https://doi.org/10.17221/348/2020-PSE

Genotype difference in the physiological characteristics of phosphorus acquisition by wheat seedlings in alkaline soils

*Feiyan Yu[1], Wei Li[1], Xiaokai Gao[1], Peng Li[1], Yihan Fu[3], Jinyong Yang[1,2], Yajuan Li[1,2], Huiqing Chang[1,2], Wenli Zhou[1,2], Xugang Wang[1,2], Lianhe Zhang[1,2,4]**

[1]Agricultural College, Henan University of Science and Technology, Luoyang, Henan, P.R. China
[2]Luoyang Key Laboratory of Plant Nutrition and Environmental Ecology, Luoyang, Henan, P.R. China
[3]Agricultural College, Henan Agricultural University, Zhengzhou, Henan, P.R. China
[4]Henan Jinxiwang Agricultural Science and Technology Company Limited, Luoyang, Henan, P.R. China
Corresponding author: lhzhang2007@126.com

Citation: Yu F.Y., Li W., Gao X.K., Li P., Fu Y.H., Yang J.Y., Li Y.J., Chang H.Q., Zhou W.L. Wang X.G., Zhang L.H. (2020): Genotype difference in the physiological characteristics of phosphorus acquisition by wheat seedlings in alkaline soils. Plant Soil Environ., 66: 506–512.

Abstract: Phosphorus (P) in soils occurs predominately as insoluble inorganic P and organic P. However, key factors controlling P acquisition by wheat (*Triticum aestivum* L.) seedlings are unclear. In this study, the difference in the physiological characteristics of P acquisition in alkaline soils was investigated in wheat seedlings of two cultivars Aikang 58 and Zhoumai 22. The results indicated that the shoot P concentration of Aikang 58 was significantly higher than that of Zhoumai 22 when supplied with 0 and 70 kg/ha of pure P under field conditions. When cultured in sterile nutrition solutions with equimolar amounts of P corresponding to KH_2PO_4, $Ca_3(PO_4)_2$, and $Ca(H_2PO_4)_2$ for 6 days, the P concentration in the shoots and roots of the seedlings of Aikang 58 was significantly higher than that of Zhoumai 22. However, the P concentration of seedlings of Aikang 58 did not exhibit a significant difference than that of Zhoumai 22 when cultured in phytic acid solution. Further studies suggested that the proton secretion rate was higher, and the root phosphatase activity was significantly lower in Aikang 58 compared with those in Zhoumai 22. After 48 h of successive P starvation, the inorganic phosphate (P_i) uptake rate of Aikang 58 was significantly higher compared with that of Zhoumai 22. However, no significant differences existed in the root morphology between the two cultivars. Hence, the higher P acquisition in the wheat seedlings of Aikang 58 was attributed to a higher rate of proton secretion and a stronger capacity for P_i uptake.

Keywords: P fertiliser; P form; calcareous soil; utilisation efficiency; P-efficient wheat cultivar

Phosphorus (P) is an essential element in higher plants and forms a key constituent of many important compounds such as nucleic acids, proteins, and ATP in plant cells. It plays a crucial role in energy transfer, signal transduction, respiration, and photosynthesis (Vance et al. 2003). Plants mainly acquire P from soils. Acquisition of P is achieved by taking up inorganic phosphate (orthophosphate, P_i) by roots. Most of the P_i is converted to organic compounds by microorganisms or becomes insoluble by interacting with cations in the soils (Chiou and Lin 2011). P primarily occurs as insoluble Ca-P, Fe-P, and Al-P and organic phosphate in agricultural soils (Raghothama 1999, Hinsinger 2001, Raghothama and Karthikeyan 2005). Since a substantial amount of P_i is converted to unavailable forms, P is frequently the most limiting element for plant growth due to low concentrations of P_i in the soil solution (Raghothama 1999). Thus, optimised amounts of P fertilisers must be applied to soil to meet the demand for the normal growth of plants (Huang et al. 2017).

