

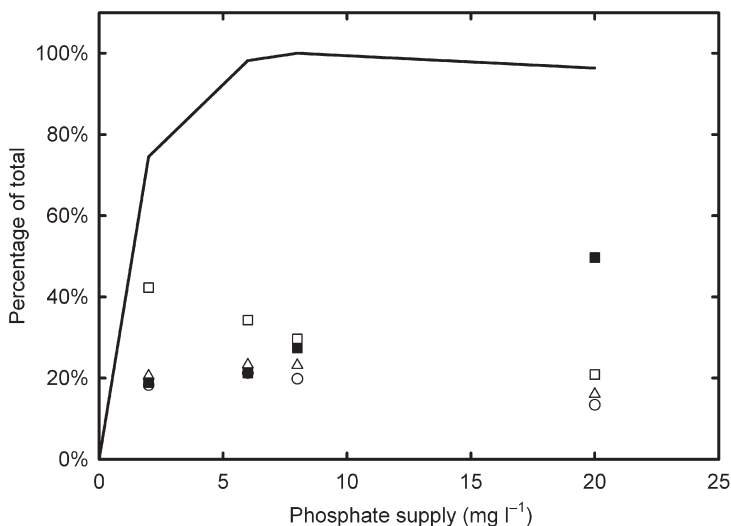
# Chapter 4

## PHOSPHORUS NUTRITION OF TERRESTRIAL PLANTS

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### INTRODUCTION

Phosphorus (P) is essential for plant growth and fecundity. It is an integral component of genetic, metabolic, structural and regulatory molecules, in many of which it cannot be substituted by any other elements. Tissue P concentrations in well fertilized plants approximate 0.4–1.5% of the dry matter (Broadley *et al.* 2004), most of which is present as nucleic acids and nucleotides, phosphorylated intermediates of energy metabolism, membrane phospholipids and, in some tissues (principally seeds), as inositol phosphates. Some P also occurs in phosphoproteins and as inorganic phosphate (Pi) and pyrophosphate (PPi). It has been estimated that small metabolites, nucleic acids and phospholipids contribute approximately equally to leaf P content in P-replete plants (Figure 4.1; Marschner 1995; Dörmann and Benning 2002). Tissue P concentrations show no systematic differences between angiosperm species grown in P-replete conditions, but strong positive correlations occur between shoot P and shoot organic-N concentrations (Broadley *et al.* 2004). When plants are sampled from their natural environment, shoot N:P mass ratios vary between about 5:1 and 40:1 (e.g. Garten 1976; Thompson *et al.* 1997; Elser *et al.* 2000a; Tessier and Raynal 2003; Güsewell 2004; McGroddy *et al.* 2004; Güsewell *et al.* 2005; Han *et al.* 2005; Niklas *et al.* 2005; Wassen *et al.* 2005; Wright *et al.* 2005; Kerkhoff *et al.* 2006) and leaf N appears to scale as the 3/4 power of leaf P (Niklas *et al.* 2005; Niklas 2008). Ratios of 10:1 approximate the maximum critical organic-N:P ratios reported for a range of crop plants (Greenwood *et al.* 1980; Güsewell 2004). In general, leaf N:P ratios below 13.5 suggest N-limited plant growth, whilst leaf N:P ratios above 16 suggest P-limited plant growth (Aerts and Chapin 2000; Güsewell and Koerselman 2002; Tessier and Raynal 2003). Stoichiometric relationships between leaf N and leaf P appear to be a consequence of the requirements of N for proteins and of P for nucleic acids, membranes and metabolism (Elser *et al.* 2000b; Niklas 2008). Plant relative growth rate (RGR) is positively correlated with rRNA concentration and negatively correlated with protein concentration (Ågren 1988; Elser *et al.* 2000b; Niklas 2008). Thus, shoots of fast-growing herbaceous species characteristic of nutrient-rich, disturbed habitats tend to have



**Fig. 4.1** The effect of P supply on leaf dry weight (line), expressed as a percentage of the maximum, and the percentage contributions of small metabolites (open triangles), nucleic acids (open squares), phospholipids (open circles) and inorganic phosphorus (filled squares) to the total leaf P content. (Data taken from Marschner 1995.)

higher concentrations of N and P, but lower N:P ratios, than shoots of slow-growing species characteristic of infertile habitats (Grime *et al.* 1997; Thompson *et al.* 1997; Grime 2001; Güsewell 2004; Niklas *et al.* 2005). Similarly, shoot N:P ratios increase during ontogeny as plant RGR declines (Güsewell 2004; Niklas 2008) and, between tissues, structural tissues have higher N:P ratios than metabolically active ones (Kerkhoff *et al.* 2006). This is consistent with the large P requirements for the growth of young tissues and the absolute cellular requirement for protein.

A lack of available P rapidly reduces plant growth rates. However, tissue P requirements and responses to P availability vary markedly between terrestrial plant species and among genotypes of a particular species (e.g. Bradshaw *et al.* 1960; Loneragan and Asher 1967; Rorison 1968; Ozanne *et al.* 1969; Greenwood *et al.* 1980, 2005, 2006; Coltman *et al.* 1986; Johnston *et al.* 1986; Alt 1987; Fageria *et al.* 1988; Föhse *et al.* 1988; Gunawardena *et al.* 1993; Gourley *et al.* 1994; Yan *et al.* 1995a,b, 2006; Beebe *et al.* 1997; Fageria and Baligar 1997, 1999; Li *et al.* 1997; Tian *et al.* 1998; Bolland *et al.* 1999; Narang *et al.* 2000; Sanginga *et al.* 2000; Baligar *et al.* 2001; Gaume *et al.* 2001; Górný and Sodikiewicz 2001; Liu *et al.* 2001; Osborne and Rengel 2002; Güsewell *et al.* 2003; Trehan and Sharma 2003; Blackshaw *et al.* 2004; Gahoonia and Nielsen 2004a,b; Zhao *et al.* 2004; Zhu and Lynch 2004; Higgs *et al.* 2005; Ozturk *et al.* 2005; White *et al.* 2005a,b; Wissuwa 2005; Oracka and Łapiński 2006; Su *et al.* 2006; Marschner *et al.* 2007; Tesfaye

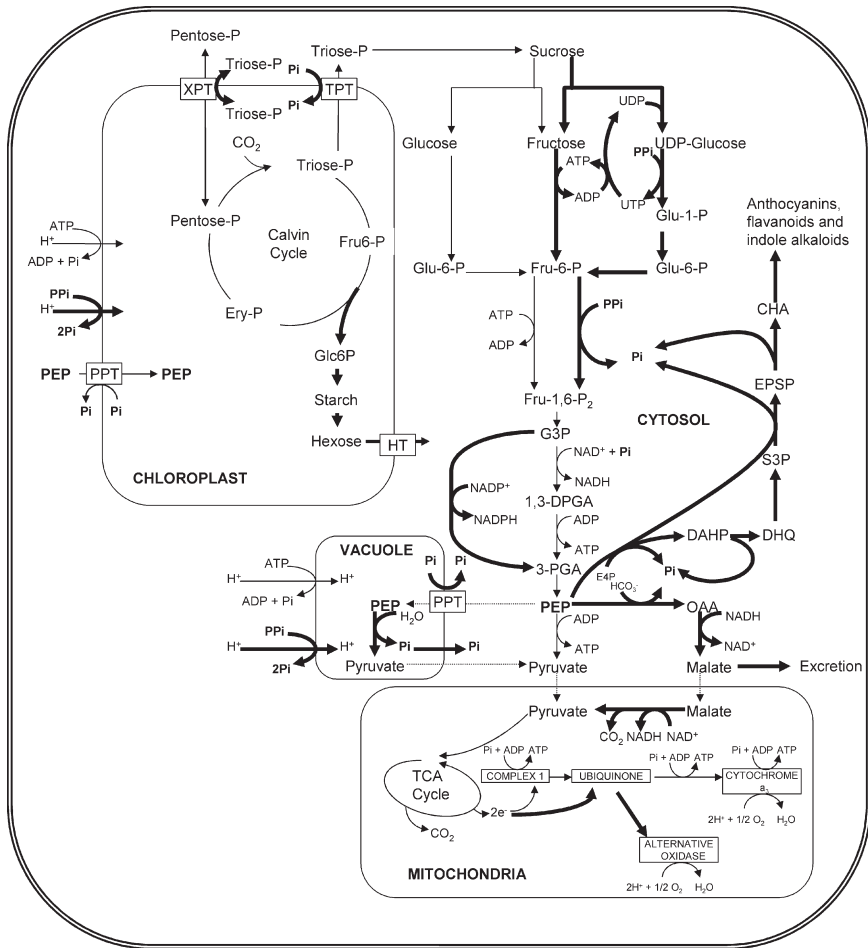
*et al.* 2007; George and Richardson 2008), suggesting significant genetic variation in the ability of plants to acclimate to reduced P availability through the conservative use of P in tissues and/or an increased capability for P acquisition. Even mild P deficiency alters cellular biochemistry, biomass allocation and root morphology to match P acquisition with plant P requirements. Typical responses of plants to P starvation include the remobilization, reduction or replacement of P in inessential cellular compounds, the exudation of metabolites and enzymes into the rhizosphere to increase P availability and changes in root morphology and/or associations with microorganisms to acquire P more effectively from the soil. In this chapter, physiological responses of plants to the vagaries of P availability will be reviewed and set in the context of their consequences for plant growth and survival in natural and agricultural ecosystems.

## PHOSPHORUS-CONTAINING COMPOUNDS IN PLANTS

Phosphorus is present in many chemical forms in plant cells (Marschner 1995). Some cellular compounds containing P are present at low concentrations or can be diminished and/or replaced with little consequence. It is the P-containing compounds that have unique cellular roles and those that are required in high concentrations by plant cells that define the absolute P requirement of plants. The acclimatory responses of plants to P starvation are directed towards maintaining essential cellular functions, either by utilizing plant P efficiently or by increasing P acquisition by the root system.

### *Nucleic acids*

Phosphorus is an essential component of DNA and RNA, in which phosphodiester bridges link the deoxyribonucleotides or ribonucleotides. The requirement for DNA and RNA is greatest in tissues undergoing rapid cell division and/or cell expansion (Ågren 1988; Elser *et al.* 2000b; Niklas 2008). The plant cannot dispense with DNA or RNA and although DNA and RNA concentrations in plant cells can be reduced during P starvation this has a significant affect on plant growth rate (Raven 2008). In addition, P is required as ADP in photosynthesis and respiration, as ATP for energy transfer reactions in, for example, nucleic acid synthesis, metabolism, cytoskeletal rearrangements and membrane transport, as GTP for energy transfer reactions during nucleic acid biosynthesis, as NADPH in biosynthetic reactions and as signaling molecules such as GTP and cAMP. It is possible for a cell to reduce some dependence on ATP by rerouting biochemical pathways and utilizing P<sub>i</sub> as an energy substrate (Figure 4.2; Plaxton and Carswell 1999; Hammond *et al.* 2004; Hammond and White 2008a), but a finite requirement for ATP cannot be avoided.



**Fig. 4.2** Alternative metabolic processes for cytosolic glycolysis, mitochondrial electron transport, chloroplast processes and tonoplast  $H^+$  pumping (bold arrows) that may enable plants to survive under P limiting conditions. Abbreviations for compounds are as follows; Glu-1-P, glucose 1-phosphate; Glu-6-P, glucose 6-phosphate; Fru-6-P, fructose 6-phosphate; Fru-1,6-P<sub>2</sub>, fructose 1,6-bisphosphate; G3P, glyceraldehyde-3-phosphate; 1,3-DPGA, 1,3-diphosphoglycerate; OAA, oxaloacetate; E4P, erythrose 4-phosphate; S3P, shikimate-3-phosphate; HT, hexose translocator; PEP, phosphoenolpyruvate; PPT, phosphoenolpyruvate/phosphate translocator; Pi, inorganic phosphate; TPT, triose phosphate/phosphate translocator; Triose-P, triose phosphates; XPT, xylulose 5-phosphate/phosphate translocator. (Figure redrawn from Plaxton and Carswell 1999 and Flügel *et al.* 2003 by Hammond and White 2008.)

### *Phosphorylated metabolites*

A considerable quantity of cellular P occurs in the many phosphorylated intermediates of metabolic pathways. Phosphorylated compounds occur, for example, in the Calvin cycle, in the photorespiratory pathway, in glycolysis, in the pentose phosphate

pathway, in nitrogen and sulfur assimilation, in the pathways of amino acid and nucleotide metabolism, and in pathways leading to the synthesis of polyphenols and lignin (Coruzzi and Last 2000; Dennis and Blakeley 2000; Malkin and Niyogi 2000; Siedow and Day 2000). In addition, where integrated metabolic transformations occur in different cellular compartments, it is often phosphorylated compounds that are transported across membranes. There is some flexibility in these metabolic pathways and, when plants lack sufficient P, alternative pathways requiring lower concentrations of phosphorylated intermediates are adopted (Figure 4.2; Plaxton and Carswell 1999; Flügge *et al.* 2003; Vance *et al.* 2003; Hammond *et al.* 2004; Hammond and White 2008a).

