Chapter 10
Phosphorus Nutrition: Rhizosphere Processes, Plant Response and Adaptations

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10.1 Introduction

Phosphorus (P) is an essential element required for cellular function and when deficient has a significant impact on plant growth and fecundity. Poor availability of P in soil and consequent P deficiency represents a major constraint to crop production globally (Runge-Metzger 1995). Soil P status is also a key factor that controls the competitive dynamics and species composition in different natural ecosystems (McGill and Cole 1981; Attiwill and Adams 1993), and thus may have significant impact on biodiversity (Wassen et al. 2005). Many plant species have evolved in P-limited environments and, as a consequence, are known to possess a number of adaptive features that can enhance the acquisition of P from soil (Raghothama 1999; Vance et al. 2003; Richardson et al. 2007). Most plants have evolved to respond to P starvation by increasing the ability of their root systems to acquire P from the soil (White et al. 2005; Hammond and White 2008; Lynch and Brown 2008; White and Hammond 2008; Fang et al. 2009). Plant root cells take up P as orthophosphate ($H_2PO_4^-$, abbreviated here as Pi), whose concentrations in the soil solution is extremely low (<10 μM). The mass flow of Pi in the soil solution is insufficient to supply the P requirements of a plant (Kirkby and Johnston 2008). Hence, roots must proliferate throughout the soil to acquire sufficient P for plant nutrition. Although some soil P is present as labile Pi bound to soil particles, most is present as sparingly soluble inorganic salts, such as calcium (Ca) phosphate in

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alkaline soils or aluminium (Al) and iron (Fe) phosphates in acidic soils, or as complex organic compounds in soil organic material or soil organisms (Hinsinger 2001; Oberson and Joner 2005; Turner 2007; Kirkby and Johnston 2008). Organic P generally accounts for around 50% of soil P, and is largely comprised of monoesters with lesser amounts of diesters and phosphonates (Newman and Tate 1980; Hawkes et al. 1984; Condron et al. 1990). In order to be available to plants, inorganic P must be either desorbed or solubilised, and organic P must be mineralised to release Pi. Once in the soil solution, Pi is acquired rapidly by plant roots such that its concentration in close proximity to the root surface is estimated to be in the order of ~0.05 to 0.2 μM (Barber 1984), which is significantly less than elsewhere in the soil environment, where soil solution concentrations are typically in the range of 1–5 μM (Bieleski 1973). Slow Pi diffusion through soil to the roots is the ultimate limitation to P supply to the root surface, and can thus restrict P acquisition.

The conserved responses of plants to P starvation that increase P acquisition include:

1. Acidification of the rhizosphere and secretion of low molecular weight organic anions and phosphatase enzymes into the soil to mobilize Pi from inorganic and organic P sources (Marschner 1995; Hinsinger 2001; Jones et al. 2003; Delhaize et al. 2007; Jain et al. 2007b; George and Richardson 2008).
2. Investment of a greater proportion of plant biomass in the root system, and alterations in the morphology of the root system to enable greater exploration of the soil volume and the exploitation of localized patches of high Pi availability (White et al. 2005; Hermans et al. 2006; Hammond and White 2008; Lynch and Brown 2008).
3. Increasing the capacity of root cells to take up Pi, thereby reducing Pi concentrations in the rhizosphere, increasing the rate of diffusion of Pi towards the rhizosphere and stimulating the release of Pi from labile sources (Marschner 1995; Bucher 2007; Jain et al. 2007b).

In addition, most plants foster symbiotic relationships with mycorrhizal fungi to increase their ability to explore the soil volume and mobilize P from remote inorganic and organic sources (Bucher 2007; Smith and Read 2007; Jansa et al. 2011). All these responses are coordinated by a small number of regulatory systems controlled by both the P status of the shoot and Pi availability in the rhizosphere (White et al. 2005; Amtmann et al. 2006; White and Hammond 2008; Hammond and White 2008).

In this chapter, we will discuss the current state of knowledge regarding (1) how plants react to limited P availability by changing their physiological response in root growth and rhizosphere biochemistry traits, (2) how they coordinate this response to P limitation, and (3) how they respond to the re-supply of P once P becomes available again. Gaps in knowledge will be identified and priorities for future research will be discussed.

10.2 Root and Rhizosphere Responses of Plants to P Deficit

10.2.1 Morphological Adjustment of Roots to P Deficiency

Most species partition a greater proportion of their total dry matter into root growth when grown under P deficiency (Bradshaw et al. 1960; Hill et al. 2006). A number of studies indicate that the capacity to adjust root mass ratio in favour of root growth is expressed most effectively by species that have evolved in fertile soils (Christie and Moorby 1975; Boot and Mensink 1990), and consequently this adjustment is considered characteristic of plants that can compete effectively in high-nutrient environments (Chapin 1980). Many species adjusting to low P conditions concurrently increase specific root length (SRL) to achieve longer or more branched roots per unit of root dry matter (Christie 1975; Fitter 1985; Hill et al. 2006) and increase their root hair length and density (Itoh and Barber 1983). Increased SRL can be achieved by reducing root mass density (Fitter 1985; Fan et al. 2003) and/or by decreasing root diameter (Hill et al. 2006). In addition, a common physiological response is root agravitropism or topsoil foraging, putting roots where concentrations of P are relatively large (Lynch 2005). The formation of specialised root structures that increase P acquisition is an alternative means by which plants adjust to low soil P levels. Most notable of these are the cluster (or proteoid) roots (dense bottle-brush-like clusters of rootlets) formed on white lupin (*Lupinus albus*) (Gardner et al. 1981; Dinkelaker et al. 1995; Keerthisinghe et al. 1998; Neumann et al. 1999). The formation of cluster roots by white lupin is induced and regulated by the P status of the shoot rather than the P concentration of the root system or the soil solution (Keerthisinghe et al. 1998; Shane et al. 2003; Shen et al. 2005). In particular, cluster roots significantly increase root-surface area and thus soil contact, and are usually found on species that are either non-mycorrhizal or weakly mycorrhizal (Skene 1998).

10.2.2 Formation of Root Hairs in Response to P Deficit

Root hair development may be sparse in high-P conditions, but both density and length increase when plants are grown on a low-P supply (Bates and Lynch 1996; Gahoonia and Nielsen 1997), thus increasing the capacity for P acquisition (Itoh and Barber 1983; Föhse et al. 1991). The benefit of increased root hair density reaches a plateau when the P-depletion zones around each root hair begin to overlap, with the optimal relationship between root hair density and length dependent on the P-diffusion coefficient of the soil (Ma et al. 2001). In a study of ten grassland species, Hill et al. (2006) concluded that root-morphology adjustments helped plants to maintain root length under a range of low-P conditions, consequently improving the potential for P uptake from P-deficient soil. However, the intrinsic morphological characteristics of each species (particularly an extensive,

fine root system), as opposed to the ability to adjust root morphology, was the most important determinant of whether a plant had a low P fertiliser requirement for maximum growth rate (Hill et al. 2006).

The use of root hair mutants has demonstrated that the presence of root hairs increases the root soil contact, evidenced by enhanced rhizosheath (soil adhering to roots) production (Haling et al. 2010; Brown et al. 2010) and this, in association with the consequent enhanced root surface area, has been demonstrated to enhance tolerance of Al-toxic (Haling et al. 2010) and P-deficient conditions (Brown et al. 2010). The major mechanism by which root hairs are beneficial to P acquisition is likely to be the greater volume of soil exploited by long root hair varieties, as evidenced by differential zones of depletion around roots of various barley root-hair mutants (Fig. 10.1) (Gahoonia and Nielsen 1997).

10.2.3 Release of Extracellular Organic Anions

Many studies have shown that organic anions modify the chemistry of the rhizosphere and mobilise various forms of inorganic and organic P. This is achieved by an increase in the dissolution of sparingly soluble P minerals, reduced sorption of P by alteration of the surface characteristics of soil particles, desorption of Pi from sorption sites (ligand exchange and ligand dissolution), and through the chelation of cations (e.g. Al and Fe in acidic soils or Ca in alkaline soils) that are commonly associated or complexed with Pi in soil (Bar-Yosef 1991; Jones and Darrah 1994; Lan et al. 1995; Jones 1998). Organic anions may also promote the growth of rhizosphere microorganisms that improve plant P acquisition. The importance of

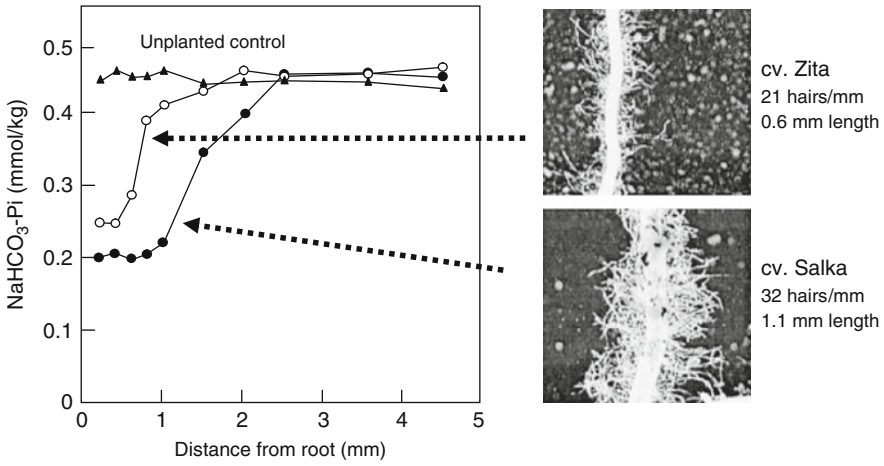


Fig. 10.1 Depletion of $NaHCO_3$-extractable inorganic P (mmol P/kg soil) from the rhizosphere of two barley cultivars (*Hordeum vulgare* cvs Zita and Salka) with different root hair morphologies. The cultivars are compared to an unplanted control soil (from Gahoonia and Nielsen 1997)

organic anions in increasing the availability of organic P, and its subsequent mineralisation by phosphatases, has also been identified recently (Jones 1998; Otani and Ae 1999; Hayes et al. 2000a; Hens et al. 2003; Li et al. 2003).

It is evident that exudation of organic anions from plant roots is facilitated by transport proteins (Neumann et al. 1999; Ryan et al. 2001). At concentrations commonly found in the rhizosphere (10–100 μM; Jones 1998) citrate and oxalate have a greater potential for P mobilisation than other organic anions. In fact, high rates of citrate exudation from cluster roots of white lupins are associated with a large capacity for P mobilisation in soil by this species (Vance et al. 2003; Richardson et al. 2007). Other plant species vary in the nature and amounts of organic anions they exude from roots (Veneklaas et al. 2003; Wouterlood et al. 2004; Pearse et al. 2006). But, generally increased organic anion efflux from roots stimulated by P-deficient conditions (Hedley et al. 1982; Lipton et al. 1987; Hoffland et al. 1989; Kirk et al. 1999), is a common phenomenon.