Supported by the Key Program for Science and Technology Development of Henan Province, Project No. 12102110102, and by the Key Science and Technology Research Project of Henan Province Department of Education, Project No. 14B210004.

https://doi.org/10.17221/348/2020-PSE

P_i concentration is predominantly dependent on soil pH and the Ca^{2+} concentration in the calcareous soil solution, and it is determined by the formation and dissolution of calcium phosphates (Hinsinger 2001, Wang et al. 2015). The solubility of Ca-P becomes low with the increases of the ratios of Ca to P in the Ca phosphatase. Huang-Huai Plain is major winter wheat producing area in China, distributing large-area calcareous soils. Because the Ca^{2+} concentration in calcareous soils is high enough and $Ca(H_2PO_4)_2$ is the main constituent of various phosphate fertilisers, $Ca(H_2PO_4)_2$ is readily converted into $CaHPO_4$ after phosphate fertilisers are added to soils (Mengel et al. 2001). Thus, the concentration of P_i in the soil solution is very low compared to insoluble Ca-P in calcareous soils. In addition, up to 80% of total P occurs as organic P that comprises mainly inositol phosphate ester in soils (Dalal 1977, McLaren et al. 2015). Inositol phosphates are rendered to P_i by hydrolysis through a phosphatase reaction (Asmar et al. 1995).

Plants have evolved a series of mechanisms to modulate their P acquisition efficiency in response to low P stress, such as secreting more organic acids (Hinsinger 2001, Raghothama and Karthikeyan 2005) and acid phosphatases (Wang et al. 2009, Liang et al. 2010), inducing the gene expression of high-affinity phosphate transporters (Sun et al. 2012, Teng et al. 2017), changing the root morphological configuration (Maharajan et al. 2019, Xu et al. 2019), increasing the ratio of root to shoot (De Souza Campos et al. 2019), forming more lateral roots (Postma et al. 2014), and increasing the length and density of root hairs (López-Bucio et al. 2003). Wheat is one of the most important crops, accounting for 22–30% of the total cultivated area in China. Substantial amounts of P fertilisers are annually added to the soil to achieve a high yield of wheat production, but the excessive application of P fertilisers readily leads to the decrease of P utilisation efficiency by converting to unavailable forms (Huang et al. 2017, Li et al. 2018). Thus, enhancing the utilisation efficiency of P fertilisers in wheat plants plays an important role to achieve a sustainable agricultural production.

Large amounts of protons and organic acids are continuously secreted by wheat roots, and this changes the rhizosphere pH and promotes more insoluble P to dissolve. Acid phosphatases are also secreted by the roots, which cause organic P hydrolysis, and its products are subsequently taken up. Soluble phosphate diffuses towards the root surface through the soil, and results in the formation of depletion zones around the roots. Thus, an efficient way for wheat seedlings to form a developed root system is to acquire more P by exploring larger volumes of soil. Although a substantial number of factors can affect the utilisation of different P sources by wheat roots, the specific characteristics that result in the varietal differences of P utilisation of different P sources are not fully understood. In the present study, the differences in the physiological characteristics of P accumulation of two wheat cultivars were investigated in order to find key factors that affect P utilisation in calcareous soils, thus providing valuable data to further improve P utilisation efficiency in the soil through genetic improvement strategies.

MATERIAL AND METHODS

Wheat seedling growth in the field. Winter wheat cultivars Aikang 58 and Zhoumai 22 were selected for this study due to be widely planted in winter wheat producing area in China, especially in the Huang-Huai Plain. Two wheat cultivars were planted in the field in the Kaiyuan campus of Henan University of Science and Technology in 2011. The FAO soil classification is Cambisol with pH 7.84. The soil texture is clay. The concentrations of organic matter (total oxidisable carbon), available N, P, and K in the soils were 2.35%, 65.51 mg/kg, 9.72 mg/kg, and 213.05 mg/kg, respectively. Two treatments were designed, including adding single superphosphate fertiliser equivalent to 0 and 70 kg/ha of pure P, respectively. The area of the plot for each cultivar was 30.0 m^2. The spacing between plants was 15 cm. Each treatment was repeated five times. The cultural management practice was performed routinely. Wheat seedlings were harvested when grown for 120 days, and the P concentration of shoots and roots were determined.