### ***Phospholipids***

In cell membranes, P occurs in phospholipids (phosphatidyl serine, phosphatidyl ethanolamine, phosphatidyl choline, phosphatidyl inositol and diphosphatidylglycerol), and the intermediate compounds of their biosynthesis (Somerville *et al.* 2000). In addition to their structural roles, phospholipids serve as substrates for the production of biochemical signals, such as inositol trisphosphate (IP<sub>3</sub>), diacylglycerol, lysophosphatidyl choline, jasmonate and free headgroups (inositol, choline, ethanolamine, serine). Membrane lipids are required in abundance by photosynthetic tissues and tissue undergoing rapid cell division and/or cell expansion. The thylakoid membrane of the chloroplast is predominantly composed of sulphoquinovosyldiacylglycerol (SQDG), digalatosyldiacylglycerol (DGDG) and monogalatosyldiacylglycerol (MGDG), which is the most abundant lipid on the planet. By using these lipids in chloroplast membranes, plants reduce their requirements for phospholipids. Furthermore, when plants are starved of P, the relative abundance of SQDG, DGDG and MGDG increases in plant membranes, thereby contributing to tissue P economy (Essigmann *et al.* 1998; Härtel *et al.* 2000; Dörmann and Benning 2002; Andersson *et al.* 2003, 2005; Jouhet *et al.* 2004; Benning and Ohta 2005; Kobayashi *et al.* 2006; Li *et al.* 2006). Interestingly, these lipids are also found in the peribacteroid membranes surrounding rhizobial symbionts in legumes, where, again, their relative abundance increases during P starvation (Gaude *et al.* 2004).

### ***Inorganic and storage P***

In P-replete plants, over 85% of the cellular Pi is located in the vacuole (Marschner 1995). However, vacuolar Pi concentrations decrease rapidly when plants lack sufficient P, to maintain cytoplasmic Pi concentration ( $[Pi]_{\text{cyt}}$ ) in the range 3–20 mM (Lee *et al.* 1990; Schachtman *et al.* 1998; Mimura 1999). If the P supplied to P-replete plants is reduced to the minimal amount required for optimal plant growth only the P in the inorganic fraction decreases substantially, which reflects the mobilization of surplus Pi from the vacuole (Figure 4.1; Marschner 1995). However,

when the P supply to plants is decreased from an optimal to a suboptimal level, the P associated with nucleic acids, lipids, small metabolites and inorganic fractions all decrease. In contrast to most other tissues, Pi concentrations in seed are low and phytate (IP<sub>6</sub>) is a dominant P fraction. In P-replete plants 50–90% of the total P in seeds occurs as phytate, but this value declines with decreasing P supply (Bielecki 1973; Marschner 1995; Mengel and Kirkby 2001). Remarkably, it is estimated that the amount of P contained in seed phytate is as much as 50% of all phosphate fertilizer applied annually on a global scale (Lott *et al.* 2000).

In addition, a small, but important, amount of P occurs in proteins. Phosphorylation and dephosphorylation of serine residues affects the activity of many enzymes (Raven 2008). Appropriate regulation of these enzymes is often critical for cellular homeostasis and, therefore, the P associated with this function is indispensable.

## **SYMPTOMS OF PHOSPHORUS IMBALANCE IN PLANTS**

The symptoms of P deficiency in plants reflect the roles of P in plant cells. Phosphorus deficiency results in a diminutive or spindly habit, acute leaf angles, suppression of tillering, prolonged dormancy, early senescence and decreased size and number of flowers and buds (Bould *et al.* 1983; Bergmann 1992; Marschner 1995; Mengel and Kirkby 2001). Symptoms of P deficiency occur first in older leaves. The development of dark green or blue-green foliage is among the first symptoms of P deficiency. Red, purple or brown pigments develop in leaves, especially along veins. This is a consequence of anthocyanin production, which is induced by increased leaf sucrose concentrations (Müller *et al.* 2005; Teng *et al.* 2005; Amtmann *et al.* 2006; Solfanelli *et al.* 2006) and is thought to protect nucleic acids from UV damage and chloroplasts from photoinhibitory damage caused by P-limited photosynthesis (Hoch *et al.* 2001). Severe P deficiency results in chloroplast abnormalities, such as a reduction in the number of grana and their morphology (Bould *et al.* 1983). There is a gradual reduction in rates of cell division, cell expansion, photosynthesis and respiration, and changes in the abundance of C, N and S metabolites and concentrations of plant growth regulator substances during P starvation (Bould *et al.* 1983; Marschner 1995).

In agriculture, P-deficiencies of crops are usually treated by the addition of P-fertilizers to the soil. This has the added advantage of increasing soil P reserves for future crops. Foliar sprays of ammonium or potassium phosphate can be used, but may cause damage to the leaves (Bould *et al.* 1983). A lack of phytoavailable Zn in the soil can also cause P toxicity in crops (Loneragan *et al.* 1982). In nature, P rarely accumulates to toxic concentrations in plant tissues, except occasionally in species adapted to soils with excessively low P availability (Shane *et al.* 2004). However, in the laboratory, when roots of P-deficient plants are transferred to solutions containing high Pi concentrations, P may accumulate to toxic levels in shoots (e.g. Green *et al.* 1973; Clarkson and Scattergood 1982; Cogliatti and Clarkson 1983). This is a consequence of an innate inability to rapidly downregulate the high Pi uptake capacity of roots of P-deficient plants.

## PHOSPHORUS AVAILABILITY TO PLANTS

Phosphorus is the 11th most abundant element in the earth's crust, and its concentration in soils generally lies between 100 and 3,000 mg P kg<sup>-1</sup> soil, or 200–6,000 kg P ha<sup>-1</sup> (Hedley *et al.* 1995; Mengel 1997).

In the soil, P is present as free Pi in the soil solution, labile Pi bound to soil particles, especially clays, as insoluble inorganic salts, such as calcium (Ca) phosphate in alkaline soils or aluminum (Al) and iron (Fe) phosphates in acidic soils, as complex organic compounds in the soil organic material, which may constitute 30–60% of the P in the topsoil, and the P in living soil biomass, which comprise about 5% of soil P (Mengel 1997; Hinsinger 2001; Oberson and Joner 2005; Turner 2007; Kirkby and Johnston 2008). These P sources must be solubilized or degraded (mineralized) to release soluble Pi for plant nutrition. The rates by which P is interconverted between these P fractions varies widely (Barber 1995; Mengel 1997), and both the amounts of P in each fraction and the rates of their interconversion are influenced by vegetation, amounts and chemical constituents of any Pi-fertilizers applied, the total P concentration in soil, soil structure, organic matter content and mineralogy, soil pH (Pi availability is highest between pH 6.5 and 7.5), temperature, soil moisture, and the abundance and identity of the soil micro-organisms present.

Nevertheless, P availability frequently limits plant growth in both natural and agricultural ecosystems (Epstein 1972; Chapin *et al.* 1986; Ågren 1988; Vance *et al.* 2003; Güsewell 2004). The simple reason for this is that both plant roots, and their associated mycorrhizal fungi, can only acquire P as orthophosphate (Schachtman *et al.* 1998; White 2003), which is present at extremely low concentrations (<10 µM) in the soil solution due to the low solubility products of inorganic P salts (Bielecki 1973; Barber 1995; Hedley *et al.* 1995; Marschner 1995). As a consequence, the diffusion of Pi through the soil solution is slow, and plant roots with their associated mycorrhizal fungi must occupy the soil volume at high density to acquire Pi at a sufficient rate for maximal growth (Bielecki 1973; Barber 1995; Marschner 1995). In addition, plant available Pi in the rhizosphere soil solution is rapidly depleted, and the replenishment of Pi in the rhizosphere soil solution from soil P sources is slow (Bielecki 1973; Barber 1995). For these reasons, conventional agriculture applies Pi-fertilizers to increase Pi concentrations in the rhizosphere to maximize crop P uptake and growth. Unfortunately, the reserves of commercially exploitable Pi rock are currently estimated to last less than 150 years (Mengel 1997; Steen 1998; Vance *et al.* 2003; Cohen 2007), so alternative strategies for P-fertilisation of crops may be required in the future.

## PLANT STRATEGIES TO INCREASE THE ACQUISITION OF P

A variety of strategies are employed by plants to mobilize and acquire Pi from the soil (Vance *et al.* 2003; Hammond *et al.* 2004; Ticconi and Abel 2004; Raghothama and Karthikeyan 2005; Rengel and Marschner 2005; White *et al.* 2005a;

Lambers *et al.* 2006; Jain *et al.* 2007b). In general, these utilize the excess carbon assimilated when plant growth is limited by factors other than photosynthesis (Mengel and Kirkby 2001; Morgan *et al.* 2005; Hermans *et al.* 2006; Hammond and White 2008a). In response to P deficiency: (1) Plant roots acidify the rhizosphere and secrete low-molecular-weight organic anions and phosphatase enzymes into the soil to mobilize Pi from inorganic and organic P sources. (2) Plants invest a greater proportion of their biomass in their root system. (3) The morphology of the root system is altered, not only to explore the soil volume more effectively but also to exploit any localized patches of high Pi availability. (4) There is a general increase in the capacity of plant roots to take up Pi, accelerating the rate of Pi uptake from the soil solution. (5) 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. None of these strategies are mutually exclusive and plants often employ several simultaneously to avert P-deficiency.

### ***Rhizosphere modification***

Roots of P-deficient plants often release protons (H<sup>+</sup>) to acidify the rhizosphere (Marschner 1995; Hinsinger 2001). In addition, they secrete low-molecular-mass organic anions, such as carboxylates and piscidic acid (Jones 1998; López-Bucio *et al.* 2000b; Hocking 2001; Ryan *et al.* 2001; Dakora and Phillips 2002; Jones *et al.* 2003; Delhaize *et al.* 2007). However, the effectiveness of these compounds in releasing Pi from soil minerals differs greatly (generally citrate > oxalate > malate = tartrate > acetate > succinate = lactate, but this order is dependent upon soil type; Jones 1998; Hinsinger 2001; Jones *et al.* 2003) and plant species differ in both the identity and quantity of the low molecular-mass organic acids they exude from their roots (e.g. Van ura and Hovadík 1965; Ohwaki and Hirata 1992; Dinkelaker *et al.* 1995; Jones 1998; Neumann and Römheld 1999; López-Bucio *et al.* 2000b; Hinsinger 2001; Dakora and Phillips 2002; Dechassa and Schenk 2004; Jain *et al.* 2007b), which may be related to their phylogeny, ecology and/or their ability to form mycorrhizal associations. Differences between genotypes of particular species in their ability to exude organic acids and to access different forms of mineral P have also been reported (Subbarao *et al.* 1997; Narang *et al.* 2000; Gaume *et al.* 2001; Ishikawa *et al.* 2002; Liao *et al.* 2006; Pearse *et al.* 2007, 2008). Although organic anions released by roots are rapidly decomposed in the soil (Jones 1998; Jones *et al.* 2003), plant roots secrete these compounds in locations where the abundance of microorganisms is low, such as the root apex or within clusters of lateral roots (Dinkelaker *et al.* 1995; Jones 1998; Gaume *et al.* 2001; Vance *et al.* 2003; Thornton *et al.* 2004; Lambers *et al.* 2006; Liao *et al.* 2006; Paterson *et al.* 2006). It is commonly observed that the release of carbon compounds increases microbial biomass and activity in the rhizosphere, but its consequences for microbial community structure and function are less well understood (Morgan *et al.* 2005).



Changes in microbial abundance and/or community structure can either promote or reduce Pi availability to plants, both directly and indirectly (Jones 1998; Barea *et al.* 2005; Morgan *et al.* 2005; Rengel and Marschner 2005; Marschner 2008).

Plant roots also secrete enzymes into the rhizosphere to release Pi from organic P compounds in the soil. These enzymes include acid phosphatases and phytases that hydrolyze organic phosphomonoesters, which are the dominant form of organic P in the soil, and apyrases and RNases that hydrolyze phosphodiesteres (Thomas *et al.* 1999; Haran *et al.* 2000; Miller *et al.* 2001; Coello 2002; Wasaki *et al.* 2003; Tomscha *et al.* 2004; Zimmermann *et al.* 2004; Jain *et al.* 2007b). Although there is significant genotypic variation in the phosphatase activities secreted by roots both between and within plant species (Tadano and Sasaki 1991; Asmar *et al.* 1995; Li *et al.* 1997; Liu *et al.* 2001; Gaume *et al.* 2001), these are not always correlated with their ability to acquire P or grow in many soils (George *et al.* 2008). This may reflect the complementarity of the many compensatory mechanisms plants employ to acclimate to low P availability. It is noteworthy that rhizosphere microorganisms also release phosphomonoesterases and phosphodiesterases that contribute to P cycling in the soil and/or induce the release of these enzymes by plants (George and Richardson 2008; Marschner 2008).

