Strategies for improving phosphorus acquisition efficiency of crop plants

Lara Ramaekers[a], Roseline Remans[c], Idupulapati M. Rao[b], Matthew W. Blair[b] and Jozef Vanderleyden[a]

[a]Center of Microbial and Plant Genetics, Department of Microbial and Molecular Systems, K.U. Leuven, Kasteelpark Arenberg 20, 3001 Heverlee, Belgium.

[b]International Center for Tropical Agriculture/Centro Internacional de Agricultura Tropical (CIAT), A.A. 6713, Cali, Colombia.

[c]The Earth Institute at Columbia University, 405 Low Library, MC 4335 535 West 116th Street New York, NY 10027, USA

Correspondence: Prof. Dr. Jozef Vanderleyden, Center of Microbial and Plant Genetics, K.U.Leuven, Kasteelpark Arenberg 20, 3001 Leuven, Belgium
Email: jozef.vanderleyden@biw.kuleuven.be
Fax : +32 16 32 19 63

---

*Prof. Dr. Jozef Vanderleyden,Center of Microbial and Plant Genetics, K.U.Leuven, Kasteelpark Arenberg 20, 3001 Leuven, Belgium

ABSTRACT

In many low input agricultural systems, phosphorus (P) is one of the most limiting mineral nutrients for plant production. The use of genetically enhanced plants with improved P acquisition efficiency may represent the most sustainable solution to increase crop yields in these systems. This review is intended to provide a short summary on adaptation mechanisms of crop plants facing P deficiency as the starting point to develop a research approach for improving P acquisition efficiency. This includes three strategies: molecular assisted plant breeding, genetic engineering and the use of agricultural practices. The natural source for improving P nutrition of plants is existing large genetic variation for traits associated with P acquisition efficiency and will therefore be emphasized in this review.

Keywords: phosphorus acquisition, phosphorus deficient soils, genetic variation, food crops

1. Introduction

Phosphorus (P) deficiency is considered a major limiting factor in crop productivity, especially in the tropics and subtropics. Compared to other major nutrients, P is by far the least mobile and least available to plants in most soil conditions (Schachtman et al., 1998; Hinsinger, 2001). Some soils such as sandy soils possess low total P contents and are not able to retain added P by fertilization (WRB soil classification system; Driessen et al., 2001). However, most soils that have little P available for the plant docontain considerable amounts of P but a large proportion is bound to different soil constituents, forming complexes of limited availability (Fairhust et al., 1999; Driessen et al., 2001).In both cases, the concentration of phosphate (Pi) in soil solution issuboptimal for crop production. Soils with low total P content can be amended with P fertilizer but are not able to retain the added P. Soils with high total P content that fix most of the P, will equally fix a large proportion of added P. In these P-fixing tropical soils, plants respond to P fertilizer application but annual P applications are needed to sustain crop yields (Sanchez, 1976). An alternative approach for both soils with low P content and P-fixing soils, is to enhance the plant´s efficiency to acquire soil P (Shenoy and Kalagudi, 2005; Lynch, 2007; Fageria et al., 2008). In this essay, we review the different mechanisms used by crop plants to improve their P acquisition efficiency. Progress in a more detailed understanding of these mechanisms holds great promise for developing strategies that build upon the observed explorative behavior of plant roots. We present a research approach involving three strategies that may lead to improved P acquisition by crop plants. Firstly, traditional plant breeding for enhanced P acquisition is a feasible strategy as shown by a range of inheritance studies and the breeding of improved common bean lines with greater P acquisition and better tolerance to low P soils. Secondly, genetic engineering can be used to introduce genes that improve P acquisition and growth of crop plants. A third strategy focuses on the use of agricultural practices to enhance plant growth under P deficient conditions through inoculation with Plant Growth-Promoting Rhizobacteria (PGPR) and mycorrhizae. Throughout this review, the inter- and intraspecific genetic variation for traits involved in P acquisition efficiency is highlighted. While this genetic variation is undoubtedly essential for improving P acquisition by plants, it may also cause divergent outcomes for a given strategy applied.

1. Plant mechanisms for improving P acquisition efficiency

Crop plants are a very diverse group with both monocot and dicot members. Dicotyledonous plants are characterized by a taproot system with a prominent primary root and basal roots arising from the mesocotyl or hypocotyl, which together form the main root axes. Monocots, on the other hand, display a shoot-borne root system with multiple root axes resulting in a fibrous root system. An extensive discussion on the root development and structure of monocots and dicots is provided by Gregory (2006). Although the root architecture in monocots and dicots differs significantly, the main adaptive root traits correlated with enhanced P acquisition are common among all vascularized plant species. P is an element that is relatively immobile in the soil. Therefore, the main strategy for P acquisition is maximal and continued soil exploration through proliferation and extension of all root types with preference for those roots that are metabolically efficient and acquire P avidly (Lynch and Ho, 2005).

Plants exposed to P deficiency activate a range of mechanisms that either result in increased acquisition of P from the soil or in a more efficient use of the internal P (Vance et al., 2003). This section focuses on plant mechanisms related to increased P acquisition. Figure 1 assembles and integrates these mechanisms in a plant model. Importantly, this figure clearly shows all possible differences between a P-efficient genotype and a P-inefficient genotype. One or several of these differences often explain the higher tolerance of P efficient genotypes to P deficiency compared to P inefficient genotypes. More extensive reviews on these mechanisms are available (Vance et al., 2003; Lambers et al., 2006; Lynch and Brown, 2006; Richardson et al., 2009b) and therefore, only a short overview with emphasis on genetic variation for these traits is provided.

1.1. Increase of root- to- shoot ratio

A common response to P deficiency is an increase in root-to-shoot dry weight ratio, due to a greater stimulation of root growth at the expense of shoot growth (Mollier and Pellerin, 1999; Hermans et al., 2006; figure 1). In a study with common bean, Nielsen et al. (2001) showed that P-efficient genotypes maintained a higher root-to-shoot ratio during their growth under P deficient conditions as compared to P-inefficient genotypes.

1.2. Redistribution of growth among root types

Low P availability also changes the distribution of growth among various root types (Drew, 1975; Hodge, 2004; Hodge, 2009). In the model plant *Arabidopsis thaliana* and various rape cultivars, a highly branched root system with reduced primary root (PR) and an increase in the number and length of lateral roots (LR) was observed when seedlings were grown under low P availability (López-Bucio et al., 2003; Pérez-Torres et al., 2008; Akhtar et al., 2008; figure 1). However, in other crop plants, elongation of the main root axes is maintained under low P (Mollier and Pellerin, 1999). This could be interpreted as exploratory behavior, allowing these roots to grow maximally until they encounter localized patches of higher P availability. The response of lateral rooting under P stress, however, shows genetic variation within species. In maize, some genotypes show an increase in LR number and length while others show a decrease. The genotypes with increased or sustained LR development have superior ability to acquire P and maintain growth (Zhu and Lynch, 2004).