Wheat seedling culture in different P sources. After surface sterilising with 10% (*v*/*v*) H_2O_2, the wheat seeds were soaked in distilled water in darkness for 6 h and then transferred to Petri plates with a diameter of 9.0 cm. Each Petri plate was evenly placed 30 grains of wheat seeds. Wheat seedlings were precultured in half strength of P-deficient Hoagland nutrient solution. After 5 days of incubation, the seedlings were transplanted to plastic containers with 18 L of the full strength of P-deficient nutrition solutions in a growth chamber, with a day/night cycle of 16/8 h (24 °C/18 °C). Each container was covered with a polyethylene board containing 24

https://doi.org/10.17221/348/2020-PSE

openings; five individual wheat seedlings were planted in each opening. The light intensity was approximately 300 μmol/m^2/s. The air humidity was controlled at 67%. The pH of this solution was adjusted to 6.0 with 1 mmol/L KOH and 1 mmol/L HCl every day (Yang et al. 2019). After 12 days of continuous incubation, the seedlings were transferred to sterile Hoagland nutrient solutions in 1 L plastic containers containing equimolar amounts (180 μmol/L) of P sources corresponding to KH_2PO_4, $Ca_3(PO_4)_2$, $Ca(H_2PO_4)_2$, and $C_6H_{18}O_{24}P_6$, respectively. The pH of the solution was not adjusted. The nutrient solutions were continually aerated with an air compressor every 3 h. The seedlings were harvested after cultured for 6 days. The solution was renewed every 2 days.

Determination of P concentration. About 0.2–0.50 g of dried samples (shoots and roots) were put into 100 mL digestion tubes, adding 5 mL of an acid mixture of concentrated HNO_3 and $HClO_4$ (4:1 *v*/*v*) and placed at room temperature overnight, and then digested completely at 150 °C (Yang et al. 2019). After cooling down, the digests were diluted with deionised water to a final volume of 25 mL. P concentration in the digested samples was determined by inductively coupled plasma optical emission spectrometer (ICP-OES, PerkinElmer, 5300DV, Massachusetts, USA).

Determination of P_i concentration. P_i measurement followed a modified method described previously by Nanamori et al. (2004). About 0.50 g of fresh roots were homogenised in 5 mL of 10% (*w*/*v*) perchloric acid, then was centrifuged at 10 000 *g* for 10 min. 0.5 mL of the supernatant was incubated with 3 mL of mixed reagents (2.5% ammonium molybdate:6 mol/L sulfuric acid:10% ascorbic acid:distilled water = 1:1:1:2, *v*/*v*) and 2 mL distilled water at 45 °C for 20 min, then the absorbance was determined at 820 nm wavelength.

Determination of P_i uptake rate. 21 days of wheat seedlings were treated for 48 h under P starvation, then transferred to the absorption solution containing 5 mmol/L MES (2-morpholino ethanesulphonic acid), 0.5 mmol/L $Ca(NO_3)_2$, and 180 μmol/L KH_2PO_4, pH 5.5. After successive uptake of P_i for 3 h, the roots were removed quickly and washed with distilled water repeatedly to clean the adsorbed P_i on the surfaces of the roots, then oven-dried and digested. P concentration of roots was determined by ICP-OES.

Determination of proton secretion. When grown in the full strength of Hoagland nutrient solution for 21 days, wheat seedlings were transferred to 100 mmol/L $CaCl_2$ solutions. After 24 h of subsequent incubation, the pH was adjusted to 6.0 with 100 μmol/L NaOH solution, then determined the volume of NaOH solution consumed. The proton secretion rate and the total amount of protons secreted by roots were calculated based on the volume of NaOH solution consumed.

Determination of phosphatase activity. 21 days of wheat seedlings were cultured in the full strength of P-deficient Hoagland nutrient solution for 3 h, then about 0.50 g of roots of wheat seedlings was transferred to 50 mL of enzyme reaction solution containing 50 mmol/L sodium acetate (pH 5.6), 5 mmol/L p-nitrophenyl-1-phosphate (Sigma), and 10 mmol/L $MgCl_2$. After incubated at 30 °C for 60 min, the roots were removed from the solution. The enzyme reaction was terminated by adding 10 mL of 1 mol/L NaOH solution. The absorbances were determined at 405 nm wavelength by monitoring the formation of para-nitrophenol (Tadano and Sakai 1991, Hurley et al. 2010).