### ***Altered biomass allocation and root system modification***

In response to P deficiency plants allocate more of their biomass to the root system, thereby increasing root growth rates and the volume of soil the root system can explore (Vance *et al.* 2003; Hutchings and John 2004; White *et al.* 2005a; Hermans *et al.* 2006; Hammond and White 2008a). To exploit the local effects of secreting organic anions and enzymes into the rhizosphere, plants increase their root length density in regions of higher P availability. In response to P deficiency, plants preferentially produce roots in the topsoil, since P is often concentrated close to the soil surface (Barber 1995; Lynch and Brown 2001; Rubio *et al.* 2003; Liao *et al.* 2004; Ho *et al.* 2005; Zhu *et al.* 2005), proliferate lateral roots in P-rich patches (Drew 1975; Robinson 1994; Hodge 2004; Hutchings and John 2004) and increase the length and density of root hairs to enlarge the effective surface area of the root system, thereby increasing the volume of soil explored for minimal biomass investment (Jungk 2001; Zhang *et al.* 2003). All these acclimatory responses increase P acquisition and plant growth, and there is considerable genetic variation both between and within plant species in these traits (e.g. O'Toole and Bland 1987; Sattelmacher *et al.* 1990; Klepper 1992; Oyanagi 1994; Barber 1995; Bonser *et al.* 1996; Manske *et al.* 2000; Lynch and Brown 2001; Stalham and Allen 2001; López-Bucio *et al.* 2002; Chevalier *et al.* 2003; Rubio *et al.* 2003; Gahoonia and Nielsen 2004a,b; Liao *et al.* 2004; Yan *et al.* 2004; Zhu and Lynch 2004; Ho *et al.* 2005; Malamy 2005; White *et al.* 2005a,b; Wissuwa 2005; Zhu *et al.* 2005, 2006; Reymond *et al.* 2006).

### ***Increased Pi uptake capacity***

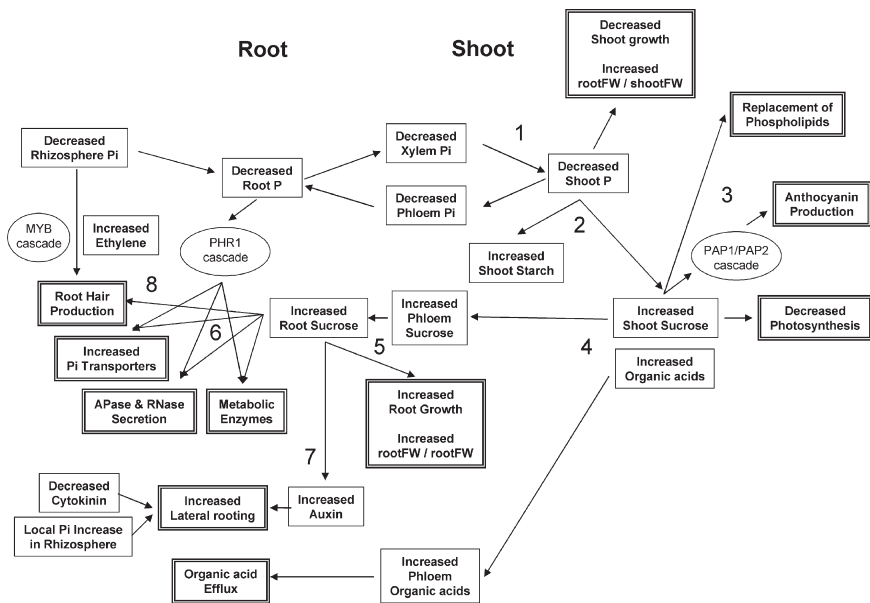
The Pi uptake capacity of plant root cells is also increased in P deficient plants (Epstein 1972; Lee *et al.* 1990; Schachtman *et al.* 1998; Smith FW *et al.* 2003; Raghothama and Karthikeyan 2005; Bucher 2007; Jain *et al.* 2007b) even in the mature, suberised parts of the root (Clarkson *et al.* 1978; Rubio *et al.* 2004), but this is not considered to be a major factor affecting P acquisition efficiency (Barber 1995; Horst *et al.* 2001; White *et al.* 2005a; Lambers *et al.* 2006). Differences in root:shoot biomass ratio, root growth rate, root hair production and root system morphology generally account for most variation in P acquisition efficiency between and within plant species (Ozanne *et al.* 1969; Fageria *et al.* 1988; Föhse *et al.* 1988, 1991; Baligar *et al.* 2001; Lynch and Brown 2001; Dechassa *et al.* 2003; Wissuwa 2003; Zhu and Lynch 2004; White *et al.* 2005a; Zhu *et al.* 2005), although the exudation of organic acids contributes to the exceptionally high P acquisition efficiency of some crops, such as brassica (Hoffland 1992; Dechassa *et al.* 2003) and white lupin (López-Bucio *et al.* 2000b).

### ***Improved symbiotic associations***

To increase their exploration of the soil, most land plants form associations with mycorrhizal fungi (Harrison 1999; Karandashov and Bucher 2005; Bucher 2007; Smith and Read 2007). This association can benefit both partners, with the fungi receiving C from the plants and the plants receiving P and other mineral elements from the fungi. It is estimated that between 4% and 20% of net photosynthate is transferred from plants to their fungal partners (Johnson *et al.* 1997; Morgan *et al.* 2005). In return, the fungal partner acquires the mineral elements for the symbiosis. The fungal hyphae enlarge the volume of soil explored, increase the surface area for Pi uptake, extend into soil pores too small for roots to enter and, in some cases, hydrolyze organic P compounds that plants cannot (Bielecki 1973; Harrison 1999; Karandashov and Bucher 2005; Morgan *et al.* 2005; Bucher 2007). Consequently, roots of mycorrhizal plants can acquire between three to five times more Pi than those of non-mycorrhizal plants when grown in low P soils (Bielecki 1973; Marschner 1995; Johnson *et al.* 1997; Smith SE *et al.* 2003; Smith and Read 2007). By contrast, when Pi is readily available to plants, the C costs of mycorrhizal associations are not compensated for by improved P nutrition and a reduced mycorrhizal colonization of roots is often observed (Johnson *et al.* 1997; Graham 2000; Morgan *et al.* 2005). It is, perhaps, also noteworthy that nodulation and nodule growth in legumes are increased as plant P status improves, and this beneficial symbiosis stimulates plant growth enormously (Marschner 1995; Vádez *et al.* 1999; Schulze *et al.* 2006; Raven 2008).

## CO-ORDINATING PLANT RESPONSES TO VARIATIONS IN P SUPPLY

Plants respond both to tissue P status, enabling the efficient use of C, N, S and P resources within the plant, and to local variations in soil Pi availability, enabling the proliferation of roots in Pi rich patches (Figure 4.3; White *et al.* 2005a; Amtmann *et al.* 2006; Hammond and White 2008a). 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 (Figure 4.3[1]; Jeschke *et al.* 1997; Mimura 1999) and the consequent reduction in the Pi available for shoot metabolism. This often results in an immediate reduction in shoot growth rate before root growth is affected (Clarkson and Scattergood 1982; Cogliatti and Clarkson 1983). A reduction in  $[Pi]_{\text{cyt}}$  impacts directly on photosynthesis, glycolysis and respiration (Plaxton and Carswell 1999; Hammond *et al.* 2004; Hammond and White 2008a), and changes in carbohydrate metabolism are reinforced by transcriptional reprogramming (Hammond *et al.* 2003, 2005; Wu *et al.* 2003; Misson *et al.* 2005; Hermans *et al.* 2006; Wasaki *et al.* 2006; Morcuende *et al.* 2007; Müller *et al.* 2007). This results in organic acids, starch and sucrose accumulating in leaves of P starved plants (Figure 4.3[2]; Rao *et al.* 1990; Cakmak *et al.* 1994; Ciereszko and Barbachowska 2000; Müller *et al.* 2004, 2005, 2007; Wissuwa *et al.* 2005; Hermans *et al.* 2006; Morcuende *et al.* 2007). Metabolism is rerouted by employing reactions that do not require Pi or adenylates



**Fig. 4.3** Hypothetical signaling cascades initiating acclimatory responses to P starvation. (Based on reviews by White *et al.* 2005a; Amtmann *et al.* 2006; and Hammond and White 2008a.)

(Plaxton and Carswell 1999; Vance *et al.* 2003; Hammond *et al.* 2004; Hammond and White 2008a) and, under severe P-deficiency, intracellular phosphatases and nucleases are induced that remobilize P from cellular metabolites and nucleic acids (Bariola *et al.* 1994; Berger *et al.* 1995; Bosse and Köck 1998; Brinch-Pedersen *et al.* 2002; Petters *et al.* 2002; Hammond *et al.* 2003; Wasaki *et al.* 2006; Morcuende *et al.* 2007; Müller *et al.* 2005, 2007). A general decrease in tissue RNA concentration is also observed (Hewitt *et al.* 2005). Increased leaf sucrose concentrations lead indirectly to (i) a reduction of photosynthesis through the downregulation of many photosystem subunits and small subunits of RuBisCo (Paul and Pellny 2003; Lloyd and Zakhleniuk 2004; Amtmann *et al.* 2006; Hermans *et al.* 2006; Rook *et al.* 2006), (ii) an increase in leaf sulfolipid and galactolipid concentrations through the upregulation of genes involved in their biosynthesis (Essigmann *et al.* 1998; Dörmann and Benning 2002; Yu *et al.* 2002; Andersson *et al.* 2003, 2005; Hammond *et al.* 2003; Frentzen 2004; Benning and Ohta 2005; Franco-Zorrilla *et al.* 2005; Misson *et al.* 2005; Cruz-Ramírez *et al.* 2006; Kobayashi *et al.* 2006; Li *et al.* 2006), and (iii) the production of anthocyanins through a transcriptional cascade involving the transcription factors TTG1-TT8/EGL3-PAP1/PAP2 (Figure 4.3[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 transporters delivering organic acids and sucrose to the phloem, which facilitates the movement of these compounds to the root (Figure 4.3[4]; Gaume *et al.* 2001; Hermans *et al.* 2006).

The preferential allocation of C to the root system, and the resulting increased root:shoot biomass ratio, appears to be a direct consequence of altered shoot metabolism and is mediated by increased translocation of sucrose to the root (Figure 4.3[5]; Hermans *et al.* 2006; Hammond and White 2008a). In addition, the sucrose delivered to the root acts as a systemic signal (indicating low shoot P status) that can initiate changes in gene expression to alter root biochemistry and remodel root morphology (Liu *et al.* 2005; Amtmann *et al.* 2006; Hermans *et al.* 2006; Hernández *et al.* 2007; Karthikeyan *et al.* 2007; Tesfaye *et al.* 2007; Hammond and White 2008a). Increased root sucrose concentrations appear to upregulate genes encoding riboregulators, Pi transporters, RNases, phosphatases and metabolic enzymes in combination with the PHR1 transcriptional cascade (Figure 4.3[6]), whilst its effects on lateral rooting occur through modulation of auxin transport (Figure 4.3[7]) and those on root hair development are contingent upon changes in auxin transport and the local production of ethylene (Figure 4.3[8]).