1.3. Stimulation of root hair growth

Another common adaptation to low P is the stimulation of root hair growth (Lynch, 2007; figure 1). By enhancing both root hair length and density, the soil volume subject to P depletion by roots significantly increases. In the model plant *Arabidopsis*, root hair density was 29% higher and low P root hairs grew three times as long as high P root hairs after 16 days of P starvation (Bates and Lynch, 1996). Substantial genetic variation for these traits is found among genotypes of different crop plants including wheat, barley (Gahoonia et al., 1997) and among recombinant inbred lines of common bean (Yan et al., 2004). In common bean, root hair length and density of basal roots are correlated with P acquisition in the field (Yan et al., 2004) suggesting that in particular the basal root hairs are important for P acquisition. Various studies also indicate that root hairs may assist in the exudation of P-mobilizing compounds such as organic acids, protons and phosphatases. These compounds are able to liberate fixed P by (i) complexing and chelating cations bound to P, (ii) competing with phosphate ions for sorption sites, (iii) dephosphorylation of organic P and (iv) by acidifying the rhizosphere so that dissolution of sparingly soluble P minerals in alkaline soils is increased (this topic has been recently reviewed by Richardson et al., 2009b). P deficient conditions caused an 81% increase in the organic acid exudation rate in some lowland rice genotypes (Hoffland et al., 2006). Similar results were reported in four common bean genotypes with a two- to threefold increase in organic acid exudation after 7 days of P starvation (Shen et al., 2002).

1.4. Topsoil foraging

In most natural soils, the topsoil is the layer with greatest bioavailability of P. As a consequence, root systems that enhance topsoil foraging will be able to acquire more P. Architectural traits associated with enhanced topsoil foraging in common bean include shallower growth of basal roots, increased adventitious rooting and greater dispersion of lateral branching from the basal roots (Lynch and Brown, 2006; Lynch, 2007; figure 1). P efficient bean genotypes produce shallower basal roots in response to low P availability compared to P inefficient bean genotypes and P acquisition significantly correlates with basal root shallowness (Liao et al., 2001). Similar results have been observed in seminal roots of maize genotypes (analogous to basal roots in dicots – Zhu et al., 2005). Adventitious roots are common in many plants. This root type arises from the hypocotyl and grows horizontally just below the soil surface. As with basal root shallowness, genotypic and P-induced adventitious rooting vary widely among common bean genotypes (Miller et al., 2003) and are moderately heritable (Ochoa et al., 2006).

1.5. Soil exploration at minimal metabolic cost

Another adaptation to P limitation that has been studied mainly in common bean is the exploration of the soil at minimal metabolic cost (Lynch and Brown, 2006; Lynch, 2007). One mechanism of reducing the root metabolic burden is to allocate relatively more biomass to root classes that are metabolically efficient in acquiring P such as adventitious roots and root hairs (figure 1). The production and maintenance of these root types needs less biomass as compared to tap and basal roots. Moreover, they greatly enlarge the absorptive surface area relative to the root volume making them more efficient in acquiring P. Miller et al. (2003) showed that at low P availability, a higher proportion of the root biomass of common bean is allocated to adventitious roots, especially in P-efficient genotypes. Another strategy to reduce P requirements of root growth is the induction of aerenchyma in roots (Fan et al., 2003; figure 1). Cortical cells are replaced with air space and the P released from the breakdown of the cortical tissue could be useful in meeting the P demands for root elongation. Substantial genotypic variation in aerenchyma formation in response to low P was observed in common bean and maize. Also in maize, root porosity seems to be strongly correlated with sustained root growth under low P (Lynch and Brown, 2006).

1.6. Association with mycorrhizae

Association of crop plants with mycorrhizal fungi can also mediate the availability of P to plants through extension of the plant root system with mycorrhizal hyphae (Bucher, 2007; figure 1). Arbuscular mycorrhiza (AM) is probably the most widespread terrestrial symbiosis and is formed by 70-90% of land plant species (Parniske, 2008). In exchange for P and other nutrients supplied to the plant, the fungal symbiont obtains reduced carbon (Jacobsen et al., 2005). An extensive review on plant-mycorrhizae associations is provided by Parniske (2008). Improved P acquisition is the main benefit of AM symbioses. The beneficial effect for symbiotic P acquisition however depends on P nutrition. Several studies in maize inoculated with mycorrhizae report an increase in P acquisition and plant growth under low P conditions but a decrease for these parameters under high P conditions (Kaeppler et al., 2000). The carbon cost of mycorrhizal symbioses could cause this detrimental effect under fertile conditions. In conditions of low available P, Kaeppler et al. (2000) reported substantial variation among maize inbred lines for mycorrhizal responsiveness (defined as growth increase upon mycorrhizal inoculation). The genotypes with the lowest shoot dry weight showed highest growth increase compared to the genotypes with higher shoot dry weight. Clearly, more studies on genotypic variation for mycorrhizal responsiveness under conditions of varying P nutrition are needed.

1.7. Increased expression of high affinity P-transporters

The concentration of P in root cells can be up to 1000-fold higher than the P-concentration in soil solution. In order to acquire P against this steep concentration gradient, P transport across the soil/root interface requires a specialized transport system. In plants, two P uptake systems have been identified, a high affinity system that is either increased or de-repressed under P deficiency and a low affinity system that is constitutively expressed (Ullrich-Eberius et al., 1984; Rausch and Bucher, 2002). Plants can possess multiple P-transporters of each system. For example, nine transporter genes have been cloned from *Arabidopsis*, at least five from potato and up to eight from barley. All cloned genes are members of the Pht1 family of plant P transporters and are highly conserved (Rausch and Bucher, 2002). Several studies report expression of *pht1* genes in different organs including root, shoot tissues and reproductive organs but highest expression is commonly found in root hairs (Mudge et al., 2002). More extensive information on P-uptake mechanisms at the root-soil interface is provided by Bucher (2007).