Root morphology analysis. 21 days of wheat seedlings were cultured in the full strength of the P-deficient Hoagland nutrient solution. After 22 days of P starvation, root systems of wheat seedlings were scanned by STD 1600 Scanner (Epson, Nagano, Japan), then analysed the scanning image by software WinRhioz (Quebec, Canada), and obtained the data of root length, root diameter, root surface area, root volume, the number of forks and crossings.

Data analysis. One-way analysis of variance (ANOVA) was performed using SPSS 13.0 for Windows (SPSS Inc., Chicago, USA) to determine the significance ($P < 0.05$) between control and treatments. Statistical differences were assessed by Student's *t*-test.

RESULTS

The difference in the total P and P concentration of wheat seedlings of two cultivars in alkaline soil. Two wheat cultivars were planted in the field to investigate the differences in the total P and P concentration of the shoots and roots between the two wheat cultivars. The results indicated that the total P and P concentration of the shoots of Aikang 58 were significantly higher than those of Zhoumai 22 when grown in alkaline soil (Figure 1A, C), irrespective of whether phosphate fertiliser was supplied or not. In contrast, there were no significant differences in total P and P concentration of the roots between the two cultivars (Figure 1B, D). Thus, the higher total P

https://doi.org/10.17221/348/2020-PSE

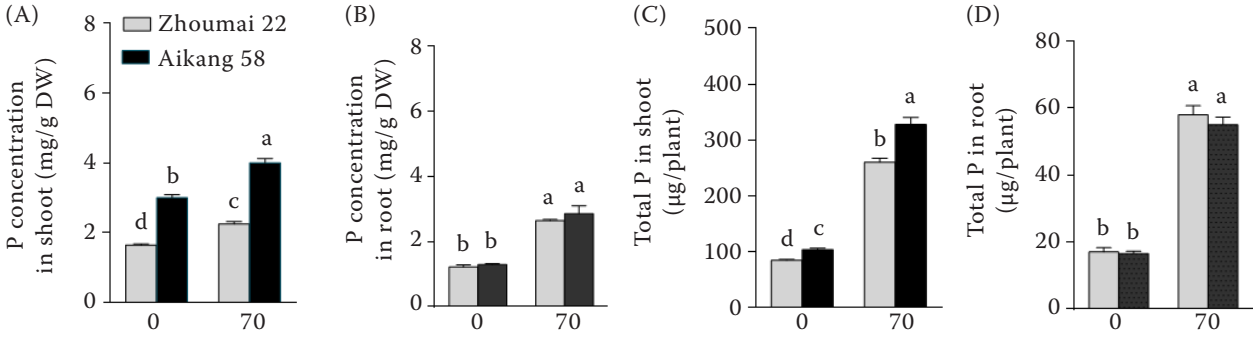

Figure 1. Differences in the phosphorus (P) concentration and the total P content in the shoots (A and C) and roots (B and D) of the two cultivars supplied with 0 and 70 kg/ha of pure P. Data are means ± standard deviation of three replicates. Letters of a, b, c and d indicate differences between the two cultivars in the same treatment ($P < 0.05$). DW – dry weight

in the shoots of Aikang 58 was attributed to the higher P concentration compared with Zhoumai 22.

Differences in the utilisation of different P sources between the two cultivars. Wheat seedlings were cultured in solutions with an equimolar amount of P sources that corresponded to KH_2PO_4, $Ca_3(PO_4)_2$, $Ca(H_2PO_4)_2$, and $C_6H_{18}O_{24}P_6$ in order to investigate the differences in the utilisation of different P sources between the two cultivars. The results showed that P concentrations in the shoots (Figure 2A) and roots (Figure 2B) of Aikang 58 were significantly higher than those of Zhoumai 22 when cultured in solutions corresponding to KH_2PO_4, $Ca_3(PO_4)_2$, and $Ca(H_2PO_4)_2$ for 6 days. When cultured in the $C_6H_{18}O_{24}P_6$ solution with an equivalent amount of P, no significant difference was found in the P concentration of the shoots and roots between the two cultivars (Figure 2).