The PHR1 protein is a MYB transcription factor that binds to an imperfect-palindromic sequence (PIBS; GNATATNC) present in the promoter regions of many genes whose expression responds to P starvation (PSR genes). These include genes encoding transcription factors, protein kinases, Pi transporters, RNases, phosphatases, metabolic enzymes and enzymes involved in the synthesis of sulfolipids and galactolipids (Figure 4.3; Rubio *et al.* 2001; Hammond *et al.* 2004; Franco-Zorrilla *et al.* 2004; Schünmann *et al.* 2004; Misson *et al.* 2005; Jain *et al.* 2007b). 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). Since the *Arabidopsis siz1* mutant constitutively exhibits phenotypic characteristics of P-deficient plants, it is hypothesized that SIZ1 acts as a repressor of plant responses to P starvation (Miura *et al.* 2005). One target of the PHR1 protein appears to be the microRNA family, miR399 (Bari *et al.* 2006; Chiou 2007). The expression of miR399 is specifically and rapidly up-regulated by P starvation (Fujii *et al.* 2005; Bari *et al.* 2006; Chiou *et al.* 2006). The target gene for miR399 is an ubiquitin E2 conjugating enzyme, also identified as the gene responsible for the *pho2* mutant phenotype (*AtUBC24*; At2g33770; Sunkar and Zhu 2004; Fujii *et al.* 2005; Aung *et al.* 2006; Bari *et al.* 2006; Chiou *et al.* 2006) and the expression of *AtUBC24* is downregulated during P starvation (Fujii *et al.* 2005; Bari *et al.* 2006; Chiou *et al.* 2006). It is thought that *AtUBC24* is a negative regulator of the expression of a subset of P starvation responsive genes, possibly through other intermediary transcription factors (Chiou 2007). Interestingly, there is some sequence similarity between miR399 and the TPS11/Mt4/At4 family of non-coding transcripts, which allows them to bind to miR399 (Shin *et al.* 2006; Chiou 2007; Franco-Zorrilla *et al.* 2007). The expression of the TPS11/Mt4/At4 family is induced rapidly and specifically in response to P starvation (Liu *et al.* 1997; Burleigh and Harrison 1999; Martín *et al.* 2000; Hou *et al.* 2005; Shin *et al.* 2006), and these non-coding transcripts sequester miR399 and serve to attenuate the miR399-mediated transcriptional responses to P starvation (Franco-Zorrilla *et al.* 2007). The recent characterization of the *At4* T-DNA knockout mutant suggests that it has a role in the internal redistribution of P from the shoots to the roots (Shin *et al.* 2006). It has a similar phenotype to the *pho2* mutant, which accumulates more P in leaves than wildtype plants (Delhaize and Randall 1995).

Recently, it has become apparent that most alterations in root morphology in response to P starvation arise from the interplay of local and systemic signals. Changes in the concentration, transport and/or sensitivity to auxin, ethylene, cytokinin and sucrose have all been implicated in the remodeling of root morphology in P-deficient plants (Martín *et al.* 2000; Forde and Lorenzo 2001; López-Bucio *et al.* 2002, 2003, 2005; Al-Ghazi *et al.* 2003; Casimiro *et al.* 2003; Casson and Lindsey 2003; Ma *et al.* 2003; Vance *et al.* 2003; Hammond *et al.* 2004; Ticconi and Abel 2004; Franco-Zorrilla *et al.* 2005; Malamy 2005; Nacry *et al.* 2005; White *et al.* 2005a; Amtmann *et al.* 2006; Jain *et al.* 2007a; Karthikeyan *et al.* 2007; Hammond and White 2008a), and the observed changes in concentrations of plant growth regulators are consistent with changes in the expression of genes known to be regulated by, or involved in the regulation of, auxin, ethylene, cytokinin and sucrose in roots of P-deficient plants (Al-Ghazi *et al.* 2003; Casson and Lindsey 2003; Uhde-Stone *et al.* 2003; Wu *et al.* 2003; Misson *et al.* 2005; Hermans *et al.* 2006; Hernández *et al.* 2007).

Contact of the root cap of P-starved plants with media lacking Pi appears to be necessary and sufficient to reduce meristematic activity in primary roots and slow their growth, in a response mediated by multicopper oxidases (Ticconi *et al.* 2004; López-Bucio *et al.* 2005; Sánchez-Calderón *et al.* 2005, 2006; Svistoonoff *et al.* 2007; Jain *et al.* 2007a). 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; Robinson 1994; López-Bucio *et al.* 2003) but appears to be initiated by changes in auxin transport (López-Bucio *et al.* 2002, 2003, 2005; Al-Ghazi *et al.* 2003; Casimiro *et al.* 2003; Casson and Lindsey 2003; Malamy 2005; Nacry *et al.* 2005; Jain *et al.* 2007a), with greater sucrose availability increasing the responsiveness to auxin (Nacry *et al.* 2005; Jain *et al.* 2007a). It is also promoted by the reduction in cytokinin concentrations in roots of P-deficient plants (Martín *et al.* 2000; López-Bucio *et al.* 2002; Franco-Zorrilla *et al.* 2002), but the changes in cytokinin signaling during P starvation appear to be a secondary consequence of crosstalk between sugar and local P-signaling cascades (Franco-Zorrilla *et al.* 2005). This phenomenon is comparable to the proliferation of specialized cluster roots in regions of local Pi enrichment observed in diverse non-mycorrhizal plant species when they lack sufficient P (Dinkelaker *et al.* 1995; Shane *et al.* 2003; Shen *et al.* 2005; Lamont 2003; Lambers *et al.* 2006). The initiation and elongation of root hairs, once thought to be root cell autonomous, and regulated solely through local interactions between increasing auxin and ethylene concentrations (Bates and Lynch 1996; Jungk 2001; Casson and Lindsey 2003; Ma *et al.* 2003; Ticconi and Abel 2004; Zhang *et al.* 2003; He *et al.* 2005; Amtmann *et al.* 2006), now also appears to be modulated by plant P status through sucrose supply to the roots, since the roots of P starved plants have more and longer root hairs when supplied with sucrose (Jain *et al.* 2007a). 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)

## **THE INFLUENCE OF P NUTRITION ON THE ECOLOGY OF TERRESTRIAL PLANTS**

The most limiting, or most toxic, mineral element in an environment is likely to determine its ecology. In terrestrial ecosystems, recent anthropogenic inputs have raised N availability and most environments are now limited by the availability of P (Chapin *et al.* 1986; Güsewell 2004; Wassen *et al.* 2005). Thus, P availability will determine both primary production and species diversity of these ecosystems. In wild plants, as in agricultural plants, competitive advantage is gained by effective P acquisition and efficient utilization of P for growth and reproduction, and wild plants show the full range of responses to low P availability described in the previous sections. One proxy for the competitive ability of a species growing on P-limited soils is a high tissue N:P ratio, although slow growing species, perennials and legumes can provide exceptions (Güsewell 2004; Niklas 2008). The remobilization of P from senescing to developing leaves (Aerts 1996; Aerts and Chapin 2000; McGroddy *et al.* 2004; Güsewell 2005), and the storage of P between growth seasons (Güsewell *et al.* 2003; Güsewell 2004), are important factors for the P economy of wild plants, as is the ability to maintain the P-demands of symbiotic N-fixation in N-limited environments (Raven 2008). Supplying reproductive tissues

with P is essential. Seeds have higher N and P concentrations and lower N:P ratios than vegetative tissues, and wild plants typically allocate between 15% and 60% of their P to reproduction depending upon P availability in their environment (Fenner 1986; Güsewell 2004). Tissue N:P ratio also determines the vulnerability of plants to herbivores, decomposers and pathogens.

In soils with extremely low P availability, such as those of Western Australia and South Africa, plants must be capable of acquiring P from less abundant and less readily-available P sources. This often requires special adaptations, and the flora of these regions is dominated by non-mycorrhizal plants that utilize tissue P efficiently and produce lateral or cluster roots that secrete citrate in local patches of P-rich soil (Dinkelaker *et al.* 1995; Lamont 2003; Lambers *et al.* 2006). Such plants include *Lupinus* and *Kennedia* (Fabales), Cyperaceae and Juncaceae (Poales), and Proteaceae (Proteales). Similarly, species that can solubilize P effectively in clayey, acid or alkaline soils often dominate the vegetation of these areas. Thus, it is noteworthy that calcicole and calcifuge plants differ in their efflux of organic acids (Ström 1997; Jones 1998). The ability to form mycorrhizal associations does not appear to be a specific adaptation to low P availability, since it was an obligate requirement for plants to colonize the land and most plant species maintain these associations (Karandashov and Bucher 2005; Smith and Read 2007). However, the costs and benefits to plants of this symbiosis depend critically on P availability and plant P requirements, and it may be disadvantageous under some circumstances (Johnson *et al.* 1997; Graham 2000; Morgan *et al.* 2005). In less extreme environments, slower-growing stress-tolerant species with low tissue P requirements and high N:P ratios often dominate when P is limiting (Thompson *et al.* 1997; Grime *et al.* 1997; Aerts and Chapin 2000; Grime 2001; Güsewell 2004). Since graminoids generally have lower tissue P concentrations and higher tissue N:P ratios than forbs, mixed pastures on soils with a low P availability are generally dominated by grasses that can also acquire Pi effectively (Güsewell 2004). It is thought that the diversity of plant species is highest in P-limited soils since P is relatively immobile in the soil and different plants show contrasting foraging strategies and/or acquire P from different sources, thereby minimizing competition (Janssens *et al.* 1998; Güsewell 2004; McCrea *et al.* 2004; Güsewell *et al.* 2005). In fact, a recent survey of temperate Eurasia suggests that P-limitation favors the persistence of endangered plant species (Wassen *et al.* 2005). However, this is not always observed. For example, shifts in the dominance of clonal graminoids can reduce the diversity of plant species on soils with low P availability through exclusion (Güsewell 2004).

Species composition changes rapidly after mineral fertilization and the long-term effects of a single fertilization event can persist for many decades, through its combined effects on plant and microbial community structures (Güsewell 2004). In the first year, the effects of fertilisation are often determined by the responses of species that dominated the original plant community that grow rapidly or are better able to exploit the timing or method of fertilisation. In subsequent years, subordinate or new species with different nutrient requirements may increase in abundance and reach dominance. Intriguingly, a heterogeneous distribution of mineral availability can increase the total biomass of plant communities more than a homogeneous

supply (Hutchings and John 2004). It is expected that P-fertilisation will promote the growth of faster-growing plants with higher P requirements for growth and lower tissue N:P ratios (e.g. Bradshaw *et al.* 1960; Mamolos *et al.* 1995; Thompson *et al.* 1997; Elser *et al.* 2000b; Güsewell *et al.* 2003). These are primarily ruderal plant species, which are often annual species or short-lived perennials with high reproductive allocation and, consequently, greater P requirements, but also include competitive plant species (Thompson *et al.* 1997; Güsewell 2004; Han *et al.* 2005). An increase in the abundance of forbs and bryophytes, relative to grasses, is often observed following P fertilization (Güsewell 2004). In addition, since P-fertilisation promotes the growth of legumes and nitrogenase activity in their nodules (Smith 1992; Stöcklin *et al.* 1998), P-fertilisation of a N-limited environment can alter plant communities dramatically by increasing N availability.

## PHOSPHORUS MANAGEMENT FOR SUSTAINABLE AGRICULTURE

Given that P limits agricultural productivity, and that Pi fertilizers are a finite resource, agronomists and plant breeders must work together to reduce the Pi-fertilizer inputs to agriculture without compromising yield or quality. This might be effected by improved agronomic strategies, greater use of alternative P-fertilizers, such as manures, animal wastes and recovered phosphates (Raven 2008), and through the development of crop genotypes that are more efficient in acquiring P from the soil and/or in utilizing P more economically in their tissues (Gahoonia and Nielsen 2004a; White *et al.* 2005a; Lambers *et al.* 2006).

In many developed countries, generous applications of P fertilizers in the past have led to an increase in soil P reserves, especially in arable areas, and many crops now show little response to P-fertilizer applications (Mengel and Kirkby 2001; Kirkby and Johnston 2008). In these circumstances, recommended fertilizer applications are often based on replacing P losses to the environment plus the P offtake by crops (e.g. Defra 2000). To reduce P fertilizer inputs to these crops, management practices should optimize the timing, placement and formulation of P-fertilizers to reduce P losses to the environment. This can be assisted by the use of decision support systems (Mengel 1997; Heathwaite *et al.* 2003; Fixen 2005; Zhang *et al.* 2007; Hammond and White 2008b), modern fertilizer placement techniques (Bryson 2005; Gregory and George 2005; White *et al.* 2005b) and the use of slow release fertilizers (Perrott and Kear 2000). These techniques can be complemented by growing crops that acquire P effectively from agricultural soils. For example, since P becomes concentrated in the surface/ploughed layers of agricultural soils, crop genotypes with a topsoil foraging phenotype would maximize P acquisition, but could make them susceptible to other edaphic or climatic stresses, such as drought. To reduce the P off-take by crops, the plant P requirements for optimal yields must be minimized. In regions where low soil P availability compromises crop production, which apparently exceed 5.7 billion hectares of potential agricultural land



worldwide, improved agronomic practice and plant breeding should aim to increase P availability and acquisition. Liming can improve P availability in Pi-fixing soils with low pH (Mengel and Kirkby 2001). In some situations, the incorporation of soil organic matter into soils will improve the use of soil and fertilizer P, since organic compounds compete with Pi for binding sites on clays (Mengel 1997; Horst *et al.* 2001). Crop traits that improve P availability and acquisition include the development of an extensive root system, the release of organic acids and enzymes into the rhizosphere and the cultivation of beneficial associations with soil microorganisms. Again, a reduced plant P requirement for optimal yields may be beneficial.