To date, no studies on plant genotypic variation in expression level or activity of P transporters and possible correlation with P acquisition efficiency have been reported. However, several mutants with aberrant phosphate transporter expression have been well described (Zakhleniuk et al., 2001; Shin et al., 2004; Xu et al., 2007) and suggest the presence of genetic variation among plant genotypes. Elucidating this genotypic variation in P transporter expression/activity level could therefore be a very promising study.

Furthermore, little is known on the molecular pathways in the plant triggering these responses to P starvation (Hammond and White, 2008; Richardson, 2009). Svistoonoff et al. (2006) provide evidence for an important role of the root cap (tip of the primary root) in sensing P deficiency and/or responding to it in *Arabidopsis*. In the root cap, *low phosphate root* 1 and 2 (LPR1 and LPR2) genes, which encode multicopper oxidases, are responsible for the ceasing of primary root growth under low P conditions. More recently, it was also shown that P-deficient *Arabidopsis* seedlings increase auxin sensitivity through increased expression of the TIR1 auxin receptor, leading to stimulation of lateral root formation under low P conditions (Pérez-Torres et al., 2008). However, increased lateral root formation seems to be independent of primary root growth inhibition. This is shown by the phosphate-insensitive *lpi3 Arabidopsis* mutant which does not show primary root growth arrest but still increases lateral root number under low P conditions (Pérez-Torres et al., 2008). Moreover, the lateral root formation of two mutants *lpr1-1* and *lpr1-2* and a near-isogenic line (NIL) carrying the recessive LPR1 allele which implies lower LPR1 expression, does not seem to be affected, although quantitative data for lateral root number and length are not available (Svistoonoff et al., 2006). Thus, primary root growth arrest and increased lateral root formation as a response to P deprivation might be regulated independently in the plant root.

Another important component of the Pi-signaling network that is being unravelled is the microRNA399(miR399)/PHO2 pathway (Dong et al., 1998; Rubio et al., 2001; Hamburger et al., 2002; Miura et al., 2005; Fujii et al., 2005). Under P deficient conditions, this pathway activates a subset of P starvation-induced genes including high affinity P-transporter genes *Pht1;8* and *Pht1;9* in *Arabidopsis*. Moreover, the phenotype of the *pho2* mutant also indicates a role for PHO2 in systemic plant responses including regulation of P allocation between shoot and root. PHO2 encodes an E2 conjugase that is modulated by the P-dependent miR399. The microRNA miR399 might be the mobile signal assuring coordinated responses to P deficiency between shoot and root (Bari et al., 2006). Bari et al. also show that P-dependent miR399 expression is conserved in rice and reveal close homologs of *Arabidopsis* PHO2 in several higher plant species including wheat, soybean and cotton. Therefore, the miR399/PHO2 pathway seems to be a conserved regulatory mechanism.

These findings are important steps towards resolving the complete signal transduction cascade for P-limitation in plants. However, the question as to how plants actually perceive P – and if it is the presence or the absence of P that acts as a signal – is key in our further understanding of the signaling pathway.

The background on the mechanisms for improving P acquisition, leads to three proven strategies for improving P efficiency of crop plants that we will discuss in the following section.

2. Strategies for improving P acquisition efficiency of crop plants

Phosphorus deficiency in soils is caused by a general low total P content of the soil or low bioavailability of P in the soil. In both cases, the main approach to benefit from applied as well as native fixed P is to target the plant root system to enhance P acquisition from the soil. Growth model simulations for rice showed that small optimizations of the root system i.e. increasing root fineness, trigger large increases in P acquisition (Wissuwa, 2003). Those large increases are mainly due to enhanced root growth as a result of higher P acquisition per unit root size. Achieving these changes can be brought about through three strategies based on molecular breeding, the deployment of transgenics, and agricultural practices as described below.

Strategy 1: Molecular assisted plant breeding for enhanced tolerance to low P soils

As mentioned in the previous section, genotypic variation for tolerance to P deficiency has been demonstrated in many food crops. This variation provides the source for developing cultivars that are superior in P acquisition and higher yielding in P deficient conditions through plant breeding (Zhang et al., 2007; Fageria et al., 2008; Hammond et al., 2008). Conventional plant breeding including phenotypic selection for improved root systems has proven to be difficult, prone to environmental effects, and time-consuming (Miklas et al., 2006). As tolerance to low P is a quantitative trait, an appropriate method to dissect its complex polygenic inheritance is through Quantitative Trait Loci (QTL) analysis. A QTL is a region in the genome that is responsible for variation in the quantitative trait of interest. Identifying and placing QTL on a genetic map is based on the statistically significant association of phenotypic differences for the trait of interest with molecular markers that constitute the genetic map (Doerge, 2001). Molecular markers found to be linked to the target trait can be used for selection in the breeding process (Marker-Assisted Selection, MAS).

A range of QTL have been identified for tolerance mechanisms to low P in various food crops (Kaeppler et al., 2000; Wissuwa et al., 2005; Beebe et al., 2006). In common bean, some of these have been notably correlated with low P adaptation in the field despite being evaluated in hydroponic or greenhouse conditions (Yan et al., 2004). An association between low P tolerance and aluminum toxicity resistance QTL has also been found in common bean and could indicate the added importance of organic acid exudation (López-Marín et al., 2009).

Despite this progress, a remaining challenge is to utilize these QTL through marker assisted breeding. Research by Heuer et al. (2009) provides one of the very few examples in which attempts are undertaken to further dissect a major QTL for phosphorus acquisition (*Pup1*) in rice. This QTL had been identified in a Kasalath (tolerant) × Nipponbare (sensitive) population. Nipponbare near-isogenic lines (NILs) carrying the *Pup1* donor allele from Kasalath increased P acquisition and grain yield by a factor of three to four relative to the sensitive Nipponbare recurrent parent under P deficient conditions. Interestingly, all NILs developed a root system similar to Nipponbare under P sufficient conditions suggesting that *Pup1* entails a specific adaptation to P deficiency. Moreover, this effect under low P did not seem to be limited to a Nipponbare genetic background or to the specific environment. Introgression of *Pup1* into the background of two other tropical rice cultivars by MAS and evaluation at other sites showed that the variability among introgression lines was high but the majority outperformed both recurrent parents (Wissuwa et al., 2005). These findings illustrate the possible fast progress that could be achieved upon transfer of the *Pup1* allele to elite breeding material lacking tolerance to P deficiency. Further efforts are ongoing to identify gene(s) underlying this locus (Heuer et al., 2009).