The heterologous expression of genes for enzymes involved in organic anion synthesis in roots has been investigated as a means to increase exudation of organic anions from roots. Overexpression of a bacterial gene encoding citrate synthase (CS) in tobacco (*Nicotiana tabacum*) has been reported to increase citrate efflux from roots of transgenic lines compared to control plants (de la Fuente-Martínez et al. 1997). However, using similar gene constructs and in some cases the same transgenic lines, Delhaize et al. (2001) could not confirm these results. Moreover, tobacco plants that overexpressed a tobacco CS, or were downregulated for iso-citrate dehydrogenase expression, showed no significant increase in citrate efflux even though in some cases the plants had greater internal citrate concentration (Delhaize et al. 2003). Notwithstanding this, it is apparent that there is potential to enhance organic acid exudation by targeting the citrate synthesis biosynthetic pathway. Overexpression of a plant gene for mitochondrial CS in *Arabidopsis thaliana* enhanced citrate efflux, with an associated small improvement in P acquisition (Koyama et al. 2000).

Genes that encode channels involved in the transport of organic anions may be another target for a gene technology approach to improving tolerance to P deficit. Citrate-permeable channels in the plasma membrane of cluster roots of white lupin have been identified (Zhang et al. 2004), and a gene encoding a malate channel has been cloned from wheat (Sasaki et al. 2004). When expressed in transgenic barley (GP-ALMT1), this gene (*TaALMT1*) resulted in increased exudation of malate, albeit in an Al-activated manner (Delhaize et al. 2004), and has been demonstrated to be beneficial to the P nutrition of plants when grown in acidic soils (Fig. 10.2) (Delhaize et al. 2009).

10.2.4 Release of Extracellular Phosphatase

A number of studies have demonstrated significant rates of organic P mineralisation in proportion to soil phosphatase activity (Trasar-Cepeda and Carballas 1991;

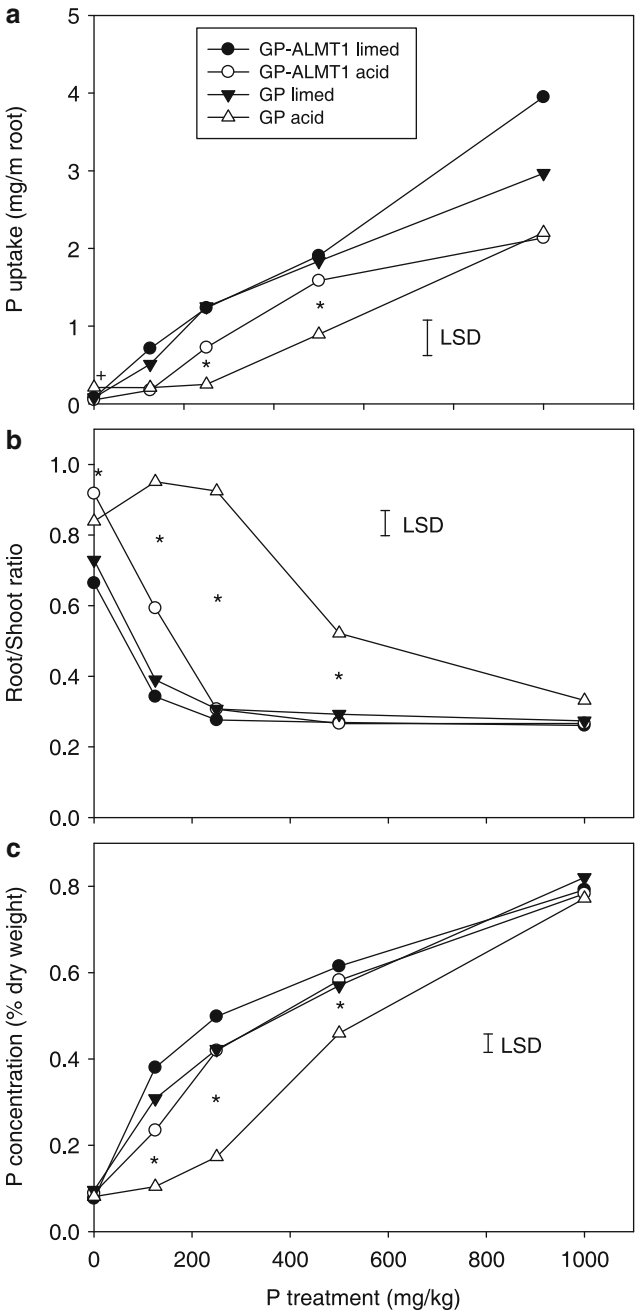


Fig. 10.2 Expression of the wheat aluminium resistance gene (*TaALMT1*) in transgenic barley enhances phosphorus uptake per unit root and reduces the root/shoot ratios of plants grown on an acid soil with a range of phosphorus supplies. Effect of phosphorus supply on phosphorus uptake

Lopez-Hernandez et al. 1998; Oehl et al. 2001; George et al. 2002). In natural ecosystems, mineralisation of soil organic P is thought to provide the major proportion of P to plants (Fox and Comerford 1992; Polglase et al. 1992). Similarly, in organic-based farming systems, and where green-manure crops are used for fertilisation, high rates of organic P cycling have been observed (Oberson et al. 1996, 2001; Nziguheba et al. 1998; Maroko et al. 1999; Oehl et al. 2004).

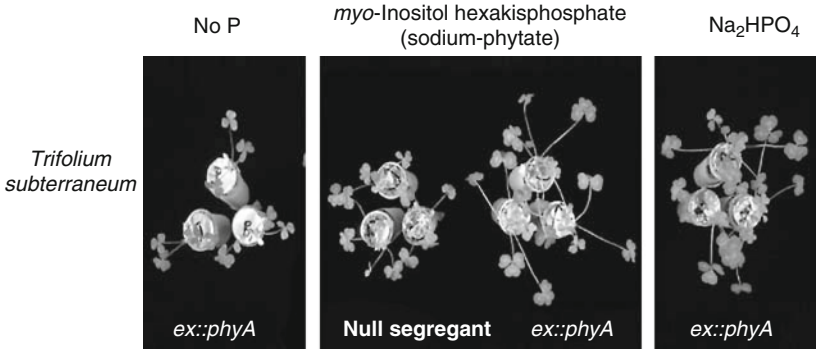
The hydrolysis of organic P is mediated by the action of phosphatase enzymes in the extracellular environment, a process that is necessary for the subsequent uptake of Pi by plant roots (see Nannipieri et al. 2011). At present there is no evidence for direct uptake of dissolved organic P compounds by plants, although organic P substrates may be hydrolysed within the root apoplast (Duff et al. 1994; George et al. 2008). Extracellular phosphatase activity of plant roots is induced under conditions of P deficiency and is associated with either root cell walls (McLachlan 1980; Dracup et al. 1984; Barrett-Lennard et al. 1993; Hayes et al. 1999; Hunter and McManus 1999) or is released directly into the rhizosphere (Tarafdar and Claassen 1988; Tadano et al. 1993; Li et al. 1997; Gaume et al. 2001). The cloning of genes encoding extracellular phosphatases from *A. thaliana* (Haran et al. 2000) and *L. albus* has provided direct evidence for extracellular secretion and regulation of phosphatase expression in response to P deficiency (Wasaki et al. 2000; Miller et al. 2001).

Extracellular secretion of phosphatases from roots is correlated with the ability of plants to obtain P from organic P sources when grown under sterile conditions (Tarafdar and Claassen 1988; Hayes et al. 2000b; Richardson et al. 2000; George et al. 2008). For example, wheat and a range of pasture species are able to utilise P from various monoester (e.g. glucose-6-phosphate) and diester (e.g. ribonucleic acid) forms, but show limited capacity to acquire P directly from *myo*-inositol hexakisphosphate (Richardson et al. 2000; George et al. 2008), despite inositol phosphates being an abundant form of organic P in many soils. It is likely that the biological importance of the different forms of organic P will be dictated by their turnover rates. Direct hydrolysis of organic P and subsequent utilisation of the mineralised Pi by roots has also been demonstrated in soil-grown plants. Depletion of various pools of extractable organic P from the rhizosphere has been linked with greater phosphatase activities around plant roots (Chen et al. 2002; George et al.

Fig. 10.2 (continued) by roots (**a**), root/shoot ratios (**b**), and shoot phosphorus concentrations (**c**) of transgenic barley (*GP*, *triangles*) and transgenic barley expressing *TaALMT1* (*GP-ALMT1*, *circles*) grown on an unamended acid ferrosol (*open symbols*) or on the same soil that had been limed (*closed symbols*). Phosphorus uptake per unit root was calculated from total shoot phosphorus only, because the phosphorus contents of roots could not be accurately determined because of adhering soil. Plants were harvested 26 days after sowing and the data for each show the treatment means ($n = 4$) and least-significant difference (*LSD*) ($P = 0.05$; untransformed data). *Asterisks* indicate where the means of the genotypes grown on the acid soil with a particular phosphorus treatment differed by more than the LSD (untransformed data), and *crosses* indicate where additional differences between genotypes were apparent using log10-transformed data (from Delhaize et al. 2009)

2002, 2006). However, the relative contribution of extracellular phosphatases derived from roots and from microorganisms in the utilisation of soil organic P is unclear because the numbers and activity of bacteria and fungi are greater within the rhizosphere than in the bulk soil (Chen et al. 2002; Richardson et al. 2005). In addition, there is some evidence that phosphatases derived from soil fungi have a greater affinity for organic P compounds compared to phosphatases derived from plant roots (Tarafdar et al. 2001). Either way, it is evident that the mineralisation of organic P occurs in the rhizosphere and could make an important contribution to the orthophosphate requirement of plants for growth.

Research efforts have been focussed on improving the ability of plants to acquire P directly from common forms of soil organic P, such as inositol phosphates. A number of studies have developed transgenic plants with heterologous expression of microbial phytases (Richardson et al. 2001; Zimmermann et al. 2003; Lung et al. 2005; Xiao et al. 2005). Transgenic plants that produce microbial phytase and release it from their roots have novel ability to hydrolyse P from *myo*-inositol hexakisphosphate and, when grown under controlled conditions, showed enhanced growth and P nutrition (Fig. 10.3) (Richardson et al. 2001; Mudge et al. 2003;



Shoot dry weight (mg/plant)	28.1	40.7	51.8	47.9
Shoot phosphorus (μg P/shoot)	48.3	103.5	299.0	305.3
Exuded root phytase activity[a] (nKat/g root dry wt)	–	1.3	107.9	–

[a]Activity for wild-type plants was 0.6 nKat/g root dry weight.

