Li W B, Zhang Q Y, Li Y H, Liu M S (2008). Assessment on phosphorus efficiency characteristics of soybean genotypes in phosphorus-deficient soils. Agric Sci China, 7(8): 958–969

Raghothama K G (1999). Phosphate acquisition. Annu Rev Plant Physiol Plant Mol Biol, 50(1): 665–693

Smith F W, Mudge S R, Rae A L, Glassop D (2003). Phosphate transport in plants. Plant Soil, 248(1/2): 71–83

Wang C, Luo D M, Xu Y L, Li Z G, Wurentuya, Sarula (2007). The screening of soybean genotypes with tolerance to phosphorus. Journal of Inner Mongolia University for Nationalities, 22(2): 150–

153 (in Chinese)
Wu J J, Zhong P, Liu L J, Liu D S, Lin W G, Dong D J (2008). Evaluation on the low phosphorous tolerance of different soybean genotypes. Soybean Science, 27(6): 983–987 (in Chinese)
Xu Q P, Luo C Y, Liao H, Yan X L, Nian H (2003). Study on the response of soybean varieties to P deficiency. Soybean Science, 22: 108–114 (in Chinese)
Yan X L, Wu P, Ling H Q, Xu G H, Xu F S, Zhang Q F (2006). Plant nutriomics in China: an overview. Annals of Botany, 98: 473–482
Yan X L, Zhang F S (1997). Plant Nutrition Genetics. Beijing: China Agricultural Press, 44–45 (in Chinese)
Yi K K, Wu Z C, Zhou J, Du L M, Guo L B, Wu Y R, Wu P (2005). OsPTF1, a novel transcription factor involved in tolerance to phosphate starvation in rice. Plant Physiol, 138(4): 2087–2096