In general, however, the achievements of MAS for tolerance to low P are limited (Steele et al., 2006). This limited success is due to difficulties such as epistatic interactions between QTL and the identification of many QTL each with only small impact. Moreover, some QTL can show poor stability across different mapping populations and environments and in new genetic backgrounds. MAS is most effective for introgression of few stable QTL with large effects (Miklas et al., 2006). It is also important to narrow down the QTL region as much as possible so that linkage drag is reduced and only target genes are transferred. With the identification of a growing number of genes involved in response to low P (Valdéz-López and Hernández, 2008; Yuan and Liu, 2008), the search for candidate genes within a QTL will be facilitated.

Strategy 2: Development of transgenic plants

Several attempts have been made to improve specific P acquisition processes in food crops through genetic engineering with specific bacterial, fungal or plant genes.

Focus has been mainly on genes enhancing solubilization of P in the soil. An overview of reported transgenic crop plants is given in table 1. López-Bucio et al. (2000) introduced a bacterial citrate synthase gene into tobacco (*Nicotiana tabacum*) and reported a two- to fourfold increase of the citrate efflux by roots of transgenic lines and superior growth and yield in low P alkaline soils. However, Delhaize et al. (2001) could not confirm these results. Many studies (summarized in table 1) also report transgenic overexpression of phytase in various food crops. Phytases are exuded into the rhizosphere and are able to hydrolyse phytate which constitutes up to 50% of the total organic P in soil (Anderson, 1980). Overexpression of phytase in potato, clover, soybean and tobacco resulted in increased P acquisition and content.

Increasing knowledge on regulatory and signalling mechanisms involved in P acquisition might identify new useful genes (Valdéz-López and Hernández, 2008; Yuan and Liu, 2008). As P transport and P solubilization are processes that seem to be closely linked to root hairs, a combined overexpression of P transporters and P solubilizers might result in synergistic effects.

Despite promising experimental results, to date, no transgenic lines have been released for commercial use. Genetic engineering is not always very robust and easily reproducible and still remains a controversial societal issue that has strict regulatory control compared to conventional crop improvement. Furthermore, plant varieties are highly diverse each with very different genetic backgrounds and varying reactions to low P soils. Therefore, transferring one gene across multiple backgrounds could give divergent outcomes.

Strategy 3: Agricultural practices to enhance plant growth in low P soils

Agricultural practices that enhance acquisition of P from the soil include the inoculation of food crops with plant growth-promoting rhizobacteria (PGPR) or mycorrhizae (Rengel and Marschner, 2005; Hodge et al., 2009). One advantage to this strategy is that the use of these microbes can complement products from plant breeding or transgenesis described above.

In the first case, PGPR can directly increase plant available P via mechanisms of solubilization and mineralization of fixed P from inorganic and organic forms. These mechanisms include the release of organic acids, protons and phosphatases into the rhizosphere. Bacteria from the genera *Pseudomonas* and *Bacillus* and fungi, primarily *Penicillum* and *Aspergillus,* are among the most powerful P solubilizers. Another mechanism which indirectly leads to increased P acquisition by plants, is the production of phytohormones (mainly auxins) by rhizobacteria that stimulate root growth (Richardson, 2001; Jacobsen et al., 2005; Richardson et al., 2009a). Inoculation with *Azospirillum*, known to produce substantial amounts of indole-3-acetic-acid (IAA), increases the length and density of root hairs as well as the appearance and elongation rates of lateral roots in many plant species (Fallik et al., 1994). Inoculation with *Azospirillum* thus triggers a natural stimulation of root adaptation to low P soils. Its effect can now be better understood in view of the recent finding of Pérez-Torres et al. (2008) that P deficiency in *Arabidopsis* seedlings increases auxin sensitivity through increased expression of the TIR1 auxin receptor, leading to stimulation of lateral root formation. However, under low P conditions, contrasting effects of *Azospirillum* on plant root development and yield have been detected among genotypes of wheat (Kucey, 1988) and common bean (Remans et al., 2008b). Remans et al. (2008a) further identified this differential response as a contrasting root sensitivity to the bacterial produced auxin and identified a QTL for root responsiveness to auxin. Nevertheless, this study highlights the possibility of breeding for cultivars with improved root responsiveness to auxin-producing bacteria. It might also explain inconsistent results and indicate that the agricultural use of PGPR is not widely applicable but depends on the genotype that is cultivated. In some cases, commercial inoculants of PGPR have been developed for agricultural use but their widespread application remains limited due to inconsistent performance in different environments and poor understanding of the mechanisms involved in their ability to promote plant growth (Richardson, 2001). However, even considering the set limitations, the use of PGPR remains a good option in terms of cost-effectiveness and potential for technological improvement.

Another valuable plant-microbe interaction, namely mycorrhizal symbiosis, is based on the mutualistic exchange of C from the plants in return for P and other nutrients from the fungus. Influx of P in roots colonized by mycorrhizal fungi can be 3 to 5 times higher than in nonmycorrhizal roots (Smith and Read, 1997). Some plant P transporters from the Pht1 family have been found to be expressed only at the plant/mycorrhiza interface during symbiosis in different food crops and are repressed under high P conditions (Bucher, 2007). The presence of these transporters is essential to avoid early degradation of this interface suggesting that the delivery of P and probably other nutrients to the plant is necessary to maintain symbiosis (Javot et al., 2007). This knowledge might indicate how improvement of the mycorrhizal P acquisition pathway is possible. However, further basic research of the symbiotic interaction is needed. The study of plant genotypic variation for responsiveness to mycorrhization and for P acquisition from mycorrhiza could provide a basis for breeding or engineering crop plants with higher responsiveness to mycorrhization and higher P acquisition through the mycorrhizal pathway.

