Plant Science 179 (2010) 302–306

Contents lists available at ScienceDirect

Plant Science

journal homepage: www.elsevier.com/locate/plantsci

Review

Acquisition or utilization, which is more critical for enhancing phosphorus efficiency in modern crops?

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ARTICLE INFO

Article history:
Received 8 February 2010
Received in revised form 7 June 2010
Accepted 19 June 2010
Available online 30 June 2010

Keywords:
P efficiency
P acquisition
P utilization
Crops

ABSTRACT

Phosphorus (P) is one of the major factors worldwide limiting crop growth. Enhancing P efficiency in plants can be achieved through improving P acquisition, utilization, or both. Which of these approaches is more critical for enhancing P efficiency in crops, particularly in intensive cropping systems? P availability is unevenly distributed through the soil profile. Most modern crop cultivars are selected through conventional breeding approaches for better adaptation to stratified soil P by root architectural and morphological traits that allow for more P acquisition from the P-rich soil surface zone. Conversely, most crops have relatively efficient P uptake capacity but low P translocation and remobilization. Hence, phosphorus utilization efficiency (PUE) becomes a significant bottleneck for further improvements in crop P efficiency. Furthermore, the modification of root systems requires additional carbon input, and thus crops might sacrifice carbohydrates for higher yield to meet demand for P acquisition. With the support from soybean transformation studies, we speculate that enhancement of PUE might become a potentially powerful strategy for increasing P efficiency in modern crops grown in intensive cropping systems.

Contents

1. Introduction

Low phosphorus (P) availability is a principal constraint to crop production worldwide. In most soils, soil and fertilizer P are easily bound by either soil organic matter or chemicals, and thus are unavailable to plants unless hydrolyzed to release inorganic phosphate (Pi) [1]. Therefore, the development of P-efficient crop varieties that can grow and yield better with low P supply is a key to improving crop production.

There are several definitions and calculation methods relevant for the discussion of crop P efficiency. Here we define crop P efficiency as the ability to produce biomass or yield under certain available P supply conditions [2–4]. Phosphorus efficiency can be divided into P acquisition efficiency (PAE) and P utilization efficiency (PUE). PAE refers to the ability of crops to take up P from soils, and PUE is the ability to produce biomass or yield using the acquired P. Enhancing P efficiency in plants can be achieved through improving P acquisition and/or utilization [5–7]. However, the contribution from PAE or PUE to crop P efficiency varies with crop species and environmental conditions.

There are three purposes of this review. First, we provide a brief overview of progress in studies on facilitating PAE and PUE. Secondly, we discuss the contribution of PAE and/or PUE to P efficiency under different conditions. Finally, we speculate on future approaches to improving crop P efficiency in modern agriculture, particularly in intensive cropping systems, which are based on high inputs (capital, labor, fertilizers, pesticides, growth regulators, etc.) to maintain high yield.

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doi:10.1016/j.plantsci.2010.06.007