Fig. 10.3 Growth, phosphorus nutrition and activity of phytase exuded from the roots of transgenic *Trifolium subterraneum*. The images show plants that release the *Aspergillus niger* phytase (ex::phyA) as an extracellular enzyme and the corresponding null-segregant transgenic control line. Plants were grown for 28 days in sterile agar either without added phosphorus (no P) or with phosphorus supplied as sodium phytate (*myo*-inositol hexakisphosphate) or disodium phosphate (Na_2HPO_4) at 0.9 mM (with respect to phosphate) (taken from George et al. 2004)

Zimmermann et al. 2003; George et al. 2004). However, when grown in a range of soils, these plants have generally shown limited capacity to access additional P over that of control plants (George et al. 2004, 2005b). These results highlight the complexity inherent in attempting to improve multimechanistic tolerance traits by a single gene approach. Whilst potential exists for manipulating P-use efficiency at a genetic scale, success will often be limited by poor understanding of the control of the mechanisms imposed by different soil environments.

10.3 Coordinating Plant Responses to Variations in P Supply

In P-replete plants, small metabolites, nucleic acids and phospholipids contribute approximately equally to leaf P content (Marschner 1995; Dörmann and Benning 2002; White and Hammond 2008). When plants lack sufficient P, they restrict their use of P to essential cellular functions and improve the ability of their root systems to acquire P from the soil.

Many of the responses of plants to P starvation appear to be initiated, or modulated, by a decrease in the delivery of Pi to the shoot and the consequent reduction in the Pi available for shoot metabolism (Fig. 10.4, response 1). This has a direct effect on photosynthesis, glycolysis and respiration, which is reinforced by transcriptional reprogramming (Plaxton and Carswell 1999; Hammond et al. 2003,

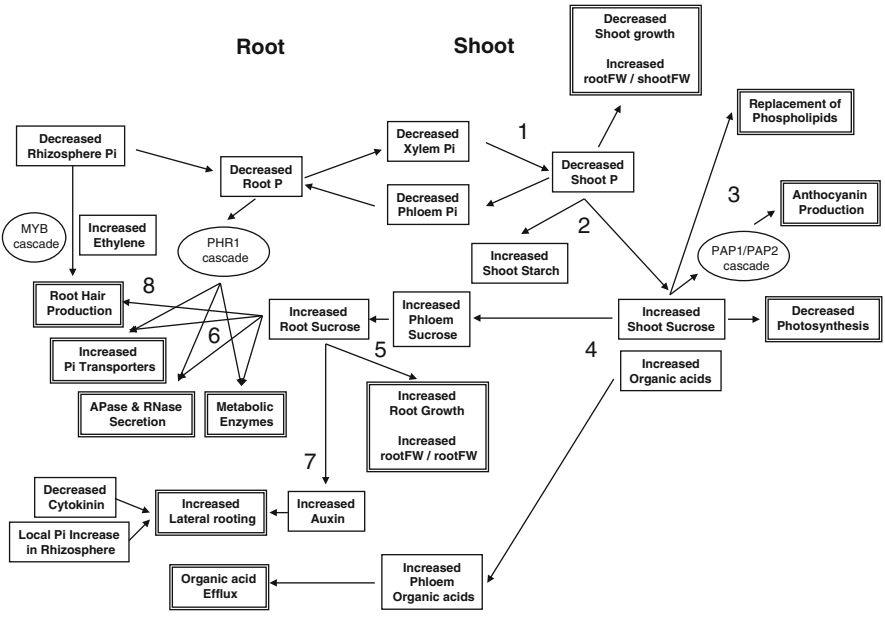


Fig. 10.4 Regulatory networks coordinating plant responses to variations in P supply. *Numbers* indicate different plant responses and are explained in the text (from White and Hammond 2008)

2005; Misson et al. 2005; Hermans et al. 2006; Wasaki et al. 2006; Morcuende et al. 2007; White and Hammond 2008). The changes in carbohydrate metabolism result in the accumulation of organic acids, starch and sucrose in leaves of P-starved plants (Fig. 10.4, response 2) (Hermans et al. 2006; Morcuende et al. 2007). Metabolism is rerouted by employing reactions that do not require Pi or adenylates and, under severe P starvation, intracellular phosphatases and nucleases are produced to remobilize P from cellular metabolites and nucleic acids (Plaxton and Carswell 1999; Hammond et al. 2003; Wasaki et al. 2006; Morcuende et al. 2007; Müller et al. 2007).

Increased leaf sucrose concentrations lead indirectly to (1) a reduction in photosynthesis through decreased expression of genes encoding many photosystem subunits and small subunits of RuBisCo (Lloyd and Zakhleniuk 2004; Amtmann et al. 2006; Hermans et al. 2006; Rook et al. 2006; Morcuende et al. 2007), (2) an increase in leaf sulfolipid and galactolipid concentrations through the upregulation of genes involved in their biosynthesis (Dörmann and Benning 2002; Hammond et al. 2003; Benning and Ohta 2005; Misson et al. 2005; Franco-Zorrilla et al. 2005; Gaude et al. 2008), and (3) the production of anthocyanins through a transcriptional cascade involving the transcription factors TTG1-TT8/EGL3-PAP1/PAP2 (Fig. 10.4, response 3) (Lloyd and Zakhleniuk 2004; Teng et al. 2005; Amtmann et al. 2006; Solfanelli et al. 2006). An increased leaf sucrose concentration also results in the upregulation of genes encoding transport proteins delivering organic acids and sucrose to the phloem, which facilitates the movement of these compounds to the root (Fig. 10.4, response 4) (Hermans et al. 2006). Details of the genes and transcription factors identified in genomics studies can be found in a range of databases that are exemplified by the Database of *Arabidopsis* Transcription Factors (Guo et al. 2005).

One consequence of the increased delivery of organic acids and sucrose to plant roots is an increase in the root/shoot biomass ratio (Fig. 10.4, response 5) (Hermans et al. 2006; Hammond and White 2008). In addition, the sucrose delivered to the root acts as a systemic signal to initiate changes in gene expression that alter root biochemistry and the morphology of the root system (Franco-Zorrilla et al. 2005; Liu et al. 2005; Amtmann et al. 2006; Hermans et al. 2006; Karthikeyan et al. 2007; Tesfaye et al. 2007; Hammond and White 2008). Increased root sucrose concentrations appear to upregulate genes encoding riboregulators, Pi transporters, RNases, phosphatases and metabolic enzymes in combination with the PHR1 transcriptional cascade (Fig. 10.4, response 6), whereas its effects on lateral rooting occur through modulation of auxin transport (Fig. 10.4, response 7) (Jain et al. 2007a; Pérez-Torres et al. 2008) and those on root hair development are contingent upon changes in auxin transport and the local production of ethylene (Fig. 10.4, response 8) (Jain et al. 2007a).

The PHR1 protein is a MYB transcription factor that binds to an imperfect-palindromic sequence (P1BS; GNATATNC) that is present in the promoter regions of many genes whose expression responds to P starvation. These include genes encoding transcription factors, protein kinases, Pi transporters, RNases, phosphatases, metabolic enzymes and enzymes involved in the synthesis of sulfolipids and

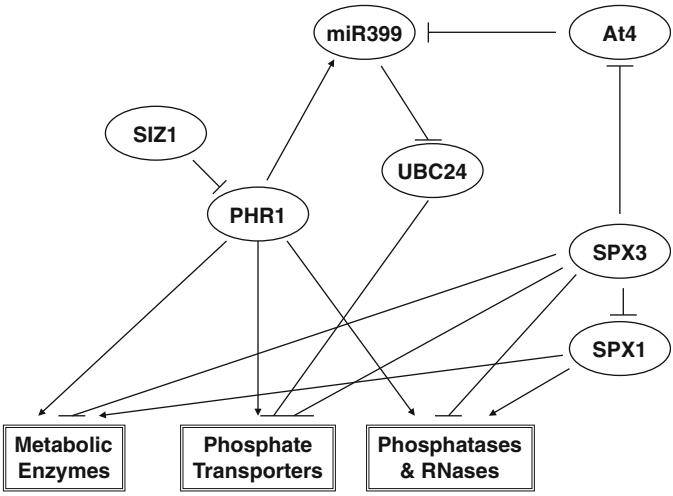


Fig. 10.5 Gene Regulatory networks impacting on PHR1-mediated acclimatory responses to P starvation. *Arrows* indicate positive regulation. *Blunt-ended lines* indicate negative regulation

galactolipids (Fig. 10.5) (Rubio et al. 2001; Hammond et al. 2004; Franco-Zorrilla et al. 2004; Misson et al. 2005; Jain et al. 2007b; Fang et al. 2009; Lin et al. 2009). The expression of *PHR1* appears to be constitutive, but the PHR1 protein is targeted by a small ubiquitin-like modifier (SUMO) E3 ligase (SIZ1), whose expression is increased by P starvation (Miura et al. 2005). The activity of SIZ1 acts as a negative regulator of plant responses to P starvation (Miura et al. 2005). The PHR1-mediated increase in Pi transport is contingent upon the activity of PHF1, an ER protein that facilitates the trafficking of PHT1-family Pi transporters, whose expression is upregulated upon P starvation (González et al. 2005). Amongst the targets of the PHR1 protein are members of the miR399 microRNA family and the SPX gene family (Bari et al. 2006; Franco-Zorrilla et al. 2007; Nilsson et al. 2007; Lin et al. 2009). The expression of *miR399s* is specifically and rapidly upregulated by P starvation (Chiou 2007). The target for miR399s is *AtUBC24*, which is downregulated during P starvation. This gene encodes the ubiquitin E2 conjugating enzyme responsible for the *pho2* mutant phenotype, which is thought to downregulate the transcription of a subset of P-starvation-responsive genes through intermediary transcription factors (Chiou 2007; Fang et al. 2009). Expression of *AtUBC24* in roots appears to be regulated systemically by shoot P status and the translocation of *miR399s* in the phloem (Buhtz et al. 2008; Lin et al. 2008; Pant et al. 2008). The rate of their translocation in the phloem is likely to be influenced indirectly by sucrose loading and unloading in the shoot and root, respectively. Members of the *TPSI1*/*Mt4*/*At4* family of non-coding transcripts, whose expression is rapidly and specifically induced in response to P starvation, appear to bind and sequester miR399s thereby attenuating miR399-mediated transcriptional responses to P starvation (Franco-Zorrilla et al. 2007). In *Arabidopsis*, the expression of *AtSPX1* and *AtSPX3* are greatly increased by P starvation (Duan et al. 2008). Increased expression of

AtSPX1 upregulates transcription of several genes, including *PAP2*, *RNS1* and *ACP5* (Duan et al. 2008). Increased expression of AtSPX3 occurs upon prolonged P starvation and appears to act in feedback regulation of plant responses to P starvation by downregulating the expression of *AtSPX1*, *At4* and genes encoding several Pi transporters, RNases and phosphatases (Duan et al. 2008).

