

Large-scale screening for *Aegilops tauschii* tolerant genotypes to phosphorus deficiency at seedling stage

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Abstract *Aegilops tauschii*, as one of wheat wild relatives, possesses a wide range of resistance to biotic/abiotic factors. To better utilize and provide the genetic basis of breeding for improving phosphorus deficiency tolerance, large-scale screening for tolerant *A. tauschii* to phosphorus deficiency was conducted using hydroponic experiment. A total of 380 *A. tauschii* genotypes were used to evaluate their phosphorus deficiency tolerance using root system at seedling stage. The results indicate that compared to applied phosphorus condition, genetic variation of the tested traits among 380 *A. tauschii* genotypes was significant under non-applied phosphorus condition. Heritability estimates showed that root dry weight, shoot dry weight, and total dry weight is highly inheritable. Principal component (PC) analysis showed that first four PCs explained 81.387 % of total variation. S value and phosphorus deficiency tolerance index (PDTI) showed that all *A. tauschii* genotypes can be divided into three groups, high (17 %), moderate (58 %) and low (25 %) tolerance groups. Compared with other cultivated wheat using S

value and PDTI, the top five tolerant *A. tauschii* genotypes have stronger ability of phosphorus deficiency tolerance than other cultivated wheat. In conclusion, we systematically evaluated large-scale *A. tauschii* genotypes, and 63 tolerant lines and some root traits used as selection criteria were selected. The top five tolerant *A. tauschii* genotypes have relative higher tolerance than other wheat, and can be further used for wheat genetic improvement and molecular breeding for abiotic stress tolerance.

Keywords *Aegilops tauschii* · Wheat · Phosphorus deficiency · Root system

Introduction

Phosphorus (P) is of definite importance for the production of food crops and the demand for P fertilizer is increasing worldwide. Terrestrial plants generally take up soil P in its inorganic form (Pi) (Marschner 1995). However, 50–80 % of the total P in agricultural soils exists as organic phosphate, in which, up to 60–80 % is myoinositol hexakisphosphate (phytate) (Iyamuremye et al. 1996; Turner et al. 2002; George and Richardson 2008). Because phytate-P is not directly available to plants, low P availability becomes one of the limiting factors to plant growth and development. Not surprisingly, application of P fertilizer is the main solution.

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However, high inputs and low recovery rates of P fertilizers not only increase the cost of crop production, but also accelerate the exhaustion of non-renewable phosphate resources (CAY 1991, 2006). It has been estimated that the P will be exhausted by the end of this century both in China (Ma et al. 2005) and worldwide (Vance et al. 2003).

In response to available P deficiency condition, plants have developed numerous adaptive mechanisms for better growth, including modification of root morphology and architecture, activation of high-affinity Pi transporters, improvement of internal phosphatase activity, and secretion of organic acids and phosphatases (Raghothama and Karthikeyan 2005; Vance et al. 2003). Plants can increase acquisition and utilization efficiency of P through these adaptive mechanisms, which are referred to as P-efficiency (Wang et al. 2010). But there are many differences in P-efficiency among different plant species. Meanwhile, mechanisms of P-efficiency can be different from one genotype to other within a given plant species, such as wheat (Levent et al. 2005), sweet maize (Lu et al. 2010) and rice (Li et al. 2005). In wheat, the differences of P-efficiency have the following characters: (i) modern cultivars exceed traditional cultivars (Horst et al. 1993), (ii) semi-dwarf plant type exceeds common plant type (Wu 1990), and (iii) cultivars that developed from distant hybridization exceed common cultivars (Zhong et al. 2003). In other words, different genotypes of plant species exist obvious genetic diversity on P-efficiency, high P-efficiency genotypes of plant species often demonstrate high tolerance to P deficiency, thereby, screening and utilizing high tolerance genotypes to P deficiency of a given plant species could be a good solution to face available P deficiency.

In the long process of biological evolution, wild species survive in various stress conditions and conserve some favorable traits, such as, drought resistance, saline-alkaline resistance, barren soil resistance, disease resistance and P deficiency resistance (Cui et al. 2004). Thus, taking advantages of these favorable traits in wild relatives or ancestors of wheat can improve wheat breeding efficiency. *Aegilops tauschii* is one of the ancestral species of wheat, which is the donor species of D genome of wheat. It possesses with a wide range of resistance/tolerances to biotic/abiotic factors (Valkoun et al. 1990; Cox et al. 1992) that can contribute to wheat improvement, (Yen and Yang 1984). In addition, screening and evaluation

of high P-efficiency genotypes more concentrated in common wheat in China and abroad at present (Yang et al. 2012; Xiong et al. 2008), excellent genetic resources of wild species also remains to excavate, so breeders increasingly focused on *A. tauschii*.

In the study, 380 *A. tauschii* genotypes from all over the world were evaluated using root system through hydroponic experiments. The digital image analysis was introduced to collect root characters, because it provides more accurate and less subjective measures than the characteristics that the human eye can detect (Bouma et al. 2000). Thus, we use digital image analysis to investigate root characters of *A. tauschii* under applied phosphorus (AP) and non-applied phosphorus (NAP) conditions at seedling stage. The objectives of this study were to establish the evaluation system of wild relatives using multiple root related traits, and to screen excellent gene resources with high tolerance to P deficiency from 380 *A. tauschii*, laying the foundation for wheat breeding for improving abiotic stresses.

Materials and methods

Plant materials

A total of 380 *Aegilops tauschii* accessions ($2n = 14$, DD), two hexaploid wheat accessions, CS and CN16, (*Triticum aestivum* L., $2n = 42$, AABBDD), two tetraploid wheat accessions, AS2255 and AS313, (*Triticum turgidum* L., $2n = 28$, AABB) and two synthetic hexaploid wheat lines, LAN-2404 and LAN-2399 ($2n = 42$, AABBDD) were used in the study. These accessions were maintained by Triticeae Research Institute of Sichuan Agricultural University (SAU). CS accession is susceptible to P deficiency (Su et al. 2006; Ren 2012). LAN-2404 and LAN-2399 were screened as tolerant genotypes under drought and nutrients deficiency stresses in our previous studies. CN16 is a native wheat cultivar possessing good comprehensive characters and is an ideal recurrent parent for back-cross breeding. These accessions were maintained by Triticeae Research Institute of Sichuan Agricultural University (SAU).

Growth conditions

All the *A. tauschii* were grown in phytotron in Wenjiang, Sichuan Province, China, during September

2012–March 2013. The materials were evaluated by hydroponic experiments under two phosphorus conditions, applied phosphorus (AP) and non-applied phosphorus (NAP) in a completely randomized design, each with four replications. The AP and NAP treatments contained normal nutrient solution with and without $\text{NH}_4\text{H}_2\text{PO}_4$ (1 mmol/L), respectively. The normal nutrient solution was modified from Hoagland's nutrient solution (Hoagland and Arnon 1950) in order to optimize growth condition of *A. tauschii*. The modified Hoagland's nutrient solution is consisted of $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ (4 mmol/L), KNO_3 (6 mmol/L); $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ (2 mmol/L), H_3BO_3 (46 $\mu\text{mol/L}$), $\text{Na}\cdot\text{Fe}\cdot\text{EDTA}$ (100 $\mu\text{mol/L}$); $\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$ (9.146 $\mu\text{mol/L}$), $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ (0.76 $\mu\text{mol/L}$), $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ (0.32 $\mu\text{mol/L}$), $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24} \cdot 4\text{H}_2\text{O}$ (0.0161 $\mu\text{mol/L}$).

Uniform seedlings grown from eight-day germinated seeds were transplanted into a hole of foamboard, a sponge stripe was needed to twine around the seedlings in case of their falling down from foamboard, and then put the foamboard with seedlings into the box which filled with nutrient solution. Make sure all the little root of seedlings must be fully exposed to nutrient solution so that they can absorb nutrients. In order to ensure the regular growth of all the seedlings after transplanting, they should be grown in normal solution with phosphorus for four days. Subsequently, normal solution with $\text{NH}_4\text{H}_2\text{PO}_4$, and without $\text{NH}_4\text{H}_2\text{PO}_4$ were used to water *A. tauschii* genotypes under AP and NAP conditions, respectively, and the solutions were replaced every 4 days. The growth environment of all seedlings was 25/22 (± 1) °C day/night temperature and 65/85 % day/night relative humidity, and a 16-hour photoperiod with 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photon flux density at the level of the plant canopy.