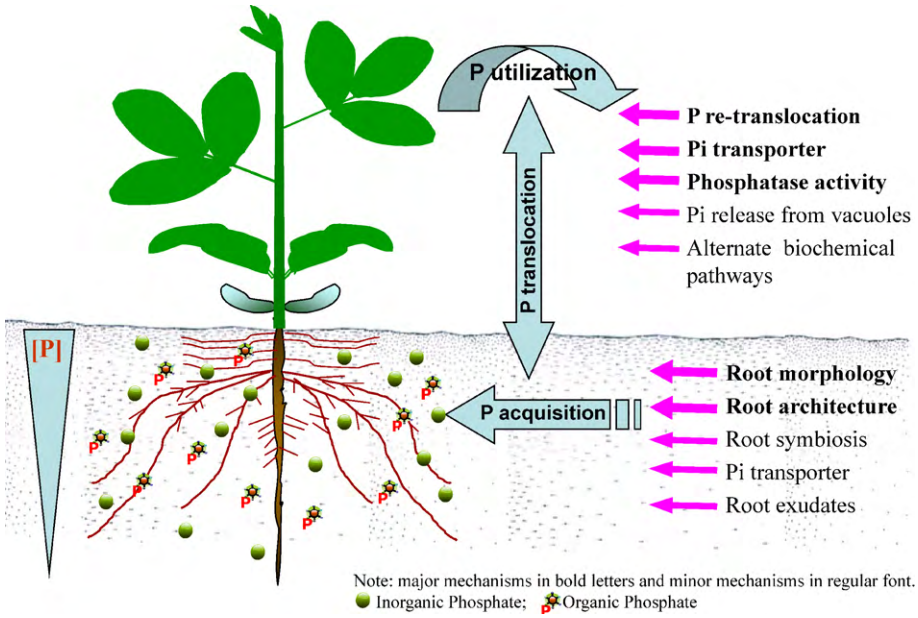

Fig. 1. Schematic representation of the possible mechanisms of P acquisition and utilization for better growth of modern crops grown in intensive cropping systems.

2. Research progress on P efficiency

Various physiological and biochemical traits are involved in enhancing crop P efficiency (Fig. 1). In P acquisition, the most important traits are root morphological characteristics and architecture. P availability is unevenly distributed through the soil profile. Root architecture determines the extent of root exploration throughout the soil profile. Root architectural parameters, branching angle of basal roots and number of lateral branching per cm root, were positively related to P efficiency in common bean [8]. Root shallowness also played a critical role in PAE in soybean [9]. Genotypic variation in root hairs significantly affects P acquisition and grain yields of barley in low P soil [10,11]. In rice, a threefold increase in plant growth was attributed to a 22% increase in root fineness under P deficiency [12]. This demonstrated that large genotypic differences in P acquisition can be caused by rather small changes in root growth-related traits [12].

The production of root exudates, such as organic anions [13] and phosphatase enzymes, may also enhance P acquisition. Exudation of organic acids into the rhizosphere has been proposed to increase P availability by mobilizing sparingly soluble mineral P and organic P sources, and thus increase plant PAE [14,15]. Overproducing citrate in transgenic tobacco plants enhanced P uptake, and thus P efficiency [16]. Over-expression of a plant gene for mitochondrial citrate synthase (CS) in *Arabidopsis thaliana* enhanced citrate excretion, and thus improved plant growth and P accumulation in low P acid soils [17]. Similarly, transgenic barley expressing the aluminium activated malate transporter gene from wheat (*TaALMT1*) showed enhanced P nutrition and grain production when grown on an acid soil [18]. However, some of the above findings failed to be repeated for the same transgenic plants or for ones that expressed the bacterial *CS* gene to a much higher level [19]. Over-expression of phytase or acid phosphatase genes leads to significant increases in exudation of phytase from roots, and therefore improves plant PAE [20–23]. However, over-expression of the extracellular phytase may not ensure improved plant P nutrition unless the soils had been amended with various combinations of phytate, phosphate and lime [21]. It can be seen that the roles of organic acid, phytase and phosphatase remain controversial due to a poor fundamental understanding about their interactions with soils [21,24].

Given soluble P, high-affinity Pi transporters also play an important role in P uptake. Analysis of knock-down rice plants revealed that OsPT6, a high-affinity Pi transporter, plays an important role in Pi uptake and translocation [25], which offers the potential to enhance the P nutrition of crops by the gene technology approach.

In addition to plant adaptations, a large range of bacterial and fungal species is able to solubilize and acquire various forms of mineral P [26]. Among these microbial species, arbuscular mycorrhizal (AM) fungi, which have a high-affinity P uptake mechanism, are particularly important to enhance P uptake for many agricultural plants under low P conditions [27]. However, AM fungi in many agricultural systems play the nonbeneficial or even parasitic roles due to the greater carbon cost of mycorrhizal roots [28]. Moreover, mycorrhizal responsiveness of modern wheat cultivars was generally lower than that of older cultivars [29]. Our results showed that a complementary relationship between root architecture and AM colonization existed in soybean P efficiency (Wang et al. in press). Soybean genotype with the shallow root architecture had higher P efficiency, but lower AM colonization. Conversely, the genotype with the deep root had higher AM colonization but lower P efficiency under low P conditions (Wang et al. in press). Therefore, it seems to be a co-evolutionary pattern among root architecture, AM colonization and P efficiency in plants. AM colonization might negate P efficiency adaptations in modern crops grown in intensive cropping systems.