Crosstalk between local and systemic signals (including auxin, ethylene, cytokinin and sucrose) controls the remodelling of root system morphology in response to P starvation (White et al. 2005; Amtmann et al. 2006; Jain et al. 2007a; Karthikeyan et al. 2007; Hammond and White 2008; White and Hammond 2008; Fang et al. 2009). The growth rate of primary roots is reduced in P-starved plants by a reduction of meristem activity, which is initiated directly by contact of the root cap with media lacking Pi and requires the activity of multicopper oxidases (Ticconi et al. 2004; Sánchez-Calderón et al. 2006; Svistoonoff et al. 2007; Jain et al. 2007a; Fang et al. 2009). The proliferation of lateral roots of P-starved plants in regions of increased Pi availability is also contingent upon growth of the primary root apex through these regions (Drew 1975), but appears to be initiated by changes in auxin transport and perception (Nacry et al. 2005; Sánchez-Calderón et al. 2006; Jain et al. 2007a; Hammond and White 2008; Pérez-Torres et al. 2008), with greater sucrose availability increasing the responsiveness to auxin (Nacry et al. 2005; Jain et al. 2007a). Specifically, the *TIR1* gene, which encodes the auxin receptor component of the ubiquitin protein ligase complex SCFTIR1, is upregulated by P starvation (Pérez-Torres et al. 2008). The upregulation of *TIR1* results in the degradation of AUX/IAA auxin response repressors, allowing the expression of ARF transcription factors, such as *ARF19*, to modulate the expression of genes that enable the initiation and emergence of lateral roots without increasing root auxin concentrations (Pérez-Torres et al. 2008). The initiation of lateral roots is also promoted by reduced cytokinin concentrations in roots of P-deficient plants, which appears to be a secondary consequence of the crosstalk between sugar and local P-signalling cascades (Franco-Zorrilla et al. 2005). This phenomenon is comparable to the proliferation of specialised cluster roots in regions of local Pi enrichment observed in diverse non-mycorrhizal plant species when they lack sufficient P (Lamont 2003; Lambers et al. 2006; Vance 2008). The initiation and elongation of root hairs are stimulated by locally elevated concentrations of auxin and ethylene, and both are stimulated when more sucrose is available to the roots (Jain et al. 2007a; Hammond and White 2008). Finally, the topsoil-foraging phenotype of P-deficient plants appears to be modulated primarily by the sensitivity of root gravitropism to ethylene, which increases with P starvation (Basu et al. 2007).

10.4 Response of Plants to P Re-supply

A root growing in soil is likely to find sites with a high concentration of potentially available P and sites with almost no P (Hodge 2009), though how the plant senses and reacts to this is yet unknown. There will be microsites with active microflora

and/or microflora where competition for nutrients is great. An individual root will then experience local P competition, P-limiting and P-sufficient conditions at different times.

As highlighted above, the physiological state of a P-deficient plant is quite specific and the response is multigenic in nature with, for example, over 1,000 genes being differentially regulated under these conditions in *Arabidopsis* (Wu et al. 2003; Hammond et al. 2003; Morcuende et al. 2007). Under conditions of P starvation, plants have increased root/shoot biomass ratio (Lynch 1995), alteration of root architecture (Williamson et al. 2001; López-Bucio et al. 2000), many more lateral roots and long root hairs (Bates and Lynch 1996). Also high-affinity P transporters are more abundant (Mudge et al. 2002; Smith et al. 2003) and organic acids and phosphatases are synthesized and secreted (Raghothama 1999; del Pozo et al. 1999; Li et al. 2002). There are fewer P-containing metabolites (Zrenner et al. 2006), phospholipids are replaced in part by sulfolipids and galactolipids (Dörmann and Benning 2002; Kelly et al. 2003), and cells have a reduced level of RNA (Hewitt et al. 2005). Vacuolar Pi has been remobilised, carbohydrates such as starch and sugars have been accumulated and anthocyanin has been produced. In addition, some plants may have begun processes of senescence or flowering (Morcuende et al. 2007).

The hypothetical transcriptional response of plants to P re-supply or upon discovery of a P resource in a heterogeneous environment would be to reverse many of these changes and we consider that this response will take several forms:

1. Initially, there is an immediate non-specific response to perturbation of the system, which is likely to be rapid and transient and shows typical characteristics of other perturbation responses, involving increased expression of genes that are likely to protect plants against abiotic and biotic stresses (AbuQamar et al. 2009). It has previously been suggested that these may be cell-autonomous and related to changes in cell membrane potential, initiating cytosolic Ca^{2+} signalling cascades (Hammond et al. 2003; Amtmann et al. 2006). There is considerable crosstalk between abiotic and biotic signalling pathways, and these are often integrated in the cytosolic Ca^{2+} signature.
2. Sensing of altered P availability and initiation of regulatory cascades, which will not necessarily be a reversal of those cascades initiated upon P starvation. These responses are also rapid, occurring within 30 min of P re-supply (Amtmann et al. 2006). Although many of these responses are regulated systemically by sucrose concentration in P-deficient plants, upon re-supply of P the necessary gene cascades change regulation far in advance of any changes in sucrose content, suggesting other signalling pathways (Amtmann et al. 2006).
3. Reversal of tissue P economy. Morcuende et al. (2007) demonstrated that upon P re-supply there is rapid (<3 h) upregulation of nucleic acid synthesis to promote growth and re-optimise metabolic pathways for energy production and reversal of sulfolipid and galactolipid synthesis, to allow sulfur to become available for protein synthesis.

4. Reducing energetic investment in costly P-tolerance mechanisms. Morcuende et al. (2007) demonstrated that expression of genes regulating root growth, organic acid and phosphatases synthesis and efflux are also rapidly downregulated upon P re-supply.
5. Upregulation of mechanisms to prevent Pi toxicity such as sequestration and complexation, due to the persistence of Pi-transport proteins.

Results from our own c-DNA microarray experiments, in which *A. thaliana* was grown in P-deficient conditions then re-supplied with P, generally support these hypotheses of the response of P-starved plants to P re-supply. There was a distinct time-dependent response in the roots (Table 10.1) but this time dependence was not obvious in the leaves (data not shown). Most transcripts reacted after 3 h. Some transcripts increased initially and decreased within 24 h. In the first 45 min of P re-supply, the largest proportion of genes differentially regulated are associated with initiating cell production and include genes associated with cell function (3.5%), DNA synthesis (5.2%), protein degradation and synthesis (8.4%), RNA processing and regulation (2.7%) and amino acid metabolism (1.3%). After 3 h of re-supply of P, many of the same genes are still differentially regulated but a number of other processes have started to occur, notably cascades involved in cell wall development and lipid metabolism (3.1%), signalling cascades (8.8%) and sulfur assimilation (4.8%), most likely promoting protein synthesis. Beyond this, and between 0.5 and 2 days after re-supplying P, while the RNA processing, protein metabolism and cell division pathways are still differentially regulated, the DNA synthesis genes have equilibrated and differential regulation of signalling cascades has moderated. Interestingly, it is only at this stage that abiotic stress genes are differentially regulated, much later than anticipated in the hypotheses. It is also at this stage that we see genes involved in carbohydrate metabolism and transporters differentially regulated.

So, from this single study it is apparent that the earliest responses of plants to P re-supply is to upregulate cellular molecular machinery, which is quickly followed by cell division and lipid and protein biosynthesis. It is only later that the plant shows a generic stress response and upregulation of specific signalling cascades and P transport. The key result from this and other studies is that the vast majority (~35%) of differentially regulated genes at all time points are of unknown origin, which means that there are a lot of response mechanisms and regulatory cascades associated with P re-supply that are yet to be understood.

10.5 Can P Starvation and Re-supply Responses Be Genetically Manipulated for Agricultural Benefit?

Increased pressure on P fertiliser usage and costs due to the depletion of non-renewable natural resources (Heffer et al. 2006; Cordell et al. 2009; Gilbert 2009), their potential negative impacts on local environments and water quality (White and

Table 10.1 Differential regulation of genes in root and shoot tissue upon re-supply of P to roots in comparison to a salt-stress control

Cell process		Number of genes	Percentage of genes differentially regulated				Cell process		Number of genes	Percentage of genes differentially regulated			
			0.75 h	3 h	12 h	48 h				0.75 h	3 h	12 h	48 h
Cell	Cell	162	3.5	2.8	2.8	–	Nucleotide metabolism	Synthesis	12	–	0.2	–	–
	Division	24	0.5	–	–	–		Degradation	10	–	0.2	–	–
	Cycle	32	0.7	0.1		–	RNA	RNA	603	–	–	11.8	–
	Vesicle transport	34	–	0.7	0.6	–		Processing	51	1.1	–	–	–
	Late embryogenesis	5	0.1	–	–	–		Transcription	27	–	–	0.5	–
Cell wall	Cell wall	73	–	1.4	1.4	–		Regulation of transcription	477	1.6	0.9	9.3	0.9
	Precursor synthesis	2	–	–	–	–	DNA	DNA	150	3.0	2.9	–	–
	Cell wall proteins	14	–	0.1	0.3	–		Synthesis/ chromatin structure	103	2.2	2.0	0.1	–
	Degradation	15	–	–	–	0.4		Unspecified	23	–	–	–	0.6
	Modification	13	–	0.2	–	0.4	Protein	Synthesis	129	1.6	2.5	2.3	2.5
Glycolysis	Glycolysis	–	–	–	0.3	–		Postranslational modification	163	0.2	2.9	3.2	3.4
	Mitochondrial e-transport/ATP synthesis	39	–	0.6	0.8	0.7		Degradation	367	6.8	7.0	6.7	0.2
Lipid	Lipid metabolism	–	–	1.7	–	–		Protein folding	21	–	–	0.4	–
	Exotics	18	–	0.3	–	–	Amino acid	Amino acid metabolism	69	1.3	1.3	1.2	–
	Phospholipase D	4	–	–	0.1	–		Synthesis	44	–	0.2	0.9	0.9
Carbohydrate (CHO) metabolism	Raffinose family	4	–	0.1	–	4.7		Degradation	28	0.5	0.5	–	0.4
	Trehalose	7	0.2	0.1	–	0.3	Hormones	Hormone metabolism	118	0.1	2.2	0.4	0.1
	Myo-inositol	2	–	–	–	–	Signalling	Signalling	248	–	4.7	–	–
	CHO metabolism	24	–	0.5	–	–		Receptor kinases	92	0.2	1.8	0.3	0.7
	Synthesis	10	–	0.2	–	–		Calcium	40	0.9	–	–	–

(*continued*)

Table 10.1 (continued)

Cell process		Number of genes	Percentage of genes differentially regulated				Cell process		Number of genes	Percentage of genes differentially regulated			
			0.75 h	3 h	12 h	48 h				0.75 h	3 h	12 h	48 h
Stress	Stress	–	–	–	3.1	–		Phosphoinositides	4	0.1	–	–	–
	PR-proteins	4	–	–	–	0.1		Miscellaneous	3	–	0.1	–	–
	Abiotic	98	–	–	1.9	–	Transport	Transport	191	0.2	0.9	3.7	4.0
	Heat	61	1.0	1.1	1.2	1.2	Nitrogen	Metabolism	5	–	–	0.1	–
	Cold	6	0.1	0.1	–	–	Sulfur	Assimilation	252	0.1	4.8	0.1	0.1
	Unspecified	22	0.4	0.4	0.3	0.4	Miscellaneous	Miscellaneous	252	5.4	0.7	1.1	1.2
Redox	Redox regulation	42	0.2	0.6	0.8	0.8	Not Assigned		1,833	33.9	33.9	35.8	35.0
Polyamine	Metabolism	3	–	–	0.1	–							

The plants were grown in a P-poor soil for 8 weeks and after that P was added to increase the P availability fourfold. At the same time, other plants were also treated with a salt stress to remove any general abiotic stress responses. Phosphorus addition resulted in an extractable P concentration increased by 20 times in the soils. Roots and above ground tissue were sampled initially, after 45 min, 3, 12, and 48 h. c-DNA microarray experiments were carried out to assess the percentage of genes differentially regulated. Missing values indicate non-detectable changes

Hammond 2008), and the energy required and carbon dioxide evolved in their production and use (Helsel 1992; Jenssen and Kongshaug 2003), have increased the need to manage P fertiliser input more carefully. Over 85% of P mined is used in food production (Heffer et al. 2006) and peak P production (akin to peak oil) is estimated to occur by 2033 (Raven 2008; Cordell et al. 2009). These pressures will be exacerbated by increasing demand on food production systems as the human population increases, and by fluctuation in oil prices (Cordell et al. 2009). The breeding of new crop varieties that yield well with reduced P fertiliser inputs is now a priority for sustainable agriculture in the future.