3. Considerations in a broader perspective

As previously discussed, there are two different types of P deficient soils: (1) soils with an overall low total P content and (2) soils with high total P but with low availability of P for the plant because of strong P retention (Driessen et al., 2001). Enhancing the plant’s efficiency to acquire P is a good strategy, whether this P originates (partly) from P fertilizer in low P soils or from endogenous soil P in highly P-fixing soils. However, the consequence of increased plant acquisition efficiency would be a lowering of the total soil P content over time. Whether this lowering will occur fast or slow, will depend on the initial total P content of the soil, the cropping intensity and crop P requirements. To avoid ending up with overall low P soil contents, it is advisable to add small amounts of P fertilizer or slow release P fertilizer, such as rock phosphate, to the soil. This strategy avoids the rapid loss of added P through soil leaching in poor soils that are unable to retain P. In P-fixing soils, addition of small amounts or slow release P fertilizer will avoid the fixation of P fertilizer which is not directly taken up by the plant. Combining this strategy with an improved plant efficiency to acquire P will ensure a higher recovery of applied P and therefore, less P fertilizer will be required. However, it has to be taken into account that P fertilizer is not always available nor affordable for small-scale poor farmers. Moreover, at the current world-wide rate of fertilizer application, the readily available sources of high-grade phosphate rocks may become rare within the next 60 to 90 years and this will make P fertilizer prices rise considerably (Runge-Metzer, 1995; Lambers et al., 2006; Yuan and Liu, 2008). Without any P additions, the soil will eventually run out of P. To reduce the dependency on P fertilizer, it would be interesting to enhance the plant's internal P use efficiency. P use efficiency is defined as the capacity to produce a large amount of organic matter per unit of P taken up (Rengel and Marschner 2005). Plants with enhanced P use efficiency show higher growth for the same amount of P taken up. Recently, Su et al. (2009) identified 6 QTL controlling P utilization efficiency in Chinese winter wheat pot and field trials. Moreover, positive linkages were observed between QTL for P acquisition efficiency and P use efficiency at two loci, showing the possibility of improving P acquisition and P use simultaneously.

Natural environments typically comprise a combination of different abiotic stresses. In acid soils for example, plant growth is inhibited principally because of toxicity from excess aluminum (Al) and lack of nutrients, especially P (von Uexküll and Mutert, 1995). Some root adaptation mechanisms to low P are also useful to cope with other abiotic stresses. Suboptimal P and iron (Fe) availability both trigger an increase in root hair density and length (Schikora and Schmidt, 2001). A well-known mechanism to prevent Al from penetrating inside the root cells is the exudation of organic acid anions complexing Al (Miyasaka et al., 1991; Delhaize et al., 1993; Ma et al., 1997). Organic acid exudation is equally used by plants to release P by complexing and chelating cations bound to P and compete for sorption sites with P on clays and Fe and Al oxides (Schachtman et al., 1998; Hinsinger et al., 2001). Breeding attempts have focused on developing larger root systems in crop plants in order to increase ability to compete for several nutrients (Malamy, 2005).

One of the mechanisms to increase access to P, is a greater topsoil exploration resulting in shallower roots under P deficiency. However, this may inadvertently result in reduced water acquisition since water availability typically increases with soil depth. As a consequence, plant genotypes selected for adaptation to low P soils may be more sensible to drought and viceversa (Ho et al., 2004; Lynch and Ho, 2005). However, Beebe et al. (2008) reported on an interesting breeding program aimed at creating breeding lines of common bean with increased yields under drought conditions. Some selected drought resistant lines also appeared to expres superior yields in a low P environment, one of which even outyielded the low P tolerant check by 41%. This finding indicates that yield potential under drought conditions and yield potential under low P conditions may not be mutually exclusive.

4. Conclusions

Tremendous genetic variation for adaptation to P deficiency exists among food crops. The study and use of this variation are pivotal for the development of crop plants with better growth rates and higher yields on P deficient soils. In turn, P efficient crop varieties with less dependency on P fertilizer are an essential ingredient of a new sustainable Green Revolution that assures food security for a growing world population.

Adaptation to low P can be achieved by genetic engineering or by molecular assisted plant breeding, with many possible traits identified so far for mechanistic input. In addition, food crops can be inoculated with plant growth-promoting rhizobacteria (PGPR) or mycorrhizae to improve their P acquisition. Combining these three strategies might provide a novel and useful approach on the road to low P adapted food crops.

5. Acknowledgments

We thank Prof. E.V. Quadros for critical reading of the manuscript. This work is supported by a grant from the Flemish Interuniversity Council (VLIR) to L.R.

6. References

Akthar, M.S., Oki, Y., Adachi, T., 2008. Genetic variation in phosphorus acquisition and utilization efficiency from sparingly soluble P-sources by *Brassica* cultivars under P-stress environment. J. Agric. Crop Sci. 194, 380-392.

Anderson, G., 1980. Assessing organic phosphorus in soil. In: Khasawneh, F.E., Sample, E.C., Kamprath, E.J., (Eds.), The Role of Phosphorus in Agriculture. American Society of Agronomy, Madison, WI, USA, pp. 411–431.

Bari, R., Datt Pant, B., Stitt, M., Scheible, W., 2006. PHO2, microRNA399 and PHR1 define a phosphate-signaling pathway in plants. Plant Phys. 141, 988-999.

Bates, T.R., Lynch, J.P., 1996. Stimulation of root hair elongation in *Arabidopsis thaliana* by low phosphorus availability. Plant Cell Environ. 19, 529-538.

Beebe, S.E., Rao, I.M., Cajiao, C., Grajales, M., 2008. Selection for drought resistance in common bean also improves yield in phosphorus limited and favorable environments. Crop Sci. 48, 582-592.

Beebe, S.E., Rojas, M., Yan, X., Blair, M.W., Pedraza, F., Muñoz, F., Tohme, J., Lynch, J.P., 2006. Quantitative trait loci for root architecture traits correlated with phosphorus acquisition in common bean. Crop Sci. 46, 413-423.

Bucher, M., 2007. Functional biology of plant phosphate uptake at root and mycorrhiza interfaces. New Phyt. 173, 11-26.

Delhaize, E., Hebb, D.M., Ryan, P.R., 2001. Expression of a *Pseudomonas aeruginosa* citrate synthase gene in tobacco is not associated with either enhanced citrate accumulation or efflux. Plant Phys. 125, 2059-2067.

Delhaize, E., Ryan, P.R., Randall, P.J., 1993. Aluminum tolerance in wheat (*Triticum aestivum* L.) II. Aluminum-stimulated excretion of malic acid from root apices. Plant Phys. 103, 695-702.

Delhaize, E., Taylor, P., Hocking, P.J., Simpson, R.J., Ryan, P.R., Richardson, A.E., 2009. 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 Biotech. J. 7(5), 391-400.

Doerge, R., 2001. Mapping and analysis of quantitative trait loci in experimental populations. Nature Rev. Gen. 3, 43-52.

Dong, B., Rengel, Z., Delhaize, E., 1998. Uptake and translocation of phosphate by *pho2* mutant and wild-type seedlings of *Arabidopsis thaliana*. Planta 205, 251-256.

Drew, M.C., 1975. Comparison of effects of a localized supply of phosphate, nitrate, ammonium and potassium on growth of seminal root system, and shoot, in barley. New Phyt. 75, 479-490.

Driessen, P., Deckers, S., Spaargaren, O., Nachtergaele, F., 2001. Lecture notes on the major soils of the world. FAO.