Data collection and analysis

Shoot characteristics and root morphology were evaluated after 18 days of transplantation. Seedlings was washed with clean water carefully and then root morphology was scanned with the scanner Epson XL 10,000 \times , using WinRHizo Pro 2008a image analysis system (Régent Instr. Inc., Quebec, Canada) to obtain root characteristics including root length (RL), root diameter (RDM), root surface area (RSA), root volume (RV), root tips (RT) and root

forks (RF). Then the plants were separated into shoot and root, stored in paper bags, and heated at 105 °C for 30 min to kill the living cells, and then dried at 75 °C until obtaining constant mass, root dry weight (RDW) and shoot dry weight (SDW) (Table 1).

In order to eliminate inherent biology and genetics difference of different *A. tauschii* genotypes, the phosphorus deficiency tolerance index (PDTI) was used as an indicator to measure diversity of different genotypes with $\text{PDTI} = T_{\text{NAP}}/T_{\text{AP}}$ (Ren 2012; Zhang et al. 2004a, b), where T_{NAP} and T_{AP} are the traits measured under NAP and AP conditions respectively. The estimate of heritability is defined by the formula $H = V_G/(V_G + V_E)$, where V_G and V_E represent estimates of genetic and environmental variances, respectively (Smith et al. 1998). Stepwise multiple linear regression was used according to Draper and Smith (1966) to determine the variable accounting for the majority of total TDW variability. Descriptive analysis, analysis of variance, correlation analysis, principal component analysis (PCA) and multiple linear stepwise regression were conducted for the tested traits using IBM SPSS Statistics for windows, Version 20.0 (IBM Corp. Released 2011). Weighting method was utilized to acquire S value of each *A. tauschii* genotype, which calculated as $S = \sum_{i=1}^k r_i Y_i / \sum_{i=1}^k r_i$, where r_i is the first i eigenvalues of principal component (PC), Y_i is the first i score of PC that calculated by SPSS factor analysis using PDTI, k is the number of PC.

Results

Variance analysis and the basic parameter estimation

Analysis of variance revealed obvious variation among genotypes for all tested traits (Table 2). The level of variation is reflected by distribution of the traits representing different P deficiency tolerance criteria (Fig. 1). Ten traits except RL in 380 *A. tauschii* genotypes have significant variation. Significant difference was also observed under the NAP and AP conditions for the tested traits except RDM. The results indicate that the tested traits were significantly influenced by phosphorus supply among 380 *A.*

tauschii genotypes and they could be used for further genetic analyses. The basic parameter estimation including mean, standard deviation and coefficient of variation also showed substantial phenotypic variation among genotypes for each trait (Table 3). Coefficient of variation under NAP condition ranged from 13.113 to 41.436 %, while under AP condition it ranged from 5.043 to 36.288 %. Compared with AP condition, the mean value of RL, RDW, SDW, RDM, RSA, RV and TDW decreased under NAP condition, on the contrary, the rest traits including RT, RF and R/S increased under NAP condition.

Fig. 1 Distribution of 10 traits phenotyped under non-applied phosphorus (NAP) and applied phosphorus (AP) conditions in 380 *Aegilops tauschii* genotypes

Heritability estimated

Heritability estimates were obtained for all the traits (Table 3), and it was generally higher under NAP condition than that under AP condition. Among them, TDW had the highest heritability (0.905 for NAP and 0.818 for AP) and RDM had the lowest heritability (0.685 for NAP and 0.550 for AP). For the other traits,

Table 1 Description of traits collected in the study

Abbreviated trait name	Full trait name	Description
RL	Root length (cm)	The average root length of four plants
RDW	Root dry weight (g)	The average root dry weight of four plants
SDW	Shoot dry weight (g)	The average shoot dry weight of four plants
RDM	Root diameter (mm)	The average root diameter of four plants
RSA	Root surface area (cm ²)	The average root surface of four plants
RV	Root volume (cm ³)	The average root volume of four plants
RT	Root tips	The average number of root tips of four plants
RF	Root forks	The average number of root forks of four plants
TDW	Total dry weight (g)	The total weight of RDW and SDW
R/S	Root to shoot ratio	The ratio of root dry weight to shoot dry weight

Table 2 Variance analysis for the measured traits under applied phosphorus (AP) and non-applied phosphorus (NAP) conditions

Variables	Type III sum of squares		Mean square		F value		P value	
	Treatment	Genotype	Treatment	Genotype	Treatment	Genotype	Treatment	Genotype
df	1	379	1	379	1	379	1	379
RL	7820.847	11850.454	7820.847	31.268	413.592	1.153	**	NS
RDW	0.028	2.106	0.028	0.012	145.004	1.553	**	**
SDW	0.174	0.534	0.174	0.001	171.607	1.316	**	**
RDM	0.67	247.532	0.67	0.653	1.283	1.666	NS	**
RSA	203099.681	3013988.737	203099.681	7952.477	31.438	1.449	**	**
RV	181.647	7842.79	181.647	20.693	9.789	1.228	**	*
RT	20918303.36	697687710.1	20918303.36	1840864.67	14.589	1.706	**	**
RF	74208542.02	6580137111	74208542.02	17361839.34	6.113	2.447	*	**
TDW	0.341	1.059	0.341	0.003	176.983	1.429	**	**
R/S	0.002	13.153	0.002	0.035	0.061	1.103	*	*

df degree of freedom; RL root length; RDW root dry weight; SDW shoot dry weight; RDM root diameter; RSA root surface area; RV root volume; RT root tips; RF root forks; TDW total dry weight; R/S root to shoot ratio, NS not significant