A higher PUE is mainly attributed to efficient re-translocation and re-use of the stored P in plants. Translocation of absorbed P from metabolically inactive sites to active sites in *Brassica napus* plants growing under low P conditions increases PUE [30,31]. Acid phosphatase contributes to the increased P utilization efficiency in bean through P remobilization from old leaves [32]. Studies with sorghum, tomato, wheat and soybean showed that P remobilization was not only a matter of senescence but occurred even in young non-mature tissues, indicating the recycling of a specific P fraction in the plants [31]. Moreover, higher P re-translocation rate from shoots to roots impels tolerant *B. napus* cultivars to establish a better root system, thereby helps plant growth under low P conditions and increases PUE [31]. Low-affinity Pi transporters from the Pht2 family, along with a number of members

of the Pht1 family, are involved in vascular loading and unloading, and thus affect PUE [33,34]. A low-affinity rice Pi transporter, OsPht1;2, functions in translocation of stored Pi in plants [25]. Another very important factor is the Pi release from the vacuoles under P stress [31]. The Pi storage in vacuoles under P sufficient conditions and the Pi release from vacuoles under P deficient conditions help plants fulfill the demands for P and maintain Pi homeostasis in plants. However, the transport mechanism for the tonoplast Pi transporters is still unclear [35]. In addition, studies showed that some enzymes in photosynthetic plants, which use Pi-independent or inorganic pyrophosphate (PPi) dependent glycolytic reactions, might facilitate a more efficient P utilization by P recycling, reduction of P consumption and utilization of alternative P pools under Pi starvation conditions [6,36,37]. Despite many mechanisms related to the increased PUE, there have been few successful examples of increased PUE by gene engineering approaches due to the complexity of interconnected biochemical pathways in plants.

3. Contribution of P acquisition and/or utilization to P efficiency

As we describe above, both PAE and PUE can contribute to improved crop P efficiency. From here the question arises about which is more critical. As more information is gathered, it appears that the relative importance of P acquisition and utilization efficiency significantly varies with soil P status [5,38].

When P supply is limited, P acquisition could be more important than P utilization. For instance, P efficiency in spring wheat was mostly determined by PAE under P deficient conditions in both acidic and calcareous soils [5]. Higher importance of PAE has also been reported in soybean and common bean in low P acidic soils [9,39]. P deficiency tolerance in rice was largely caused by genotypic differences in P uptake, and PUE had negligible effect [35,40]. Improving P efficiency based on PAE in P-efficient genotypes has been suggested as a potential approach for maintaining pigeon pea and rapeseed yield potentials in soils with low P bioavailability [41,42].

On the other hand, with adequate P supply, PUE could be considered more important than PAE for crop P efficiency. PUE played a dominant role explaining variations in grain yield under high P supply conditions in spring wheat, especially in calcareous soils [5]. Genotypic variation among different potato genotypes results in differences in PUE but not PAE [43,44], at least in pot experiments.

There are many physiological and biochemical processes related to P acquisition and utilization efficiency, and most are associated with genotypic variation [6,45]. This suggests that P efficiency mechanisms could be mostly under genetic control, and thus differ among crop species, as well as among genotypes within a given species. In maize, high P efficiency was due to enhanced P acquisition rather than to an enhanced P utilization under low P condition [46]. Results from a set of genotype and environment studies also indicates that P efficiency in maize is mainly due to the function of P acquisition rather than utilization efficiency in both high and low P acidic soils [7]. In another wheat germplasm screening study, some genotypes showed higher PAE as indicated by higher shoot P content and concentration in a P deficient calcareous soil. Conversely, in the same study, the genotypes with similar shoot P concentration or content showed significant differences in P efficiency, indicating higher PUE in these genotypes [47]. These results differ from the study cited above [5]. Therefore, systematic characterization and identification of P efficiency in a given species should be conducted in large germplasm resources to obtain reliable results. [47].