The P-use efficiency (PUE) of plants has been defined in many ways (Gourley *et al.* 1994; Baligar *et al.* 2001; Greenwood *et al.* 2005; Gregory and George 2005; White *et al.* 2005a). The following four definitions are used most often: (1) the increase in yield per unit P in the soil, which is often referred to as agronomic P efficiency (APE), (2) the amount of P in a plant divided by its root biomass, which is referred to as P acquisition efficiency (PAE), (3) the amount of P in a plant divided by the amount of P in the soil, which is referred to as P uptake efficiency (PUPE), and (4) crop yield divided by amount of P in the plant, which is referred to as tissue, or physiological, P utilization efficiency (PUtE). It will be apparent that APE is the product of PUPE and PUtE. For this reason, genetic strategies to increase the yield of crops on low P soils have focused on improving P acquisition by roots and tissue P utilization efficiency.

Earlier in this chapter, it was observed that greater root:shoot biomass ratios, root growth rates and root hair production, together with the proliferation of lateral roots in regions of local P availability and the exudation of organic acids and enzymes into the rhizosphere are the traits required for effective P mobilization and acquisition by plants. There is considerable genetic variation in all these traits in most crops, which might be selected through conventional breeding programs. In addition, it has been suggested that knowledge of the mechanisms whereby plants sense and respond to P availability in soils could facilitate selection, breeding and GM approaches to improve crop production on soils with low P availability (Vance *et al.* 2003; Hammond *et al.* 2004; White *et al.* 2005a; Jain *et al.* 2007b). The transcriptional cascades controlling appropriate facets of root morphology and/or the release of organic acids and enzymes into the rhizosphere could be targeted. Transgenic plants secreting more and/or different organic acids and hydrolytic enzymes into the rhizosphere have been engineered (Koyama *et al.* 2000; López-Bucio *et al.* 2000a,b; Richardson *et al.* 2001; Mudge *et al.* 2003; Zimmermann *et al.* 2003; George *et al.* 2004, 2005a,b; Xiao *et al.* 2005, 2006; George and Richardson 2008). However, although these genetic manipulations have shown promising results, they have not always been successful in promoting plant growth in natural soils (Delhaize *et al.* 2001; George *et al.* 2004, 2005a,b; George and Richardson 2008).

There is considerable variation both between and within crop species in the critical tissue P concentration required for maximum growth (Fageria *et al.* 1988; Fageria and Baligar 1997, 1999; Baligar *et al.* 2001; Osborne and Rengel 2002; Bentsink

*et al.* 2003; Trehan and Sharma 2003; Zhu and Lynch 2004; Ozturk *et al.* 2005; White *et al.* 2005a,b). However, differences in the response of yield to P fertilisation do not appear to be correlated with PUE (Greenwood *et al.* 1980; Alt 1987; Föhse *et al.* 1988; Fageria and Baligar 1999; Ozturk *et al.* 2005). Thus, selection for greater PUE does not appear to be an effective strategy for developing crops that yield well on soils with low P availability. However, genotypes of crops that yield well and have lower tissue P concentrations can be used to reduce P-fertilizer inputs to soils on that require only maintenance P fertilisation.

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## REFERENCES

- Aerts R (1996) Nutrient resorption from senescing leaves of perennials: are there general patterns? *J Ecol* 84: 597–608
- Aerts R, Chapin FS (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv Ecol Res* 30: 1–67
- Ågren GI (1988) Ideal nutrient productivities and nutrient proportions in plant growth. *Plant Cell Environ* 11: 613–620
- Al-Ghazi Y, Muller B, Pinloche S, Tranbarger TJ, Nacry P, Rossignol M, Tardieu F, Dumas P (2003) Temporal responses of *Arabidopsis* root architecture to phosphate starvation: evidence for the involvement of auxin signalling. *Plant Cell Environ* 26: 1053–1066
- Alt D (1987) Influence of P- and K-fertilization on yield of different vegetable species. *J Plant Nutr* 10: 1429–1435
- Amtmann A, Hammond JP, Armengaud P, White PJ (2006) Nutrient sensing and signalling in plants: potassium and phosphorus. *Adv Bot Res* 43: 209–257
- Andersson MX, Stridh MH, Larsson KE, Liljenberg C, Sandelius AS (2003) Phosphate-deficient oat replaces a major portion of the plasma membrane phospholipids with the galactolipid digalactosyldiacylglycerol. *FEBS Lett* 537: 128–132
- Andersson MX, Larsson KE, Tjellström H, Liljenberg C, Sandelius AS (2005) Phosphate-limited oat. The plasma membrane and the tonoplast as major targets for phospholipid-to-glycolipid replacement and stimulation of phospholipases in the plasma membrane. *J Biol Chem* 280: 27578–27586
- Asmar F, Gahoonia TS, Nielsen NE (1995) Barley genotypes differ in activity of soluble extracellular phosphatase and depletion of organic phosphorus in the rhizosphere soil. *Plant Soil* 172: 117–122
- 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
- Baligar VC, Fageria NK, He ZL (2001) Nutrient use efficiency in plants. *Commun Soil Sci Plant Anal* 32: 921–950
- Barber SA (1995) *Soil Nutrient Bioavailability: A Mechanistic Approach*. Wiley, New York
- Barea JM, Pozo MJ, Azcón R, Azcón-Aguilar C (2005) Microbial co-operation in the rhizosphere. *J Exp Bot* 56: 1761–1778
- 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

- Bariola PA, Howard CJ, Taylor CB, Verburg MT, Jaglan VD, Green PJ (1994) The *Arabidopsis* ribonuclease gene *RNS1* is tightly controlled in response to phosphate limitation. *Plant J* 6: 673–685
- 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
- Beebe S, Lynch J, Galwey N, Tohme J, Ochoa I (1997) A geographical approach to identify phosphorus-efficient genotypes among landraces and wild ancestors of common bean. *Euphytica* 95: 325–336
- Benning C, Ohta H (2005) Three enzyme systems for galactoglycerolipid biosynthesis are coordinately regulated in plants. *J Biol Chem* 280: 2397–2400
- Bentsink L, Yuan K, Koorneef M, Vreugdenhil D (2003) The genetics of phytate and phosphate accumulation in seeds and leaves of *Arabidopsis thaliana*, using natural variation. *Theor Appl Genet* 106: 1234–1243
- Berger S, Bell E, Sadka A, Mullet JE (1995) *Arabidopsis thaliana Atvsp* is homologous to soybean *VspA* and *VspB*, genes encoding vegetative storage protein acid phosphatases, and is regulated similarly by methyl jasmonate, wounding, sugars, light and phosphate. *Plant Mol Biol* 27: 933–942
- Bergmann W (1992) Nutritional Disorders of Plants. Visual and Analytical Diagnosis. Gustav Fischer, Jena, Germany
- Bielecki RL (1973) Phosphate pools, phosphate transport, and phosphate availability. *Ann Rev Plant Physiol* 24: 225–252
- Blackshaw RE, Brandt RN, Janzen HH, Entz T (2004) Weed species response to phosphorus fertilization. *Weed Sci* 42: 406–412
- Bolland MDA, Siddique KHM, Loss SP, Baker MJ (1999) Comparing responses of grain legumes, wheat and canola to applications of superphosphate. *Nutr Cycl Agroecosyst* 53: 157–175
- Bonser AM, Lynch J, Snapp S (1996) Effect of phosphorus deficiency on growth angle of basal roots in *Phaseolus vulgaris*. *New Phytol* 132: 281–288
- Bosse D, Köck M (1998) Influence of phosphate starvation on phosphohydrolases during development of tomato seedlings. *Plant Cell Environ* 21: 325–332
- Bould C, Hewitt EJ, Needham P (1983) Diagnosis of Mineral Disorders in Plants. Volume 1: Principles. HMSO, London
- Bradshaw AD, Chadwick MJ, Jowett D, Lodge RW, Snaydon RW (1960) Experimental investigations into the mineral nutrition of several grass species. Part III: phosphate level. *J Ecol* 48: 631–637
- Brinch-Pedersen H, Sorensen LD, Holm PB (2002) Engineering crop plants: getting a handle on phosphate. *Trends Plant Sci* 7: 118–125
- Broadley MR, Bowen HC, Cotterill HL, Hammond JP, Meacham MC, Mead A, White PJ (2004) Phylogenetic variation in the shoot mineral concentration of angiosperms. *J Exp Bot* 55: 321–336
- Bryson R (2005) Proceedings of the International Fertiliser Society 577. Improvements in Farm and Nutrient Management Through Precision Farming. IFS, York
- Bucher M (2007) Functional biology of plant phosphate uptake at root and mycorrhiza interfaces. *New Phytol* 173: 11–26
- Burleigh SH, Harrison MJ (1999) The down-regulation of *Mt4*-like genes by phosphate fertilization occurs systemically and involves phosphate translocation to the shoots. *Plant Physiol* 119: 241–248
- Cakmak I, Hengeler C, Marschner H (1994) Partitioning of shoot and root dry matter and carbohydrates in bean plants suffering from phosphorus, potassium and magnesium deficiency. *J Exp Bot* 45: 1245–1250
- Casimiro I, Beekman T, Graham N, Bhalerao R, Zhang H, Casero P, Sandberg G, Bennett MJ (2003) Dissecting *Arabidopsis* lateral root development. *Trends Plant Sci* 8: 165–171
- Casson SA, Lindsey K (2003) Genes and signalling in root development. *New Phytol* 158: 11–38
- Chapin FS, Vitousek PM, Vanclve K (1986) The nature of nutrient limitation in plant-communities. *Am Nat* 127: 48–58

- Chevalier F, Pata M, Nacry P, Doumas P, Rossignol M (2003) Effects of phosphate availability on the root system architecture: large scale analysis of the natural variation between *Arabidopsis* accessions. *Plant Cell Environ* 26: 1839–1850
- 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
- Ciereszko I, Barbachowska A (2000) Sucrose metabolism in leaves and roots of bean (*Phaseolus vulgaris* L.) during phosphate deficiency. *J Plant Physiol* 156: 640–644
- Clarkson DT, Scattergood CB (1982) Growth and phosphate transport in barley and tomato plants during the development of, and recovery from, phosphate stress. *J Exp Bot* 33: 865–875
- Clarkson DT, Sanderson J, Scattergood CB (1978) Influence of phosphate-stress on phosphate absorption and translocation by various parts of the root system of *Hordeum vulgare* L. (barley). *Planta* 139: 47–53
- Coello P (2002) Purification and characterization of secreted acid phosphatase in phosphorus-deficient *Arabidopsis thaliana*. *Physiol Plant* 116: 293–298
- Cogliatti DH, Clarkson DT (1983) Physiological changes in, and phosphate uptake by potato plants during development of, and recovery from phosphate deficiency. *Physiol Plant* 58: 287–294
- Cohen D (2007) Earth's natural wealth: an audit. *New Scientist* 2605: 35–41
- Coltman RR, Gerloff GC, Gabelman WH (1986) Equivalent stress comparisons among tomato strains differentially tolerant to phosphorus deficiency. *J Am Soc Hort Sci* 111: 422–426
- Coruzzi G, Last R (2000) Amino acids. In: Buchanan BB, Gruissem W, Jones RL (eds), *Biochemistry & Molecular Biology of Plants*. ASPP, Rockville, MD, pp 358–419
- Cruz-Ramírez A, Oropeza-Aburto A, Razo-Hernández F, Ramírez-Chávez E, Herrera-Estrella L (2006) Phospholipase D $\zeta$ 2 plays an important role in extraplasmidic galactolipid biosynthesis and phosphate recycling in *Arabidopsis* roots. *Proc Natl Acad Sci USA* 103: 6765–6770
- Dakora FD, Phillips DA (2002) Root exudates as mediators of mineral acquisition in low-nutrient environments. *Plant Soil* 245: 35–47
- Dechassa N, Schenk MK (2004) Exudation of organic anions by roots of cabbage, carrot, and potato as influenced by environmental factors and plant age. *J Plant Nutr Soil Sci* 167: 623–629
- Dechassa N, Schenk MK, Claassen N, Steingrobe B (2003) Phosphorus efficiency of cabbage (*Brassica oleraceae* L. var. *capitata*), carrot (*Daucus carota* L.), and potato (*Solanum tuberosum* L.). *Plant Soil* 250: 215–224
- Defra (2000) Fertiliser Recommendations for Agricultural and Horticultural Crops (RB209) (7th edition). HMSO, Norwich
- Delhaize E, Randall PJ (1995) Characterization 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 is not associated with either enhanced citrate accumulation or efflux. *Plant Physiol* 125: 2059–2067
- Delhaize E, Gruber BD, Ryan PR (2007) The roles of organic anion permeases in aluminium resistance and mineral nutrition. *FEBS Lett* 581: 2255–2262
- Dennis DT, Blakeley SD (2000) Carbohydrate metabolism. In: Buchanan BB, Gruissem W, Jones RL (eds), *Biochemistry & Molecular Biology of Plants*. ASPP, Rockville, MD, pp 630–675
- Dinkelaker B, Hengeler C, Marschner H (1995) Distribution and function of proteoid roots 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
- 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
- Elser JJ, Fagan WF, Denno RF, Dobberfuhl DR, Folarin A, Huberty A, Interlandi S, Kilham SS, McCauley E, Schulz KL, Siemann EH, Sterner RW (2000a) Nutritional constraints in terrestrial and freshwater food webs. *Nature* 408: 578–580
- Elser JJ, Sterner RW, Gorokhova E, Fagan WF, Markow TA, Cotner JB, Harrison JF, Hobbie SE, Odell GM, Weider LJ (2000b) Biological stoichiometry from genes to ecosystems. *Ecol Lett* 3: 540–550