* and ** represent significance level of $P < 0.05$ and $P < 0.01$ respectively

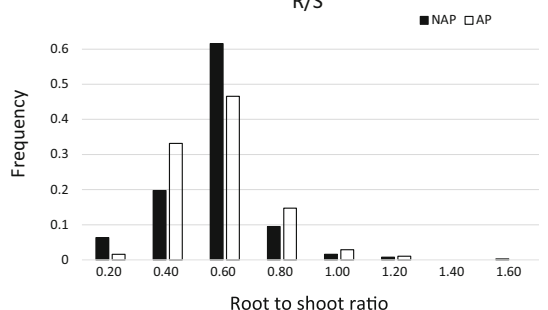
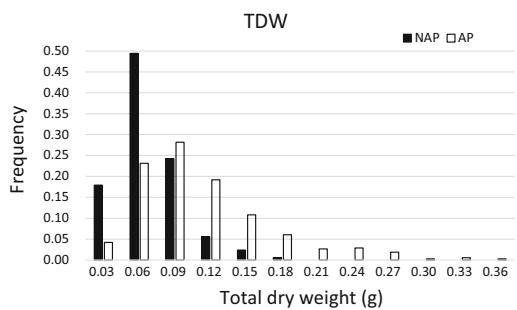
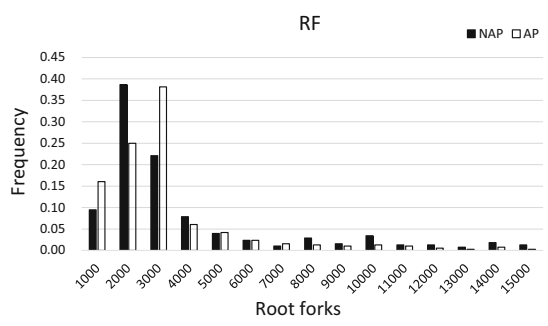
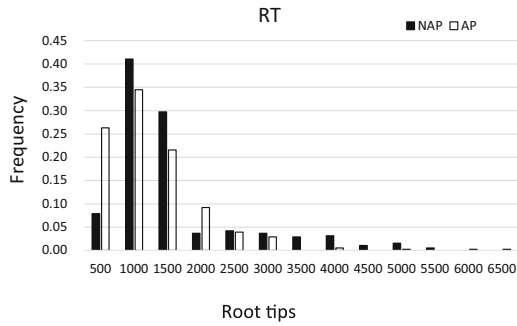
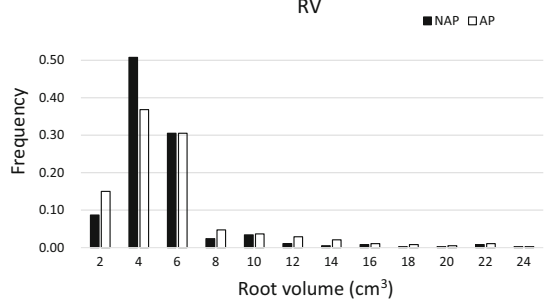
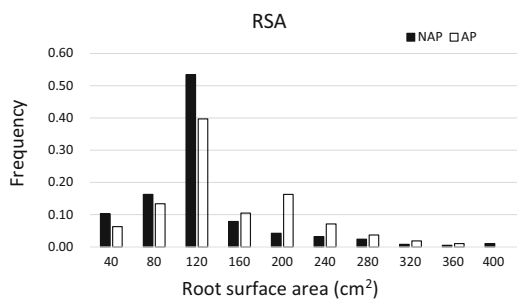
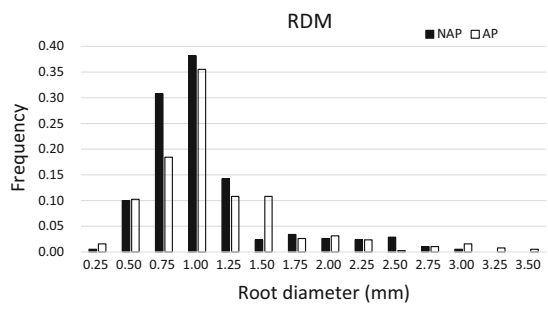
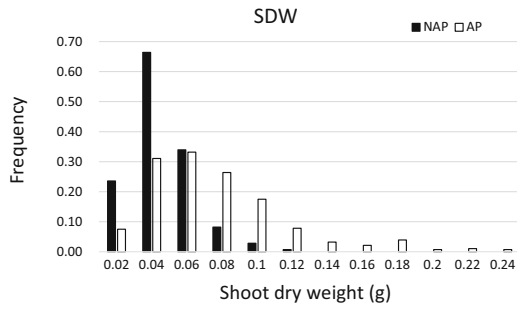
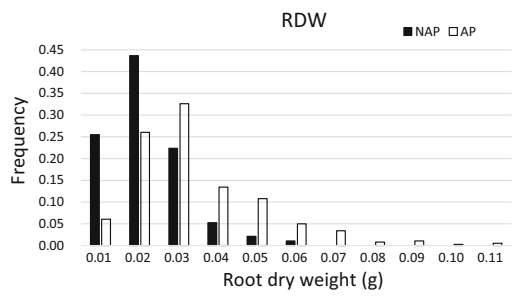
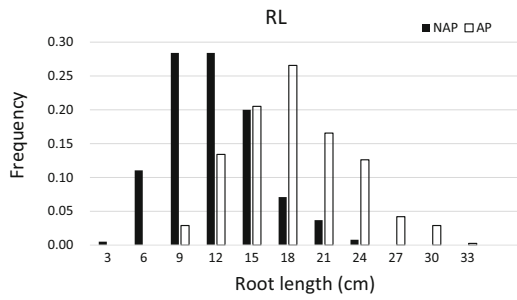


Table 3 Means, standard deviation (Sd), coefficients of variation (CV %) and heritability estimates for the tested traits under non-applied phosphorus (NAP) and applied phosphorus (AP) conditions

Traits	Mean		Sd		CV %		Heritability	
	NAP	AP	NAP	AP	NAP	AP	NAP	AP
RL	10.418	16.834	3.835	4.807	36.814	28.555	0.740	0.618
RDW	0.018	0.03	0.006	0.01	34.736	33.875	0.900	0.801
SDW	0.037	0.067	0.012	0.021	31.913	31.898	0.868	0.796
RDM	0.838	0.897	0.291	0.267	34.788	29.714	0.685	0.550
RSA	70.838	103.533	11.708	25.671	16.528	24.795	0.838	0.753
RV	2.077	3.055	0.336	0.712	16.174	23.301	0.823	0.759
RT	896.288	564.48	142.425	80.432	15.891	14.249	0.756	0.659
RF	3014.707	2389.75	395.323	120.521	13.113	5.043	0.797	0.733
TDW	0.054	0.097	0.017	0.026	30.859	26.937	0.905	0.818
R/S	0.484	0.361	0.201	0.131	41.436	36.288	0.841	0.725

RL root length; RDW root dry weight; SDW shoot dry weight; RDM root diameter; RSA root surface area; RV root volume; RT root tips; RF root forks; TDW total dry weight; R/S root to shoot ratio

heritability estimates were relatively high, ranging from 0.618 (RL under AP condition) to 0.900 (RDW under NAP condition). It is noteworthy that biomass-related traits like RDW, SDW and TDW showed high heritability estimate (0.900 for NAP and 0.801 for AP; 0.868 for NAP condition and 0.796 for AP condition; 0.905 for NAP condition and 0.818 for AP condition; respectively). RSA (0.838 for NAP and 0.753 for AP), RV (0.823 for NAP and 0.759 for AP), RT (0.756 for NAP and 0.659 for AP) and RF (0.797 for NAP and 0.733 for AP) had an intermediate level of heritability. These results indicate that RDW, SDW and TDW are highly inheritable and can be used as a good indicator for screening *A. tauschii* genotypes for phosphorus deficiency tolerance.

Genetic correlations among tested traits

Pearson correlations among 10 traits were calculated (Table 4), and there are 28 and 27 correlation pairs reached the significant levels under NAP and AP conditions, respectively. Root-related traits, such as RT and RF ($r = 0.888$ and $r = 0.745$ for NAP and AP, respectively), RDW and SDW ($r = 0.837$ and $r = 0.821$ for NAP and AP, respectively), RL and RDW ($r = 0.655$ and $r = 0.643$ for NAP and AP, respectively) showed relatively high correlations under two P treatments. TDW was significantly correlated with SDW (0.978 for NAP and 0.985 for AP) and RL (0.655 for NAP and 0.735 for AP).

Principal component analysis (PCA) and multiple linear regression analysis

Bartlett test of sphericity Chi square value was 2293.627, which reached significant level at $P < 0.001$ and indicated there is high correlation among various traits. Therefore, PCA were performed for all the tested traits (Table 5) and plot for the first principal component (PC1) and the second principal component (PC2) are shown in Fig. 2. The first four principal components (PCs) were selected and the cumulative contribution of them was 81.387 %. The eigenvalue of first PC was 3.046, explained 35.463 % of phenotype variation. RDW, SDW and TDW were the three major factors among corresponding characteristic vector. They represent the plant biomass and can be defined as biomass factor. The eigenvalue of second PC was 2.204, explained 22.036 % of phenotype variation. RSA, RV, RT and RF were the four major factors among corresponding characteristic vector, and they influence the ability of obtaining phosphorus nutrition and can be defined as phosphorus obtaining factor. The eigenvalue of third principal component was 1.253, contributed to 12.534 % of phenotype variation. R/S was the only one major factor and it suggests the environment is conducive to root growth or shoot growth. The eigenvalue of fourth PC was 1.136, with 11.355 % of explained phenotype variation, and RDM was the only one major factor. RL, RT, RF and R/S were negative values and it

Table 4 Genetic correlation among selected traits under applied phosphorus (AP) and non-applied phosphorus (NAP) conditions