4. P acquisition and utilization in intensive cropping systems

Due to long-term agricultural practices, especially high P fertilization and long-term organic residue accumulation, available P content in the most cultivated soils with intensive cropping systems becomes higher and higher. Taking Ludhiana of India as an example, available P in the soil increased from the initially low status ($8.0\,kg\,ha^{-1}$) to very high ($85.8\,kg\,ha^{-1}$) due to continuous application of P fertilizer during 22 years of crop rotation [48]. In wheat-maize rotation systems in the North China Plain, the available soil P concentration has increased to 15–30 $mg\,kg^{-1}$ at present from 5–10 $mg\,kg^{-1}$ in the 1980s due to increasing inputs of chemical P fertilizer [49]. Therefore, a review concluded that modern varieties have often been selected under high-nutrient input conditions in order to obtain high yield [4]. Under this condition, some genes related to efficient nutrient acquisition will be lost since all nutrients are directly available to plants, and plant adaptive traits to nutrient deficiency often result in the additional carbon cost [4]. Our results also showed that wild soybean genotypes had higher infection rates with AM under low P conditions compared to modern high yielding varieties (Wang et al., in press). However, in our opinion, most modern cultivars are selected through conventional breeding approaches for better adaptation to stratified soil P distributions, so as to acquire more P from the P-rich soil surface zone. For example, there is a notable correlation between root architecture and P efficiency in soybean. Modern cultivars have shallow root architecture and higher PAE, while wild soybean genotypes have deep root architecture and lower PAE, and the root architecture and PAE of semi-wild soybean is intermediate between modern cultivars and wild soybean [9]. Hence, PAE has already been selected, PUE then becomes a significant bottleneck for further improvement of crop P efficiency in modern cultivars.

Furthermore, the modification of root systems usually requires additional carbon input, and thus crops might have to sacrifice carbohydrates that could be used for higher yields to meet the demand for P acquisition [50,51]. For example, in wheat, over 50% of the carbohydrates were translocated to roots for root growth and maintenance and for the absorption of ions. Of them, anion uptake only costs about 20% of the translocated carbohydrates [52]. However, in rice, large genotypic differences in P uptake from a P deficient soil can be attributed to 22% change in root growth-related parameters, suggesting relatively small carbon costs in roots for P acquisition [12]. Even though carbohydrate supply from leaves to roots was not a limiting factor to lower plant biomass under P deficiency in rice, the P-efficient rice genotypes preferentially re-translocated more P to roots to stimulate root growth and P uptake [53]. A series of studies in India, Bangladesh, and Mexico found that in only 50% of cases was root length density of wheat germplasm grown in intensive cropping system significantly and positively correlated with grain yield, and positive correlations decreased when fertilizer supply was increased [50]. This also suggested that the benefits of large root systems generally diminish with high fertilizer input, especially in intensive cropping systems. Likewise, larger root systems do not necessarily lead to improved water use efficiency even in low water soils, but rooting depth does [54]. Improved total root volume in the deeper soil (80–100 cm) was responsible for improved water use efficiency [50].

Our genetic transformation studies also support the conclusion that PUE is a bottleneck for P efficiency in modern soybean cultivars. When a modern shallow and large rooted soybean cultivar with high P efficiency was transformed to overexpress an Arabidopsis purple APase gene (*AtPAP15*) with phytase activity, different lines differed in growth performance in a field site with moderate P supply [23]. The transgenic line with enhanced secreted phytase grew better than the wild type when phytate was the sole P source

in sand culture, but lost this effect in the field. Conversely, a line with enhanced APase activity in shoots had higher P remobilization ability and grew best in the field. This suggests that the modern cultivar we used as a wild-type control is able to acquire sufficient P from the growth medium, but short to remobilize P. Therefore, we speculate that enhancement of PUE might become a potentially powerful strategy for increasing P efficiency in modern crops grown in intensive cropping systems.