- Epstein E (1972) Mineral Nutrition of Plants: Principles and Perspectives. Wiley, New York
- Essigmann B, Güler S, Narang RA, Linke D, Benning C (1998) Phosphate availability affects the thylakoid lipid composition and the expression of *SQD1*, a gene required for sulfolipid biosynthesis in *Arabidopsis thaliana*. Proc Natl Acad Sci USA 95: 1950–1955
- Fageria NK, Baligar VC (1997) Phosphorus use efficiency by corn genotypes. J Plant Nutr 20: 1267–1277
- Fageria NK, Baligar VC (1999) Phosphorus-use efficiency in wheat genotypes. J Plant Nutr 22: 331–340
- Fageria NK, Wright RJ, Baligar VC (1988) Rice cultivar evaluation for phosphorus use efficiency. Plant Soil 111: 105–109
- Fenner M (1986) The allocation of minerals to seeds in *Senecio vulgaris* plants subjected to nutrient shortage. J Ecol 74: 385–392
- Fixen PE (2005) Proceedings of the International Fertiliser Society 569. Decision Support Systems in Integrated Crop Nutrient Management. IFS, York
- Flügge U-I, Häusler RE, Ludewig F, Fischer K (2003) Functional genomics of phosphate antiport systems of plastids. Physiol Plant 118: 475–482
- Föhse D, Claassen N, Jungk A (1988) Phosphorus efficiency of plants. I. External and internal P requirement and P uptake efficiency of different plant species. Plant Soil 110: 101–109
- 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
- Forde B, Lorenzo H (2001) The nutritional control of root development. Plant Soil 232: 51–68
- Franco-Zorrilla JM, Martín AC, Solano R, Rubio V, Leyva A, Paz-Ares J (2002) Mutations at *CRE1* impair cytokinin-induced repression of phosphate starvation responses in *Arabidopsis*. Plant J 32: 353–360
- 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. Nature Genet 39: 1033–1037
- Frentzen M (2004) Phosphatidylglycerol and sulfoquinovosyldiacylglycerol: anionic membrane lipids and phosphate regulation. Curr Opin Plant Biol 7: 270–276
- Fujii H, Chiou TJ, Lin SI, Aung K, Zhu JK (2005) A miRNA involved in phosphate-starvation response in *Arabidopsis*. Current Biol 15: 2038–2043
- Gahoonia TS, Nielsen NE (2004a) Root traits as tools for creating phosphorus efficient crop varieties. Plant Soil 260: 47–57
- Gahoonia TS, Nielsen NE (2004b) Barley genotypes with long root hairs sustain high grain yields in low-P field. Plant Soil 262: 55–62
- Garten CT (1976) Correlations between concentrations of elements in plants. Nature 261: 686–688
- Gaude N, Tippmann H, Flemetakis E, Katinakis P, Udvardi M, Dormann P (2004) The galactolipid digalactosyldiacylglycerol accumulates in the peribacteroid membrane of nitrogen-fixing nodules of soybean and *Lotus*. J Biol Chem 279: 34624–34630
- Gaume A, Mächler F, De León 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: White PJ, Hammond JP (eds), The Ecophysiology of Plant-Phosphorus Interactions. Springer, Dordrecht, The Netherlands, pp 247–270
- 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, Richardson AE, Smith JB, Hadobas PA, Simpson RJ (2005a) 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, Simpson RJ, Hadobas PA, Richardson AE (2005b) Expression of a fungal phytase gene in *Nicotiana tabacum* improves phosphorus nutrition in plants grown in amended soil. *Plant Biotech J* 3: 129–140
- 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 explain differences in the P nutrition of plants when grown in soil. *Environ Exp Bot* (in press)
- Górny AG, Sodikiewicz T (2001) Genetic analysis of the nitrogen and phosphorus utilization efficiencies in mature spring barley plants. *Plant Breeding* 120: 129–132
- Gourley CJP, Allan DL, Russelle MP (1994) Plant nutrient efficiency: a comparison of definitions and suggested improvement. *Plant Soil* 158: 29–37
- Graham JH (2000) Assessing the costs of arbuscular mycorrhizal symbiosis in agroecosystems. In: Podilha GK, Douds DD (eds), *Current Advances in Mycorrhizae Research*. APS Press, St Paul, MN, pp 127–142
- Green DG, Ferguson WS, Warder FG (1973) Accumulation of toxic levels of phosphorus in the leaves of phosphorus-deficient barley. *Can J Plant Sci* 53: 241–246
- Greenwood DJ, Cleaver TJ, Turner MK, Hunt J, Niendorf KB, Loquens SMH (1980) Comparison of the effects of phosphate fertilizer on the yield, phosphate content and quality of 22 different vegetable and agricultural crops. *J Agric Sci* 95: 457–469
- Greenwood DJ, Stellacci AM, Meacham MC, Broadley MR, White PJ (2005) Phosphorus response components of different *Brassica oleracea* genotypes are reproducible in different environments. *Crop Sci* 45: 1728–1735
- Greenwood DJ, Stellacci AM, Meacham MC, Mead A, Broadley MR, White PJ (2006) Relative values of physiological parameters of P response of different genotypes can be measured in experiments with only two P treatments. *Plant Soil* 281: 159–172
- Gregory PJ, George TS (2005) Soil Management for Nutrient Use Efficiency - An Overview. *Proceedings* 564, International Fertiliser Society, York.
- Grime JP (2001) *Plant Strategies, Vegetation Processes, and Ecosystem Properties* (2nd edition). Wiley, Chichester
- Grime JP, Thompson K, Hunt R, Hodgson JG, Cornelissen JHC, Rorison IH, Hendry GAF, Ashenden TW, Askew AP, Band SR, Booth RE, Bossard CC, Campbell BD, Cooper JEL, Davison AW, Gupta PL, Hall W, Hand DW, Hannah MA, Hillier SH, Hodgkinson DJ, Jalili A, Liu Z, Mackey JML, Matthews N, Mowforth MA, Neal AM, Reader RJ, Reiling K, Ross-Fraser W, Spencer RE, Sutton F, Tasker DE, Thorpe PC, Whitehouse J (1997) Integrated screening validates primary axes of specialisation in plants. *Oikos* 79: 259–281
- Gunawardena SFBN, Danso SKA, Zapata F (1993) Phosphorus requirement and sources of nitrogen in three soybean (*Glycine max*) genotypes, Bragg, nts 382 and Chippewa. *Plant Soil* 151: 1–9
- Güsewell S (2004) N:P ratios in terrestrial plants: variation and functional significance. *New Phytol* 164: 243–266
- Güsewell S (2005) Nutrient resorption of wetland graminoids is related to the type of nutrient limitation. *Funct Ecol* 19: 344–354
- Güsewell S, Koerselman W (2002) Variation in nitrogen and phosphorus concentrations of wetland plants. *Perspect Plant Ecol Evol Syst* 5: 37–61
- Güsewell S, Bollens U, Ryser P, Klötzli F (2003) Contrasting effects of nitrogen, phosphorus and water regime on first- and second-year growth of 16 wetland plant species. *Funct Ecol* 11: 754–765
- Güsewell S, Bailey KM, Roem WJ, Bedford BL (2005) Nutrient limitation and botanical diversity in wetlands: can fertilisation raise species richness? *Oikos* 109: 71–80
- Hammond JP, White PJ (2008a) Sucrose transport in the phloem: integrating root responses to phosphorus starvation. *J Exp Bot* 59: 93–109

- Hammond JP, White PJ (2008b) Diagnosing phosphorus deficiency in crops. In: White PJ, Hammond JP (eds), *The Ecophysiology of Plant-Phosphorus Interactions*. Springer, Dordrecht, The Netherlands, pp 225–246
- 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
- Han W, Fang J, Guo D, Zhang Y (2005) Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. *New Phytol* 168: 377–385
- 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
- Harrison MJ (1999) Molecular and cellular aspects of the arbuscular mycorrhizal symbiosis. *Annu Rev Plant Physiol Plant Mol Biol* 50: 361–389
- Härtel H, Dörmann P, Benning C (2000) DGD1-independent biosynthesis of extraplastidic galactolipids after phosphate deprivation in *Arabidopsis*. *Proc Natl Acad Sci USA* 97: 10649–10654
- He Z, Ma Z, Brown KM, Lynch JP (2005) Assessment of inequality of root hair density in *Arabidopsis thaliana* using the Gini coefficient: a close look at the effect of phosphorus and its interaction with ethylene. *Ann Bot* 95: 287–293
- Heathwaite L, Sharpley A, Bechmann M (2003) The conceptual basis for a decision support framework to assess the risk of phosphorus loss at the field scale across Europe. *J Plant Nutr Soil Sci* 166: 447–458
- Hedley MJ, Mortvedt JJ, Bolan NS, Syers JK (1995) Phosphorus fertility management in agroecosystems. In: Tiessen H (ed), *Phosphorus in the Global Environment. Transfers Cycles and Management*, Wiley, Chichester, pp 59–92
- 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
- Hernández G, Ramírez M, Valdés-López O, Tesfaye M, Graham MA, Czechowski T, Schlereth A, Wandrey M, Erban A, Cheung F, Wu HC, Lara M, Town CD, Kopka J, Udvardi MK, Vance CP (2007) Phosphorus stress in common bean: root transcript and metabolic responses. *Plant Physiol* 144: 752–767
- 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
- 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
- Hipps NA, Davies MJ, Dodds P, Buckley GP (2005) The effects of phosphorus nutrition and soil pH on the growth of some ancient woodland indicator plants and their interaction with competitor species. *Plant Soil* 271: 131–141
- Ho MD, Rosas JC, Brown KM, Lynch JP (2005) Root architectural tradeoffs for water and phosphorus acquisition. *Funct Plant Biol* 32: 737–748
- Hoch WA, Zeldin EL, McCown BH (2001) Physiological significance of anthocyanins during autumnal leaf senescence. *Tree Physiol* 21: 1–8
- Hocking P (2001) Organic acids exuded from roots in phosphorus uptake and aluminium tolerance of plants in acid soils. *Adv Agron* 74: 63–97
- Hodge A (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytol* 162: 9–24

- Hoffland E (1992) Quantitative evaluation of the role of organic acid exudation in the mobilization of rock phosphate by rape. *Plant Soil* 140: 279–289
- Horst WJ, Kamh M, Jibrin JM, Chude VO (2001) Agronomic measures for increasing P availability to crops. *Plant Soil* 237: 211–223
- Hou XL, Wu P, Jiao FC, Jia QJ, Chen HM, Yu J, Song XW, Yi KK (2005) Regulation of the expression of *OsIPS1* and *OsIPS2* in rice via systemic and local Pi signalling and hormones. *Plant Cell Environ* 28: 353–364
- Hutchings MJ, John EA (2004) The effects of environmental heterogeneity on root growth and root/shoot partitioning. *Ann Bot* 94: 1–8
- Ishikawa S, Adu-Gyamfi JJ, Nakamura T, Yoshihara T, Watanabe T, Wagatsuma T (2002) Genotypic variability in phosphorus solubilising activity of root exudates by pigeon pea grown in low-nutrient environments. *Plant Soil* 245: 71–81
- 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 Breeding Rev* 29: 359–419
- Janssens F, Peeters A, Tallwin JRB, Bakker JP, Bekker RM, Fillat F, Oomes MJM (1998) Relationship between soil chemical factors and grassland diversity. *Plant Soil* 202: 69–78
- Jeschke WD, Kirkby EA, Peuke AD, Pate JS, Hartung W (1997) Effects of P deficiency on assimilation and transport of nitrate and phosphate in intact plants of castor bean (*Ricinus communis* L.). *J Exp Bot* 48: 75–91
- Johnson NC, Graham JH, Smith FA (1997) Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytol* 135: 575–586
- Johnston AE, Lane PW, Mattingly GEG, Poulton PR, Hewitt MV (1986) Effects of soil and fertilizer P on yields of potatoes, sugar beet, barley and winter wheat on a sandy clay loam soil at Saxmundham, Suffolk. *J Agric Sci* 106: 155–167
- Jones DL (1998) Organic acids in the rhizosphere - a critical review. *Plant Soil* 205: 25–44
- Jones DL, Dennis PG, Owen AG, van Hees PAW (2003) Organic acid behavior in soils - misconceptions and knowledge gaps. *Plant Soil* 248: 31–41
- Jouhet J, Maréchal E, Baldan B, Bligny R, Joyard J, Block MA (2004) Phosphate deprivation induces transfer of DGDG galactolipid from chloroplast to mitochondria. *J Cell Biol* 167: 863–874
- Jungk A (2001) Root hairs and the acquisition of plant nutrients from soil. *J Plant Nutr Soil Sci* 164: 121–129
- Karandashov V, Bucher M (2005) Symbiotic phosphate transport in arbuscular mycorrhizas. *Trends Plant Sci* 10: 22–29
- 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
- Kerkhoff AJ, Fagan WF, Elser JJ, Enquist BJ (2006) Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. *Am Nat* 168: E103–E122
- Kirkby EA, Johnston AE (2008) Soil and fertilizer phosphorus in relation to crop nutrition. In: White PJ, Hammond JP (eds), *The Ecophysiology of Plant-Phosphorus Interactions*. Springer, Dordrecht, The Netherlands, pp 177–223
- Klepper B (1992) Development and growth of crop root systems. *Adv Soil Sci* 19: 1–25
- Kobayashi K, Masuda T, Takamiya K-I, Ohta H (2006) Membrane lipid alteration during phosphate starvation is regulated by phosphate signaling and auxin/cytokinin cross-talk. *Plant J* 47: 238–248
- Koyama H, Kawamura 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
- Laegreid M, Bøckman OC, Kaarstad O (1999) *Agriculture, Fertilizers and the Environment*. CABI, Wallingford