	RL	RDW	SDW	RDM	RSA	RV	RT	RF	TDW	R/S
<i>NAP</i>										
RL	1	0.655**	0.630**	-0.138**	-0.108*	-0.147**	0.164**	0.180**	0.655**	0.139**
RDW		1	0.837**	-0.064	-0.021	-0.056	0.210**	0.206**	0.932**	0.416**
SDW			1	-0.103*	0.049	-0.017	0.275**	0.284**	0.978**	-0.063
RDM				1	0.266**	0.420**	-0.086	0.018	-0.093	0.086
RSA					1	0.498**	0.182**	0.295**	0.025	-0.095
RV						1	0.006	0.105*	-0.033	-0.076
RT							1	0.888**	0.261**	-0.015
RF								1	0.266**	-0.033
TDW									1	0.115*
R/S										1
<i>AP</i>										
RL	1	0.643**	0.734**	-0.210**	0.026	-0.182**	-0.014	0.043	0.735**	-0.312**
RDW		1	0.821**	-0.091	0.113*	-0.092	0.048	-0.004	0.907**	0.067
SDW			1	-0.149**	0.038	-0.146**	0.014	0.041	0.985**	-0.376**
RDM				1	0.441**	0.355**	0.215**	0.329**	-0.137**	0.091
RSA					1	0.387**	0.412**	0.562**	0.062	0.012
RV						1	0.146**	0.191**	-0.136**	0.088
RT							1	0.745**	0.025	-0.034
RF								1	0.029	-0.159**
TDW									1	-0.258**
R/S										1

RL root length; RDW root dry weight; SDW shoot dry weight; RDM root diameter; RSA root surface area; RV root volume; RT root tips; RF root forks; TDW total dry weight; R/S:root to shoot ratio

* and ** represent significance level of $P < 0.05$ and $P < 0.01$ respectively

shows that excessive RDM increasing will reduce the value of RL, RT, RF and R/S.

To establish selection indices involving multiple P deficiency tolerant traits, multiple linear regression was performed for the tested traits. Here, we built the regression to explain total dry weight through stepwise regression that contains regression models in which the choice of predictive variables was carried out (Table 6). The final stepwise model built based on P deficiency criteria explained 88.2 % and 86.6 % of phenotypic variation for dry weight under NAP and AP conditions. The built model included six important traits for NAP condition, their relative contribution are: RL (40.9 %), RDW (39.1 %), RDM (7.2 %), RSA (0.6 %), RT (0.3 %) and RF (0.1 %). There are seven important traits for AP condition, their relative contribution are: RL (42.3 %), RDW (38.6 %), RDM (4.0 %), RSA (0.7 %), RV (0.5 %), RT (0.3 %) and RF (0.2 %).

Screening for *A. tauschii* tolerant genotypes using root system

We used weighting method to calculate S value for each *A. tauschii* genotype, and the phosphorus deficiency tolerance index (PDTI) for each trait was calculated as well. The genotypes with relatively higher and lower S value and PDTI are shown in the Table 7. According to the principle of high S value with high tolerance ability, among 380 *A. tauschii*, AS623282 had the highest S value of 3.853 and AS623395 had lowest S value of -1.257, which was selected as extremely tolerant and sensitive genotypes, respectively. Overall, there are 63, 221 and 96 genotypes with high ($S \geq 0.5$), moderate ($-0.5 \leq S < 0.5$) and low tolerant ability ($S < -0.5$), accounting for 17, 58 and 25 %, respectively. PDTI calculated for *A. tauschii* genotypes also reflect the capability of P deficiency tolerance, and plants often enhance P deficiency

Table 5 Principal component analysis (PCA)

Variables	PC 1	PC 2	PC 3	PC 4
RL	0.398	-0.037	0.114	-0.205
RDW	0.462	-0.156	0.288	0.078
SDW	0.455	-0.225	-0.354	0.105
RDM	0.089	0.018	0.239	0.710
Characteristic vector				
RSA	0.117	0.522	-0.103	0.223
RV	0.081	0.483	-0.059	0.380
RT	0.292	0.354	0.080	-0.417
RF	0.217	0.486	0.021	-0.236
TDW	0.502	-0.233	-0.188	0.102
R/S	0.057	-0.042	0.816	-0.036
Eigenvalues	3.046	2.204	1.253	1.136
Contribution %	35.463	22.036	12.534	11.355
Cumulative contribution %	35.463	52.499	65.032	81.387

RL root length; RDW root dry weight; SDW shoot dry weight; RDM root diameter; RSA root surface area; RV root volume; RT root tips; RF root forks; TDW total dry weight; R/S root to shoot ratio; PC principal component

tolerant ability with increasing PDTI. It is observed that *A. tauschii* with a higher S value also has a higher PDTI (Table 7), which illustrates the two selection indicators are effective for screening *A. tauschii* under P

deficiency condition. Among 63 *A. tauschii* genotypes that possess high tolerance under phosphorus deficiency, we found most of them come from the west of Asia and distribute nearby Caspian Sea (Table 8; Fig. 3) through analysis on their geographic origin. It can be seen that 63 *A. tauschii* genotypes were found in 12 countries, of which 13 from Iran, nine from Turkey and eight from Afghanistan. They distributed mainly in a zone of Turkey-Iran-Afghanistan, which is in keeping with the road of *A. tauschii* spreading.

Comparison of tolerance ability among different origin of *A. tauschii*

PDTI for each traits and average S value across all the test traits were used to compare different P deficiency tolerance among different origin of *A. tauschii*. Table 8 listed their average S values for *A. tauschii* genotypes from each origin. China, Turkey, Uzbekistan and Azerbaijan had higher S value, which were 0.212, 0.210, 0.049 and 0.011, respectively. The percentage of the selected tolerant genotypes was 13.333, 22.500, 23.529 and 17.647 % of the total accessions from China, Turkey, Uzbekistan and Azerbaijan, respectively. For PDTI, we compared their values for 10 traits in nine countries, each with more than 10 *A. tauschii* genotypes (Fig. 4). The nine countries included Afghanistan, Armenia, Azerbaijan, China, Iran, Pakistan, Tajikistan, Turkey and

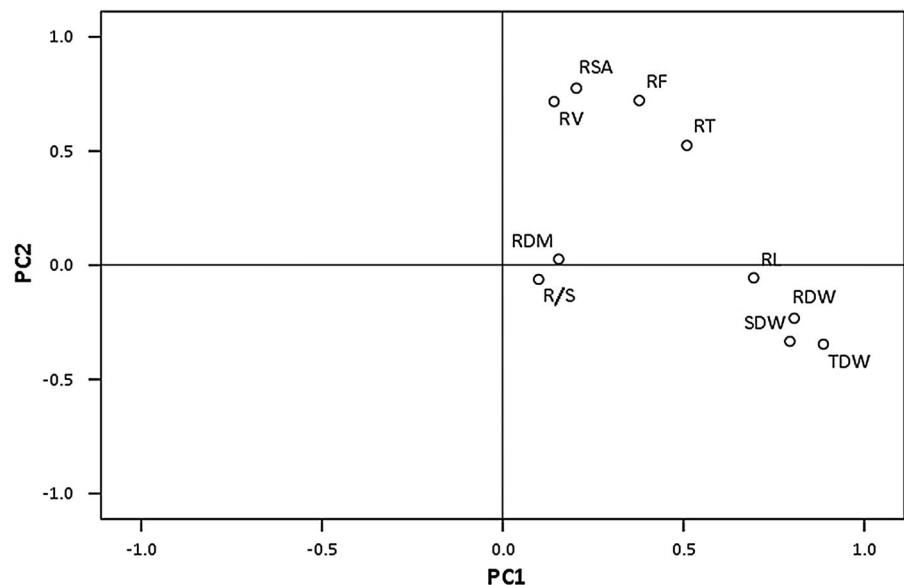
Fig. 2 Scatter plot of the first two principal components (PC) from PCA

Table 6 Multiple linear stepwise regression to explain total dry weight (TDW) from root traits built with *Aegilops tauschii* genotypes means

P treatment	Final stepwise model	R ²	P value
NAP	TDW = 0.006 + 0.001RL + 2.273RDW - 0.001RDM + 0.00001245RSA + 0.0000001801RT + 0.0000003546RF	0.882	<0.001
AP	TDW = -0.022 + 0.003RL + 2.535RDW - 0.001RDM - 0.00003642RSA - 0.00008523RV - 0.000003952RT + 0.000001918RF	0.866	<0.001

NAP non-applied phosphorus; AP applied phosphorus; TDW total dry weight; RL root length; RDW root dry weight; RDM root diameter; RSA root surface area; RV root volume; RT root tips; RF root fork