5. Concluding remarks

Phosphorus efficient plants play a major role in increasing crop yields due to shortage of inorganic P fertilizer resources, limited land and water resources, and increasing environmental concerns. Research in the improvement of P efficiency often attributes more to PAE under limited P supply, and to PUE under high P conditions. Therefore, the improvement of both P acquisition and P utilization efficiency in the given species under different P supply conditions in the different soil types seems to be the perfect breeding approach. However, current conventional breeding strategies are mainly implemented through selection of biomass or yield under high fertility soils, such as super hybrid rice varieties, which require more P fertilizer than other rice strains to achieve an economically optimum yield. This is not only costly but also subject to environmental influences. Therefore, PUE will be a significant bottleneck for further improvements in crop P efficiency, which should be a potentially powerful strategy for increasing P efficiency in modern crops grown in intensive cropping systems.

With rapid advances in molecular techniques, more and more QTLs and/or genes are being identified for involvement in P acquisition and internal utilization. The most of work has been done in *A. thaliana*, a model species. In rice, the P uptake 1(*Pup1*) locus is the only known QTL for P uptake [55], and OsPTF1 is a transcription factor that enhances P uptake of transgenic rice plants in P deficient soil [56]. High-affinity Pi transporters also help plants acquire more P from the low P soils, and low-affinity Pi transporters are constitutively expressed and take part in Pi transport to different parts of the plant in high P conditions. However, until now there have been few successful examples of improving PAE in plants using these specific QTLs and/or genes, and no reports for specific gene effects on PUE because of complexities tied to mechanisms of P internal utilization [4,6]. Nevertheless, these results open more possibilities for bioengineering more P efficient cultivars and reducing use of P fertilizer while increasing crop yields.

The challenges now are to achieve a greater understanding of the mechanisms and regulation of P acquisition and internal utilization efficiency, and to develop closer collaboration between physiologists and plant breeders to bring the achievements of the basic studies on P efficiency into plant breeding. Finally, carbon costs of P efficiency needs to be taken into account in crop improvement programs to fully realize more economical and ecologically sustainable agriculture.

Acknowledgements

This research is supported by the National Natural Science Foundation of China (30890131 and 30971853). We thank Dr. Tom Walk for critical review on this manuscript.