Differences in P_i uptake rate, proton secretion rate, and phosphatase activity between the two wheat cultivars. The differences in P_i uptake rate, proton secretion rate, and phosphatase activity between the two wheat cultivars were investigated. After 48 h of P starvation, the root P concentration of Aikang 58 was slightly higher than those of Zhoumai 22, but there was no significant difference. After the successive uptake of P_i for 48 h, the root P concentration of Aikang 58 was significantly higher than those of Zhoumai 22. The uptake rate of phosphate was significantly higher than that of Zhoumai 22 (Figure 3A). The former was 1.4-times higher than the latter. In addition, the proton secretion rate of Aikang 58 was significantly higher than that of Zhoumai 22 (Figure 3B). The former was 1.53- and 1.24-times higher, respectively, than the latter. However, the acid phosphatase activity in the roots of Zhoumai 22

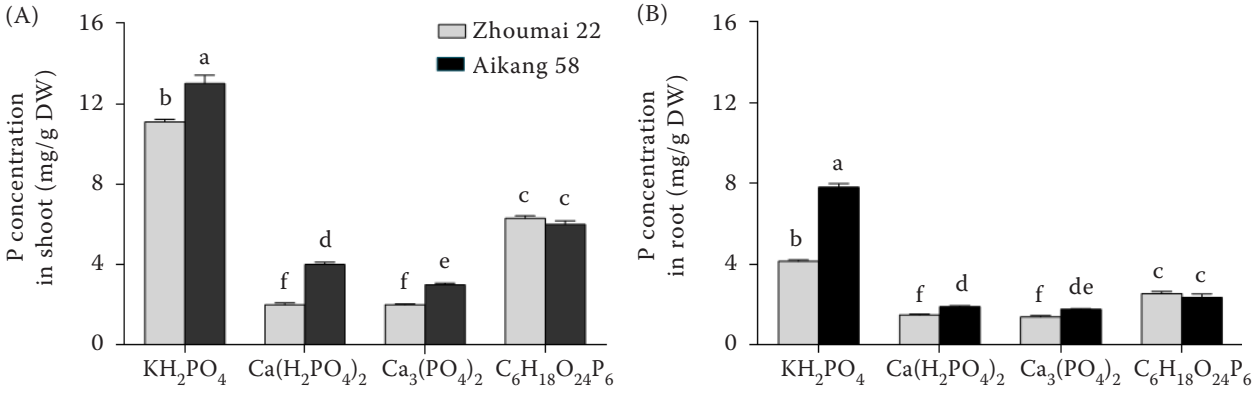

Figure 2. Difference in the phosphorus (P) concentrations in the shoots (A) and roots (B) of two wheat cultivars grown in solutions supplied with different P sources. Data are means ± standard deviation of three replicates. Letters of a, b, c, d, e and f indicate differences between the two cultivars in the same treatment ($P < 0.05$). DW – dry weight

https://doi.org/10.17221/348/2020-PSE

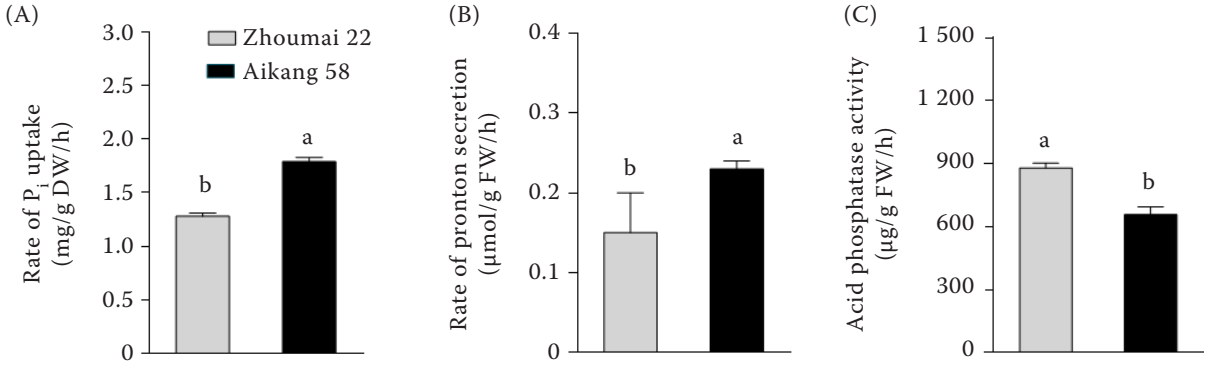

Figure 3. Differences in inorganic phosphate (P_i) uptake rate, proton secretion rate, and phosphatase activity between the two wheat cultivars under normal cultivation conditions. Data are means ± standard deviation of three replicates. Letters of a and b indicate differences between the two cultivars in the same treatment ($P < 0.05$). DW – dry weight; FW – fresh weight

was significantly higher compared with Aikang 58 (Figure 3C). The former was 1.29-times higher than the latter.