Fageria, N.K., Baligar, V.C., Li, Y.C., 2008. The role of nutrient efficient plants in improving crop yields in the twenty first century. J. Plant Nutr. 31, 1121-1157.

Fairhust, T., Lefroy, E., Mutert, E., Batjes, N.H., 1999. The importance, distribution and causes of phosphorus deficiency as a constraint to crop production in the tropics. Agrofor. Forum 9, 2-8.

Fallik, E., Sarig, S., Okon, Y., 1994. Morphology and physiology of plant roots associated with *Azospirillum*. In: Okon, Y. (Ed.), *Azospirillum*/plant associations. CRC Press, Boca Raton, pp. 77-86.

Fan, M.S., Zhu, J., Richards, C., Brown, K.M., Lynch, J.P., 2003. Physiological roles for aerenchyma in phosphorus-stressed roots. Funct. Plant Biol. 30(5), 493-506.

Fujii, H., Chiou, T.J., Lin, S.I., Aung, K., Zhu, J.K., 2005. A miRNA involved in phosphate-starvation response in *Arabidopsis.* Curr. Biol. 15, 2038-2043.

Gahoonia, T.S., Care, D., Nielsen, N.E., 1997. Root hairs and phosphorus acquisition of wheat and barley cultivars. Plant Soil 191, 181-188.

George, T.S., Richardson, A.E., Hadobas, P.A., Simpson, R.J., 2004. Characterization of transgenic *Trifolium subterraneum* L. which expresses *phyA* and releases extracellular phytase, growth and phosphorus nutrition in laboratory media and soil. Plant Cell Environ. 27, 1351-1361.

George, T.S., Simpson, R.J., Hadobas, P.A., Richardson, A.E., 2005. Expression of a fungal phytase gene in *Nicotiana tabacum* improves phosphorus nutrition of plants grown in amended soils. Plant Biotech. J. 3, 129-140.

Gregory, P., 2006. Plant Roots, Growth, activity and interaction with soils. Blackwell Publishing, Oxford.

Hamburger, D., Rezzonico, E., MacDonald-Comber Petétot, J., Somerville, C., Poirier, Y., 2002. Identification and characterization of the *Arabidopsis* PHO1 gene involved in phosphate loading to the xylem. Plant Cell 14, 889-902.

Hammond, J.P., Broadley, M.R., White, P.J., King, G.J., Bowen, H.C., Hayden, R., Meacham, M.C., Mead, A., Overs, T., Spracklen, W.P., Greenwood, D.J., 2008. Shoot yield drives phosphorus use efficiency in *Brassica oleraceae* and correlates with root architecture traits. J. Exp. Bot. 60, 1953-1968.

Hammond, J.P., White, P.J., 2008. Sucrose transport in the phloem, integrating root responses to phosphorus starvation. J. Exp. Bot. 59, 93-109.

Hermans, C., Hammond, J.P., White, P.J., Verbruggen, N., 2006. How do plants respond to nutrient shortage by biomass allocation? Trends Plant Sci. 11, 610-617.

Heuer, S., Lu, X., Chin, J.H., Tanaka, J.P., Kanamori, H., Matsumoto, T., De Leon, T., Ulat, V.J., Ismail, A.M., Yano, M., Wissuwa, M., 2009. Comparative sequence analysis of the major quantitative trait locus *phosphorus uptake 1* (*Pup1*) reveal a complex genetic structure. Plant Biotech. J. 7, 456-471.

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

Ho, M.D., McCannon, B.D., Lynch, J.P., 2004. Optimization modelling of plant root architecture for water and phosphorus acquisition. J. Theor. Biol. 226, 331-340.

Hodge, A., 2004. The plastic plant: root responses to heterogeneous supplies of nutrients. New Phyt. 162, 9-24.

Hodge, A., 2009. Root decisions. Plant Cell Environ. 32, 628-640.

Hodge, A., Berta, G., Doussan, C., Merchan, F., Crespi, M., 2009. Plant root growth, architecture and function. Plant Soil 321, 153-187.

Hoffland, E., Wei, C., Wissuwa, M., 2006. Organic acid exudation by lowland rice (*Oryza sativa* L.) at zinc and phosphorus deficiency. Plant Soil 283, 155-162.

Jacobsen, I., Leggett, M.E., Richardson, A.E., 2005. Rhizosphere microorganisms and plant phosphorus uptake. In: Sims, J.T. and Sharpley, A.N. (Eds.), Phosphorus, agriculture and the environment. Soil Sci. Soc. America, Madison, pp. 437-494.

Javot, H., Penmetsa, R.V., Terzaghi, N., Cook, D.R., Harrison, M.J., 2007. A *Medicago truncatula* phosphate transporter indispensable for the arbuscular mycorrhizal symbiosis. Proc. Natl. Acad. Sci. U.S.A. 104, 1720-1725.

Kaeppler, S.M., Parke, J.L., Muelle, S.M., Senior, L., Stuber, C., Tracy, W.F., 2000. Variation among maize inbred lines and determination of QTL for growth at low phosphorus and responsiveness to arbuscular mycorrhizal fungi. Crop Sci. 40, 358-364.

Kucey, R.M.N., 1988. Plant growth-altering effects of *Azospirillum brasilense* and *Bacillus* C-11-25 on two wheat cultivars. J. Appl. Bact. 64, 187-196.

Lambers, H., Shan, M.W., Cramer, M.D., Pearse, S.J., Veneklaas, E.J., 2006. Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. Ann. Bot. 98, 693-713.

Li, G., Yang, S., Li, M., Qiao, Y., Wang, J., 2009. Functional analysis of an *Aspergillus ficuum* phytase gene in *Saccharomyces cerevisiae* and its root-specific, secretory expression in transgenic soybean plants. Biotechn. Letter 31, 1297-1303.

Liao, H., Rubio, G., Yan, X., Cao, A., Brown, K.M., Lynch, J.P., 2001. Effect of phosphorus availability on basal root shallowness in common bean. Plant Soil 232, 69-79.

López-Bucio, J., Cruz-Ramírez, A., Herrera-Estrella, L., 2003. The role of nutrient availability in regulating root architecture. Curr. Opin. Plant Biol. 6, 280-287.

López-Bucio, J., de la Vega, O.M., Guevara-García, A., Herrera-Estrella, L., 2000. Enhanced phosphorus uptake in transgenic tobacco plants that overproduce citrate. Nature 18, 450-453.