Breeding crops that acquire and/or use P more efficiently is one strategy to reduce the use of P fertilisers. Such crops could produce comparable yields with lower inputs of inorganic Pi fertilisers or have reduced physiological P requirements and tissue P concentrations, thus reducing the amount of P removed by the crop and, thereby, the amount of P needed to maintain the availability of Pi in the soil. New varieties can be bred conventionally, based on trait-focused screens of germplasm collections. However, a great deal of information is now available about how plants regulate P homeostasis and acquisition from the soil, particularly at the genetic level (Franco-Zorrilla et al. 2004; Jain et al. 2007b; Hammond and White 2008; White and Hammond 2008: Fang et al. 2009; Lin et al. 2009). Mutants with allelic variation and/or altered expression of genes affecting P acquisition or P use within the plant have been generated. Several of these mutants illustrate strategies for developing crop plants that acquire and/or use P more efficiently.

Mutations that improve P acquisition from the soil could improve crop growth when P availability in the soil is poor. Transgenic plants that secrete microbial phytases into the rhizosphere have the potential to release P from inositol phosphates and show enhanced growth and P nutrition when inositol hexaphosphate is the major source of P (Richardson et al. 2001; Mudge et al. 2003; Zimmermann et al. 2003; George et al. 2004, 2005a). However, when grown in most soils, these plants have comparable growth and P nutrition to control plants (George et al. 2004, 2005b). Similarly, overexpression of a bacterial gene encoding citrate synthase in tobacco has been reported to increase citrate efflux from roots and to increase the availability of P from Ca-P (de la Fuente-Martínez et al. 1997; López-Bucio et al. 2000), but an effect on plant growth and P acquisition is not always observed (Delhaize et al. 2001). The expression of a wheat malate transporter gene (*ALMT1*) in barley has been shown to be effective in increasing P uptake by transgenic plants, but only in severely acidic soil conditions (Delhaize et al. 2009). Increased expression of specific phosphate transporters has been shown to increase biomass accumulation in tobacco cell cultures under P-limiting conditions (Mitsukawa et al. 1997), but did not enhance P uptake rates or growth of transgenic barley in soil (Rae et al. 2004).

Mutations altering root morphology also have the potential to enable plants to acquire more P. For example, barley genotypes with long root hairs have higher yields than genotypes with no root hairs on soils with low P availability (Brown et al. 2010), and genotypes of bean, maize and brassica with larger root systems have better growth under P-limiting conditions (Rubio et al. 2003; Liu et al. 2004; Hammond et al. 2009). The overexpression of miR399, or the downregulation of

UBC24 (*pho2*) expression, results in greater accumulation of P (Delhaize and Randall 1995; Aung et al. 2006; Bari et al. 2006; Chiou et al. 2006). A T-DNA insertional knockout of AtSIZ1 caused *Arabidopsis* to exhibit exaggerated Pi starvation responses, including cessation of primary root growth, extensive lateral root and root hair development, increase in root/shoot biomass quotient, and greater anthocyanin accumulation, even though intracellular Pi levels in *siz1* plants were similar to those in the wild type. All three mutants exhibit constitutive P-deficiency symptoms, including increased P uptake, which might be beneficial in some agricultural systems.

Mutations that improve crop growth when soil P availability is low, through better physiological utilisation of P, may also be useful in breeding crops for reduced P inputs. For example, OsPTF1, a bHLH transcription factor from rice, whose expression increases in the roots of P-starved plants, has been shown to enhance tolerance to P starvation (Yi et al. 2005). Also, transgenic tobacco cells that lack an alternative oxidase had improved growth under P-limiting conditions (Parsons et al. 1999).

10.6 Concluding Remarks

Management of soil P remains a crucial issue for the economic and environmental sustainability of agriculture and natural ecosystems globally. It is therefore essential that we have appropriate understanding of the mechanisms by which plants are able to acquire P from soil. In this chapter, various processes and physiological traits of plants that facilitate the availability and acquisition of P from soil have been outlined and some possibilities for deploying these traits into agricultural germplasm discussed. Better understanding of these processes and development of improved germplasm may ultimately improve the P-use efficiency of agriculture systems and provide valuable information for wider-scale land and resource management. However, at present it is evident that the full extent of the complexity of the gene-by-gene, and gene-by-environment interactions that are associated with plant P nutrition are not well appreciated, and that our comprehension of the functional redundancy and compatibility of different mechanisms both within individual plants and between coexisting organisms is poor. It is therefore important that a systems approach to P management continues to be developed for a more sustainable agriculture.

References

AbuQamar S, Luo HL, Laluk K, Mickelbart MV, Mengiste T (2009) Crosstalk between biotic and abiotic stress responses in tomato is mediated by the *AIM1* transcription factor. Plant J 58:347–360

Amtmann A, Hammond JP, Armengaud P, White PJ (2006) Nutrient sensing and signalling in plants: potassium and phosphorus. Adv Bot Res 43:209–257

Attiwill PM, Adams MA (1993) Nutrient cycling in forests. New Phytol 124:561–582

Aung K, Lin SI, Wu CC, Huang YT, Su CL, Chiou TJ (2006) *pho2*, a phosphate overaccumulator, is caused by a nonsense mutation in a microRNA399 target gene. Plant Physiol 141:1000–1011

Barber SA (1984) Soil nutrient bioavailability: a mechanistic approach. Wiley, New York

Bari R, Pant BD, Stitt M, Scheible WR (2006) PHO2, microrna399, and PHR1 define a phosphate-signaling pathway in plants. Plant Physiol 141:988–999

Barrett-Lennard EG, Dracup M, Greenway H (1993) Role of extracellular phosphatase in the phosphorus-nutrition of clover. J Exp Bot 44:1595–1600

Bar-Yosef B (1991) Root excretions and their environmental effects. Influence on availability of phosphorus. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots: the hidden half. Dekker, New York, pp 529–557

Basu P, Zhang YJ, Lynch JP, Brown KM (2007) Ethylene modulates genetic, positional, and nutritional regulation of root plagiogravitropism. Funct Plant Biol 34:41–51

Bates TR, Lynch JP (1996) Stimulation of root hair elongation in *Arabidopsis thaliana* by low phosphorus availability. Plant Cell Environ 19:529–538

Benning C, Ohta H (2005) Three enzyme systems for galactoglycerolipid biosynthesis are coordinately regulated in plants. J Biol Chem 280:2397–2400

Bieleski RL (1973) Phosphate pools, phosphate transport and phosphate availability. Annu Rev Plant Physiol 24:225–252

Boot GA, Mensink M (1990) Size and morphology of root systems of perennial grasses from contrasting habitats as affected by nitrogen supply. Plant Soil 129:291–299

Bradshaw AD, Chadwick MJ, Jowett D, Lodge RW, Snaydon RW (1960) Experimental investigations into the mineral nutrition of several grass species. III. Phosphate level. J Ecol 48:631–637

Brown LK, George TS, Thompson JA, Wright G, Lyon J, Hubbard SF, White PJ (2010) What are the implications of variation in root hair length on P-limited yield in barley (*Hordeum vulgare* L.)? Plant Cell Environ (in press)

Bucher M (2007) Functional biology of plant phosphate uptake at root and mycorrhiza interfaces. New Phytol 173:11–26

Buhtz A, Springer F, Chappell L, Baulcombe D, Kehr J (2008) Identification and characterization of small RNAs from the phloem of *Brassica napus*. Plant J 53:739–749

Chapin FS (1980) The mineral nutrition of wild plants. Annu Rev Ecol Syst 11:233–260

Chen CR, Condron LM, Davis MR, Sherlock RR (2002) Phosphorus dynamics in the rhizosphere of perennial ryegrass (*Lolium perenne* L.) and radiata pine (*Pinus radiata* D. Don). Soil Biol Biochem 34:487–499

Chiou TJ (2007) The role of microRNAs in sensing nutrient stress. Plant Cell Environ 30:323–332

Chiou TJ, Aung K, Lin SI, Wu CC, Chiang SF, Su CI (2006) Regulation of phosphate homeostasis by microRNA in *Arabidopsis*. Plant Cell 18:412–421

Christie EK (1975) Physiological responses of semiarid grasses. II. The pattern of root growth in relation to external phosphorus concentration. Aust J Agric Res 26:437–446

Christie EK, Moorby J (1975) Physiological responses of semiarid grasses. I. The influence of phosphorus supply on growth and phosphorus absorption. Aust J Agric Res 26:423–436

Condron LM, Frossard E, Tiessen H, Newman RH, Stewart JWB (1990) Chemical nature of organic phosphorus in cultivated and uncultivated soils under different environmental conditions. J Soil Sci 41:41–50

Cordell D, Drangert J-O, White S (2009) The story of phosphorus: global food security and food for thought. Glob Environ Change 19:292–305

de la Fuente-Martínez JM, Ramirez-Rodriguez V, Cabrera-Ponce JL, Herrera-Estrella L (1997) Aluminum tolerance in transgenic plants by alteration of citrate synthesis. Science 276: 1566–1588

del Pozo JC, Allona I, Rubio V, Leyva A, De la Pena A, Aragoncillo C, Paz-Ares J (1999) Type 5 acid phosphatase gene from *Arabidopsis thaliana* is induced by phosphate starvation and by some other types of phosphate mobilising/oxidative stress conditions. Plant J 19:579–589

Delhaize E, Randall PJ (1995) Characterisation of a phosphate-accumulator mutant of *Arabidopsis thaliana*. Plant Physiol 107:207–213

Delhaize E, Hebb DM, Ryan PR (2001) Expression of a *Pseudomonas aeruginosa* citrate synthase gene in tobacco is not associated with either enhanced citrate accumulation or efflux. Plant Physiol 125:2059–2067

Delhaize E, Ryan PR, Hocking PJ, Richardson AE (2003) Effects of altered citrate synthase and isocitrate dehydrogenase expression on internal citrate concentrations in tobacco (*Nicotiana tabacum* L.). Plant Soil 248:137–144