The difference in root morphology between the two cultivars. The morphological differences in the root system between the two cultivars under P-deficient conditions were investigated. The root length, root surface area, root volume, number of forks, and crossings of Aikang 58 were less than those of Zhoumai 22, but the root diameter was slightly higher than that of Zhoumai 22 (Table 1). All the differences were not significant.

DISCUSSION

In this study, it was found that the shoot P concentration of Aikang 58 was significantly higher than that of Zhoumai 22 under the field conditions, regardless of whether P fertiliser was added or not (Figure 1). P in soils occurs predominately as insoluble inorganic P and organic P. Thus, the difference in shoot P concentration of two cultivars mainly depended on the capacity of P acquisition in alkaline soils. Further studies suggested that Aikang 58 had higher P concentrations in the seedlings when cultured in solutions with an equimolar amount of P corresponding to KH_2PO_4, $Ca(H_2PO_4)_2$, and $Ca_3(PO_4)_2$. $Ca(H_2PO_4)_2$ added to the solution is postulated to be quickly transformed into $CaHPO_4$ because the Ca^{2+} concentration in Hoagland solution is high. The majority of $Ca_3(PO_4)_2$ and $CaHPO_4$ is present in insoluble forms in solutions. Because the proton secretion rate of Aikang 58 was significantly higher than that of Zhoumai 22, more $Ca_3(PO_4)_2$ and $CaHPO_4$ were dissolved, thus resulting in an increase of soluble P in the solution. In addition, the P_i uptake rate of Aikang 58 was significantly higher than that of Zhoumai 22. Therefore, the seedlings of Aikang 58 could readily take up more P when cultured in solutions containing $Ca_3(PO_4)_2$ and $Ca(H_2PO_4)_2$. It resulted in higher P concentrations in the seedlings of Aikang 58 compared with that of Zhoumai 22 when grown in solutions with an equimolar amount of P corresponding to KH_2PO_4, $Ca_3(PO_4)_2$, and $Ca(H_2PO_4)_2$. $Ca(H_2PO_4)_2$ is the main constituent of various phosphate fertilisers, thus $Ca(H_2PO_4)_2$ is readily converted into dissolved $CaHPO_4$ after phosphate fertilisers are added to calcareous soils (Mengel et al. 2001). Protons secreted by wheat roots can stimulate insoluble inorganic P to dissolve (Hinsinger 2001). Due to the higher rate

Table 1. Differences in the root morphological characteristics between the two wheat cultivars at 22 days of phosphorus (P) deficiency

	Root length (cm)	Surface area (cm^2)	Root diameter (mm)	Root volume (cm^3)	Forks	Crossings
Zhoumai 22	189.56 ± 26.36[a]	15.65 ± 1.25[a]	0.25 ± 0.02[a]	0.12 ± 0.05[a]	320 ± 11[a]	127 ± 28[a]
Aikang 58	183.84 ± 27.11[a]	14.08 ± 2.47[a]	0.30 ± 0.02[a]	0.11 ± 0.05[a]	309 ± 42[a]	106 ± 14[a]

Data are means ± standard deviation of three replicates. Letters of a and b indicate differences between the two cultivars in the same treatment ($P < 0.05$)

https://doi.org/10.17221/348/2020-PSE

of proton secretion by Aikang 58, it was postulated that the pH in the rhizosphere solution reduced more than Zhoumai 22, thus increasing the available P levels in the rhizosphere solution by dissolving more Ca phosphates. Thus, a decrease in the pH of the rhizosphere solution in calcareous soils benefits to increase the availability of insoluble inorganic P and enhances P_i uptake. In addition, the activity of P_i transporter strongly depends on pH and declines sharply at pH 8.0 (Sun et al. 2012). It was postulated that a decrease in the pH of the rhizosphere solution also benefited to increase the activity of P_i transporter and enhance P_i uptake.