López-Marín, H.D., Rao, I.M., Blair, M.W., 2009. Quantitative trait loci for root morphology traits under aluminum stress in common bean (*Phaseolus vulgaris* L.). Theor. Appl. Gen. 119(3), 449-458.

Lung, S., Chan, W., Yip, W., Wang, L., Young, E.C., Lim, B.L., 2005. Secretion of beta-propeller phytase from tobacco and *Arabidopsis* roots enhances phosphorus utilization. Plant Sci. 169, 341-349.

Lynch, J.P., 2007. Roots of the second green revolution. Austr. J. Bot. 55, 493-512.

Lynch, J.P., Brown, K.M., 2006. Whole-plant adaptations to low phosphorus availability. In: Huang, B. (Ed.), Plant-Environment Interactions. CRC Press Inc., Boca Raton, pp. 209-242.

Lynch, J.P., Ho, M.D., 2005. Rhizoeconomics, Carbon costs of phosphorus acquisition. Plant Soil 269, 45-56.

Ma, X., Wright, E., Ge, Y., Bell, J., Yajun, X., Bouton, J.H., Wang, Z., 2009. Improving phosphorus acquisition of white clover (*Trifolium repens* L.) by transgenic expression of plant-derived phytase and acid phosphatase genes. Plant Sci. 176, 479-488.

Ma, J.F., Zheng, S.J., Matsumoto, H., Hiradate, S., 1997. Detoxifying aluminium with buckwheat. Nature 390, 569-570.

Malamy, J.E., 2005. Intrinsic and environmental response pathways that regulate root system architecture. Plant Cell Environ. 28, 67-77.

Miklas, P.N., Kelly, J.D., Beebe, S.E., Blair, M.W., 2006. Common bean breeding for resistance against biotic and abiotic stresses, from classical to MAS breeding. Euphytica 147, 105-131.

Miller, C.R., Ochoa, I., Nielsen, K.L., Beck, D., Lynch, J.P., 2003. Genetic variation for adventitious rooting in response to low phosphorus availability, potential utility for phosphorus acquisition from stratified soils. Funct. Plant Biol. 30, 973–985.

Miura, K., Rus, A., Sharkhuu, A., Yokoi, S., Karthikeyan, A.S., Raghothama, K.G., Baek, D., Koo, Y.D., Jin, J.B., Bressan, R.A., Yun, D., Hasegawa, P.M., 2005. The Arabidopsis SUMO E3-ligase SIZ1 controls phosphate deficiency responses. Proc. Natl. Acad. Sci. U.S.A. 102, 7760-7765.

Miyasaka, S.C., Buta, J.G., Howell, R.K., Foy, C.D., 1991. Mechanism of aluminum tolerance in snapbeans – Root exudation of citric acid. Plant Phys. 96, 737-743.

Mollier, A., Pellerin, S., 1999. Maize root system growth and development as influenced by P deficiency. J. Exp. Bot. 50, 487-497.

Mudge, S.R., Rae, A.L., Diatloff, E., Smith, F.W., 2002. Expression analysis suggests novel roles for members of the Pht1 family of phosphate transporters in *Arabidopsis*. Plant J. 31(3), 341-353.

Nielsen, K.I., Eshel, A., Lynch, J.P., 2001. The effect of phosphorus availability on the carbon economy of contrasting common bean genotypes. J. Exp. Bot. 52 (355), 329-339.

Ochoa, I.E., Blair, M.W., Lynch, J.P., 2006. QTL analysis for adventitious root formation in common bean under contrasting phosphorus availability. Crop Sci. 46, 1609-1621.

Park, M.R., Baek, S.H., de los Reyes, B.G., Yun, S.J., 2007. Overexpression of a high-affinity phosphate transporter gene from tobacco (NtPT1) enhances phosphate uptake and accumulation in transgenic rice plants. Plant Soil 292(1-2), 259-269.

Parniske, M., 2008. Arbuscular mycorrhiza: the mother of plant root endosymbioses. Nat. Rev. Microbiol. 6(10), 763-775.

Pérez-Torres, C., López-Bucio, J., Cruz-Ramírez, A., Ibarra-Laclette, E., Dharmasiri, S., Estelle, M., Herrera-Estrella, L., 2008. Phosphate availability alters lateral root development in *Arabidopsis* by modulating auxin sensitivity via a mechanism involving the TIR1 auxin receptor. Plant Cell 20, 3258-3272.

Rae, A.L., Jarmey, J.M., Mudge, S.R., Smith, F.W., 2004. Over-expression of a high-affinity phosphate transporter in transgenic barley plants does not enhance phosphate uptake rates. Funct. Plant Biol. 31(2), 141-148.

Ranathunge, K., Steude, E., Lafitte, R., 2003. Control of water uptake by rice (*Oryza sativa* L.), role of the outer part of the root. Planta 217, 193-205.

Rausch, C., Bucher, M., 2002. Molecular mechanisms of phosphate transport in plants. Planta 216, 23-37.

Remans, R., Beebe, S., Blair, M., Manrique, G., Tovar, E., Rao, I., Croonenborghs, A., Torres-Gutierrez, R., El-Howeity, M., Michiels, J., Vanderleyden, J., 2008a. Physiological and genetic analyses of root responsiveness to auxin-producing plant growth-promoting rhizobacteria in common bean (*Phaseolus vulgaris* L.). Plant Soil 302(1-2), 149-161.

Remans, R., Ramaekers, L., Schelkens, S., Hernandez, G., García, A., Luis Reyes, J., Mendez, N., Toscano, V., Mulling, M., Galvez, L., Vanderleyden, J., 2008b. Effect of *Rhizobium-Azospirillum* coinoculation on nitrogen fixation and yield of two contrasting *Phaseolus vulgaris* genotypes cultivated across different environments in Cuba. Plant Soil 312(1-2), 25-37.

Rengel, Z., Marschner, P., 2005. Nutrient availability and management in the rhizosphere: exploiting genotypic differences. New Phyt. 168, 305-312.

Richardson, A.E., 2001. Prospects for using soil microorganisms to improve the acquisition of phosphorus by plants. Austr. J. Plant Phys. 28, 897-906.

Richardson, A.E., 2009. Regulating the phosphorus nutrition of plants, molecular biology meeting agronomic needs. Plant Soil 322, 17-24.

Richardson, A.E., Barea, J., McNeill, A.M., Prigent-Combaret, C., 2009a. Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. Plant Soil 339, 305-339.

Richardson, A.E., Hadobas, P.A., Simpson, R.J., 2001. Phytate as a source of phosphorus for the growth of transgenic *Trifolium subterraneum* L.. Plant nutrition – Food security and sustainability of agro-ecosystems 92, 560-561.