Delhaize E, Ryan PR, Hebb DM, Yamamoto Y, Sasaki T, Matsumoto H (2004) Engineering high level aluminum tolerance in barley with the ALMT1 gene. Proc Natl Acad Sci USA 101:15249–15254

Delhaize E, Gruber BD, Ryan PR (2007) The roles of organic anion permeases in aluminium resistance and mineral nutrition. FEBS Lett 581:2255–2262

Delhaize E, Taylor P, Hocking PJ, Simpson RJ, Ryan PR, Richardson AE (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 Biotechnol J 7:391–400

Dinkelaker B, Hengeler C, Marschner H (1995) Distribution and function of proteoid and other root clusters. Bot Acta 108:183–200

Dörmann P, Benning C (2002) Galactolipids rule in seed plants. Trends Plant Sci 7:112–118

Dracup MNH, Barrett-Lennard EG, Greenway H, Robson AD (1984) Effect of phosphorus deficiency on phosphatase activity of cell walls from roots of subterranean clover. J Exp Bot 35:466–480

Drew MC (1975) Comparison of the effects of a localized supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system, and the shoot, in barley. New Phytol 75:479–490

Duan K, Yi K, Dang L, Huang H, Wu W, Wu P (2008) Characterization of a sub-family of *Arabidopsis* genes with the SPX domain reveals their diverse functions in plant tolerance to phosphorus starvation. Plant J 54:965–975

Duff SMG, Sarath G, Plaxton WC (1994) The role of acid phosphatases in plant phosphorus metabolism. Physiol Plant 90:791–800

Fan M, Zhu J, Richards C, Brown KM, Lynch JP (2003) Physiological roles for aerenchyma in phosphorus-stressed roots. Funct Plant Biol 30:493–506

Fang Z, Shao C, Meng Y, Wua P, Chen M (2009) Phosphate signaling in *Arabidopsis* and *Oryza sativa*. Plant Sci 176:170–180

Fitter AH (1985) Functional significance of root morphology and root system architecture. In: Fitter AH, Atkinson D, Read DJ, Useher MB (eds) Ecological interactions in soil-plant, microbes and animals. Blackwell, London, pp 87–106

Föhse D, Claassen N, Jungk A (1991) Phosphorus efficiency of plants. II. Significance of root radius, root hairs and cation-anion balance for phosphorus influx in seven plant species. Plant Soil 132:261–272

Fox TR, Comerford NB (1992) Rhizosphere phosphatase activity and phosphatase hydrolyzable organic phosphorus in two forested spodosols. Soil Biol Biochem 24:579–583

Franco-Zorrilla JM, González E, Bustos R, Linhares F, Leyva A, Paz-Ares J (2004) The transcriptional control of plant responses to phosphate limitation. J Exp Bot 55:285–293

Franco-Zorrilla JM, Martín AC, Leyva A, Paz-Ares J (2005) Interaction between phosphate-starvation, sugar, and cytokinin signaling in *Arabidopsis* and the roles of cytokinin receptors CRE1/AHK4 and AHK3. Plant Physiol 138:847–857

Franco-Zorrilla JM, Valli A, Todesco M, Mateos I, Puga MI, Rubio-Somoza I, Leyva A, Weigel D, García JA, Paz-Ares J (2007) Target mimicry provides a new mechanism for regulation of microRNA activity. Nat Genet 39:1033–1037

Gahoonia TS, Nielsen NE (1997) Variation in root hairs of barley cultivars doubled soil phosphorus uptake. Euphytica 98:177–182

Gardner WK, Parbury DG, Barber DA (1981) Proteoid root morphology and function in *Lupinus albus*. Plant Soil 60:143–147

Gaude N, Nakamura Y, Scheible W, Ohta H, Dörmann P (2008) Phospholipase C5 (NPC5) is involved in galactolipid accumulation during phosphate limitation in leaves of *Arabidopsis*. Plant J 56:28–39

Gaume A, Machler F, Deleon C, Narro L, Frossard E (2001) Low-P tolerance by maize (*Zea mays* L.) genotypes: significance of root growth, and organic acids and acid phosphatase root exudation. Plant Soil 228:253–264

George TS, Richardson AE (2008) Potential and limitations to improving crops for enhanced phosphorus utilization. In: Hammond JP, White PJ (eds) The ecophysiology of plant–phosphorus interactions. Springer, Dordrecht, pp 247–270

George TS, Gregory PJ, Robinson JS, Buresh RJ (2002) Changes in phosphorus concentrations and pH in the rhizosphere of some agroforestry and crop species. Plant Soil 246:65–73

George TS, Richardson AE, Hadobas PA, Simpson RJ (2004) Characterisation of transgenic *Trifolium subterraneum* L. which expresses *phyA* and releases extracellular phytase: growth and P nutrition in laboratory media and soil. Plant Cell Environ 27:1351–1361

George TS, Simpson RJ, Hadobas PA, Richardson AE (2005a) Expression of a fungal phytase gene in *Nicotiana tabacum* improves phosphorus nutrition in plants grown in amended soil. Plant Biotechnol J 3:129–140

George TS, Richardson AE, Smith JB, Hadobas PA, Simpson RJ (2005b) Limitations to the potential of transgenic *Trifolium subterraneum* L. plants that exude phytase when grown in soils with a range of organic P content. Plant Soil 278:263–274

George TS, Turner BL, Gregory PJ, Richardson AE (2006) Depletion of organic phosphorus from oxisols in relation to phosphatase activities in the rhizosphere. Eur J Soil Sci 57:47–57

George TS, Gregory PJ, Hocking PJ, Richardson AE (2008) Variation in root-associated phosphatase activities in wheat contributes to the utilisation of organic P substrates in vitro, but does not effectively predict P-nutrition in different soils. Environ Exp Bot 64:239–249

Gilbert N (2009) The disappearing nutrient. Nature 461:716–718

González E, Solano R, Rubio V, Leyva A, Paz-Ares J (2005) PHOSPHATE TRANSPORTER TRAFFIC FACILITATOR1 is a plant-specific SEC12-related protein that enables the endoplasmic reticulum exit of a high-affinity phosphate transporter in *Arabidopsis*. Plant Cell 17: 3500–3512

Guo A, He K, Liu D, Bai S, Gu X, Wei L, Luo J (2005) DATF: a database of *Arabidopsis* transcription factors. Bioinformatics 21:2568–2569, http://datf.cbi.pku.edu.cn. Accessed 30 July 2010

Haling RE, Simpson RJ, Delhaize E, Hocking PJ, Richardson AE (2010) Effect of lime on root growth, morphology and the rhizosheath of cereals growing in an acid soil. Plant Soil 327:199–212

Hammond JP, White PJ (2008) Sucrose transport in the phloem: integrating root responses to phosphorus starvation. J Exp Bot 59:93–109

Hammond JP, Bennett MJ, Bowen HC, Broadley MR, Eastwood DC, May ST, Rahn C, Swarup R, Woolaway KE, White PJ (2003) Changes in gene expression in *Arabidopsis* shoots during phosphate starvation and the potential for developing smart plants. Plant Physiol 132:578–596

Hammond JP, Broadley MR, White PJ (2004) Genetic responses to phosphorus deficiency. Ann Bot 94:323–332

Hammond JP, Broadley MR, Craigon DJ, Higgins J, Emmerson Z, Townsend H, White PJ, May ST (2005) Using genomic DNA-based probe-selection to improve the sensitivity of high-density oligonucleotide arrays when applied to heterologous species. Plant Methods 1:10

Hammond JP, Broadley MR, White PJ, King GJ, Bowen HC, Hayden R, Meacham MC, Mead A, Overs T, Spracklen WP, Greenwood DJ (2009) Shoot yield drives phosphorus use efficiency in *Brassica oleracea* and correlates with root architectural traits. J Exp Bot 60:1953–1968

Haran S, Logendra S, Seskar M, Bratanova M, Raskin I (2000) Characterization of *Arabidopsis* acid phosphatase promoter and regulation of acid phosphatase expression. Plant Physiol 124:615–626

Hawkes GE, Powlson DS, Randall EW, Tate KR (1984) A ^{31}P nuclear magnetic resonance study of the phosphorus species in alkali extracts of soils from long-term field experiments. J Soil Sci 35:35–45

Hayes JE, Richardson AE, Simpson RJ (1999) Phytase and acid phosphatase activities in roots of temperate pasture grasses and legumes. Aust J Plant Physiol 26:801–809

Hayes JE, Richardson AE, Simpson RJ (2000a) Components of organic phosphorus in soil extracts that are hydrolysed by phytase and acid phosphatase. Biol Fertil Soils 32:279–286

Hayes JE, Simpson RJ, Richardson AE (2000b) The growth and phosphorus utilisation of plants in sterile media when supplied with inositol hexaphosphate, glucose 1-phosphate or inorganic phosphate. Plant Soil 220:165–174

Hedley MJ, White RE, Nye PH (1982) Plant-induced changes in the rhizosphere of rape (*Brassica napus* var. Emerald) seedlings. III. Changes in L value, soil phosphate fractions and phosphatase activity. New Phytol 91:45–56

Heffer P, Prud'homme MPR, Muirheid B, Isherwood KF (2006) Phosphorus fertilisation: issues and outlook. Proceedings 586. International Fertiliser Society, York

Helsel ZR (1992) Energy and alternatives for fertiliser and pesticide use. In: Fluck RC (ed) Energy in world agriculture, vol 6. Elsevier, Oxford, pp 177–210

Hens M, Turner BL, Hocking PJ (2003) Chemical nature and bioavailability of soil organic phosphorus mobilized by organic anions. In: Rengel Z (ed) Proceedings of the second international symposium on phosphorus dynamics in the soil-plant continuum. Uniprint: University of Western Australia, Perth, pp 16–17

Hermans C, Hammond JP, White PJ, Verbruggen N (2006) How do plants respond to nutrient shortage by biomass allocation? Trends Plant Sci 11:610–617

Hewitt MM, Carr JM, Williamson CL, Slocum RD (2005) Effects of phosphate limitation on expression of genes involved in pyrimidine synthesis and salvaging in *Arabidopsis*. Plant Physiol Biochem 43:91–99

Hill JO, Simpson RJ, Moore AD, Chapman DF (2006) Morphology and response of roots of pasture species to phosphorus and nitrogen nutrition. Plant Soil 286:7–19

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

Hodge A (2009) Root decisions. Plant Cell Environ 32:628–640

Hoffland E, Findenegg GR, Nelemans JA (1989) Solubilization of rock phosphorus by rape. II. Local root exudation of organic acids in response to P-starvation. Plant Soil 113:161–165

Hunter DA, McManus MT (1999) Comparison of acid phosphatase in two genotypes of white clover with different responses to applied phosphate. J Plant Nutr 22:679–692

Itoh S, Barber SA (1983) Phosphorus uptake by six plant species as related to root hairs. Agron J 75:457–461