References

[1] M.S. Akhtar, Y. Oki, T. Adachi, Genetic variability in phosphorus acquisition and utilization efficiency from sparingly soluble P-sources by *Brassica* cultivars under P-stress environment, J. Agron. Crop Sci. 194 (2008) 380–392.
[2] G.D. Batten, A review of phosphorus efficiency in wheat, Plant Soil 146 (1992) 163–168.
[3] J.P. Lynch, The role of nutrient-efficiency crops in modern agriculture, J. Crop Prod. 1 (1998) 241–264.
[4] M. Wissuwa, M. Mazzola, C. Picard, Novel approaches in plant breeding for rhizosphere-related traits, Plant Soil 321 (2009) 409–430.
[5] G.G.B. Manske, J.I. Ortiz-Monasterio, M. van Ginkel, R.M. González, R.A. Fischer, S. Rajaram, P.L.G. Vlek, Importance of P uptake efficiency versus P utilization for wheat yield in acid and calcareous soils in Mexico, Eur. J. Agron. 14 (2001) 261–274.
[6] V.V. Shenoy, G.M. Kalagudi, Enhancing plant phosphorus use efficiency for sustainable cropping, Biotechnol. Adv. 23 (2005) 501–513.
[7] S.N. Parentoni, C.L.S. Júnior, Phosphorus acquisition and internal utilization efficiency in tropical maize genotypes, Pesqui. Agropecu. Bras. 43 (2008) 893–901.
[8] J.P. Lynch, S.E. Beebe, Adaptation of beans (*Phaseolus vulgaris* L.) to low phosphorus availability, HortScience 30 (1995) 1165–1171.
[9] J. Zhao, J. Fu, H. Liao, Y. He, H. Nian, Y. Hu, L. Qiu, Y. Dong, X. Yan, Characterization of root architecture in an applied core collection for phosphorus efficiency of soybean germplasm, Chin. Sci. Bull. 49 (2004) 1611–1620.
[10] T.S. Gahoonia, N.E. Nielsen, Variation in root hairs of barley cultivars doubled soil phosphorus uptake, Plant Soil 98 (1997) 177–182.
[11] T.S. Gahoonia, N.E. Nielsen, Root traits as tools for creating phosphorus efficient crop varieties, Plant Soil 260 (2004) 47–57.
[12] M. Wissuwa, How do plants achieve tolerance to phosphorus deficiency? Small causes with big effects, Plant Physiol. 133 (2003) 1947–1958.
[13] P.R. Ryan, E. Delhaize, D.L. Jones, Function and mechanism of organic anion exudation from plant roots, Annu. Rev. Plant Physiol. Plant Mol. Biol. 52 (2001) 527–560.
[14] B. Dinkelaker, V. Römheld, H. Marschner, Citric acid excretion and precipitation of calcium citrate in the rhizosphere of white lupin (*Lupinus albus* L.), Plant Cell Environ. 12 (1989) 285–292.
[15] J.F. Johnson, C.P. Vance, D.L. Allan, Phosphorus deficiency in *Lupinus albus*. Altered lateral root development and enhanced expression of phosphoenolpyruvate carboxylase, Plant Physiol. 112 (1996) 31–41.
[16] J. Lopez-Bucio, O.M. de la Vega, A. Guevara-Garia, L. Herrera-Estrella, Enhanced phosphorus uptake in transgenic tobacco plants that overproduce citrate, Nat. Biotechnol. 18 (2000) 450–453.
[17] H. Koyama, A. Kawamura, T. Kihara, T. Hara, E. Takita, D. Shibata, Overexpression of mitochondrial citrate synthase in *Arabidopsis thaliana* improved growth on a phosphorus limited soil, Plant Cell Physiol. 41 (2000) 1030–1037.
[18] E. Delhaize, P. Taylor, P.J. Hocking, R.J. Simpson, P.R. Ryan, A.E. Richardson, Transgenic barley (*Hordeum vulgare* L.) expressing the wheat aluminium resistance gene (*TaALMT1*) shows enhanced phosphorus nutrition and grain production when grown on an acid soil, Plant Biotechnol. J. 7 (2009) 391–400.