This study showed that P concentration in the seedlings of Aikang 58 was slightly less than that of Zhoumai 22 when cultured in phytic acid solution. Phosphatase excreted by the root system can hydrolyse organic P to P_i, thus contributing to more efficient absorption of the roots. Although the rate of P_i uptake by Aikang 58 was higher, the activity of acid phosphatase was significantly lower than that of Zhoumai 22. It was postulated that the concentration of the P_i decomposed from phytic acid in the solutions was lower, resulting in less P_i uptake by the seedlings of Aikang 58. Therefore, higher P concentration in the seedlings of Zhoumai 22 contributed to a higher activity of acid phosphatase secreted by roots, thus decomposing more phytic acid, releasing much P_i, and promoting P_i uptake. Previous studies have shown that soybean plants that overexpressing acid phosphatase genes significantly increase yields in acidic soils (Wang et al. 2009). The activity of acid phosphatase is affected greatly by pH, and it reaches a maximum at pH 4.3. However, the activity is very low under alkaline conditions (Tadano et al. 1993). In this study, it was found that the seedlings were readily able to capture more P from phytic acid than $Ca_3(PO_4)_2$ and $Ca(H_2PO_4)_2$ when supplied with an equal amount of P. Since Aikang 58 and Zhoumai 22 were planted in the alkaline soils, it was postulated that the activity of acid phosphatase was significantly reduced. Thus, the seedlings do not acquire more P from organic P than from Ca phosphates in the alkaline soils. Both of the cultivars acquired more P from inorganic P than from organic P. It is difficult for Zhoumai 22 to display an advantage in capturing organic P from alkaline soils compared with Aikang 58.

In conclusions, the selection and breeding of P-efficient wheat cultivars are ideal strategies to improve the utilisation efficiency of phosphate fertiliser and reduce the consumption of P fertiliser. In this study, the higher P concentration in the wheat seedlings of Aikang 58 was attributed to a higher rate of proton secretion and a stronger capacity for inorganic phosphate uptake by roots. These findings suggested that the rate of proton secretion and P_i uptake are important indicators for screening P-efficient wheat cultivars.

REFERENCES

Asmar F., Singh T., Gahoonia, Nielsen N.E. (1995): Barley genotypes differ in activity of soluble extracellular phosphatase and depletion of organic phosphorus in the rhizosphere soil. Plant and Soil, 172: 117–122.

Chiou T.J., Lin S.I. (2011): Signaling network in sensing phosphate availability in plants. Annual Review of Plant Biology, 62: 185–206.

Dalal R.C. (1977): Soil organic phosphorus. Advances in Agronomy, 29: 83–117.

De Souza Campos P.M., Cornejo P., Rial C., Borie F., Varela R.M., Seguel A., López-Ráez J.A. (2019): Phosphate acquisition efficiency in wheat is related to root:shoot ratio, strigolactone levels, and PHO_2 regulation. Journal of Experimental Botany, 70: 5631–5642.

Hinsinger P. (2001): Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. Plant and Soil, 237: 173–195.

Huang M., Wang Z.H., Luo L.C., Wang S., Hui X.L., He G., Cao H.B., Ma X.L., Huang T.M., Zhao Y., Diao C.P., Zheng X.F., Zhao H.B., Liu J.S., Malhi S. (2017): Soil testing at harvest to enhance productivity and reduce nitrate residues in dryland wheat production. Field Crops Research, 212: 153–164.

Hurley B.A., Tran H.T., Marty N.J., Park J., Snedden W.A., Mullen R.T., Plaxton W.C. (2010): The dual-targeted purple acid phosphatase isozyme AtPAP26 is essential for efficient acclimation of *Arabidopsis* to nutritional phosphate deprivation. Plant Physiology, 153: 1112–1122.

López-Bucio J., Cruz-Ramírez A., Herrera-Estrella L. (2003): The role of nutrient availability in regulating root architecture. Current Opinion in Plant Biology, 6: 280–287.