Jain A, Poling MD, Karthikeyan AS, Blakeslee JJ, Peer WA, Titapiwatanakun B, Murphy AS, Raghothama KG (2007a) Differential effects of sucrose and auxin on localized phosphate deficiency-induced modulation of different traits of root system architecture in *Arabidopsis*. Plant Physiol 144:232–247

Jain A, Vasconcelos MJ, Raghothama KG, Sahi SV (2007b) Molecular mechanisms of plant adaptation to phosphate deficiency. Plant Breed Rev 29:359–419

Jansa J, Finlay R, Wallander H, Smith FA, Smith SE (2011) Role of mycorrhizal symbioses in phosphorus cycling. In: Bünemann EK, Oberson A, Frossard E (eds) Phosphorus in action: biological processes in soil phosphorus cycling. Soil biology, vol 26. Springer, Heidelberg. doi:10.1007/978-3-642-15271-9_6

Jenssen TK, Kongshaug G (2003) Energy consumption and greenhouse gas emissions in fertiliser production. Proceedings 509. International Fertiliser Society, York

Jones DL (1998) Organic acids in the rhizosphere – a critical review. Plant Soil 205:25–44

Jones DL, Darrah PR (1994) Role of root derived organic acids in the mobilization of nutrients in the rhizosphere. Plant Soil 166:247–257

Jones DL, Dennis PG, Owen AG, van Hees PAW (2003) Organic acid behavior in soils – misconceptions and knowledge gaps. Plant Soil 248:31–41

Karthikeyan AS, Varadarajan DK, Jain A, Held MA, Carpita NC, Raghothama KG (2007) Phosphate starvation responses are mediated by sugar signaling in *Arabidopsis*. Planta 225:907–918

Keerthisinghe G, Hocking PJ, Ryan PR, Delhaize E (1998) Effect of phosphorus supply on the formation and function of proteoid roots of white lupin (*Lupinus albus* L.). Plant Cell Environ 21:467–478

Kelly AA, Froehlich JE, Dörmann P (2003) Disruption of the two digalactosyldiacylglycerol synthase genes DGD1 and DGD2 in *Arabibopsis* reveals the existence of an additional enzyme of galactolipid synthase. Plant Cell 15:2694–2706

Kirk GJD, Santos EE, Findenegg GR (1999) Phosphate solubilization by organic anion secretion from rice (*Oryza sativa* L.) growing in aerobic soil. Plant Soil 211:11–18

Kirkby EA, Johnston AE (2008) Soil and fertilizer phosphorus in relation to crop nutrition. In: Hammond JP, White PJ (eds) The ecophysiology of plant–phosphorus interactions. Springer, Dordrecht, pp 177–223

Koyama H, Kanamura A, Kihara T, Hara T, Takita E, Shibata D (2000) Overexpression of mitochondrial citrate synthase in *Arabidopsis thaliana* improved growth on a phosphorus limited soil. Plant Cell Physiol 41:1030–1037

Lambers H, Shane MW, Cramer MD, Pearse SJ, Veneklaas EJ (2006) Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. Ann Bot 98:693–713

Lamont BB (2003) Structure, ecology and physiology of root clusters – a review. Plant Soil 248:1–19

Lan M, Comerford NB, Fox TR (1995) Organic anions effect on phosphorus release from spodic horizons. Soil Sci Soc Am J 59:1745–1749

Li M, Osaki M, Rao IM, Tadano T (1997) Secretion of phytase from the roots of several plant species under phosphorus-deficient conditions. Plant Soil 195:161–169

Li D, Zhu H, Liu K, Liu X, Leggewie G, Urdvardi M, Wang D (2002) Purple acid phosphatase of *Arabidopsis thaliana*. Comparative analysis and differential regulation by phosphate deprivation. J Biol Chem 277:27772–27781

Li L, Tang C, Rengel Z, Zhang F (2003) Chickpea facilitates phosphorus uptake by intercropped wheat from an organic phosphorus source. Plant Soil 248:297–303

Lin SI, Chiang SF, Lin WY, Chen JW, Tseng CY, Wu PC, Chiou TJ (2008) Regulatory network of microRNA399 and PHO2 by systemic signaling. Plant Physiol 147:732–746

Lin WY, Lin SI, Chiou TJ (2009) Molecular regulators of phosphate homeostasis in plants. J Exp Bot 60:1427–1438

Lipton DS, Blanchar RW, Blevins DG (1987) Citrate, malate, and succinate concentration in exudates from P-sufficient and P-stressed *Medicago sativa* L. seedlings. Plant Physiol 85:315–317

Liu Y, Mi G, Chen F, Zhang J, Zhang F (2004) Rhizosphere effect and root growth of two maize (*Zea mays* L.) genotypes with contrasting P efficiency at low P availability. Plant Sci 167:217–223

Liu JQ, Samac DA, Bucciarelli B, Allan DL, Vance CP (2005) Signaling of phosphorus deficiency-induced gene expression in white lupin requires sugar and phloem transport. Plant J 41:257–268

Lloyd JC, Zakhleniuk OV (2004) Responses of primary and secondary metabolism to sugar accumulation revealed by microarray expression analysis of the *Arabidopsis* mutant, *pho3*. J Exp Bot 55:1221–1230

López-Bucio J, de la Vega OM, Guevara-García A, Herrera-Estrella L (2000) Enhanced phosphorus uptake in transgenic tobacco plants that overproduce citrate. Nat Biotechnol 18:450–453

Lopez-Hernandez D, Brossard M, Frossard E (1998) P-isotopic exchange values in relation to P mineralization in soils with very low P-sorbing capacities. Soil Biol Biochem 30:1663–1670

Lung S-C, Chan W-L, Yip W, Wang L, Yeung EC, Lim BL (2005) Secretion of beta-propeller phytase from tobacco and *Arabidopsis* roots enhances phosphorus utilisation. Plant Sci 169:341–349

Lynch JP (1995) Root architecture and plant productivity. Plant Physiol 109:7–13

Lynch JP (2005) Root architecture and nutrient acquisition. In: BassiriRad H (ed) Nutrient acquisition by plants: an ecological perspective. Springer, Berlin, pp 147–183

Lynch JP, Brown KM (2008) Root strategies for phosphorus acquisition. In: White PJ, Hammond JP (eds) The ecophysiology of plant–phosphorus interactions. Springer, Dordrecht, pp 83–116

Ma Z, Walk TC, Marcus A, Lynch JP (2001) Morphological synergism in root hair length, density, initiation and geometry for phosphorus acquisition in *Arabidopsis thaliana*: a modeling approach. Plant Soil 236:221–235

Maroko JB, Buresh RJ, Smithson PC (1999) Soil phosphorus fractions in unfertilized fallow-maize systems on two tropical soils. Soil Sci Soc Am J 63:320–326

Marschner H (1995) Mineral nutrition of higher plants, 2nd edn. Academic, London

McGill WB, Cole CV (1981) Comparative aspects of cycling of organic C, N, S and P through soil organic matter. Geoderma 26:267–286

McLachlan KD (1980) Acid phosphatase activity of intact roots and phosphorus nutrition of plants. I. Assay conditions and phosphatase activity. Aust J Agric Res 31:429–440

Miller SS, Liu JQ, Allan DL, Menzhuber CJ, Fedorova M, Vance CP (2001) Molecular control of acid phosphatase secretion into the rhizosphere of proteoid roots from phosphorus-stressed white lupin. Plant Physiol 127:594–606

Misson J, Raghothama KG, Jain A, Jouhet J, Block MA, Bligny R, Ortet P, Creff A, Somerville S, Rolland N, Doumas P, Nacry P, Herrerra-Estrella L, Nussaume L, Thibaud M-C (2005) A genome-wide transcriptional analysis using *Arabidopsis thaliana* Affymetrix gene chips determined plant responses to phosphate deprivation. Proc Natl Acad Sci USA 102:11934–11939

Mitsukawa N, Okumura S, Shirano Y, Sato S, Kato T, Harashima S, Shibata D (1997) Overexpression of an *Arabidopsis thaliana* high-affinity phosphate transporter gene in tobacco cultured cells enhances cell growth under phosphate limited conditions. Proc Natl Acad Sci USA 94:7098–7102

Miura K, Rus A, Sharkhuu A, Yokoi S, Karthikeyan AS, Raghothama KG, Baek D, Koo YD, Jin JB, Bressan RA, Yun D-J, Hasegawa PM (2005) The *Arabidopsis* SUMO E3 ligase SIZ1 controls phosphate deficiency responses. Proc Natl Acad Sci USA 102:7760–7765

Morcuende R, Bari R, Gibon Y, Zheng WM, Pant BD, Bläsing O, Usadel B, Czechowski T, Udvardi MK, Stitt M, Scheible WR (2007) Genome-wide reprogramming of metabolism and regulatory networks of *Arabidopsis* in response to phosphorus. Plant Cell Environ 30:85–112

Mudge SR, Rae AL, Diatloff E, Smith FW (2002) Expression analysis suggests novel roles for members of the Pht1 family of phosphate transporters in *Arabidopsis*. Plant J 31:341–353

Mudge SR, Smith FW, Richardson AE (2003) Root-specific and phosphate-regulated expression of phytase under the control of a phosphate transporter promoter enables *Arabidopsis* to grow on phytate as a sole phosphorus source. Plant Sci 165:871–878

Müller R, Morant M, Jarmer H, Nilsson L, Nielsen TH (2007) Genome-wide analysis of the *Arabidopsis* leaf transcriptome reveals interaction of phosphate and sugar metabolism. Plant Physiol 143:156–171

Nacry P, Canivenc G, Muller B, Azmi A, Van Onckelen H, Rossignol M, Doumas P (2005) A role for auxin redistribution in the responses of the root system architecture to phosphate starvation in *Arabidopsis*. Plant Physiol 138:2061–2074

Nannipieri P, Giagnoni L, Landi L, Renella G (2011) Role of phosphatase enzymes in soil. In: Bünemann EK, Oberson A, Frossard E (eds) Phosphorus in action: biological processes in soil phosphorus cycling. Soil biology, vol 26. Springer, Heidelberg. doi:10.1007/978-3-642-15271-9_9

Neumann G, Massonneau A, Martinoia A, Römheld V (1999) Physiological adaptations to phosphorus deficiency during proteiod root development in white lupin. Planta 208:373–382

Newman RH, Tate KR (1980) Soil phosphorus characterization by ^{31}P-nuclear magnetic resonance. Commun Soil Sci Plant Anal 11:835–842

Nilsson L, Müller R, Nielsen TH (2007) Increased expression of the MYB-related transcription factor, PHR1, leads to enhanced phosphate uptake in *Arabidopsis thaliana*. Plant Cell Environ 30:1499–1512

Nziguheba G, Palm CA, Buresh RJ, Smithson PC (1998) Soil phosphorus fractions and adsorption as affected by organic and inorganic sources. Plant Soil 198:159–168

Oberson A, Joner EJ (2005) Microbial turnover of phosphorus in soil. In: Turner BL, Frossard E, Baldwin DS (eds) Organic phosphorus in the environment. CABI, Wallingford, pp 133–164