- 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
- Lee RB, Ratcliffe RG, Southon TE (1990)  $^{31}\text{P}$  NMR measurements of the cytoplasmic and vacuolar Pi content of mature maize roots: relationships with phosphorus status and phosphate fluxes. *J Exp Bot* 41: 1063–1078
- 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 M, Welti R, Wang X (2006) Quantitative profiling of Arabidopsis polar glycerolipids in response to phosphorus starvation. Roles of phospholipases D $\zeta$ 1 and D $\zeta$ 2 in phosphatidylcholine hydrolysis and digalactosyldiacylglycerol accumulation in phosphorus-starved plants. *Plant Physiol* 142: 750–761
- Liao H, Yan X, Rubio G, Beebe SE, Blair MW, Lynch JP (2004) Genetic mapping of basal root gravitropism and phosphorus acquisition efficiency in common bean. *Funct Plant Biol* 31: 959–970
- Liao H, Wan H, Shaff J, Wang X, Yan X, Kochian LV (2006) Phosphorus and aluminum interactions in soybean in relation to aluminum tolerance. Exudation of specific organic acids from different regions of the intact root system. *Plant Physiol* 141: 674–684
- Liu C, Muchhal US, Raghothama KG (1997) Differential expression of TPS11, a phosphate starvation-induced gene in tomato. *Plant Mol Biol* 33: 867–874
- Liu J, Li Y, Tong Y, Gao J, Li B, Li J, Li Z (2001) Chromosomal location of genes conferring the tolerance to Pi starvation stress and acid phosphatase (APase) secretion in the genome of rye (*Secale cereale* L.). *Plant Soil* 237: 267–274
- Liu J, 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
- Loneragan JF, Asher CH (1967) Responses of plants to phosphate concentration in solution culture. II. Role of phosphate absorption and its relation to growth. *Soil Sci* 103: 311–318
- Loneragan JF, Grunes DL, Welch RM, Aduayi EA, Tengah A, Lazar VA, Cary EE (1982) Phosphorus accumulation and toxicity in leaves in relation to zinc supply. *Soil Sci Soc Am J* 46: 345–352
- López-Bucio J, de la Vega OM, Guevara-García A, Herrera-Estrella L (2000a) Enhanced phosphorus uptake in transgenic tobacco plants that overproduce citrate. *Nature Biotech* 18: 450–453
- López-Bucio J, Nieto-Jacobo MF, Ramírez-Rodríguez V, Herrera-Estrella L (2000b) Organic acid metabolism in plants: from adaptive physiology to transgenic varieties for cultivation in extreme soils. *Plant Sci* 160: 1–13
- López-Bucio J, Hernández-Abreu E, Sánchez-Calderón L, Nieto-Jacobo MF, Simpson J, Herrera-Estrella L (2002) Phosphate availability alters architecture and causes changes in hormone sensitivity in the Arabidopsis root system. *Plant Physiol* 129: 244–256
- 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, Hernández-Abreu E, Sánchez-Calderón L, Pérez-Torres A, Rampey RA, Bartel B, Herrera-Estrella L (2005) An auxin transport independent pathway is involved in phosphate stress-induced root architectural alterations in Arabidopsis. Identification of *BIG* as a mediator of auxin pericycle cell activation. *Plant Physiol* 137: 681–691
- Lott JNA, Ockenden I, Raboy V, Batten GD (2000) Phytic acid and phosphorus in crop seeds and fruits: a global estimate. *Seed Sci Res* 10: 11–33

- Lynch JP, Brown KM (2001) Topsoil foraging - an architectural adaptation of plants to low phosphorus availability. *Plant Soil* 237: 225–237
- Ma Z, Baskin TI, Brown KM, Lynch JP (2003) Regulation of root elongation under phosphorus stress involves changes in ethylene responsiveness. *Plant Physiol* 131: 1381–1390
- Malamy JE (2005) Intrinsic and environmental response pathways that regulate root system architecture. *Plant Cell Environ* 28: 67–77
- Malkin R, Niyogi K (2000) Photosynthesis. In: Buchanan BB, Gruissem W, Jones RL (eds), *Biochemistry & Molecular Biology of Plants*. ASPP, Rockville, MD, pp 568–628
- Mamolos AP, Veresoglou DS, Barbayiannis N (1995) Plant species abundance and tissue concentrations of limiting nutrients in low-nutrient grasslands: a test of competition theory. *J Ecol* 83: 485–495
- Manske GGB, Ortiz-Monasterio JI, Van Grinkel M, González R, Rajaram S, Molina E, Vlek PLG (2000) Traits associated with improved P-uptake efficiency in CIMMYT's semidwarf spring bread wheat grown on an acid Andisol in Mexico. *Plant Soil* 221: 189–204
- Marschner H (1995) *Mineral Nutrition of Higher Plants* (2nd edition). Academic, London
- Marschner P (2008) The effect of rhizosphere microorganisms on P uptake by plants. In: White PJ, Hammond JP (eds), *The Ecophysiology of Plant-Phosphorus Interactions*. Springer, Dordrecht, The Netherlands, pp 165–176
- Marschner P, Solaiman Z, Rengel Z (2007) Brassica genotypes differ in growth, phosphorus uptake and rhizosphere properties under P-limiting conditions. *Soil Biol Biochem* 39: 87–98
- Martín AC, del Pozo JC, Iglesias J, Rubio V, Solano R, de la Peña A, Leyva A, Paz-Ares J (2000) Influence of cytokinins on the expression of phosphate starvation responsive genes in *Arabidopsis*. *Plant J* 24: 559–567
- McCrea AR, Trueman IC, Fullen MA (2004) Factors relating to soil fertility and species diversity in both semi-natural and created meadows in the West Midlands of England. *Eur J Soil Sci* 55: 335–348
- McGroddy ME, Daufresne T, Hedin LO (2004) Scaling of C:N:P stoichiometry in forests worldwide: implications of terrestrial Redfield-type ratios. *Ecology* 85: 2390–2401
- Mengel K (1997) Agronomic measures for better utilization of soil and fertilizer phosphates. *Eur J Agron* 7: 221–233
- Mengel K, Kirkby EA (2001) *Principles of Plant Nutrition* (5th edition). Kluwer, Dordrecht, The Netherlands
- Miller SS, Liu J, 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
- Mimura T (1999) Regulation of phosphate transport and homeostasis in plant cells. *Int Rev Cytol* 191: 149–200
- Misson J, Raghothama KG, Jain A, Jouhet J, Block MA, Bligny R, Ortet P, Creff A, Somerville S, Rolland N, Dumas P, Nacry P, Herrera-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
- 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
- Morgan JAW, Bending GD, White PJ (2005) Biological costs and benefits to plant-microbe interactions in the rhizosphere. *J Exp Bot* 56: 1729–1739
- 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, Nilsson L, Krintel C, Nielsen TH (2004) Gene expression during recovery from phosphate starvation in roots and shoots of *Arabidopsis thaliana*. *Physiol Plant* 122: 233–243
- Müller R, Nilsson L, Nielsen LK, Nielsen TH (2005) Interaction between phosphate starvation signalling and hexokinase-independent sugar sensing in *Arabidopsis* leaves. *Physiol Plant* 124: 81–90
- 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
- Narang RA, Bruene A, Altmann T (2000) Analysis of phosphate acquisition efficiency in different *Arabidopsis* accessions. *Plant Physiol* 124: 1786–1799
- Neumann G, Römheld V (1999) Root excretion of carboxylic acids and protons in phosphorus-deficient plants. *Plant Soil* 211: 121–130
- Niklas KJ (2008) Carbon/nitrogen/phosphorus allometric relations across species. In: White PJ, Hammond JP (eds), *The Ecophysiology of Plant-Phosphorus Interactions*. Springer, Dordrecht, The Netherlands, pp 9–30
- Niklas KJ, Owens T, Reich PB, Cobb ED (2005) Nitrogen/phosphorus leaf stoichiometry and the scaling of plant growth. *Ecol Lett* 8: 636–642
- 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
- Ohwaki Y, Hirata H (1992) Differences in carboxylic acid exudation among P-starved leguminous crops in relation to carboxylic acid contents in plant tissues and phospholipid level in roots. *Soil Sci Plant Nutr* 38: 235–243
- Oracka T, Łapiński B (2006) Nitrogen and phosphorus uptake and utilization efficiency in D(R) substitution lines of hexaploid triticale. *Plant Breeding* 125: 221–224
- Osborne LD, Rengel Z (2002) Screening cereals for genotypic variation in efficiency of phosphorus uptake and utilisation. *Aust J Agric Res* 53: 295–303
- O'Toole JC, Bland WL (1987) Genotypic variation in crop plant root systems. *Adv Agron* 41: 91–145
- Oyanagi A (1994) Gravitropic response growth angle and vertical distribution of roots of wheat (*Triticum aestivum* L.). *Plant Soil* 165: 323–326
- Ozanne PG, Keay J, Biddiscombe EF (1969) The comparative applied phosphate requirement of eight annual pasture species. *Aust J Biol Sci* 20: 809–818
- Ozturk L, Eker S, Torun B, Cakmak I (2005) Variation in phosphorus efficiency among 73 bread and durum wheat genotypes grown in a phosphorus-deficient calcareous soil. *Plant Soil* 269: 69–80
- Paterson E, Sim A, Standing D, Dorward M, McDonald AJS (2006) Root exudation from *Hordeum vulgare* in response to localized nitrate supply. *J Exp Bot* 57: 2413–2420
- Paul MJ, Pellny TK (2003) Carbon metabolite feedback regulation of leaf photosynthesis and development. *J Exp Bot* 54: 539–547
- Pearse SJ, Venaklaas EJ, Cawthray G, Bolland MDA, Lambers H (2007) 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
- Pearse SJ, Venaklaas EJ, Cawthray G, Bolland MDA, Lambers H (2008) Rhizosphere processes do not explain variation in P acquisition from sparingly soluble forms of P among *Lupinus albus* accessions. *Aust J Agric Res* 59: (in press)
- Perrott KW, Kear MJ (2000) Laboratory comparison of nutrient release rates from fertilizers. *Commun Soil Sci Plant Anal* 31: 2007–2017
- Petters J, Göbel C, Scheel D, Rosahl S (2002) A pathogen-responsive cDNA from potato encodes a protein with homology to a phosphate starvation-induced phosphatase. *Plant Cell Physiol* 43: 1049–1053