Richardson, A.E., Hocking, P.J., Simpson, R.J., George, T.S., 2009b. Plant mechanisms to optimise acces to soil phosphorus. Crop Past. Sci. 60, 124-143.

Rubio, V., Linhares, F., Solano, R., Martin, A.C., Iglesias, J., Leyva, A., Paz-Ares, J., 2001. A conserved MYB transcription factor involved in phosphate starvation signaling both in vascular plants and in unicellular algae. Genes Dev. 15, 2122-2133.

Runge-Metzer, A., 1995. Closing the cycle: Obstacles to efficient P management for improved global food security. In: Tiessen, B. (Ed.), Phosphorus in the global environment: Transfers, cycles and Management. John Wiley and Sons, New York, pp. 27-42.

Sanchez, P.A., 1976. Properties and management of soils in the Tropics. John Wiley and Sons, New York, USA.

Schachtman, D.P., Reid, R.J., Ayling, S.M., 1998. Update on phosphorus uptake. Phosphorus uptake by plants: from soil to cell. Plant Phys. 116, 447-453.

Schikora, A., Schmidt, W., 2001. Acclimative changes in root epidermal cell fate in response to Fe and P deficiency: a specific role for auxin? Protoplasma 218, 67-75.

Shen, H., Yan, X., Zheng, S., Wang, X., 2002. Exudation of organic acids in common bean as related to mobilization of aluminum- and iron-bound phosphates. Env. Exp. Bot. 48, 1-9.

Shenoy, V.V., Kalagudi, G.M., 2005. Enhancing plant phosphorus use efficiency for sustainable cropping. Biotechn. Adv. 23, 501-513.

Shin, H., Shin, H.S., Dewbre, G.R., Harrison, M.J., 2004. Phosphate transport in *Arabidopsis*: Pht1;1 and Pht1;4 play a major role in phosphate acquisition from both low- and high-phosphate environments. Plant J. 39(4), 629-642.

Smith, S.E., Read, D.J., 1997. Mycorrhizal symbiosis. Academic Press, New York.

Steele, K.A., Price, A.H., Shashidhar, H.E., Witcombe, J.R., 2006. Marker-assisted selection to introgress rice QTLs controlling root traits into an Indian upland rice variety. Theor. Appl. Gen. 112, 208-221.

Svistoonoff, S., Creff, A., Reymond, M., Sigoillot-Claude, C., Ricaud, L., Blanchet, A., Nussaume, L., Desnos, T., 2007. Root tip contact with low-phosphate media reprograms plant root architecture. Nature Gen. Letter 39(6), 792-796.

Su, J., Li, H., Li, B., Jing, R., Tong, Y., Li, Z., 2009. Detection of QTLs for phosphorus use efficiency in relation to agronomic performance of wheat grown under phosphorus sufficient and limited conditions. Plant Sci. 176, 824-836.

Tesfaye, M., Temple, S.J., Allan, D.L., Vance, C.P., Samac, D.A., 2001. Overexpression of malate dehydrogenase in transgenic alfalfa enhances organic acid exudation synthesis and confers tolerance to aluminum. Plant Phys. 127, 1836-1844.

Ullrich-Eberius, C., Novacky, A., Van Bel, A., 1984. Phosphate uptake in *Lemna gibba* G1, energetics and kinetics. Planta 161, 46-52.

Valdéz-López, O., Hernández, G., 2008. Transcriptional regulation and signaling in phosphorus starvation, what about legumes? J. Integr. Plant Biol. 50(10), 1213-1222.

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

von Uexküll, H.R., Mutert, E., 1995. Global extent, development and economic impact of acid soils. Plant Soil 171, 1-5.

Wasaki, J., Maruyama, H., Tanaka, M., Yamamura, T., Dateki, H., Shinano, T., Ito, S., Osaki, M., 2009. 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, 107-113.

Wissuwa, M., 2003. How do plants achieve tolerance to phosphorus deficiency? Small causes with big effects. Plant Phys. 133, 1947-1958.

Wissuwa, M., Gatdula, K., Ismail, A., 2005. Candidate gene characterization at the *Pup1* locus, a major QTL increasing tolerance to phosphorus deficiency. In: Toriyama, K., Heong, K.L., Hardy, B. (Eds.), Rice is life, Scientific perspectives for the 21st century. IRRI, Manila, pp. 83-85.

Xu, G.H., Chague, V., Melamed-Bessudo, C., Kapulnik, Y., Jain, A., Raghothama, K.G., Levy, A.A., Silber, A., 2007. Functional characterization of LePT4: a phosphate transporter in tomato with mycorrhiza-enhanced expression. J. Exp. Bot. 58(10), 2491-2501.

Yan, X., Liao, H., Beebe, S.E., Blair, M.W., Lynch, J.P., 2004. QTL mapping of root hairs and acid exudation traits and their relationship to phosphorus uptake in common bean. Plant Soil 265, 17-29.

Yang, H., Knapp, J., Koirala, P., Rajagopal, D., Ann Peer, W., Silbart, L.K., Murphy, A., Gaxiola, R., 2007. Enhanced phosphorus nutrition in monocots and dicots over-expressing a phosphorus-responsive type I H+-pyrophosphatase. Plant Biotechn. J. 5, 735-745.

Yuan, H., Liu, D., 2008. Signaling components involved in plant responses to phosphate starvation. J. Integr. Plant Biol. 50(7), 849-859.

Zakhleniuk, O.V., Raines, C.A., Lloyd, J.C., 2001. *pho3*: a phosphorus-deficient mutant of *Arabidopsis thaliana* (L.) Heynh. Planta 212(4), 529-534.

Zhang, Q.F., 2007. Strategies for developing green super rice. Proc. Natl. Acad. Sci. U.S.A. 104, 16402-16409.

Zhu, J.M., Kaeppler, S., Lynch, J., 2005. Topsoil foraging and phosphorus acquisition efficiency in maize. Funct. Plant Biol. 32, 749-762.

Zhu, J.M., Lynch, J.P., 2004. The contribution of lateral rooting to phosphorus acquisition efficiency in maize seedlings. Funct. Plant Biol. 31, 949-958.

Zimmermann, P., Zardi, G., Lehmann, M., Zeder, C., Amrhein, N., Frossard, E., Bucher, M., 2003. Engineering the root-soil interface via targeted expression of a synthetic phytase gene in trichoblasts. Plant Biotechn. J. 1, 353–360.