Table 7 Top 10 genotypes with extremely high tolerance and bottommost 10 genotypes with extremely low tolerance selected from 380 *Aegilops tauschii* based on phosphorus deficiency tolerance index (PDTI) and S value

Genotype	PDTI										S value
	RL	RDW	SDW	RDM	RSA	RV	RT	RF	TDW	R/S	
AS623282	1.763	3.167	2.185	1.919	4.287	1.241	1.545	1.813	2.180	1.903	3.853
AS623011	1.356	3.000	2.111	1.657	3.292	1.516	1.380	1.396	2.800	1.263	3.508
AS623285-1	1.570	2.500	1.143	1.126	3.721	1.483	0.635	0.782	1.444	1.188	3.051
AS623305	0.941	2.000	0.791	1.081	1.214	1.322	0.733	0.736	0.733	1.100	2.325
AS623020	0.584	0.786	0.840	1.232	1.433	1.103	0.620	1.254	0.821	0.935	2.228
AS623296	0.734	0.667	0.718	0.784	2.615	0.952	2.927	2.060	0.711	0.929	2.093
AS623103	0.791	0.533	0.400	1.632	2.715	1.029	1.239	1.496	0.438	1.333	2.047
AS623083	0.664	0.663	0.955	0.772	2.916	0.519	1.602	1.092	0.852	0.695	2.012
AS623144	0.412	0.470	0.575	1.115	2.260	1.248	0.418	0.399	0.543	0.817	1.716
AS623023	1.473	1.000	1.700	1.232	1.116	0.858	4.991	6.697	1.438	0.588	1.703
AS623118	0.432	0.222	0.407	0.639	0.759	0.571	0.232	0.507	0.333	0.545	-0.977
AS623254	0.601	0.222	0.360	0.179	0.160	0.645	0.253	0.631	0.324	0.617	-0.980
AS623017	0.425	0.182	0.333	0.528	0.092	0.049	0.200	0.734	0.272	0.545	-0.984
AS623384	0.264	0.235	0.328	0.475	0.279	0.671	0.297	0.674	0.293	0.718	-1.023
AS623413	0.347	0.294	0.219	0.743	0.142	0.105	0.249	0.850	0.245	0.345	-1.033
AS623243	0.419	0.242	0.266	0.293	0.105	0.44	0.27	0.61	0.25	0.91	-1.114
AS623236	0.255	0.192	0.231	0.795	0.697	0.130	0.236	0.188	0.219	0.833	-1.138
AS623184	0.426	0.250	0.250	0.240	0.073	0.057	0.268	0.348	0.250	0.988	-1.141
AS623077	0.292	0.222	0.376	0.300	0.891	0.374	0.141	0.293	0.327	0.591	-1.177
AS623395	0.365	0.077	0.250	0.601	0.585	0.398	0.092	0.446	0.182	0.308	-1.257

RL root length; RDW root dry weight; SDW shoot dry weight; RDM root diameter; RSA root surface area; RV root volume; RT root tips; RF root fork; TDW total dry weight; R/S The root to shoot ratio

Uzbekistan, and there are 51, 14, 34, 15, 81, 42, 12, 40 and 17 genotypes respectively (Table 8). The four countries China, Turkey, Uzbekistan and Azerbaijan with higher S value also have larger PDTI value for traits, RDW, SDW, RSA, RV, RT, RF and TDW than others (Fig. 4). The results suggest the *A. tauschii* from China, Turkey, Uzbekistan and Azerbaijan have relatively higher P deficiency tolerance ability.

Comparison of tolerance ability between *A. tauschii* and other wheat

According to the S value, AS623282, AS623011, AS623285-1, AS623305 and AS623020 are listed as the top five genotypes with high tolerance ability. To compare the tolerance ability to phosphorus deficiency between *A. tauschii* that have been screened out and other cultivated wheat, tetraploid wheat (AS2255 and

Table 8 Comparison of tolerance ability among different geographic origin of *A. tauschii* using average S value

Origins	<i>A. tauschii</i> genotypes	Average S value	<i>A. tauschii</i> with high tolerance	Percentage of <i>A. tauschii</i> with high tolerance
Afghanistan	51	−0.106	8	15.686 %
Armenia	14	−0.253	1	7.143 %
Azerbaijan	34	0.011	6	17.647 %
China	15	0.212	2	13.333 %
Dagestan, Russian Federation	3	−0.150	0	0
Former Soviet Union	2	0.079	0	0
Georgia	3	−0.399	0	0
India	2	−0.114	0	0
Iran	81	−0.080	13	16.049 %
Kazakhstan	3	−0.009	1	33.333 %
Pakistan	42	−0.090	4	9.524 %
Syrian Arab Republic	4	0.636	3	75.000 %
Tajikistan	12	−0.044	2	16.667 %
Turkey	40	0.210	9	22.500 %
Turkistan	1	0.351	0	0
Turkmenistan	4	0.365	1	25.000 %
Unknown	47	−0.108	7	14.894 %
Uzbekistan	17	0.049	4	23.529 %
Western Asia	5	0.273	2	40.000 %
Total	380		63	

Fig. 3 The geographic distribution of 63 *Aegilops tauschii* genotypes (the zone sketched with red curve) with high tolerance to phosphorus deficiency

AS313), hexaploid wheat (CS and CN16) and synthetic hexaploid wheat (LAN-2404 and LAN-2399) were used in the study. The selected *A. tauschii* genotypes have higher PDTI and S values than other

cultivated wheat (Table 9). CS shows susceptible character under P deficiency in our study and previous reports (Su et al. 2006; Ren 2012). Synthetic hexaploid wheat, LAN-2404 and LAN-2399, were hybrids

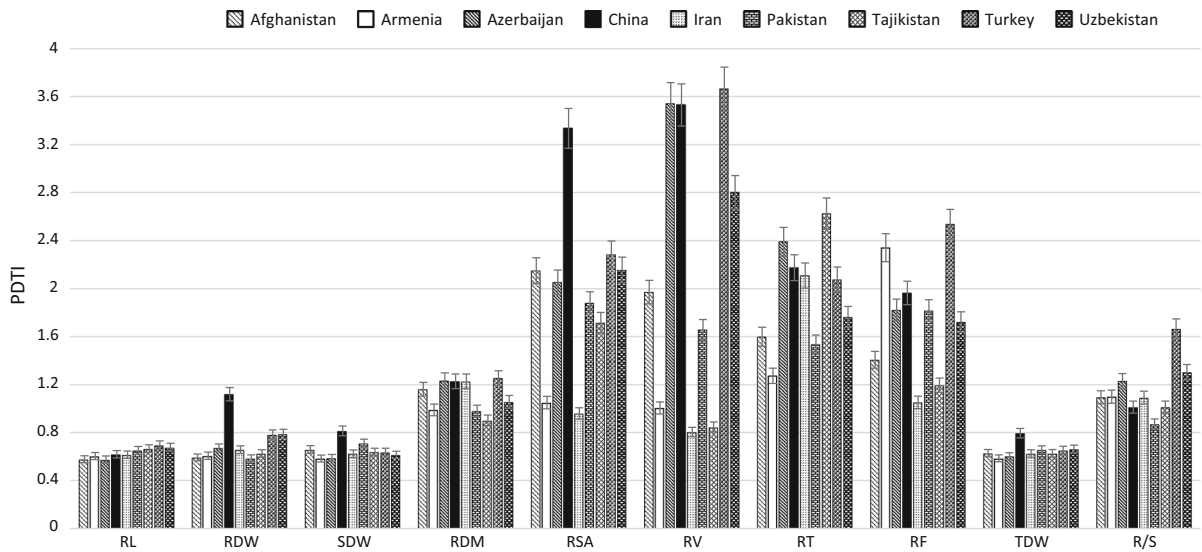


Fig. 4 Comparison of P deficiency tolerance among *Aegilops tauschii* from nine countries using phosphorus deficiency tolerance index (PDTI) of ten traits