- 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
- Raghothama KG, Karthikeyan AS (2005) Phosphate acquisition. *Plant Soil* 274: 37–49
- Rao IM, Fredeen AL, Terry N (1990) Leaf phosphate status, photosynthesis, and carbon partitioning in sugar beet. *Plant Physiol* 92: 29–36
- Raven JA (2008) Phosphorus and the future. In: White PJ, Hammond JP (eds), *The Ecophysiology of Plant-Phosphorus Interactions*. Springer, Dordrecht, The Netherlands, pp 271–283
- Rengel Z, Marschner P (2005) Nutrient availability and management in the rhizosphere: exploiting genotypic differences. *New Phytol* 168: 305–312
- Reymond M, Svistoonoff S, Loudet O, Nussaume L, Desnos T (2006) Identification of QTL controlling root growth response to phosphate starvation in *Arabidopsis thaliana*. *Plant Cell Environ* 29: 115–125
- 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
- Robinson D (1994) The responses of plants to non-uniform supplies of nutrients. *New Phytol* 127: 635–674
- 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
- Rorison IM (1968) The response to phosphorus of some ecologically distinct plant species. I. Growth rates and phosphorus absorption. *New Phytol* 67: 913–923
- 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
- Rubio G, Sorgonà A, Lynch JP (2004) Spatial mapping of phosphorus influx in bean root systems using digital autoradiography. *J Exp Bot* 55: 2269–2280
- 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
- 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, Cruz-Ramírez A, Nieto-Jacobo F, Dubrovsky JG, Herrera-Estrella L (2005) Phosphate starvation induces a determinate developmental program in the roots of *Arabidopsis thaliana*. *Plant Cell Physiol* 46: 174–184
- 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
- Sanginga N, Lyasse O, Singh BB (2000) Phosphorus use efficiency and nitrogen balance of cowpea breeding lines in a low P soil derived from savanna zone in West Africa. *Plant Soil* 220: 119–128
- Sattelmacher B, Kuene R, Malagamba P, Moreno U (1990) Evaluation of tuber bearing *Solanum* species belonging to different ploidy levels for its yielding potential at low soil fertility. *Plant Soil* 129: 227–233
- Schachtman DP, Reid RJ, Ayling SM (1998) Phosphorus uptake by plants: from soil to cell. *Plant Physiol* 116: 447–453
- Schulze J, Temple G, Temple SJ, Beschow H, Vance CP (2006) Nitrogen fixation by white lupin under phosphorus deficiency. *Ann Bot* 98: 731–740
- Schünemann PHD, Richardson AE, Vickers CE, Delhaize E (2004) Promoter analysis of the barley *Ph1;1* phosphate transporter gene identifies regions controlling root expression and responsiveness to phosphate deprivation. *Plant Physiol* 136: 4205–4214
- 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

- Shane MW, McCully ME, Lambers H (2004) Tissue and cellular phosphorus storage during development of phosphorus toxicity in *Hakea prostrata* (Proteaceae). *J Exp Bot* 55: 1033–1044
- 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
- Shin H, Shin HS, Chen R, Harrison MJ (2006) Loss of *At4* function impacts phosphate distribution between the roots and the shoots during phosphate starvation. *Plant J* 45: 712–726
- Siedow JN, Day DA (2000) Respiration and photorespiration. In: Buchanan BB, Gruissem W, Jones RL (eds), *Biochemistry & Molecular Biology of Plants*. ASPP, Rockville, MD, pp 676–728
- Smith FW, Mudge SR, Rae AL, Glassop D (2003) Phosphate transport in plants. *Plant Soil* 248: 71–83
- Smith SE, Read DJ (2007) *Mycorrhizal Symbiosis* (3rd edition). Elsevier, London
- Smith SE, Smith FA, Jakobsen I (2003) Mycorrhizal fungi can dominate phosphate supply to plants irrespective of growth responses. *Plant Physiol* 133: 16–20
- Smith VH (1992) Effects of nitrogen: phosphorus supply ratios on nitrogen fixation in agricultural and pastoral ecosystems. *Biogeochemistry* 18: 19–35
- 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
- Somerville C, Browse J, Jaworski JG, Ohlrogge JB (2000) Lipids. In: Buchanan BB, Gruissem W, Jones RL (eds), *Biochemistry & Molecular Biology of Plants*. ASPP, Rockville, MD, pp 456–527
- Stalham MA, Allen EJ (2001) Effect of variety, irrigation regime and planting date on depth, rate, duration and density of root growth in the potato (*Solanum tuberosum*) crop. *J Agric Sci* 137: 251–270
- Steen I (1998) Phosphorus availability in the 21st century: management of a non-renewable resource. *Phosphorus Potassium* 217: 25–31
- Stöcklin J, Schweizer K, Körner C (1998) Effects of elevated CO<sub>2</sub> and phosphorus addition on productivity and community composition of intact monoliths from calcareous grassland. *Oecologia* 116: 50–56
- Ström L (1997) Root exudation of organic acids: importance to nutrient availability and the calcifuge and calcicole behaviour of plants. *Oikos* 80: 459–466
- Su J, Xiao Y, Li M, Liu Q, Li B, Tong Y, Jia J, Li Z (2006) Mapping QTLs for phosphorus-deficiency tolerance at wheat seedling stage. *Plant Soil* 281: 25–36
- Subbarao GV, Ae N, Otani T (1997) Genotypic variation in the iron- and aluminium-phosphate solubilising activity of pigeon pea root exudates under P deficient conditions. *Soil Sci Plant Nutr* 43: 295–305
- Sunkar R, Zhu J-K (2004) Novel and stress-regulated microRNAs and other small RNAs from *Arabidopsis*. *Plant Cell* 16: 2001–2019
- 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, Sasaki H (1991) Secretion of acid phosphatase by the roots of several crop species under phosphorus-deficient conditions. *Soil Sci Plant Nutr* 37: 129–140
- 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
- Tessier JT, Raynal DJ (2003) Use of nitrogen to phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation. *J Appl Ecol* 40: 523–534
- Thomas C, Sun Y, Naus K, Lloyd A, Roux S (1999) Apyrase functions in plant phosphate nutrition and mobilizes phosphate from extracellular ATP. *Plant Physiol* 119: 543–551
- Thompson K, Parkinson JA, Band SR, Spencer RE (1997) A comparative study of leaf nutrient concentrations in a regional herbaceous flora. *New Phytol* 136: 679–689

- Thornton B, Paterson E, Midwood AJ, Sim A, Pratt SM (2004) Contribution of current carbon assimilation in supplying root exudates of *Lolium perenne* measured using steady-state  $^{13}\text{C}$  labeling. *Physiol Plant* 120: 434–441
- Tian G, Carsky RJ, Kang BT (1998) Differential phosphorus responses of leguminous cover crops on soil with variable history. *J Plant Nutr* 21: 1641–1653
- Ticconi CA, Abel S (2004) Short on phosphate: plant surveillance and countermeasures. *Trends Plant Sci* 9: 548–555
- Ticconi CA, Delatorre CA, Lahner B, Salt DE, Abel S (2004) Arabidopsis *ptr2* reveals a phosphate-sensitive checkpoint in root development. *Plant J* 37: 801–814
- Tomscha JL, Trull MC, Deikman J, Lynch JP, Guiltinan MJ (2004) Phosphatase under-producer mutants have altered phosphorus relations. *Plant Physiol* 135: 334–345
- Trehan SP, Sharma RC (2003) External phosphorus requirement of different potato (*Solanum tuberosum*) cultivars resulting from different internal requirements and uptake efficiencies. *Indian J Agric Sci* 73: 54–56
- 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
- Uhde-Stone C, Zinn KE, Ramirez-Yáñez M, Li A, Vance CP, Allan DL (2003) Nylon filter arrays reveal differential gene expression in proteoid roots of white lupin in response to phosphorous deficiency. *Plant Physiol* 131: 1064–1079
- Vádez V, Lasso JH, Beck DP, Drevon JJ (1999) Variability of  $\text{N}_2$ -fixation in common bean (*Phaseolus vulgaris* L.) under P deficiency is related to P use efficiency. *Euphytica* 106: 231–242
- Vance CP, Uhde-Stone C, Allan DL (2003) Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. *New Phytol* 157: 423–447
- Van ura V, Hovadík A (1965) Root exudates of plants. II. Composition of root exudates of some vegetables. *Plant Soil* 22: 21–32
- Wasaki J, Yonetani R, Kuroda S, Shinano T, Yazaki J, Fujii F, Shimbo K, Yamamoto K, Sakata K, Sasaki T, Kishimoto N, Kikuchi S, Yamagishi M, Osaki M (2003) Transcriptomic analysis of metabolic changes by phosphorus stress in rice plant roots. *Plant Cell Environ* 26: 1515–1523
- 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, Olde Venterink H, Lapshina ED, Tanneberger F (2005) Endangered plants persist under phosphorus limitation. *Nature* 437: 547–550
- White PJ (2003) Ion transport. In: Thomas B, Murphy DJ, Murray BG (eds), *Encyclopaedia of Applied Plant Sciences*. Academic, London, pp 625–634
- White PJ, Broadley MR, Greenwood DJ, Hammond JP (2005a) Genetic Modifications to Improve Phosphorus Acquisition by Roots. *Proceedings 568*, International Fertiliser Society, York
- White PJ, Broadley MR, Hammond JP, Thompson AJ (2005b) Optimising the potato root system for phosphorus and water acquisition in low-input growing systems. *Aspects Appl Biol* 73: 111–118
- Wissuwa M (2003) How do plants achieve tolerance to phosphorus deficiency? Small causes with big effects. *Plant Physiol* 133: 1947–1958
- Wissuwa M (2005) Combining a modeling with a genetic approach in establishing associations between genetic and physiological effects in relation to phosphorus uptake. *Plant Soil* 269: 57–68
- Wissuwa M, Gamat G, Ismail AM (2005) Is root growth under phosphorus deficiency affected by source or sink limitations? *J Exp Bot* 56: 1943–1950
- Wright IJ, Reich PB, Cornelissen JHC, Falster DS, Garnier E, Hikosaka K, Lamont BB, Lee W, Oleksyn J, Osada N, Poorter H, Villar R, Warton DI, Westoby M (2005) Assessing the generality of global leaf trait relationships. *New Phytol* 166: 485–496

- Wu P, Ma L, Hou X, Wang M, Wu Y, Liu F, Deng XW (2003) Phosphate starvation triggers distinct alterations of genome expression in *Arabidopsis* roots and leaves. *Plant Physiol* 132: 1260–1271
- Xiao K, Harrison MJ, Wang Z-Y (2005) Transgenic expression of a novel *M. truncatula* phytase gene results in improved acquisition of organic phosphorus by *Arabidopsis*. *Planta* 222: 27–36
- Xiao K, Katagi H, Harrison M, Wang ZY (2006) Improved phosphorus acquisition and biomass production in *Arabidopsis* by transgenic expression of a purple acid phosphatase gene from *M. truncatula*. *Plant Sci* 170: 191–202
- Yan X, Beebe SE, Lynch JP (1995a) Genetic variation for phosphorus efficiency of common bean in contrasting soil types. II. Yield response. *Crop Sci* 35: 1094–1099
- Yan X, Lynch JP, Beebe SE (1995b) Genetic variation for phosphorus efficiency of common bean in contrasting soil types. I. Vegetative response. *Crop Sci* 35: 1086–1093
- Yan X, Liao H, Beebe SE, Blair MW, Lynch JP (2004) QTL mapping of root hair and acid exudation traits and their relationship to phosphorus uptake in common bean. *Plant Soil* 265: 17–29
- Yan Y, Wu P, Ling H, Xu G, Xu F, Zhang Q (2006) Plant nutriomics in China: an overview. *Ann Bot* 98: 473–482
- Yu B, Xu C, Benning C (2002) *Arabidopsis* disrupted in *SQD2* encoding sulfolipid synthase is impaired in phosphate-limited growth. *Proc Natl Acad Sci USA* 99: 5732–5737
- Zhang K, Greenwood DJ, White PJ, Burns IG (2007) A dynamic model for the combined effects of N, P and K fertilizers on yield and mineral composition; description and experimental test. *Plant Soil* 298: 81–98
- Zhang YJ, Lynch JP, Brown KM (2003) Ethylene and phosphorus availability have interacting yet distinct effects on root hair development. *J Exp Bot* 54: 2351–2361
- Zhao J, Fu J, Liao H, He Y, Nian H, Hu Y, Qiu L, Dong Y, Yan X (2004) Characterisation of root architecture in an applied core collection for phosphorus efficiency of soybean germplasm. *Chinese Sci Bull* 49: 1611–1620
- Zhu J, Lynch JP (2004) The contribution of lateral rooting to phosphorus acquisition efficiency in maize (*Zea mays*) seedlings. *Funct Plant Biol* 31: 949–958
- Zhu J, Kaepler SM, Lynch JP (2005) Topsoil foraging and phosphorus acquisition efficiency in maize (*Zea mays*). *Funct Plant Biol* 32: 749–762
- Zhu J, Mickelson SM, Kaepler SM, Lynch JP (2006) Detection of quantitative trait loci for seminal root traits in maize (*Zea mays* L.) seedlings grown under differential phosphorus levels. *Theor Appl Genet* 113: 1–10
- 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 Biotech J* 1: 353–360
- Zimmermann P, Regierer B, Kossmann J, Frossard E, Amrhein N, Bucher M (2004) Differential expression of three purple acid phosphatases from potato. *Plant Biol* 6: 519–528