[19] E. Delhaize, D.M. Hebb, P.R. Ryan, Expression of a *Pseudomonas aeruginosa* citrate synthase gene is not associated with either enhanced citrate accumulation or efflux, Plant Physiol. 125 (2001) 2059–2067.
[20] A.E. Richardson, P.A. Hadobas, J.E. Hayes, Extracellular secretion of *Aspergillus* phytase from *Arabidopsis* roots enables plants to obtain phosphorus from phytate, Plant J. 25 (2001) 641–649.
[21] T.S. George, R.J. Simpson, P.A. Hadobas, A.E. Richardson, Expression of a fungal phytase gene in *Nicotiana tabacum* improves phosphorus nutrition of plants grown in amended soils, Plant Biotechnol. J. 3 (2005) 129–140.
[22] J. Wasaki, H. Maruyama, M. Tanaka, T. Yamamura, H. Dateki, T. Shinano, S. Ito, M. Osaki, Overexpression of the *LASAP2* gene for secretory acid phosphatase in white lupin improves the phosphorus uptake and growth of tobacco plants, Soil Sci. Plant Nutr. 55 (2009) 107–113.
[23] X. Wang, Y. Wang, J. Tian, B. Lim, X. Yan, H. Liao, Overexpressing *AtPAP15* enhances phosphorus efficiency in soybean, Plant Physiol 151 (2009) 233–240.
[24] D.L. Jones, P.G. Dennis, A.G. Owen, P.A.W. van Hees, Organic acid behavior in soils – misconceptions and knowledge gaps, Plant Soil 248 (2003) 31–41.
[25] P. Ai, S. Sun, J. Zhao, X. Fan, W. Xin, Q. Guo, L. Yu, Q. Shen, P. Wu, A.J. Miller, G. Xu, Two rice phosphate transporters, OsPht1;2 and OsPht1;6, have different functions and kinetic properties in uptake and translocation, Plant J. 57 (2009) 798–809.
[26] T.S George, A.E. Richardson, Potential and limitations to improving crops for enhanced phosphorus utilization, in: P.J. White, J.P. Hammond (Eds.), Ecophysiology of Plant–Phosphorus Interactions, Springer, Netherlands, 2008, pp. 247–270.
[27] A.O. Adesemoye, J.W. Kloepper, Plant-microbes interactions in enhanced fertilizer-use efficiency, Appl. Microbiol. Biotechnol. 85 (2009) 1–12.
[28] M.H. Ryan, J.H. Graham, Is there a role for arbuscular mycorrhizal fungi in production agriculture? Plant Soil 244 (2002) 263–271.
[29] Y.G. Zhu, S.E. Smith, A.R. Barritt, F.A. Smith, Phosphorus (P) efficiencies and mycorrhizal responsiveness of old and modern wheat cultivars, Plant Soil 237 (2001) 249–255.
[30] M.S. Akhtar, Y. Oki, T. Adachi, Y. Murata, M.H.R. Khan, Relative phosphorus utilization efficiency, growth response, and phosphorus uptake kinetics of *Brassica* cultivars under a phosphorus stress environment, Commun. Soil Sci. Plant Anal. 38 (2007) 1061–1085.
[31] M.S. Akhtar, Y. Oki, T. Adachi, Intraspecific variations of phosphorus absorption and remobilization, P forms, and their internal buffering in Brassica cultivars exposed to a P-stressed environment, J. Integr. Plant Biol. 50 (2008) 703–716.
[32] S. Kouas, A. Debez, T. Slatni, N. Labidi, J.J. Drevon, C. Abdelly, Root proliferation, proton efflux, and acid phosphatase activity in common bean (*Phaseolus vulgaris*) under phosphorus shortage, J. Plant Biol. 52 (2009) 395–402.
[33] F.W. Smith, S and P transport systems in plants, Plant Soil 232 (2001) 109–118.