Table 9 A comparison of phosphorus deficiency tolerance index (PDTI) and S value between first five extremely tolerant genotypes with tetraploid wheat (AS2255 and AS313),

hexaploid wheat (CS and CN16) and synthetic hexaploid wheat (LAN-2404 and LAN-2399)

Wheat accession	PDTI										S value
	RL	RDW	SDW	RDM	RSA	RV	RT	RF	TDW	R/S	
AS623282	1.763	3.167	2.185	1.919	4.287	1.241	1.545	1.813	2.180	1.903	3.853
AS623011	1.356	3.000	2.111	1.657	3.292	1.516	1.380	1.396	2.800	1.263	3.508
AS623285-1	1.570	2.500	1.143	1.126	3.721	1.483	0.635	0.782	1.444	1.188	3.051
AS623305	0.941	2.000	0.791	1.081	1.214	1.322	0.733	0.736	0.733	1.100	2.325
AS623020	0.584	0.786	0.840	1.232	1.433	1.103	0.620	1.254	0.821	0.935	2.228
CS	0.702	0.656	0.702	1.007	0.515	0.519	0.378	0.515	0.688	0.935	-1.049
CN16	0.691	0.806	0.798	1.087	0.602	0.654	0.355	0.524	0.800	1.011	-0.387
LAN-2404	0.644	0.720	0.840	1.205	0.738	0.889	0.338	0.695	0.806	0.857	0.196
LAN-2399	0.606	0.726	0.733	0.764	1.078	0.818	1.018	1.098	0.878	1.145	0.320
AS2255	0.478	0.792	0.765	1.032	0.324	0.334	0.259	0.281	0.772	1.036	-1.721
AS313	0.506	0.656	0.777	0.929	0.434	0.404	0.430	0.452	0.744	0.844	-1.487

RL root length; RDW root dry weight; SDW shoot dry weight; RDM root diameter; RSA root surface area; RV root volume; RT root tips; RF root forks; TDW total dry weight; R/S root to shoot ratio

crossing by tetraploid wheat and *A. tauschii*. They were selected as tolerant genotypes under drought and nutrient deficiency environments in our previous study. Here, we found it showed moderate tolerance to P deficiency. In addition, the synthetic hexaploid wheat (LAN-2404 and LAN-2399) had higher S value

than tetraploid wheat (AS2255 and AS313) and hexaploid wheat (CS and CN16). The results showed that the top five *A. tauschii* genotypes selected based on S value and PDTI have higher tolerance in response to phosphorus deficiency than other cultivated wheat tested in the study.

Discussion

The importance of root morphological traits for germplasm evaluation

Plants with an extensive root system can absorb more nutrients under conditions of nutrient stress than can plants with a less extensive system. To survive during low phosphorus stress, plants modify their root system to increase the acquisition of phosphorus by increasing the root/shoot ratio, altering root morphology and architecture, stimulating lateral root initiation, and increasing the density and elongation of root hairs (Hammond and White 2008; Hermans et al. 2006; Jain et al. 2007; Lynch 2007). In the present study, compared with AP condition, root tips (RT), root forks (RF), root/shoot ratio (R/S) increased under NAP condition, which is consistent with previous studies. Therefore, root morphology should be considered as an important factor to evaluate germplasms. Nevertheless, very little research has been done on root morphology for evaluation of phosphorus deficiency tolerance for a long time, due to difficulty in root sampling and detection methods. With the aid of the WinRHizo digital images analysis system, this work become feasible, especially for early assessment of root system (Magalhães et al. 2011). The data measured by this analytical system is fast and accurate, and displays great efficiency in early discrimination of phosphorus deficiency tolerance genotypes.

Evaluation of phosphorus deficiency tolerance at seedling stage

A large number of studies in many plant species have shown that phosphorus supply is critical for optimum crop yield in early season, withholding phosphorus during early plant growth will limit crop growth and production from which the plant may not recover. Phosphorus limitation later in the season has a much smaller impact on crop production than do limitations early in growth (Grant et al. 2001). In other words, plants of seedling stage are sensitive to phosphorus stress and most researchers choose seedling stage as period to evaluate tolerance of nutrient deficiency (Kong et al. 2010; Zhao et al. 2011; Guo et al. 2012; Li et al. 2012; Ren 2012;). Besides, the traits related to P deficiency tolerance at seedling stage are associated with crop productivity and yield, and plants with high

tolerance to P deficiency at seedling stage tend to get higher yield (Liu et al. 2005; Zhang et al. 2008; Tahir et al. 2011; Teng et al. 2013). There are several advantages for evaluation of *A. tauschii* genotypes at seedling stage in our study. First of all, the experiment environments can be well controlled so that uniform stress can be applied. Second, compared with the whole stage of plants, phenotypic variation caused by experimental errors can be controlled better because the plants are much more uniform at an early seedling stage. Thirdly, large-scale and high-throughput screening can be carried out in a phytotron using digital images analysis system. It greatly shorten screening period and would be labor-saving and time-saving.

Traits and their relative importance in P deficiency tolerance evaluation

There is a spate of reports about evaluation traits which associated with P tolerant genotypes in China and abroad, but, they can't reach an agreement. In wheat, evaluation traits mainly includes the following three aspects (Sun and Zhang 2002; Bai et al. 2007): (i) root-related traits, for example, root configuration, root length, root weight, lateral root length, root tips, root forks, root diameter, root surface area, root volume and root shoot ratio; (ii) yield-related traits, such as plant height, tiller number, thousand seed weight, biomass and grain yield; (iii) physiology and biochemistry-related traits, for example, acid phosphatase activity, the total organic acid, PH of rhizosphere, chlorophyll content. At present, root or shoot dry weight (biomass traits) and grain yield become the basic and most reliable evaluation traits, root-related traits are frequently and widely used in evaluation of phosphorus deficiency tolerance in numerous crop species (Hammond et al. 2009). Application of evaluation traits are the key points of precise screening germplasm for P deficiency tolerance and statistical model is help for trait selection. Thus, PCA and multiple linear regression analysis were used in the present study. The central idea of PCA is to reduce the dimensionality of a data set consisting of a large number of interrelated variables, while retaining as much as possible of the variation present in the data set (Jolliffe 2002). In this study, the first four PCs contributed more than 80 % of total variations, and biomass factor and P obtaining factor become the main

indicators, which are useful for germplasm screening under P deficiency stress. Multiple linear regression analysis shows that RL, RDW and RDM have larger contribution to TDW under both NAP and AP condition. Taken together, the results suggested biomass related traits such as RDW, SDW and TDW become preferred indicators in the evaluation, which is consistent with previous conclusions (Yang et al. 2010; Hammond and White 2008; Hermans et al. 2006). In addition, root-related traits such as RSA, RV, RT and RF make a major contribution to our evaluation and they can also be used as important selection criteria in other researches.

Utilizing the resources of wheat wild relatives, *A. tauschii*

Wild *A. tauschii* related to cultivated wheat possess numerous genes of agronomic interest and can be valuable sources of resistance to diseases, pests and extreme environmental factors. These genes can be incorporated into the wheat genome via intergenetic crossing, following, where necessary, the development of chromosome addition and substitution lines from the resulting hybrids. The *A. tauschii* are the most closely related to wheat, exhibit great genetic diversity, the exploitation of which has been the subject of experimentation for more than a century (Annamária et al. 2008). Many of the species in the *Aegilops* genus have good resistance to disease and insect pests (Gill et al. 1983, 1985, 1987; Raupp et al. 1993, 1995, 1997; Zaharieva et al. 2001). Among other things, some *Aegilops* species are excellent sources of resistance to various rusts and powdery mildew (Damania and Pecetti 1990; Dimov et al. 1993). Many agronomically useful traits (disease and insect resistance, stress tolerance) have been incorporated into the wheat (Cox and Hatchett 1994; Raupp et al. 1993; Friebe et al. 1996).