Oberson A, Besson JM, Maire N, Sticher H (1996) Microbial processes in soil organic transformations in conventional and biological cropping systems. Biol Fertil Soils 21:138–148

Oberson A, Friesen DK, Rao IM, Bühler S, Frossard E (2001) Phosphorus transformations in an oxisol under contrasting land-use systems: the role of the microbial biomass. Plant Soil 237:197–210

Oehl F, Oberson A, Sinaj S, Frossard E (2001) Organic phosphorus mineralization studies using isotopic dilution techniques. Soil Sci Soc Am J 65:780–787

Oehl F, Frossard E, Fliessbach A, Dubois D, Oberson A (2004) Basal organic phosphorus mineralization in soils under different farming systems. Soil Biol Biochem 36:667–675

Otani T, Ae N (1999) Extraction of organic phosphorus in andosols by various methods. Soil Sci Plant Nutr 45:151–161

Pant BD, Buhtz A, Kehr J, Scheible W-R (2008) MicroRNA399 is a long-distance signal for the regulation of plant phosphate homeostasis. Plant J 53:731–738

Parsons HL, Yip JYH, Vanlerberghe GC (1999) Increased respiratory restriction during phosphate-limited growth in transgenic tobacco cells lacking alternative oxidase. Plant Physiol 121:1309–1320

Pearse SJ, Venaklaas EJ, Cawthray G, Bolland MDA, Lambers H (2006) Carboxylate composition of root exudates does not relate consistently to a crop species' ability to use phosphorus from aluminium, iron or calcium phosphate sources. New Phytol 173:181–190

Pérez-Torres C-A, 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

Plaxton WC, Carswell MC (1999) Metabolic aspects of the phosphate starvation response in plants. In: Lerner HR (ed) Plant responses to environmental stresses: from phytohormones to genome reorganisation. Dekker, New York, pp 349–372

Polglase PJ, Attiwill PM, Adams MA (1992) Nitrogen and phosphorus cycling in relation to stand age of *Eucalyptus regnans* F. Muell. III. Labile inorganic and organic P, phosphatase activity and P availability. Plant Soil 142:177–185

Rae AL, Jarmey JM, Mudge SR, Smith FW (2004) Over-expression of a high-affinity phosphate transporter in transgenic barley plants does not enhance phosphate uptake rates. Funct Plant Biol 31:141–148

Raghothama KG (1999) Phosphate acquisition. Annu Rev Plant Physiol Plant Mol Biol 50: 665–693

Raven JA (2008) Phosphorus and the future. In: White PJ, Hammond JP (eds) The ecophysiology of plant–phosphorus interactions. Springer, Dordrecht, pp 271–283

Richardson AE, Hadobas PA, Hayes JE (2000) Phosphomonoesterase and phytase activities of wheat (*Triticum aestivum* L.) roots and utilisation of organic phosphorus substrates by seedlings grown in sterile culture. Plant Cell Environ 23:397–405

Richardson AE, Hadobas PA, Hayes JE (2001) Extracellular secretion of *Aspergillus* phytase from *Arabidopsis* roots enables plants to obtain phosphorus from phytate. Plant J 25:641–649

Richardson AE, George TS, Hens M, Simpson RJ (2005) Utilisation of soil organic phosphorus by higher plants. In: Turner BL, Frossard E, Baldwin DS (eds) Organic phosphorus in the environment. CABI, Wallingford, pp 165–184

Richardson AE, George TS, Jakobsen I, Simpson RJ (2007) Plant utilization of inositol phosphates. In: Turner BL, Richardson AE, Mullaney EJ (eds) Inositol phosphates: linking agriculture and the environment. CABI, Wallingford, pp 242–260

Rook F, Hadingham SA, Li Y, Bevan MW (2006) Sugar and ABA response pathways and the control of gene expression. Plant Cell Environ 29:426–434

Rubio V, Linhares F, Solano R, Martín AC, 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

Rubio G, Liao H, Yan XL, Lynch JP (2003) Topsoil foraging and its role in plant competitiveness for phosphorus in common bean. Crop Sci 43:598–607

Runge-Metzger A (1995) Closing the cycle: obstacles to efficient P management for improved global security. In: Tiessen H (ed) Phosphorus in the global environment: transfers, cycles and management. Wiley, Chichester, pp 27–42

Ryan PR, Delhaize E, Jones DL (2001) Function and mechanism of organic anion exudation from plant roots. Annu Rev Plant Physiol Plant Mol Biol 52:527–560

Sánchez-Calderón L, López-Bucio J, Chacón-López A, Gutiérrez-Ortega A, Hernández-Abreu E, Herrera-Estrella L (2006) Characterization of low phosphorus insensitive mutants reveals a crosstalk between low P-induced determinate root development and the activation of genes involved in the adaptation of *Arabidopsis* to P deficiency. Plant Physiol 140:879–889

Sasaki T, Yamomoto Y, Ezaki B, Katsuhara M, Ahn SJ, Ryan PR, Delhaize E, Matsumoyo H (2004) A wheat gene encoding an aluminium-activated malate transporter. Plant J 37:645–653

Shane MW, de Vos M, De Roock S, Lambers H (2003) Shoot P status regulates cluster-root growth and citrate exudation in *Lupinus albus* grown with a divided root system. Plant Cell Environ 26:265–273

Shen J, Li H, Neumann G, Zhang F (2005) Nutrient uptake, cluster root formation and exudation of protons and citrate in *Lupinus albus* as affected by localized supply of phosphorus in a split-root system. Plant Sci 168:837–845

Skene KR (1998) Cluster roots: some ecological considerations. J Ecol 86:1060–1064

Smith SE, Read DJ (2007) Mycorrhizal symbiosis, 3rd edn. Elsevier, London

Smith FW, Mudge SR, Rae AL, Glassop D (2003) Phosphate transport in plants. Plant Soil 248:71–83

Solfanelli C, Poggi A, Loreti E, Alpi A, Perata P (2006) Sucrose-specific induction of the anthocyanin biosynthetic pathway in *Arabidopsis*. Plant Physiol 140:637–646

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. Nat Genet 39:792–796

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 Soil 155(156):95–98

Tarafdar JC, Claassen N (1988) Organic phosphorus compounds as a phosphorus source for higher plants through the activity of phosphatases produced by plant roots and microorganisms. Biol Fertil Soils 5:308–312

Tarafdar JC, Yadav RS, Meena SC (2001) Comparative efficiency of acid phosphatase originated from plant and fungal sources. J Plant Nutr Soil Sci 164:279–282

Teng S, Keurentjes J, Bentsink L, Koornneef M, Smeekens S (2005) Sucrose-specific induction of anthocyanin biosynthesis in *Arabidopsis* requires the MYB75/PAP1 gene. Plant Physiol 139:1840–1852

Tesfaye M, Liu J, Allan DL, Vance CP (2007) Genomic and genetic control of phosphate stress in legumes. Plant Physiol 144:594–603

Ticconi CA, Delatorre CA, Lahner B, Salt DE, Abel S (2004) *Arabidopsis pdr2* reveals a phosphate-sensitive checkpoint in root development. Plant J 37:801–814

Trasar-Cepeda MC, Carballas T (1991) Liming and the phosphatase activity and mineralization of phosphorus in an acidic soil. Soil Biol Biochem 23:209–215

Turner BL (2007) Inositol phosphates in soil: amounts, forms and significance of the phosphorylated inositol stereoisomers. In: Turner BL, Richardson AE, Mullaney EJ (eds) Inositol phosphates: linking agriculture and the environment. CABI, Wallingford, pp 186–206

Vance CP (2008) Plants without arbuscular mycorrhizae. In: Hammond JP, White PJ (eds) The ecophysiology of plant–phosphorus interactions. Springer, Dordrecht, pp 117–142

Vance CP, Ehde-Stone C, Allan DL (2003) Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. New Phytol 157:423–447

Veneklaas EJ, Stevens J, Cawthray GR, Turner S, Grigg AM, Lambers H (2003) Chickpea and white lupin rhizosphere carboxylates vary with soil properties and enhance phosphorus uptake. Plant Soil 248:187–197

Wasaki J, Omura M, Ando M, Dateki H, Shinano T, Osaki M, Ito H, Matsui H, Tadano T (2000) Molecular cloning and root specific expression of secretory acid phosphatase from phosphate deficient lupin (*Lupinus albus* L.). Soil Sci Plant Nutr 46:427–437

Wasaki J, Shinano T, Onishi K, Yonetani R, Yazaki J, Fujii F, Shimbo K, Ishikawa M, Shimatani Z, Nagata Y, Hashimoto A, Ohta T, Sato Y, Miyamoto C, Honda S, Kojima K, Sasaki T, Kishimoto N, Kikuchi S, Osaki M (2006) Transcriptomic analysis indicates putative metabolic changes caused by manipulation of phosphorus availability in rice leaves. J Exp Bot 57: 2049–2059

Wassen MJ, Venterink HO, Lapshina ED, Tanneberger L (2005) Endangered plants persist under phosphorus limitation. Nature 437:547–550

White PJ, Hammond JP (2008) Phosphorus nutrition of terrestrial plants. In: White PJ, Hammond JP (eds) The ecophysiology of plant–phosphorus interactions. Springer, Dordrecht, pp 51–81

White PJ, Broadley MR, Greenwood DJ, Hammond JP (2005) Genetic modifications to improve phosphorus acquisition by roots. Proceedings 568. International Fertiliser Society, York

Williamson LC, Ribrioux SPCP, Fitter AH, Leyser HMO (2001) Phosphate availability regulates root system architecture in *Arabidopsis*. Plant Physiol 126:875–890

Wouterlood M, Cawthray GR, Scanlon TT, Lambers H, Veneklaas EJ (2004) Carboxylate concentrations in the rhizosphere of lateral roots of chickpea (*Cicer arietinum*) increase during plant development, but are not correlated with phosphorus status of soil or plants. New Phytol 162:745–753

Wu P, Ma L, Hou X, Wang M, Wu Y, Liu F, Deng XW (2003) Phosphate starvation triggers distinct alterations if genome expression in *Arabidopsis* roots and leaves. Plant Physiol 132:1260–1271

Xiao K, Harrison MJ, Wang ZY (2005) Transgenic expression of a novel *Medicago truncatula* phytase gene results in improved acquisition of organic phosphorus by *Arabidopsis*. Planta 222:27–36

Yi K, Wu Z, Zhou J, Du L, Guo L, Wu Y, Wu P (2005) OsPTF1, a novel transcription factor involved in tolerance to phosphate starvation in rice. Plant Physiol 138:2087–2096

Zhang WH, Ryan PR, Tyerman SD (2004) Citrate-permeable channels in the plasma membrane of cluster roots from white lupin. Plant Physiol 136:3771–3783

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 Biotechnol J 1:353–360

Zrenner R, Stitt M, Schmidt R, Sonnewald U, Boldt R (2006) Pyramidine and purine biosynthesis and degradation in plants. Annu Rev Plant Biol 57:805–836