Li C.X., Li Y.Y., Li Y.J., Fu G.Z. (2018): Cultivation techniques and nutrient management strategies to improve productivity of rainfed maize in semi-arid regions. Agricultural Water Management, 210: 149–157.

Liang C.Y., Tian J., Lam H.M., Lim B.L., Yan X.L., Liao H. (2010): Biochemical and molecular characterization of PvPAP3, a novel purple acid phosphatase isolated from common bean enhancing extracellular ATP utilization. Plant Physiology, 152: 854–865.

Maharajan T., Ceasar S.A., Krishna T.P.A., Ignacimuthu S. (2019): Phosphate supply influenced the growth, yield and expression of PHT1 family phosphate transporters in seven millets. Planta, 250: 1433–1448.

https://doi.org/10.17221/348/2020-PSE

McLaren T.I., Smernik R.J., McLaughlin M.J., McBeath T.M., Kirby J.K., Simpson R.J., Guppy C.N., Doolette A.L., Richardson A.E. (2015): Complex forms of soil organic phosphorus – a major component of soil phosphorus. Environmental Science and Technology, 49: 13238–13245.

Mengel K., Kirkby E., Kosegarten H., Appel T. (2001): Principles of Plant Nutrition. 5th Edition. Dordrecht, Kluwer Academic Publishers, 369–372. ISBN 978-94-010-1009-2

Nanamori M., Shinano T., Wasaki J., Yamamura T., Rao I. M., Osaki M. (2004): Low phosphorus tolerance mechanisms: phosphorus recycling and photosynthate partitioning in the tropical forage grass, *Brachiaria* hybrid cultivar Mulato compared with rice. Plant Cell Physiology, 45: 460–469.

Postma J.A., Dathe A., Lynch J.P. (2014): The optimal lateral root branching density for maize depends on nitrogen and phosphorus availability. Plant Physiology, 166: 590–602.

Sun S.B., Gu M., Cao Y., Huang X.P., Zhang X., Ai P.H., Zhao J.N., Fan X.R., Xu G.H. (2012): A constitutive expressed phosphate transporter, ospht1;1, modulates phosphate uptake and translocation in phosphate-replete rice. Plant Physiology, 159: 1571–1581.

Tadano T., Sakai H. (1991): Secretion of acid phosphatase by the roots of several crop species under phosphorus-deficient conditions. Soil Science and Plant Nutrition, 37: 129–140.

Tadano T., Ozawa K., Sakai H., Osaki M., Matsui H. (1993): Secretion of acid phosphatase by the roots of crop plants under phosphorus-deficient conditions and some properties of the enzyme secreted by lupin roots. Plant and Soil, 155: 95–98.

Teng W., He X., Tong Y.P. (2017): Transgenic approaches for improving use efficiency of nitrogen, phosphorus and potassium in crops. Journal of Integrative Agriculture, 16: 2657–2673.

Vance C.P., Uhde-Stone C., Allan D.L. (2003): Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. New Phytologist, 157: 423–447.

Wang X.R., Wang Y.X., Tian J., Lim B.L., Yan X.L., Liao H. (2009): Overexpressing *AtPAP15* enhances phosphorus efficiency in soybean. Plant Physiology, 151: 233–240.

Wang Y.L., Zhang H.L., Tang J.W., Xu J.B., Kou T.J., Huang H.M. (2015): Accelerated phosphorus accumulation and acidification of soils under plastic greenhouse condition in four representative organic vegetable cultivation sites. Scientia Horticulturae, 195: 67–73.

Xu J.M., Wang Z.Q., Wang J.Y., Li P.F., Jin J.F., Chen W.W., Fan W., Kochian L.V., Zheng S.J., Yang J.L. (2019): Low phosphate represses histone deacetylase complex1 to regulate root system architecture remodeling in *Arabidopsis*. New Phytologist, 225: 1732–1745.

Yang J.Y., Yu F.Y., Fu Z.H., Fu Y.H., Liu S.N., Chen M.L., Li Y.J., Sun Q.Z., Chang H.Q., Zhou W.L., Wang X.G., Zhang L.H. (2019): Pathway and driving forces of selenite absorption in wheat leaf blades. Plant, Soil and Environment, 65: 609–614.

Received: July 9, 2020
Accepted: September 16, 2020
Published online: October 1, 2020