Since 1990s, a large amount of synthetic wheat were introduced in China from International Maize and Wheat Improvement Center (CIMMYT), opened a new insight for mining good genes, breeding innovation, creating novel breeding materials and nurturing new wheat cultivars. Representatively, a new commercial wheat cultivar, Chuanmai 42 (CM42), was derived from synthetics (*Triticum durum* × *Aegilops tauschii*) by Sichuan Academy of Agricultural Sciences of China. It was resistant or

immune to Chinese new stripe rust races, and was a heavy and large spike variety with high quality. The average yield of CM42 exceeded 6t/ha in regional testing of two years and it was the first officially released variety from synthetics in the world (Zhang et al. 2004a; Li et al. 2006). Recently, another new wheat cultivar, Shumai969 (unpublished, derived from synthetic wheat SHW-L1 and CM42), was authorized by Sichuan province of China, which represents big breakthrough of wheat yield in Sichuan. These successful commercial wheat cultivars suggest *A. tauschii* can enhance efficiency for wheat improvement. Additionally, two synthetic hexaploid wheat (Lan-2399 and Lan-2404) used in our study showed better P deficiency tolerance than other wheat, because the synthetic wheat were derived from *A. tauschii* crossing with tetraploid wheat. We found the tetraploid wheat had low tolerance to P deficiency, so tolerant genes for P deficiency may come from *A. tauschii*. Large-scale screening of *A. tauschii* help us to discover more tolerant *gemplasms* for P deficiency. CN16 is a native commercial wheat cultivar with good comprehensive agronomic characters, and it can be use as a recurrent parent for transferring excellent tolerant genes and for developing new wheat cultivars.

Judging from what we have discussed above, P deficiency tolerance ability should be one of the essential of *A. tauschii*, and the good genes also could be utilizing in wheat breeding. However, there is few people did screen job for phosphorus deficiency tolerance, let alone breed high P-efficient common wheat. Here, a natural *A. tauschii* population was used for genetic evaluation for phosphorus deficiency resistance. The results indicate the *A. tauschii* from China, Turkey, Uzbekistan and Azerbaijan have relatively higher P deficiency tolerance ability than that from others. Using PDTI for each traits and average S value across all the test traits, 63 *A. tauschii* genotypes with high tolerance under phosphorus deficiency was identified. Most of them were from Western Asia and distributed around the zone of Turkey-Iran-Afghanistan, which is in keeping with the road of *A. tauschii* spreading. *Aegilops* species are found in Mediterranean climates, being indigenous from the Canary Islands to the western part of Asia, in Afghanistan and West China (van Slageren 1994). Their ability to spread so widely was probably due to their great adaptability, which also explains why they carry so many agronomically valuable traits such as

drought tolerance (Molnár et al. 2004), salt tolerance (Colmer et al. 2006) and phosphorus deficiency tolerance. These genotypes with high tolerance such as AS623282, AS623011, AS623285-1, AS623305 and AS623020 can be used as germplasm resources that could widen the genetic diversity of cultivated wheat, as a result, to shorten the procedure of wheat breeding for tolerance to phosphorus deficiency.

In conclusion, we systematically evaluated large-scale *A. tauschii* genotypes, and several tolerant and sensitive genotypes were selected. Root related traits used in the study such as RDW, SDW, TDW, RSA, RV, RT and RF could be used as selection criteria to evaluate and screen other wheat related germplasm resources. The top five tolerant *A. tauschii* genotypes, AS623282, AS623011, AS623285-1, AS623305 and AS623020 that have relative higher tolerance than other wheat can be further used for wheat genetic improvement and molecular breeding for abiotic stress tolerance.

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References

- Annamária S, Istvá M, Márta ML (2008) Utilisation of *Aegilops* (goatgrass) species to widen the genetic diversity of cultivated wheat. *Euphytica* 163:1–19
- Bai DY, Feng GH, Zhang HY, Chen RZ, Wang XJ (2007) Screening of wheat genotypes with high phosphorus efficiency under low phosphorus stress. *J Triticeae Crops* 27:407–410
- Bouma TJ, Nielsen KL, Koutstaal B (2000) Sample preparation and scanning protocol for computerized analysis of root length and diameter. *Plant Soil* 218:185–196
- CAY (1991) China Agriculture Yearbook. Chinese Agricultural Press, Beijing
- CAY (2006) China Agriculture Yearbook. Chinese Agricultural Press, Beijing
- Colmer TD, Flowers TJ, Munns R (2006) Use of wild relatives to improve salt tolerance in wheat. *J Exp Bot* 57:1059–1078
- Cox TS, Hatchett JH (1994) Hessian fly resistance gene *H26* transferred from *Triticum tauschii* to common wheat. *Crop Sci* 34:958–960
- Cox TS, Raupp WJ, Wilson DL, Gill BS, Leath S, Bockus WW et al (1992) Resistance to foliar diseases in a collection of *Triticum tauschii* germplasm. *Plant Dis* 76:1061–1064
- Cui DQ, Hao X, Li Y, Liu YY (2004) Progress of genetic study on phosphorus efficiency of wheat. *J Triticeae Crops* 24:110–113
- Damania AB, Pecetti L (1990) Variability in a collection of *Aegilops* species and evaluation for yellow rust resistance at two location in northern Syria. *J Genet Breed* 44:97–102
- Dimov A, Zaharieva M, Mihova S (1993) Rust and powdery mildew resistance in *Aegilops* accessions from Bulgaria. In: Damania AB (ed) Biodiversity and wheat improvement. Wiley, New York, pp 165–169
- Draper NR, Smith H (1966) Applied regression analysis. Wiley, New York, p 7407
- Friebe B, Jiang J, Raupp WJ, McIntosh RA, Gill BS (1996) Characterization of wheat alien translocations conferring resistance to diseases and pests: current status. *Euphytica* 71:59–83
- George TS, Richardson AE (2008) Potential and limitations to improving crops for enhanced phosphorus utilization. In: White PJ, Hammond JP (eds) Ecophysiology of plant-phosphorus interactions. Springer, Dordrecht, pp 247–270
- Gill BS, Browder LE, Hatchett JH, Harvey TL, Martin TJ, Raupp WJ, Sharma HC, Waines JG (1983) Disease and insect resistance in wild wheats. In: Sakamoto S (ed) Proc 6th Int Wheat Genet Symp, Faculty of Agriculture, Kyoto University, Japan, pp 783–792
- Gill BS, Sharma HC, Raupp WJ, Browder LE, Hatchett JH, Harvey TL (1985) Evaluation of *Aegilops species* for resistance to wheat powdery mildew, wheat leaf rust, Hessian fly and greenbug. *Plant Breed* 69:314–316
- Gill BS, Hatchett JH, Raupp WJ (1987) Chromosomal mapping of Hessian fly resistance gene *H13* in the D genome of wheat. *J Hered* 78:97–100
- Grant CA, Flaten DN, Tomaszewicz DJ, Sheppard SC (2001) The importance of early season phosphorus nutrition. *Can J Plant Sci* 81:211–224
- Guo Y, Kong FM, Xu YF, Zhao Y, Liang X, Wang YY et al (2012) QTL mapping for seedling traits in wheat grown under varying concentrations of N, P and K nutrients. *Theor Appl Genet* 124:851–865
- Hammond JP, White PJ (2008) Sucrose transport in the phloem: integrating root responses to phosphorus starvation. *J Exp Bot* 59:93–109
- Hammond JP, Broadley MR, White PJ, King GJ, Bowen HC, Hayden R, Meacham MC, Mead A, Overs T, Spracklen WP, Greenwood DJ (2009) Shoot yield drives phosphorus use efficiency in *Brassica oleracea* and correlates with root architecture traits. *J Exp Bot* 60:1953–1968
- Hermans C, Hammond JP, White PJ, Verbruggen N (2006) How do plants respond to nutrient shortage by biomass allocation? *Trends Plant Sci* 11:610–617
- Hoagland DR, Arnon IR (1950) The water culture method for growing plants without soils. *Circ Calif Agric Exp Stn* 347:4–32
- Horst WJ, Abdou M, Wiesler F (1993) Genotypic differences in phosphorus efficiency of wheat. *Plant Soil* 155:293–296
- Iyamuremye F, Dick RP, Baham J (1996) Organic amendment and phosphorus dynamics: II. Distribution of soil phosphorus fractions. *Soil Sci* 161:436–443
- Jain A, Vasconcelos MJ, Raghothama KG, Sahi SV (2007) Molecular mechanisms of plant adaptation to phosphate