[34] F.W. Smith, S.R. Mudge, A.L. Rae, D. Glassop, Phosphate transport in plants, Plant Soil 248 (2003) 71–83.
[35] M. Panigrahy, D.N. Rao, N. Sarla, Molecular mechanisms in response to phosphate starvation in rice, Biotechnol. Adv. 27 (2009) 389–397.
[36] M.E. Theodoru, W.C. Plaxton, Metabolic adaptations of plant respiration to nutritional phosphate deprivation, Plant Physiol. 101 (1993) 339–344.
[37] W.C. Plaxton, Metabolic aspects of phosphate starvation in plants, in: J.P. Lynch, J. Deikman (Eds.), Phosphate in Plant Biology: Regulatory Roles in Molecular, Cellular, Organismic, and Ecosystem Processes, vol. 19, American Society of Plant Physiologists, Maryland, 1998, pp. 229–240.
[38] M.L. Huang, X.P. Deng, Y.Z. Zhao, S.L. Zhou, S. Inanaga, S. Yamada, K. Tanaka, Water and nutrient use efficiency in diploid, tetraploid and hexaploid wheats, J. Integr. Plant Biol. 49 (2007) 706–715.
[39] S.E. Beebe, M. Rojas-Pierce, X. Yan, M.W. Blair, F. Pedraza, F. Muñoz, J. Tohme, J.P. Lynch, Quantitative trait loci for root architecture traits correlated with phosphorus acquisition in common bean, Crop Sci. 46 (2006) 413–423.
[40] M. Wissuwa, N. Ae, Genotypic variation for tolerance to phosphorus deficiency in rice and the potential for its exploitation in rice improvement, Plant Breeding 120 (2001) 43–48.
[41] K. Fujita, Y. Kai, M. Takayanagi, H. El-Shemy, J.J. Adu-Gyamfi, P.K. Mohapatr, Genotypic variability of pigeonpea in distribution of photosynthetic carbon at low phosphorus level, Plant Sci. 166 (2004) 641–649.
[42] H. Zhang, Y. Huang, X. Ye, L. Shi, F. Xu, Genotypic differences in phosphorus acquisition and the rhizosphere properties of *Brassica napus* in response to low phosphorus stress, Plant Soil 320 (2009) 91–102.
[43] T. Balemi, M.K. Schenk, Genotypic variation of potato for phosphorus efficiency and quantification of phosphorus uptake with respect to root characteristics, J. Plant Nutr. Soil Sci. 172 (2009) 669–677.
[44] T. Balemi, M.K. Schenk, Genotypic difference of potato in carbon budgeting as a mechanism of phosphorus utilization efficiency, Plant Soil 322 (2009) 91–99.
[45] R.B. Clark, R.R. Duncan, Improvement of plant mineral nutrition through breeding, Field Crops Res. 27 (1991) 219–240.
[46] I. Corrales, M. Amenós, C. Poschenrieder, J. Barceló, Phosphorus efficiency and root exudates in two contrasting tropical maize varieties, J. Plant Nutr. 30 (2007) 887–900.
[47] L. Ozturk, S. Eker, B. Torun, I. Cakmak, Variation in phosphorus efficiency among 73 bread and durum wheat genotypes grown in a phosphorus-deficient calcareous soil, Plant Soil 269 (2005) 69–80.
[48] D.K. Benbi, C.R. Biswas, Nutrient budgeting for phosphorus and potassium in a long-term fertilizer trial, Nutr. Cycl. Agroecosys. 54 (1999) 125–132.
[49] F.S. Zhang, Research and Application of an Integrated Nutrient Resource Management Technique to Harmonize High Crop Yield and Environment Protection, China Agricultural University Press, Beijing, 2008, pp. 110–111.
[50] G.G.B. Manske, P.L.G. Vlek, Root architecture-wheat as a model plant, in: Y. Waisel, A. Eshel, U. Kafkafi (Eds.), Plant Roots: The Hidden Half, 3rd ed., Marcel Dekker, New York, Basel, 2002, pp. 249–259.
[51] J.P. Lynch, M.D. Ho, Rhizoeconomics: carbon costs of phosphorus acquisition, Plant Soil 269 (2005) 45–56.
[52] H. Lambers, O.W. Atkin, I. Scheurwater, Respiratory patterns in roots in relation to their function, in: Y. Waisel, A. Eshel, U. Kafkafi (Eds.), Plant Roots: The Hidden Half, 2nd ed., Marcel Dekker, New York, 1996, pp. 323–362.
[53] M. Wissuwa, G. Gamat, A.M. Ismail, Is root growth under phosphorus deficiency affected by source or sink limitations? J. Exp. Bot. 56 (2005) 1943–1950.
[54] A. Hodge, G. Berta, C. Doussan, F. Merchan, M. Crespi, Plant root growth, architecture and function, Plant Soil 321 (2009) 153–187.
[55] M Wissuwa, J. Wegner, N. Ae, M. Yano, Substitution mapping of *Pup1*: a major QTL increasing phosphorus uptake of rice from a phosphorus-deficient soil, Theor. Appl. Genet. 105 (2002) 890–897.
[56] K. Yi, Z. Wu, J. Zhou, L. Du, L. Guo, Y. Wu, P. Wu, OsPTF1, a novel transcription factor involved in tolerance to phosphate starvation in rice, Plant Physiol. 138 (2005) 2087–2096.