- deficiency. In: Janick J (ed) Plant breeding reviews. Wiley, NJ, pp 359–419
- Jolliffe IT (2002) Principal component analysis, 2nd edn. Springer, New York, pp 1–10
- Kong ZX, Yang LL, Zhang ZZ, Ma ZQ (2010) Screening of wheat germplasm tolerant to low phosphorus. *J Triticeae Crops* 30:591–595
- Levent O, Selim E, Bulent T, Ismail C (2005) Variation in phosphorus efficiency among 73 bread and durum wheat genotypes grown in a phosphorus-deficient calcareous soil. *Plant Soil* 269:69–80
- Li YF, Luo AC, Wang WM, Cai BX, Hu XY, Yang X (2005) Genotypic variation of rice in yield, phosphorus uptake and utilization at different phosphorus supply. *Chin J Soil Sci* 36:365–368
- Li GQ, Li ZF, Yang WY, Zhang Y, He ZH, Xu SC, Singh RP, Qu YY, Xia XC (2006) Molecular mapping of stripe rust resistance gene *YrCH2* in Chinese wheat cultivar Chuanmai 42 and its allelism with *Yr24* and *Yr26*. *Theor Appl Genet* 112:1434–1440
- Li CY, Zhang H, Ma L, Li C (2012) Comprehensive evaluation on physiological indices of nitrogen absorption and utilization in winter wheat at the seedling stage. *Plant Nutr Fertil Sci* 18:523–530
- Liu Y, Li ZC, Mi GH, Zhang HL, Mu P, Wang XK (2005) Screening and identification for tolerance to low-phosphorus stress of rice germplasm (*Oryza sativa* L.). *Acta Agron Sin* 31:238–242
- Lu DL, Yan FB, Lu WP (2010) Genotypic difference of phosphorus uptake and utilization in sweet maize varieties. *J Yangzhou Univ* 31:60–64
- Lynch JP (2007) Roots of the second green revolution. *Aust J Bot* 55:493–512
- Ma WQ, Zhang FS, Zhang WF (2005) Fertilizer production and consumption and the resources, environment, food security and sustainable development in China. *Resour Sci* 27:33–40
- Magalhães PC, De Souza TC, Cantão FRO (2011) Early evaluation of root morphology of maize genotypes under phosphorus deficiency. *Plant Soil Environ* 57:135–138
- Marschner H (1995) Functions of mineral nutrients: macronutrients. *Miner Nutr High Plants* 2:379–396
- Molnár I, Gáspár L, Sárvári É, Dulai S, Hoffmann B, Molnár-Láng M, Galiba G (2004) Physiological and morphological responses to water stress in *Aegilops biuncialis* and *Triticum aestivum* genotypes with differing tolerance to drought. *Funct Plant Biol* 31:1149–1159
- Raghothama KG, Karthikeyan AS (2005) Phosphate acquisition. *Plant Soil* 274:37–49
- Raupp WJ, Amri A, Hatchett JH, Gill BS, Wilson DL, Cox TS (1993) Chromosomal location of Hessian fly-resistance genes *H22*, *H23* and *H24* derived from *Triticum tauschii* in the D genome of wheat. *J Hered* 84:142–145
- Raupp WJ, Gill BS, Friebe B, Wilson DL, Cox TS, Sears RG (1995) The Wheat Genetic Resource Center: Germplasm conservation, evaluation and utilization. *Proc 8th Int Wheat Genet Symp*, China Agricultural Sciencetech Press, Beijing, China pp 469–475
- Raupp WJ, Friebe B, Wilson DL, Cox TS, Gill BS (1997) Kansas State's Wheat Genetics Resource Center provides unique oasis for germplasm research. *Diversity* 13:21–23
- Ren YZ (2012) Effects of low phosphorus stress on different wheat varieties at seedling stage. *Chin Agric Sci Bull* 28:40–44
- Smith SE, Kuehl RO, Ray IM, Hui R, Soleri D (1998) Evaluation of simple methods for estimating broad-sense heritability in stands of randomly planted genotypes. *Crop Sci* 38:1125–1129
- Su JY, Xiao YM, Li M, Liu QY, Li B, Tong YP, Jia JZ, Li ZS (2006) Mapping QTLs for phosphorus-deficiency tolerance at wheat seedling stage. *Plant Soil* 281:25–36
- Sun HG, Zhang FS (2002) Morphology of wheat roots under low-phosphorus stress. *Chin J Appl Ecol* 13:295–299
- Tahir S, Alam SM, Ahmad Z (2011) Wheat yield and phosphorus fertilizer efficiency as influenced by pre-incubated use of single superphosphate and poultry litter and its time of application. *J Plant Nutr* 34:1034–1040
- Teng W, Deng Y, Chen XP, Xu XF, Chen RY, Lv Y et al (2013) Characterization of root response to phosphorus supply from morphology to gene analysis in field-grown wheat. *Exp Bot* 64:1403–1411
- Turner BL, Paphazy MJ, Haygarth PM, Mckelvie ID (2002) Inositol phosphates in the environment. *Philos Trans R Soc Lond B Biol Sci* 357:449–469
- Valkoun J, Dostal J, Kucerová D (1990) *Triticum* × *Aegilops* hybrids through embryo culture. *Biotechnol Agric For* 13:152–166
- Van Slageren MW (1994) Wild wheats: a monograph of *Aegilops* L. and *Amblyopyrum* (Jaub & Spach) Eig (Poaceae). Wageningen Agricultural University Papers, Wageningen, The Netherlands, pp 7–94
- Vance CP (2001) Plant nutrition in a world of declining renewable resources. *Plant Physiol* 127:390–397
- Vance CP, Uhde-Stone C, Allan DL (2003) Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. *New Phytol* 157:423–447
- Wang XR, Shen JB, Liao H (2010) Acquisition or utilization, which is more critical for enhancing phosphorus efficiency in modern crops. *Plant Sci* 179:302–305
- Wu ZS (1990) Wheat breeding. Chinese Agricultural Press, Beijing
- Xiong YS, Yuan JF, Hao FX, Zhao SJ, Peng CL, Xu XY (2008) Advance on wheat genotype diversity with high nutrient efficiency. *Hubei Agric Sci* 47:1084–1087
- Yang M, Ding GD, Shi L, Feng J, Xu FS, Meng JL (2010) Quantitative trait loci for root morphology in response to low phosphorus stress in *Brassica napus*. *Theor Appl Genet* 121:181–193
- Yang XB, Zhang XZ, Li TX, Wu DY (2012) Differences in phosphorus utilization efficiency among wheat cultivars. *Chin J Appl Ecol* 23:60–66
- Yen J, Yang JL (1984) *Aegilops tauschii* in Yili Xinjiang region. *Crops J* 3:1–8
- Zaharieva M, Monneveux P, Henry M, Rivoal R, Valkoun J, Nachit MM (2001) Evaluation of a collection of wild wheat relative *Aegilops geniculata* Roth and identification of potential sources for useful traits. *Euphytica* 119:33–38
- Zhang LM, He LY, Li JS, Xu SZ (2004a) Investigation of Maize Inbred Lines on Tolerance to Low-Phosphorus Stress at Seedling Stage. *Sci Agric Sin* 37:1955–1959
- Zhang Y, Yang WY, Hu XR, Yu Y, Zou YC, Li QM (2004b) Analysis of agronomic characters of new wheat variety

- Chuanmai 42 derived from synthetics (*Triticum duru Aegilops tauschii*). *Southwest China J Agric Sci* 17:141–145
- Zhang JH, Gao SB, Yang KC, Zhang ZM, Lin HJ, Huang N et al (2008) Screening and identification for tolerance to low phosphorus stress of Maize germplasm resources. *J Plant Genet Resour* 9:335–339
- Zhao HT, Wang RF, Xu YF, An DG (2011) Screening and evaluating low nitrogen tolerant wheat genotype at seedling stage. *Chin J Eco-Agric* 19:1199–1204
- Zhong GC, Mu SM, Zhang ZB (2003) Distant hybridization of triticeae. Science Press, Beijing